PROCEEDINGS

of the

Biological Society of Washington

VOLUME 96
1983

Vol. 96(1) published 25 March 1983
Vol. 96(2) published 7 July 1983
Vol. 96(3) published 31 October 1983
Vol. 96(4) published 29 December 1983

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 1982–1983

OFFICERS

President
PAUL J. SPANGLER

Vice President
DAVID L. PAWSON

Secretary
CATHERINE J. KERBY

Treasurer
LESLIE W. KNAPP

COUNCIL

Elected Members

JANET C. GOMON
GORDON HENDLER
RICHARD S. HOUBRICK
ROY W. McDIARMID
JAMES C. TYLER

TABLE OF CONTENTS

Volume 96

INDEX TO NEW TAXA

VOLUME 96

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

ARTHROPODA

Crustacea

Insecta

(ISSN 0006-324X)

Proceedings
of the
BIOLOGICAL SOCIETY
of
WASHINGTON

Volume 96 25 March 1983 Number 1

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 $10.00 include subscription to the *Proceedings of the Biological Society of Washington. Library subscriptions to the Proceedings are: $18.00 within the U.S.A., $23.00 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 Instutution, 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.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 1–6

DESCRIPTION OF *EUALUS LINEATUS* NEW SPECIES, WITH A REDESCRIPTION OF *HEPTACARPUS HERDMANI* (WALKER) (CARIDEA: HIPPOLYTIDAE)

Mary K. Wicksten and Terrance H. Butler

Abstract.—A small striped hippolytid shrimp has been identified as *Eualus herdmani* by several authors. Examination of the holotype of *Spirontocaris herdmani* Walker revealed that this unique specimen should be assigned instead to the genus *Heptacarpus,* and that it differs from an undescribed species assigned to it in the literature. *Heptacarpus herdmani* is redescribed. The common subtidal striped shrimp of the western coast of North America is described herein as a new species, *E. lineatus.*

Species of *Eualus* live in boreal to cool temperate waters of the northern and southern hemispheres (Wicksten 1979). A small striped shrimp of this genus has been collected subtidally along the Pacific coast from Alaska to western Mexico. This shrimp has been identified as *E. herdmani* (Walker). However, specimens of this animal do not agree completely with the description given by Walker (1898). We borrowed specimens from the Allan Hancock Foundation (AHF), and the U.S. National Museum (USNM) to compare them with the holotype, borrowed from the British Museum (Natural History).

This paper describes as a new species *E. lineatus,* previously misidentified as *E. herdmani. Spirontocaris herdmani* is redescribed and assigned to *Heptacarpus.*

This work was supported in part by a fellowship from the Allan Hancock Foundation and a minigrant from Texas A&M University. Figures 1–2 were prepared by Alastair Denbigh, Pacific Biological Station.

Heptacarpus herdmani (Walker)

Spirontocaris herdmani Walker, 1898:277–278, pl. 16, fig. 2.
Heptacarpus herdmani.—Holmes, 1900:204.
Spirontocaris herdmani.—Rathbun, 1904:100–101 (in part).
Eualus herdmani.—Holthuis, 1947:11 (in part).—Word and Charwat, 1976:103–104 (in part).—Butler, 1980:197–198 (in part).
Not *Eualus herdmani* of Hobson and Chess, 1974:579 (=*Eualus lineatus* n. sp.)

Description.—Rostrum horizontal, reaching beyond second segment of antennular peduncle and almost to end of scaphocerite. Two dorsal teeth on carapace, series of 3 to end of eyestalk, distal half of rostrum without dorsal teeth. Apex of rostrum sharp. Rostrum with 1 prominent ventral tooth just behind tip, slight knob behind tooth.

Carapace smooth, dorsum straight. Very small knob at level of suborbital spine. No supraorbital spines. Antennal spines strong, prominent; pterygostomian spine very small and sharp.

Abdomen smooth. Pleurae of segments 1–4 rounded, those of segments 5 and 6 with sharp points. Telson with 3 pairs of lateral spines. Spines at apex of telson broken.

Eye darkly pigmented, round.

Stylocerite reaching end of first segment of antennular peduncle. First segment with 2 lateral spines. Second segment less than 0.5× length of first, with 1 spine. Third segment and flagella broken. Entire peduncle "about 0.5× length of antennal scale" (Walker 1898).

Basis of second antenna with sharp ventral spine, large blunt knob above. Scaphocerite broken, but broad. Flagella missing.

Mouthparts dehydrated and fused in holotype. First and second maxillipeds with exopods. Third maxilliped without exopod, but with epipod, "reaching beyond end of antennal scales" (Walker 1898).

First pereopods strongly chelate, overreaching scaphocerite, with epipods. Fingers shorter than palm, with tuft of setae at tip. Propodus about 2× length of carpus, merus about equal to propodus. Ischium about 0.5× length of merus.

Second pereopods chelate, with epipods. Fingers of chela shorter than palm. Carpus with 7 segments, the third of these the longest. Merus and ischium about equal, both about 0.5× length of carpus.

Third pereopods with long, curved simple dactyls. Dactyls with a few long setae on curved margin, about 0.33× length of propodus. Carpus about 0.5× propodus, with overhanging knob at articulation with propodus. Merus longer than propodus, with 2 spines. Ischium about 0.5× merus. Fourth and fifth pereopods similar to third, all without epipods. Fourth merus with 4 lateral spines, fifth merus without spines.

Pleopods dehydrated in holotype. Eggs small, numerous. Uropods broad, ovate.

Type-locality.—"Puget Sound" (Walker 1898).

Remarks.—The unique holotype of *Heptacarpus herdmani* has been broken and dehydrated so that many fine details cannot be observed. However, the lack of an exopod on the third maxilliped clearly shows that the species does not belong to the genus *Eualus*. Indeed, Walker noted the lack of an exopod in his original description.

Heptacarpus herdmani is related to *H. paludicola* Holmes, and *H. flexus* (Rathbun) in having epipods on the first and second pereopods. *Heptacarpus paludicola* differs from *H. herdmani* in having 6–8 dorsal rostral spines and 2–4 ventral rostral spines, sharp points on the pleura of the fourth abdominal segment, and bifid dactyls with 5 spines on the third to fifth pereopods. *Heptacarpus flexus* has a very slender rostrum with 4–5 dorsal spines and 5–8 ventral spines, a pronounced hump on the dorsal surface of the third abdominal segment, and a suborbital spine consisting of a prominent knob.

One may ask who was responsible for the confusion between *H. herdmani* and the species of *Eualus*. Rathbun (1904:60) grouped *Spirontocaris herdmani* with species having both an exopod and an epipod on the third maxilliped and epipods on the first, second, and third pereopods. Specimens from the U.S. National Museum labelled *S. herdmani* in Rathbun's handwriting belong to the new species of *Eualus*, not *Heptacarpus* (nor *Spirontocaris*, as now interpreted). Apparently, Rathbun missed Walker's mention of the lack of exopods on the third maxillipeds, or assumed that he made an error in his description.

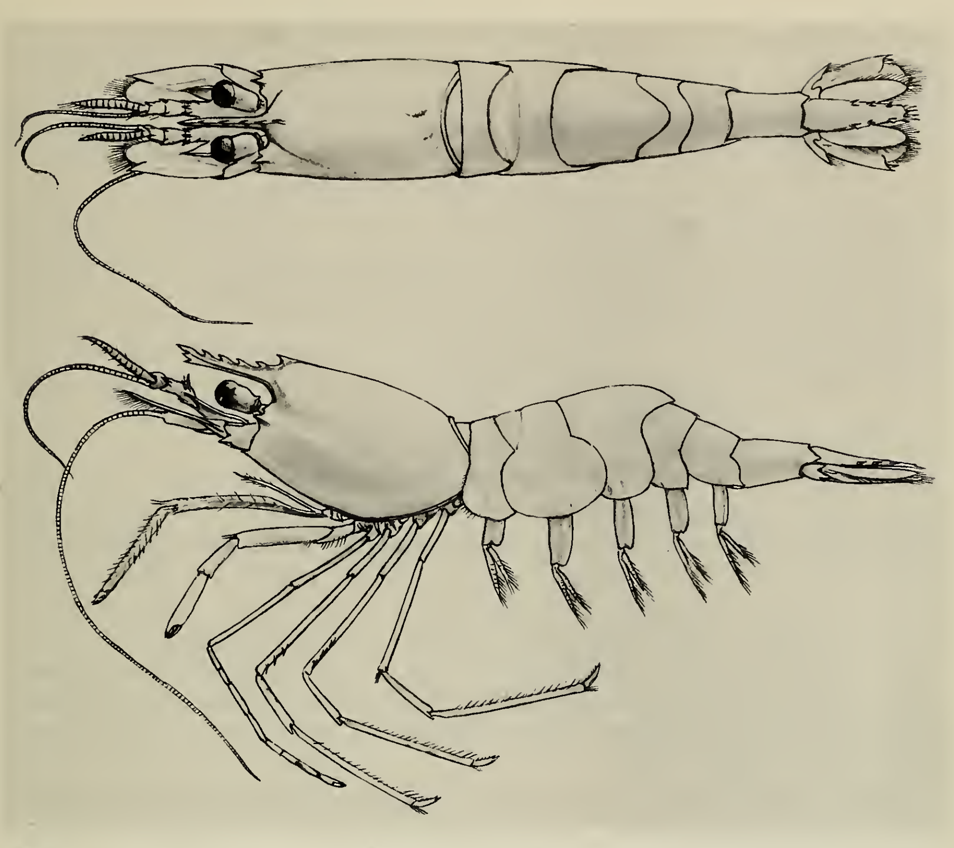


Fig. 1. *Eualus lineatus*: Dorsal and lateral views of female, carapace length 3.1 mm.

As now interpreted, the only known specimen of *H. herdmani* is the holotype from Puget Sound, either from Washington, U.S.A. or the Canadian side. No depth or substrate were mentioned for the specimen, but the long, simple dactyls suggest that the species lived on a soft bottom. Perhaps future dredging or sampling with SCUBA gear will discover more specimens of this poorly known shrimp.

Eualus lineatus, new species
Figs. 1–2

Spirontocaris herdmani.—Rathbun, 1904:100–101 (in part).
Eualus herdmani.—Holthuis, 1947:11 (in part).—Hobson and Chess, 1974:579.—Word and Charwat, 1976:103–104 (in part).—Butler, 1980:197–198 (in part).

Description.—Rostrum short, reaching second segment of antennular peduncle, straight, with 3–6 dorsal teeth and 1–3 ventral teeth, all of dorsal margin toothed.

Carapace smooth, dorsum straight. Small suborbital spine, moderate antennal spine with supporting carina, moderate pterygostomial spine.

Abdomen smooth. Pleura of segments 1–3 rounded, pleura of fourth segment with weak posterolateral spine, fifth with strong posterolateral spine. Median dorsal margin of third segment strongly produced posteriorly. Telson with 3 pairs dorsolateral spines.

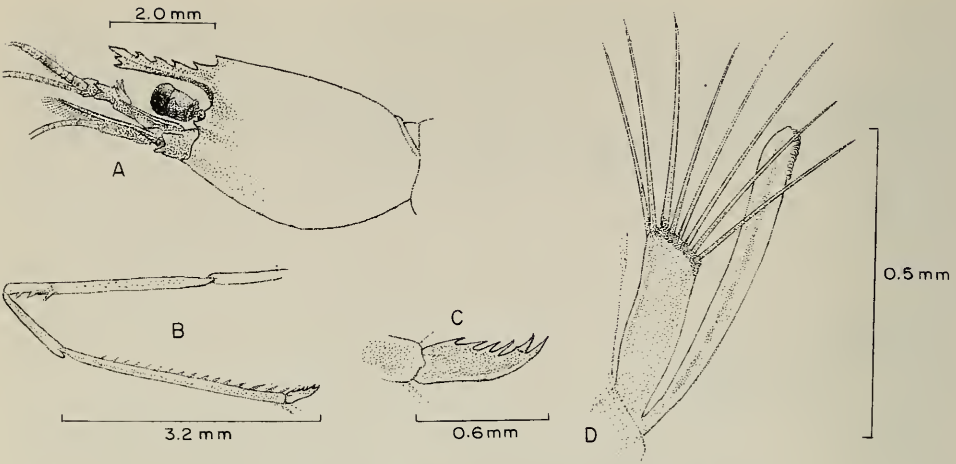


Fig. 2. *Eualus lineatus*: A, Anterior lateral view of female, carapace length 3.1 mm; B, Left third pereopod of female; C, Dactyl of left third pereopod of same female; D, Appendix masculina of male, carapace length 4.1 mm.

Eyes moderately large, darkly pigmented.

Stylocerite reaching end of first segment of antennular peduncle. First segment with 3 moderate dorsal spines. Second segment about 0.5× length of first, with 2 strong spines. Third segment shorter than second, with 2 spines. Inner flagellum more than 2× length of outer.

Basis of second antenna with sharp ventral spine, large blunt upper lobe. Scaphocerite oblong, shorter than carapace, lamella slightly longer than spine. Flagellum slightly exceeding body length.

Mandible with slender incisor process, ending in small teeth. Molar process with spinules. Two-jointed palp present. First maxilla with lower endite slender, upper broad; palp faintly bilobed. Second maxilla with lower endite reduced, upper endite larger, bilobed; palp and scaphognathite well developed. First maxilliped with exopod and 2-jointed palp; epipod bilobed, caridean lobe very small; endites of coxa and basis separated by notch. Second maxilliped with exopod, podobranch, and epipod. Third maxilliped with exopod and epipod, exceeding antennular peduncle, stout and setose.

First pereopod shorter than third maxilliped, stout, with epipod. Fingers of chela less than 0.5× length of palm. Carpus slightly shorter than palm. Merus about 2× length of carpus. Ischium less than 0.5× merus. Second pereopod chelate, longer than first pereopod, with epipod. Fingers shorter than length of palm. Carpus with 7 segments, the third and fourth the longest. Merus about 0.6× length of carpus, slightly longer than ischium. Third pereopod slightly longer than second, with epipod. Dactyl stout, about 0.2× length of propodus, with 5 spines. Propodus with 16–19 spinules in 2–3 rows. Carpus about 0.4× length of propodus. Merus about same length as propodus, with 3 spines. Ischium less than 0.5× length of merus. Fourth pereopod about as long as third. Dactyl stout, similar to that of third pereopod. Propodus with 15 spinules in single row. Merus with 2–3 spines. Fifth pereopod as long as fourth. Dactyl about 0.2× length of propodus, with 4–5 small spines. Propodus with 14–22 spinules in 1 or 3 rows. Merus with 0–1 spine. No epipods on pereopods 3–5.

Second pleopod with appendix interna. Appendix masculina little more than half length of appendix interna, stout, apex truncated, with 8 long spinules. Uropods reaching end of telson, with long tooth on outer margin.

Type-material.—HOLOTYPE: female, total length 21.0 mm. 1.5 mi. SW of Gull Island, off Santa Cruz Island, California (33°56′00″N, 119°50′55″W), 89 m, mud and sponge bottom, 8 Nov 1941, *Velero III* sta. 1435-41, AHF type number 4129.—Paratype: female. San Juan Islands, Washington, summer 1930, John C. Queen, collector, USNM.—Paratypes: female, carapace length 3.1 mm, west shore Jesse Island, British Columbia (49°12′N, 123°57′W), 30 Apr 1972; female, carapace length 3.4 mm, Boca del Infierno Bay, Nootka Sound, British Columbia (49°38′N, 126°37′W), 21 May 1973, National Museum of Canada.

Other material.—41 specimens from 24 stations, AHF and USNM, Naha Bay, Alaska; coast of British Columbia, Puget Sound, off Depoe Bay, Oregon; southern California from Redondo Beach and off Long Beach; Santa Cruz, Santa Rosa, and Santa Catalina Islands; Bahía San Gabriel, Isla Espíritu Santo, Gulf of California, Mexico; 17–140 m, among rocks, kelp, sand or mud; on wreck (MKW). 34 specimens from Burnaby Narrows, Queen Charlotte Islands (52°22′N, 131°21′W) to Jesse Island (49°12′N, 123°57′W), intertidally on sand and gravel to 232 m on mud, 1928–1973 (THB).

Records in literature.—Sitka, Alaska to Puget Sound (Butler 1980); Santa Monica Bay, Palos Verdes Peninsula, Santa Catalina Island, and Point Loma, California (Word and Charwat 1976).

Color in life.—Red diagonal lines on carapace and first and second abdominal segments, red spots and blotches on third to sixth abdominal segments, telson, uropods, and protopodites of pleopods, smaller red spots on all anterior appendages, including eye stalk and pereopods (Butler 1980, color plate 1C).

Parasites.—Parasitized by *Bopyroides hippolytes* (Butler, 1980). An unidentified rhizocephalan on a specimen from Neah Bay, Washington.

Remarks.—*Eualus lineatus* is related to *E. avinus* (Rathbun), *E. pusiolus* (Krøyer), and *E. berkeleyorum* Butler in having epipods on the first 3 pereopods. In *Eualus avinus* the rostrum is arched over the eye, and bears 12–14 upper teeth and 1–3 ventral teeth. The dactyl of the third pereopod is slender and simple. *Eualus pusiolus* has a straight rostrum shorter than the second segment of the antennular peduncle, with 2–5 upper teeth and at most 1 lower tooth. The dactyl of the third pereopod is stout. *Eualus berkeleyorum* has a straight rostrum with 8–11 dorsal teeth and 2–5 ventral teeth. The dactyls of its third pereopods are slender and simple. It does not have a ventral spine on the pleura of the fourth abdominal segment.

Most specimens of *E. lineatus* have been taken by trawls. One specimen was collected by a SCUBA diver on the wreck of the *Olympic,* off Long Beach, California. A first stage larva of the species has been hatched in the laboratory (Butler 1980). The species is eaten by rockfishes (*Sebastes* spp.) off Santa Catalina Island, California (Hobson and Chess 1974).

Etymology.—The name of the species refers to the red lines on the carapace and body of the shrimp.

Literature Cited

Butler, T. H. 1980. Shrimps of the Pacific coast of Canada.—Canadian Bulletin of Fisheries and Aquatic Sciences 202, 280 pp.

Hobson, E. S., and J. R. Chess. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California.—United States National Marine Fisheries Service Fishery Bulletin 74(3):567–598.

Holmes, S. J. 1900. Synopsis of California stalk-eyed Crustacea.—Occasional Papers of the California Academy of Sciences 7:1–262, pls. 1–4.

Holthuis, L. B. 1947. The Hippolytidae and Rhynchocinetidae collected by the *Siboga* and *Snellius* expeditions with remarks on other species. The Decapoda of the *Siboga* Expedition Part IX.—Siboga Expeditie Monographie 39a^8:1–100.

Rathbun, M. J. 1904. Decapod crustaceans of the northwest coast of North America.—Harriman Alaska Expedition, Series 10, 210 pp.

Walker, A. O. 1898. Crustacea collected by W. A. Herdman in Puget Sound, Pacific coast of North America, September, 1897.—Proceedings and Transactions of the Liverpool Biological Society 12:268–287.

Wicksten, M. K. 1979. Zoogeographical affinities of the broken back shrimp (Caridea: Hippolytidae) of western South America.—Proceedings of the International Symposium on Marine Biogeography and Evolution in the Southern Hemisphere. Vol. 2. New Zealand Division of Scientific and Industrial Research Information Series 137:627–634.

Word, J. Q., and D. Charwat. 1976. Invertebrates of southern California coastal waters. II. Natantia.—El Segundo: Southern California Coastal Water Research Project. 238 pp.

(MKW) Department of Biology, Texas A&M University, College Station, Texas 77843; (THB) Pacific Biological Station, Nanaimo, British Columbia V9R 5K6, Canada.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 7–28

HYDROIDA FROM ESTUARIES OF SOUTH CAROLINA, USA: FAMILIES SERTULARIIDAE AND PLUMULARIIDAE

Dale R. Calder

Abstract.—Six species of Sertulariidae and five species of Plumulariidae were identified in collections of hydroids from estuaries of South Carolina. *Sertularia exigua* Allman, 1877, is synonymized with *Dynamena cornicina* McCrady, 1859, and *Aglaophenia rigida* Allman, 1877, is placed in synonymy with *A. trifida* L. Agassiz, 1862. *Aglaophenia trifida* occurs in two distinct colony forms in estuaries of South Carolina, but the two variants are not regarded as separate taxa. *Obelia marginata* Allman, 1877, from the Atlantic Ocean and *Campanularia marginata* Bale, 1884, from Australia belong to the genus *Thyroscyphus* Allman, 1877. *Thyroscyphus balei,* new name, is proposed as a replacement name for the junior secondary homonym *T. marginatus* (Bale, 1884).

The assemblage has a distinct warm water affinity. All 11 species range at least as far south as the Caribbean, while but four occur north of the Carolina coast on substrates other than pelagic *Sargassum.* Only two of the species, *Sertularella conica* and *Aglaophenia rigida,* are restricted to the western Atlantic. No representatives of either family were collected below salinities of 15‰ in the study area.

Studies by McCrady (1859) and Fraser (1912) form the basis for much of the information presently available on hydroids of estuarine and nearshore areas between Cape Hatteras, North Carolina, and Cape Canaveral, Florida. Other records of hydroids from the Carolinian region are scattered in various taxonomic papers covering broad geographic areas, such as those of Allman (1877), Jäderholm (1896), Nutting (1900, 1904, 1915), Stechow (1923), Fraser (1943, 1944) and Vervoort (1972). Additional data are given in investigations of fouling communities (McDougall 1943; Dean and Bellis 1975; Sutherland 1977, 1981; Sutherland and Karlson 1977; Karlson 1978), and faunal studies (Pearse 1936; Pearse and Williams 1951; Stephenson and Stephenson 1952; Wells 1961; Wells, Wells, and Gray 1964; Cain 1972; Howard and Frey 1975), as well as miscellaneous other publications (Verrill 1872; Fewkes 1881; Brooks 1886; Mayer 1910a, b; Sandifer *et al.* 1974; Calder 1976; Calder and Hester 1978). Despite its dated systematics, Fraser's (1944) monograph continues to be the most comprehensive source of information on hydroids of the region.

Hydroids occur from marine to freshwater environments and are an important constituent of epibenthic assemblages in estuaries. This paper is a systematic account of the species belonging to the families Sertulariidae and Plumulariidae found in estuaries of South Carolina.

Materials and Methods

Hydroids were sorted from benthic samples collected between 1973 and 1978 at 130 stations in estuaries of South Carolina. These stations encompassed the

Table 1.—Locations, depths, substrate types, and observed bottom salinity ranges for stations where hydroids of the families Sertulariidae and Plumulariidae were collected in estuaries of South Carolina.

Station	Location	N	W	Depth (m)	Substrate	Salinity (‰)
LRA7	Little River Inlet	33°51′40″	78°32′31″	4	sand, shell	33
LRA8	Little River Inlet	33°52′00″	78°32′48″	2	sand, shell	33
MI07	Murrells Inlet	33°30′00″	79°01′34″	3	sand, shell	34
MI09	Murrells Inlet	33°33′12″	79°01′43″	2	sand, shell	34
MI10	Murrells Inlet	33°33′25″	79°01′44″	3	sand, shell	34
MI12	Murrells Inlet	33°33′16″	79°01′08″	1	sand, shell	34
MI13	Murrells Inlet	33°33′28″	79°01′35″	2	sand, shell	34
MI15	Murrells Inlet	33°33′37″	79°01′24″	1	sand, shell	34
MI16	Murrells Inlet	33°33′18″	79°02′02″	3	sand, shell	34
MI17	Murrells Inlet	33°33′08″	79°02′14″	1	silty sand, shell	34
YB02	Winyah Bay	33°13′21″	79°11′14″	5	sand, shell	—
NS00	North Santee River	33°09′00″	79°14′09″	0	sand, shell	—
NS01	North Santee River	33°08′34″	79°14′48″	3	sand, shell	—
NB02	North Santee River	33°10′00″	79°14′30″	1	sand, shell	—
BB01	Bulls Bay	32°57′27″	79°36′57″	4	mud, shell	34
BB02	Sewee Bay	32°57′27″	79°38′15″	2	mud, shell	34
SB03	Sewee Bay	32°56′51″	79°38′33″	2	mud, shell	32–35
SB04	Sewee Bay	32°56′47″	79°38′30″	3	mud, shell	32–35
SB05	Sewee Bay	32°56′35″	79°39′07″	4	mud, shell	32–35
SB07	Sewee Bay	32°56′24″	79°39′00″	2	mud, sand, shell	31–35
SB08	Sewee Bay	32°56′17″	79°38′45″	2	mud, shell	31–35
SB10	Sewee Bay	32°55′49″	79°39′25″	4	mud, shell	31–34
SB13	Sewee Bay	32°55′57″	79°38′29″	4	mud, shell	31–35
SB15	Sewee Bay	32°55′23″	79°39′37″	4	mud, shell	31–34
SB18	Sewee Bay	32°55′27″	79°38′27″	2	mud, shell	30–35
B003	Bulls Bay	32°55.9′	79°36.2′	5	mud, sand	28–34
B002	Prices Creek	32°54.2′	79°40.7′	8	sand, shell	29–34
CI01	Capers Inlet	32°51′30″	79°42′35″	3	sand, shell	34
B001	Inlet Creek	32°47.5′	79°49.5′	4	sand, shell	23–33
CH00	Charleston Harbor	32°45′20″	79°51′40″	20	sand, shell	—
J003	Charleston Harbor	32°44.9′	79°51.6′	10	mud, shell	22–33
J002	Charleston Harbor	32°47.1′	79°53.2′	3	mud	16–28
J001	Charleston Harbor	32°45.4′	79°55.1′	7	mud, sand	16–25
CH02	Charleston Harbor	32°46′18″	79°53′17″	12	mud, shell	—
KP01	Stono Inlet	32°37′25″	79°59′26″	10	sand, shell	29
KP02	Stono River	32°38′03″	80°00′32″	10	sand, shell	28
KP04	Stono River	32°40′29″	80°00′10″	7	sand, shell	24
KP07	Kiawah River	32°37′29″	80°04′33″	6	sand, shell	25
KP08	Kiawah River	32°36′54″	80°06′43″	2	mud, shell	24
E001	Wadmalaw Sound	32°41.2′	80°10.4′	7	sand, shell, mud	17–27
DE10	North Edisto River	32°39′06″	80°15′25″	11	sand, shell	22–33
E003	North Edisto River	32°38.8′	80°15.7′	7	sand, shell	19–31
E002	Toogoodoo Creek	32°41.3′	80°17.3′	4	sand, shell, mud	21–26
DE04	North Edisto River	32°37′41″	80°16′34″	7	sand, mud, shell	22–33
DE05	North Edisto River	32°37′22″	80°16′16″	10	pebbles	21–34
DE06	North Edisto River	32°36′53″	80°15′55″	10	sand, shell	27–31
E005	Steamboat Creek	32°36.2′	80°17.7′	7	sand, mud, shell	23–29
DE07	North Edisto River	32°36′33″	80°15′10″	9	sand, shell	27–31
DE08	North Edisto River	32°36′21″	80°14′00″	8	sand	24–34
E006	North Edisto River	32°36.5′	80°14.8′	8	sand	25–30
E007	North Edisto River	32°35.9′	80°13.5′	8	mud	26–31

Table 1.—Continued.

Station	Location	N	W	Depth (m)	Substrate	Salinity (‰)
AC01	Adams Creek	32°35′48″	80°12′22″	3	sand, shell	—
E008	North Edisto River	32°33.6′	80°10.7′	10	sand, shell	29–31
DE01	Dawho River	32°37′25″	80°17′05″	4	mud	19–29
D004	South Edisto River	32°29.7′	80°21.2′	7	sand	24–33
H003	St. Helena Sound	32°30.9′	80°27.9′	5	sand, mud, shell	21
BR08	Beaufort River	32°24′46″	80°40′53″	6	sand, shell	—
P002	Colleton River	32°16.2′	80°43.7′	6	mud, sand	27–32
P001	Port Royal Sound	32°16.2′	80°48.5′	8	sand, mud, shell	24–31
P006	Chechessee River	32°17′30″	80°45′00″	9	sand	30
G001	Calibogue Sound	32°10.9′	80°47.8′	7	sand, mud, shell	25–30

region from Little River Inlet in the northeast to the Wright River in the southwest, and extended from the mouth to the head of various estuarine systems in the state. Representatives of the families Sertulariidae and Plumulariidae were found at 61 of these stations (Table 1). Most specimens were obtained in epifaunal collections made with modified oyster dredges and otter trawls, but a few were sorted from infaunal samples taken using Petersen grabs. Collections were preserved in 10% neutralized formaldehyde.

Bottom water samples, taken in conjunction with most benthic collections, were obtained with Van Dorn bottles and analyzed for salinity in the laboratory with a Beckman RS7B induction salinometer.

Hydroids occurring on pelagic *Sargassum* are allochthonous to South Carolina estuaries and were not included in this study. The synonymy list for each species includes published records from estuaries between Cape Hatteras, North Carolina, and Cape Canaveral, Florida. Descriptions and illustrations are based entirely on specimens from estuaries of South Carolina. The terminology employed largely follows that used in the monograph on South African hydroids by Millard (1975). A reference collection has been deposited in the Department of Invertebrate Zoology, Royal Ontario Museum.

Systematic Account

Family Sertulariidae Fleming, 1828

Dynamena Lamouroux, 1812

Dynamena cornicina McCrady, 1859

Figs. 1, 2

Dynamena cornicina McCrady, 1859:204.—Calder, 1976:169.—Calder and Hester, 1978:91.

Sertularia cornicina.—Verrill, 1874:408, 411, 733.—Fraser, 1912:374, fig. 38; 1944: 279, fig. 266.

Sertularia exigua Allman, 1877:24, pl. 16, figs. 7, 8.

Sertularia complexa Clarke, 1879:245, pl. 4, figs. 26–28.

Sertularia moluccana Pictet, 1893:50, pl. 2, figs. 42, 43.

Desmoscyphus palkensis Thornely, 1904:119, pl. 2, figs. 7A, B.

Sertularia densa Stechow, 1919:93, fig. J1.

Sertularia cornicina f. *pinnata* Jarvis, 1922:339.

Collection records.—Sta. MI07, dredge, 29 May 1975. Sta. MI09, dredge, 29 May 1975. Sta. MI10, dredge, 29 May 1975. Sta. MI12, dredge, 29 May 1975. Sta. MI13, dredge, 29 May 1975. Sta. MI15, dredge, 29 May 1975. Sta. MI16, dredge, 29 May 1975. Sta. BB02, dredge, 11 Aug 1977. Sta. SB03, dredge, 22 Aug 1977. Sta. SB04, dredge, 25 July 1978. Sta. SB07, dredge, 22 Aug 1977. Sta. SB10, dredge, 22 Aug 1977, 25 July 1978. Sta. SB13, dredge, 25 July 1978. Sta. SB15, dredge, 22 Aug 1977. Sta. B003, dredge, 12 Aug 1974, 22 Oct 1974, 13 Oct 1975. Sta. B002, dredge, 23 Oct 1973, 15 Apr 1974, 12 Aug 1974, 22 Oct 1974, 13 Oct 1975, 5 Jan 1976. Sta. B001, dredge, 16 Oct 1974, 2 Apr 1976. Sta. J003, dredge, 1 Aug 1975, 1 Apr 1976. Sta. KP07, dredge, 15 Mar 1977. Sta. KP08, dredge, 16 Mar 1977. Sta. DE04, dredge, 21 Nov 1977, 17 Oct 1978. Sta. DE05, dredge, 17 Oct 1978. Sta. DE07, dredge, 21 Nov 1977. Sta. E008, dredge, 2 Oct 1974. Sta. D004, dredge, 9 Jan 1974. Sta. BR08, dredge, 27 Mar 1974, 8 Oct 1975. Sta. P002, dredge, 4 Oct 1973, 5 Apr 1974, 7 Aug 1974, 8 Oct 1974. Sta. P001, dredge, 4 Oct 1973, 7 Aug 1974, 8 Oct 1974. Sta. P006, trawl, 7 Aug 1974. Sta. G001, dredge, 4 Oct 1973, 7 Aug 1974, 8 Oct 1974, 8 Apr 1975, 8 Oct 1975.

Description.—Unbranched colonies reaching 2 cm high; color in life bright yellow. Hydrocaulus monosiphonic, straight, arising from a creeping hydrorhiza; basal part athecate, length variable but usually about 1 mm long, articulating with upper thecate part by an oblique hinge-joint; thecate part divided by oblique nodes, internodes 491–784 μm long, each with an opposite pair of frontally-placed hydrothecae; thecate part of a few hydrocauli having an irregularly-placed athecate internode marked by an oblique hinge-joint distally. Hydrothecae cylindrical, distal half curved outward, contiguous frontally, not touching across back of internode; abcauline wall concave except for an occasional basal bulge, 293–386 μm long; contiguous part of adcauline wall straight, 246–363 μm long, free part convex, 199–293 μm long; diameter at base of hydrotheca 129–188 μm. Hydrothecal orifice oval, 129–158 μm wide from adcauline to abcauline wall; margin with 2 prominent lateral teeth and a smaller median adcauline tooth, occasionally renovated. Operculum consisting of a large abcauline and a smaller adcauline valve divided by a median line. Perisarc of abcauline wall expanded just below margin, but intrathecal teeth lacking.

Gonothecae oval, resembling chinese lanterns with about 6 rounded, transverse ridges, 680 μm wide, 1000 μm long from base to orifice, arising by short pedicels from hydrorhiza. Walls round in cross-section, orifice round, 365 μm in diameter, at end of short collar.

Remarks.—Charleston Harbor, South Carolina, is the type-locality of this circumglobal hydroid. According to Nutting (1904), McCrady's (1859) types of this species were destroyed by fire in Charleston during the American Civil War. I was unable to locate any of McCrady's hydrozoan material at the Charleston Museum.

Sertularia exigua, originally described by Allman (1877) from Cape Fear, North Carolina, is regarded as a synonym of *D. cornicina.* Allman's types of *S. exigua* could not be located at the Museum of Comparative Zoology where they were originally deposited (Nutting 1904), but his descriptions and illustrations of the species are indistinguishable from *D. cornicina.* The back of the hydrothecal pairs, rather than the front, is shown in Allman's drawings of the species.

Dynamena cornicina is often a substrate for the hydroid *Hebella scandens*

(Bale 1888), and it was probably hydrothecae of the latter that McCrady (1859) presumed, with considerable reservation, to be gonothecae.

Known range.—Western Atlantic: Massachusetts to Brazil; Bermuda. Elsewhere: Circumglobal, tropical and temperate waters.

Dynamena quadridentata (Ellis and Solander, 1786)
Fig. 3

Sertularia quadridentata Ellis and Solander, 1786:57, pl. 5, fig. G.
Pasythea (*Sertularia*) *quadridentata*.—Lamouroux, 1812:183.
Pasythea quadridentata.—Lamouroux, 1816:156.—Fraser, 1912:372, fig. 36.
Pasythea nodosa Hargitt, 1908:114, figs. 13–15.
Pasya quadridentata.—Stechow, 1923:166.
Pasya elongata Stechow and Müller, 1923:469, pl. 27, fig. 8.
Dynamena gibbosa Billard, 1924:650, fig. 2G.
Dynamena quadridentata.—Billard, 1925:194, fig. 42.
Dynamena quadridentata var. *elongata* Billard, 1925:195, fig. 43A, B, C, D.
Dynamena quadridentata var. *nodosa* Billard, 1925:197, fig. 43E.

Collection record.—Sta. J003, dredge, 1 Apr 1976.

Description.—Hydrorhiza with distinct internal ridges of perisarc. Colonies 4.5 mm high; hydrocaulus monosiphonic, straight, unbranched; basal portion athecate, short, with an oblique hinge-joint distally; thecate part divided either by oblique and frequently indistinct nodes, or by oblique hinge-joints. Internodes variable in length with 1–3 opposite pairs of frontally-situated hydrothecae; hydrothecal pairs usually contiguous for a varying distance in front, not touching across back of internode. Base of hydrotheca above abutting adcauline wall of hydrotheca below when 2 or more pairs of hydrothecae present per internode. Hydrothecae varying from nearly cylindrical to somewhat tumid, narrowest just below margin; abcauline wall 187–281 μm long; solitary pair, or proximal pairs of a group curved outward with axes oblique to internode, adcauline wall convex, abcauline wall concave except for basal bulge; distal pair of a group with adnate portions of adcauline wall straight, axes parallel to internode, margin curved abruptly outward, abcauline wall concave. Hydrothecal margin oval with 2 prominent lateral teeth and a smaller median adcauline tooth. Operculum consisting of a large abcauline and a smaller adcauline valve. Intrathecal teeth present.

Gonothecae absent.

Remarks.—This species is common on pelagic *Sargassum*, but was collected from benthic algae at only one station in the study area.

Known range.—Western Atlantic: North Carolina to Brazil; Bermuda; northward to Massachusetts on floating *Sargassum*. Elsewhere: Circumglobal, tropical and warm temperate waters.

Sertularella Gray, 1848

Sertularella conica Allman, 1877
Fig. 4

Sertularella conica Allman, 1877:21, pl. 15, figs. 6, 7.—Fraser, 1912:373, fig. 37.
Sertularella gayi.—Verrill, 1900:571; 1907:319, fig. 170 [not *Sertularella gayi* (Lamouroux, 1821)].

Sertularella inconstans.—Calder and Hester, 1978:91 (not *Sertularella inconstans* Billard, 1919).

Collection record.—Sta. CH00, trawl, 22 May 1974.

Description.—Unbranched, sympodial colonies reaching 1 cm high. Hydrocaulus monosiphonic, geniculate, divided into internodes by oblique nodes sloping alternately in opposite directions, an annulation often evident above each node; perisarc thick. Internodes variable in length, first very short; each internode with a distal hydrotheca; diameter at nodes 135–181 μm. Hydrothecae alternate, slender, flask-shaped, widest at juncture of adcauline wall and internode, narrowest just below margin, walls with 4–8 distinct annulations; adcauline wall convex, length adnate 211–257 μm, length free 293–445 μm; abcauline wall slightly convex basally, slightly concave distally, 398–562 μm long. Hydrothecal margin with 4 distinct, equal teeth, operculum of 4 valves; aperture quadrate or irregularly oval, 187–211 μm wide from adcauline to abcauline tooth; 3 well-developed internal teeth, 2 additional smaller ones occasionally evident.

Gonothecae absent.

Remarks.—This species is very similar to *Sertularella robusta* Coughtrey, 1876, as described by Pennycuik (1959), Ralph (1961), Blanco (1968), Vervoort (1972), Watson (1973), and Vervoort and Vasseur (1977). The latter species occurs over a wide area in the southern hemisphere. *Sertularella conica* has been observed in Bermuda (Calder, unpublished) and was recorded earlier from Bermuda by Verrill (1900, 1907) as *Sertularella gayi* (Lamouroux, 1821). Bennitt's (1922) record of *S. tenella* (Alder, 1856) from Bermuda may also have been based on this species. *Sertularella conica* is readily distinguished from *S. gayi* in having internal teeth below the margin of the hydrotheca. Fraser's (1913, 1944) accounts of this species from the Canso Banks, Nova Scotia, as well as those from the eastern Pacific (Fraser 1937, 1948), do not correspond with *S. conica.* Specimens identified as *S. conica* from the Tortugas by Gemerden-Hoogeveen (1965) also appear to be based on material of another species.

Sertularella conica was collected once in estuaries of South Carolina. Specimens were found growing on hydrocauli of *Aglaophenia trifida* taken at the entrance of Charleston Harbor.

Known range.—Western Atlantic: North Carolina to the Caribbean Sea; Bermuda.

Sertularia Linnaeus, 1758

Sertularia distans Lamouroux, 1816

Fig. 5

Sertularia distans Lamouroux, 1816:191. Not *Dynamena distans* Lamouroux, 1816:180, pl. 5, figs. 1a, 1b [=*Dynamena pumila* (Linnaeus, 1758)].

Sertularia gracilis Hassall, 1848:2223.

Dynamena gracilis.—Marktanner-Turneretscher, 1890:240 (part).

Sertularia pourtalesi Nutting, 1904:59, pl. 5, fig. 5.

Sertularia stookeyi Nutting, 1904:59, pl. 5, figs. 6, 7.—Fraser, 1912:375, fig. 39.—Calder, 1976:169.—Calder and Hester, 1978:91.

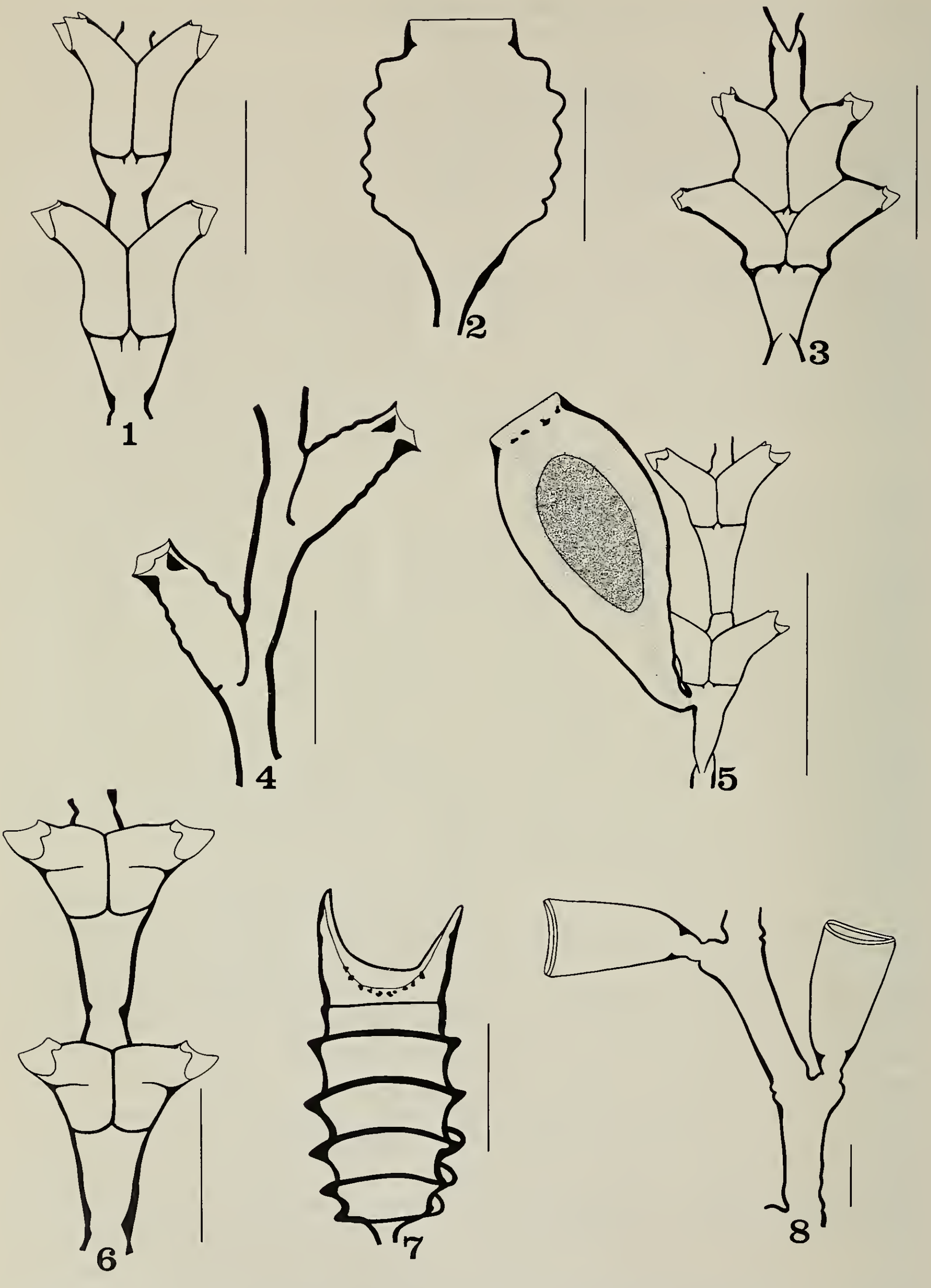
Sertularia heterodonta Ritchie, 1909a:79, fig. 4 [not *Dynamena heterodonta* (Jarvis, 1922)].

Sertularia distans var. *garcilis* Billard, 1912:465.
Tridentata heterodonta.—Stechow, 1923:205.
Tridentata pourtalesi.—Stechow, 1923:205.
Tridentata stookeyi.—Stechow, 1923:205.
Tridentata gracilis.—Stechow, 1923:208, fig. G.
Sertularia distans gracilis Millard, 1964:49.
Tridentata distans.—Hirohito, 1969:23, fig. 16.

Collection records.—Sta. BB01, dredge, 11 Aug 1977. Sta. BB02, dredge, 11 Aug 1977. Sta. SB03, dredge, 22 Aug 1977, 28 Apr 1978, 25 July 1978. Sta. SB04, dredge, 22 Aug 1977. Sta. SB05, dredge, 22 Aug 1977. Sta. SB07, dredge, 22 Aug 1977. Sta. SB10, dredge, 22 Aug 1977. Sta. SB15, dredge, 22 Aug 1977, 25 May 1978. Sta. B003, dredge, 22 Oct 1974. Sta. B002, trawl, 23 Apr 1973, 23 July 1973, 23 Oct 1973; dredge, 14 Jan 1974, 15 Apr 1974, 12 Aug 1974, 22 Oct 1974, 16 Apr 1975, 13 Oct 1975, 5 Jan 1976. Sta. B001, dredge, 9 Oct 1973, 17 Jan 1974, 12 Apr 1974, 15 Aug 1974, 16 Oct 1974, 13 Oct 1975, 2 Jan 1976, 2 Apr 1976. Sta. J003, Petersen grab, 1 Oct 1973; dredge, 1 Oct 1973. Sta. CH02, dredge, 10 Oct 1973. Sta. J002, dredge, 14 Oct 1975. Sta. KP01, dredge, 14 Mar 1977. Sta. KP02, dredge, 14 Mar 1977. Sta. KP04, dredge, 14 Mar 1977. Sta. KP07, dredge, 15 Mar 1977. Sta. DE10, dredge, 7 Mar 1978. Sta. E003, dredge, 2 Apr 1974, 2 Aug 1974. Sta. E002, trawl, 15 Sep 1973. Sta. DE04, dredge, 15 Dec 1977. Sta. DE05, dredge, 21 Nov 1977, 17 Oct 1978. Sta. DE06, dredge, 21 Nov 1977, 13 June 1978. Sta. E005, dredge, 7 Jan 1974. Sta. DE07, dredge, 21 Nov 1977, 15 Dec 1977. Sta. DE08, dredge, 7 Mar 1978, 17 Oct 1978. Sta. E006, trawl, 7 Aug 1973; dredge, 1 Feb 1974. Sta. E007, dredge, 5 Aug 1974, 9 Oct 1975, 11 Jan 1976. Sta. E008, trawl, 9 Apr 1973, 2 July 1973, 5 Sep 1973; dredge, 2 Oct 1973, 7 Jan 1974, 3 Apr 1974, 2 Oct 1974. Sta. D004, dredge, 3 Oct 1973, 9 Jan 1974. Sta. BR08, dredge, 8 Oct 1975. Sta. P002, dredge, 5 Apr 1974, 8 Oct 1974. Sta. P001, dredge, 5 Apr 1974. Sta. G001, dredge, 8 Oct 1974.

Description.—Colonies up to 2 cm high; usually unbranched but occasionally with one or more branches; branch arising either from an apophysis inserting just below a hydrotheca or from renovation of an old hydrotheca. Hydrocaulus monosiphonic, straight, arising from a creeping hydrorhiza; basal part of variable length but usually less than 500 μm long, consisting of 1 or 2 athecate internodes marked by oblique hinge-joints; thecate part divided by slightly oblique and often obscure nodes, internodes 398–620 μm long, each with an opposite pair of frontally-placed hydrothecae; thecate part of some hydrocauli having one or more irregularly-placed athecate internodes with oblique hinge-joints distally. Hydrothecae horn-shaped, curved outward; pair usually contiguous but occasionally separated frontally, not touching across back of internode; abcauline wall concave, 181–222 μm long; adcauline wall 246–281 μm long, length contiguous 0–105 μm, diameter at base of hydrotheca 64–117 μm. Hydrothecal orifice oval, 70–94 μm wide from adcauline to abcauline wall; margin with 2 prominent lateral teeth and a small median adcauline tooth. Operculum consisting of an abcauline valve and an adcauline valve with a median line. Intrathecal teeth lacking. Hydranth with an abcauline caecum.

Gonothecae oval, with about 4 faint, rounded ridges, maximum diameter 351–433 μm, length from base to orifice 749–842 μm, arising by short pedicels from



Figs. 1–8. Family Sertulariidae. 1, *Dynamena cornicina*, hydrothecae, station P001; 2, *Dynamena cornicina*, gonotheca, station P001; 3, *Dynamena quadridentata*, hydrothecae, station J003; 4, *Sertularella conica*, hydrothecae, station CH00; 5, *Sertularia distans*, hydrothecae and gonotheca, station E002; 6, *Sertularia marginata*, hydrothecae, station D004; 7, *Sertularia marginata*, gonotheca, station D004; 8, *Thyroscyphus marginatus*, hydrothecae, station B002, scale bars = 500 μm.

hydrocaulus at bases of hydrothecae. Walls oval or nearly round in cross-section; orifice round, 211–252 μm in diameter, at end of a short collar; submarginal teeth present.

Remarks.—Specimens from South Carolina were compared with Nutting's (1904) type–material of *S. stookeyi* from the Great Bahama Banks (USNM 19710) and are inseparable from them morphologically. *Sertularia stookeyi* has been included in the synonymy of *S. distans* Lamouroux, 1816 by Cornelius (1979).

Sertularia distans is widespread in estuaries of South Carolina in salinities above 21‰. It frequently occurs in dense masses on the axes of dead specimens of the octocoral *Leptogorgia virgulata*.

Known range.—Western Atlantic: Massachusetts to Brazil; Bermuda. Elsewhere: Circumglobal, tropical and temperate waters.

Sertularia marginata (Kirchenpauer, 1864)

Figs. 6, 7

Dynamena marginata Kirchenpauer, 1864:13, fig. 8. Not *Sertularia marginata* Allman, 1877:23, pl. 16, figs. 1, 2 (=*Sertularia striata* Totton, 1930).
Sertularia flosculus Thompson, 1879:104, pl. 17, fig. 2.
Sertularia amplectens Allman, 1885:141, pl. 16, figs. 3, 4.
Desmoscyphus pectinatus Allman, 1888:71 (part).
Desmoscyphus gracilis Allman, 1888:71, pl. 34, figs. 2, 2a–c.
Desmoscyphus inflatus Versluys, 1899:42, figs. 11–13.
Sertularia inflata.—Jäderholm, 1903:286.
Sertularia versluysi Nutting, 1904:53, pl. 1, figs. 4–9.—Fraser, 1912:375, fig. 40.
Sertularia pluma Hartlaub, 1905:661.
Sertularia marginata.—Bale, 1913:125 (part).—Calder, 1976:169.—Calder and Hester, 1978:91.
Amphisbetia marginata.—Stechow, 1921:258.
Tridentata flosculus.—Stechow, 1923:204.
Tridentata inflata.—Stechow, 1923:205.
Sertularia marginata f. *typica* Vannucci, 1949:248.
Sertularia marginata f. *laxa* Vannucci, 1949:248, pl. 3, fig. 46.

Collection records.—Sta. J003, dredge, 1 Oct 1973. Sta. J002, dredge, 14 Oct 1975. Sta. J001, trawl, 8 Oct 1973. Sta. D004, dredge, 3 Oct 1973. Sta. H003, dredge, 10 Oct 1975.

Description.—Hydroids up to 6.5 cm high, arising from a tangled hydrorhiza. Hydrocaulus straight, monosiphonic, alternately branched, perisarc thick; basal part athecate, length variable but usually several mm long, occasionally with one or more transverse or slightly oblique nodes, separated from upper thecate part by an oblique hinge-joint; thecate part divided by rather indistinct transverse nodes, internodes short, each with an apophysis and an axillary hydrotheca basally and a pair of subopposite hydrothecae distally, hydrothecal pair separated front and back. Apophyses given off alternately from opposite sides of hydrocaulus, separated from hydroclade by a transverse node, node sometimes obscure. Hydrocladia unbranched, reaching 1 cm long, directed upward; first internode short, athecate, node transverse proximally, an oblique hinge-joint distally; remaining internodes each with one pair of frontally-placed hydrothecae, nodes oblique, often indistinct or entirely obliterated. Hydrothecae in opposite pairs, pair occasionally separated but usually contiguous frontally, not touching across back of internode; each hydrotheca expanded basally, turned abruptly outward and slightly upward distally, tapering towards margin; abcauline wall concave, 176–222 μm long with a prominent intrathecal septum; contiguous part of adcauline wall straight, length contiguous 0–211 μm, free part convex, 129–304 μm long. Hydrothecal orifice oval, margin with very small median adcauline tooth and 2 large, pointed lateral teeth appearing unequal in size due to angle of aperture. Operculum consisting of a large abcauline and a smaller adcauline valve divided by a median line.

Gonothecae resembling Chinese lanterns, 760 μm wide, 1400 μm long from base to orifice, arising by short pedicels from hydrocaulus just above axillary hydrothecae. Walls oval in cross-section, with 5–6 transverse ridges; orifice hemispherical, bounded by 2 spines; spines horn-shaped, 255–350 μm long.

Remarks.—Van Gemerden-Hoogeveen (1965) recognized that *Sertularia inflata* (Versluys, 1899) was very difficult to separate from *S. marginata,* but she believed that they could be distinguished on the basis of differences in gonotheca arrangement and shape as well as hydrotheca shape. However, I have followed Billard (1925), Vannucci Mendes (1946), Ralph (1961), Mammen (1965a), Millard and Bouillon (1974), Millard (1975), Garcia *et al.* (1980), and others in regarding *S. inflata* as a synonym of *S. marginata.*

Known range.—Western Atlantic: North Carolina to Brazil; Bermuda; northward to Massachusetts on floating *Sargassum.* Elsewhere: Circumglobal, tropical and subtropical waters.

Thyroscyphus Allman, 1877

Thyroscyphus marginatus (Allman, 1877), new combination

Fig. 8

Obelia marginata Allman, 1877:9, pl. 6, figs. 1, 2.
Campanularia insignis Fewkes, 1881:129.
Not *Campanularia marginata* Bale, 1884:154, pl. 1, fig. 2.
Lytoscyphus marginata.—Ritchie, 1909b:260.
Lytoscyphus marginatus.—Billard, 1910:8.
Campanularia marginata.—Nutting, 1915:44, pl. 6, figs. 5–7.
Leptoscyphus marginatus.—Jäderholm, 1920:3.
Cnidoscyphus marginatus.—Splettstösser, 1929:88, 125, figs. 83–88.—Calder, 1976: 169.—Calder and Hester, 1978:91.

Collection record.—Sta. B002, dredge, 12 Aug 1974.

Description.—Specimen fragmentary, 2.8 cm high; hydrocaulus 0.8 mm wide, monosiphonic, straight basally, zigzag distally, divided by transverse nodes; perisarc thick. Each internode with a distal apophysis bearing a hydrotheca; every third internode with a second apophysis near the first; second apophysis large, supporting a branch; branches and hydrothecae given off alternately from opposite sides of hydrocaulus. Branches nearly perpendicular to hydrocaulus, lacking secondary branches in present material; internodes zigzag, similar to those of hydrocaulus but more slender. Hydrothecae 1112–1264 μm long from apophysis to margin, cone-shaped; pedicel very short; base asymmetrical, with adcauline wall convex, abcauline wall nearly straight; diaphragm distinct, basal chamber small; margin entire, with a ring-like edge; aperture round, 562–655 μm wide.

Gonothecae absent.

Remarks.—I follow Millard (1975) in regarding the genus *Cnidoscyphus* Splettstösser, 1929, as a synonym of *Thyroscyphus* Allman, 1877. *Obelia marginata* Allman, 1877 from the Atlantic belongs to *Thyroscyphus,* as does *Campanularia marginata* Bale, 1884, from Australia (Bale 1915). A new name, *Thyroscyphus balei,* is proposed here for the junior secondary homonym *T. marginatus* (Bale 1884). *Thyroscyphus marginatus* is common to abundant in tropical and subtropical waters of the western North Atlantic, apparently reaching the northern limit of its range off the coast of the Carolinas (Nutting 1915; Fraser 1944; Cain 1972). While it is frequent on hard banks off the coasts of Georgia and the Carolinas, only one fragmentary colony was collected during this study in estuarine areas of South Carolina.

Known range.—Western Atlantic: North Carolina to Venezuela; Bermuda. Elsewhere: Tropical west coast of Africa.

Family Plumulariidae L. Agassiz, 1862
Subfamily Halopterinae Millard, 1962
Monostaechas Allman, 1877
Monostaechas quadridens (McCrady, 1859)
Fig. 9

Plumularia quadridens McCrady, 1859:199.

Monostaechas dichotoma Allman, 1877:37, pl. 22, figs. 1–5.

Monostaechas quadridens.—Nutting, 1900:75, pl. 13, figs. 1–4.—Fraser, 1912: 380, fig. 46; 1943:95; 1944:334, fig. 343.—Calder, 1976:169.—Calder and Hester, 1978:91.

Monostaechas fisheri var. *simplex* Billard, 1913:16, fig. 7 (not *Monostaechas fisheri* Nutting, 1905).

Monostaechas quadridens f. *stechowi* Leloup, 1935:2, figs. 2, 3.

Collection record.—Sta. P006, trawl, 12 Jan 1976.

Description.—Colonies reaching 8.5 cm high; hydrocaulus monosiphonic, 260 μm in diameter, perisarc thick. Basal internodes very long, athecate, with numerous movable, 2 chambered nematothecae, most of which are missing in present specimens, giving rise via two curved apophyses to a pair of opposite upward-directed branches just below a hydrothecate segment, athecate and thecate segments of hydrocaulus separated by an oblique hinge-joint. Branches resembling hydrocaulus and rebranched in like manner, the whole colony thus appearing to be dichotomously branched; some distal branches with a single branch-bearing apophysis below thecate segment. Hydrothecate segments up to 1 cm long, consisting of alternating hydrothecate and athecate internodes. Thecate internodes 456–644 μm long with an oblique hinge-joint proximally and a transverse node distally, each such internode with a hydrotheca, a movable median inferior nematotheca with a scoop-shaped aperture, a reduced median superior nematotheca, and a pair of movable trumpet-shaped lateral nematothecae on distinct apophyses adnate to hydrothecal wall. Athecate internodes 316–538 μm long with a transverse node proximally and an oblique hinge-joint distally, with 1–2 movable nematothecae, each with a scoop-shaped aperture. Hydrotheca cup-shaped, 263–316 μm deep; main axis oblique to internode; abcauline wall slightly convex, 222–269 μm long; free part of adcauline wall straight or slightly concave, 105–164 μm long; margin entire, circular, aperture diameter 269–322 μm.

Gonothecae absent.

Remarks.—McCrady's (1859) type-material of *M. quadridens* from the Charleston Harbor area was found floating in the water, and specimens collected in an otter trawl from Port Royal Sound during this study were also all unattached. Attached hydroids of *M. quadridens* are abundant on ledges of the inner continental shelf off South Carolina, and the species is probably carried into estuaries of the state by water currents.

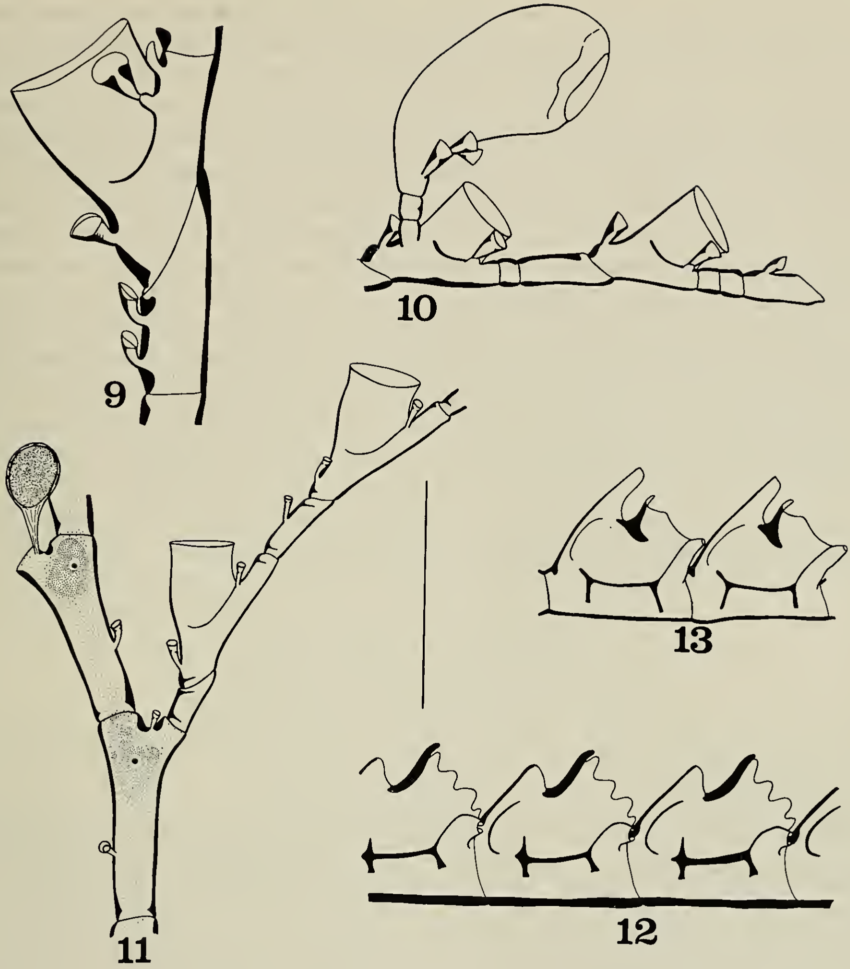
Known range.—Western Atlantic: Massachusetts to Brazil. Elsewhere: Circumglobal, tropical and subtropical waters.

Schizotricha Allman, 1883
Schizotricha tenella (Verrill, 1874)
Fig. 10

Plumularia tenella Verrill, 1874:731.
Schizotricha tenella.—Nutting, 1900:80, pl. 4, figs. 4, 5.—Fraser, 1912:383, fig. 52.—Calder, 1976:169.—Calder and Hester, 1978:91.
Halopteris tenella.—Vervoort, 1968:108.

Collection records.—Sta. LRA7, dredge, 21 Apr 1976. Sta. LRA8, dredge, 21 Apr 1976. Sta. MI07, dredge, 29 May 1975. Sta. MI09, dredge, 29 May 1975. Sta. MI12, dredge, 29 May 1975. Sta. MI13, dredge, 29 May 1975. Sta. MI15, dredge, 29 May 1975. Sta. MI16, dredge, 29 May 1975. Sta. MI17, dredge, 29 May 1975. Sta. BB01, dredge, 11 Aug 1977. Sta. BB02, dredge, 11 Aug 1977. Sta. SB03, dredge, 22 Aug 1977, 28 Apr 1978, 25 July 1978. Sta. SB04, dredge, 22 Aug 1977, 25 July 1978. Sta. SB08, dredge, 22 Aug 1977, 25 May 1978, 25 July 1978. Sta. SB13, dredge, 22 Aug 1977, 28 Apr 1978, 25 July 1978. Sta. SB18, dredge, 22 Aug 1977, 25 Apr 1978, 25 July 1978. Sta. B002, dredge, 15 Apr 1974, 22 Oct 1974, 5 Jan 1976. Sta. B001, dredge, 2 Apr 1976. Sta. E001, dredge, 2 Apr 1974, 2 Aug 1974. Sta. E003, dredge, 2 Apr 1974, 2 Aug 1974, 3 Oct 1974. Sta. E008, dredge, 2 Oct 1974. Sta. DE01, dredge, 13 June 1978. Sta. DE05, dredge, 21 Nov 1977, 15 Dec 1977, 13 June 1978, 17 Oct 1978. Sta. DE06, dredge, 21 Nov 1977, 15 Dec 1977, 13 June 1978. Sta. DE07, dredge, 21 Nov 1977, 17 Oct 1978. Sta. DE10, dredge, 21 Nov 1977, 13 June 1978, 17 Oct 1978. Sta. BR08, dredge, 27 Mar 1974, 8 Oct 1975.

Description.—Colonies up to 3 cm high. Hydrocaulus monosiphonic, slightly zigzag, unbranched, basal region with hydrothecae, nematothecae, and hydrocladia often missing, divided beyond basal region into alternating hydrothecate and athecate internodes. Internodes of variable length and diameter, usually longer and thicker toward proximal end of hydrocaulus. Hydrothecate internodes with an oblique joint proximally and a transverse or slightly oblique node distally, the latter often indistinct; each thecate internode with one hydrotheca, one median inferior nematotheca, 2 lateral nematothecae, an occasional median superior nematotheca, and an apophysis near base of hydrotheca. Athecate internodes with a slightly oblique node proximally and an oblique joint distally, 1–4 nematothecae.



Figs. 9–13. Family Plumulariidae. 9, *Monostaechas quadridens,* hydrotheca, station P006; 10, *Schizotricha tenella,* hydrothecae and gonotheca, station BR08; 11, *Plumularia floridana,* hydrothecae and gonotheca, station B001; 12, *Aglaophenia trifida,* hydrothecae, station CH00; 13, *Macrorhynchia philippina,* hydrothecae, station BR08, scale bars = 500 μm.

Apophyses long, given off alternately from opposite sides of hydrocaulus, supporting unbranched or alternately branched hydrocladia. Hydrocladia up to 7 mm long, typically consisting of a series of 3 types of internodes; a very short athecate internode lacking nematothecae, nodes transverse at both ends; a longer athecate internode with 0–2 trumpet-shaped median nematothecae, proximal node transverse, distal node oblique; a long hydrothecate internode with a median inferior nematotheca, a hydrotheca, and a pair of trumpet-shaped lateral nematothecae, node oblique proximally, transverse distally. Nematothecae on both hydrocaulus and hydrocladia 2-chambered, movable. Hydrotheca cup-shaped, main axis oblique to hydroclade, abcauline wall nearly straight, 111–158 μm long, free adcauline wall concave, length 70–94 μm, margin entire, opening circular, aperture diameter 140–176 μm.

Gonotheca cornucopia-shaped with 3 nematothecae near base, 562–690 μm long, 263–316 μm wide, borne on a 2-segmented pedicel inserting near base of hydrotheca on hydrocaulus and hydrocladia.

Remarks.—Vannucci (1949) included this species in the synonymy of *Halopteris diaphana* (Heller, 1868). I regard the two as separate species for the following reasons. The presence of three types of hydrocladial internodes in *S. tenella* immediately distinguishes it from *H. diaphana,* which has but two types. Hydrocladia are usually branched in *S. tenella* and unbranched in *H. diaphana.* Finally, the largely temperate water *S. tenella* attains a much larger colony size than the tropical and subtropical *H. diaphana.*

Schizotricha tenella is the most widespread plumularian hydroid in temperate estuaries of the east coast of the United States (Nutting 1900, 1901; Fraser 1912, 1944; Calder 1971, 1976; Watling and Maurer 1972; Calder and Hester 1978). It is both euryhaline, penetrating up–estuary to a salinity of about 15‰, and eurythermal, having been collected during this study over a temperature range from 9–32°C.

Known range.—Western Atlantic: Massachusetts to the Caribbean Sea. Elsewhere: Eastern Pacific, from Southern California to Panama.

Subfamily Plumulariinae Agassiz, 1862

Plumularia Lamarck, 1816

Plumularia floridana Nutting, 1900

Fig. 11

Plumularia floridana Nutting, 1900:59, pl. 2, figs. 4, 5.—Fraser, 1912:381, fig. 49.—Calder, 1976:169.—Calder and Hester, 1978:91.

Collection records.—Sta. NS01, dredge, 6 Apr 1976. Sta. SB03, dredge, 25 July 1978. Sta. SB04, dredge, 25 July 1978. Sta. SB08, dredge, 25 July 1978. Sta. SB18, dredge, 22 Aug 1977. Sta. B002, dredge, 15 Apr 1974, 12 Aug 1974. Sta. B001, dredge, 16 Oct 1974, 13 Oct 1975, 2 Apr 1976. Sta. CH00, dredge, 13 Oct 1975. Sta. CH02, dredge, 10 Oct 1973. Sta. J002, trawl, 9 Oct 1973. Sta. E003, dredge, 8 Jan 1974, 2 Aug 1974, 3 Oct 1974. Sta. E005, dredge, 3 Oct 1974. Sta. E007, dredge, 2 Oct 1973. Sta. AC01, Petersen grab, 6 June 1973. Sta. DE01, dredge, 21 Oct 1977. Sta. DE04, dredge, 21 Nov 1977, 13 June 1978. Sta. DE05, dredge, 13 June 1978, 17 Oct 1978.

Description.—Hydrocaulus monosiphonic, straight, unbranched, reaching 2.5 cm high, divided beyond basal region by distinct, transverse nodes; internodes 293–480 μm long, 70–105 μm wide at nodes, each with a distal apophysis and 2 nematothecae, one beside apophysis and another proximal one on side opposite apophysis; apophyses given off alternately from opposite sides of hydrocaulus, giving rise to unbranched hydrocladia with 1–5 hydrothecae; hydrocladia up to 2 mm long, nodes alternately transverse and oblique, hydroclade with 1–3 short basal internodes lacking hydrothecae and nematothecae, remaining internodes alternately hydrothecate and athecate, internodes with 2 internodal septa, one near each extremity, often indistinct; thecate internodes 257–351 μm long with a median inferior nematotheca, a hydrotheca, and a pair of lateral nematothecae, lateral nematothecae not reaching hydrothecal margin; athecate internodes 94–257 μm long, usually with one median nematotheca, all nematothecae movable, 2-chambered, cone-shaped; hydrotheca cup-shaped, main axis oblique to hydroclade, abcauline wall 129–164 μm long, length adcauline wall free 70–105 μm, margin entire, aperture diameter 117–164 μm.

Female gonotheca oval with thin perisarc, 211–281 μm long, 99–123 μm wide when fully developed, borne on slender pedicels from anterior side of apophysis base, each containing one ovum or developing planula, additional ova visible in coenosarc of hydrocaulus, planula escaping from rupture at distal end of gonotheca.

Remarks.—This species closely resembles descriptions of *Plumularia alicia* Torrey, 1902 from California and Oregon, USA (Torrey 1902; Fraser 1937), *Plumularia* sp. from Queensland, Australia (Pennycuik 1959), and *P. pennycuikae* Millard and Bouillon, 1973 from the Seychelles (Millard and Bouillon 1973), Bonin Islands (Hirohito 1974), and Mozambique (Millard 1975). *Plumularia floridana* differs from these species chiefly in having one instead of two nematothecae in the axil between hydrocaulus and apophysis. *Plumularia indica* from India (Mammen 1965b) is similar, and like *P. floridana* has a single axillary nematotheca. If not conspecific, these hydroids must all be very closely related.

Known range.—Western Atlantic: North Carolina to Brazil; Bermuda; northward to Massachusetts on floating *Sargassum*. Elsewhere: Eastern Pacific, from Southern California to Ecuador.

Subfamily Aglaopheniinae Stechow, 1911

Aglaophenia Lamouroux, 1812

Aglaophenia trifida L. Agassiz, 1862

Fig. 12

Aglaophenia cristata.—McCrady, 1859:202 [not *Plumularia cristata* Lamarck, 1816 = *Aglaophenia pluma* (Linnaeus, 1758)].

Aglaophenia trifida L. Agassiz, 1862:358.—Calder, 1976:169.—Calder and Hester, 1978:91.

Aglaophenia rigida Allman, 1877:43, pl. 25, figs. 5–9.—Jäderholm, 1896:17.—Fraser, 1912:378, fig. 44.

Collection records.—Sta. YB02, dredge, 6 Jan 1977. Sta. NS00, trawl, 17 Dec 1974. Sta. NB02, trawl, 19 Dec 1974. Sta. CH00, trawl, 22 May 1974.

Description.—Colonies growing in tangled masses reaching 20 cm high. Hydrocaulus monosiphonic, wiry, slender, reaching 0.5 mm wide basally, occasionally unbranched but usually with long, widely-separated branches. Branches given off from front of hydrocaulus either singly or in pairs, frequently rebranched in like manner; paired branches when present arising from contiguous internodes. Hydrocaulus and branches divided by oblique nodes into short internodes measuring 300–560 μm long, each internode with one apophysis and 3 nematothecae, one proximal to, one on, and one in the axil of each apophysis, apophyses given off alternately from fronto-lateral surface of internodes. Hydrocladia reaching 13 mm long, nearly straight, absent only at base of hydrocaulus and some older branches, divided at regular intervals by slightly oblique nodes; internodes 281–351 μm long, 94–164 μm wide at nodes, each with one hydrotheca, one median inferior nematotheca, one pair of lateral nematothecae, and 2 internodal septa, one at base of intrathecal septum, the other at base of lateral nematothecae.

Hydrothecae cone-shaped, 269–328 μm long, 164–187 μm wide at aperture, occupying most of internode, orifice of one hydrotheca adjacent to base of next, adcauline wall convex, distal half of abcauline wall concave with thick perisarc, plane of orifice sloping. Margin with one median and 4 pairs of lateral teeth, teeth rounded, short intrathecal septum present basally. Nematothecae tubular, one-chambered, immovable; median nematotheca adnate to hydrotheca for much of its length, reaching halfway to hydrothecal margin, length free 23–47 μm; lateral nematothecae adnate to hydrotheca, reaching nearly to orifice.

Corbulae pod-shaped, 4 mm long, 770 μm wide, each occurring in place of a distal hydrocladium, borne on short pedicels consisting of an internode with one hydrotheca; either side of corbula with 11–13 gonohydrocladia, each with a row of about 6 nematophores; interior of corbula with oval gonothecae.

Remarks.—Two distinct colony forms of this species were found in estuaries of South Carolina. Hydroids from several shallow subtidal and intertidal areas (stations YB02, NS00, NB02), appeared to be dichotomously branched because the long branches arose singly from the hydrocaulus. A different colony form was evident in specimens collected from deeper water at station CH00 near the Charleston Harbor entrance. These hydroids had long branches arising in pairs from the hydrocaulus, their hydrocladia were longer, and the diameters of their hydrocauli were greater. Nevertheless, hydrothecae of the two forms were indistinguishable and the variation in colony form is believed to be environmentally induced.

Specimens of this species from Sullivans Island and Charleston, South Carolina, were identified by McCrady (1859) as *Aglaophenia cristata*. However, he believed that it was probably distinct from the species described from Europe by Lamarck (1816) as *Plumularia cristata* [=*Aglaophenia pluma* (Linnaeus, 1758)]. Agassiz (1862) provided a new name, *A. trifida,* for this hydroid but did not describe or illustrate it. Despite Fraser's (1944) apparent views to the contrary, Agassiz should be recognized as the author of the species because he provided the necessary "indication" required under Article 16 (ICZN).

There is nothing in the original description of *Aglaophenia rigida* by Allman (1877), or in subsequent descriptions of that species by later authors, that can be used to distinguish it from *A. trifida*. Although Nutting (1900) and Fraser (1944) reported differences in the number of marginal teeth between the two species, with eight in *A. rigida* and nine in *A. trifida,* such differences are nonexistent. The types of *A. rigida* (MCZ 2109) have nine marginal teeth. Accordingly, the species are regarded here as synonyms, with the name *A. trifida* L. Agassiz, 1862 having priority over *A. rigida* Allman, 1877.

Aglaophenia trifida bears considerable resemblance to descriptions of the cosmopolitan *A. pluma* (Linnaeus, 1758). Nutting (1900) compared specimens of *A. trifida* with material of *A. pluma* from Plymouth, England, and concluded that the two were different species. He observed that the abcauline wall of the hydrotheca distal to the median inferior nematotheca is less concave in *A. trifida* and that the corbulae of this species were much longer and more slender. For the present I prefer to treat *A. trifida* as a distinct species, but it may eventually be shown to be conspecific with *A. pluma*. Records of *A. pluma* from the western North Atlantic as *A. dichotoma* (Leloup 1937; Fraser 1944) and *A. pluma pluma* (van Gemerden-Hoogeveen 1965) are probably based on hydroids identical with those identified here as *A. trifida*.

Known range.—Western Atlantic: North Carolina to the Caribbean Sea.

Macrorhynchia Kirchenpauer, 1872
Macrorhynchia philippina Kirchenpauer, 1872
Fig. 13

Aglaophenia (*Macrorhynchia*) *philippina* Kirchenpauer, 1872:29, 45, pls. 1, 2, 7, fig. 2b.
Aglaophenia urens.—Bale, 1884:155, pl. 14, fig. 6, pl. 17, fig. 9 (not *Aglaophenia urens* Kirchenpauer, 1872).
Lytocarpus phillipinus.—Bale, 1888:786, pl. 21, figs. 5–7 (*lapsus*).
Lytocarpus philippinus.—Marktanner-Turneretscher, 1890:274, pl. 6, fig. 16.—Fraser, 1912:379, fig. 45.—Calder, 1976:169.—Calder and Hester, 1978:91.
Lytocarpia philippina.—Stechow, 1919:132, fig. Z1.
Macrorhynchia philippina.—Stechow, 1923:241.

Collection records.—Sta. B003, dredge, 12 Aug 1974. Sta. B002, dredge, 13 Oct 1975. Sta. CI01, trawl, 5 Oct 1976. Sta. BR08, dredge, 8 Oct 1975. Sta. P006, trawl, 7 Aug 1974.

Description.—Irregularly, pinnately, or twice-pinnately branched colonies reaching 10 cm high. Hydrocaulus and branches curved gradually backward, polysiphonic except at distal ends, bearing hydrocladia except when these are broken off proximally; nodes indistinct; apophyses short, given off alternately from front of anterior stolon only, each apophysis bearing one rudimentary nematotheca and one axillary nematotheca, an additional nematotheca on stolon between adjacent apophyses. Hydrocladia up to 7 mm long, curved outward, nodes straight; internodes 257–374 μm long, 75–100 μm wide at nodes, each with one hydrotheca, one median inferior nematotheca, one pair of lateral nematothecae, and 2 septa. Hydrothecae boot-shaped, 257–316 μm long, 140–187 μm wide at aperture; abcauline wall with a distinct inward-projecting intrathecal septum, adcauline wall with a short intrathecal septum basally; margin with low, rounded lateral teeth and an acute median tooth. Nematothecae tubular, one-chambered, immovable; median inferior nematotheca long, adnate to hydrotheca proximally, reaching beyond margin of hydrotheca distally, length free 82–140 μm, internal aperture diameter 11–19 μm; lateral nematothecae projecting a short distance beyond hydrothecal margin distally, otherwise adnate to hydrotheca.

Phylactocarpia up to 2.5 mm long, occurring in place of hydrocladia. Basal internode of phylactocarp with a hydrotheca, a median inferior nematotheca, a pair of lateral nematothecae, and 2 internodal septa; terminal internode also hydrothecate, or with nematothecae only; intermediate internodes modified, one or more bearing gonothecae, nematothecae well-developed. Gonothecae disc-shaped, 1217–1287 μm wide, 1193–1463 μm high, 550–667 μm thick; 1–3 per phylactocarp.

Remarks.—Following authors such as Stechow (1923), Vannucci Mendes (1946), Mammen (1965b) and Gravier (1970), Kirchenpauer's (1872) subgenus *Macrorhynchia* is recognized as a distinct genus, and *Lytocarpus* Allman, 1883 is regarded as a synonym.

According to the literature (Gravely 1927; Halstead 1965), this hydroid is capable of stinging humans.

Known range.—Western Atlantic: North Carolina to Brazil; Bermuda. Elsewhere: Circumglobal, tropical and subtropical waters.

Acknowledgments

Materials for this study were collected while I was a staff member of the Marine Resources Research Institute, Charleston, South Carolina. Field work was supported by funds from the Coastal Plains Regional Commission (Contract No. 10340031), the U.S. Army Corps of Engineers (Contract Nos. DACW60-75-C-0016, DACW60-76-C-0017, DACW60-77-C-0013), and the South Carolina Coastal Council. Thanks are due to Magdalene Maclin, Billy Boothe, David Knott, and Dr. Robert Van Dolah for assistance in the field. I am also indebted to Dr. K. P. Sebens of the Museum of Comparative Zoology at Harvard University and Dr. F. M. Bayer of the National Museum of Natural History, Smithsonian Institution, for the loan of specimens. Mr. A. Sanders kindly permitted access to invertebrate collections at the Charleston Museum in a search for any hydrozoan materials collected by John McCrady. Finally, I thank an anonymous reviewer for constructive criticisms.

Literature Cited

Agassiz, L. 1862. Contributions to the natural history of the United States of America. Volume 4.—Little, Brown and Company, Boston, 380 pp.

Alder, J. 1856. A notice of some new genera and species of British hydroid zoophytes.—Annals and Magazine of Natural History (2)18:353–362.

Allman, G. J. 1877. Report on the Hydroida collected during the exploration of the Gulf Stream by L. F. de Pourtalès, assistant United States Coast Survey.—Memoirs of the Museum of Comparative Zoology at Harvard College 5(2):1–66.

———. 1883. Report on the Hydroida dredged by H.M.S. Challenger during the years 1873–1876. Part I. Plumularidae.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–1876, Zoology 7:1–54.

———. 1885. Description of Australian, Cape and other Hydroida, mostly new, from the collection of Miss H. Gatty.—Journal of the Linnaean Society 19:132–161.

———. 1888. Report on the Hydroida dredged by H.M.S. Challenger during the years 1873–1876. Part II. The Tubularinae, Corymorphinae, Campanularinae, Sertularinae, and Thalamophora.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873–1876, Zoology 23:1–90.

Bale, W. M. 1884. Catalogue of the Australian hydroid zoophytes.—Australian Museum, Sydney, 198 pp.

———. 1888. On some new and rare Hydroida in the Australian Museum collection.—Proceedings of the Linnaean Society of New South Wales 3:745–799.

———. 1913. Further notes on Australian hydroids. II.—Proceedings of the Royal Society of Victoria (new series) 26:114–147.

———. 1915. Report on the Hydroida collected in the Great Australian Bight and other localities. Part III.—Zoological Results of the Fishing Experiments carried out by F.I.S. "Endeavour" 3:241–336.

Bennitt, R. 1922. Additions to the hydroid fauna of the Bermudas.—Proceedings of the American Academy of Arts and Sciences 57:241–259.

Billard, A. 1910. Revision d'une partie des hydroïdes du British Museum.—Annales Sciences Naturelles, Zoologie 11:1–67.

———. 1912. Hydroïdes de Roscoff.—Archives de Zoologie Expérimentale et Générale 51:459–478.

———. 1913. Les hydroïdes de l'expédition du Siboga. I. Plumulariidae.—Siboga-Expeditie, Monographie 7a:1–115.

———. 1919. Note sur quelques espèces nouvelles de Sertularella de l'expédition du "Siboga."—Archives de Zoologie Expérimentale et Générale 58:18–23.

———. 1924. Note sur quelques espèces la plupart nouvelles de synthecides et de sertularides du "Siboga."—Bulletin de la Société Zoologique de France 49:646–652.

———. 1925. Les hydroïdes de l'Expédition du Siboga. II. Synthecidae et Sertularidae.—Siboga-Expeditie, Monographie 7b:115–232.

Blanco, O. M. 1968. Nueva contribucion al conocimiento de la fauna marina hidroide.—Revista del Museo de la Plata (Nueva Serie), Sección Zoologia 10:195–224.

Brooks, W. K. 1886. The life-history of the Hydromedusae: A discussion of the origin of the medusae, and of the significance of metagenesis.—Memoirs of the Boston Society of Natural History 3:359–430.

Cain, T. D. 1972. Additional epifauna of a reef off North Carolina.—Journal of the Elisha Mitchell Scientific Society 88:79–82.

Calder, D. R. 1971. Hydroids and Hydromedusae of southern Chesapeake Bay.—Virginia Institute of Marine Science Special Papers in Marine Science 1, 125 pp.

———. 1976. The zonation of hydroids along salinity gradients in South Carolina estuaries.—*In* G. O. Mackie, ed., Coelenterate Ecology and Behavior, Plenum Press, New York, pp. 165–174.

———, and B. S. Hester. 1978. Phylum Cnidaria.—*In* R. G. Zingmark, ed., A Checklist of the Biota of the Coastal Zone of South Carolina, University of South Carolina Press, Columbia, pp. 87–93.

Clarke, S. F. 1879. Report on the Hydroida collected during the exploration of the Gulf Stream and Gulf of Mexico by Alexander Agassiz, 1877–1878.—Bulletin of the Museum of Comparative Zoology at Harvard College 5:239–252.

Cornelius, P. F. S. 1979. A revision of the species of Sertulariidae (Coelenterata: Hydroida) recorded from Britain and nearby seas.—Bulletin of the British Museum (Natural History), Zoology Series 34:243–321.

Coughtrey, M. 1876. Critical notes on the New Zealand Hydroida.—Transactions and Proceedings of the New Zealand Institute 8:298–302.

Dean, T. A., and V. J. Bellis. 1975. Seasonal and spatial distribution of epifauna in the Pamlico River estuary, North Carolina.—Journal of the Elisha Mitchell Scientific Society 91:1–12.

Ellis, J., and D. Solander. 1786. The natural history of many curious and uncommon zoophytes, collected from various parts of the globe by the late J. Ellis. . . . Systematically arranged and described by the late Daniel Solander. . . . London, 208 pp.

Fewkes, J. W. 1881. Reports on the results of dredgings, under the 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." XI. Report on the Acalephae.—Bulletin of the Museum of Comparative Zoology at Harvard College 8:127–140.

Fleming, J. 1828. A History of British Animals. Bell and Bradfute, Edinburgh, 565 pp.

Fraser, C. M. 1912. Some hydroids of Beaufort, North Carolina.—Bulletin of the United States Bureau of Fisheries 30:339–387.

———. 1913. Hydroids from Nova Scotia.—Victoria Memorial Museum Bulletin Number 1:157–186.

———. 1937. Hydroids of the Pacific coast of Canada and the United States.—University of Toronto Press, Toronto, 207 pp.

———. 1943. Distribution records of some hydroids in the collection of the Museum of Comparative Zoölogy at Harvard College, with description of new genera and new species.—Proceedings of the New England Zoological Club 22:75–98.

———. 1944. Hydroids of the Atlantic Coast of North America.—University of Toronto Press, Toronto, 451 pp.

———. 1948. Hydroids of the Allan Hancock Pacific expeditions since March, 1938.—Allan Hancock Pacific Expeditions 4:179–335.

Garcia, P., A. Aguirre, and D. Gonzalez. 1980. Contribucion al conocimiento de los hidrozoos de las costas Españolas. Parte III. "Sertulariidae."—Boletin del Instituto Español de Oceanografia 6:5–67.

Gemerden-Hoogeveen, G. C. H. van. 1965. Hydroids of the Caribbean: Sertulariidae, Plumulariidae and Aglaopheniidae.—Studies on the Fauna of Curaçao and other Caribbean Islands 22:1–87.

Gravely, F. H. 1927. The littoral fauna of Krusadai Island in the Gulf of Manaar. Hydrozoa.—Bulletin of the Madras Government Museum (New Series, Natural History) 1:7–20.

Gravier, N. 1970. Libération de médusoides par *Macrorhynchia philippina* Kirchenpauer, 1872 (Hydroida, Plumulariidae).—Recueil des Travaux de la Station Marine d'Endoume (Fascicule Hors Série), Supplement Numereau 10:253–257.

Gray, J. E. 1848. List of the specimens of British animals in the collection of the British Museum. Part 1. Centroniae or radiated animals. London.

Halstead, B. W. 1965. Poisonous and venomous marine animals of the world. I. Invertebrates.—United States Government Printing Office, Washington, D.C., 994 pp.

Hargitt, C. W. 1908. Notes on a few coelenterates of Woods Hole.—Biological Bulletin 14:95–120.

Hartlaub, C. 1905. Die Hydroiden der magalhaenischen Region und chilenischen Küste.—Zoologische Jahrbücher, Supplement 6:497–714.

Hassall, A. H. 1848. Definitions of three new British zoophytes.—Zoologist 6:2223.

Heller, C. 1868. Die Zoophyten und Echinodermen des Adriatischen Meeres.—Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 18:1–88.

Hincks, T. 1868. A history of the British hydroid zoophytes, Vol. I.—John van Voorst, London, 338 pp.

Hirohito, Emperor of Japan. 1969. Some hydroids of the Amakusa Islands.—Biological Laboratory, Imperial Household, Tokyo, 32 pp.

———. 1974. Some hydroids of the Bonin Islands.—Biological Laboratory, Imperial Household, Tokyo, 55 pp.

Howard, J. D., and R. W. Frey. 1975. Estuaries of the Georgia coast, U.S.A.: Sedimentology and biology. I. Introduction.—Senckenbergiana Maritima 7:1–31.

Jäderholm, E. 1896. Ueber aussereuropäische Hydroiden des Zoologischen Museums der Universität Upsala.—Bihang till Svenska Vetenskapsakademiens Handlingar 21 IV(6):1–20.

———. 1903. Aussereuropäische Hydroiden im Swedischen Reichsmuseum.—Arkiv för Zoologi 1: 259–312.

———. 1920. On some exotic hydroids in the Swedish Zoological State Museum.—Arkiv för Zoologi 13(3):1–11.

Jarvis, F. E. 1922. The hydroids from the Chagos, Seychelles, and other islands and from the coasts of British East Africa and Zanzibar.—Transactions of the Linnaean Society of London (Zoology) 18:331–360.

Karlson, R. 1978. Predation and space utilization patterns in a marine epifaunal community.—Journal of Experimental Marine Biology and Ecology 31:225–239.

Kirchenpauer, G. H. 1864. Neue Sertulariden aus verschiedenen Hamburgischen Sammlungen, nebst allgemeinen Bemerkungen über Lamouroux's Gattung Dynamena.—Verhandlungen der K. Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher 31(3):1–16.

———. 1872. Ueber die Hydroidenfamilie Plumularidae, einzelne Gruppen derselben und ihre Fruchtbehälter. I. *Aglaophenia* Lx.—Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg 5:1–52.

Kühn, A. 1913. Entwicklungsgeschichte und Verwandtschaftsbeziehungen der Hydrozoen. I. Teil. Die Hydroiden.—Ergebnisse und Fortschritte der Zoologie 4:1–284.

Lamarck, J. P. B. A. de M. 1816. Histoire naturelle des animaux sans vertèbres. Ed. 2. Paris, 568 pp.

Lamouroux, J. V. F. 1812. Extrait d'un mémoire sur la classification des polypiers coralligènes non entièrement pierreux.—Nouveau Bulletin des Sciences pour la Société Philomatique de Paris 3:181–188.

———. 1816. Histoire des polypiers coralligènes flexibles, vulgairement nommés zoophytes. Caen, 560 pp.

———. 1821. Exposition méthodique des genres de l'ordre des polypiers, avec leur description et celle des principales espèces. Paris, 115 pp.

Leloup, E. 1935. Hydropolypes calyptoblastiques et siphonophores récoltés au cours de la croisière (1934–35) du navire-école Belge "Mercator".—Bulletin du Musée Royal d'Histoire Naturelle de Belgique 11:1–6.

———. 1937. Résultats scientifiques des croisières du navire-école Belge "Mercator". Vol. I. Hydroida.—Mémoires du Musée Royal d'Histoire Naturelle de Belgique 2, 9:91–121.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, secundem Classes, Ordines, Genera, Species, cum characteribus, differentiis, Synonymis, Locis, Editio Decima, Reformata. Holmiae, 824 pp.

Mammen, T. A. 1965a. On a collection of hydroids from South India. II. Suborder Thecata (excluding Family Plumulariidae).—Journal of the Marine Biological Association of India 7:1–57.

———. 1965b. On a collection of hydroids from South India. III. Family Plumulariidae.—Journal of the Marine Biological Association of India 7:291–324.

Marktanner-Turneretscher, G. 1890. Die Hydroiden des K.K. naturhistorischen Hofmuseums.—Annalen des Naturhistorischen Museums in Wien 5:195–286.

Mayer, A. G. 1910a. Medusae of the world. I. The Hydromedusae.—Carnegie Institution of Washington Publication 109:1–230.

———. 1910b. Medusae of the world. II. The Hydromedusae.—Carnegie Institution of Washington Publication 109:231–498.

McCrady, J. 1859. Gymnopthalmata of Charleston Harbor.—Proceedings of the Elliott Society of Natural History 1:103–221.

McDougall, K. D. 1943. Sessile marine invertebrates of Beaufort, North Carolina.—Ecological Monographs 13:321–374.

Millard, N. A. H. 1962. The Hydrozoa of the south and west coasts of South Africa. Part I. The Plumulariidae.—Annals of the South African Museum 46:261–319.

———. 1964. The Hydrozoa of the south and west coasts of South Africa. Part II. The Lafoeidae, Synthecidae and Sertulariidae.—Annals of the South African Museum 48:1–56.

———. 1975. Monograph on the Hydroida of southern Africa.—Annals of the South African Museum 68:1–513.

———, and J. Bouillon. 1973. Hydroids from the Seychelles (Coelenterata).—Musée Royal de l'Afrique Centrale, Annales, Serie IN-8, Sciences Zoologiques 206:1–106.

———, and ———. 1974. A collection of hydroids from Moçambique, East Africa.—Annals of the South African Museum 65:1–40.

Nutting, C. C. 1900. American hydroids. Part I. The Plumularidae.—Smithsonian Institution, United States National Museum Special Bulletin 4(1):1–285.

———. 1901. The hydroids of the Woods Hole region.—Bulletin of the United States Bureau of Fisheries 19:325–386.

———. 1904. American hydroids. Part II. The Sertularidae.—Smithsonian Institution, United States National Museum Special Bulletin 4(2):1–325.

———. 1905. Hydroids of the Hawaiian Islands collected by the steamer Albatross in 1902.—Bulletin of the United States Fish Commission 23:931–959.

———. 1915. American hydroids. Section III. The Campanularidae and Bonneviellidae.—Smithsonian Institution, United States National Museum Special Bulletin 4(3):1–126.

Pearse, A. S. 1936. Estuarine animals at Beaufort, North Carolina.—Journal of the Elisha Mitchell Scientific Society 52:174–222.

———, and L. G. Williams. 1951. The biota of the reefs off the Carolinas.—Journal of the Elisha Mitchell Scientific Society 67:133–161.

Pennycuik, P. R. 1959. Faunistic records from Queensland. Part V.—Marine and brackish water hydroids.—Papers from the Department of Zoology, University of Queensland 1:141–210.

Pictet, C. 1893. Étude sur les hydraires de la Baie d'Amboine.—Revue Suisse de Zoologie 1:1–64.

Ralph, P. M. 1961. New Zealand thecate hydroids. Part III—Family Sertulariidae.—Transactions of the Royal Society of New Zealand 88:749–838.

Ritchie, J. 1909a. Supplementary report on the hydroids of the Scottish National Antarctic Expedition.—Transactions of the Royal Society of Edinburgh 47:65–101.

———. 1909b. Two unrecorded Challenger hydroids from the Bermudas with a note on the synonymy of *Campanularia insignis*.—Zoologist 13:260–263.

Sandifer, P. A., T. I. J. Smith, and D. R. Calder. 1974. Hydrozoans as pests in closed-system culture of larval decapod crustaceans.—Aquaculture 4:55–59.

Splettstösser, W. 1929. Beiträge zur Kenntnis der Sertulariiden. *Thyroscyphus* Allm., *Cnidoscyphus* nov. gen., *Parascyphus* Ritchie.—Zoologische Jahrbücher, Systematik, Ökologie und Geographie der Tiere 58:1–134.

Stechow, E. 1911. Über Hydroiden der Deutschen Tiefsee-Expedition. Ein neues Genus thekater Hydroiden.—Zoologischer Anzeiger 37:193–197.

———. 1919. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, nebst Angaben über einige Kirchenpauer'sche Typen von Plumulariden.—Zoologische Jahrbücher, Systematik, Ökologie und Geographie der Tiere 42:1–172.

———. 1921. Neue Genera und Species von Hydrozoen und anderen Evertebraten.—Archiv für Naturgeschichte 87:248–265.

———. 1923. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete.—Zoologische Jahrbücher, Systematik, Ökologie und Geographie der Tiere 47:29–270.

———, and H. C. Müller. 1923. Hydroiden der Aru-Inseln.—Senckenbergische Naturforschende Gesellschaft 35:459–478.

Stephenson, T. A., and A. Stephenson. 1952. Life between tide-marks in North America. II. Northern Florida and the Carolinas.—Journal of Ecology 40:1–49.

Sutherland, J. P. 1977. Effect of *Schizoporella* (Ectoprocta) removal on the fouling community at Beaufort, North Carolina, USA.—*In* B. C. Coull, ed., Ecology of marine benthos. University of South Carolina Press, Columbia, pp. 155–176.

———. 1981. The fouling community at Beaufort, North Carolina: A study in stability.—American Naturalist 118:499–519.

———, and R. H. Karlson. 1977. Development and stability of the fouling community at Beaufort, North Carolina.—Ecological Monographs 47:425–446.

Thompson, D'A. W. 1879. On some new and rare hydroid zoophytes (Sertulariidae and Thuiariidae) from Australia and New Zealand.—Annals and Magazine of Natural History (5)3:97–114.

Thornely, L. R. 1904. Report on the Hydroida collected by Professor Herdman, at Ceylon, in 1902.—Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar II, Supplementary Report 8:107–126.

Torrey, H. B. 1902. The Hydroida of the Pacific coast of North America, with especial reference to the species in the collection of the University of California.—University of California Publications, Zoology 1:1–104.

Totton, A. K. 1930. Coelenterata.—Part V.—Hydroida.—British Antarctic ("Terra Nova") Expedition, 1910, Natural History Reports, Zoology 5(5):131–252.

Vannucci, M. 1949. Hydrozoa do Brasil.—Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Zoologia 14:219–265.

Vannucci Mendes, M. 1946. Hydroida Thecaphora do Brasil.—Arquivos de Zoologia do Estado de São Paulo 4:535–597.

Verrill, A. E. 1872. On Radiata from the coast of North Carolina.—American Journal of Science (3)3:432–438.

———. 1874. Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical features of the region.—Report of the Commissioner of Fisheries for 1871–1872:295–747.

———. 1900. Additions to the Anthozoa and Hydrozoa of the Bermudas.—Transactions of the Connecticut Academy of Arts and Sciences 10:551–572.

———. 1907. Characteristic life of the Bermuda coral reefs.—Transactions of the Connecticut Academy of Arts and Sciences 12:204–319.

Versluys, J., Jr. 1899. Hydraires calyptoblastes recueillis dans la Mer des Antilles pendant l'une des croisières accomplies par le Comte R. de Dalmas sur son yacht Chazalie.—Mémoires de la Société Zoologique de France 12:29–58.

Vervoort, W. 1968. Report on a collection of Hydroida from the Caribbean region, including an annotated checklist of Caribbean hydroids.—Zoologische Verhandelingen 92:1–124.

———. 1972. Hydroids from the Theta, Vema, and Yelcho cruises of the Lamont-Doherty Geòlogical Observatory.—Zoologische Verhandelingen 120:1–247.

———, and P. Vasseur. 1977. Hydroids from French Polynesia with notes on distribution and ecology.—Zoologische Verhandelingen 159:1–98.

Watling, L., and D. Maurer. 1972. Shallow water hydroids of the Delaware Bay region.—Journal of Natural History 6:643–649.

Watson, J. E. 1973. Pearson Island Expedition 1969–9. Hydroids.—Transactions of the Royal Society of South Australia 97:153–200.

Wells, H. W. 1961. The fauna of oyster beds, with special reference to the salinity factor.—Ecological Monographs 31:239–266.

———, M. J. Wells, and I. E. Gray. 1964. The calico scallop community in North Carolina.—Bulletin of Marine Science of the Gulf and Caribbean 14:561–593.

Department of Invertebrate Zoology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6, Canada.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 29–37

CREEDIA ALLENI AND *CREEDIA PARTIMSQUAMIGERA* (PERCIFORMES: CREEDIIDAE), TWO NEW MARINE FISH SPECIES FROM AUSTRALIA, WITH NOTES ON OTHER AUSTRALIAN CREEDIIDS

Joseph S. Nelson

Abstract.—Two new species of trachinoid fishes, *Creedia alleni* and *C. partimsquamigera,* are described. *Creedia alleni,* known from three specimens collected along coastal Western Australia, is distinguished from all other creediids in having only three soft rays, in addition to a spine, in each pelvic fin. *Creedia partimsquamigera,* known from nine specimens from New South Wales, is similar to *C. haswelli* (Ramsay) in fin ray counts but differs in lacking scales on the anterior portion of the body except along the lateral line and before the dorsal fin, and differs further from the other two species of *Creedia* in having a blunter snout and a blunt maxilla extending well behind the eye. *Creedia partimsquamigera* and *C. haswelli* exhibit sexual dimorphism, with males having longer pectoral and pelvic fins than females. Notes are given on the three other creediids from Australia, namely, *C. haswelli, Limnichthys fasciatus* Waite, and *L. donaldsoni* Schultz (newly found in Australia).

The family Creediidae (including Limnichthyidae) currently contains 12 described species in seven genera (Nelson 1979). Herein I describe two new species, one from near Perth, Western Australia, and the other from Sydney, New South Wales. New material of *Limnichthys fasciatus* from Western Australia and of *L. donaldsoni* and *Creedia haswelli* from eastern Australia is reported.

Methods

Measurements were made to the nearest 0.1 mm with needle-point dial calipers and are expressed as thousandths (‰) of standard length (SL). Radiographs were made of the specimens of the two new species. Abbreviations refer to the following museums: AMNH, American Museum of Natural History, New York; AMS, Australian Museum, Sydney; NMV, National Museum of Victoria, Melbourne; QVM, Queen Victoria Museum, Launceston; TFDA, Tasmanian Fisheries Development Authority, Hobart; UAMZ, University of Alberta Museum of Zoology, Edmonton; UCLA, Department of Zoology, University of California, Los Angeles; WAM, Western Australian Museum, Perth.

Creedia alleni, new species
Fig. 1

Holotype.—WAM P25808-005, 40.0 mm SL, probably a female, off Garden Island, near Fremantle, Western Australia, 32°15.7′S, 115°39′E, collected with beam trawl in 20 m, 29 June 1977. Bottom: sand and weed.

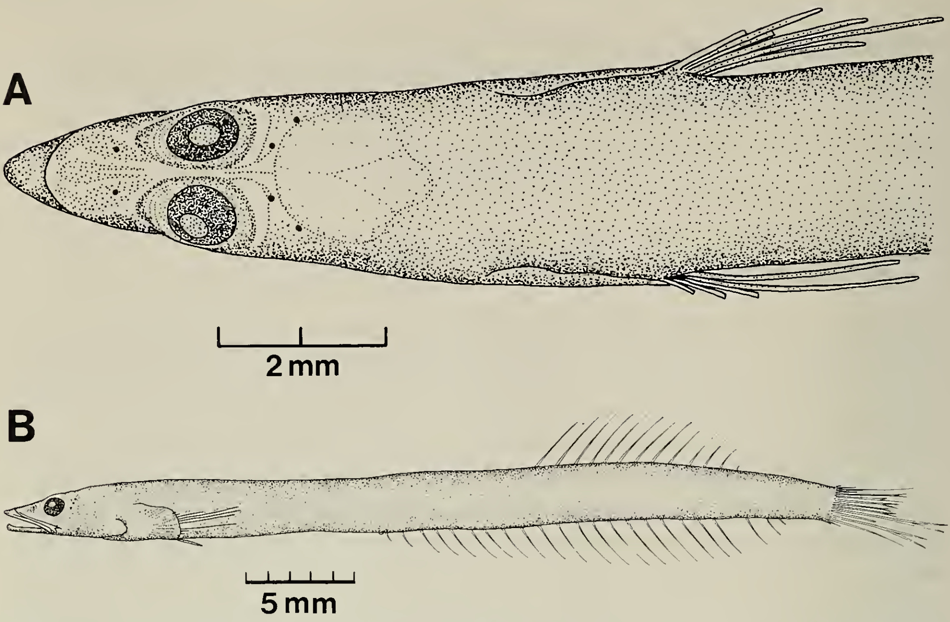


Fig. 1. *Creedia alleni*, holotype, WAM P25808-005, 40 mm SL. A, Dorsal view of head region; B, Lateral view.

Paratypes.—WAM P25346-028, 34.5 mm SL, off Gage Roads, Carnac Island, between Rottnest Island and Fremantle, Western Australia, 32°02′S, 115°40′E, collected with dredge, 30 June 1975, subsequently stained; WAM P25347-001, 28.2 mm SL, same locality, 24 July 1975.

Diagnosis.—A creediid with a I,3 pelvic fin (Fig. 2). All other creediids have the pelvic fins absent or I,4–5 (most I,5). Differs further from *C. haswelli* in having, on average, slightly fewer dorsal-fin rays (12 or 13 vs. 13–16), anal-fin rays (24 vs. 24 or more and usually 25 or 26), and vertebrae (41 or 42 vs. 42–45, usually 43 or 44). The two tear-shaped epurals (observable in stained specimen only), may be unique in creediids (the epurals are relatively narrow in all other species with two).

Description.—Morphometric and meristic data are given in Table 1. Snout relatively elongate, sloping gradually in dorsal profile. Upper jaw with fleshy extension anterior to lower jaw; maxilla extending posteriorly to, or slightly beyond vertical at center of eye; posterior tip of maxilla with well-developed notch (fork), lower lobe of fork longer than upper, upper lobe hidden under sheath when mouth closed. Bony dorsal projection at symphysis of lower jaw (Fig. 3). Lower jaw bordered by one row of pointed cirri of relatively uniform length (about 17 per side in the holotype, 16 in larger paratype, and 11 in smaller paratype). Eyes dorsal; interorbital distance small (fleshy width about 5‰ SL and bony width about half that); small, fleshy sheath covers lowermost part of eye. Tongue long and slender with slightly expanded, blunt, anterior tip. Ventral opercular flap extends far forward, overlapping branchiostegal membrane; posterior portion of gill cover overlaps base of pectoral fin. Branchiostegal rays seven (only six definitely seen in holotype). Bone of gill cover splintered (clearly visible in unstained

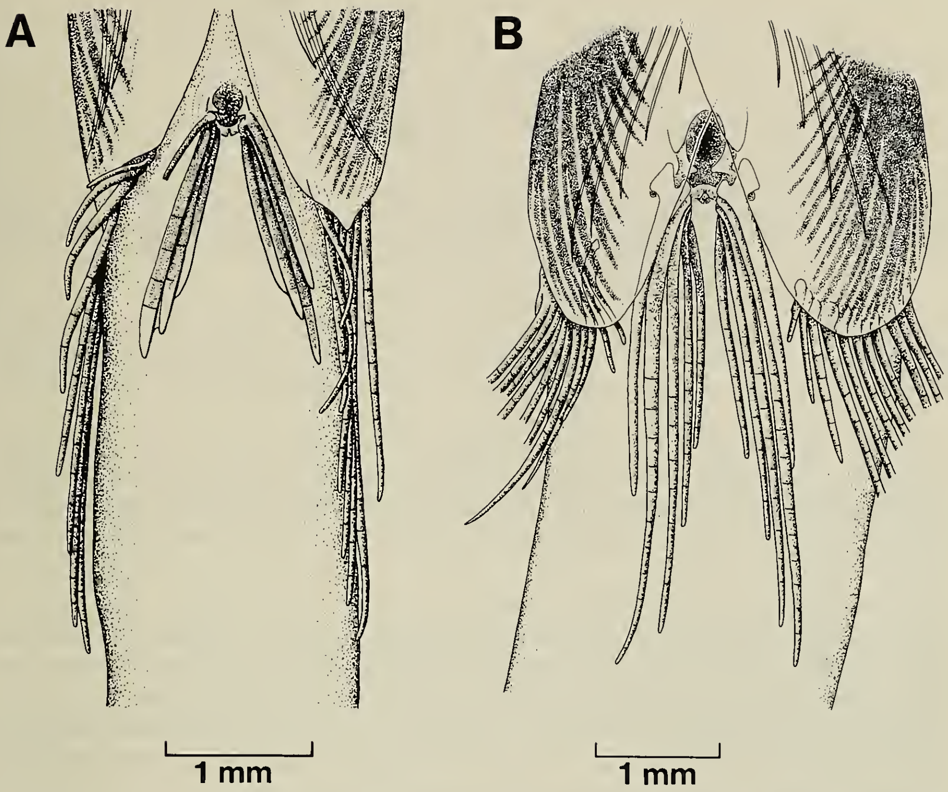


Fig. 2. Pelvic fin region of *Creedia*. A, *Creedia alleni*, paratype, WAM P25346-028, 34.5 mm SL, stained (right pelvic spine broken); B, *C. haswelli*, AMS IB.1114, 44 mm SL, New South Wales, cleared and stained.

material with transmitted light), subopercle and interopercle heavily indented but preopercle bone very lightly incised and no splintering seen on opercle of stained paratype (Fig. 3). Body completely scaled and cheeks with at least some scales (most or all scales lost but scale pockets are present). Lateral line (clearly seen only in smaller paratype) arising at upper edge of gill cover, descending steeply at posterior portion of pectoral fin, and running parallel to and near ventral profile; tenth pored scale (at bottom of descending portion near tip of pectoral fin) and following scales on lateral line with elongate posterior lobes. Base of pelvic fins slightly anterior to base of pectoral fins; inter-pelvic fin distance very small (distance between innermost rays about or less than 3‰ SL). Dorsal, anal, pectoral, and pelvic rays unbranched. Caudal fin with nine branched rays (11 principal rays). Stained paratype with narrow neural and haemal spines in caudal peduncle region (similar to *Limnichthys polyactis* [Nelson 1979, fig. 3A] except that last haemal spine is also narrow); two large, contiguous tear-shaped epurals with apex at distal end, expanding proximally to broadly rounded proximal end; anterior epural broader, sloping strongly anteriorly at proximal end, distal third narrow, and anterior surface concave; posterior epural with shorter narrow distal part, sides gradually diverging proximally (epural shape clear only in the stained spec-

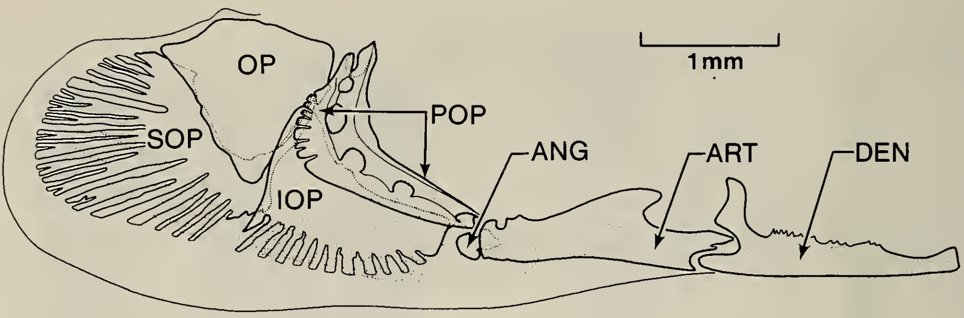


Fig. 3. *Creedia alleni,* paratype, WAM P25346-028, 34.5 mm SL, stained, right lower jaw and opercular region. Abbreviations: ANG, angular; ART, articular; DEN, dentary; IOP, interopercle; OP, opercle; POP, preopercle; SOP, subopercle. Gill cover membrane pulled down on ventral surface.

imen and its radiograph). Stained paratype with single row of well-developed teeth along upper and lower jaws, ending well before anterior tip, and patch of well-developed teeth in middle of expanded anterior tip of premaxilla (unstained specimens appear similar); weakly-developed teeth appear to be present on vomer.

No color pattern is apparent.

Etymology.—The species is named after Gerald R. Allen, Curator of Fishes at the Western Australian Museum, who brought the specimens of the new species to my attention, in recognition of his many contributions to ichthyology.

Discussion.—*Creedia alleni* is very similar to *C. haswelli,* and aside from the number of pelvic-fin rays, differs from other creediids in having the lowest number of dorsal-fin rays, and, possibly, in the shape of the epurals.

Table 1.—Morphometric and meristic data of the three type specimens of *Creedia alleni* (WAM) and nine type specimens of *Creedia partimsquamigera* (first seven AMS and last two NMV). Proportional measurements expressed as thousandths of standard length. * denotes decapitated specimen.

	C. alleni			*C. partimsquamigera*								
	Holotype	Paratypes		Holotype	Paratypes							
Standard length (mm)	40	35	28	55	67	59	57	55*	52	39	64	49
Sex	♀?	—	—	♀	♀	♀	♀	♀	♂?	♂?	♀	♂?
Body depth	72	70	78	61	63	61	60	61	—	56	56	53
Depth of caudal peduncle	34	35	41	35	32	32	30	32	33	32	31	33
Predorsal length	630	640	624	580	606	596	592	596	—	580	590	585
Preanal length	446	459	450	460	456	462	451	438	—	448	466	462
Pectoral fin length	—	101	109	55	61	59	54	54	111	97	53	112
Pelvic fin length	48	51	58	35	39	36	34	36	75	62	33	69
Head length	206	222	223	174	172	171	170	173	163	174	175	169
Head width	62	61	60	56	59	57	55	53	—	54	58	53
Snout length	44	49	53	39	36	36	32	34	34	38	36	34
Length of orbit	31	35	32	22	21	22	20	21	—	22	18	20
Dorsal-fin rays	13	12	12	16	16	15	15	14	15	16	16	15
Anal-fin rays	24	24	24	25	28	27	26	26	26	27	25	25
Pectoral-fin rays	12	12	12	13	12	12	12	12	12	12	13	12
Pelvic-fin rays	I,3	I,3	I,3	I,4	I,4	I,4	I,4	I,4	I,4	I,4	I,4	I,4
Lateral-line scales	*c.* 42	*c.* 42	*c.* 40	46	46	47	44	45	—	46	45	45
Vertebrae	41	41	42	45	45	46	46	—	—	47	45	46

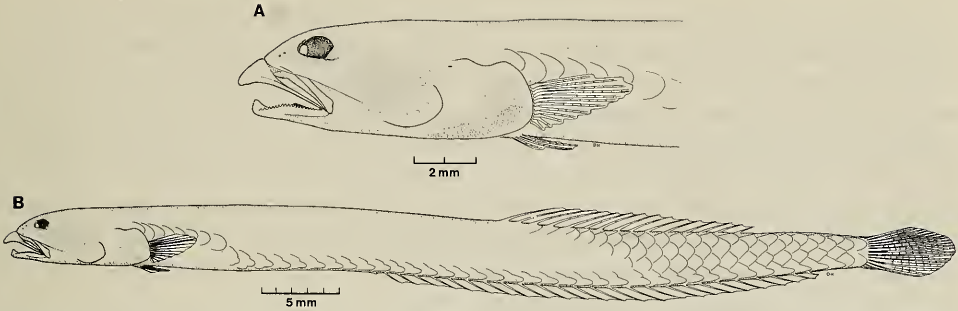


Fig. 4. *Creedia partimsquamigera,* holotype, AMS I.21420-001, 54 mm SL. A, Lateral view of head region; B, Lateral view.

Creedia partimsquamigera, new species
Fig. 4

Holotype.—AMS I.21420-001, 54.5 mm SL, ripe female, Coogee Beach, Sydney, New South Wales, 33°56′S, 151°16′E, 26 January 1980. Depth 10–15 m, in clean sand.

Paratypes.—AMS I.21420-005, 4 specimens, 52–67 mm SL (two specimens cleared and stained, including the smallest which was decapitated at capture), taken with the holotype. AMS I.22868-001, 2 specimens, 39 and 57 mm, Clovelly, Sydney, New South Wales, 33°53′S, 151°15′E, 9 September 1981. NMV-A2229, 2 specimens, 49 and 64 mm SL, Bondi Bay, Sydney, New South Wales, 33°54′S, 151°17′E, 6 August 1980. All 9 specimens were collected by R. H. Kuiter with a handnet.

Diagnosis.—A creediid with scales absent from anterior half of body except for the lateral line and a paired predorsal row, and 14–16 dorsal-fin rays. Differs further from *C. haswelli* and *C. alleni* in having a snout with a convex profile, the maxilla extending well behind the eye, the posterior tip of maxilla blunt, not forked, and the three or so elongate-most pectoral rays of males branched.

Description.—Morphometric and meristic data are given in Table 1. Snout relatively short, strongly convex in dorsal profile. Upper jaw with fleshy extension anterior to lower jaw; maxilla extending posteriorly to well behind eye; posterior tip of maxilla blunt, notch weak if present, upper portion of maxilla hidden under sheath when mouth closed. Bony dorsal projection at symphysis of lower jaw. Lower jaw bordered by one row of blunt cirri, some alternating in length, about 12–20 per side. Eyes dorsal; total interorbital width about 9–12‰ SL, bony width about half that; fleshy sheath covers lowermost part of eye. Tongue long and slender. Ventral opercular flap extends far forward, overlapping branchiostegal membrane; posterior portion of gill cover overlaps base of pectoral fin. Branchiostegal rays 7. Bone of gill cover splintered, subopercle and interopercle heavily indented, preopercle lightly indented, opercle lacks splintering. Scales present along lateral line, along base of dorsal fin and extending forward along midline in two adjacent rows to as far as about half distance from origin of dorsal fin to nape, and on body behind anterior portion of dorsal fin (usually about level of fifth or sixth ray); scales absent from anterior part of body except as noted. Lateral line arising at upper edge of gill cover, descending steeply near posterior tip of pectoral fin (behind in females and before in males), and running parallel to and near ventral profile; ventral lateral-line scales with elongate posterior lobes. Base of pelvic fins slightly anterior to base of pectoral fins; inter-pelvic fin distance very small, less than base length of fin. Dorsal, anal, pectoral, and pelvic rays unbranched except three or so elongate-most pectoral rays and perhaps elongate-most pelvic ray in males branched. Caudal fin usually with 9 branched rays. Single row of well-developed teeth along upper and lower jaws, ending well before anterior tip, and patch of well-developed teeth on relatively small expansion at anterior tip of premaxilla; vomerine teeth well-developed.

Little to no color pattern is apparent in the preserved material. However, in color transparencies provided by R. H. Kuiter of the 64 mm paratype there are two stripes extending along the length of the body, one dorso-lateral and the other mid-lateral, and about 5 short, closely-set saddles just behind the nape.

Etymology.—The specific name *partimsquamigera* is Latin (masculine) for partly scaled.

Discussion.—*Creedia partimsquamigera* differs from the other species of *Creedia* in several characters (see Diagnosis). The absence of scales on much of the body is a feature similar to that found in the two nominal species of *Chalixodytes* Schultz. However, *Creedia partimsquamigera* has an abruptly descending lateral line unlike that of *Chalixodytes* (the key in Nelson 1978, is in error on this point) and is further similar to *Creedia haswelli* in the reduced number of dorsal-fin rays and having marked sexual dimorphism in pectoral- and pelvic-fin length (see later for evidence of this in *C. haswelli*).

The type material of *C. haswelli* (and of *C. clathrisquamis* Ogilby, regarded as conspecific with *C. haswelli*) is from the Sydney area as is that of *C. partimsquamigera*. Denise S. Rennis has kindly confirmed for me that the four type specimens of *C. haswelli* and the one of *C. clathrisquamis* have completely scaled bodies.

Other Australian creediids

Creedia haswelli (Ramsay).—This species is known from southeastern Australia from the Furneaux Islands off northeastern Tasmania (Scott 1969), northeastern Tasmania (Scott 1982), Victoria, New South Wales, and, on the basis of material not previously studied, from the vicinity of King Island in Bass Strait, and from western South Australia.

Marked sexual dimorphism exists in the pectoral- and pelvic-fin length as determined from the large series from Bass Strait (NMV 2219–2228, 111 specimens). Nine specimens of each sex have the following fin lengths (in ‰ SL): females (3.5–4.9 cm SL), pectoral 90–102 and pelvic 45–54; males (3.0–4.9 cm SL), pectoral 167–201 and pelvic 97–116. In the males the longest pectoral ray is the third or fourth dorsalmost while the longest pelvic ray is the outermost soft ray. Female *C. haswelli* thus have a pectoral fin length similar to that of *Tewara cranwellae* Griffin while in males it is more similar to that of *Limnichthys fasciatus* Waite, *L. rendahli* Parrott, and *L. polyactis* Nelson. Other than in *C. partimsquamigera*, such a marked sexual dimorphism in fin length is unknown in creediids. Scott (1969) noted serrations on the posterior lobe of the lateral-line scales. This feature shows some sexual dimorphism. In the NMV material (60 specimens examined) most females have a smooth margin to the posterior lobe while most males have a serrated border on at least the lower margin (the serrations consist of small, isolated, flaplike projections which can be curled up and easily missed although some males do seem to lack them). A few females have a weakly serrated lower margin, similar to some males. Three hardened specimens from Tasmania (QVM 1980/5/38, males as judged from the length of the paired fins) have a serrated ventral margin, similar to the NMV males. One male from South Australia (AMS I.10412, see below) has exceptionally long projections and at least one male from New South Wales (AMS I.18547-001) has moderately long projections on both the upper and lower margins. A few notches are also present on the anterior portion of the lobe in many specimens, both males and females, but occurrence of these notches was not studied in detail.

Of 30 specimens radiographed, 6 have 42 vertebrae, 14 have 43, 9 have 44, and 1 has 45.

The South Australian material (AMS E1004, one specimen *c.* 36 mm, 32°31′S, 133°18′E, south of St. Francis Island, 55 m, dorsal and anal fin rays not countable, and AMS I.10412, two specimens 37 and 38 mm, 32°35′S, 133°18′E, south of St. Francis Island, 64 m) has a pelvic fin of I,4, a dorsal fin with 14 rays, and an anal fin with 24 and 25 rays.

Most specimens of *Creedia haswelli,* as with other creediids, are known from less than 100 m depth. One 40 mm ripe female (TFDA) collected off King Island, Bass Strait, however, was from 200 m.

With the inclusion of *C. alleni* and *C. partimsquamigera,* the genus *Creedia* is diagnosed as follows: dorsal fin with 12–16 rays and anal fin with 24–28 rays; pelvic fin I,3 or I,4; isolated "patch" of well-developed teeth on anterior tip of premaxillary bone; lateral line descending abruptly near tip of pectoral fin and running adjacent to anal fin base; lateral-line scales 40–47, those behind pectoral fin with posterior extension and not trilobate; marked sexual dimorphism in length of pectoral and pelvic fins (the condition in *C. alleni* is not known).

Limnichthys fasciatus Waite.—Whitley (1945) erected the subspecies *L. fasciatus major* from one Western Australian specimen on the basis of it having only 21 dorsal-fin rays and 24 anal-fin rays. In a previous study (Nelson 1978) I counted 26 and 28 rays, respectively, in the same specimen but because it and three other specimens from Western Australia had relatively short predorsal distances I provisionally recognized the subspecies. An examination of a few characters in additional material of this species from Western Australia (AMNH 31323, three specimens 28–48 mm SL of five sent and nine in collection, Great Australian Bight, 34°56′S, 118°12′E; UCLA W55-186, seven specimens, one of which is cleared and stained, 29–41 mm SL, Nancy Cove, Rottnest Island, 32°00′S, 115°30′E, off Perth) did not reveal any marked differences in proportional measurements or meristic characters in comparison with material from eastern Australia and elsewhere although the predorsal distance is in the lower range for the species. The 10 specimens have the following characteristics: predorsal distance 445–475‰ SL ($\bar{x} = 463$); preanal distance 394–450 ($\bar{x} = 426$); dorsal-fin rays 24–27 ($\bar{x} = 25.5$); anal-fin rays 27–29 ($\bar{x} = 27.9$); pectoral-fin rays 11–13 ($\bar{x} = 11.9$); branched caudal-fin rays 8, lateral line descending gradually to end of base of anal fin; one to several rows of minute teeth on upper and lower jaws and ending well before tip and no teeth at tip of premaxilla (generally only one row for most of toothed portion in upper jaw); vomerine teeth numerous, minute, in two patches; about 15–21 cirri along margin of lower jaw (each side) with some cirri alternating from long to short along posterior part of jaw; some long cirri in three specimens of UCLA sample with two or three filaments off a wide tip, other UCLA and all AMNH specimens with pointed cirri (I have not examined the cirri in other *L. fasciatus* in detail but specimens from Lord Howe Island, UAMZ 3765, have pointed cirri); and cleared and stained specimen with two slender epurals and lacking preopercular splintering. The color pattern is present in the AMNH material and apparent, though faintly, in one UCLA specimen. The pattern is similar to that found in *L. fasciatus* elsewhere with bars extending ventrally from the dorsal saddles and approaching and usually joining expansions along the well-developed lateral band as shown in Nelson (1978, fig. 1C). Although there is no firm basis at present for recognizing a separate subspecies in Western Australia, further study is warranted of suspected differences between Western Australian material and that from elsewhere in the number of rows of teeth in the lower jaw and in the presence or absence of branching of the cirri bordering the lower jaw.

Limnichthys donaldsoni Schultz.—Small specimens (8–19 mm SL) sent to me by D. F. Hoese from Yonge Reef, Lizard Island area, Queensland (15 specimens, AMS I.19472-122, 14°35′S, 145°36′E), Great Detached Reef, Queensland (50 specimens, AMS I.20750-004, 11°39′S, 143°59′E), and Cape Melville, Queensland (21 specimens, AMS I.20774-008, 14°10′S, 144°30′E) appear to represent *L. donaldsoni*. The few larger specimens from which accurate counts could be made have 20 or 21 dorsal-fin rays and 24 or 25 anal-fin rays (relatively low compared to previous counts made on this species). The only specimens with clear markings have nine short dorsal saddles with no lateral band (unlike the pattern in *L. fasciatus*). This is the first evidence of *L. donaldsoni* in Australia and is a considerable southern extension in its known range. *Limnichthys fasciatus* is present at Lizard Island (AMS I.19473-189) and has a color pattern characteristic for that species (i.e., at least some dorsal saddles extending down to extensions on the well-developed lateral band; about 6–9 dorsal saddles in specimens 12–27 mm SL) and higher dorsal- and anal-fin ray counts than *L. donaldsoni*.

Acknowledgments

I thank G. R. Allen (WAM) and D. F. Hoese (AMS) for bringing specimens of *Creedia* in their care to my attention and making them available for description. I also thank M. F. Gomon (NMV), R. H. Green and E. O. G. Scott (QVM), P. Last (TFDA), D. S. Rennis (AMS), D. E. Rosen and C. Hutchings (AMNH), and J. Seigel and B. W. Walker (UCLA) for the loan of specimens. B. Hutchins (WAM) and D. F. Hoese read an earlier version of the manuscript and provided useful information. R. H. Kuiter kindly provided information on the Coogee Beach habitat and color transparencies of creediid material. I am grateful to K. A. Garbrah for his advice on Latin names. The figures were prepared, under supervision, by Diane Hollingdale. W. E. Roberts (UAMZ) provided museum assistance. The study was supported by grant No. A5457 of the Natural Sciences and Engineering Research Council of Canada.

Literature Cited

Nelson, J. S. 1978. *Limnichthys polyactis*, a new species of blennioid fish from New Zealand, with notes on the taxonomy and distribution of other Creediidae (including Limnichthyidae).—New Zealand Journal of Zoology 5:351–364.

———. 1979. Some osteological differences between the blennioid fishes *Limnichthys polyactis* and *L. rendahli*, with comments on other species of Creediidae.—New Zealand Journal of Zoology 6:273–277.

Scott, E. O. G. 1969. Observations on some Tasmanian fishes: Part XVI.—Australian Zoologist 15(2):160–177.

———. 1982. Notes on fishes in the collection of the Queen Victoria Museum, Launceston. Pt. 1.—Records of the Queen Victoria Museum, Launceston. No. 74, 31 pp.

Whitley, G. P. 1945. New sharks and fishes from western Australia. Pt. 2.—Australian Zoologist 11(1):1–42.

Department of Zoology, The University of Alberta, Edmonton, Alberta T6G 2E9, Canada.

Note added in press.—One specimen of *Creedia alleni* (AMS I.23416-001), with I, 3 pelvics, from 34°32′S, 115°01′E, and 5 specimens of what is probably *C. haswelli* (AMS I.23412-001 to I.23415-001), with I, 4 pelvics counted in the 4 undamaged ones, from 32°42′S, 131°27′E to 34°32′S, 121°16′E, were examined after this paper was in press. The two species are thus now known to be relatively close to one another.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 38–49

TELEOST FISH REMAINS (OSTEOGLOSSIDAE, BLOCHIIDAE, SCOMBRIDAE, TRIODONTIDAE, DIODONTIDAE) FROM THE LOWER EOCENE NANJEMOY FORMATION OF MARYLAND

Robert E. Weems and Stephen R. Horman

Abstract.—Six taxa of teleost fishes have been recognized from the Nanjemoy Formation of Maryland. So far, all collected remains have been fragmentary. The recognized taxa are: *Brychaetus muelleri, Cylindracanthus rectus, Sarda delheidi, Cybium* sp., *Triodon antiquus,* and *Kyrtogymnodon* sp. No previous records of teleosts from this formation are known.

Except for a preliminary report on the remains described herein (Horman and Weems 1976), no specific reports of teleosts from the Nanjemoy Formation of Maryland or Virginia are known, though Fallah (1964) referred to a *Cylindracanthus* specimen collected from the Pamunkey Group, which could have come from either the Aquia or Nanjemoy Formation. Collecting during the last 15 years has yielded sparse but reasonably diagnostic fragmentary remains, which represent what could have been an abundant and diverse teleost fauna. Two or more bones from the same individual, fish or tetrapod, have never been reported from the Nanjemoy. This lack of even semi-articulated remains is in marked contrast to conditions in the underlying Paleocene Aquia Formation and the overlying Miocene Calvert Formation. The sparsity of identifiable fish bones in the Nanjemoy may be the result of a very low rate of clastic influx and a hard substrate, so that skeletons that fell to the sea bottom became totally disarticulated and broken up. Bryozoan colonies on some bones suggest that the remains lay on the sea bed for some time before burial.

All teleost remains described herein were collected from the bluffs upriver and downriver from Popes Creek, Maryland (Fig. 1). In these bluffs, Clark and Martin (1901) recognized two members within the Nanjemoy Formation, a lower Potapaco Member and an upper Woodstock Member (Fig. 2). Though separated in these bluffs by a prominent layer of calcareous nodules, the members are largely defined on faunal grounds, and to our knowledge, an ability to map these members outside of the vicinity of the Popes Creek bluffs on physical stratigraphic grounds has not been demonstrated. Because the base of the Nanjemoy (the contact with the underlying Marlboro Clay) and the top of the Nanjemoy (the unconformable contact with the overlying basal phosphate bed of the Calvert Formation) are mappable stratigraphic contacts, the Nanjemoy as a whole is a mappable stratigraphic unit (Glaser 1971; Teifke 1973). Our work was done in the type area where the marker horizon between the two Nanjemoy members is readily seen; hence their names are retained for this report. Elsewhere, the members might be only biostratigraphic subdivisions of the Nanjemoy.

Only the uppermost 15 feet of the Potapaco Member is exposed above Popes Creek, so we have no basis for disputing Clark and Martin's (1901) estimate that

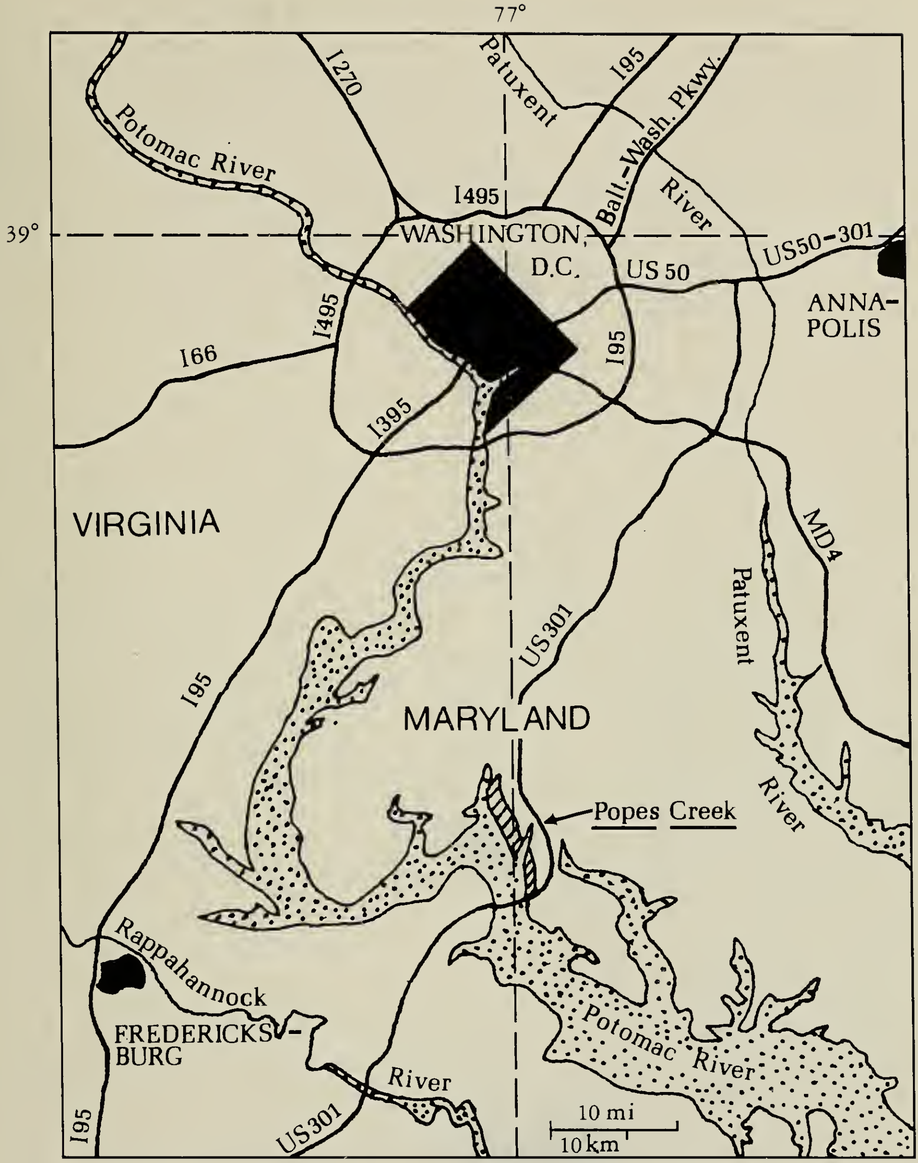
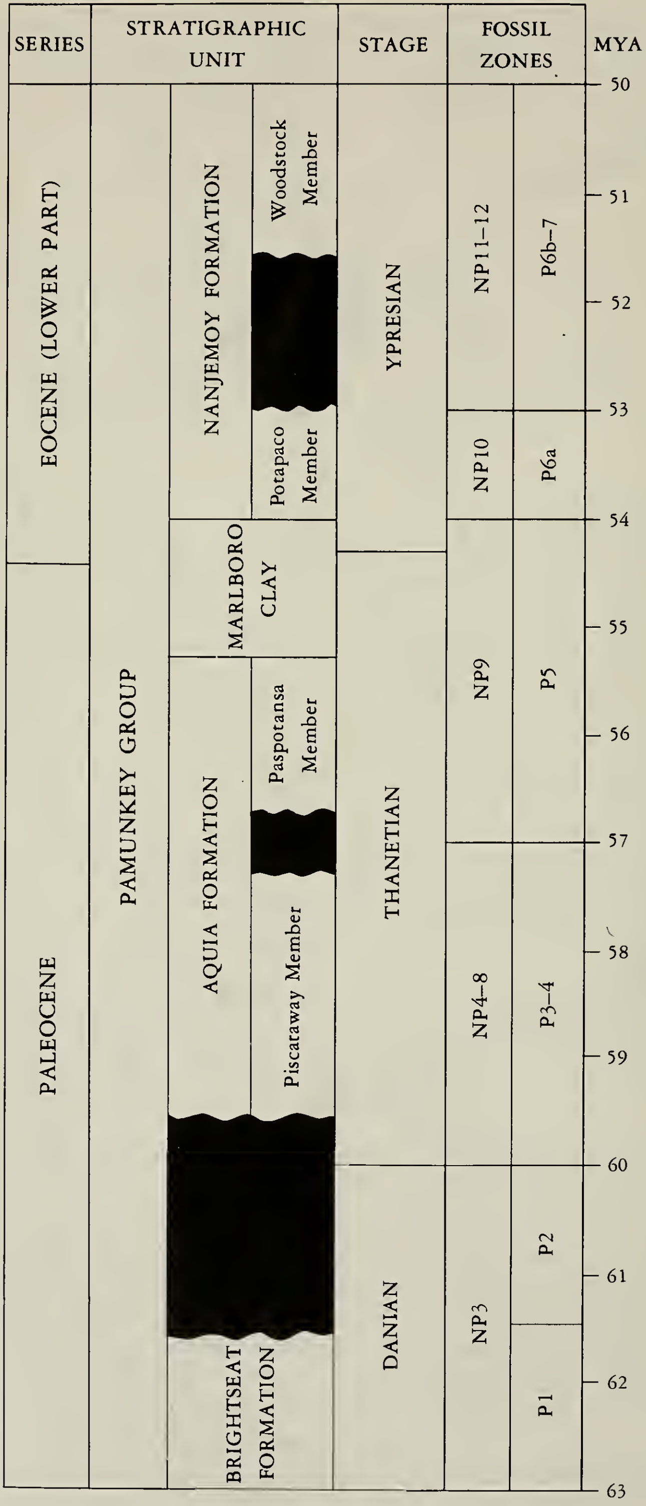


Fig. 1. Location of the bluffs along the Potomac River near Popes Creek, Maryland (ruled area).

this member is about 70 feet thick. Our own estimates on the thickness of the Woodstock Member, however, suggest that this member as Clark and Martin defined it at Popes Creek is 80 feet thick in the outcropping area instead of the 50 to 60 feet they reported (Clark and Martin 1901:66). Curiously, their diagrammatic column of the Pamunkey Group indicates a thickness for the Woodstock of about 80 feet, suggesting that the published thickness may have been a typographical error. According to our estimates, Popes Creek marks the spot at which 50 feet of the Woodstock has passed below sea level. North of Popes Creek, a thin and apparently laterally impersistent layer of coarse sand and phosphate


SERIES
STRATIGRAPHIC UNIT
STAGE
FOSSIL ZONES
MYA
EOCENE (LOWER PART)
PALEOCENE
PAMUNKEY GROUP
NANJEMOY FORMATION
Woodstock Member
Potapaco Member
MARLBORO CLAY
AQUIA FORMATION
Paspotansa Member
Piscataway Member
BRIGHTSEAT FORMATION
YPRESIAN
THANETIAN
DANIAN
NP11–12
P6b–7
NP10
P6a
NP9
P5
NP4–8
P3–4
NP3
P2
P1
50
51
52
53
54
55
56
57
58
59
60
61
62
63

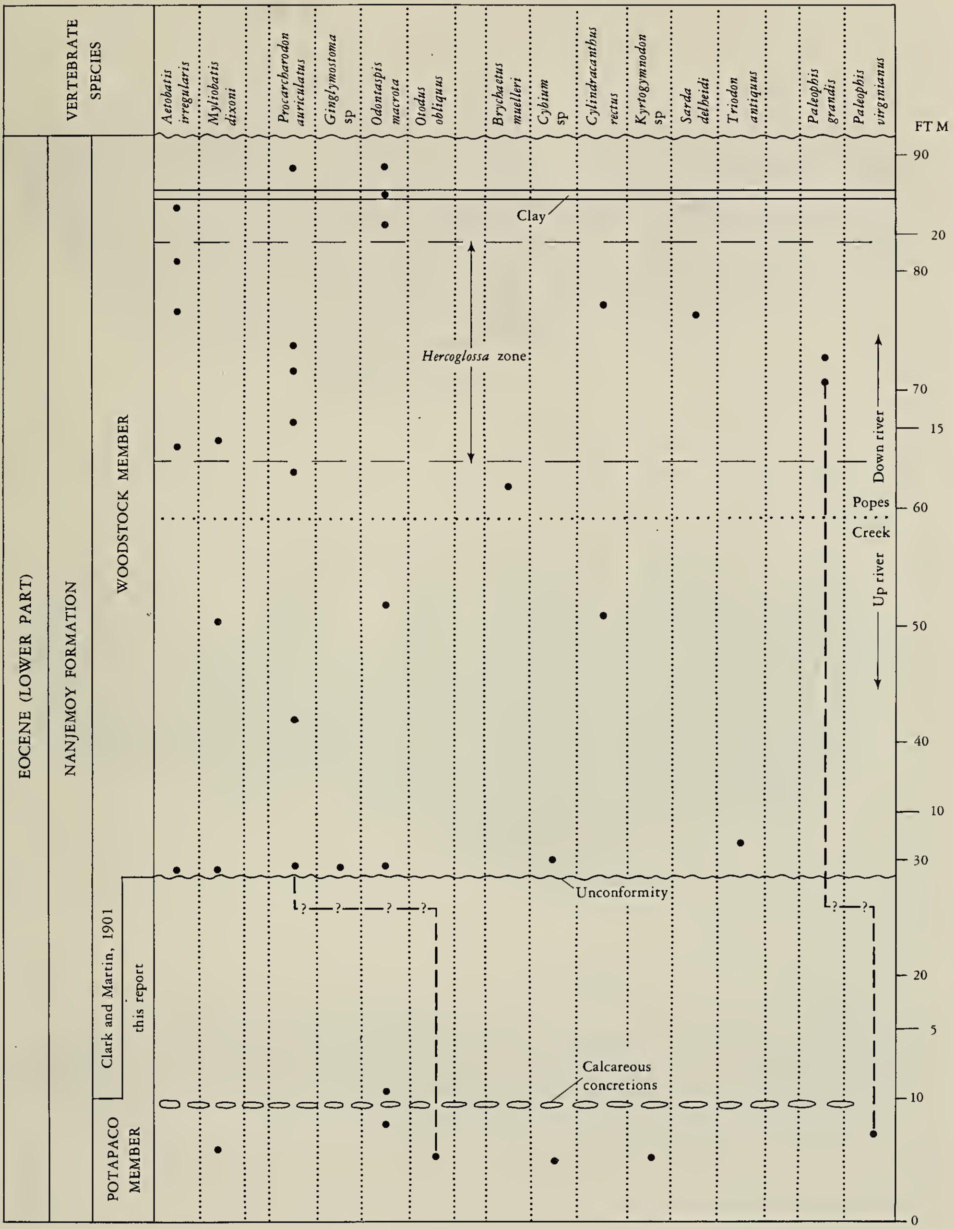


Fig. 3. Known range of some species of vertebrates collected from the Nanjemoy Formation at Popes Creek, Maryland. Except for *Myliobatis, Aetobatis, Ginglymostoma,* and *Odontaspis,* which are relatively abundant, dots represent single collected specimens.

⟵

Fig. 2. Stratigraphic column of the Pamunkey Group (from Clark and Martin 1901, and Gibson *et al.* 1980), showing the age ranges of the various formations and groups. MYA = millions of years ago.

pebbles offers the only well defined datum from which thickness estimates can be based. This bed is considered to be 20 feet above the base of the Woodstock Member as defined by Clark and Martin (1901). South of Popes Creek, the only persistent marker bed is a thin, 1–4 inch thick layer of carbonaceous plastic light-gray clay 76 feet above the base of the Woodstock and 4 feet from its top as exposed. Specimens of the large nautiloid, *Hercoglossa tuomeyi* Clark and Martin, are known only from an interval 55–70 feet above the base of the Woodstock. Figure 3 portrays graphically the estimated position of these horizons, as well as the position of the teleost remains described below and some other vertebrate remains.

Besides teleosts, rare fragmentary remains of crocodiles, turtles, and the "sea snake" *Paleophis* are found in the Nanjemoy. Teeth of sharks and skates are more common than other vertebrate remains. Teeth of the shark *Otodus obliquus* Agassiz occur throughout the Aquia Formation and Potapaco Member, and those of the shark *Procarcharodon auriculatus* (de Blainville) are found throughout the Woodstock Member, but teeth of the two species do not occur together. The serrated tooth margin of *P. auriculatus* is the only difference between the two species; hence, these forms may represent a single lineage. If so, the two forms are good index fossils for distinguishing each respective member. In addition, the ray *Aetobatis irregularis* Leriche has not been reported in the Potapaco Member even though it is common throughout the Woodstock Member. Vertebrae of *Paleophis* are rare; only *P. virginianus* Lynn is present in the Potapaco, whereas the Woodstock vertebrae are referrable to *P. grandis* (Marsh). Thus, there seems to be a detectable vertebrate biostratigraphic break between the Potapaco and the Woodstock comparable to that found in the invertebrate assemblages (Clark and Martin 1901), though the phosphate pebble bed 20 feet above the basal concretion bed seems a more reasonable location for a time break. This break probably affects the teleost distributions as well, but the teleost sample is far too sparse for any prediction to be made on which species might be confined to one member or the other.

On the basis of the first appearance of *Procarcharodon auriculatus,* Leriche (1943) wanted to correlate the Woodstock with the Lutetian (Middle Eocene) of Europe, but since then *P. auriculatus* has been reported from the Ypresian (Lower Eocene) of Britain as far down as approximately the base of nannoplankton zone NP13 (Hooker *et al.* 1980). On the basis of microfossil correlations, the Woodstock recently has been placed in the slightly older lower to middle Ypresian fossil zones NP11 and 12 (Gibson *et al.* 1980). Since control on the boundaries of Paleogene nannoplankton zones in Britain is not good (Hooker *et al.* 1980), this slight difference in the time of first appearance for *P. auriculatus* on either side of the Atlantic may be more apparent than real. If it is real, then *P. auriculatus* appeared slightly earlier in the western Atlantic than in the eastern Atlantic. In either case, an Ypresian age for the Woodstock is compatable with all available data. The underlying Marlboro Clay of late Paleocene and early Eocene age (Gibson *et al.* 1980) overlies the Aquia Formation, which has been well documented as Late Paleocene in age (Loeblich and Tappan 1957; Bybell and Govoni 1977; Gibson *et al.* 1980). Thus, these data indicate that the Potapaco Member also must be Early Eocene (Ypresian) in age.

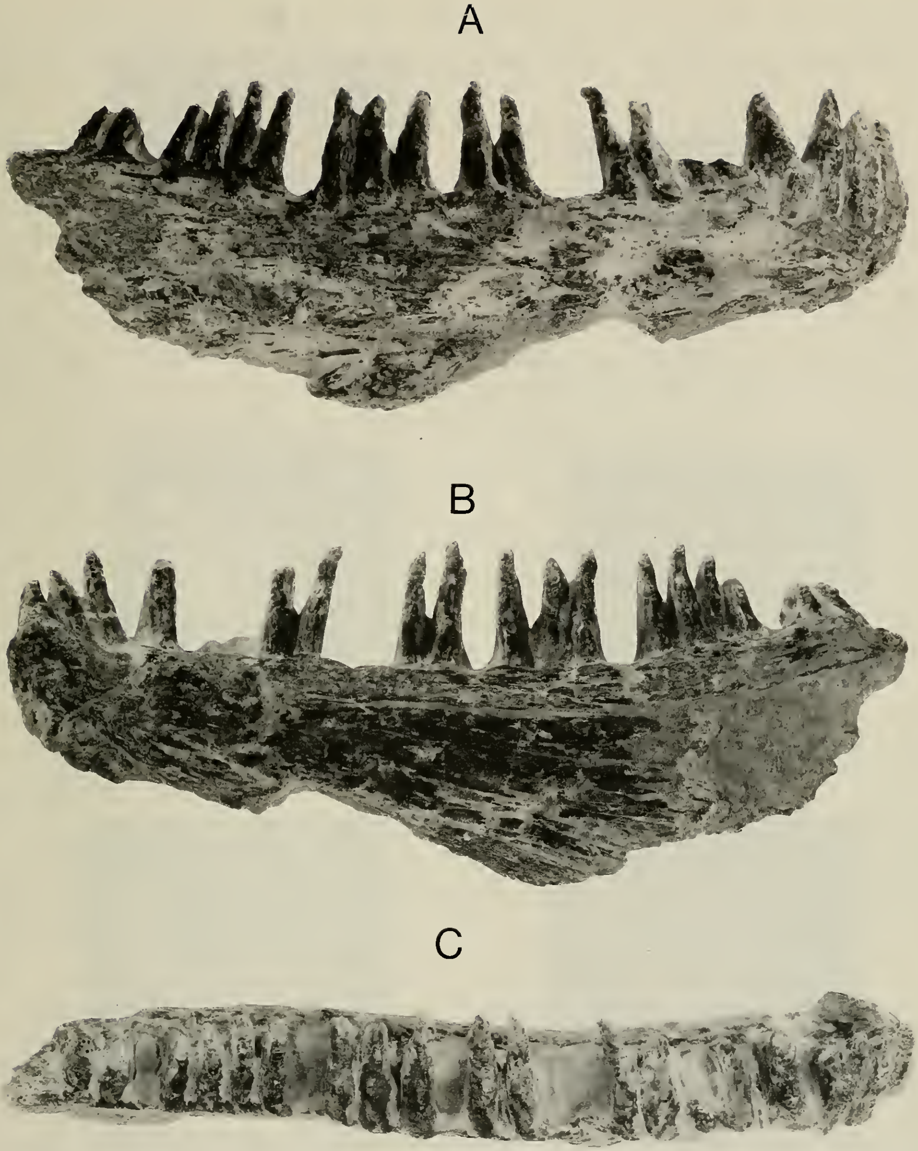


Fig. 4. Right dentary of *Brychaetus muelleri* in external (A), internal (B), and dorsal (C) aspects. Length 17 cm.

Order Osteoglossiformes
Family Osteoglossidae
Brychaetus muelleri Woodward

Material.—Right dentary containing 17 teeth and 8 empty alveoli (USNM 265383), Fig. 4.

Locality.—Bluff 100 yards south of Popes Creek, Maryland, within uppermost

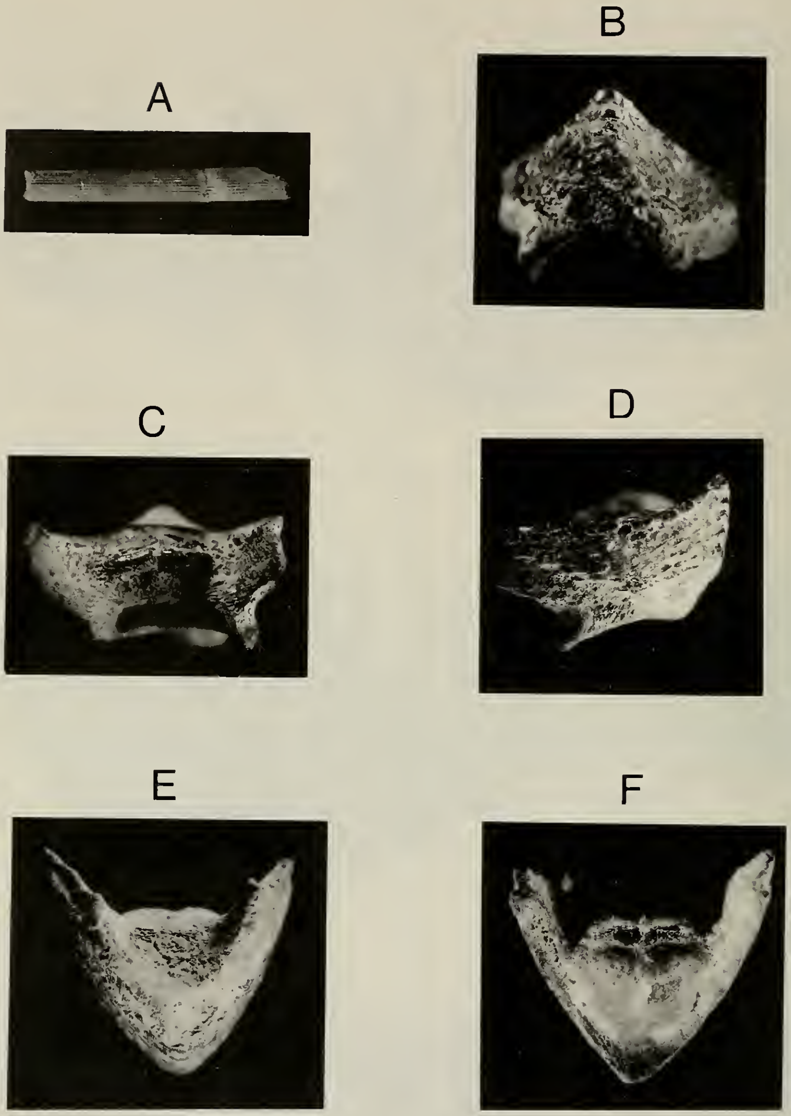


Fig. 5. A. Rostral fragment of *Cylindracanthus rectus*. Length 5.25. cm. B–F. Dentary of *Triodon antiquus* in anterior (B), posterior (C), right-lateral (D), ventral (aboral) (E), and dorsal (oral) (F) aspects. Length along midline, 6 mm; width at rear of jaw rami, 10 mm.

10 feet of the Woodstock Member, Nanjemoy Formation ("Zone 17" of Clark and Martin 1901), coll. John Glaser, 1972.

Discussion.—This large dentary with its hollow, laterally wide, anteroposteriorly compressed, and lingually recurved teeth is highly distinctive and readily referrable to *B. muelleri* (compare with Casier 1966). This teleost is by far the largest known from the Nanjemoy and probably was one of the most formidable marine carnivores of its time. *Phareodus*, a related osteoglossid from the Eocene Green River shales, is only about one-sixth as large, has a proportionally deeper jaw, and teeth that are not nearly so lingually recurved. *Brychaetus* has not been previously reported from the Lower Eocene of North America (Horman and Weems 1976).

Order Perciformes
Family Blochiidae
Cylindracanthus rectus (Agassiz)

Material.—Two rostral fragments, one of which (USNM 265384) is shown in Fig. 5(A).

Locality.—(1) Bluff ⅛ mile north of Popes Creek, Maryland, 4 feet above beach, Woodstock Member, Nanjemoy Formation, coll. Robert E. Weems, 1973; (2) USNM 265384, bluff ½ mile south of Popes Creek, Maryland, 2 feet above beach, Woodstock Member, Nanjemoy Formation, coll. Robert E. Weems, 1975.

Discussion.—Fragmentary rostra referred to this genus are fairly common in lower Tertiary sediments of North America and Europe (for example, Fallah 1964). Several species have been named, but most are based on such fragmentary material that their validity is questionable. The specimens described here are fully comparable with *C. rectus,* the first named species of the genus, and are thus placed in that taxon. Until a great deal more well-preserved material becomes available, it is impossible to tell whether this is a discrete taxon or only a catch-all category for rostral fragments of any of several closely related fishes.

Family Scombridae
Sarda delheidi (Leriche)

Material.—Right dentary (USNM 265383) with 6 teeth and at least 10 empty alveoli (Fig. 6A–C).

Locality.—Bluff 1 mile south of Popes Creek, Maryland, 1 foot above beach and 15 feet below gray carbonaceous clay bed, Woodstock Member, Nanjemoy Formation (''Zone 17'' of Clark and Martin 1901), coll. Robert E. Weems, December 1973.

Cybium sp.

Material.—Three isolated teeth (Fig. 6D–F).

Localities.—1) USNM 265389, bluff 2 miles north of Popes Creek, Maryland, coll. Robert E. Weems, 1973. 2) USNM 265385, USNM 265386, bluff 1 mile north of Popes Creek, Maryland, 1 foot above beach in phosphate lag deposit, Woodstock Member, Nanjemoy Formation (''Zone 16'' of Clark and Martin 1901), coll. Stephen R. Horman and Robert E. Weems, July 1968.

Discussion.—Isolated teeth of this sort have been traditionally assigned to *Cybium,* (compare with Casier 1966, Leriche 1905), and occasionally even species level identifications have been attempted. The teeth illustrated here are not certainly identifiable to species but are fully comparable with teeth generally assigned to this genus.

Order Tetraodontiformes
Family Triodontidae
Triodon antiquus Leriche

Material.—Fused dentary beak (USNM 265387) with dental battery (Fig. 5B–F).

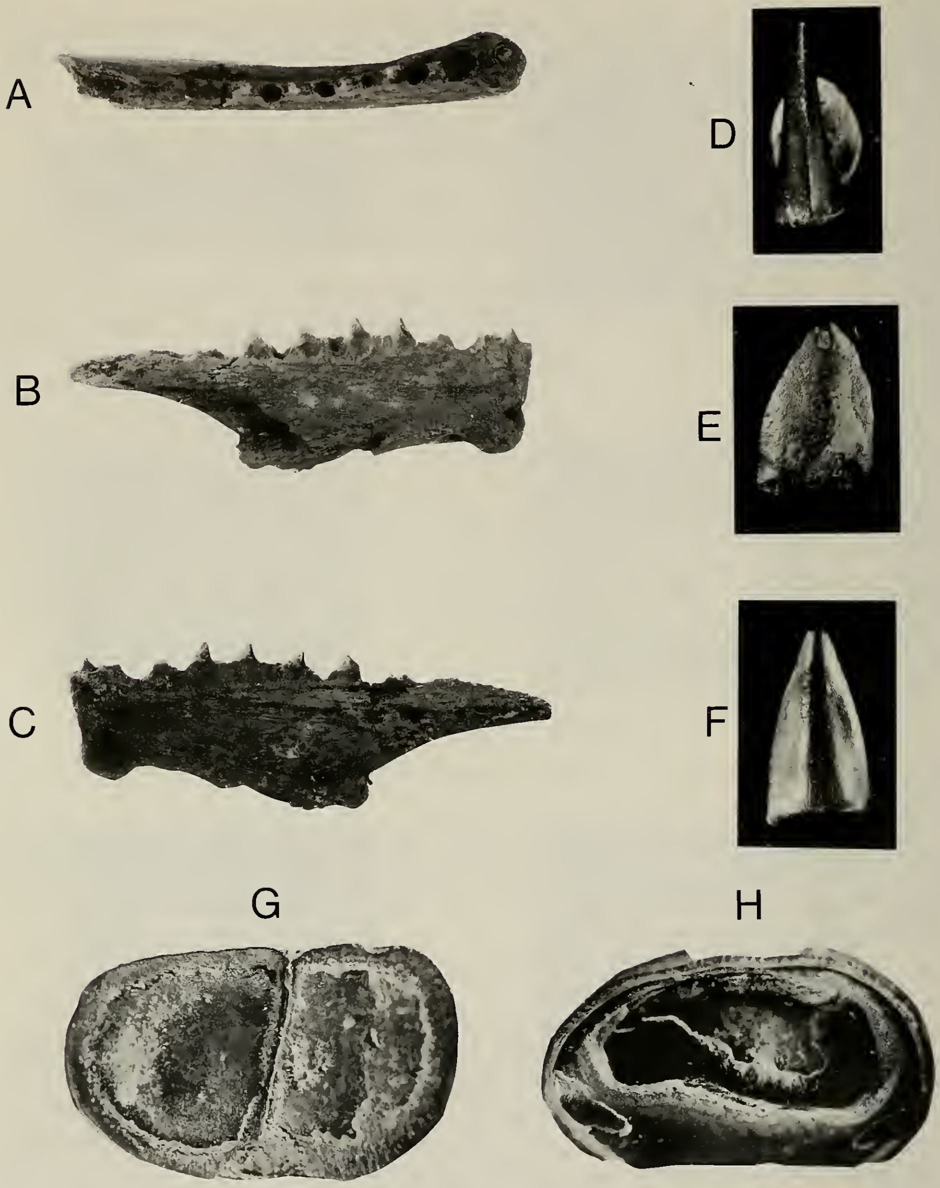


Fig. 6. A–C. Right dentary of *Sarda delheidi* in dorsal (oral) (A), external (B), and internal (C), aspects. Length 9.4 cm. D–F. Teeth referrable to *Cybium* sp. Height about 8 mm. G–H. Dental plate of *Kyrtogymnodon* sp. in internal (G) and external (H) aspects. Length 9 mm, width 15 mm.

Locality.—Bluff 1 mile north of Popes Creek, Maryland, 3 feet above beach and 2 feet above phosphate lag deposit, Woodstock Member, Nanjemoy Formation (''Zone 16'' of Clark and Martin 1901), coll. Robert E. Weems and Stephen R. Horman, July 1968.

Discussion.—This fused dentary beak obviously belongs among the tetraodontiform fishes. The Molidae and Diodontidae, however, lack the scalelike teeth covering the beak margin, and the diodontidae have the tooth plates stacked imbricately, not arranged anteroposteriorly as in the Triodontidae. The only living species of this family is *Triodon bursarius* (Tyler, 1962). Fossil species of this genus are *Triodon antiquus* Leriche (1905) and *T. cabindensis* Leriche (1920). Our specimen of *Triodon* has a beak nearly as long as wide, differing markedly from the extremely laterally elongate beak of *T. cabindensis*. In general proportions it is like *T. antiquus*, being about the same size and shape. Most specimens of *T. antiquus* have beaks notably wider than long, however, whereas in this specimen the proportions are nearly equal, thus giving an exceptionally sharp and angular appearance to this beak when seen from dorsal aspect. This appears to have resulted only from proportional changes related to growth. Most figured specimens of *T. antiquus* (Leriche 1905; Casier 1946, 1960) are smaller than this specimen. When specimens are compared by absolute size, instead of relative size, the beak curvatures are quite comparable, suggesting that the differences in apparent curvature may be due to the greater individual age of our specimen than that of most of the figured specimens from Europe, whose jaw rami had not grown to be so elongate. Only two of the European specimens reach a size comparable to our specimen. In most of the figured specimens of *T. antiquus*, only juveniles have a single pair of teeth on the inferior oral surface. By the time specimens reach sizes approaching that of our specimen, one or more pairs of lateral teeth erupt as well. Thus our specimen is unusual in this respect, but in view of the highly variable nature of the dentition in figured specimens of *T. antiquus*, it is not truly distinctive when based on only a single specimen. Therefore, unless enough material becomes available to allow a statistical comparison between the European and American populations, this specimen is best referred to the highly variable *Triodon antiquus*.

This is the first record of this family from either North America or the Western Hemisphere. Today, the family is restricted to the Indian Ocean and in the past is known to have ranged into Europe and West Africa only during the Eocene. Apparently, at that time the family also managed to cross the North Atlantic into North America. If McKenna (1972) is correct in postulating a landbridge between Europe and North America through Early Eocene time, this would have afforded a warm shallow dispersal route for this family, whose distribution today suggests that it may be restricted to warm waters.

Family Diodontidae

Kyrtogymnodon sp.

Material.—Oral tooth plate, USNM 265388, (Fig. 6G–H, containing a pair of tooth batteries each containing stacks of three teeth.

Locality.—2 miles north of Popes Creek, Maryland, along a low bluff at the mouth of Nanjemoy Creek in the uppermost 10 feet of the Potapaco Member of the Nanjemoy Formation ("Zone 15" of Clark and Martin 1901), coll. Robert E. Weems, 1973.

Discussion.—Tavani (1955) reviewed the known diodontids and arranged them within four genera. Although his suggestions concerning the definitions of genera are accepted here, it is by no means certain that species characters can be recognized from a single pair of fused plates. Moreover, it may well be that the total number of presently described species exceeds the true numbers of species represented, since individual variants may have been separately described. Therefore, the pair of fused dental plates illustrated here are merely designated *Kyrtogymnodon* sp. until better remains permit a specific diagnosis. This plate is assigned to *Kyrtogymnodon* because wear is restricted almost wholly to the central region of the most-erupted tooth. This suggests that the entire tooth battery was stacked nearly vertically so that only one tooth was worn at a time. In *Progymnodon, Oligodiodon,* and *Diodon* the batteries are stacked obliquely so that the edges of at least several teeth are functioning at the same time. If this assignment to *Kyrtogymnodon* is correct, this is by far the oldest known occurrence of this genus. Previously it has only been described from the Pliocene (Tavani 1955).

Summary

The known teleost remains from the Nanjemoy Formation can be stratigraphically arranged as follows:

Woodstock Member—*Cylindracanthus rectus* (Agassiz)
Triodon antiquus Leriche
Brychaetus muelleri Woodward
Sarda delheidi (Leriche)
Cybium sp.
Potapaco Member— *Kyrtogymnodon* sp.
Cybium sp.

These species probably represent only a small fraction of the total number of teleost species originally present; conditions during deposition seem to have destroyed all remains except those from species that had exceptionally durable skeletal elements. All remains are fragmentary, and no associated skeletal materials are known.

Literature Cited

Bybell, L. M., and D. C. Govoni. 1977. Preliminary calcareous nannofossil zonation of the Brightseat and Aquia Formations (Paleocene) of Maryland and Virginia—stratigraphic implications.—American Association of Petroleum Geologists, National Meeting (Washington, D.C.), Program and Abstracts, p. 67.

Casier, E. 1946. La faune ichthyologique de l'Ypresien de la Belgique.—Memoires du Musée Royal d'Histoire Naturelle de Belgique 104:1–267.

———. 1960. Note sur la collection des poissons Paléocenes et Eocenes de l'Enclave de Cavinda (Congo).—Annales du Musée Royal du Congo Belge (3) 1 (2):1–47.

———. 1966. Faune ichthyologique du London Clay.—British Museum (Natural History): London. 2 vols., 496 pp.

Clark, W. B., and G. C. Martin. 1901. The Eocene deposits of Maryland.—Maryland Geological Survey, Eocene, pp. 19–92.

Fallah, W. 1964. *Cylindracanthus* from the Eocene of the Carolinas.—Journal of Paleontology 38: 128–129.

Gibson, T. G., G. W. Andrews, L. M. Bybell, N. O. Frederiksen, T. Hansen, J. E. Hazel, D. M. McLean, R. J. Witmer, and D. S. van Nieuwenhaise. 1980. Geology of the Oak Grove Core, Part 2: Biostratigraphy of the Tertiary strata of the core.—Virginia Division of Mineral Resources, Publication 20:14–30.

Glaser, J. D. 1971. Geology and mineral resources of southern Maryland.—Maryland Geological Survey, Report of Investigations 15:1–84.

Hooker, J. J., A. N. Insole, R. T. J. Moody, C. A. Walker, and D. J. Ward. 1980. The distribution of cartilaginous fish, turtles, birds and mammals in the British Paleogene.—Tertiary Research 3(1):1–12.

Horman, S. R., and R. E. Weems. 1976. Eocene fish and reptiles from the Nanjemoy Formation in Maryland.—Geological Society of America, Abstracts of 25th Annual Northeastern/Southeastern Section 8(2):198.

Leriche, M. 1905. Les poissons Eocene de la Belgique.—Extrait Memoire Musée Royal d'Histoire Naturelle Belgique 3:49–228.

———. 1920. Notes sur la Paleontologie du Congo. III. Note préliminaire sur des poissons nouveaux du Paléocene et de l'Eocene de la region cotière du Congo.—Revue Zoologique Afrique 8:85.

———. 1943. Le synchronisme des formations Tertiares des deux côtes de l'Atlantique, d'apres leur faune ichthyologique.—Comptes Rendue de Séances de l'Academie des Sciences 210:589–592.

Loeblich, A. R., and H. Tappan. 1957. Correlation of the Gulf and Atlantic Coastal Plain Paleocene and lower Eocene formations by means of planktonic Foraminifera.—Journal of Paleontology 31:1109–1137.

McKenna, M. C. 1972. Was Europe connected directly to North America prior to the Middle Eocene?—*In* Dobzhansky, Hecht, and Steere eds. Evolutionary Biology, vol. 6, pp. 179–188. New York: Appleton-Century-Crofts.

Tavani, G. 1955. Osservazioni su alcuni Plectognathi (Gymnodonti).—Atti Societe Toscana Scienze Naturalle Memorie ser. A, 62:177–200.

Teifke, R. H. 1973. Stratigraphic units of the Lower Cretaceous through Miocene series, *in* Geological Studies, Coastal Plain of Virginia.—Virginia Division Mineral Resources Bulletin 83: 1–78.

Tyler, J. C. 1962. *Triodon bursarius,* a plectognath fish connecting the scleroderms and gymnodonts.—Copeia 4:793–801.

(REW) United States Geological Survey, Stop 928, Reston, Virginia 22092; (SRH) Naval Surface Weapons Laboratory, Dahlgren, Virginia 22448.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 50–58

REDESCRIPTION OF THE BIGEYE SHINER, *NOTROPIS BOOPS* (PISCES: CYPRINIDAE)

Brooks M. Burr and Walter W. Dimmick

Abstract.—The wide-ranging yet poorly known bigeye shiner, *Notropis boops*, is redescribed from examination of 567 specimens from throughout the range of the species. Significant geographic variation was not found in any of the 20 morphological characters examined. Numbers of lateral-line scales and caudal vertebrae were slightly higher in the northern and eastern parts of the species' range. Populations of *N. boops* have been severely decimated in both Ohio and Illinois due to excessive siltation from poor agricultural practices; it is a common species throughout the central portion of its range.

The bigeye shiner, *Notropis boops* Gilbert, is a mostly common inhabitant of the central Mississippi basin, although it is disappearing or rare in some areas on the edges of its range, e.g., Ohio (Trautman 1981), Illinois (Smith 1979), and Alabama (Ramsey 1976). Since its original description (Gilbert 1884), little information has been published on the systematics of *N. boops*, except for its inclusion in atlases, checklists, and state fish books. Recently, Gilbert (1978) listed the type material of *Notropis boops*, Smith and Hocutt (1981) reported on variation in pharyngeal tooth formulae in Missouri, and Lehtinen and Echelle (1979) analyzed the reproductive cycle of the species in Oklahoma.

Because of its rather wide range on both sides of the Mississippi River and the paucity of systematic information available on the species, we undertook a study of geographical variation in *N. boops*. Examination of 20 morphological characters on 567 specimens from throughout the range of the species revealed that geographic variation is minimal. The objectives of this paper are to redescribe *N. boops* and to map and discuss its distribution.

Methods

Counts and measurements followed those described by Hubbs and Lagler (1964). In examination of the cephalic lateral line, the terminology, abbreviations, and counting procedures of Snelson (1971) were followed. Vertebral counts were made from radiographs. The first vertebra bearing a well-developed haemal spine was considered to be the first caudal element; all those anterior were considered trunk vertebrae.

All meristic characters were analyzed initially for sexual or geographic variation in minor drainages. When no significant sexual, intra- or interdrainage variation was apparent, the data were pooled into two major groups of populations—those occurring east of the Mississippi River and those occurring west of the river.

Material Examined

The following material was examined. Numbers of specimens counted or measured are in parentheses. Institutional abbreviations are identified in Acknowledgments. Complete collection data are on deposit at the Department of Zoology, Southern Illinois University at Carbondale.

Notropis boops Gilbert

OHIO RIVER BASIN. *Scioto R. drainage.*—OH: Pike Co.: OSU 12334 (10). Scioto Co.: UMMZ 86011 (2). *Kentucky R. drainage.*—KY: Franklin Co.: UMMZ 144395 (3). Lincoln Co.: INHS 79062 (10). *Kinniconick Cr.*—KY: Lewis Co.: UL 5444 (5). *Harrods Cr.*—KY: Oldham Co.: UL 4779 (5). *Salt R.-Rolling Fork drainage.*—KY: Anderson Co.: UL 3175 (10). Jefferson Co.: UL 4774 (6). Madison Co.: UMMZ 125060 (4). Shelby Co.: UL 5372 (6). *Blue R.*—IN: Washington Co.: OSU 28646 (9). *Green R. drainage.*—KY: Casey Co.: UMMZ 169436 (1). Muhlenberg Co.: SIUC 1915 (10). *Wabash R. drainage.*—IN: Carrol Co.: OSU 27890 (2). Hamilton Co.: OSU 30104 (9). Lawrence Co.: UMMZ 167923 (3). Montgomery Co.: OSU 27169 (5). Parke Co.: UMMZ 144536 (1). Putnam Co.: OSU 27500 (8). Shelby Co.: OSU 29861 (10). IL: Edgar Co.: INHS 2937 (8). Shelby Co.: INHS 21720 (6). Vermilion Co.: INHS 12241 (8). *Cumberland R. drainage.*—TN: Smith-Wilson Co.: UT 44.249 (20). Williams Co.: INHS 83116 (1); UMMZ 175215 (10). KY: Cumberland Co.: INHS 78328 (10). *Tennessee R. drainage.*—AL: Jackson Co.: AU 12003 (10). Limestone Co.: UMMZ 200821 (2); UMMZ 200870 (1). TN: Bedford Co.: UMMZ 121290 (10); UT 44.709 (21). Benton Co.: UT 44.964 (4). KY: Calloway Co.: SIUC 291 (4); SIUC 308 (10); SIUC 383 (5); SIUC 388 (1). Marshall Co.: SIUC 1530 (6).

MISSISSIPPI RIVER BASIN. *Kaskaskia R. drainage.*—IL: Moultrie Co.: INHS 8915 (10). *Cuivre R. drainage.*—MO: Pike Co.: UMMZ 149205 (10). *Meramec R. drainage.*—MO: Franklin Co.: SIUC uncat. (5). Gasconade Co.: UMMZ 148339 (10). trib., Mississippi R.—MO: Perry Co.: UMMZ 149843 (8). *Miller Cr.*—IL: Alexander Co.: INHS 6047 (10). *St. Francis R. drainage.*—MO: Wayne Co.: SIUC uncat. (6). *White R. drainage.*—MO: Butler Co.: UT 44.942 (10). Carter Co.: UMMZ 193194 (5). Ripley Co.: UT 44.1826 (10). Shannon Co.: SIUC uncat. (8). Taney Co.: UMMZ 151181 (10). Clark Natl. Forest: UMMZ 117265 (8). AR: Madison Co.: UT 44.897 (9). Seary Co.: UMMZ 123532 (6). Van Buren Co.: INHS 123570 (10); INHS 81072 (10).

MISSOURI RIVER BASIN. *Gasconade R. drainage.*—MO: Gasconade Co.: INHS 80497 (3).

ARKANSAS RIVER BASIN. *Caney R. drainage.*—KS: Chautauqua Co.: KU 14424 (9). *Grouse Cr.*—Cowley Co.: KU 8616 (8). *Neosho R. drainage.*—KS: Cherokee Co.: KU 3192 (10); UMMZ 144939 (3); UMMZ 155100 (3); UMMZ 155175 (1); UMMZ 160379 (3). OK: Delaware Co.: UMMZ 103170 (10). *Illinois R. drainage.*—AR: Washington Co.: INHS 82466 (10). OK: Adair Co.: UT 48.1848 (3). Sequoyah Co.: UMMZ 137825 (6). *trib., Arkansas R.*—AR: Crawford Co.: UMMZ 123741 (10); UMMZ 123826 (10). *Fourche La Fave R. drainage.*—AR: Yell Co.: INHS 81092 (10).

RED RIVER BASIN. *Blue R. drainage.*—OK: Johnston Co.: OUMZ 30478 (10); OUMZ 40205 (4); UMMZ 156760 (4). *Kiamichi R. drainage.*—OK: LeFlore Co.: UMMZ 80947 (6). *Little R. drainage.*—OK: McCurtain Co.: INHS 80736 (10). AR: Polk Co.: UMMZ 170884 (10). *Saline R. drainage.*—AR: Sevier Co.: UMMZ 128088 (3). *Ouachita R. drainage.*—AR: Polk Co.: INHS 81032 (10). Montgomery Co.: SIUC 2494 (5). Saline Co.: SIUC 3645 (2); SIUC 3700 (5).

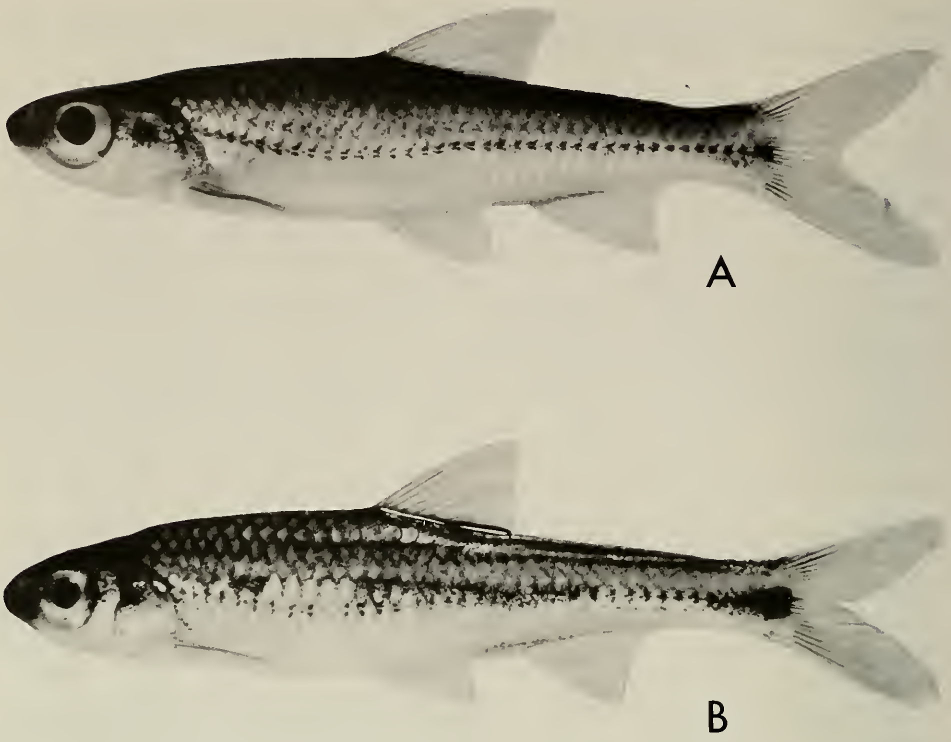


Fig. 1. A, *N. boops,* 54 mm SL female (SIUC 2494), Caddo River, Montgomery County, Arkansas, 9 October 1981; B, *N. xaenocephalus,* 55 mm SL male (INHS 75095), Stamp Creek, Bartow County, Georgia, 9 June 1976.

Notropis xaenocephalus (Jordan)

MOBILE BAY BASIN. *Etowah R. drainage.*—GA: Bartow Co.: INHS 75095 (10). *Oostanaula R. drainage.*—GA: Murray Co.: SIUC 2895 (10); SIUC 2884 (2). GA: Gordon Co.: SIUC 2904 (5).

Notropis boops Gilbert, 1884
Fig. 1

Types.—Syntypes of *N. boops* were collected by C. H. Gilbert from Salt Creek, Brown County, Indiana (10 specimens), and from Flat Rock Creek, Rush County, Indiana, by W. P. Shannon (about 30 specimens) (Gilbert 1884). C. R. Gilbert (1978) found and listed the following syntypes (numbers of specimens and their range in SL are in parentheses): Salt Creek—USNM 34982 (3, 44–46), MCZ 35961 (1, 54); 6 specimens not located. Flat Rock Creek—CAS-SU 3794 (20, 47–61); about 10 specimens not located. Some doubt exists regarding the status of the CAS-SU specimens because nothing in the jar indicated they were types and Gilbert was listed as the collector. Gilbert (1978) recommended that a lectotype be chosen from among the Salt Creek specimens. A lectotype of *N. boops* (45.6 mm SL) is herein selected and retains the original number USNM 34982. The lectotype conforms to the characters in the description that follows. The remain-

Table 1.—Proportional measurements (expressed in thousandths of SL) for *Notropis boops* in breeding condition summarizing sexual dimorphism. Specimens measured were 45–58 mm SL and were from the following drainages: Wabash (INHS 2937), Tennessee (UMMZ 200821), Mississippi (INHS 6047), White (INHS 81072), Arkansas (INHS 81092), and Ouachita (INHS 81032, 82466).

Character	Sex	n	Range	$\bar{x}$	*t*-Value	*P*
Head length	M	31	239–287	254	0.3536	N.S.
	F	19	245–266	253		
Head width	M	31	121–152	133	1.5504	N.S.
	F	19	124–140	130		
Head depth	M	30	138–176	150	1.1960	N.S.
	F	19	138–156	148		
Eye diameter	M	31	72–94	82	0.7226	N.S.
	F	19	76–96	83		
Snout length	M	31	58–71	65	1.8892	N.S.
	F	19	56–69	63		
Upper jaw length	M	30	48–76	62	0.3077	N.S.
	F	19	53–72	61		
Bony interorbital length	M	31	52–75	64	1.8051	N.S.
	F	19	53–72	62		
Anal fin length	M	31	139–191	167	2.7872	<.01
	F	19	139–182	159		
Dorsal fin length	M	31	138–267	228	0.7204	N.S.
	F	19	194–239	223		
Pelvic fin length	M	31	149–184	166	4.3382	<.005
	F	19	143–175	155		
Pectoral fin length	M	31	167–218	192	5.2201	<.005
	F	19	151–199	178		
Preanal length	M	30	631–688	671	3.2045	<.005
	F	19	672–702	681		
Prepelvic length	M	30	461–533	485	1.9223	N.S.
	F	19	462–510	492		
Predorsal length	M	31	469–553	491	1.8442	N.S.
	F	19	472–523	499		
Postdorsal length	M	31	500–609	532	1.5905	N.S.
	F	19	485–545	524		
Body width	M	31	112–150	128	0.8994	N.S.
	F	19	113–150	131		
Body depth	M	31	127–277	208	1.4403	N.S.
	F	19	130–256	223		
Caudal ped. depth	M	31	82–103	89	0.1100	N.S.
	F	19	79–94	87		
Caudal ped. length	M	31	113–256	220	0.3516	N.S.
	F	19	122–241	217		

ing syntypes now become paralectotypes bearing their original catalog numbers except those from USNM 34982 which now bear catalog number USNM 232410.

Diagnosis.—A moderate-sized species of *Notropis* (largest specimen measured is 66 mm SL); peritoneum black; intestine short (76.5–98.0% SL) with a single lengthwise loop; eye large (less than 3.5 times into head); anal-fin rays usually 8; pharyngeal teeth usually 1,4—4,1; no breeding colors.

Table 2.—Counts of lateral-line scales in *Notropis boops*.

Region	34	35	36	37	38	39	40	n	$\bar{x}$
East of Mississippi R.		23	91	86	17	3	1	221	36.5
West of Mississippi R.	3	25	125	81	18			225	35.9

Description.—Proportional measurements are shown in Table 1. General body shape and pigmentary features are illustrated in Fig. 1.

Dorsal-fin rays 7(1), 8(324). Anal-fin rays 7(5), 8(488), 9(24); $\bar{x}$ = 8.0. Left pectoral-fin rays 13(5), 14(61), 15(270), 16(160), 17(17), 18(1); $\bar{x}$ = 15.2. Pelvic-fin rays 7-6(1), 7-7(6), 7-8(13), 8-8(474), 8-9(8), 9-9(5). Principal caudal-fin rays 18(9), 19(449), 20(1), 21(4); $\bar{x}$ = 19.0.

Lateral-line scales 34–40 (Table 2). Body-circumference scales 21(7), 22(156), 23(144), 24(99), 25(37), 26(31), 27(2); $\bar{x}$ = 23.2. Body-circumference scales above lateral line 10(6), 11(360), 12(63), 13(47) ($\bar{x}$ = 11.3); below lateral line 8(4), 9(189), 10(160), 11(119), 12(4) ($\bar{x}$ = 9.8). Predorsal scale rows 10(1), 11(3), 12(100), 13(239), 14(119), 15(36); $\bar{x}$ = 13.2. Caudal-peduncle scale rows above lateral line 5(502), 6(6) ($\bar{x}$ = 5.0); below lateral line 5(506), 6(1), 7(1) ($\bar{x}$ = 5.0). Breast and nape completely scaled. Total gill rakers on first arch (all rudiments counted) 8(2), 9(6), 10(7), 11(4); $\bar{x}$ = 9.7.

Numbers of trunk, caudal, and total vertebrae are shown in Table 3. Pharyngeal teeth (sampled from throughout range) 1,4—4,0(6); 1,4—4,1(42). Teeth with prominent terminal hooks, but narrow grinding surfaces.

Lateral line on body complete to caudal base. Supratemporal canal broadly interrupted at dorsal midline; ST pore counts 2,2(20). Supraorbital canal without interruptions and not joining infraorbital canal behind eye; SO pore counts 7(5), 8(12), 9(2), 10(1); $\bar{x}$ = 8.0. Infraorbital canal complete; IO pore counts 10(2), 11(5), 12(12), 13(1); $\bar{x}$ = 11.6. Preoperculomandibular canal without interruptions; POM pore counts 9(7), 10(11), 11(2); $\bar{x}$ = 9.8.

Peritoneum black ventrally, silvery with scattered melanophores on dorsal surface of body cavity. Intestine short with a single lengthwise loop (Type I of Kafuku 1958). In 10 adults 48–59, $\bar{x}$ = 54 mm SL, ascending section 22.8–32.8, $\bar{x}$ = 28.6% SL; total intestinal length 76.5–98.0, $\bar{x}$ = 87.8% SL. Gas bladder two-chambered; total length 31.6–37.6, $\bar{x}$ = 33.8% SL, posterior chamber length 21.2–23.7, $\bar{x}$ = 22.7% SL. Peritoneal tunic covers anterior chamber. Pneumatic duct attached to dorsal surface of anterior chamber. Bladder lacks spiral markings or striations.

Distinct black lateral stripe about 1–1½ scale rows wide from tip of snout and lower jaw to caudal base. Caudal spot vague or lacking. Distinct, usually unpigmented stripe above black lateral stripe, about 1 scale row wide. Pre- and postdorsal stripe narrow, about 3–5 melanophores wide; stripe slightly expanded at origin of dorsal fin. Lateral-line pores on anterior half of body outlined with melanophores. Scales above unpigmented lateral stripe with melanophores on posterior edge of scale pocket; free scale edge forming a posterior band on exposed field leaving anterior central portion unpigmented. Thin black line on posterior edge of scale giving double-banded appearance to each scale. Top of head dark and uniformly pigmented. Body unpigmented ventral to lateral line, except

Table 3.—Counts of vertebrae (including the Weberian apparatus as four and the urostylar vertebra as one) in *Notropis boops*. East of Mississippi River = Wabash (INHS 2937), Cumberland (INHS 78328, UT 44.249), Tennessee (SIUC 308, UT 44.709), and Mississippi (INHS 6047) drainages; west of Mississippi River = Missouri (INHS 80497), White (INHS 81072), Arkansas (INHS 81092), Ouachita (INHS 81032), and Red (INHS 80736) drainages.

	Trunk					Caudal					Total					
Region	17	18	19	20	$\bar{x}$	16	17	18	19	$\bar{x}$	35	36	37	38	n	$\bar{x}$
East of Mississippi R.	1	2	55	18	19.2	2	43	29	2	17.4	1	34	37	4	76	36.6
West of Mississippi R.		1	30	18	19.3	15	29	5		16.8	3	31	15		49	36.2

some melanophores outline base of anal fin. Rays of dorsal and caudal fins outlined by melanophores. Rays of pectoral, pelvic, and anal fins occasionally outlined with a few scattered melanophores.

Numerous collections of breeding individuals from throughout the range of the species indicate that no breeding colors develop except for some creamy white in the membranes of the dorsal, caudal, and pectoral fins. Living individuals are generally greenish dorsally, silver in lateral aspect, and white ventrally.

Tubercles well-developed in breeding males from April through August, poorly developed in females and non-breeding males. Peak of tubercle development appears to be in May. Males with large dense tubercles dorsal and posterior to eyes, on front of snout (below and anterior to nares), and mandibles. Top of head with minute tubercles densely distributed. Ventral surface of head, gill membranes, preopercle, and opercle with sparsely scattered small tubercles. Small tubercles outline scales above lateral line, being prominent anteriorly and dorsally, and decreasing in size posteriorly and ventrally. Scales below lateral line and anterior to anal fin faintly outlined with tubercles. Small tubercles in single rows, mostly medially and distally, on branched and unbranched portions of all anal-fin rays, first 2 pelvic-fin rays, and first 5–7 dorsal-fin rays. Pectoral-fin tubercles on dorsal side of first 3–8 rays, occurring in double rows proximally and distally and densest (usually 4 rows) medially. Those on first unbranched ray rather evenly distributed in 2–4 rows on middle two-thirds of ray. Females rarely develop tubercles on chin; they are smaller and more sparsely distributed than those found on chin of males.

Variation.—No significant sexual differences in meristic characters were noted. Excluding dimensions directly affected by gonadal development, males in breeding condition display significantly greater values for lengths of the anal, pectoral, and pelvic fins, and the preanal distance (see Student's *t*-Tests, Table 1).

The urogenital papilla of adult females is enlarged and protruded during the spawning season; the papilla of males is only slightly swollen. There are no significant sexual differences in pigmentation pattern.

Notropis boops is remarkably uniform in external morphological features throughout its rather extensive range. Only two characters were found to exhibit some variation, the number of vertebrae and the number of lateral-line scales. Variation is slight in both characters, but the pattern of variation is similar. Specimens from east of the Mississippi River and in the northern part of the species' range average slightly higher numbers of lateral-line scales and caudal vertebrae (Tables 2–3). The variation in these two characters follows a general trend re-

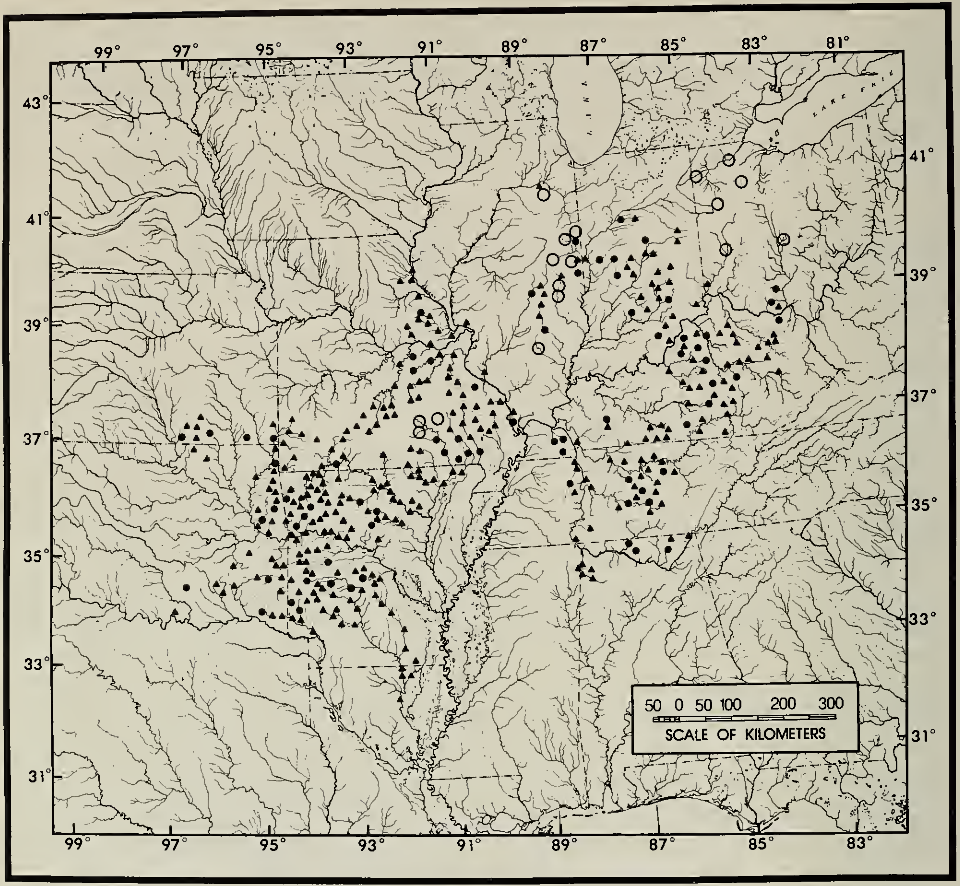


Fig. 2. Range of *N. boops*. Solid dots represent localities from which specimens were examined; triangles represent localities from the literature; open circles represent localities where the species presumably no longer occurs.

ported for many fishes in which the number of elements (e.g., vertebrae) progressively increases to the north (Barlow 1961).

Smith and Hocutt (1981) examined pharyngeal tooth counts in 100 individuals of *N. boops* from Big River, Missouri, and reported the following variation: 64% had a 1,4—4,1 count, 19% a 1,4—4,0 count, 8% a 0,4—4,0 count, 7% a 0,4—4,1 count, 1% a 1,4—3,1 count, and 1% a 1,5—4,1 count. Pharyngeal tooth counts from throughout the range of the species agree for the most part with those of Smith and Hocutt and indicate that a tooth is occasionally lost from the minor row.

Comparisons.—Among the species of *Notropis, N. boops* most closely resembles *N. xaenocephalus* (Jordan) as Swift (1970) originally suggested. These two species are extremely similar in overall body shape and pigmentation pattern (Fig. 1). *Notropis xaenocephalus* is, however, readily distinguished from *N. boops* by the following characters: pharyngeal teeth usually 2,4—4,2, anal-fin rays usually 7, peritoneum silvery with scattered melanophores, caudal spot well-developed, and tuberculation on the head, body, and fins less extensive.

Distribution

Notropis boops occurs in the central Mississippi basin where its range extends from the Scioto River drainage, Ohio, west to the lower Red River drainage, Oklahoma, south to the Ouachita River drainage, Louisiana, and north to the Illinois River drainage, Illinois (Fig. 2). Its reported occurrence in the Cache Creek drainage (Comanche County) of southwestern Oklahoma (Miller and Robison 1973) is not verified by specimens.

In recent years some populations of *N. boops* have been severely decimated, particularly in western Ohio (Trautman 1981) and east-central Illinois (Smith 1979) because of excessive siltation and turbidity. The continued use of poor agricultural practices in these states has modified many of the clear, gravel-bottomed streams that *N. boops* formerly inhabited (Fig. 2).

The species is on the endangered or rare fish list for Mississippi (Clemmer *et al.* 1975) and is of special concern in Alabama (Ramsey 1976). Although *N. boops* is rare or disappearing on the edges of its range it is common and abundant throughout most of Arkansas, eastern Oklahoma, southern Missouri, southeastern Kansas and central Kentucky and Tennessee.

Acknowledgments

We are grateful to the following ichthyologists and their institutions for information on types, loans of specimens, and/or providing one of us (BMB) with laboratory space: L. M. Page, Illinois Natural History Survey (INHS); F. B. Cross and J. T. Collins, University of Kansas (KU); K. Hartel, Museum of Comparative Zoology (MCZ); E. A. Lachner, U.S. National Museum of Natural History (USNM); T. M. Cavender, Ohio State University Museum of Zoology (OSU); L. G. Hill, University of Oklahoma Museum of Zoology (OUMZ); W. D. Pearson, University of Louisville (UL); R. M. Bailey, University of Michigan Museum of Zoology (UMMZ); D. A. Etnier, University of Tennessee (UT). K. Schmitt, Scientific Photography and Illustration Facility of the Southern Illinois University at Carbondale (SIUC) Graduate School, assisted in preparation of the figures.

Literature Cited

Barlow, G. W. 1961. Causes and significance of morphological variation in fishes.—Systematic Zoology 10(3):105–117.

Clemmer, G. H., R. D. Suttkus, and J. S. Ramsey. 1975. A preliminary check-list of endangered and rare fishes of Mississippi, pp. 6–11. *In* A preliminary list of rare and threatened vertebrates in Mississippi.—Mississippi Game and Fish Commission, Jackson.

Gilbert, C. H. 1884. A list of fishes collected in the East Fork of White River, Indiana, with descriptions of two new species.—Proceedings of the United States National Museum 7(423): 199–205.

Gilbert, C. R. 1978. Type catalogue of the North American cyprinid fish genus *Notropis*.—Bulletin of the Florida State Museum, Biological Sciences 23(1):1–104.

Hubbs, C. L., and K. F. Lagler. 1964. Fishes of the Great Lakes region.—University of Michigan Press, Ann Arbor. 213 pp.

Kafuku, T. 1958. Speciation in cyprinid fishes on the basis of intestinal differentiation, with some references to that among catostomids.—Bulletin of the Freshwater Fisheries Research Laboratory 8:45–78.

Lehtinen, S., and A. A. Echelle. 1979. Reproductive cycle of *Notropis boops* (Pisces: Cyprinidae) in Brier Creek, Marshall County, Oklahoma.—The American Midland Naturalist 102(2):237–243.

Miller, R. J., and H. W. Robison. 1973. The fishes of Oklahoma.—Oklahoma State University Press, Stillwater. 246 pp.

Ramsey, J. S. 1976. Freshwater fishes, pp. 53–65. *In* H. Boschung (ed.). Endangered and threatened plants and animals of Alabama.—Bulletin Alabama Museum of Natural History No. 2.

Smith, P. W. 1979. The fishes of Illinois.—University of Illinois Press, Urbana. 314 pp.

Smith, R. E., Jr., and C. H. Hocutt. 1981. Formulae variations of pharyngeal tooth counts in the cyprinid genus *Notropis*.—Copeia 1981(1):222–224.

Snelson, F. F., Jr. 1971. *Notropis mekistocholas,* a new herbivorous cyprinid fish endemic to the Cape Fear River basin, North Carolina.—Copeia 1971(3):449–462.

Swift, C. C. 1970. A review of the eastern North American cyprinid fishes of the *Notropis texanus* species group (subgenus *Alburnops*), with a definition of the subgenus *Hydrophlox,* and materials for a revision of the subgenus *Alburnops*.—Ph.D. thesis, Florida State University, Tallahassee. 515 pp.

Trautman, M. B. 1981. The fishes of Ohio.—Ohio State University Press, Columbus. 782 pp.

(BMB) Department of Zoology, Southern Illinois University at Carbondale, Carbondale, Illinois 62901; (WWD) Museum of Zoology, Louisiana State University, Baton Rouge, Louisiana 70893.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 59–66

SYNONYMY AND DISTRIBUTION OF *PHYLLOMEDUSA BOLIVIANA* BOULENGER (ANURA: HYLIDAE)

David C. Cannatella

Abstract.—The correct name for the large, black-eyed species of *Phyllomedusa* from Bolivia, adjacent Brazil and northern Argentina is *Phyllomedusa boliviana*; *P. pailona* Shreve is a junior subjective synonym. The tadpole is a generalized phyllomedusine type. With the exception of the syntypes, none of the specimens referred to *P. boliviana* in the literature has been identified correctly.

Boulenger (1902) described *Phyllomedusa boliviana* on the basis of a male and female from Chulumani, on the eastern slopes of the Andes in Bolivia. Until the revision by Funkhouser (1957), no additional specimens were referred to that species. Funkhouser did not examine the type specimens, and her relegation of several specimens from Buena Vista, Bolivia, to this species was based solely on the description of the species.

In the course of studies on the systematics of phyllomedusine frogs, I have examined all of Funkhouser's material and one of the syntypes of *P. boliviana*. None of the specimens examined by her can be ascribed to that species. Rather, they represent an undescribed species apparently related to *P. tarsius, P. trinitatis,* and *P. venusta,* and will be treated in a paper dealing with the systematics of these species.

In addition, I have collected *P. boliviana* at the type-locality and also in northern Argentina, where the species is known as *Phyllomedusa pailona,* described from El Pailón, Bolivia, by Shreve (1959). Live specimens from Chulumani and Argentina are similiar in the possession of a blackish-brown iris and eyelid edged in red. Direct comparison of the holotype and paratypes of *P. pailona* with the syntype of *boliviana* leads me to conclude that only one species is represented, and that *Phyllomedusa boliviana* is the proper name for the species.

Materials and Methods

Measurements were taken as described by Duellman (1970). The following abbreviations are used: snout–vent length, SVL; standard length (distance from tip of snout to tip of coccyx) SL; tibia length, TIB; foot length, FOOT; head length, HLEN; head width, HWID; interorbital distance, IOD; internarial distance, IND; length of eyelid, ELID; length of eye, EYE; horizontal diameter of tympanum, TYMP; distance from anterior corner of eye to nostril, ENOS. Color notes from life are taken from the field notes of the author. The following museum acronyms were employed: American Museum of Natural History, AMNH; British Museum (Natural History), BMNH; Carnegie Museum, CM; Instituto Miguel Lillo (Tucumán, Argentina), IML; University of Kansas Museum of Natural History, KU; Museo Argentino de Ciencias Naturales, (Buenos Aires, Argentina), MACN; Museum of Comparative Zoology, MCZ; University of Michigan Museum of Zoology, UMMZ; United States National Museum of Natural History, USNM.

Phyllomedusa boliviana Boulenger
Fig. 1

Phyllomedusa boliviana Boulenger, 1902:395. Syntypes, BMNH 1901.8.2.49–50 (RR 1947.2.22.32–33) from Chulumani, Bolivia, 2000 m, P. O. Simons, collector.

Phyllomedusa (*Pithecopus*) *boliviana*.—Lutz, 1950:602, 621.

Phyllomedusa pailona Shreve, 1959:1. Holotype, MCZ 29677, El Pailón, 5 km from the eastern shore of the Río Grande, Depto. Santa Cruz, Bolivia, 350 m, Carl Gans and F. S. Pereira, collectors.—Duellman, 1968:6.—Duellman, 1977: 163.

Pithecopus pailonus.—Lutz, 1966:236.—Laurent, 1967:232.

Diagnosis.—A large species of *Phyllomedusa* having 1) the first toe longer than, and opposable to, the second; 2) distinct, well-developed parotoid glands; 3) prevomerine teeth present in adults; 4) no calcar or dermal appendages; 5) a lightly reticulated palpebral membrane; 6) iris black-brown in life; 7) in life, upper eyelid edged with red, tubercles on flank white, tipped with red; concealed surfaces of hindlimb pale yellow-green with no markings.

Redescription of male syntype.—Head wider than body; snout short, rounded in dorsal view; in lateral view, truncate and inclined posteriorly from lip to nostril; canthus rostralis rounded, distinct; loreal region barely concave; lips thin and not flared; nostrils not protuberant, directed laterally; internarial region flat; eyes not protuberant; pupil vertically elliptical; palpebrum finely reticulated; parotoid gland well-developed, extending from eyelid to a point level with the insertion of the arm; supratympanic fold moderately developed, barely obscuring upper edge of tympanum; tympanum distinct, oval; anterior edge of tympanum separated from posterior corner of eye by distance of 1 mm. Axillary membrane absent; upper arm slender, forearm robust; ulnar fold low; relative lengths of fingers 1-2-4-3 from shortest to longest; finger discs about three-fifths diameter of tympanum; subarticular tubercles large, round to conical; supernumerary tubercles lacking on fingers; palmar tubercle barely distinct; prepollex enlarged, elliptical, bearing thin, horny nuptial excrescence; fingers lacking webbing.

Leg of moderate length, slender; no calcar or dermal ornamentation; inner tarsal fold absent; outer tarsal fold barely distinct; relative lengths of toes 2-1-3-5-4 from shortest to longest; toe discs rounded, shorter than those on fingers; inner metatarsal tubercle elliptical, low, flattened; outer metatarsal tubercle absent; no webbing between toes; subarticular tubercles large, round to conical; no supernumerary tubercles on toes.

Anal opening directed posteriorly at midlevel of thighs; anal opening a short tube, no flap; supra-anal fold present; pair of large tubercles present inferior and lateral to anus; skin of dorsal surfaces smooth, no tubercles; skin of chin and pectoral region finely areolate; skin of belly and ventral surface of thigh tubercular; skin of remaining ventral surfaces of limbs smooth, except for that of forearm and tarsus, which bears a few discrete tubercles; anterior flank tuberculate, posterior flank smooth; tongue lanceolate, barely notched posteriorly; free

Fig. 1. *Phyllomedusa boliviana,* male, KU 182969, SVL 64.8 mm.

for about one-half its length; prevomerine teeth present; dentigerous processes of prevomer small, separated medially by distance equal to width of one process, processes directed posteromedially at midlevel of elliptical choana; vocal slit short, extending from posterolateral corner of tongue to corner of mouth; vocal sac single, median, subgular.

In preservative, dorsal surfaces pale blue; dorsal surfaces of finger and toe discs gray; ventral surface of chin pale brown, with few diffuse cream spots; ventral surface of belly and thigh cream; ventral aspects of forearm and tarsus pale brown, with discrete white tubercles; ventral surfaces of hand and foot pale brown; ventral surfaces of shank and inner aspect of tarsus pale gray with pale brown mottling; anterior and posterior aspect of thigh pale blue-violet; few, indistinct white tubercles present on posterior aspect of thigh; anal region pale brown; paired anal tubercles and supra-anal fold white; white stripe present along heel, tarsus, and lateral border of fifth toe; border of upper eyelid, lower lip, and anterior flank white; most tubercles of anterior flank capped with small spot of dark gray pigment; white stripe at point of insertion of arm, demarcating the blue color of upper arm from cream region of chest; this stripe and lip stripe bordered inferiorly by thin gray line.

The male syntype is in excellent condition, except that the outer two toes of each foot are slightly desiccated. Also, there is a 1 cm incision in the midventral region. The female specimen is similar to the male syntype in most respects; Duellman (pers. comm.), however, noted that the palpebrum of the female was not reticulated.

Measurements of the syntypes (male/female) in mm.—SVL 54.3/75.2, TIB 23.9/

Fig. 2. Distribution of *P. boliviana.* Key to localities: 1. Caranavi; 2. Chulumani; 3. El Pailón; 4. Jaciara; 5. Aguas Blancas, Río Pescado, and Finca Jakulica; 6. Yuto.

31.1, FOOT 18.0/23.7, HLEN 18.8/22.0, HWID 18.6/23.8, IOD 5.2/8.1, IND 4.1/5.1, ELID 4.2/5.7, EYE 6.1/8.3, TYMP 3.2/4.2, ENOS 5.0/5.2.

Coloration in life.—Dorsal surfaces, face, and tympanum lime green; upper eyelid edged with red; venter gray, with pale yellow splotches; lower lip, supra-anal fold, and tarsal fold white, edged with pale red; tubercles on flank white, tipped with red; tarsal fold white; ventral surfaces of hand and foot flesh-colored; axilla and concealed region of elbow pale yellow; groin, concealed surface of shank, tarsus, and thigh pale yellow-green with a hint of orange; anal region dark gray; paired anal tubercles pale yellow; finger and toe discs off-white; iris dark brown, almost black (D. Cannatella field notes, 12 December 1978).

The above notes are based on a sample of Argentinian specimens (KU 182969–90). Specimens from Chulumani, Bolivia (KU 183436–38) differed in the following points: the tubercles on the ventral surface of the forearm and tarsus, and the supra-anal fold were red-orange; the ulnar and tarsal stripes were white with a red-orange wash.

Distribution.—This species is known from the Andean slopes and eastern lowlands of Bolivia, and the lowlands of western Brazil and northern Argentina, at elevations of 350–2000 m (Fig. 2). Duellman (1977) followed Funkhouser (1957) in including Peru within the species' range, on the basis of her misidentified specimens. Likewise, the specimens from Restauraçao, Brazil, on which Heyer (1977) remarked, were compared to misidentified "*boliviana*"; the frogs from Restauraçao are not *boliviana*, but are referrable to the undescribed species from Buena Vista mentioned above.

Variation.—The syntypes of *P. boliviana* and the type-series of *P. pailona*

Table 1.—Measurements (mm) of *P. boliviana* from northern Argentina; mean ± 2 standard errors; range in parentheses.

Measurement	Males (n = 19)	Females (n = 3)
SVL	67.7 ± 1.18 (63.6–74.2)	76.8 ± 3.54 (74.8–80.3)
SL	65.3 ± 1.18 (60.5–70.8)	72.3 ± 3.10 (69.9–75.2)
TIB	28.4 ± 0.47 (27.1–30.9)	31.4 ± 0.59 (30.8–31.8)
FOOT	23.1 ± 0.49 (20.8–24.6)	25.7 ± 1.36 (24.4–26.7)
HLEN	23.2 ± 0.28 (22.0–24.6)	24.6 ± 1.40 (23.9–26.0)
HWID	23.0 ± 0.28 (22.2–24.3)	24.6 ± 0.54 (24.2–25.1)
IND	5.4 ± 0.12 (4.9–6.0)	5.9 ± 0.43 (5.5–6.2)
ENOS	5.4 ± 0.06 (5.2–5.6)	6.0 ± 0.30 (5.7–6.2)
TYMP	4.1 ± 0.13 (3.6–4.4)	4.5 ± 0.20 (4.4–4.7)

differ in ventral coloration. The syntypes of *P. boliviana* and the KU specimens from Chulumani and Caranavi, Bolivia, have flank tubercles tipped with dark brown spots; the venters are dark brown with areas of pale mottling (some have no pale areas). Also, the venter of the male syntype of *P. boliviana* is slightly paler than those of the KU specimens.

One of the specimens of the type-series of *P. pailona* has just a hint of such flank spots (CM 36278) and the others lack them. Moreover, two of these have a white lateral stripe on the anterior flanks, bordered below by a dark blue stripe. The venters of these frogs are almost immaculate, a diagnostic feature noted by Shreve (1959).

Most of the frogs from Jaciara, Brazil, have a hint of the dark tips on the flank tubercles, and all have a more discrete lateral stripe as well, bordered below by a dark blue-gray stripe or wider area. The venters of this series are pale gray, slightly darker than the type-series of *pailona*, but not as dark as the Chulumani series.

The frogs from Agua Blanca, Argentina, consist of two series: one recently collected by me and the other collected by Dr. Raymond Laurent. The specimens collected by me have dark brown venters with pale mottling, and a few discrete dark spots on the flank tubercles. The older specimens have immaculate venters with almost no hint of the flank tubercle spots. The KU specimens from Finca Jakulica and Angosto del Pescado, Argentina are colored similarly to the recent KU specimens from Agua Blanca.

It appears that the striking differences in ventral coloration between the type-specimens of both nominal species are due to some preservation difference and/or fading over time. Additionally, all of the recently collected KU specimens have dark blue dorsal surfaces, and those of the other specimens are pale blue.

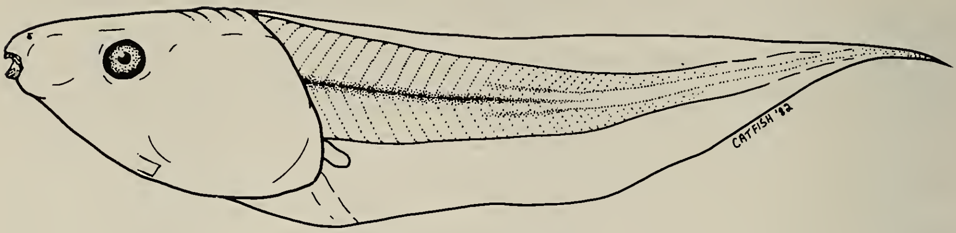


Fig. 3. Larva of *Phyllomedusa boliviana,* KU 183822.

In the preserved specimens there is also variation in the presence of a reticulated palpebrum, but this is clearly a preservation artifact. All of the specimens collected by me (KU 182969–90 and KU 183436–40) possessed a reticulated palpebrum in life. However, these specimens were stored for several months in formalin before transfer to ethanol, and the reticulation has been lost in all of them. All other specimens that I have examined still possess the reticulation.

Measurements of the specimens collected in northern Argentina are summarized in Table 1. Males from the vicinity of Chulumani, Bolivia range from 54.3 to 70.2 mm SVL (n = 3). The two males from Caranavi are 53.5 and 57.2 mm SVL. Those from El Pailón, Bolivia (n = 4) range from 56.1 to 64.7 mm SVL, and the males from Jaciara are 62.1–68.3 mm in SVL (n = 6).

Justification of synonymy.—Direct comparison of the type-specimens of *P. boliviana* and *P. pailona* leaves little doubt that the two names have been applied to the same species. Shreve based his comparison on material of "*boliviana*" that had been misidentified by Funkhouser (1957). As noted above, the immaculate venter of *P. pailona* is due to preservation artifacts. The iris color alone will diagnose *P. boliviana* from all other *Phyllomedusa.* Additionally, the combination of reticulated palpebrum, large parotoid glands, and absence of pattern on the posterior flanks and concealed surfaces of the hindlimbs will distinguish this species from all others of the genus.

Natural history.—At Aguas Blancas, Argentina, specimens were collected 0.5–1.0 m above ground in vegetation near ruts filled with water at the side of a highway. The males were calling; the call is a 'tup-tup-tup,' repeated every 2–10 seconds. At Angosto del Pescado and Finca Jakulica, individuals were collected around ponds or ditches filled with water, about 1 m above ground in vegetation; the males were calling in the same fashion. Barrio (1976) described the mating call of this species from the Río Pescado, Argentina.

In Bolivia, individuals were calling from vegetation about 1 m above ground; none were collected near standing water, however. All specimens collected by me were taken at night. Laurent (1967) remarked on the natural history of the species in Argentina.

Tadpoles.—The lot of tadpoles was collected by day from a muddy roadside ditch, where KU 183439–40 were taken on the previous night. Tadpoles of *Ololygon rubra* were collected in the same ditch.

In general, the larvae of *P. boliviana* resemble those phyllomedusine larvae described by Cannatella (1980, 1982). The following description is based on KU 183822, which consists of seven tadpoles. A representative larva at Stage 32

(Gosner 1960) with a SVL of 15.0 mm and total length of 42.5 mm is illustrated in Fig. 3. Body slightly deeper than wide, deepest and widest at two-thirds the length of the body; top of head slightly convex; snout rounded in lateral profile; snout rounded in dorsal view; nostrils dorsolateral; internarial distance slightly greater than width of oral disc; eyes dorsolateral and directed laterally; spiracle a flap-like tube, ventral and sinistral to midline; spiracular opening at a point about midlength of the body; mouth anteroventral; cloacal tube short, dextral to base of caudal fin; caudal musculature slender, tapering gradually to posterior end of fin; myomeres weakly developed; at midlength of the tail the depth of the caudal musculature slightly less than depth of ventral fin, but greater than depth of dorsal fin; caudal musculature extending to tip of tail; dorsal fin shallow anteriorly, not extending onto body; dorsal fin deepest at two-thirds its length from anterior; ventral fin deepest at its midlength.

Mouth relatively small, with a shallow lateral fold; medial portion of upper lip lacking papillae; elsewhere, papillae present in one or two rows along borders; upper beak broadly curved and uniformly serrate; lower beak V-shaped and uniformly serrate; two upper and three lower rows of denticles; upper rows of same length; second upper row broadly interrupted medially; three lower rows of denticles uninterrupted; first two lower rows about same length; third row about one-half as long as upper two; denticles of third row smaller and fewer in number.

In life, dorsum transparent with gold and black pigments; lateral surfaces gold; venter transparent, with some gold pigment anteriorly; tail clear with fine distribution of melanophores; area above eye heavily pigmented with gold; iris white with black and gold flecks. In preservative, sides and top of head and body translucent, with scattered melanophores; intense concentration of melanophores covering gut, and obscuring view of intestines; caudal musculature flesh-colored; dorsal and ventral fins transparent, with fine distribution of melanophores in posterior one-half of dorsal and ventral fins, but not extending to tip of tail.

Eggs.—Three clutches of eggs were examined (IML 1349). One clutch is a lot of hatchling tadpoles. The second is a clutch of 154 tadpoles about to hatch from the egg membranes; the egg mass is still enveloped in a folded leaf. The third clutch is also encased in a folded leaf and consists of 142 eggs in the first stages of cleavage; the mean diameter of 20 eggs is 2.6 mm. A few of the eggs appear to be unfertilized and are smaller in size, and empty egg cases are found at the upper and lower ends of the cylindrical clutch in the same fashion as described for *P. hypocondrialis* by Pyburn (1980), and *P. duellmani* by Cannatella (1982).

Specimens examined.—ARGENTINA: *Jujuy:* Ruta Yuto-Ledesma, a 7 km de bifurcación, IML 1305(7), 1307(8); Bifurcación ruta Yuto, 1306(2), 1308; Pozo Colque (cerca de Yuto), 1309(3); Alrededores de Yuto, 1310; Yuto, UMMZ 127406; *Salta:* Río Pescado, IML 1345(24), 1397(8), 1349 (eggs); Aguaray, 1467(6); Abra Grande, Orán, 1682(2); Agua Blanca, 460 m, 1685 (11), 2145 (4), 2171, KU 182969–71, KU 128940–44, 128945 (skeleton); Angosto del Pescado 620 m, IML 2706(24), 1349(3) (three clutches eggs), KU 182972–75; Finca Jakulica, 560 m, 182976–90.

BRAZIL: *Mato Grosso:* Jaciara, UMMZ 127908, USNM 164097, MCZ 44942, AMNH 72450, KU 92322–25, 92326–27 (skeletons).

BOLIVIA: *La Paz:* 4.4 km E Chulumani, 1760 m, KU 183436; 2.1 km E Chulumani, 1900 m, 183437–38; Chulumani, 2000 m, BMNH 1947.2.22.33 (syntype); 15.7 km S Caranavi, 900 m, KU 183439–40, 183822 (larvae); *Santa Cruz:* Río

Grande, Cabezas, MACN 3483(5); El Pailón, 350 m, CM 36278–79 and MCZ 29679 (paratypes of *P. pailona*); MCZ 29677 (holotype of *P. pailona*).

Acknowledgments

For loan of specimens and provision of working space I thank Charles W. Myers, Alice G. C. Grandison, Jose M. Gallardo, Raymond F. Laurent, Arnold G. Kluge, W. Ronald Heyer, C. J. McCoy, and Pere Alberch. Raymond Laurent was a gracious host during my stay in Argentina, and Esteban LaVilla and Omar Pagaburo greatly assisted me there in the field. Thomas Berger travelled with me in Bolivia. William E. Duellman shared data on the female syntype of *P. boliviana* and also criticized the manuscript. Collecting permits for Bolivia and Argentina were granted by Gastón Bejarano B. of the Departamento Nacional de Vida Silvestre, Parques Nacionales, Caza y Pesca, of Bolivia and Malcolm D. Craig, Dirección Nacional de Fauna Silvestre, Argentina. Field work was supported by a grant (DEB 76-09986, William E. Duellman, principal investigator) from the National Science Foundation, and by a National Science Foundation Graduate Fellowship to the author.

Literature Cited

Barrio, A. 1976. Estudio cariotipico y analisis audioespectrografico de los cantos de las especies de *Phyllomedusa* (*Anura, Hylidae*) que habitan en la Argentina.—Physis 35(90):65–74.

Boulenger, G. A. 1902. Descriptions of new batrachians and reptiles from the Andes of Peru and Bolivia.—Annals and Magazine of Natural History (7)10:394–402.

Cannatella, D. C. 1980. A review of the *Phyllomedusa buckleyi* group (Anura: Hylidae).—Occasional Papers of the Museum of Natural History of the University of Kansas (87):1–40.

———. 1982. Leaf-frogs of the *Phyllomedusa perinesos* group (Anura: Hylidae).—Copeia 1982(3): 501–513.

Duellman, W. E. 1968. The genera of phyllomedusine frogs (Anura: Hylidae).—University of Kansas Publications, Museum of Natural History 18(1):1–10.

———. 1970. The hylid frogs of Middle America.—Monograph of the Museum of Natural History, University of Kansas (1):1–753.

———. 1977. Liste der rezenten Amphibien und Reptilien: Hylidae, Centrolenidae, Pseudidae.—Das Tierreich (95):1–225.

Funkhouser, A. 1957. A review of the Neotropical tree-frogs of the genus *Phyllomedusa*.—Occasional Papers of the Natural History Museum of Stanford University (5):1–90.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification.—Herpetologica 16(3):183–190.

Heyer, W. R. 1977. Taxonomic notes on frogs from the Madeira and Purus Rivers, Brasil.—Papéis Avulsos de Zoologia, São Paulo 31(8):141–162.

Laurent, R. F. 1967. Redescubrimiento de *Pithecopus pailonus* (Shreve) en Argentina.—Acta Zoologica Lilloana 22:231–248.

Lutz, B. 1950. Anfibios anuros da colecao Adolpho Lutz. Hylidae in the Adolpho Lutz collection of the Instituto Oswaldo Cruz.—Memórias do Instituto Oswaldo Cruz 11(3):599–637.

———. 1966. *Pithecopus ayeaye*, a new Brazilian hylid with vertical pupils and grasping feet.—Copeia 1966(2):236–240.

Pyburn, W. F. 1980. The function of eggless capsules and leaf in nests of the frog *Phyllomedusa hypochondrialis* (Anura: Hylidae).—Proceedings of the Biological Society of Washington 93(1): 153–167.

Shreve, B. 1959. A new Phyllomedusa from Bolivia (Salientia, Hylidae).—Breviora (113):1–3.

Museum of Natural History and Department of Systematics and Ecology, The University of Kansas, Lawrence, Kansas 66045.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 67–78

STUDIES OF THE COASTAL MARINE FAUNA OF SOUTHERN SINALOA, MEXICO. IV. REPORT ON THE CARIDEAN CRUSTACEANS

M. E. Hendrickx, M. K. Wicksten, and A. M. van der Heiden

Abstract.—As a result of a large scale survey of the coastal marine fauna of southern Sinaloa, Mexico, 29 species of caridean shrimps are reported for a wide variety of habitats. Information is provided on their currently known distribution in the Eastern Pacific region.

Since 1979, a large scale survey of the marine coastal fauna has been underway in the southeastern part of the Gulf of California. One of the main results obtained so far is the updating of a provisional inventory of the species of marine and estuarine invertebrates and fishes found in southern Sinaloa (van der Heiden and Hendrickx 1982; Hendrickx and van der Heiden in press). Much information also has been gained regarding the occurrence of these species in different habitats.

There have been almost no faunistic studies on invertebrates on a regional basis in the Gulf of California. The most comprehensive works available are those of Parker (1963) and Brusca (1980). Both, however, are incomplete, mentioning only some of the wide variety of species to be found in the area. This paper records the caridean shrimps found so far in southern Sinaloa, and provides information on their habitats. Further studies are underway, however, and additional species may be found to be present in the area, especially in less accessible habitats such as the nearshore rocky subtidal.

Material and methods.—The material on which this study of caridean shrimps is based comes from a wide spectrum of habitats with differing environmental conditions. Specimens from shallow water coastal systems came from estuaries, coastal lagoons, and rocky intertidal habitats. Material from the Bay of Mazatlán was taken during a 2-year sampling program aboard the boat *FC-1* of the Secretaría de Educación Pública in Mazatlán. Specimens from the continental shelf were collected during a three-leg project (SIPCO project) aboard the oceanographic vessel *El Puma* of the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. Sampling in shallow water was done by hand collecting, cast nets, trawls, small grabs, or small dredges. Aboard ship, bottom grabs, dredges, beam trawls, or otter trawls were used according to the capabilities of the ships that were available. A map of the sampling areas is given in Fig. 1.

Family Pasiphaeidae

Leptochela serratorbita Bate, 1888

Material.—Bay of Mazatlán, Van Veen grab: 2 males (April 1980), 1 ovigerous female (Jan 1980).

Previous Eastern Pacific records.—Cape San Lucas, Baja California Sur; Topolobampo, Sinaloa (Chace 1937).

Range.—Tropical and warm temperate western Atlantic (Chace 1972), southern Gulf of California.

Habitat.—At Cape San Lucas, 15–30 m on sandy bottom (Chace 1937); in Bay of Mazatlán, 10–27 m on fine sand.

Family Palaemonidae

Palaemon (*Palaemon*) *gracilis* (Smith, 1871)

Material.—Caimanero lagoon, cast net, 23 specimens (June 1978; Sept 1978; 4 ovigerous).

Previous Eastern Pacific records.—Nicaragua and Panama (Holthuis 1952b).

Range.—Caimanero lagoon south to Río Lara, southern Panama.

Habitat.—Rivers, streams and coastal waterways throughout its range, in fresh to brackish water (up to 8‰ salinity).

Macrobrachium americanum Bate, 1868

Material.—Río Baluarte, 4 specimens (1979).

Previous Eastern Pacific records.—Numerous records, from Mexico to Peru (Holthuis 1952b).

Range.—Mulege, Baja California Sur to northern Peru (Holthuis 1952a).

Habitat.—Freshwater streams in southern Sinaloa (Río Presidio, Río Baluarte, and Río Quelite).

Macrobrachium digueti (Bouvier, 1895)

Material.—Río Baluarte, 3 specimens (Nov 1978, Aug 1980).

Previous Eastern Pacific records.—Baja California, Mexico; Guatemala, Panama, and Ecuador (Holthuis 1952b); Peru (Méndez 1981).

Range.—Mulege, Baja California Sur; Río Baluarte, Sinaloa south to Río Moche, Peru.

Habitat.—Fresh water.

Macrobrachium occidentale Holthuis, 1950

Material.—Río Baluarte, 2 specimens (Nov 1978).

Previous Eastern Pacific records.—Guatemala, El Salvador and Panama (Holthuis 1952b).

Range.—Río Baluarte, Sinaloa south to Panama.

Habitat.—Specimens from the Río Baluarte were collected in fresh water.

Macrobrachium tenellum (Smith, 1869)

Material.—Huizache-Caimanero lagoon complex, 3 specimens (July 1978); Caimanero lagoon, cast net, 7 ovigerous females (Sept 1978); Estero El Verde, hand net, 3 specimens (July 1979).

Previous Eastern Pacific records.—Numerous records, Mexico to Peru (Holthuis 1952b).

Range.—Mulege, Baja California Sur to northern Peru (Holthuis 1952a).

Habitat.—So far, the species has been reported only in fresh water. The ani-

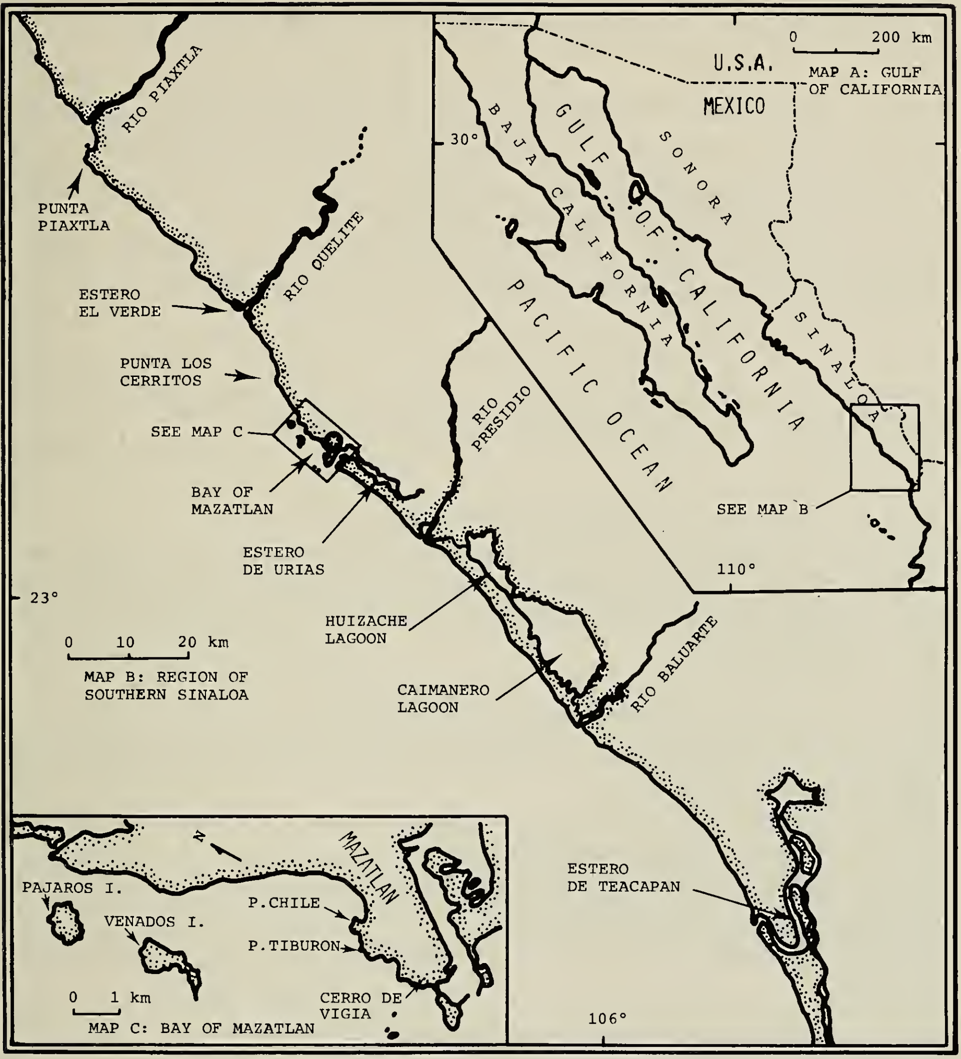


Fig. 1. Location of the sampling areas. Map A: Gulf of California; Map B: Region of Southern Sinaloa; Map C: Bay of Mazatlán.

mals from near Mazatlán, however, were collected in brackish water. The salinity ranged up to 20‰. In Estero El Verde, *M. tenellum* was found in beds of widgeon grass (*Ruppia* sp.).

Palaemonetes (*Palaemonetes*) *hiltoni* Schmitt, 1921

Material.—Estero El Verde, 11 specimens, 9 ovigerous (June and Dec 1979; Jan and May 1980); Caimanero lagoon, cast net, 61 specimens (date not recorded).

Previous Eastern Pacific records.—Southern California, U.S.A., Sonora and Sinaloa, Mexico (Holthuis 1952b).

Range.—San Pedro, California south to Sinaloa.

Habitat.—Animals from estero El Verde were taken among widgeon grass (*Ruppia* sp.) with a small hand net at 0.4–1 m at a salinity of 20–22‰.

Periclimenes (*Periclimenes*) *infraspinis* (Rathbun, 1902)

Material.—Bay of Mazatlán, Van Veen grab, 3 specimens (Aug 1979).

Previous Eastern Pacific records.—Southern California, U.S.A.; Gulf of California, Costa Rica, Galapagos Islands (Holthuis 1951).

Range.—San Diego, U.S.A., south to the Galapagos Islands (Brusca 1980).

Habitat.—The specimens were taken on a sandy bottom at 9 m.

Neopontonides dentiger Holthuis, 1951

Material.—Bay of Mazatlán, trawl, 1 ovigerous female (Sept 1979); off Punta Piaxtla (23°34′N, 106°57′W), trawl, 1 specimen (Apr 1981).

Previous Eastern Pacific record.—Off Cape San Francisco, Ecuador (Holthuis 1951, 1952a).

Range.—The species is known only from these 3 records.

Habitat.—Holthuis (1951) reported the holotype from a mud-rock bottom at 4 m. Material from Sinaloa was found a sand-rock bottom at 8 m in the Bay of Mazatlán, and on a muddy bottom with colonies of gorgonians attached to stones at 66 m off Punta Piaxtla.

Pontonia margarita Smith, 1869

Material.—Bay of Mazatlán: 1 male and 1 female (Sept 1979), 2 males and 2 ovigerous females (June 1980).

Previous Eastern Pacific records.—Numerous records, from the Gulf of California to the Galapagos Islands (Holthuis 1951).

Range.—From the Gulf of California to the Galapagos Islands, Ecuador (Holthuis 1951).

Habitat.—Specimens were found as commensals of the pearl oyster *Pinctada mazatlanica*.

Family Gnathophyllidae

Gnathophyllum panamense Faxon, 1893

Material.—Punta Los Cerritos, north of Mazatlán, rocky shore, 1 specimen (May 1981).

Previous Eastern Pacific records.—Gulf of California south to Panama (Brusca 1980).

Range.—Gulf of California south to the Galapagos Islands (Wicksten in press).

Habitat.—Rocky intertidal zone to 17 m, sometimes found in tidepools.

Family Hippolytidae

Lysmata californica (Stimpson, 1866)

Material.—Bay of Mazatlán, trawled, 3 specimens, 1 ovigerous (Nov 1979).

Previous Eastern Pacific records.—California, U.S.A.; west coast of Baja California, Gulf of California, to Panama (Abele and Patton 1976; Brusca 1980; Standing 1981).

Range.—Tomales Bay, California to Panama.

Habitat.—Common in rocky intertidal areas (Brusca 1980). Taken at 9 and 24 m on muddy sand or fine sand off Mazatlán.

Trachycaris restrictus (A. Milne-Edwards, 1878)

Material.—Off Punta Piaxtla, trawled, 1 ovigerous female (Apr 1981).

Previous Eastern Pacific records.—Gulf of California, Panama (Wicksten in press).

Range.—Tropical eastern and western Atlantic (Chace 1972); Gulf of California to Panama.

Habitat.—The specimen from off Punta Piaxtla was taken on a muddy bottom at 66 m.

Thor paschalis (Heller, 1862)

Material.—Bay of Mazatlán, Van Veen grab, 1 specimen (Nov 1979); Pichilingue, Bay of La Paz, Baja California, rocky shore, 3 specimens (Mar 1980).

Previous Eastern Pacific records.—Gulf of California, southwestern Mexico, Panama (Wicksten in press).

Range.—Indo-West Pacific region (Bruce 1976); Gulf of California to Panama.

Habitat.—At La Paz, the animals were found under stones in a rocky intertidal area. The animal from the Bay of Mazatlán was collected on a bottom of stones and shell fragments.

Latreutes antiborealis Holthuis, 1952c

Material.—Bay of Mazatlán, Van Veen grab, 1 specimen (Nov 1980).

Previous Eastern Pacific records.—Numerous records, Gulf of California to Chile (Wicksten and Méndez in press).

Range.—Gulf of California to Chile.

Habitat.—The specimen from the Bay of Mazatlán was collected on fine to very fine sand at 6 m.

Family Processidae

Processa spp.

Material.—Off Teacapán, Sinaloa (22°24′N, 105°54′W), Van Veen grab, 1 ovigerous female (Aug 1980); Bay of Mazatlán, Van Veen grab, 24 specimens from 12 different grab samples (Aug 1979–Mar 1981).

Habitat.—The animal from off Teacapán was taken at 37 m on silty sand; the rest came from 7–25 m on sandy mud to muddy sand, sometimes with shell fragments.

Remarks.—Individuals of this genus are common in the Bay of Mazatlán. Most of these specimens belong to an undescribed species being studied by M. K. Wicksten and M. Méndez. Others have not yet been identified to species.

Family Alpheidae

Synalpheus digueti Coutière, 1909

Material.—Pájaros Island, Bay of Mazatlán, rocky intertidal zone, 1 specimen (Apr 1980); Punta Chile, Bay of Mazatlán, rocky intertidal zone, 3 specimens (Oct 1980).

Previous Eastern Pacific records.—"Lower California" (Coutière 1909); Arena Bank, Gulf of California (Chace 1937); Panama (Abele and Patton 1976); Isla Malpelo, Colombia (Abele 1975).

Range.—Southern Gulf of California to Colombia.

Habitat.—Lower midlittoral to sublittoral zones, among stones or within crevices in rocky intertidal; also associated with sponges in lower intertidal zone.

Synalpheus nobilii Coutière, 1909

Material.—About 5 km N of Mazatlán, 2 specimens (1 ovigerous) (Dec 1979); Punta Chile, Bay of Mazatlán, 1 ovigerous female (Oct 1980); foot of Cerro de Vigía, Bay of Mazatlán, 2 specimens (1 ovigerous) (Oct 1980); Cerro de Vigía, 5 specimens (2 ovigerous) (Nov 1980).

Previous Eastern Pacific records.—Gulf of California (Wicksten in press); Clipperton Island (Chace 1962); Panama (Abele 1976); Isla Malpelo, Colombia (Abele 1975); Ecuador (Coutière 1909); Galapagos Islands (Schmitt 1939).

Range.—Gulf of California to the Galapagos Islands.

Habitat.—All specimens except the female from Punta Chile came from beneath tufts of coralline algae in the lower midlittoral zone of rocky shores.

Synalpheus biunguiculatus (Stimpson, 1860)

Material.—Punta Piaxtla, rocky shore, 2 specimens (1 ovigerous) (Oct 1979); Punta Chile, Bay of Mazatlán, rocky shore, 2 ovigerous females (Oct 1980); foot of Cerro de Vigía, Bay of Mazatlán, 5 specimens (1 ovigerous) (Oct 1980); Estero de Teacapán, 2 specimens (Mar 1980), 4 specimens (Apr 1980), 1 specimen (May 1980).

Previous Eastern Pacific records.—Gulf of California, southwestern Mexico, and Galapagos Islands (Wicksten in press); Clipperton Island (Chace 1962), Panama (Abele 1976), Isla Malpelo, Colombia (Abele 1975).

Range.—Hawaiian Islands (Stimpson 1860; Banner 1953), Gulf of California south to Galapagos Islands.

Habitat.—Specimens from Punta Piaxtla and the Bay of Mazatlán were found under sponges on rocks and under stones. The animals from Estero de Teacapán were collected on oyster racks with *Striostrea iridescens* and barnacles (*Balanus* sp.) at a salinity of 40‰ in March 1980).

Synalpheus apioceros sanjosei Coutière, 1909

Material.—Punta Piaxtla, rocky shore, 1 ovigerous female (Oct 1980); Bay of Mazatlán, 1 specimen (June 1979); Punta Chile, Bay of Mazatlán, rocky shore, 7 specimens (2 ovigerous) (Apr 1980), 1 ovigerous female (Oct 1980); Isla Pájaros, Bay of Mazatlán, rocky shore, 4 specimens (Apr 1980); foot of Cerro de Vigía, Bay of Mazatlán, rocky shore, 2 specimens (Dec 1980), 2 specimens (1 ovigerous) (Oct 1980), 3 specimens (1 ovigerous) (Nov 1980).

Previous Eastern Pacific records.—Southern Gulf of California (Brusca 1980); Isla San José, Baja California Sur (Coutière 1909).

Range.—Scammon's Lagoon, west coast of Baja California throughout Gulf of California (Wicksten in press).

Habitat.—In the Bay of Mazatlán, one animal was taken in June 1979 among the calcareous tubes of the gregarious polychaete *Filograna implexa* on sand at 9.5 m. All other specimens came from the lower midlittoral zone to the sublittoral fringe on rocky shores, where the species usually is found under sponges attached to stones or in small cavities.

Automate dolichognatha De Man, 1888

Material.—Off coast of Sinaloa (23°10′N, 106°28′W), Van Veen grab, 1 specimen (Apr 1981).

Previous Eastern Pacific records.—Isla Clarion, Panama, Isla Cocos, Colombia, Ecuador, and Galapagos Islands (Wicksten 1981).

Range.—Tropical western Atlantic, tropical Indo-West Pacific region, tropical eastern Pacific from Sinaloa to the Galapagos Islands (Wicksten 1981).

Habitat.—Commonly found in rocky intertidal zones (Wicksten 1981). The specimen from southern Sinaloa was collected by dredging on a silty sand bottom at 28 m.

Automate rugosa Coutière, 1900

Material.—Off Punta Piaxtla, Van Veen grab, 1 specimen (Apr 1981); off Mazatlán, Van Veen grab, 4 specimens (Apr 1981); entrance to Estero de Urías (Mazatlán Harbour), sediment sample, 1 specimen (Apr 1980).

Previous Eastern Pacific records.—Isla Cedros and Turtle Bay, Mexico; Gulf of Panama (Wicksten 1981; Coutière 1909).

Range.—Isla Cedros, west coast of Baja California; Sinaloa, Gulf of California, south to the Gulf of Panama.

Habitat.—Specimens were taken from sediment samples of muddy sand collected at 27–70 m.

Alpheus armillatus H. Milne Edwards, 1837

Material.—Punta Chile, Bay of Mazatlán, rocky shore, 2 specimens (Oct 1980), 1 specimen (Nov 1980); between Punta Chile and Punta Tiburón, Bay of Mazatlán, under stones, 4 specimens (1 ovigerous) (Apr 1980); Estero de Urías, Mazatlán Harbour, 1 specimen (Nov 1981).

Previous Eastern Pacific records.—Widely distributed in the Gulf of California (Wicksten in press).

Range.—Tropical and warm temperature western Atlantic (Chace 1972); Gulf of California.

Habitat.—The species is common in the rocky intertidal zone of the Bay of Mazatlán, where it lives in burrows under stones. Small specimens have been found under sponges and in small crevices. The species occurs from the lower midlittoral zone to the sublittoral fringe.

Alpheus floridanus Kingsley, 1878

Material.—Bay of Mazatlán, trawl, 1 specimen (Mar 1979), Van Veen grab, 1 specimen (Jan 1980); Off Cerro de Vigía, Bay of Mazatlán, Van Veen grab, 1 ovigerous female (Nov 1980); off Mazatlán (23°04′N, 106°16′W) trawl, 1 specimen (Mar 1981).

Previous Eastern Pacific records.—Bahía Gonzaga, Mexico; Isla Taboga, Panama (Wicksten in press).

Range.—Eastern Atlantic from Guinea to Congo, Gulf of Mexico to Brazil (Chace 1972); Gulf of California, Panama.

Habitat.—The animals were collected at 20–25 m on muddy sand, often with a significant amount of clay. Contrary to what has been reported for the western Atlantic coast, none of the specimens was taken intertidally.

Alpheus leviusculus Dana, 1852

Material.—South of Punta Chile, Bay of Mazatlán, rocky shore, 5 specimens (2 ovigerous) (Feb 1980; Apr 1980); Punta Chile, rocky shore, 3 specimens (Oct 1980).

Previous Eastern Pacific records.—Galapagos Islands (Sivertsen 1933; Hult 1939).

Range.—Wake Island, Canton Island (Banner and Banner 1964); Gulf of California to Colombia (Wicksten in press), Galapagos Islands.

Since the publication of the report of Banner and Banner (1982) on the alpheids of Australia, it may be necessary to consider the specimens from Sinaloa as members of a new subspecies that would be distinct to both *A. l. leviusculus* (Indo-West Pacific region) and *A. l. bouvieri* (Atlantic region).

Habitat.—Alpheus leviusculus was collected under stones, among sand, and in gravel in rocky intertidal areas. It commonly burrows in the lower midlittoral zone and sublittoral fringe.

Alpheus cf. *A. malabaricus* Fabricius, 1775

Material.—Estero El Verde (23°25′30″N, 106°33′30″W) bottom dredge, 1 specimen (May 1979); El Tanque Canal, Caimanero Lagoon, cast net at night, 3 specimens (May 1979); Estero de Urías, Mazatlán Harbour, in mud, 2 specimens (Nov 1981).

Previous Eastern Pacific records.—Vicinity of Mazatlán (Wicksten in press).

Range.—The specimens from Mazatlán belong to the *A. malabaricus* complex and their relationship with other members of this complex will be treated in a forthcoming paper (Wicksten in press).

Habitat.—In southern Sinaloa, the species seems to be restricted to coastal lagoons and mangrove channels. The specimens from Estero de Urías were collected in mud, on a small flat bank bordered by mangrove trees at a salinity of 36‰ and a temperature of 31°C. Other specimens were collected on shallow muddy sand bottoms in a lagoon at a salinity of 37‰.

Table 1.—Species of Carideans in Different Habitats

Rivers, estuaries and lagoons:
- *Alpheus malabaricus*
- *Macrobrachium* spp.
- *Palaemon gracilis*
- *Palaemonetes hiltoni*

Intertidal-subtidal rocky areas:
- *Alpheus armillatus*
- *Alpheus leviusculus*
- *Alpheus schmitti*
- *Gnathophyllum panamense*
- *Synalpheus apioceros sanjosei*
- *Synalpheus biunguiculatus*
- *Synalpheus digueti*
- *Synalpheus nobilii*

Offshore soft or mixed bottoms:
- *Alpheus floridanus*
- *Automate dolichognatha*
- *Automate rugosa*
- *Latreutes antiborealis*
- *Leptochela serratorbita*
- *Lysmata californica*
- *Neopontonides dentiger*
- *Ogyrides* sp.
- *Periclimenes infraspinis*
- *Pontonia margarita*
- *Processa* spp.
- *Thor paschalis*
- *Trachycaris restrictus*

Alpheus schmitti Chace, 1972

Material.—Punta Chile, Bay of Mazatlán, rocky shore, 2 specimens (Feb 1980).

Previous Eastern Pacific records.—The species is known only from this record.

Range.—Florida Keys, Antigua Island, Grenada, Tobago (Chace 1972); Mazatlán, Sinaloa.

Habitat.—Lower midlittoral zone, under stones.

Family Ogyrididae

Ogyrides sp.

Material.—Bay of Mazatlán, 58 specimens (Aug 1980–Apr 1981).

Previous Eastern Pacific records.—Southwestern Mexico (Wicksten in press).

Range.—Because of the uncertainty of the specific identity, the range is uncertain. Other specimens of *Ogyrides* have been taken in southwestern Mexico and off Southern California, U.S.A. There may be more than one species in the area.

Habitat.—In the Bay of Mazatlán, the species is common on soft bottoms.

Discussion

At least 29 species of carideans including a least two species of *Processa* and one or more species of *Ogyrides*, are known now from the coast of Sinaloa. The fauna contains many wide-ranging species, some of which are known only from a few specimens.

Certain species are characteristic of different depths or habitats (Table 1). Those of the coastal estuaries and lagoons are particularly interesting, having been poorly studied elsewhere in western Mexico.

The caridean fauna of Mazatlán differs somewhat from that found in other parts of the Gulf of California. The small shrimp *Palaemon ritteri*, common at Guaymas and Puerto Peñasco, has not been taken at Mazatlán. *Thor paschalis* and *Hippolyte williamsi*, common elsewhere among *Sargassum* spp., also are uncommon or not reported from the area. Perhaps the degree of exposure to waves or the temperature of the water may be responsible for the difference in the caridean faunas.

Literature Cited

Abele, L. G. 1975. The macruran decapod Crustacea of Malpelo Island.—Smithsonian Contributions to Zoology 176:69–85.

———. 1976. Comparative species composition and relative abundance of decapod crustaceans in marine habitats of Panamá.—Marine Biology 38:263–278.

———, and W. K. Patton. 1976. The size of coral heads and the community biology of associated decapod crustaceans.—Journal of Biogeography 3:35–47.

Banner, A. H. 1953. The Crangonidae, or snapping shrimp of Hawaii.—Pacific Science 12(1):3–144.

———, and D. M. Banner. 1964. Contributions to the knowledge of the alpheid shrimp of the Pacific Ocean, IX. Collections from the Phoenix and Line Islands.—Pacific Science 18(1):83–100.

———, and ———. 1966. The alpheid shrimp of Thailand.—Siam Society Monographs Series, No. 3. 168 pp.

———, and ———. 1982. The alpheid shrimp of Australia. Part III. The remaining alpheids, principally the genus *Alpheus* and the family Ogyridae.—Records of the Australian Museum, 34(1–2):1–357.

Bate, C. S. 1868. On a new genus, with four new species, of freshwater prawns.—Proceedings of the Zoological Society of London, 1868:363–368.

———. 1888. Report on the Crustacea Macrura collected by the H.M.S. *Challenger* during the years 1873–76.—Reports of the Voyages of the H.M.S. *Challenger,* Zoology 24:i–xc, 1–942.

Bouvier, E. L. 1895. Sur les Palémons recueillis dans les eaux douces de la Basse-Californie par M. Diguet.—Bulletin du Muséum d'Histoire Naturelle de Paris 1:159–162.

Bruce, A. J. 1976. Shrimps from Kenya.—Zoologische Verhandelingen, Leiden 145:1–72.

Brusca, R. C. 1980. A handbook to the common intertidal invertebrates of the Gulf of California.—University of Arizona Press, Tucson, 513 pp.

Chace, F. A., Jr. 1937. The Templeton Crocker Expedition. VII. Caridean decapod Crustacea from the Gulf of California and the west coast of Lower California.—Zoologica 22(2):109–138.

———. 1962. The non-brachyuran decapod crustaceans of Clipperton Island.—Proceedings of the United States National Museum 113(3466):605–635.

———. 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.

Coutière, H. 1900. Sur quelques Alpheidae des Côtes américaines (Collection de l'U.S. National Museum, Washington).—Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 131:356–358.

———. 1909. The American species of snapping shrimps of the genus *Synalpheus.*—Proceedings of the United States National Museum 36(1659):1–93.

Dana, J. D. 1852. Crustacea. Part I. U.S. Exploring Expedition, during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N., 13:1–1620.

Fabricius, J. C. 1775. Systema Entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus. Flensburg and Leipzig, 832 pp.

Faxon, W. 1893. 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, Lieut. Commander Z. L. Tanner, U.S.N., commanding. VI. Preliminary descriptions of new species of Crustacea.—Bulletin of the Museum of Comparative Zoology Harvard University 24(7):149–220.

Heller, C. 1862. Beiträge zur Crustaceen-Fauna des Roten Meeres. Zweiter Teil.—Sitzungsberichte der Akademie der Wissenschaften in Wien 44(1):241–295.

Hendrickx, M. E., and A. M. van der Heiden. (in press). Study of the invertebrate fauna of southern Sinaloa, México.—*In* A. Ayala-Castañares, F. B. Phleger, R. Schwartzlose y A. Laguarda, eds., The Gulf of California: Origin, Evolution, Waters, Marine Life & Natural Resources. Universidad Nacional Autónoma de México, Mexico City.

Holthuis, L. B. 1950. Preliminary descriptions of twelve new species of palaemonid prawns from American waters (Crustacea Decapoda).—Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 53:93–99.

———. 1951. A general revision of the Palaemonidae (Crustacea Decapoda Natantia) of the Americas. I. The subfamilies Euryrhynchinae and Pontoniinae.—Occasional Papers of the Allan Hancock Foundation 11:1–332.

———. 1952a. The Palaemonidae collected by the *Siboga* and *Snellius* expeditions, with remarks on other species. II. Subfamily Pontoniinae.—Siboga Expeditie $39a^{10}$:1–249.

———. 1952b. A general revision of the Palaemonidae. II. The subfamily Palaemoninae.—Occasional Papers of the Allan Hancock Foundation 12:1–396.

———. 1952c. Reports of the Lund University Chile Expedition 1948–49. The Crustacea Decapoda Macrura of Chile.—Lunds Universitets Årsskrift, N.F. Avd. 2, 7(10):1–109.

Hult, J. 1939. Crustacea Decapoda from the Galapagos Islands collected by Mr. Rolf Blomberg.—Arkiv for Zoologi 30A(5):1–18.

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

Man, J. G. 1888. Bericht über die von Herrn Dr. J. Brock im indischen Archipel gessammelten Decapoden und Stomatopoden.—Archiv für Naturgeschichte 53(1):215–600.

Méndez, M. 1981. Claves de identificación y distribución de los langostinos y camarones (Crustacea: Decapoda) del mar y ríos de la costa del Perú.—Boletín del Instituto del Mar de Perú-Callao. 5:1–170.

Milne-Edwards, A. 1878. Description de quelques espèces nouvelles de crustacés provenant du voyage aux îles du Cap-Vert de MM. Bouvier et de Cessac.—Bulletin de la Société philomathématique de Paris, (7), 2:225–232.

Milne-Edwards, H. 1837. Histoire naturelle des crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. 2. Paris: Roret. 532 pp.

Parker, R. H. 1963. Zoogeography and ecology of macroinvertebrates, particularly mollusks, in the Gulf of California and the continental slope off México.—Videnskabelige Meddelelse fra Dansk Natur-historisk Forening 126:1–178.

Rathbun, M. J. 1902. Description of new decapod crustaceans from the west coast of North America.—Proceedings of the United States National Museum 24(1272):885–905.

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

———. 1939. Decapod and other Crustacea collected on the Presidential Cruise of 1938.—Smithsonian Miscellaneous Collections 98(6):1–29.

Sivertsen, E. 1933. The Norwegian Zoological Expedition to the Galapagos Islands 1925, conducted by Alf Wollebaek. VII. Littoral Crustacea Decapoda from the Galapagos Islands.—Meddelelser fra det Zoologiske Museum, Oslo 38:1–23.

Smith, S. I. 1869. *In* Verrill, A. E. On the parasitic habits of Crustacea.—American Naturalist 3: 239–250.

———. 1871. List of the Crustacea collected by J. A. McNiel in Central America.—Reports of the Peabody Academy of Science, 1869:87–98.

Standing, J. D. 1981. Occurrences of shrimps (Natantia: Penaeidea and Caridea) in central California and Oregon.—Proceedings of the Biological Society of Washington 94(3):774–786.

Stimpson, W. 1860. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit W. Stimpson. Pars VIII. Crustacea Macrura.—Proceedings of the Academy of Natural Sciences of Philadelphia 12:22–47.

———. 1866. Descriptions of new genera and species of macrurous Crustacea from the west coast of North America.—Proceedings of the Chicago Academy of Sciences 1:46–48.

van der Heiden, A. M., and M. E. Hendrickx. 1982. Inventario de la fauna marina y costera del sur de Sinaloa, México. Segundo Informe de Avance, Revisado y aumentado.—Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Estación Mazatlán. 135 pp.

Wicksten, M. K. 1981. The species of *Automate* (Caridea: Alpheidae) in the eastern Pacific Ocean.—Proceedings of the Biological Society of Washington 94(4):1104–1109.

———. (in press). Shallow water caridean shrimps of the Gulf of California.—Occasional Papers of the Allan Hancock Foundation. New Series.

———, and M. Méndez. (in press). Neuvos registros de camarones carideos del Perú.

(MEH and AMVDH) Instituto de Ciencias del Mar y Limnología, UNAM, Estación Mazatlán, P.O. Box 811, Mazatlán, Sinaloa, México; (MKW) Department of Biology, Texas A&M University, College Station, Texas 77843-3258.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 79–83

THREE NEW SPECIES OF *OCHROTRICHIA* (*METRICHIA*) FROM CHIAPAS, MEXICO (TRICHOPTERA: HYDROPTILIDAE)

Joaquin Bueno-Soria

Abstract.—Three new species of *Ochrotrichia* (*Metrichia*) (Trichoptera: Hydroptilidae), are described and figured: *Ochrotrichia* (*M.*) *lacuna Ochrotrichia* (*M.*) *riva* and *Ochrotrichia* (*M.*) *avon*. All species were discovered to occur around a waterfall named "Cascada de Misolha" in Chiapas, Mexico.

In a recent collecting trip in Mexico, I found several undescribed species of *Ochrotrichia* (*M.*) from a waterfall named "Cascada de Misolha," located at 20 km southeast from Palenque, Chiapas, on the road to Ocosingo.

Banks (1907), described *Orthotrichia nigritta* from Texas, which was made the type of the genus *Metrichia* by Ross (1938). The genus was reduced to the status of subgenus by Flint (1968), and been revised by Flint (1972), Denning and Blickle (1972), and Marshall (1979). Heretofore only five species of *Ochrotrichia* (*Metrichia*) have been known from Mexico: *Ochrotrichia* (*M.*) *aberrans* Flint, *Ochrotrichia* (*M.*) *nigritta* (Banks), *Ochrtrichia* (*M.*) *quadrata* Flint, *Ochrotrichia* (*M.*) *trigonella* Flint, and *Ochrotrichia* (*M.*) *trispinosa* Bueno. In this paper three new species are described.

Ochrotrichia (*M.*) *lacuna*, new species
Figs. 1–3

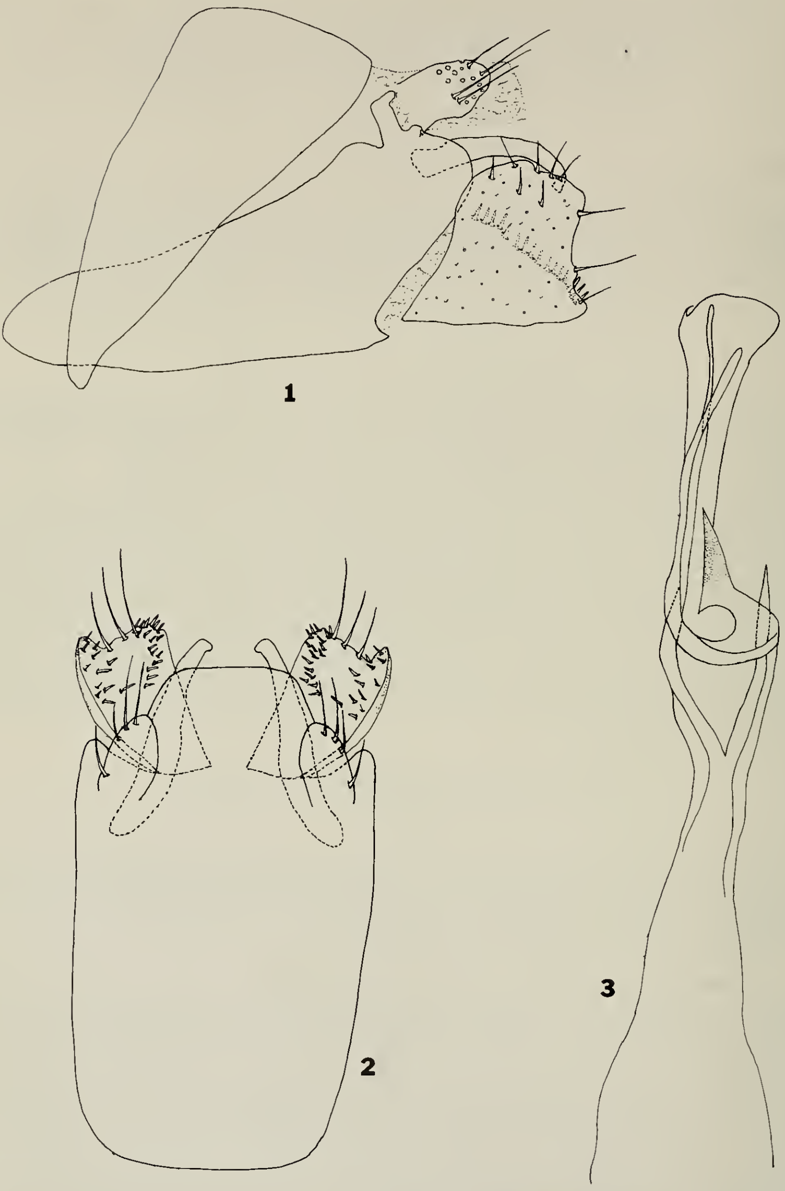
This species appears to be related to *Ochrotrichia* (*M.*) *biungulata* Flint, particularly in the shape of the claspers, but differs rather strongly in the structure of the aedeagus. The two, unequal, subapical hooks and internal tubule and lateral spine arising just basad of them are distinctive.

Adult.—Length of forewing, 2 mm. Color uniformly fuscous. Male abdomen with 2 pairs of internal sacs: 1 long, annulate pair between segments 5 and 6, and a small round pair between 6 and 7. Male genitalia: Ninth segment more than one and one-half times as long as high in lateral aspect, posterior margin slightly angulate. Cercus elongate. Dorsolateral hooks slightly decurved, basolateral scale very small. Claspers slightly longer than high in lateral aspect, apex slightly concave, with several small, black, peglike setae in a line on ventromesal margin. Aedeagus with two hooks arising subapically, one much longer than other, with an internal tubule and lateral process arising just basad of hooks.

Material.—Holotype, male. MEXICO: Chiapas, "Cascada de Misolha," 20 km SE from Palenque, 18 May 1981, J. Bueno and H. Velasco. Deposited in Instituto de Biologia UNAM (IBUNAM).

Ochrotrichia (*M.*) *riva*, new species
Figs. 4–6

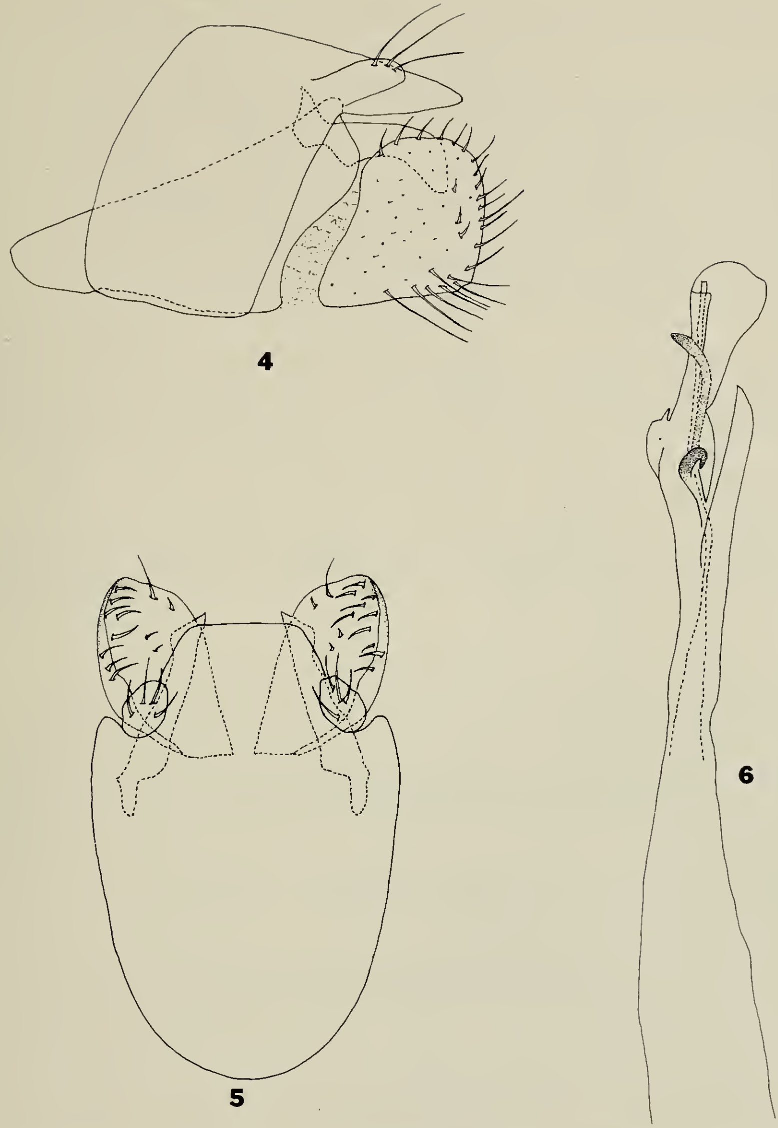
Although abundantly distinct, this species is related to *Ochrotrichia* (*M.*) *quadrata* Flint by the shape in lateral view of the clasper and the hooks on the ae-



Figs. 1–3. *Ochrotrichia* (*M.*) *lacuna*, new species. 1, Male genitalia lateral. 2, Tenth terga and claspers in dorsal view. 3, Aedeagus in dorsal view.

deagus. However, the small rectangular claspers, with a few spines at the apex, and the long process of the aedeagus are distinctive.

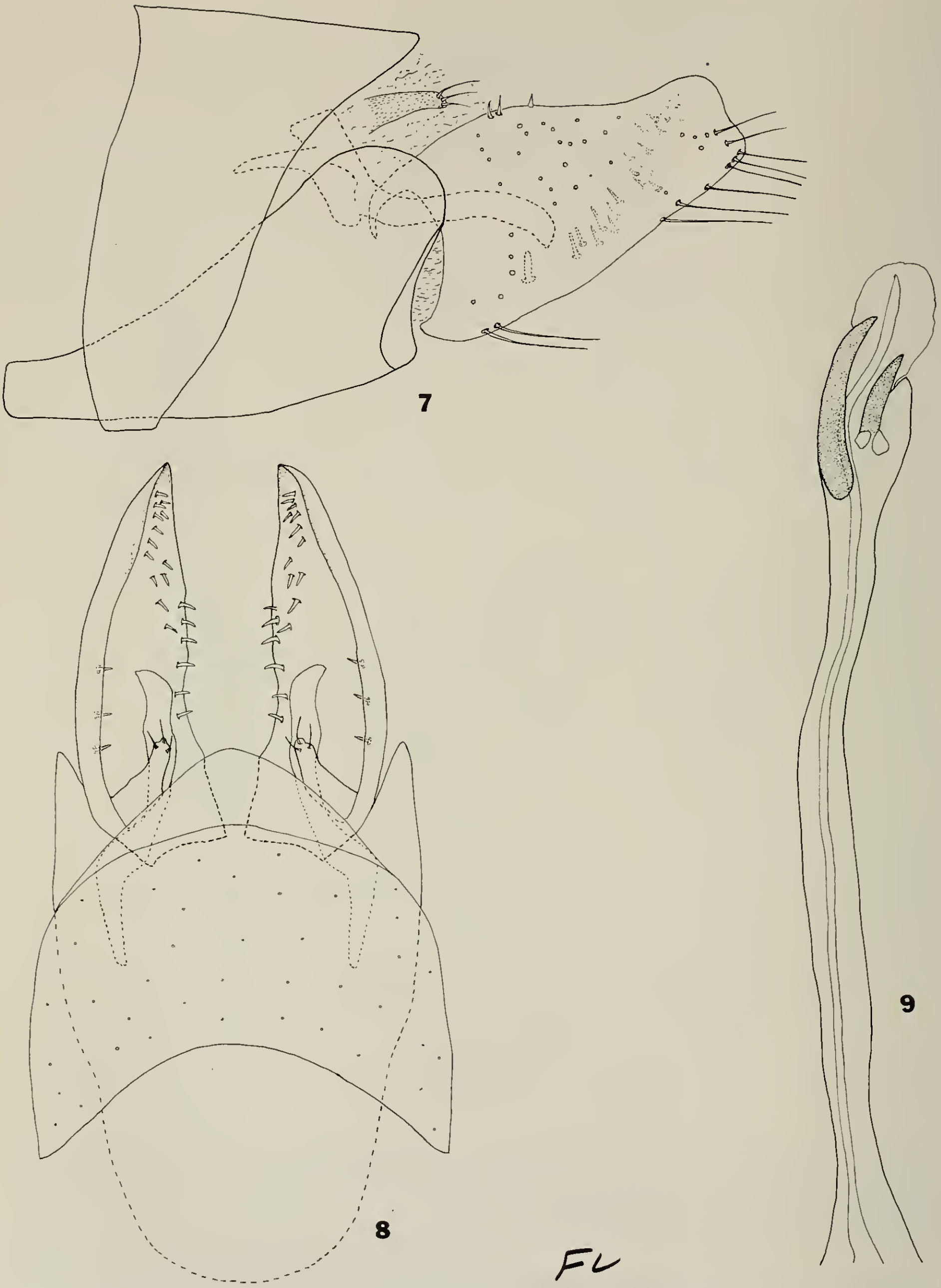
Adult.—Length of forewing, 3 mm. Color dark-brown in alcohol. Male abdomen without any sacs between the segments. Male genitalia: Ninth segment almost twice as long as high in lateral aspect, posterior margin nearly vertical. Cercus rounded. Dorsolateral hooks long, wide, somewhat curved, basolateral



Figs. 4–6. *Ochrotrichia* (*M.*) *riva*, new species. 4, Male genitalia lateral. 5, Tenth tergum and claspers in dorsal view. 6, Aedeagus in dorsal view.

scale slightly curved. Clasper rectangular in lateral aspect, posterior margin truncate and bearing a few long spines. Aedeagus with two hooks arising subapically, one short and very dark, other much longer and paler, with a long lateral process arising basad of hooks.

Material.—Holotype, male. MEXICO: Chiapas, "Cascada de Misolha," 20 km SE from Palenque, 18 May 1981, J. Bueno and H. Velasco (IBUNAM). Paratypes, same data as holotype, 17 males (IBUNAM); same, but C. M. & O. S. Flint Jr., 2 males. Deposited in the United States National Museum (USNM).



Figs. 7–9. *Ochrotrichia* (*M.*) *avon*, new species. 7, Male genitalia lateral. 8, Tenth tergum and claspers in dorsal view. 9, Aedeagus in dorsal view.

Ochrotrichia (*M.*) *avon*, new species
Figs. 7–9

This species appears to be quite different from the two preceding species, differing rather strongly in the shape of the aedeagus. The paired slightly separated, subapical hooks, and the long internal tubule arising from the base of the aedeagus, are distinctive.

Adult.—Length of forewing 2 mm. Color uniformly fuscous. Male abdomen with a pair of short, dark, sacs within fifth segment, opening between fifth and sixth. Male genitalia: Ninth segment more than one and one-half times as long as high in lateral aspect, posterior margin angulate. Cercus narrow and elongate. Dorsolateral hook distintly decurved, basolateral scale very small. Claspers clearly longer than high in lateral aspect, apex truncate, with several long setae and black spines on ventromesal margin. Aedeagus with two stout, black, subapical hooks arising almost contiguosly, one much longer than the other, with a very long internal tubule.

Material.—Holotype, male. MEXICO: Chiapas, ''Cascada de Misolha''. 20 km SE from Palenque, 18 May 1981, J. Bueno and H. Velasco (IBUNAM). Paratypes, same data as holotype, but C. M. & O. S. Flint Jr., 1 male (USNM).

Acknowledgments

I acknowledge the help of Dr. Oliver S. Flint, Jr. for his aid in the revision of the manuscript, and Dr. P. J. Spangler for the facilities used in the elaboration of the manuscript.

Literature Cited

Banks, N. 1907. New Trichoptera and Psocidae.—Journal of the New York Entomological Society 15:162–166.

Denning, D. G., and Blickle, R. L. 1972. A review of the genus *Ochrotrichia* (Trichoptera: Hydroptilidae).—Annals of the Entomological Society of America 65:141–151.

Flint, O. S., Jr. 1968. The Caddisflies of Jamaica (Trichoptera).—Bulletin of the Institute of Jamaica, Science Series 19:1–68.

———. 1972. Studies of Neotropical Caddis Flies, XIII: The Genus *Ochrotrichia* from Mexico and Central America (Trichoptera: Hydroptilidae).—Smithsonian Contributions to Zoology 118: 1–28.

Marshall, J. E. 1979. A Revision of the genera of the Hydroptilidae (Trichoptera).—Bulletin of the British Museum (Natural History), Entomological Series 39(3):1–239.

Ross, H. H. 1938. Lectotypes of North American Caddis Flies in the Museum of Comparative Zoology.—Psyche 45:1–61.

Instituto de Biologia, U.N.A.M., Apartado Postal 70-153, Mexico 04510, D.F.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 84–88

STREPTOSPINIGERA HETEROSETA, A NEW GENUS AND SPECIES OF EUSYLLINAE (POLYCHAETA: SYLLIDAE) FROM THE WESTERN SHELF OF FLORIDA

Jerry D. Kudenov

Abstract.—*Streptospinigera heteroseta* is a new genus and species of Eusyllinae from the western continental shelf of Florida, in the Gulf of Mexico. Although it is most closely allied to *Streptosyllis* in having enlarged anterior setae, it also exhibits similarities to both *Astreptosyllis* and *Syllides*.

Specimens initially identified as *Streptosyllis* Webster and Benedict, 1884 (Polychaeta: Syllidae: Eusyllinae), were examined as part of a revision of this genus (Kudenov and Dorsey in preparation), and found to represent an undescribed genus and species. Both genera possess enlarged anterior setae, but, the new genus differs from *Streptosyllis* in having composite spinigers and capillariform dorsal superior simple setae. This new taxon is described herein and compared to *Streptosyllis* and the other related genera *Astreptosyllis* Kudenov and Dorsey, 1982, and *Syllides* Örsted, 1845.

Specimens were collected as part of the Bureau of Land Management's Outer Continental Self Baseline Environmental Survey in the Gulf of Mexico (Dames and Moore 1979), involving Mississippi, Alabama, and Florida (MAFLA study). Type-specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Streptospinigera, new genus

Type-species.—*Streptospinigera heteroseta* new species, by original designation.

Diagnosis.—Prostomium with 3 pairs of eyes, 3 antennae; palps fused basally, directed anteriorly and ventrally (visible from above), distally rounded, blunt. Pharynx unarmed. Proventriculus occupying up to 4 segments. Peristomium with 2 pairs of tentacular cirri, these cylindrical, smooth, slightly club-shaped. Dorsal cirri smooth, long and cylindrical to short and subulate anteriorly, abruptly becoming strongly annulate posteriorly. Ventral cirri not extending beyond parapodial lobes. Parapodia uniramous, supported by a single neuroaciculum, distally beak-shaped to truncate, anterior ones twice as thick as the rest. Notoacicula slender, spindle-shaped when present. Superior dorsal simple seta present, lacking distal hood, distally falcate, thick anteriorly, abruptly becoming slender, capillariform thereafter. Composite falcigers lacking distal hoods, thick anteriorly, abruptly becoming slender thereafter. Composite spinigers present medially and posteriorly, having slender shafts and prolonged blades. Inferior ventral simple seta absent. Pygidium terminal, with 1 midventral and 2 dorsolateral anal cirri.

Remarks.—*Streptospinigera* is clearly most closely allied to *Streptosyllis* in having enlarged acicula accompanied by enlarged superior dorsal simple setae and composite falcigers in anterior-most setigers. *Streptospinigera* differs from

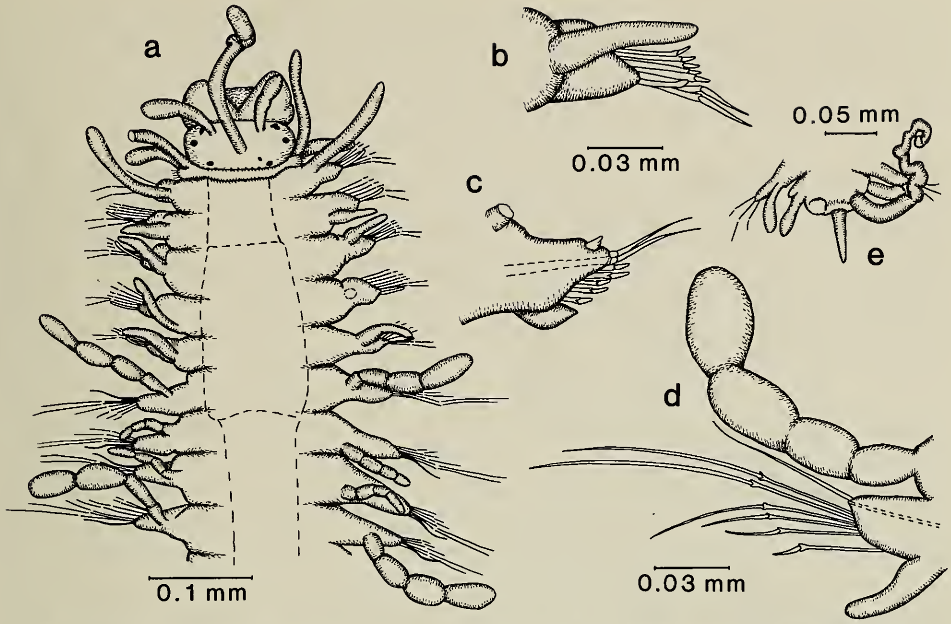


Fig. 1. *Streptospinigera heteroseta*: a, b, d, e Holotype: a, Anterior end, dorsal view, pharynx partly extended; b, Right parapodium from setiger 3, dorsal view; c, Paratype: Left parapodium from setiger 3, view of anterior facing surface; d, Right parapodium from setiger 18, view of anterior facing surface; e, Pygidium, dorsal view.

Streptosyllis in having both composite spinigers and capillariform dorsal simple setae, and in lacking prolonged ventral cirri and distal hoods on all setae. *Streptospinigera* is also somewhat similar to *Astreptosyllis* in that both have enlarged composite falcigers in anterior setigers. *Astreptosyllis* differs from *Streptospinigera* in lacking both enlarged acicula and dorsal simple setae, in lacking composite spinigers, and in having prolonged ventral cirri. *Streptospinigera* is less similar to *Syllides* in that the latter lacks enlarged setae and composite spinigers. However, *Syllides* and *Streptospinigera* have both falcate and capillariform dorsal simple setae, and lack prolonged ventral cirri and setal hoods. Only the type-species, described below, is known.

Etymology.—The generic name derives from the Greek, *streptos,* meaning twisted, the Latin, *spinatus,* meaning with spines, and the Latin, *gero,* meaning to bear. Gender: feminine.

Streptospinigera heteroseta, new species
Figs. 1, 2

Material examined.—FLORIDA, GULF OF MEXICO: off Tampa, MAFLA 2207E, 27°57′00.4″N, 83°09′00.3″W, fine to very fine sand, 19 m, coll. Dames and Moore for BLM, Aug 1977; holotype (USNM 74489). Station 151, Florida Middle Ground-II, dredge, 7 Nov 1978; paratype (USNM 74490).

Description.—A small species, measuring at least 1 mm long, 0.05 mm wide without parapodia for 23 setigers (holotype). Paratype incomplete, measuring 1 mm long, 0.08 mm wide without parapodia for 14 setigers. Body generally lacking

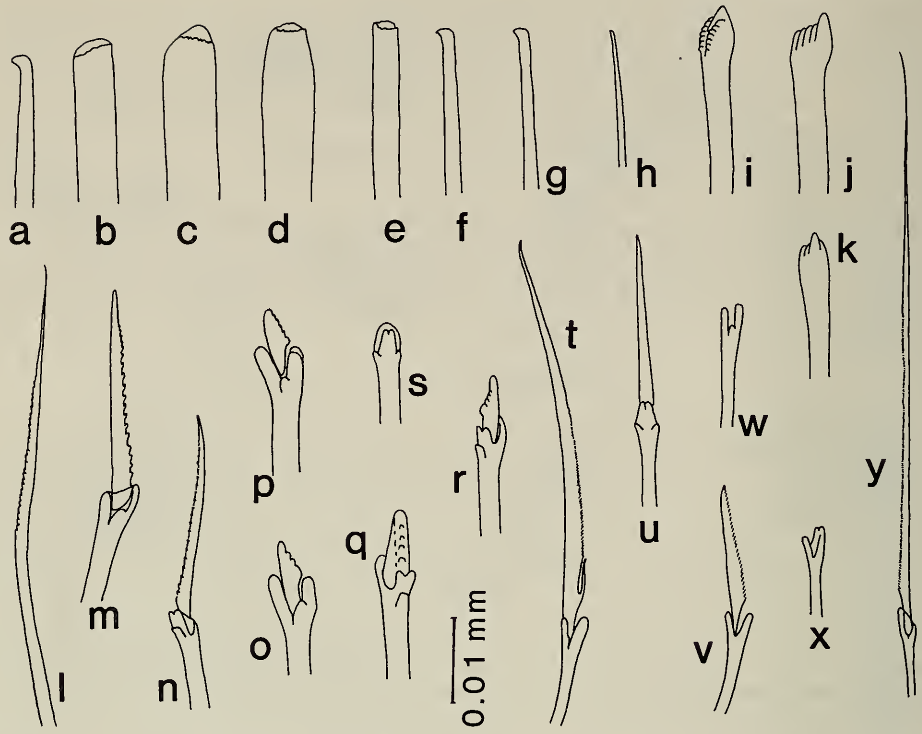


Fig. 2. *Steptospinigera heteroseta*: a–g, j–y Holotype; h–i, Paratype: a, Aciculum, setiger 1, dorsal view; b, Same, setiger 2, dorsal view; c, Same, setiger 3, dorsal view; d, Same, setiger 4, dorsal view; e, Same, setiger 5, dorsal view; f, Same, setiger 6, dorsal view; g, Same, setiger 17, dorsal view; h, Notaciculum, setiger 7, dorsal view; i, Dorsal superior simple seta, setiger 3, ventrolateral view; j, Same, setiger 3, lateral view; k, Same, setiger 3, ventral view; l, Capillariform dorsal superior simple seta, setiger 7, lateral view; m, Enlarged long bladed composite falciger, setiger 3, lateral view of anterior facing surface; n, Same, dorsolateral view of posterior facing surface; o, Enlarged short bladed composite falciger, setiger 3, lateral view of anterior surface; p, Same, setiger 3; q, Same, setiger 4, dorsolateral view of anterior surface; r, Same, setiger 4, dorsolateral view of posterior surface; s, Shaft tip of enlarged, short bladed falciger, setiger 3, dorsal view; t, Slender, long bladed falciger, setiger 9, lateral view of anterior surface; u, Same, setiger 9, dorsal view; v, Same, setiger 9, lateral view of anterior surface; w, Shaft tip of slender composite falciger, lateral view of anterior surface; x, Same, ventrolateral view of anterior surface; y, Composite spiniger, setiger 9, lateral view, posterior surface.

pigmentation in alcohol; articles of annulated dorsal cirri each with dense brown pigment granules; with ciliary patches on prostomium, dorsal ceratophores and pygidium, and on raised, paired epaulettes on peristomium (Fig. 1a).

Prostomium wider than long, with 3 pairs of eyes (right posterior eye as 2 separate spots in holotype), all in hexagonal arrangement (Fig. 1a). Antennae smooth, slightly club-shaped distally; lateral antennae inserted between anterior pigment-patches (Fig. 1a); median antenna long, inserted between last 2 pairs of eyes (Fig. 1a). Palps large, directed anteriorly and ventrally, laterally incised, lacking palpal cirri. Pharynx partly extended in holotype, unarmed, extending through setiger 2 (Fig. 1a); number, shape of terminal papillae unknown. Proventriculus barrel-shaped, with around 30 rows of muscle points, extending from setiger 3 through 6 (Fig. 1a). Peristomium a complete ring dorsally and laterally, with 2 pairs of tentacular cirri, these smooth, slightly club-shaped distally (Fig. 1a); with paired, mound-shaped epaulettes, these ciliated, located above each dorsal tentacular cirrus (Fig. 1a).

Anterior most parapodia distally truncate (Fig. 1b, c), becoming elongate, conical posteriorly (Fig. 1d). Dorsal cirri of setiger 1 long, resembling antennae and tentacular cirri (Fig. 1a); those of setigers 2–5 short, smooth, subulate to cylindrical, extending beyond parapodial lobes but not setal fascicles (Fig. 1a); those from setiger 6 to end of body each with 4 articles, alternating in length as follows: those of setigers 6, 9, 11, 13, 16, 18 all long and well developed (Fig. 1a, d) while all others from setiger 7 short (Fig. 1a). Ventral cirri smooth throughout, being inflated in setigers 1–3 (Fig. 1c), subulate thereafter (Fig. 1d).

Neuroacicula of setigers 2–5 (or 6 in paratype) thick-shafted, distally truncate (Fig. 2b–e); those from setigers 1, 6–7 to end of body slender, distally beak-shaped (Fig. 2a, f, g). Notoaciculum accompanied by tufts of smooth capillaries (Fig. 2h) present from setiger 7 to end of body in paratype. Superior dorsal simple seta present in all setigers; those of setigers 1–5 enlarged, distally conical with a ventral subterminal notch and paired, lateral serrated ridges (Fig. 2i–k); those from setiger 6 to end of body slightly bent, slender setae with transversely serrated ventral cutting surfaces (Fig. 2l).

Setigers 1–5 each with 8–10 thick-shafted composite falcigers including 2–3 having long and 6–7 having short unidentate blades (Fig. 2m–r), all with saw-tooth cutting margins, lacking distal hoods and sheaths; shaft tips with dorsal superior branch terminating in an incised lobe (Fig. 2s) with either paired subdistal denticles (Fig. 2p, s) or an unpaired median flap (Fig. 2n, q, r); with ventral inferior branch entire, rounded (Fig. 2s); shaft tips of long bladed falcigers sometimes forming clear, cup-shaped sockets for blade. (Fig. 2m, n)

Setigers 6 to end of body each with 7–10 slender composite setae per fascicle including 2–3 superior spinigers each having long, minutely serrated blades (Fig. 2y) and 5–7 falcigers having unidentate blades with finely serrated cutting margins (Fig. 2t–v), sometimes with pronounced basal spurs (Fig. 2t), all becoming shorter ventrally within a fascicle; shaft tips similar to those of setigers 1–5 except dorsal superior branch inconspicuously incised (Fig. 2w, x), generally smooth, lacking subterminal denticles.

Pygidium short, equalling length of last 2 prepygidial segments, with anal cirri including 1 short midventral and 2 long dorsolateral cirri (left one missing, scar conspicuous); all smooth (Fig. 1e).

Remarks.—*Streptospinigera heteroseta* differs from all known species of *Streptosyllis* in having composite spinigers and two kinds of superior dorsal simple setae. It is most closely related to the *Streptosyllis websteri–S. bidentata–S. cryptopalpa* species subgroup in that compound setae of anterior fascicles have both long and short appendages. *Streptospinigera heteroseta* differs from the species of this subgroup in having anteriorly, rather than ventrally, directed palps. *Streptosyllis latipalpa* is similar to *Streptospinigera heteroseta* in having similarly oriented palps. However, *Streptosyllis latipalpa* has only short-bladed composite setae in anterior fascicles.

Etymology.—The specific name, *heteroseta,* derives from the Greek, *heteros,* meaning different, and the Latin, *seta,* meaning bristles; it is used as a noun in apposition.

Acknowledgments

I am indebted to J. M. Uebelacker and P. G. Johnson of Barry A. Vittor and Associates, Mobile, Alabama, for allowing me to examine these syllids. I am also grateful to K. Fauchald, National Museum of Natural History, for critically commenting on this paper, and to S. J. Williams, Allan Hancock Foundation, for providing technical assistance.

Literature Cited

Dames, T., and W. Moore. 1979. Final report—The Mississippi, Alabama, Florida, Outer Continental Shelf Baseline Environmental Survey MAFLA 1977/1978, Vols. I-A,B, for the U.S. Bureau of Land Management, Washington, D.C. NTIS PB-294 288. New Orleans, Louisiana.

Kudenov, J. D., and J. H. Dorsey. 1982. *Astreptosyllis acrassiseta,* a new genus and species of the subfamily Eusyllinae (Polychaeta: Syllidae) from Australia.—Proceedings of the Biological Society of Washington 95:575–578.

———. A revision of the genus *Streptosyllis* (Polychaeta: Syllidae: Eusyllinae).—Proceedings of the Biological Society of Washington. In preparation.

Örsted, A. S. 1845. Fortegnelse over Dyr, samlede i Christianiafjord ved Drøbak fra 21–24 July 1844.—Naturhistorisk Tidssrkrift København Series 2, 1:400–427.

Webster, H. E., and J. E. Benedict. 1884. The Annelida Chaetopoda from Provincetown and Wellfleet, Mass.—Annual Report of the Commissioner for Fish and Fisheries for 1881:699–747, 8 pls.

Department of Biological Sciences, University of Alaska, Anchorage, 3221 Providence Drive, Anchorage, Alaska 99508.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 89–102

THE IDENTITY OF *PETROLISTHES MARGINATUS* STIMPSON, 1859, AND THE DESCRIPTION OF *PETROLISTHES DISSIMULATUS,* N. SP. (CRUSTACEA: DECAPODA: PORCELLANIDAE)

Robert H. Gore

Abstract.—Petrolisthes marginatus, briefly described by Stimpson, but erroneously illustrated as such by Benedict, is shown to be a composite of three nominal species, *Petrolisthes marginatus* s. s., *Petrolisthes cessacii* (A. Milne Edwards) a junior subjective synonym, and an undescribed species (*P. marginatus* sensu Benedict). The latter form is described and illustrated as *Petrolisthes dissimulatus.*

Petrolisthes marginatus Stimpson, 1859, is a member of a genus of cryptic, often fast-moving porcellanid crabs that inhabit crevices and interstices in reefs and other hard, more or less permanent substrata. Stimpson briefly described but did not illustrate *P. marginatus,* using a single specimen collected at Barbados by a Mr. Gill. Stimpson's original specimen was presumably destroyed in the Great Chicago Fire (see Evans 1967), and apparently no syntypic material was deposited by Stimpson in any other museums.

Petrolisthes marginatus was nevertheless considered to be well-characterized, based on a combination of Stimpson's brief original description, plus a subsequent illustration asserted to be this species by Benedict (1901). The species is tropical, but not very common, being recorded from Fernando de Noronha (Pocock 1890), the Caribbean Sea (Young 1900), a few other localities in the western Atlantic (Haig 1956), and eventually but erroneously from several areas in the tropical eastern Pacific (Haig 1960). Specimens from the latter region were re-examined by Chace (1962) and placed in a new species, *Petrolisthes haigae,* which became the trans-Panamanian geminate form of *P. marginatus* sensu Stimpson (see below).

Benedict's (1901) illustration that he attributed to *P. marginatus* was that of a porcellanid collected at Ponce, Puerto Rico. Although his perfunctory description added little to Stimpson's sparse characterization, the accompanying figure was more detailed, and showed a small crab with quadridentate cheliped meri, lacking walking legs, and bearing two small clearly visible epibranchial spines. These spines had not been mentioned by Stimpson in his original description, but later authors (e.g. Schmitt 1924a, b, 1935; Chace 1956, 1962; Gore 1974) followed Benedict's lead and used them as criteria in identifying, or distinguishing between *P. marginatus* sensu Benedict, and other closely related but single-spined congeners such as *Petrolisthes amoenus* (Guérin, 1855), *Petrolisthes haigae* Chace, 1962, or *Petrolisthes cessacii* (A. Milne Edwards, 1878).

Petrolisthes cessacii has long been considered to be closely related to *Petrolisthes marginatus.* The original description of the former by A. Milne Edwards, as *Porcellana Cessacii,* was also without an illustration and characterized a crab attaining a relatively large size (17 × 16 mm, cl × cw), possessing a strongly advanced frontal region produced into a point ("affecte la forme d'un bec"), a cheliped carpus having three or four denticulations on its anterior margin and a large spine terminating its posterior margin. There was no mention of any epibranchial spination, and the remaining characters in the description could easily have been applied to any of several species of porcellanid crabs known at that time. For the purposes of this paper, however, the large size, advanced front, tri- or quadridentate cheliped carpus with a strong posterior spine provide evidence of similarity with *Petrolisthes marginatus* Stimpson (see below).

Balss (1914) provided a brief figure of *P. cessacii,* but Chace's (1956) illustration of the species was by far the most detailed. Literature records from Chace's study suggested that *P. cessacii* was a rather common porcellanid crab, apparently restricted to the tropical-subtropical eastern Atlantic Ocean. However, Gore (1974) noted a range extension for the species to the western Caribbean Sea, and in the same study placed Pocock's (1890) specimens of *P. marginatus* from Fernando de Noronha, Brazil, into synonymy with *P. cessacii.* Gore considered Fernando de Noronha as the first, albeit "misidentified," western Atlantic record for Milne Edwards' species. This action followed Coelho (1970) who previously had listed *P. cessacii* from the coast of Brazil without further comment. As a comparison of the illustrations provided by Chace and by Gore shows, the western African and western Caribbean forms are quite similar.

Most recently, R. B. Manning and F. A. Chace (in prep.) identified some specimens of porcellanid crabs collected from Ascension Island in the South Central Atlantic as *P. marginatus.* A comparison of this material with specimens of *P. cessacii* convinced them (in litt.) that *Petrolisthes cessacii* (A. Milne Edwards, 1878) was a junior synonym of *Petrolisthes marginatus* Stimpson, 1859. This being so, specimens identified as *P. cessacii* from Brazil (Coelho 1970; Coelho and Araujo Ramos 1972), Colombia (Werding 1977), the western Caribbean Sea (Gore 1974), and the coast of Mexico (Rickner 1975) were probably *P. marginatus* as well. What was more important, however, was that the specimen reported and illustrated by Benedict (1901) as *P. marginatus,* and perpetuated as such by subsequent authors, was now seen to differ substantially from Stimpson's description of the species, and because it was misidentified it would require a name.

Manning and Chace's conclusions were briefly incorporated in a report on Central American Porcellanidae by Gore (1982), in which the first occurrence of *P. marginatus* on the Caribbean coast of Panama was noted. In the present report, I provide a revised synonymy for *Petrolisthes marginatus* Stimpson, expand Stimpson's original description by including Chace's (1956) diagnosis for *P. cessacii,* and give a detailed description and illustration for the new species previously misidentified by Benedict.

In the taxonomic treatment that follows, carapace length (cl) precedes carapace width (cw) measured in mm across the longest or widest parts of the cephalothorax. Paratypic material of the new species from Colombia, part of the personal collection of Dr. Bernd Werding, was returned to him; the remaining paratypic and holotypic material has been returned to the National Museum of Natural History, Washington, D.C. Repository abbreviations follow the appropriate material and are explained in the Acknowledgment section.

Petrolisthes marginatus Stimpson, 1859
Fig. 1

Petrolisthes marginatus Stimpson, 1858:227 [nomen nudum]; 1859:74 [p. 28 on separate].—Pocock, 1890:513.—Young, 1900:394.—Haig, 1956:26 [in part, including color notes and reference to Buccoo Reef specimen]; 1962:176 [in part, 1 ♀, "Danish West Indies"; not Virgin Islands specimens].—Gore, 1982:17. Not Nobili, 1897:4 [=*Petrolisthes armatus* (Gibbes, 1850), *fide* Nobili, 1901: 12].

Porcellana Cessacii A. Milne-Edwards, 1878:229 [p. 10 on separate].

Petrolisthes Cessaci.—A. Milne Edwards and Bouvier, 1900:346.

Petrolisthes cessaci.—Balss, 1914:101, fig. 6.—Lebour, 1959:128, 136, fig. 10 [megalopa, identification by implication].[1]—Gauld, 1960:64.

Petrolisthes Cecoci.—Balss, 1914:100 [erroneous spelling, legend, fig. 6].

Petrolisthes cessacii.—Sourie, 1954:84, 112, 236, 239, 253, 256, 294, 295, 304.—Chace, 1956:14, fig. 4A–E.—Holthuis and Manning, 1970:242 [discussion], 243.—Coelho, 1970:233 [listed].—Coelho and Araujo Ramos, 1972:173.—Gore, 1974: 710, fig. 4; 1982:17 [discussion].—Rickner, 1975:163.—Werding, 1977:176, 197, 199, fig. 19.

Petrolisthes armatus.—Miers, 1881:432.—Balss, 1922:108 [listed].—Haig, 1962: 178 [discussion].—Coelho, 1966:55 [references to Pocock and Nobili].—Fausto-Filho, 1974:8. Not *Petrolisthes armatus* (Gibbes, 1850).

Material.—MEXICO: Vera Cruz, Isla de Lobos; coral reef; 8 June 1973; coll. J. A. Rickner 1 ♂; AHF 1974–9.—PANAMA (Atlantic): Golfo de San Blas, Pico Feo; *Thalassia* flat; 0–1 m; 7 Apr 1973; coll. Newman and party; 1 ♂, 1 ♀ ovigerous; USNM 292580.—OLD PROVIDENCE ISLAND; 13°31.55′N, 81°20.55′W; 0–1 m; 30 Jan 1972; R/V *John Elliott Pillsbury,* sta P-1350; 1 ♂, 1 ♀ ovigerous; IRCZM 89:3741.—Same station; 3 ♂♂, 1 ♀; UMML 32:5515.—Same station; 3 ♀♀ ovigerous; RMNH 30407.—Same locality; low cay; boulders; 0–1 m; 14 Dec 1980; coll. B. Werding; 1 juvenile; personal collection.—COLOMBIA: Santa Marta, Aguja; Playa Brava; under stones; 1.5 m; Dec 1978; coll. B. Werding; 2 ♂♂, 2 ♀♀ ovigerous; personal collection.—Same area; Morro Grande; intertidal, under stones; May 1980; coll. B. Werding; 3 ♂♂, 9 ♀♀ (7 ovigerous); personal collection.—Same area; Burrucuca; intertidal, among stones; 12 Jul 1976; coll. B. Werding; 1 ♂, 1 ♀; personal collection.—Same locality; shore; Nov 1976; coll. B. Werding; 1 ♂; AHF 726-01.—Same area; Punta de Betin; intertidal, among stones; Nov 1976; B. coll. Werding; 1 ♂; personal collection.—Same area; Tagange; intertidal; Feb 1976; coll. B. Werding; 1 ♂; personal collection.—Same area; Islas Rosario; May 1977; coll. B. Werding; 1 ♂; personal collection.—CURACAO: southwest coast, west of Willemstad; under stones on shore; Jan–Feb 1957; coll. B. van Bergeyk; 1 ♀ ovigerous; LBH 1151.—Same; Fuik Bay;

---

[1] The megalopa Lebour attributed to *Petrolisthes cessacii* may not belong to this species, because the figure she provided shows no epibranchial spines. Megalopae of other *Petrolisthes* species that I have examined invariably exhibit such spines if they occur in the species in the adult stage. The megalopa illustrated by Lebour could therefore be one of several species of *Petrolisthes* which occur on, or in the vicinity of, the west African coast. On the possibility that Lebour overlooked the postlarval epibranchial spines, and without evidence attributing this megalopa to another species, I will provisionally maintain Lebour's identification within the synonymy of *P. marginatus*.

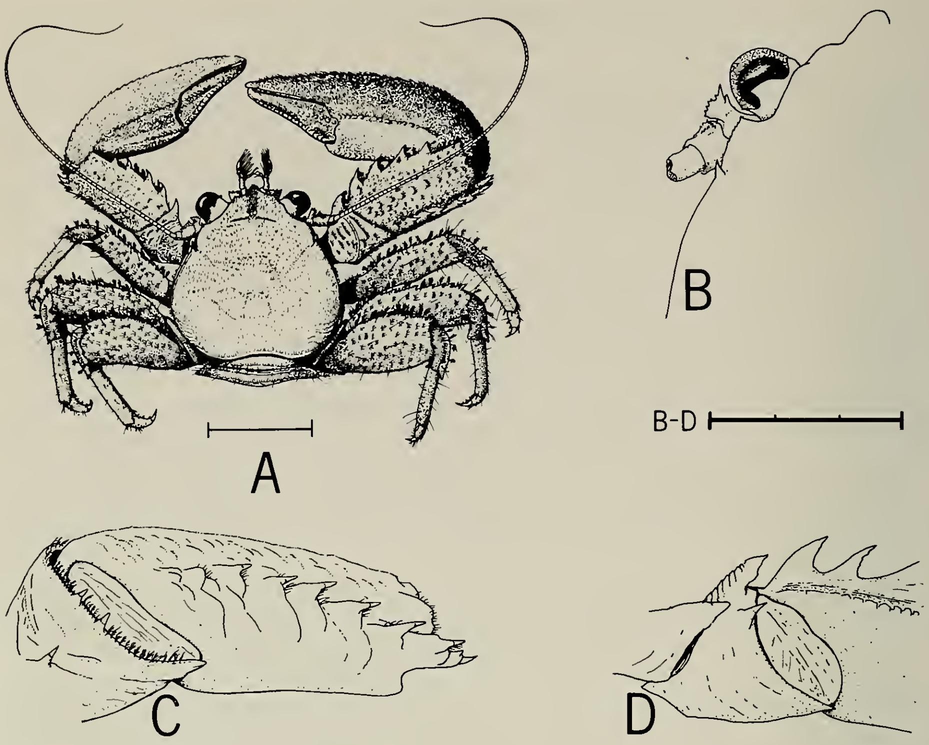


Fig. 1. *Petrolisthes marginatus.* A, Male, R/V *John Elliot Pillsbury,* Sta. P-1350, Old Providence Island, UMML 32:5515; B, Epibranchial and lateral margin of carapace, showing spination; C, Right cheliped, posteroventral view of marginal spines; D, Left cheliped, mesioventral view, note single meral spine. Scale A = 5 mm; B–D = 3 mm.

NW landing; intertidal, among stones; 0–1 m; 13 Jan 1957; coll. L. B. Holthuis; 1 ♀ crushed; LBH Nr 1051.—KLEIN BONAIRE: Old landing by Bonaire; coral debris on shore; 0–1 m; 17 Oct and 8 Nov 1930; coll. P. W. Hummelinck; 1 ♂, 1 ♀ crushed; PWH 1049a.—Same locality; east coast by landing place; rock, sand, tidal zone; 13 Sep 1948; coll. P. W. Hummelinck; 2 ♂♂, 1 ♀ ovigerous, 1 juvenile; PWH 1049a.—"DANISH WEST INDIES": 15 Dec 1911; col.? C. Meng; 1 ♀; no other data; UZMC collection.—VIRGIN ISLANDS: St. John, Europa Bay; Feb 1959; coll. Randall and Kumpf; 1 ♂, 1 ♀ ovigerous; UMML 32:1595.—SABA, NETHERLANDS ANTILLES: E. Fort Bay; rocks, tidal zone and lower; 21 Jul 1949; coll. P. W. Hummelinck; 1 ♀ ovigerous; RMNH 8458.—AVES (Islote Aves): W of Dominica; N reef, rocks, tidal zone; 12 May 1949; coll. P. W. Hummelinck; 1 ♀; RMNH 8456.—TRINIDAD: Maracas Bay; southwest corner; intertidal; 18 Jul 1968; R/V *John Elliott Pillsbury,* sta P-701; 1 ♀ ovigerous; UMML 32:5481.—TOBAGO (British West Indies): Buccoo Reef; shore; 20 Apr 1939; *Velero III,* Hancock Expedition; 1 ♂; A41-39.—BRAZIL: Fernando (de) Noronha; coll. H. M. Ridley; no other data; 3 ♂♂; BMNH 1888.19.—WEST AFRICA: Senegal; Pointe des Almadies; 30 Jul 1973; 1 ♂, 1 ♀ ovigerous; MNHN

Ga 551.—Same; Gulf of Guinea; Fernando Poo; 3°45′N, 8°48′E; R/V *John Elliott Pillsbury,* sta P-258 shore; 15 May 1965; 2 ♂♂, 3 ♀♀; RMNH 23976.—Same; Annobon; 1°25′S, 5°38′E; R/V *John Elliott Pillsbury,* sta 271, shore; 19 May 1965; 7 ♂♂, 3 ♀♀ (2 ovigerous); RMNH 23975.

Diagnosis.—Carapace about as wide as long, covered with short pubescence, usually distinct, occasionally almost invisible, smooth except for few faint rugae posterolaterally; single sharp or blunt epibranchial spine, rarely with nub of second immediately behind. Front with prominent median lobe, projecting well beyond lateral lobes, latter nearly transverse, orbital margins oblique. Merus of chelipeds armed anteroventrally with single, usually acute spine; carpus with 3–5, usually 4, minutely serrate, spine-tipped, nearly equal-sized teeth; posterior margin with 2–6 oblique rugae produced apically into spines, strong, hooked, bifid spine at posterodistal angle. Chelae pubescent, bearing distinct granular ridge from dactylar to chelar bases, separating flattened upper part of manus from slanting outer part. Walking legs spinulous on anterior margins of meri, numbers ranging from 4–8, posterodistal angles produced into 1 or 2 teeth on legs 1 and 2, unarmed on walking leg 3. (Modified from Chace 1956:15.)

Distribution.—Western Africa from Cape Verde Islands to Annobon, on the mainland from Senegal to Ghana; Ascension Island, South Central Atlantic Ocean; Fernando de Noronha and São Luiz, Brazil, north to Trinidad, Tobago Island, vicinity of Santa Marta, Colombia, Curaçao, Bonaire, Old Providence Island, Panama, Mexico, and the northern Leeward Islands. In the littoral and shallow sublittoral to about 2 m.

Remarks.—With the placing of *Petrolisthes cessacii* into synonymy, *Petrolisthes marginatus* becomes another of a small group of essentially tropical porcellanid crabs in the genus *Petrolisthes* having amphi-oceanic or amphi-continental distribution. In addition to *P. marginatus,* now known from western Africa, Ascension Island, eastern South America and the Caribbean Sea, the group includes *Petrolisthes armatus* (Gibbes, 1850) from western Africa, eastern tropical North, Central and South America, and the tropical eastern Pacific; *Petrolisthes galathinus* (Bosc, 1802) from warm-temperate and tropical eastern North America, tropical Central and South America and the eastern Pacific; *Petrolisthes tonsorius* Haig, 1960 from the southwestern Caribbean Sea and tropical eastern Pacific; and *Petrolisthes tridentatus* Stimpson, 1859, from the Caribbean Sea, and tropical eastern South America and eastern Pacific. These species have presumably been able to cross oceanic or isthmian barriers either by dispersal or by vicariance events. The geographically separated populations at least have not undergone speciation recognizable through presently employed morphological criteria. At least 14 other species of *Petrolisthes* have extensive tropical distributions encompassing the western Indian Ocean and to either Japan or to Samoa or Hawaii in the Pacific Ocean (Haig 1964, 1974, in litt.).

The relegation of *P. cessacii* into junior synonymy with *P. marginatus* appears to be justified at present based on morphology. Whether the eastern and western Atlantic populations are reproductively isolated or will remain so, given the potential for long distance larval dispersal, remains uncertain. It would be extremely interesting, for example, to see if differences in larval morphology are exhibited among the African, Ascension Island, and western Atlantic populations.

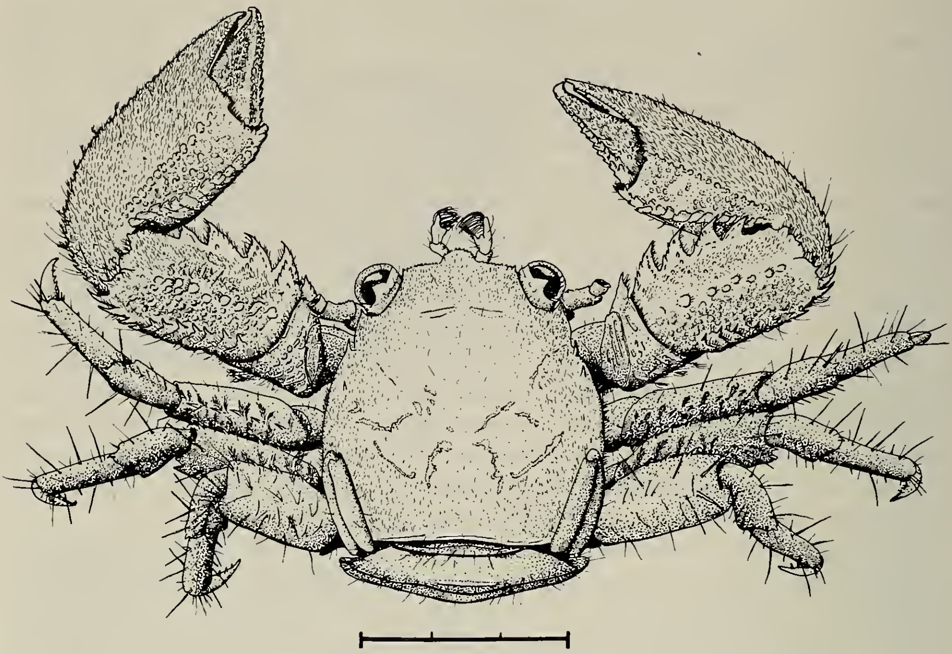


Fig. 2. *Petrolisthes dissimulatus*, holotype, ovigerous female, St. John, Virgin Islands, USNM 190893. Scale line = 3 mm.

Petrolisthes dissimulatus, new species
Figs. 2, 3, 4

Petrolisthes marginatus.—Benedict, 1901:134, pl. 3, fig. 1.—Schmitt, 1924a:73; 1924b:88; 1935:185, 187.—Boschma, 1931:374.—Chace, 1956: 24 [discussion]; 1962:622 [discussion].—Haig, 1956:17, 26 (in part, Curaçao specimen only); 1962:176 (in part, except 1 ♀, "Danish West Indies").—Gore, 1974:711 [discussion]. Not *P. marginatus* Stimpson, 1859.

Holotype.—1 ♀, ovigerous; St. John, Virgin Islands, coral reef of lagoon point, west side of bay; 6 Apr 1937; W. L. Schmitt; USNM 190893.

Paratypes.—2 ♂♂, same data as holotype; USNM 190894.—PUERTO RICO: Playa de Ponce; 1899; USFC Steamer *Fish Hawk*; J. E. Benedict; 1 ♀; USNM 42351.—VIRGIN ISLANDS: St. Thomas; 10 Nov 1917?; no other data; UZMC collection.—"DANISH WEST INDIES": 15 Dec 1911; C. Meng; 3 ♂♂, 2 ♀♀ (1 ovigerous); no other data; UZMC collection.—BARBADOS (Univ. Iowa Barbados-Antigua Exped.): 15 May 1918; W. L. Schmitt; 1 ♂, 2 ♀♀ ovigerous; USNM 57971.—Same; from coral head; 4 Jun 1918; W. L. Schmitt; 1 ♂; USNM 57972.—Same; Okra Reef; 13 May 1918; W. L. Schmitt; 1 ♂, 2 ♀♀ ovigerous, 1 cheliped; USNM 68648.—Same; 15 May 1918; W. L. Schmitt; 4 ♂♂, 1 ♀ ovigerous; USNM 68649.—Same; coral heads; 4 Jun 1918; W. L. Schmitt; 1 ♀; USNM 68650.—Same; old coral; 31 May 1918; W. L. Schmitt; 1 ♂, 2 ♀♀ ovigerous; USNM 68651.—CURAÇAO: Santa Marta Bay, by St. Nicolaas; coral blocks, open sea shore; 4 Feb 1957; coll. L. B. Holthuis; 1 ♂; LBH nr. 1083.—

Same; Piscadera Bay; sand and muddy sand with stones, algae, sponges, etc.; 0–1.5 m; 12 Nov and Dec 1956; coll. L. B. Holthuis; 1 ♂, 2 ♀♀ (1 ovigerous); LBH nr. 1002.—Same; Willemstad; strand of Marie Pompoen; among stones; 26 Dec 1956; coll. L. B. Holthuis; 3 ♂♂; LBH nr. 1028.—Same; Fuik Bay; NW landing; among stones; 0–1 m; 13 Jan 1957; coll. L. B. Holthuis; 6 ♂♂, 3 ♀♀; LBH nr. 1051.—Same; Vista Alegre; shore; 23 Apr 1939; "Velero III" Hancock Expedition; 1 ♀ ovigerous; USNM 98105 [A46-39].—COLOMBIA: Santa Marta; Aguja, Playa Brava; under stones; 1.5 m; Dec 1978; coll. B. Werding; 1 ♂, 1 ♀; personal collection.—Same; Islas Rosario; May 1977; coll. B. Werding; 1 ♂, 3 ♀♀ (2 ovigerous); personal collection.

Measurements.—Holotype, 4.1 × 4.0 mm; paratype males, 1.8 × 1.8 to 6.5 × 5.9 mm; paratype females, 3.1 × 3.0 to 5.8 × 5.4 mm; ovigerous females, 3.9 × 3.6 to 5.7 × 5.6 mm.

Diagnosis.—Carapace rounded, smooth, pubescent; frontal region produced, trilobate, truncate anteriorly, prominent rounded denticulate median lobe, lateral lobes rectangularly rounded, serrated; orbital margin nearly normal to plane of lateral lobe; 2 epibranchial spines; manus broad, flattened, distinct longitudinal row of low tubercles extending along outer surface from dactylar to chela bases; merus with 2 sharp spines on anteroventral margin; carpus less than twice as long as wide, anterior margin with 4 serrated teeth having curved needlelike tips, posterior margin distal extension a single curved spine; walking legs spinulous on anterior margins of meri, posterodistal angles of legs 1 and 2 produced into sharp tooth, that of leg 3 unarmed.

Description.—Cephalothorax subcircular to slightly rectangular, longer than broad, flattened posteriorly, smooth, covered with fine pubescence predominantly on frontal, and anterior and posterior branchial areas; frontal region produced, trilobate, lateral lobes rectangularly rounded, minutely dentate especially at inner orbital angle, anterior margins nearly transverse, front thus appearing truncate; prominent, rounded, slightly deflexed, denticulate, median lobe, subequal to lateral lobes, shallow, median sulcus extending posteriorly to paired, slightly elevated protogastric lobes; orbital margin nearly straight, strongly concave posteriorly, forming parabolic arc, mesial and posterior margins appearing as rounded right angle; no supraocular spines or spinules, but minute denticles often present; outer orbital angle a sharp spine directed obliquely outward, followed by small serrations decreasing in size posteriorly; epibranchial angle with single large curved acute spine above, a second, often less acute, occasionally only a nub, immediately behind; remainder of carapace unarmed; lateral margins from epibranchial angle to posterior branchial region bearing thin ridge forming general dorsal outline of cephalothorax.

First movable antennal article with large, lamellar projection bearing several smaller teeth leading to strong single, or bifid, spine at tip, second with longitudinal row of small acute conical denticles or tubercles, third smooth, rounded; flagellar articles lightly setose.

Third maxilliped ischium exhibiting several raised, granular, transverse ridges, these appearing more like rugae on merus; mesial triangular projection of latter with distinct spinule at apex; remaining articles lightly rugose or smooth.

Cheliped merus rough, granular, large serrated, spinelike tooth on anterior margin, followed by pair of small, curved spinules on posterodorsal margin, sec-

Fig. 3. *Petrolisthes dissimulatus,* Benedict's specimen, paratype female, Playa de Ponce, Puerto Rico; USNM 42351. Scale line = 3 mm.

ond pair (rarely 3), more closely spaced, often extremely sharp or needlelike on anteroventral margin; article pubescence sparse but produced into several long tufts on posterior margin; carpus about 1.4 × longer than wide, covered dorsally with very low, rounded granules scarcely raised from surface of article, plus isolated raised tubercles interspersed throughout, all often obscured by thick, fine pubescence; anterior margin bearing 4 strong, serrated, distinctly curved teeth which decrease in size distally, and having spinelike or needlelike tips; prominent medial longitudinal ridge formed by irregular row of large, flattened tubercles extends to medial distal margin, many of these tubercles carrying fanlike row of simple setae; posterior margin with series of 6–11 elongate, raised, ridgelike setose rugae, those proximally ending in single, thin, upright spine pointing dorsally, those more distally becoming wider, increasingly horizontal in orientation, that of distalmost extension at posterodistal angle a single, strongly curved spine; another smaller spine adjacent on posterodorsal medial lobe; manus broad, flattened, with low granules nearly obscured by fine pubescence as on carpus; longitudinal crest of enlarged, flattened tubercles on upper quarter of outer surface, extending from dactylar to carpal junctions, second row, more elongated and flattened, defining proximal upper margin, both rows forming oblique isoceles triangle; ventral margin of hand a combination of small, conical teeth or crenulate tubercles in irregular double row to tip of fixed finger; another single row defines anterior cutting edge of latter, becoming completely smooth at finger base; gape interiorly with thick tuft of pubescence; movable finger trihedral, upper margin defined by a longitudinal row of enlarged, adpressed or imbricate teeth, coupled with less distinct adjacent second row, both joining that on manus; dactylar tip curved, crossing over interiorly to similarly curved tip of fixed finger; cutting edges of both without noticeable exterior gape.

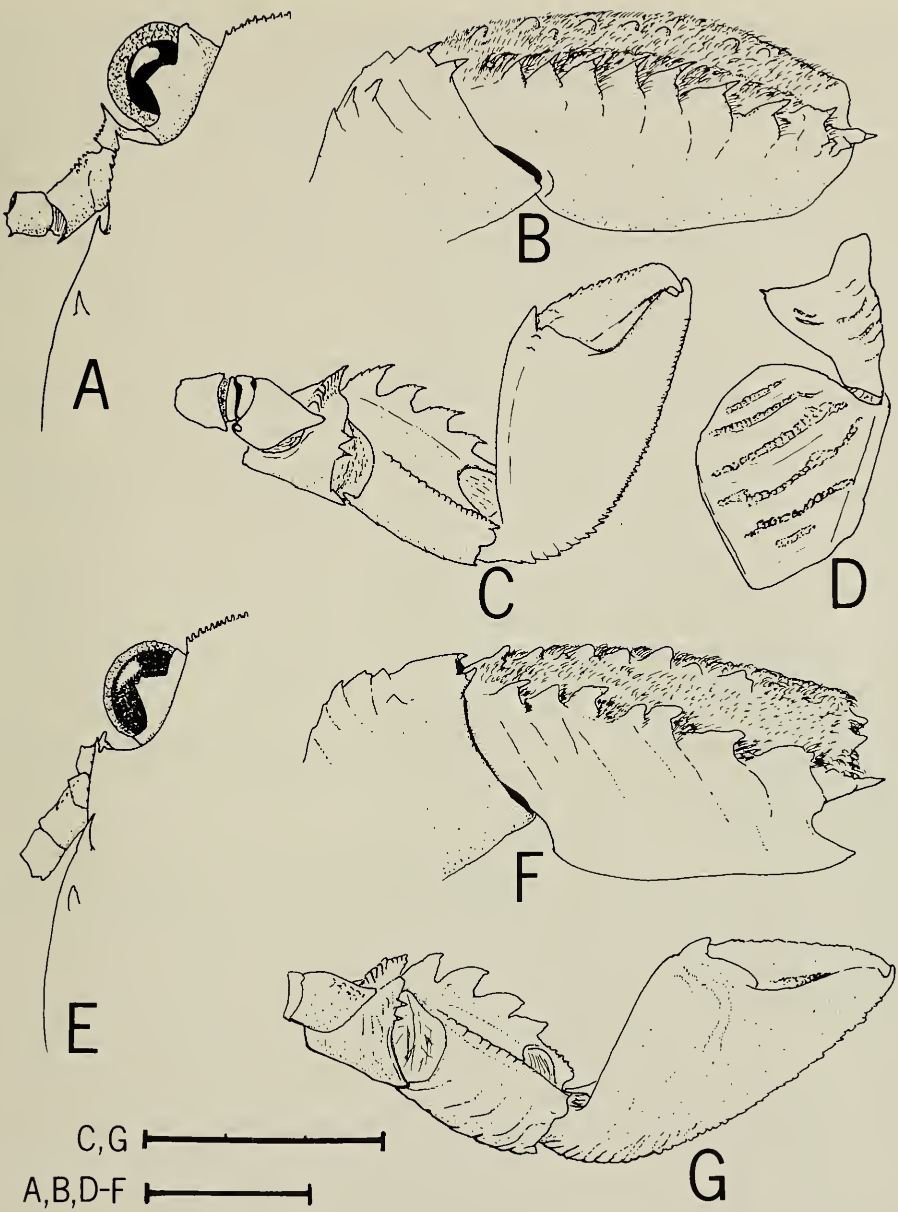


Fig. 4. *Petrolisthes dissimulatus*. A, C, D, Holotype female, USNM 190893; B, Paratype male, St. John's, Virgin Islands, USNM 190894; E–G, Benedict's specimen, paratype female, Playa de Ponce, Puerto Rico; USNM 42351. A, E, Epibranchial and lateral margin of carapace, showing spination; B, F, Right cheliped, posteroventral view of marginal spines; C, G, Left cheliped, mesioventral view; note double meral spines; D, Left maxilliped 3. Scale A, B, D, F = 1 mm; C, G, = 3 mm.

Walking legs smooth to faintly rugose; anterior margin of meri with many fine plumose hairs, these less numerous on carpus, all segments with scattered long, non-plumose setae; anterior margins of meri variably spined, that of first and second with 5–9, third with 3–4 (rarely 7) sharp, curved spinules; posterodistal angle of legs 1 and 2 produced into single, occasionally double tooth, third unarmed; distal dorsal margin of carpi with single strong tooth or spine; propodi with 2 widely-spaced ventral spines, stronger pair or triad at distoventral margin; dactyls with 3 accessory spinules nearly equal in length to each other, subequal to dactylar tip; ventral bases of all pereopods with sharp spinule posteriorly, best seen in individuals having autotomized appendages. Telson with 7 plates.

Variations.—The most consistent variation was in the sharpness of spines and spinules. On the meri and carpi of the chelipeds this ranged from distinctly curved and needlelike, to merely acute, to somewhat blunt. Signs of wear and breakage were often seen. Although the epibranchial spines were usually acute, in several instances the second and smaller spine was less sharp, often blunt, or appearing as a nub, quite difficult to discern in the surrounding pubescence. Some variation was also seen in the pilosity on the carapace and chelipeds but is probably attributable to wear and exigencies of long years of perservation.

Color.—All specimens had faded in alcohol to creamy white. According to Benedict (1901) his specimen was pink when first examined. Schmitt (1924b) stated that Barbadoan specimens in alcohol were salmon pink, marked with reddish flecks along the margins and tubercles of the chelipeds, and with red bands on the carpus and propodus of the walking legs.

Ecology.—The species has been collected from littoral and shallow sublittoral coralline rubble and rocky habitats associated with coral reefs. Ovigerous females are known only from April and May.

Distribution.—The Caribbean Sea; the Antilles from Puerto Rico, the Virgin Islands, Barbados, and Curaçao; Colombia from Santa Marta and Islas Rosario.

Relationships.—*Petrolisthes dissimulatus* exhibits some relationship to several western Atlantic or eastern Pacific porcellanids. It superficially resembles the Caribbean species *Petrolisthes amoenus* (Guérin) in general carapace shape and cheliped morphology and armature, but differs in lacking a supraocular spine and the smaller spinules on the lateral margins of the carapace seen in *P. amoenus*. *Petrolisthes amoenus* is also less pubescent, and does not exhibit the distinctive granular ridges on the upper outer quarter of the manus. The new species bears a close resemblance to what may be its eastern Pacific geminate species, *Petrolisthes hirtispinosus* Lockington, 1878. Both possess granular ridges on the manus, but *P. dissimulatus* can be easily distinguished from *P. hirtispinosus* (and *P. amoenus* as well) by the double epibranchial spines, and the truncate, nearly transverse frontal margin. The new species also shows a general resemblance to *Petrolisthes monodi* Chace, 1956, a somewhat variable species from northwestern Africa, but can be separated using the characters previously delineated for distinguishing it from New World relatives.

Etymology.—The specific epithet is Latin, meaning feigned, disguised, or hidden, and refers to the fact that the new species was confused with *P. marginatus* for so many years.

Discussion.—Five morphological characters were emphasized both in Stimpson's original description of *P. marginatus,* and in Benedict's description and illustration of what is now *P. dissimulatus*. These are 1) the shape and prominence of the frontal region, 2) the shape and size of the cheliped carpal teeth, 3) the presence of a ridge on the upper surface of the manus, 4) the color of the specimens, and 5) the overall size of the material at hand.

According to Stimpson, in *P. marginatus* the median lobe of the front is prominent, the four teeth on the anterior margin of the cheliped carpus are equal-sized and very sharp, the ridge extending from the anterior angle of the carpus to the inner base of the finger on the chelipeds is of moderate prominence, the color of the species was deep purplish-crimson, and the carapace length was "about half an inch" [ca. 12 mm].

In Benedict's description and illustration the outline of the front from the median lobe to the angle of the orbit is straight, the cheliped carpus bears four sharp marginal teeth which decrease in size distally, a granular ridge extends from the gape of the fingers to the anterior edge of the carpus, the color of the specimen was pink, and the carapace length of the illustrated specimen is approximately 4 mm, based on a listed magnification of 3½×. The female specimen of *P. dissimulatus* from Playa de Ponce (USNM 42351) is 3.9 × 3.6 mm and agrees with the figured specimen not only in general measurements, but also in carapace and cheliped morphology, even down to the damaged distalmost marginal tooth on the right cheliped, and is thus the specimen Benedict studied (see Figs. 2, 3, 4).

Although *P. dissimulatus* agrees in a very general way with Stimpson's original description of *P. marginatus,* when the two forms are placed side by side the differences are immediately seen (compare Figs. 1 and 4 herein). For example, in *P. marginatus* the median lobe of the front is always quite prominent and much narrower than that of *P. dissimulatus*. The lateral margins of the front slope more or less obliquely backward to the inner orbital angle in *P. marginatus* whereas in *P. dissimulatus* they are nearly transverse or "straight" as noted by Benedict (1901) and Schmitt (1935). The cheliped carpal teeth in *P. marginatus* are sharply pointed, equal-sized or nearly so, or diminish only gradually in size. In *P. dissimulatus* these same teeth are not only sharply pointed but may have needlelike tips which curve distally, and the teeth decrease rapidly in size. The granular ridge on the upper surface of the manus is about the same in both species, but is slightly less prominent in *P. marginatus* than *P. dissimulatus*.

Beginning with Stimpson (1859), many authors (Young 1900; Chace 1956; Haig 1956; Holthuis and Manning 1970; Gore 1974; Werding 1977) have alluded to the often striking hues of purple, crimson or Van Dyke red in *P. marginatus* (and as *P. cessacii*). Unfortunately, there are no references to color for *P. dissimulatus* other than Benedict's or Schmitt's brief notes mentioned above. At present it seems likely that *P. dissimulatus* is probably red, with banded red and white walking legs, and thus slightly different in color from *P. marginatus*.

The two species are also distinguishable in size. Recall that Stimpson's specimen was about 12 mm cl, and *P. marginatus* can grow to nearly 18 mm cl (based on a molted carapace from Isla Aves, Venezuela; Manning in litt.). Ovigerous females range from 7–12.6 mm cl in West Africa (Chace 1956; Holthuis and Manning 1970), and 9.5–17.5 mm cl in the Caribbean region (Gore 1974, unpublished data). On the other hand, *P. dissimulatus* apparently does not grow larger than about 6.5 mm cl, and ovigerous females range from 3.9–5.7 mm cl, so that the species is clearly smaller than *P. marginatus*.

Finally, *P. dissimulatus* is quickly distinguished not only from *P. marginatus,* but from all other porcellanids in the western Atlantic Ocean with the exception of *Petrolisthes rosariensis* Werding, 1977, by the presence of double epibranchial spines. In *P. marginatus* an extremely small nub of a second spine, more like an enlarged tubercle than a spine or spinule, may occasionally occur behind one epibranchial spine or the other, but this remains the exception not the rule. Moreover, *P. rosariensis* is easily separated because its chelipeds and carapace are covered with transverse piliferous rugae much as in *P. galathinus,* to which it is closely related. Neither *P. dissimulatus* nor *P. marginatus* has transverse piliferous rugae anywhere on the carapace or chelipeds.

Acknowledgments

I thank Drs. Raymond B. Manning and Fenner A. Chace, Jr., National Museum of Natural History, Washington, D.C. for alerting me to this problem and providing literature sources, and much of their own data. I also thank the following colleagues for searching their respective collections for specimens of the three species considered in this report: Dr. Jacques Forest, Muséum National d'Histoire Naturelle, Paris (MNHN); Janet Haig, Allan Hancock Foundation, University of Southern California (AHF); Williard D. Hartmann, Yale Peabody Museum, New Haven (YPM); Bernd Hauser, Muséum d'Histoire Naturelle de Genève (MHNG); Lipke B. Holthuis, Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); R. W. Ingle, British Museum (Natural History), London (BMNH); Herbert Levi, Museum of Comparative Zoology, Harvard (MCZ); Raymond B. Manning (USNM); A. Solem, Field Museum of Natural History, Chicago (FMNH); Gilbert L. Voss, University of Miami (UMML); and Torben Wolff, Universitets Zoologiske Museum, Copenhagen (UZMC). Dr. George Davis, Academy of Natural Sciences, Philadelphia (ANSP) graciously provided access to stored collections, and Dr. Bernd Werding, Institut für Allgemeine und Spezielle Zoologie, Giessen, generously loaned specimens of the new species and *P. marginatus* from his private collection.

Literature Cited

Balss, H. 1914. Decapode Crustaceen von den Guinea-Inseln, Süd-Kamerun und dem Congogebiet.—Ergibnisse der Zweiten Deutschen Zentral-Afrika-Expedition 1910–1911 unter Führung Adolph Friedrichs, Herzog zu Mecklenburg 1, Zoologie:97–108, figs. 1–12.

———. 1922. Crustacea VII: Decapoda Brachyura (Oxyrhyncha und Brachyrhyncha) und geographische Übersicht über Crustacea Decapoda.—*In* W. Michaelsen, Beiträge zur Kenntnis der Meeresfauna Westafrikas 3(3):69–110.

Benedict, J. E. 1901. The Anomuran collections made by the Fish Hawk expedition to Porto Rico.—Bulletin of the U.S. Fish Commission 20(2):129–148, 3 figs., pls. 4–6.

Boschma, H. 1931. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. LV. Rhizocephala.—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 89:297–380, text-figs. 1–57.

Chace, F. A., Jr. 1956. Porcellanid crabs.—Expédition Océanographique Belge dans les eaux côtières Africaines de l'Atlantique Sud (1948–1949), Résultats Scientifiques 3(5):1–54, figs. 1–14.

———. 1962. The non-brachyuran decapod crustaceans of Clipperton Island.—Proceedings of the United States National Museum 113(3466):605–635, figs. 1–7.

Coelho, P. A. 1966. Lista dos Porcellanidae (Crustácea, Décapoda. Anomura) do Litoral de Pernambuco e dos Estado Vizinhos.—Trabajos de la Instituto Oceanográfico de Universidade do Recife 5/6:51–68.

———. 1970. A distribuição dos Crustáceos Decápodos Reptantes do norte do Brasil.—Trabajos de la Instituto Oceanográfico de Universidade Federal de Pernambuco, Recife 9/11:223–238, fig. 1.

———, and M. de Araújo Ramos. 1972. A constituição e a distribuição de Fauna de Decápodos do litoral leste da América do Sul entre as Latitudes de 5° N e 59° S.—Trabajos de la Instituto Oceanográfico de Universidade Federal de Pernambuco, Recife 13:133–236, figs. 1–4.

Evans, A. C. 1967. Syntypes of Decapoda described by William Stimpson and James Dana in the collections of the British Museum (Natural History).—Journal of Natural History 1(3):399–411.

Fausto Filho, J. 1974. Stomatopod and decapod crustaceans of the Archipelago of Fernando de Noronha, Northeast Brazil.—Arquivos de Ciências do Mar (Fortaleza) 14(1):1–35.

Gauld, D. T. 1960. Decapoda Anomura. An annotated check list of the Crustacea of Ghana. III.—Journal of the West African Scientific Association 6(1):64–67.

Gore, R. H. 1974. Biological results of the University of Miami Deep-Sea expeditions, 102. On a small collection of porcellanid crabs from the Caribbean Sea (Crustacea, Decapoda. Anomura).—Bulletin of Marine Science 24(3):700–721, figs. 1–5.

———. 1982. Porcellanid crabs from the Pacific and Atlantic coasts of Central America (Crustacea Decapoda: Anomura).—Smithsonian Contributions to Zoology 363:i–iv, 1–34.

Haig, J. 1956. The Galatheidea (Crustacea Anomura) of the Allan Hancock Atlantic Expedition with a review of the Porcellanidae of the western North Atlantic.—Allan Hancock Atlantic Expedition 8:1–43, 1 pl.

———. 1962. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916, LXXIX: Porcellanid crabs from eastern and western America.—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 124:171–192, figs. 1–5.

———. 1964. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916. 81. Porcellanid crabs from the Indo-West Pacific, Part 1.—Videnskabelige Meddelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 126:355–386, figs. 1–4.

———. 1974. The anomuran crabs of Western Australia: Their distribution in the Indian Ocean and adjacent seas.—Journal of the Marine Biological Association of India 14(2):443–451.

Holthuis, L. B., and R. B. Manning. 1980. The R/V *Pillsbury* Deep-Sea Biological Expedition to the Gulf of Guinea, 1964–65. 12. The Porcellanidae, Hippidae, and Albuneidae (Crustacea, Decapoda).—Studies in Tropical Oceanography 4(2):241–255, fig. 1.

Lebour, M. V. 1959. The larval decapod Crustacea of tropical West Africa.—Atlantide Report 5: 119–143, figs. 1–21.

Miers, E. J. 1881. Crustacea. *In* Report on a collection made by Mr. T. Conry in Ascension Island.—Annals and Magazine of Natural History, (5) 8:432–434.

Milne Edwards, A. 1878. Description de quelques espèces nouvelles de Crustacés provenant du voyage aux îles du Cap-Vert de M. M. Bouvier et de Cessac.—Bulletin de la Société Philomathique de Paris, (7):225–232.

———, and E. L. Bouvier. 1900. Crustacés Décapodes. I. Brachyures et Anomoures. Première partie.—Expédition scientifiques du *Travailleur* et due *Talisman* pendant les Années 1880, 1881 1882, et 1883. 396 pp., 32 pls. Paris: Masson.

Nobili, G. 1897. Decapodi et Stomatopodi raccolti dal Dr. Enrico Festa nel Darien a Curaçâo, La Guayra, Porto Cabello, Colon, Panama, ecc.—Bollettino Musei di Zoologia ed Anatomia Comparata della R. Università di Torino 12(280):1–8.

———. 1901. Viaggio del Dr. Enrico Festa nella Repubblica dell'Ecuador e regioni vicine, 23: Decapodi e Stomatopodi.—Bollettino Musei di Zoologia ed Anatomia Comparata dell R. Università di Torino 16(415):1–58.

Pocock, R. I. 1890. Crustacea. *In* Ridley, Notes on the zoology of Fernando Noronha.—Journal of the Linnean Society of London, Zoology 20:506–526.

Rickner, J. A. 1975. Notes on members of the family Porcellanidae (Crustacea: Anomura) collected on the east coast of Mexico.—Proceedings of the Biological Society of Washington 88(16):159–166.

Schmitt, W. L. 1924a. The macruran, anomuran and stomatopod Crustacea. Bijdragen tot de kennis der fauna van Curaçao.—Resultaten eener reis van Dr. C. J. Van Der Horst in 1920, 23:61–81, figs. 1–7, pl. VIII.

———. 1924b. 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. I–IV.

———. 1935. Crustacea Macrura and Anomura of Porto Rico and the Virgin Islands.—Scientific Survey of Porto Rico and the Virgin Islands, New York Academy of Sciences 15(2):125–227, figs. 1–80, pls. I–IV.

Sourie, R. 1954. Contribution à l'étude écologique des côtes rocheuses du Sénégal.—Mémoirs de l'Institut Français d'Afrique Noire 38:1–342, pls. 1–23.

Stimpson, W. 1858. Prodromus descriptionis animalium evertebratorum, quae in expeditione ad Oceanum Pacificum Septentrionalem, a Repubblica Federata Missa, Cadwaladaro Ringgold et Johanne Rodgers ducibus, observavit et descriptsit, pars VII, Crustacea Anomura, I: Teleosomi.—Proceedings of the Academy of Natural Sciences of Philadelphia (1859) 10:225–252.

———. 1859. Notes on North American Crustacea, No. I.—Annals of the Lyceum of Natural History in New York 7:49–93, 1 pl.

Werding, B. 1977. Los Porcelanidos (Crustace: Anomura: Porcellanidae) de la region de Santa Marta, Colombia.—Annales de Instituto de Investigaciones Marinas de Punta de Betín 9:173–214, figs. 1–29.

Young, C. G. 1900. The stalk-eyed Crustacea of British Guiana, West Indies, and Bermuda. John M. Watkins, London. 514 pp., 7 pls.

66-1 Drexelbrook Dr., Drexel Hill, Pennsylvania 19026.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 103–109

GEOGRAPHIC VARIATION IN *CHLOROSPINGUS OPHTHALMICUS* IN COLOMBIA AND VENEZUELA (AVES: THRAUPIDAE)

Storrs L. Olson

Abstract.—Geographic variation in the montane species *Chlorospingus ophthalmicus* was studied in specimens from the Andes of Colombia and Venezuela. There are two distinct subspecies groups in this area that were formerly treated as separate species. The white postocular spot is lacking in the *flavopectus* group, which has five representatives in Colombia, including two described as new (*C. o. trudis* n. subsp. and *C. o. exitelus* n. subsp.). Additional taxa are found in Ecuador and Peru. In the *ophthalmicus* group there are five named subspecies in Colombia and Venezuela, as well as two populations of intergrades or undetermined status. In this group, the subspecies *C. o. jacqueti* has three curiously disjunct populations separated by distinct intervening forms. Specimens of the *flavopectus* group are reported from a locality only 40 km from the nearest known population of the *ophthalmicus* group, which suggests the possibility of determining whether two distinct species are actually involved. Further field work and collecting are needed to resolve some of the intriguing problems in the evolutionary history of *C. ophthalmicus* in Colombia and Venezuela.

The Common Bush-Tanager, *Chlorospingus ophthalmicus,* exhibits complex variation through its extensive range from Mexico through Argentina. A large series of specimens from Colombia in the National Museum of Natural History, Smithsonian Institution (USNM), most of which had not previously been identified to subspecies, prompted the following revision. To effect this, I assembled material from other institutions, including representation from Venezuelan populations. Although I have included my observations on the Venezuelan specimens, these are tentative and more material will have to be consulted before the systematics and distribution of some of the forms of *C. ophthalmicus* are properly understood in that country. The spelling of Colombian place names, and their location by department, conforms with that of Paynter and Traylor (1981) and is not necessarily that found on specimen labels or in my previous publications. The distribution of the various populations of *C. ophthalmicus* in Colombia and Venezuela is shown in Fig. 1.

Chlorospingus ophthalmicus jacqueti Hellmayr, 1921

Type-locality.—Galipán, Cerro del Avila, near Caracas, Venezuela.

Characters.—White postocular spot and dark throat speckles present. Throat only slightly tinged with buffy. Crown color relatively light, rather grayish brown. Yellow breast-band only moderately suffused with orangish.

Range.—Inexplicably disjunct. Found in northern Venezuela from Miranda west to Carabobo, then in Trujillo (and extreme eastern Mérida according to

Fig. 1. Distribution of *Chlorospingus ophthalmicus* in Colombia and Venezuela based on material examined in this study. Some specimens (AMNH and MCZ) were examined after the map had been prepared and a few localities are therefore not shown here. Department boundaries in Colombia do not reflect several of the more recent shifts and splits. Hatching indicates areas above 1000 feet elevation.

Storer [1970]), and finally on the western slope of the eastern Andes of Colombia in southern Cesar, Norte de Santander, and northern Santander.

Specimens examined.—VENEZUELA. MIRANDA: Pico de Naiguatá (1, USNM; 1, CM). DISTRITO FEDERAL: El Limon (4, CM). ARAGUA: Cordillera de la Costa, Rancho Grande (7, USNM; 1, LSU); Colonia Tovar (5, CM; 1, USNM). CARABOBO: La Cumbre de Valencia (8, CM). TRUJILLO: Guamito (10, CM; 2, MCZ).

COLOMBIA. CESAR: La Palmita (22, CM). NORTE DE SANTANDER: Ramírez (2, CM); Las Ventanas (7, CM). SANTANDER: Corcova [not in Paynter and Traylor] (2, LACM); Cachirí (2, FM); Hacienda Las Vegas (1, USNM).

Remarks.—Although the distribution of this subspecies makes no sense, I am forced to concur with Zimmer (1946, 1947) that the birds from the west slope of the northern part of the eastern Andes of Colombia are inseparable from Venezuelan *jacqueti.* These birds are separated from those of Trujillo by the very different subspecies *eminens* and *venezuelanus,* and those of Trujillo are in turn separated from those of northern Venezuela by an unnamed dark-capped form from Lara and the very distinctive race *falconensis* of Falcón and Yaracuy. K. C. Parkes (in litt. 12 July 1982) notes that there are slight differences in coloration of the dorsum and undertail coverts between the three disjunct populations of *jacqueti*. Nevertheless, these populations are clearly much more similar to one another than to any of the intervening forms.

Chlorospingus ophthalmicus subsp. indet.

Characters.—Near *jacqueti* but crown noticeably darker, less grayish, though not as dark as in *venezuelanus*; buffiness of throat and orangish of breast band not as marked as in *venezuelanus* or *falconensis*.

Range.—Venezuela, in Lara and northern Trujillo.

Specimens examined.—VENEZUELA. LARA: Anzoátegui (3, CM); Guárico (4, CM). TRUJILLO: Páramo de Rosas (2, CM).

Remarks.—The darker crown in specimens from Lara and Páramo de Rosas has already been noted by Hellmayr (1936:403, footnote). It is consistent and prevents these birds from being assigned to *jacqueti*. They could perhaps be considered as intergrades with *venezuelanus*, as Hellmayr was inclined to do, but the intervening population of apparently typical *jacqueti* from Guamito, Trujillo, complicates such an interpretation. Specimens of *C. ophthalmicus* from a number of additional localities from Mérida through Yuracuy would be desirable.

Chlorospingus ophthalmicus falconensis Phelps and Gilliard, 1941

Type-locality.—San Luis Mountains, above San Luis, Falcón, Venezuela.

Characters.—Crown much darker than in *jacqueti*, but browner and not as dark blackish as in *venezuelanus*. Throat buffier and breast band more orangish than in either *jacqueti* or *venezuelanus*.

Range.—Venezuela, in the states of Falcón and Yaracuy.

Specimens examined.—VENEZUELA. FALCON: San Luis (1, USNM). YARACUY: Lagunita de Aroa (1, CM).

Chlorospingus ophthalmicus venezuelanus Berlepsch, 1893

Type-locality.—Mérida, Venezuela.

Characters.—Crown much darker than in any of the other subspecies having a white postocular spot, with the exception of *eminens*. Differs from *eminens* (and *jacqueti*) in the buffier throat and more orangish breast band.

Range.—Southwestern Venezuela in the Andes of Mérida, Táchira, and portions of Lara (according to Storer [1970], no specimens from Lara or Táchira seen).

Specimens examined.—VENEZUELA. MERIDA: Culata (2, USNM); Escorial (1, ANSP); Heights Tabay (4, CM).

Chlorospingus ophthalmicus ponsi Phelps and Phelps, 1952

Type-locality.—Cerro Tamuypejocha, Sierra Perijá, Zulia, Venezuela.

Characters.—Like *jacqueti* but throat decidedly buffier, with more pronounced speckling, breast band more orangish. Crown much lighter than in *venezuelanus* or *falconensis*. Not as richly colored ventrally as *falconensis*.

Range.—The Sierra de Perijá in Zulia, Venezuela, and Cesar and La Guajira, Colombia.

Specimens examined.—COLOMBIA. CESAR: Hiroca (10, USNM). LA GUAJIRA: La Africa (3, USNM); Tierra Nueva (8, USNM); Monte Elias (2, USNM).

Remarks.—Hitherto this subspecies was known only from the vicinity of the type-locality, the above specimens being the first recorded for Colombia. They match the original description of *ponsi* perfectly except that I do not find the crown to be any darker than in *jacqueti*. There is considerable individual variation in the darkness of the crown in both subspecies, however.

Chlorospingus ophthalmicus eminens Zimmer, 1946

Type-locality.—Gramalote, Norte de Santander, Colombia.

Characters.—Very similar to *venezuelanus* in the dark crown, differing only in the less buffy, nearly white throat and less orangish breast band.

Range.—Colombia, on the eastern slope of the eastern Andes in southern Norte de Santander and Boyacá.

Specimens examined.—COLOMBIA. NORTE DE SANTANDER: Gramalote (1, ANSP); Palo Gordo (3, USNM). BOYACA: Hacienda La Primavera (4, FM).

Remarks.—Apparently intergrades with the westernmost of the three disjunct populations of *jacqueti* (see following account).

Chloropsingus ophthalmicus jacqueti > *eminens*

Characters.—Nearest *jacqueti* but crown darker, more blackish brown, less gray. Crown not as dark as in *eminens,* throat buffier and breast band more orangish.

Range.—Colombia in Norte de Santander, geographically intermediate between *eminens* to the east and *jacqueti* to the west.

Specimens examined.—COLOMBIA: NORTE DE SANTANDER: Buenos Aires (8, USNM); Alto del Pozo (1, USNM); 8 mi. S of Convención, (3, USNM); Ocaña, beyond Pueblo Nuevo (1, USNM).

Remarks.—The above series is quite distinct from either *jacqueti* or *eminens* and shows little variation, so that it would be possible to designate it as a new subspecies. I believe that at present, however, these birds should be regarded as intergrades. They are very similar to the unnamed dark-capped birds from Lara, Venezuela, and differ only in their somewhat buffier throats.

Chlorospingus ophthalmicus flavopectus (Lafresnaye, 1840)

Type-locality.—Santa Fé de Bogotá, Colombia.

Characters.—Differs from all of the preceding subspecies in lacking the white postocular spot; crown gray without any brownish cast; throat white, nearly without speckles; size larger.

Range.—Colombia, on the western slope of the eastern Andes from Santander through Cundinamarca.

Specimens examined.—COLOMBIA. SANTANDER: Above Virolín (4, USNM). BOYACA: Páramo de Agüero (1, USNM); Arcabuca, 3 km SW (1, MVZ); Lago de Tuquina [not in Paynter and Traylor] (1, FM). CUNDINAMARCA: La Aguadita (2, ANSP); Subia (2, AMNH); Aguabonita (2, AMNH); El

Roble (2, AMNH); "Santa Fé de Bogotá" (1, USNM); "Bogotá" (1, MCZ [holotype]; 4, USNM).

Remarks.—Hellmayr (1936) and earlier authors considered *flavopectus,* along with certain forms from Ecuador and Peru, to be specifically distinct from *ophthalmicus.* It was not until Zimmer's (1947) revision that the two species were combined. The forms of the *flavopectus* group (which in Colombia includes *flavopectus, trudis, macarenae, nigriceps,* and *exitelus*) seem so distinct from those in the *ophthalmicus* group that I have reservations about Zimmer's action and I wonder if the earlier treatment may not have been correct after all. There is a possibility that further collecting and field work in Santander could resolve this (see following account).

Chlorospingus ophthalmicus trudis, new subspecies

Holotype.—CM 59494, male, La Pica, Santander, Colombia. Collected 12 February 1917 by M. A. Carriker, Jr., original number 21063.

Characters.—Most similar to *flavopectus* but dorsum lighter, more yellowish-green, less olivaceous; crown lighter, more brownish gray; auriculars brownish rather than black; inner webs of rectrices not blackish but brownish-gray or greenish. Averages smaller, with a visibly smaller bill (wing chord 64.8–72.1 mm, average 68.6, n = 8; vs. 67.4–76.4, average 72.3, n = 9, in *flavopectus* [72.2 mm in holotype]).

Range.—Known so far only from the type-locality. Meyer de Schauensee (1948: 320) describes La Pica as a campsite at 2800 m on "the stretch of mountain trail crossing the ridge known as Cruz de Piedra, between San Andrés and Málaga, north of Molagavita."

Specimens examined.—Holotype and 8 topotypes with essentially the same data (6, CM; 2, ANSP; 1, MCZ).

Etymology.—Latin *trudis,* a pointed pole or pike, one of several meanings for the Spanish word *pica,* in reference to the type-locality.

Remarks.—This form is removed about 85 km to the north of the nearest specimens of *flavopectus* that I examined (near Virolín). Differentiation may have been affected by the barrier afforded by the valley of the Río Chicamoca. Of more significance is the fact that less than 40 km separate *trudis* from populations of *jacqueti* to the north (at Hacienda Las Vegas) and there is no such barrier evident between them. It would be of great interest to determine how these two completely different forms interact if and where they come in contact.

Chlorospingus ophthalmicus macarenae Zimmer, 1947

Type-locality.—Mt. Macarena, Metá, Colombia.

Characters.—Like *flavopectus* but smaller, throat slightly buffier, yellow breast band more restricted and more intensely colored, greenish flanks more extensive and yellower, belly white not grayish.

Range.—Colombia, confined to the Macarena Mountains east of the eastern Andes in Metá.

Specimens examined.—COLOMBIA. META: La Macarena (12, FM).

Remarks.—This is a well marked isolate obviously allied with the *flavopectus* group.

Chlorospingus ophthalmicus nigriceps Chapman, 1912

Type-locality.—Miraflores, 6800 ft., Central Andes, east of Palmira, Cauca, Colombia.

Characters.—Similar to *flavopectus* in lacking the white postocular spot but crown very dark, blackish; throat and sometimes part of pectoral band heavily speckled with blackish; green of dorsum darker, suffused with blackish.

Range.—Colombia, western slope of the southern end of the eastern Andes and both slopes of the southern end of the central Andes.

Specimens examined.—COLOMBIA. QUINDIO: Laguneta (7, ANSP). HUILA: Moscopán (2, CM; 1, FM); Tijeras, Moscopán (5, USNM; 3, FM; 2, MVZ); La Plata (1, ANSP); Buenavista (6, ANSP); La Candela (16, ANSP; 1, AMNH); Andalucía (1, USNM). TOLIMA: Toche (5, ANSP; 1, MCZ); Río Toche (1, USNM; 1, MCZ); El Edén (1, AMNH). VALLE DEL CAUCA: E. of Palmira (1, AMNH, holotype).

Remarks.—Previously published records from the northern part of the central Andes in Antioquia pertain to the following new subspecies.

Chlorospingus ophthalmicus exitelus, new subspecies

Holotype.—USNM 403747, female, ovary enlarged. Ventanas, Valdívia, Antioquia, Colombia, 7000–7400 feet. Collected 11 June 1948 by M. A. Carriker, Jr., original number 13878.

Characters.—Nearest *nigriceps* but crown decidedly lighter, grayish instead of black; speckling on throat reduced and lighter in color; green of dorsum lighter, more yellowish. Crown darker than in *flavopectus*, in which there is almost no speckling on the throat.

Range.—Colombia, both slopes of the northern end of the central Andes in Antioquia.

Specimens examined.—COLOMBIA. ANTIOQUIA: Ventanas, Valdívia (3, USNM, including holotype); Hacienda Zulaiba (2, USNM); Envigado (1, USNM); Sabanalarga [not the Sabanalarga in Atlántico in Paynter and Traylor] (1, AMNH, Niceforo, collector); "Medellín" (1, AMNH); "Antioquia" [Salmon, collector] (1, MCZ); Santa Elena (6, AMNH, intergrades with *nigriceps*).

Etymology.—Greek *exitelos*, a lessening or fading, in reference to the diminution in intensity of the features that are characteristic of *nigriceps*.

Remarks.—This subspecies is easily separated from *nigriceps* to the south. The birds from Sabanalarga and Medellín mentioned by Meyer de Schauensee (1951: 1062) under *nigriceps* are definitely referable to this subspecies, as probably are those from Retiro (not seen). There apparently is but one record of *C. ophthalmicus* in the western Andes. Meyer de Schauensee (1951:1062) lists *C. o. nigriceps* from Concordia, an old Salmon collecting site. This is presumably based on the record of "*C. flavipectus*" from Concordia mentioned in Sclater and Salvin (1879). As this is near the narrowest part of the Cauca Valley, with the foothills of the Central Andes being in places only a few hundred meters from the steep eastern slopes of the western Andes (W. L. Brown, in litt. 21 July 1982), dispersal of *C. ophthalmicus* from one range to the other at this point is not unlikely. The birds from the western Andes would almost certainly pertain to *C. o. exitelus*.

A series of six specimens from Santa Elena, Antioquia, is quite variable, some of the individuals having dark crowns, while others have lighter crowns. This series appear to be composed of intergrades between *exitelus* and *nigriceps*. None has the crown as dark as in *nigriceps*, however, but the throat is more heavily speckled than in *exitelus*.

Acknowledgments

For lending specimens crucial to this study I am indebted to Frank B. Gill, Academy of Natural Sciences of Philadelphia (ANSP); Kenneth C. Parkes, Carnegie Museum of Natural History, Pittsburgh (CM); John W. Fitzpatrick and Melvin A. Traylor, Jr., Field Museum of Natural History, Chicago (FM); John P. O'Neill, Louisiana State University, Baton Rouge (LSU); and Ned K. Johnson, Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). I also examined specimens in the collections of the American Museum of Natural History, New York (AMNH), and the Museum of Comparative Zoology, Harvard University (MCZ). For reading and commenting on the manuscript I am grateful to W. L. Brown, S. L. Hilty, Kenneth C. Parkes, and Raymond A. Paynter, Jr. This is contribution number 12 of the Wetmore Papers, a project supported in part by trust funds from the Smithsonian Institution for completing unfinished work and study of undescribed material left by the late Alexander Wetmore. Janine Higgins prepared the map.

Literature Cited

Hellmayr, C. E. 1936. Catalogue of Birds of the Americas. Part 9.—Field Museum of Natural History, Zoological Series 13(9):1–458.

Meyer de Schauensee, R. 1948. The birds of the Republic of Colombia. Part 1.—Caldasia 5:251–380.

———. 1951. The birds of the Republic of Colombia. Part 4.—Caldasia 5:873–1112.

Paynter, R. A., Jr., and M. A. Traylor, Jr. 1981. Ornithological gazetteer of Colombia.—Harvard University, Cambridge, Massachusetts.

Sclater, P. L., and O. Salvin. 1879. On the birds collected by the late Mr. T. K. Salmon in the State of Antioquia, United States of Columbia.—Proceedings of the Zoological Society of London 1879:486–550.

Storer, R. W. 1970. Subfamily Thraupinae. Pp. 246–408 *in* R. A. Paynter, Jr., editor. Check-list of Birds of the World. Vol. 13.—Museum of Comparative Zoology, Cambridge, Massachusetts.

Zimmer, J. T. 1946. A new subspecies of tanager from northeastern Colombia.—Journal of the Washington Academy of Sciences 36(11):389–390.

———. 1947. Studies of Peruvian birds. No. 52.—American Museum Novitates 1367:1–26.

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

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 110–114

FUNCTION OF THE TEETH AND VESTIBULAR ORGAN IN THE CHAETOGNATHA AS INDICATED BY SCANNING ELECTRON MICROSCOPE AND OTHER OBSERVATIONS

Robert Bieri, Dolores Bonilla, and Fernando Arcos

Abstract.—Ultrastructure of the teeth of chaetognaths indicates that they may function to pierce the exoskeleton of copepods. The vestibular ridge behind the posterior teeth has a series of pores that may excrete a poison that immobilizes copepods.

A series of recently published SEM photographs of the hooks and teeth (armature) of several species of chaetognaths (Cosper and Reeve 1970; Nagasawa and Marumo 1973, 1979; Bone and Pulsford 1978; Spero, Hagan, and Vastano 1979) permits comparison with some SEM photographs we have made. The anterior and posterior teeth have a distinct microstructure at the tips reminiscent of a stone drill. We postulate that they puncture copepod exoskeletons to speed the penetration of digestive enzymes and hasten absorption of digested material. The teeth also have lightly serrate, knife-like edges and thus also can cut or shear.

A series of pores in the papillae of the vestibular organ, visible in earlier SEM studies may be the openings of ducts for the secretion of a toxin. The toxin could flow down the grooves of the teeth and penetrate the prey through the puncture holes. If these hypotheses are confirmed, then the epithet, "Arrowworms, Tigers of the Sea" should be changed to "Arrowworms, Cobras of the Sea."

Methods.—Each study published to date has used different methods of killing, preservation, and sample manipulation. The methods of Bone and Pulsford (1978) and of Spero, Hagan, and Vastano (1979) have given the finest pictures of soft tissue. We used both formalin and dilute (0.4%) gluteraldehyde for killing and fixing. The latter gave better preservation of the soft tissues, but where live animals are not available, formalin killed specimens can give useful information. We used both acetone and isoamylacetate for final dehydration and found that the armature of chaetognaths is sufficiently rugged that we could dry specimens from acetone using a heat lamp and still get good gold plating.

Results.—Spero, Hagan, and Vastano very generously allow us to publish here their previously unpublished, superb SEM picture of the head of *Sagitta hispida* (Fig. 1). This is useful for orientation and shows the microstructure of the teeth (Fig. 1). The hooks or seizing jaws are on either side of the head. The two paired rows of smaller anterior teeth and larger posterior teeth are clearly visible, as are the papillae along the ridge of the vestibular organs under each set of posterior teeth. For comparison, Fig. 2 shows the head of *Pterosagitta draco*. The muscular "hood" is partly drawn over the hooks on the right side of the head. Five, possibly six anterior teeth on the right side of the head and six or seven on the other side are visible but the posterior teeth are too numerous to count accurately. The velvet-like tissue around the mouth, clearly shown in Fig. 1, is badly con-

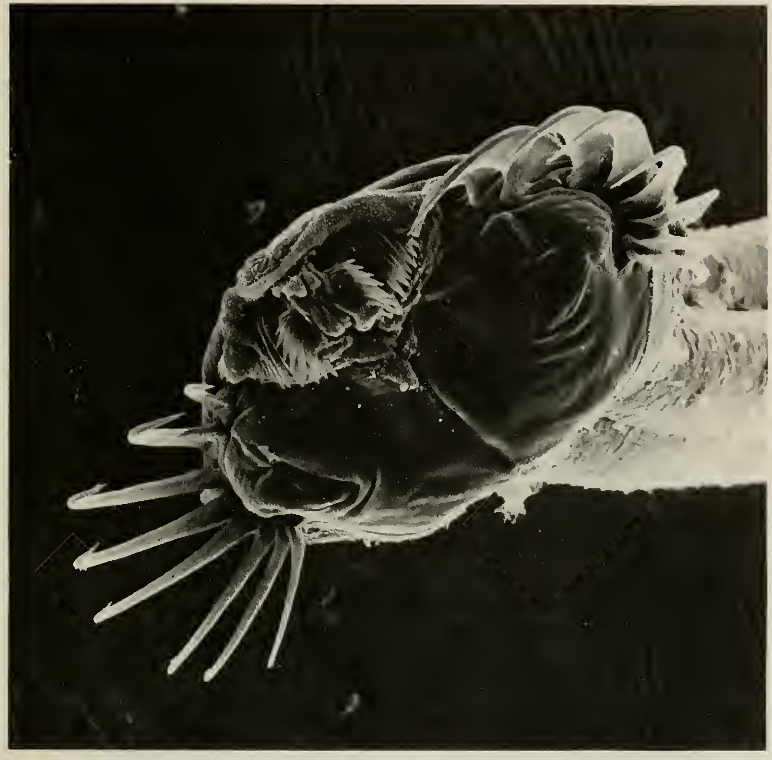
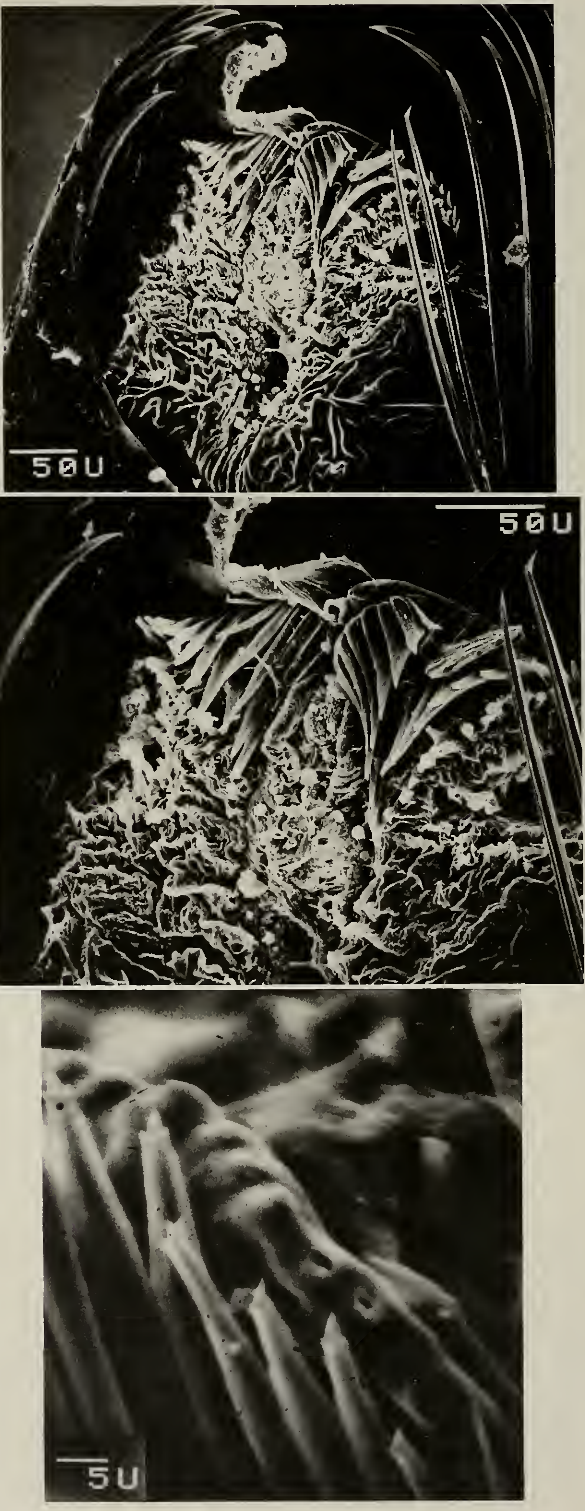


Fig. 1. SEM of the head of *Sagitta* seen from the front and below. The hooks (also called seizing jaws and spines) are arranged on either side of the head. The anterior and posterior teeth are arranged in two pairs of rows, the anterior teeth projecting diagonally and the posterior teeth hanging down in this preparation. Photo courtesy of Spero. Hagan, and Vastano.

tracted either by the formalin fixation or by the dehydration. The vestibular organ is strongly wrinkled and contracted and shows up as a series of white knobs on narrow stalks. The knobs are shown enlarged in Fig. 3. This severe distortion of the soft tissues proved fortuitous because it strongly emphasizes the pores present in each papilla of the vestibular organ. Refering back to Fig. 1, it is barely possible to see that they are present also in *Sagitta hispida*. We also found them present in *Sagitta peruviana* (Fig. 4). Here the pores are clearly evident although it is not clear if they are present in every papilla as they appear to be in *Pterosagitta draco*. The pores, though small, are shown clearly in Fig. 1 of *Sagitta hispida* in Cosper and Reeve (1970).

The microstructure of the teeth seems to be essentially the same in all three species. Though somewhat blurred, the tip structure shows up best in Fig. 4. There are four cusps at the tip, one is longer and the other three are shorter and subequal in length. The tips of several different teeth are outlined in Fig. 5. All can be interpreted as different views of the 4-cuspate form. Close examination of Fig. 2 of Cosper and Reeve (1970) shows the same quadri-cuspate structure.

Discussion.—The shape of the tips of the teeth seems well suited for quick penetration of the longest cusp into a rigid surface followed by a splitting or


50U
50U
5U

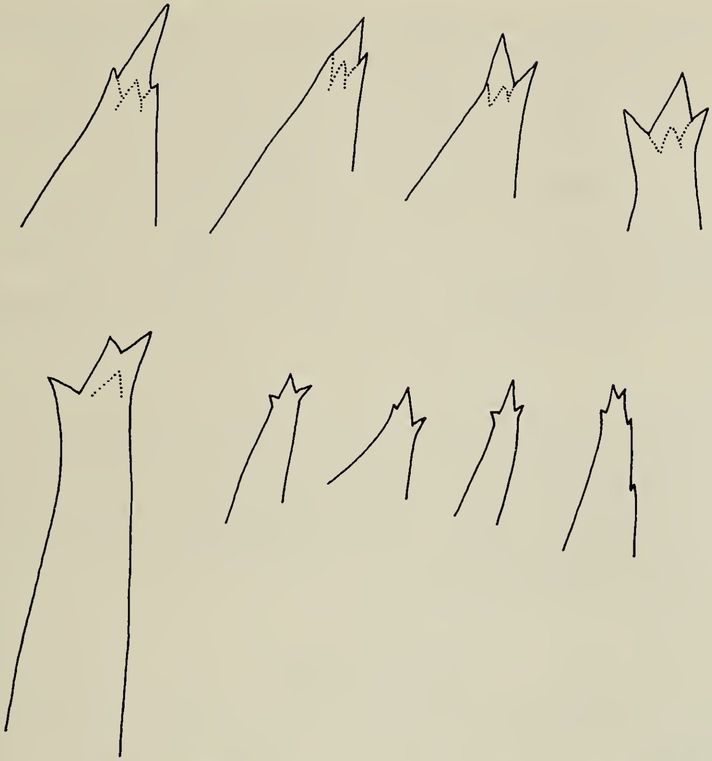


Fig. 5. Outlines of anterior and posterior teeth taken from SEM photos showing how the quadridentate pattern can appear as a single, bifid or trifid point. The larger sketches are of *Sagitta peruviana*, the smaller of *Pterosagitta draco* and are not drawn to scale.

perforating of the exoskeleton by the three following cusps. The serrate, knife-like edges of the teeth could serve as slicing or cutting edges on soft-bodied animals such as fish larvae. Robert Miller (personal communication) stated that during his experimental studies on fish, unidentified sagittas cut many of the larvae cleanly in half.

For the pores in the vestibular organ, three possible functions suggested themselves. They could hold prey by suction. They could secrete digestive enzymes, or an immobilizing toxin. In reviewing the literature related to head structure, digestive physiology, and feeding behavior (summarized by Hyman 1959) we could find no indication of the internal structure of the vestibular organs. Parry

←

Fig. 2. Head of *Pterosagitta draco* showing hooks (partly covered by the hood on the right side of the head) anterior and posterior teeth, and the vestibular region highly distorted in preparation. Below the posterior teeth on the right side of the head the papillae of the vestibular organ appear as white knobs.

Fig. 3. Enlargement of the same specimen as in Fig. 2 showing the vestibular ridge of the vestibular organ below the posterior teeth. Because of distortion the papillae appear as tubes.

Fig. 4. Vestibular organ of *Sagitta peruviana* behind the posterior teeth. Pores in the vestibular ridge are clearly evident as is the cuspate or quadridentate shape of the teeth.

(1947) found no toxin in the secretion from the anterior part of the pharynx. On the other hand, in describing the feeding behavior of *Spadella* which he found essentially the same as in *Sagitta setosa*, he wrote, "As the prey is clasped against the mouth region it is probably coated with secretion produced by the granular cells. By this means the appendages would be entangled and the copepod prevented from escaping. That the prey is not killed is shown by its circulating blood and gut peristalsis which can be observed for some time after swallowing. On the other hand, a copepod which has been relinquished is unable to move away." (Parry 1947:25).

It seems to us that the vestibular organ could secrete a toxin specifically blocking locomotion. Clearly this would be a great advantage to the arrowworm because moving spines of even an herbivorous copepod could damage the mouth tissues. If the copepod's circulation and gut movements continued to function as observed by Parry, it would speed the dispersion of the digestive enzymes. The teeth and hooks seem adequate to hold the prey against the mouth. The very close proximity of the pores of the vestibular ridge to the posterior teeth indicate a functional relationship between the two. The ridges of the posterior teeth, shown most clearly in Fig. 2 of Cosper and Reeve (1970) could direct a toxic secretion into the punctured body.

Acknowledgments

The authors extend sincere thanks to the Departamento de Microscopia Electronica del Instituto Nacional de Hygiene, Guayaquil, for the use of their equipment and facilities.

Literature Cited

Bone, A., and A. Pulsford. 1978. The arrangement of ciliated sensory cells in *Spadella* (Chaetognatha).—Journal of the Marine Biological Association of the United Kingdom 58:565–570.

Cosper, T. C., and M. R. Reeve. 1970. Structural details of the mouthparts of a chaetognath as revealed by scanning electron microscopy.—Bulletin of Marine Science 20:441–445.

Hyman, L. H. 1959. The invertebrates, 5, Smaller Coelomate groups. McGraw-Hill, New York, 783 pp.

Nagasawa, S., and R. Marumo. 1973. Structure of grasping spines of six chaetognath species observed by scanning electron microscopy.—Bulletin of the Plankton Society of Japan 19: 63–75.

———, and ———. 1979. Identification of chaetognaths based on morphological characteristics of hooks.—La Mer 17(4):14–24.

Parry, D. A. 1947. Structure and function of the gut in *Spadella cephaloptera* and *Sagitta setosa*.—Journal of the Marine Biological Association of the United Kingdom 26:16–36.

Spero. H., D. Hagan, and A. Vastano. 1979. An SEM examination of *Sagitta tenuis* (Chaetognatha), utilizing a special sedation and handling procedure.—Transactions of the American Microscopical Society 98:139–141.

(RB) Antioch College, Yellow Springs, Ohio 45389; (DB, FA) Instituto Oceanografico del Armado, Casilla 4950, Guayaquil, Ecuador.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 115–120

SYSTEMATICS AND DISTRIBUTION OF SHREWS OF THE GENUS *CROCIDURA* (MAMMALIA: INSECTIVORA) IN VIETNAM

Lawrence R. Heaney and Robert M. Timm

Abstract.—Three noncommensal species of white-tooth shrews (*Crocidura*) are found in Vietnam; from smallest to largest, they are *C. horsfieldi indochinensis*, *C. attenuata*, and *C. fuliginosa dracula*. All are probably widespread, although their distributions remain incompletely known in Vietnam.

Shrews of the genus *Crocidura* are the most widespread and diverse insectivores in the Oriental faunal region (Chasen 1940; Ellerman and Morrison-Scott 1951). However, there are few specimens from most areas, and this is especially true of the continental portions of southeast Asia. We recently surveyed the holdings of the American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), and U.S. National Museum of Natural History (USNM), and have encountered a number of misidentified specimens and important unpublished records of three species of *Crocidura* from Vietnam. Because past investigators have been hampered by a lack of adequate descriptions and illustrations, we provide these here, along with reidentifications of previously published, misidentified specimens. Localities are mapped or listed in gazetteers by Moore and Tate (1965), Osgood (1932), and Van Peenen *et al.* (1969). We do not treat the common commensal species of the subgenus *Suncus*, *C. murina*, in this paper; see Van Peenen *et al.* (1969) for a list of localities for this species in southern Vietnam.

All cranial measurements were taken by Heaney with dial calipers graduated to 0.05 mm. External measurements were taken from the collectors labels. The following cranial measurements were taken: condyloincisive length, condyles to anterior tip of incisors; braincase breadth, greatest breadth, roughly mastoidal; interorbital breadth, taken at anterior end of orbit; rostral length, anterior tip of incisor to anteriormost portion of orbit, in the infraorbital foramen; postpalatal depth, measured from just posterior to posterior lip of palate to closest point on cranial surface; rostral breadth, calipers held dorsally to rostrum, measurement taken at margin of P^2 and P^3, in ''notch''; postpalatal length, taken from posterior edge of postpalatal lip to anteriormost point on foramen magnum; condyle to glenoid, calipers placed in glenoid fossa, drawn up against posteriormost point on occipital condyles; I^1 to M^3, greatest length of toothrow, at alveolus of M^3 to anteriormost point on I^1; P^4 to M^3, taken labially at alveolus; M^2 to M^2, greatest width taken at anterior labial margins of second upper molars; palatal width at M^3, alveolar distance between lingual margins of third upper molars.

Crocidura attenuata Milne-Edwards

Crocidura attenuata Milne-Edwards, 1872:263.

These shrews are virtually identical to the species that follow in pelage characteristics; thus, the following description of the pelage applies equally well to

Table 1.—External and cranial measurements of white-toothed shrews from Vietnam. Values are means ± standard deviation (and range).

Measurements	*Crocidura attenuata* (n = 9)	*Crocidura fuliginosa* (n = 17)	*Crocidura horsfieldi* (n = 4)
Length of head and body	83.9 ± 3.6 (79–88)	92.5 ± 5.9 (83–101)	66.0 (65–67)
Length of tail	50.0 ± 6.5 (45–61)	71.2 ± 4.3 (62–80)	48.5 (47–50)
Length of hind foot	14.3 ± 0.71 (13–15)	16.2 ± 1.2 (15–18)	13.0 (13)
Condyloincisive length	20.88 ± 0.95 (19.6–22.4)	23.63 ± 0.43 (22.9–24.2)	17.77 (17.7–17.9)
Braincase breadth	9.51 ± 0.27 (9.1–9.9)	10.23 ± 0.18 (9.9–10.5)	8.13 (8.0–8.2)
Interorbital breadth	4.58 ± 0.22 (4.2–4.9)	4.93 ± 0.12 (4.7–5.1)	3.95 (3.8–4.1)
Rostral length	8.18 ± 0.25 (7.9–8.6)	9.52 ± 0.28 (8.8–9.8)	6.6 (6.4–6.7)
Postpalatal depth	3.77 ± 0.14 (3.5–3.9)	4.18 ± 0.13 (3.9–4.4)	3.48 (3.4–3.6)
Rostral breadth	2.67 ± 0.19 (2.3–3.0)	2.71 ± 0.11 (2.6–2.9)	2.28 (2.0–2.6)
Postpalatal length	9.25 ± 0.47 (8.6–9.9)	10.41 ± 0.29 (10.0–11.0)	8.27 (7.9–8.5)
Condyle to glenoid	8.20 ± 0.39 (7.7–8.7)	8.97 ± 0.15 (8.8–9.2)	7.20 (7.2)
I^1 to M^3	9.08 ± 0.36 (8.6–9.7)	10.65 ± 0.21 (10.3–11.0)	7.48 (7.3–7.6)
P^4 to M^4	5.09 ± 0.21 (4.9–5.5)	5.99 ± 0.15 (5.7–6.2)	4.20 (4.1–4.4)
M^2 to M^2 (labial)	6.39 ± 0.38 (5.7–6.8)	6.95 ± 0.21 (6.5–7.4)	5.35 (4.9–5.7)
Palatal width at M^3	2.84 ± 0.17 (2.6–3.1)	2.99 ± 0.08 (2.8–3.1)	2.20 (2.0–2.3)

all three species. Dorsal pelage soft, dense; color grayish brown, hairs often tipped with silver, slate gray at base. Ventral pelage shorter, slightly more grayish. Ear covered inside and out with fine, scattered brown hairs; these hairs are densest along edge, giving ear a brownish fringe. Distal septum of ear with stiff brown hairs protruding beyond margin. Fore-feet and hind-feet with sparse covering of brown hairs on dorsum; ventral surface naked of hairs. Tail thinly covered with brown hairs. Long hairs sparse but present on proximal two-thirds of tail, absent from distal third. Ventral surface of tail paler, grading into darker dorsum.

Crocidura attenuata differs from *C. fuliginosa* externally in its generally smaller size (Table 1), and especially in its proportionately and absolutely shorter tail; the average tail to head and body ratio is 0.50. *Crocidura attenuata* differs externally from *C. horsfieldi* in being considerably larger (head and body more than 79 mm as opposed to less than 67 mm), and in having a proportionately shorter tail.

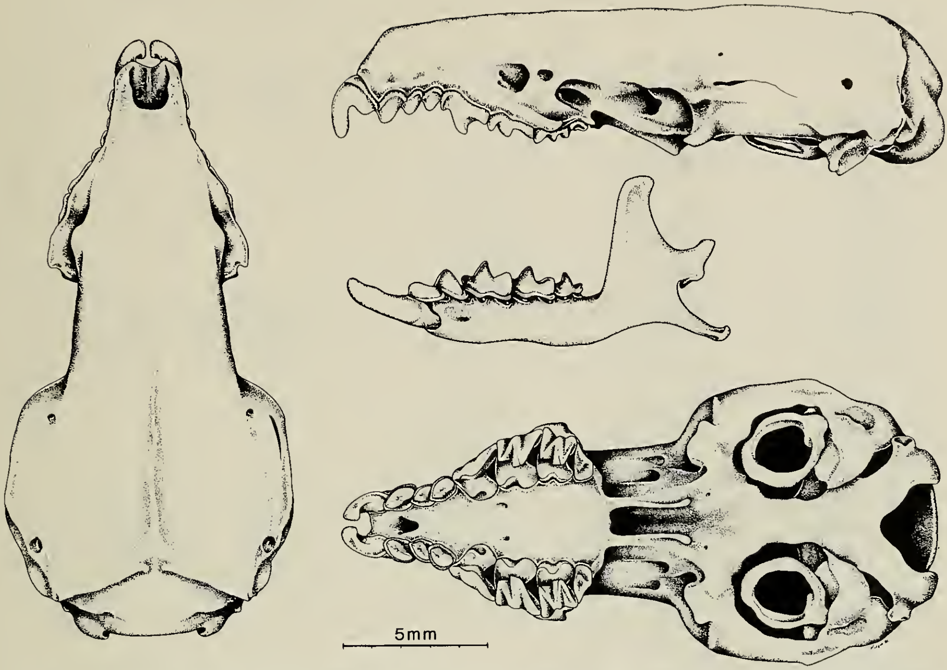


Fig. 1. Dorsal, lateral, and ventral views of the cranium and lateral view of the mandible of *Crocidura attenuata* from Mt. Langbian, Tuyen Duc Province, Vietnam (FMNH 46640). Approximately ×4.

The skull of *C. attenuata* (Figs. 1, 2) is similar to those of *C. fuliginosa* and *C. horsfieldi* in most respects. It differs from *C. fuliginosa* in being generally smaller; having a shorter and less massive toothrow, especially in having narrower molars (Fig. 2); having the second upper unicuspid conspicuously smaller than first or third; more rounded (U-shaped) base to the basisphenoid between the pterygoid processes; and a narrower strut of the maxillary over the infraorbital canal (Fig. 2). *Crocidura attenuata* differs from *C. horsfieldi* in having a larger skull (Table 1); a proportionately broader anterior tip to the rostrum; more procumbent incisors; and in having the third unicuspid about three-fourths the size of the first, rather than about half (Fig. 2).

These are the first specimens reported from Vietnam. As noted by Jenkins (1976), *C. attenuata* often has been confused with *C. fuliginosa,* and most of the specimens we examined have been reported previously in the literature as *C. fuliginosa*. Our identifications are based on measurements provided by Jenkins (1976), on comparisons with specimens (FMNH) from near the type locality of *C. attenuata* (see Allen 1938), and the illustrations and description published by Milne-Edwards (1872). Only one of the specimens from the USNM reported by Van Peenen *et al.* (1969) as *C. fuliginosa* is actually that species; the others are *C. attenuata.* The specimens cited here indicate that *C. attenuata* is widespread in southern Vietnam at elevations from near sea level to 1700 m. We note that the cranium of a *Crocidura* from Thailand figured by Lekagul and McNeely (1977: 31) and identified as *C. fuliginosa* is actually *C. attenuata,* whereas the skull and

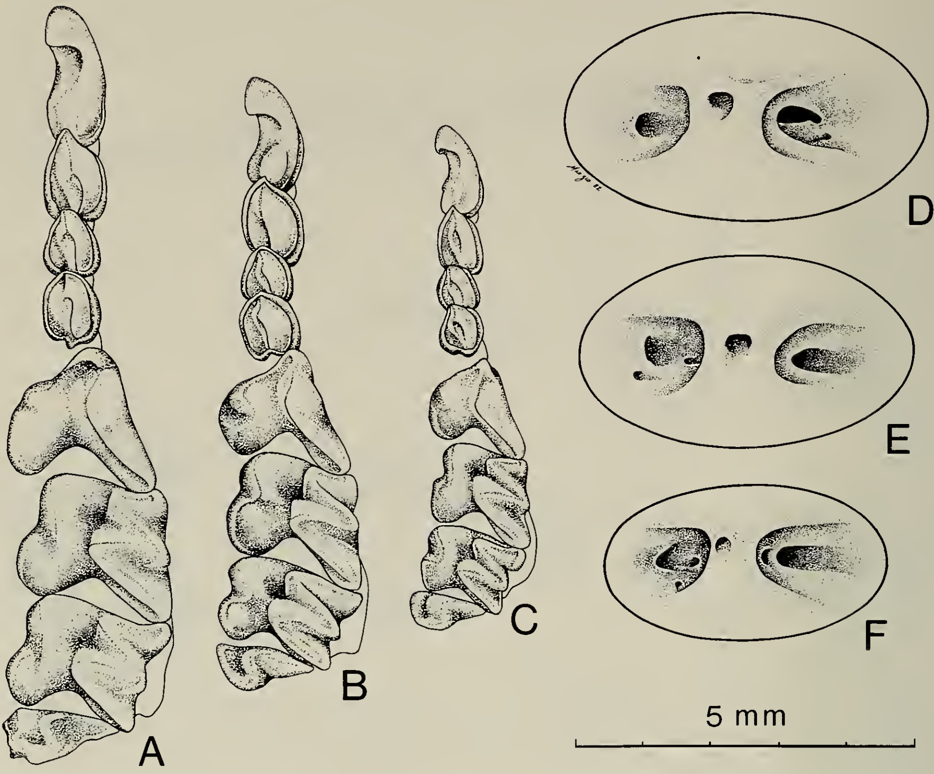


Fig. 2. Maxillary toothrows of *Crocidura fuliginosa* (A; FMNH 32422 from Chapa, Tonkin), *C. attenuata* (B; FMNH 46640 from Langbian Peak, Tuyen Duc Prov.), and *C. horsfieldi* (C; FMNH 39029 from Chapa, Mt. Fan Si Pan, Tonkin); and infraorbital regions of *C. fuliginosa* (D; USNM 357438 from Con Son Island), *C. attenuata* (E; FMNH 46641 from Langbian Peak, Tuyen Duc Prov.), and *C. horsfieldi* (F; USNM 357862 from An Khe Military Base, Binh Dinh Prov.). All drawings to same scale, approximately ×9.

measurements Lekagul and McNeely (1977:34) attribute to *C. attenuata* are those of *C. fuliginosa*.

As noted by Jenkins (1976), the subspecific status of Indochinese specimens is uncertain, although Lekagul and McNeely (1977) thought Thai specimens probably represented *C. a. attenuata*.

Specimens examined.—VIETNAM: *Quan Tri Prov.:* 2.3 km E, 8 km S Thon Ke Tri Peak, elev. 70 m (1 USNM); *Thua Thien Prov.:* 8 km W, 3.7 km N Nui Ke, elev. 30 m (1 USNM); 9.1 km W, 3.6 km N Nui Ke, elev. 30 m (1 USNM); *Tuyen Duc Prov.:* Fyan, elev. 1200 m (1 USNM); Mt. Langbian (no elevation given; 3 FMNH); Mt. Langbian, elev. 1700 m (2 USNM).

Crocidura fuliginosa dracula Thomas

Crocidura fuliginosa dracula Thomas, 1912:686.

As noted above, these shrews have pelage virtually identical to that of the other species, although we note that the skin on the hind feet of this species appears to be paler dorsally than that of *C. attenuata* or *C. horsfieldi*. *Crocidura fuliginosa* differs cranially from *C. attenuata* as noted above; it differs from *C. horsfieldi* most conspicuously in its vastly larger size (Table 1, Fig. 2), and also in its proportionately larger P^4.

Crocidura fuliginosa is widespread in southeast Asia (Jenkins 1976; Medway 1977), and has been reported previously from Vietnam (Osgood 1932); most of the specimens we examined were reported by Osgood. As noted above, Van Peenen *et al.* (1969) reported this species from Con Son Island; their other records are here referred to *C. attenuata*. We have records of *C. fuliginosa* only from Con Son Island and from northern Vietnam, from elevations from 40 m to ca. 1600 m, although the species is known to occur in southern Thailand and Malaysia (Lekagul and McNeely 1977; Medway 1977). This species apparently occurs sympatrically with *C. horsfieldi* near Chapa in northwestern Tonkin. Van Peenen *et al.* (1969) cited Thomas (1927) as reporting a specimen of *C. fuliginosa* from Dakto, but Thomas actually referred to it as "*Crocidura* sp.," and we consider its identity to be uncertain. Our identifications are based on the discussion of the status of *C. fuliginosa* by Medway (1977), on comparison with specimens (FMNH) from China (see Allen 1938), and on data provided by Jenkins (1976). The recognition of *dracula* as a valid species by Lekagul and McNeeley (1977) is based on their confusion regarding *C. fuliginosa* and *C. attenuata* (see above); our examination of specimens supports the recognition by Jenkins (1976) of *dracula* as a subspecies of *fuliginosa*.

Specimens examined.—VIETNAM: *Con Son Prov.:* Con Son Island, 1 km S, 0.3 km W Airfield Bldg., elev. 40 m (1 USNM); *Annam:* Hoi-Xuan (1 FMNH); *Tonkin:* Ba Nam Nhung (1 FMNH); Chapa, elev. 5000 ft (10 FMNH); Lai Chau, elev. 500 ft (1 AMNH, 2 FMNH); Muong Mo (1 FMNH).

Crocidura horsfieldi indochinensis Robinson and Kloss

Crocidura horsfieldi indochinensis Robinson and Kloss, 1922:88.

This species is similar in appearance to *C. attenuata*, but differs in its smaller size, proportionately longer tail (tail to head and body ratio averages 0.74), and several cranial features noted above (Fig. 2). It is conspicuously different from *C. fuliginosa* in its much smaller size.

Robinson and Kloss (1922) described *indochinensis* on the basis of a single specimen from Dalat (5000 ft elev.), Langbian Plateau (=Mt. Langbian), Tuyen Duc Prov., southern Annam (Vietnam); they provided (among others) the following measurements: tail, 50; hind foot, 12.2; greatest length of skull, 17.2; maxillary toothrow to tip of incisors, 7.4; mastoid breadth, 8.1. These measurements fit well within the range of those presented here, and it is on this basis that we refer our specimens to this taxon. Osgood (1932) reported two specimens from Chapa, in extreme northwestern Vietnam, and Anthony (1941) extended the known distribution to northeastern Burma. Ellerman and Morrison-Scott (1951) were the first to list *indochinensis* as a subspecies of *C. horsfieldi*, but offered no explanation for doing so. This treatment was followed by Jenkins, who stated that the holotype of *indochinensis* was similar to topotypes of *C. horsfieldi*. We list *indochinensis* as a subspecies of *C. horsfieldi* strictly on that basis. Lekagul and McNeely (1977) also followed this treatment, listing specimens from Chengmai and Kao Yai Park in Thailand. Specimens we examined all were taken at or above 600 m elevation. We note that *C. attenuata* and *C. h. indochinensis* have both been taken on Mt. Langbian.

Specimens examined.—VIETNAM: *Tonkin:* Chapa, Mt. Fan Si Pan (1 FMNH); *Binh Dinh Prov.:* An Khe Military Base, elev. approx. 600 m (2 USNM); *Tuyen Duc Prov.:* Mt. Langbian, elev. 1700 m (1 USNM).

Acknowledgments

We thank G. G. Musser and R. W. Thorington for permission to examine specimens under their care, K. F. Koopman and R. S. Voss for their comments on the manuscript, Rosanne Miezio for her fine illustrations, and G. Lake for assistance with preparing the manuscript.

Literature Cited

Allen, G. M. 1938. The mammals of China and Mongolia. Natural History of Central Asia, 11: xxv+620 pp.—American Museum of Natural History, New York.

Anthony, H. E. 1941. Mammals collected by the Vernay-Cutting Burma Expedition.—Field Museum of Natural History, Zoological Series 27:37–123.

Chasen, F. N. 1940. A handlist of Malaysian mammals.—Bulletin of the Raffles Museum, Singapore 15:xx+1–209.

Ellerman, J. R., and T. C. S. Morrison-Scott. 1951. Checklist of Palearctic and Indian mammals 1758–1946.—British Museum (Natural History), London, 810 pp.

Jenkins, P. D. 1976. Variation in Eurasian shrews of the genus *Crocidura* (Insectivora: Soricidae).—Bulletin of the British Museum (Natural History), Zoology 30(7):269–309.

Lekagul, B., and J. A. McNeely. 1977. Mammals of Thailand.—Kurusapha Ladprao Press, Bangkok. li+758 pp.

Medway, L. 1977. Mammals of Borneo: field keys and an annotated checklist.—Monographs of the Malaysian Branch of the Royal Asiatic Society 7:xii+1–172.

Milne-Edwards, A. 1872. Recherches pour servir a l'histoire naturelle des mammifères.—G. Masson, Paris.

Moore, J. C., and G. H. H. Tate. 1965. A study of the diurnal squirrels, Sciurinae, of the Indian and Indochinese subregions.—Fieldiana: Zoology 48:1–351.

Osgood, W. H. 1932. Mammals of the Kelley-Roosevelts and Delacour Asiatic Expeditions.—Field Museum of Natural History, Zoological Series 18(10):193–339.

Robinson, H. C., and C. B. Kloss. 1922. New Mammals from French Indo-China and Siam.—Annals and Magazine of Natural History (9) 9:87–99.

Thomas, O. 1912. New species of *Crocidura* and *Petaurista* from Yunnan.—Annals and Magazine of Natural History (8)9:686–688.

———. 1927. The Delacour exploration of French Indo-China. Mammals.—Proceedings of the Zoological Society of London 1927:41–58.

Van Peenen, P. F. D., P. F. Ryan, and R. H. Light. 1969. Preliminary identification manual for mammals of South Vietnam.—United States National Museum, Washington. vi+310 pp.

(LRH) Museum of Zoology and Division of Biological Sciences, University of Michigan, Ann Arbor, Michigan 48109; (RMT) Division of Mammals, Field Museum of Natural History, Chicago, Illinois 60605-2496.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 121–126

PARVULODESMUS PROLIXOGONUS, A NEW GENUS AND SPECIES OF XYSTODESMID MILLIPED FROM SOUTH CAROLINA (POLYDESMIDA)

Rowland M. Shelley

Abstract.—The minute xystodesmid milliped, *Parvulodesmus prolixogonus,* is described as a new genus and species from a sample collected 30 years ago in Abbeville, South Carolina. The principal diagnostic character is a long, slender acropodite, which overlaps the sterna of segments 4–6 and curves dorsad into a small apical loop. The species is assigned to the tribe Rhysodesmini on the basis of gonopodal traits, small body size, and sternal hairs.

For the past six years I have been investigating the endemic xystodesmid milliped fauna of piedmont South Carolina, diagnosing three new genera in the tribe Apheloriini—*Croatania, Brevigonus,* and *Furcillaria* (Shelley 1977, 1980, 1981a), and describing other species in a revision of *Sigmoria* (1981b) and a second paper on *Brevigonus* (1981c). I have visited the area around Abbeville, Abbeville County, four times searching for a purported new species of the tribe Rhysodesmini that Leslie Hubricht collected in the early 1950s. Richard L. Hoffman, who examined the milliped at the time of its collection, told me of its existence and that it represented a new genus. Unfortunately, no gonopod drawings were available, and the preserved specimens were not in his private collection nor in any major museum in the eastern United States. Re-collection of the species therefore seemed necessary, and I visited Abbeville in spring, summer, and fall, to allow for seasonal occurrence. These efforts, however, were unsuccessful.

In 1981 the milliped collection of the late William T. Keeton, former Professor of Biology at Cornell University, was transferred to Dr. Hoffman to be incorporated into his holdings. While casually perusing this material one day, I chanced upon the long lost sample from Abbeville, which contained two males and two females in good condition. However, the gonopods had been removed from one male and were not in the vial. Consequently, the critically important genitalic features can only be determined from the other male, which I designate the holotype. These are the smallest xystodesmids I know of, smaller even than *Gyalostethus monticolens* (Chamberlin) or *Pleuroloma pinicola* Shelley, and I agree completely with Dr. Hoffman that they represent a new genus and species in the tribe Rhysodesmini.

Parvulodesmus, new genus

Type species.—Parvulodesmus prolixogonus, new species.

Description.—A genus of minute rhysodesmine xystodesmids with the following characteristics:

Body composed of head and 20 segments in both sexes; W/L ratio 21–24%. Head of normal appearance, smooth; epicranial suture distinct, not bifid; facial setae reduced, epicranial and interantennal absent. Antennae moderately long, with 4 small, apical sensory cones.

Terga smooth, strictures faint. Collum large and broad, but not extending beyond ends of following tergite. Paranota strongly depressed; peritremata flat and inconspicuous on all segments, ozopores opening laterad.

Caudal segments normal for family.

Pregonopodal sterna of males with variable concave depressions; postgonopodal sterna of males and all sterna of females flat and unmodified, with small clusters of setae beside leg coxae. Gonapophyses of males short and apically expanded. Coxae without ventrodistal spines or tubercles; prefemoral spines short and blunt, greatly reduced, absent from some legs.

Gonopodal aperture relatively large, elliptical. Gonopods with very long acropodites, overlapping apically but otherwise parallel to each other, extending forward from aperture between legs of segments 6, 5, and 4, lying in sternal depressions. Coxae small, without apophyses. Prefemora small, with short, acicular processes. Acropodites long, thin, and flat, curving dorsad into narrow loops apically, with medial subterminal digitiform processes.

Cyphopodal aperture narrow, encircling second legs. Cyphopods minute but with comparatively large, rugulose receptacles overlying ventral valves. Valves small and subequal; operculum not detectable but presumed present under free end of valves.

Species.—One is known; others may also occur in piedmont South Carolina.

Relationships.—*Parvulodesmus* appears to be most closely related to several undiagnosed rhysodesmine species in the Gulf Coastal Plain of southern Alabama. These species, which constitute one or possibly two new genera, also have long gonopodal acropodites that overlap two or more sterna anterior to the gonopodal aperture.

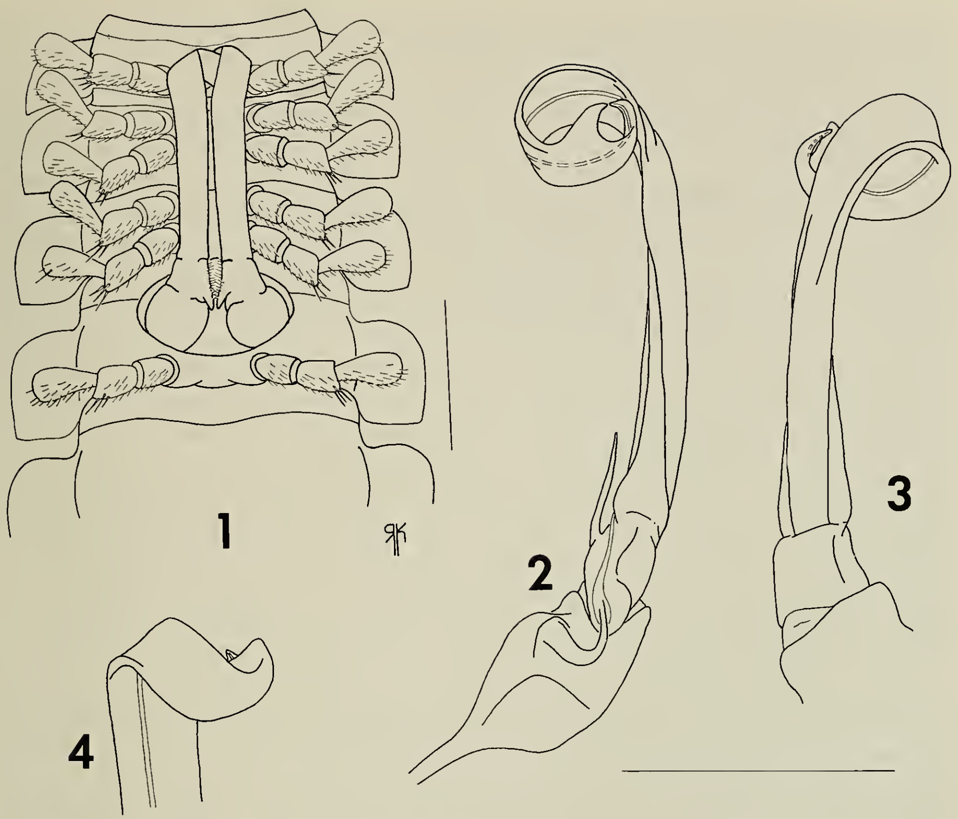
Parvulodesmus prolixogonus, new species
Figs. 1–4

Type specimens.—Male holotype, and one male and two female paratypes (collection of R. L. Hoffman) collected by Leslie Hubricht, 1 May 1952, from Abbeville, Abbeville Co., South Carolina.

Diagnosis.—With the characters of the genus.

Holotype.—Length 14.7 mm, maximum width 3.1 mm, W/L ratio 21.1%, depth/width ratio 58.1%. Color in life unknown; all specimens completely blanched by preservative, without any evidence of stripes or other pigmentation patterns.

Head capsule smooth, polished; epicranial suture thin but distinct, terminating in slight impression in interantennal region, not bifid. Antennae moderately long and slender; reaching back to middle of fourth tergite, becoming progressively more hirsute distally, with 4 apical sensory cones, no other sensory structures apparent, first antennomere subglobose, 2–6 clavate, 7 short and truncate; relative lengths of antennomeres $3 > 2 > 4 > 5 = 6 > 1 > 7$. Genae not margined laterally, with distinct medial impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Facial setae as follows: epicranial, interantennal, frontal, and genal not detected, subantennal 1-1, clypeal about 8-8, labral about 12-12.



Figs. 1–4. *Parvulodesmus prolixogonus*. 1, Gonopods *in situ*, ventral view of holotype. 2, Left gonopod of holotype, medial view. 3, Telopodite of the same, lateral view. 4, Distal half of acropodite, oblique dorsal view. Scale line for fig. 1 = 1.00 mm; line for other figs. = 1.00 mm for each.

Terga smooth, polished. Collum broad, ends not produced beyond those of following tergite. Paranota strongly depressed, angled sharply ventrad and continuing slope of dorsum; anterior corners rounded, caudolateral corners blunt on all segments; posterior edges of paranota only slightly discontinuous with dorsum. Peritremata thin and inconspicuous, only slightly elevated above paranotal surface; ozopores located near middle of peritremata, opening laterad.

Sides of metazonites finely granular, without noticeable grooves or impressions. Strictures faint, indistinct. Sterna of segments 4–6 with concave central depressions, deepest on segment 4, to accommodate stems of gonopodal acropodites; without lobes or other processes. Postgonopodal sterna without lobes, caudal edges straight; with shallow transverse grooves between leg pairs and short, longitudinal grooves between caudal legs; with 2 to 4 long, slender setae in small clusters near coxae of both leg pairs. Pregonopodal legs densely hirsute; postgonopodal legs becoming progressively less hirsute caudally. Coxae without projections; prefemora apically blunt and rounded, without spines; tarsal claws hooked, of normal length on all legs. Hypoproct rounded; paraprocts with margins slightly thickened.

Gonopodal aperture elliptical, with slight indentations anteriolaterad, margins elevated above metazonal surface, not thickened. Gonopods *in situ* (Fig. 1) with telopodites projecting ventrad from aperture, extending anteriad in parallel arrangement over sterna of segments 6, 5, and 4, apices overlapping and interlocking between third pair of legs. Gonopod structure as follows (Figs. 2–4): Coxa small, without apophysis. Prefemur small, with short, acicular process arising on dorsal side, extending beyond juncture of prefemur and acropodite for about ⅛ of length of latter. Acropodite demarcated from prefemur by slight constriction, in form of thin, narrow blade extending linearly from prefemur, with apical loop of narrow diameter; loop located at about ⅔ length, curving dorsad from stem of acropodite, with subterminal digitiform projection on medial edge subtending small circular area between solenomerite; solenomerite short, apically acute, directed subanteriad. Prostatic groove arising in pit in base of prefemur, crossing to dorsal side of acropodite at juncture with prefemur, running along inner surface of apical loop and opening terminally on solenomerite.

Male paratype.—The male paratype agrees with the holotype in all particulars except facial setae, which are as follows: epicranial and interantennal absent, subantennal 1-1, frontal 1-1, genal 2-2, clypeal about 8-8, labral about 12-12, merging with clypeal series and continuing along genal margins for about one-third of lengths, about 4 setae on each side. Gonopodal variation is unknown, since the paratype gonopods were previously dissected and lost.

Female paratype.—Length 13.1 mm, maximum width 3.2 mm. W/L ratio 24.4%, depth/width ratio 62.5%. Agreeing closely with males in somatic features except paranota more strongly depressed, creating appearance of more highly arched body, and lacking sternal depressions of pregonopodal segments of males. Cyphopods with comparatively large, subtriangular receptacle visible in aperture, lying over and obscuring valves, surface rugulose; valves small and subequal, located dorsad to receptacle, opening anteriad, surfaces finely granulate.

Distribution.—Known only from the type locality.

Remarks.—The prefemoral process of *P. prolixogonus* can be easily overlooked or mistaken for a seta or cotton fiber, when the gonopod is placed on cotton for drawing. It is colorless, translucent, and closely appressed to the prefemur and base of the acropodite. Its shortness relative to the extremely long acropodite makes it look like a macroseta, and it blends into the acropodite and becomes nearly invisible in any view except medial, which reveals the narrow gap between them. The process is also very fragile and can be easily broken during gonopod dissection.

Parvulodesmus prolixogonus is assigned to the tribe Rhysodesmini because of the small body size, the hairs on the sterna, the parallel arrangement of the gonopods, and the acicular prefemoral process. These traits are all more typical of the Rhysodesmini than any other southeastern xystodesmid tribe. Small body size is shared with the genera *Gyalostethus, Caralinda,* and the undescribed Alabama taxa; hirsute sterna are exhibited by two species of *Pleuroloma*; and all rhysodesmine genera except *Caralinda* display acicular prefemoral processes and parallel gonopods. One rhysodesmine trait not observed was the sternal remnant connecting the gonopodal coxae. I neglected to check this character before dissecting the gonopods of the holotype, and the nature of the remnant will have to be determined from fresh material.

In trying to discover more specimens near Abbeville, I checked a wide variety of biotopes in every habitat I could think of. I also wrote the collector, but he could only remember that the sample was taken near the railroad. Many of the places I investigated were urbanized sites in or near Abbeville, and one trip came during the last week of April, the same time of year that the type sample was collected. Thus, I think I checked, at the proper time of year, the kinds of sites Hubricht did. On the thought that Abbeville might be at the range periphery where the species is least common, I investigated distant parts of the county and adjacent McCormick, Greenwood, and Anderson counties, to try to find an area of greater abundance. Although not specifically looking for *Parvulodesmus,* I have also investigated thoroughly during the past six years the entire Piedmont of South Carolina and, to a lesser extent, the tier of counties along the southern side of the Savannah River in Georgia. However, trying to find such a tiny animal in such a large area with no habitat information is exceedingly difficult, and it is not surprising that none of these activities were successful. I think that the situation with *Parvulodesmus* may be similar to that of *Caralinda* in southern Georgia, Alabama, and neighboring Florida. In this genus single species were described by Hoffman (1978) and me (1979), but I have recently discovered a large amount of *Caralinda* from the Florida panhandle in the Florida State Collection of Arthropods, containing two or three more new species. Thus, *Caralinda* consists of four to five species and occupies a much larger area than previously thought. Similarly, *Parvulodesmus* may also consist of two or more species and occupy a much larger area in South Carolina than just Abbeville County. However, I have exhausted all my knowledge and field experience trying to find more individuals, and my only further thought is that May might be the time of least abundance. Perhaps the species of *Parvulodesmus,* like *Nannaria conservata* Chamberlin (Shelley 1975), are most abundant during the winter months and are prevalent in December, January, and February. I leave this idea for future investigators, who may be challenged by the rarity of *Parvulodesmus,* or local biologists, who live in the Abbeville-Greenwood area and can sample in winter and continuously throughout the year. A continuous, long-term effort of this kind may be required to find *Parvulodesmus* again.

Acknowledgments

I thank Richard L. Hoffman, for the privilege of describing these new taxa, and Renaldo G. Kuhler, N.C. State Museum scientific illustrator, who prepared Figure 1. This study was aided by financial assistance by the National Science Foundation, Grant No. DEB 7702596.

Literature Cited

Hoffman, Richard L. 1978. A new genus and species of rhysodesmine milliped from southern Georgia (Polydesmida: Xystodesmidae).—Proceedings of the Biological Society of Washington 91:365–373.

Shelley, Rowland M. 1975. The identity of *Nannaria conservata* Chamberlin, with notes on an abnormal male and descriptions of two new species of *Nannaria* from North Carolina (Diplopoda: Polydesmida: Xystodesmidae).—Proceedings of the Biological Society of Washington 88:179–188.

———. 1977. The milliped genus *Croatania* (Polydesmida: Xystodesmidae).—Proceedings of the Biological Society of Washington 90:302–325.

———. 1979. A new milliped of the genus *Caralinda* from north Florida (Polydesmida: Xystodesmidae).—Florida Entomologist 62:184–187.

———. 1980. The status of *Cleptoria shelfordi* Loomis, with the proposal of a new genus in the milliped family Xystodesmidae (Polydesmida).—Brimleyana 3:31–42.

———. 1981a. A new xystodesmid milliped genus and three new species from piedmont South Carolina (Polydesmida).—Proceedings of the Biological Society of Washington 94:949–967.

———. 1981b. Revision of the milliped genus *Sigmoria* (Polydesmida: Xystodesmidae).—Memoirs of the American Entomological Society No. 33, 140 pp.

———. 1981c. A new milliped of the genus *Brevigonus* from South Carolina, with comments on the genus and *B. shelfordi* (Loomis) (Polydesmida: Xystodesmidae).—Brimleyana 6:51–60.

North Carolina State Museum of Natural History, P.O. Box 27647, Raleigh, North Carolina 27611.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 127–133

CURIDIA DEBROGANIA, A NEW GENUS AND SPECIES OF AMPHIPOD (CRUSTACEA: OCHLESIDAE) FROM THE BARRIER REEFS OF BELIZE, CENTRAL AMERICA

James Darwin Thomas

Abstract.—The family Ochlesidae is amended to include the new genus *Curidia,* which differs from all other members by possessing maxillipedal palps. *Curidia debrogania* is described and compared to other genera and species within the family Ochlesidae.

Curidia debrogania is plesiomorphic by possession of maxillipedal palps, suggesting this member of the small, cryptic family might have originated in the tropical Western Atlantic. Distribution records and ecological notes are included.

Family Ochlesidae

Accessory flagellum absent; palp of maxilliped absent or uniarticulate; mouthparts projecting subconically; mandible with molar reduced or lacking; coxae 1–4 subacuminate; telson entire.

Curidia, new genus

Diagnosis.—Article 1 and 2 of antenna 1 each with long ventrodistal cusp, peduncular article 1 longer than 2, flagellum 4-articulate, article 2 longest, exceeding peduncular article 1 in length. Coxa 1 rounded ventrally, coxae 2 and 3 dominant, elongate. Upper and lower lips apically acute; mandible with molar; first maxilla with palp, outer plate styliform; second maxilla with both plates styliform, outer plate longest; maxilliped with elongate inner plate, outer plate slightly armed, palp present, consisting of slender unarmed article bearing terminal seta.

Etymology.—The name *Curidia* is from the Greek, Kouridios, "wedded," (gender feminine), and is in reference to Stebbing's original designation of the type-genus *Ochlesis,* which means "disturbance." This designation referred to the lack of maxillipedal palps in the type species, *O. innocens* Stebbing, 1910. The presence or absence of these palps is a primary distinction between the hyperiidean and gammaridean amphipods. Hence, Stebbing felt that the lack of these structures was a significant "disturbance," or "disruption" among the Gammarideans. The presence of maxilliped palps in the genus *Curidia* allows the family Ochlesidae to be included without exception among the Gammarideans.

Curidia debrogania, new species

Description.—Male: body strongly compressed and very thin dorsally; pleonite 2 with rounded process dorsally; urosomite 1 thin and elongate; epimeron 3, posteroventral margin with upturned hook; head small with acute lateral cephalic lobe, eye prominent, composed of 21 ommatidia; article 1 of antenna 1 longer

Fig. 1. *Curidia debrogania*, holotype, male, 1.59 mm, JDT Bel 48, Carrie Bow Cay, Belize.

than article 2, articles 1 and 2 each with large ventrodistal cusp, cusp of article 1 extending to end of article 3, cusp of article 2 extending halfway along flagellum; accessory flagellum absent; primary flagellum 4-articulate, article 2 elongate, apical and ventral margins with long aesthetascs; antenna 2 shorter and less robust than antenna 1, article 4 with ventral cusp extending halfway along article 5; flagellum 4-articulate, article 2 slightly smaller than article 1; upper lip large, triangular; mandibles massive, styliform, incisors simple, left mandible with small lacinia mobilis, molar small, circular, weakly triturative, ratio of palp articles 1–3, 35:45:57, article 3 with double row of small facial ridges and 3 short spines distally; lower lip slender, apices extended, mandibular projections produced and narrowly rounded; maxilla 1, inner plate small with 1 apical and 1 subapicomedial seta, outer plate attenuated, styliform and slightly recurved distally, medial margin bearing 5 hooked spines subapically, preceded proximally by marginal row of fine setae, palp uniarticulate, borne on raised process and bearing single long terminal seta; maxilla 2, inner plate styliform with 7 pectinate spines (5 medial, 1 apical, 1 subapical) and 4 short setae on medial margin, outer plate longer and thinner than inner plate, bearing several long apical setae, plus single basofacial spine and 6 short setae on lateral margin; maxilliped, inner plate thin, elongate (0.77 times outer plate), with 3 facial and 2 distomedial plumose setae, short apical nail, and numerous short setae on distolateral margin, outer plate curled orally, apical margin rounded with 4 subapical spines and plumose seta, 2 mediofacial setae on oral margin, palp uniarticulate, bearing long terminal seta extending beyond outer plate; coxa 1 small, dentate on anteroventral margin; coxa 2 elongate, anterior margin produced; coxa 3 also elongate with straight anterior margin, posterior margin produced; coxa 4 smaller than coxae 1–3, anteroventral margin truncate; coxae 5 and 6 similar, with posteroventral margins produced; coxa 7

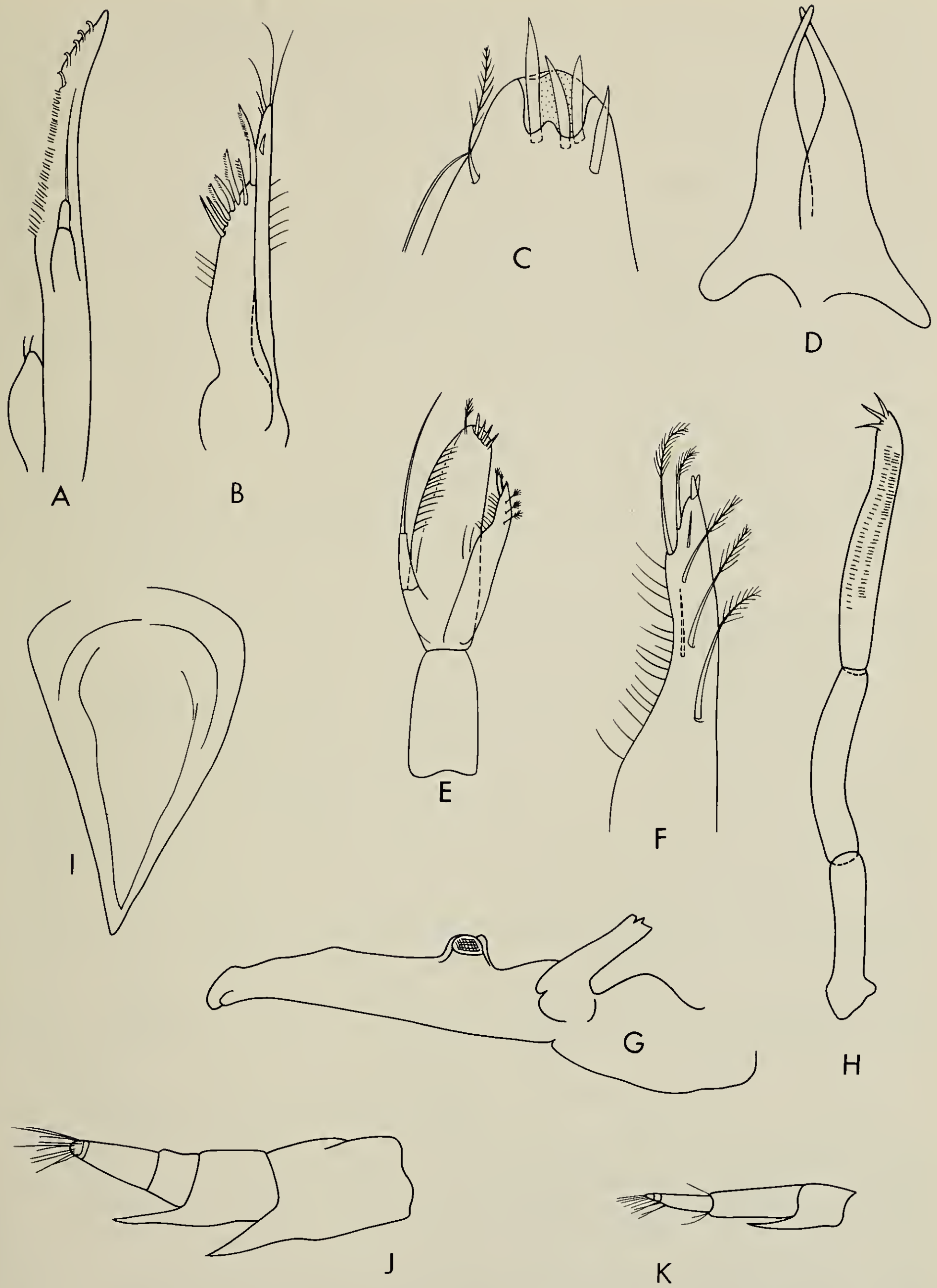


Fig. 2. *Curidia debrogania,* A–I, holotype, male, 1.59 mm, JDT Bel 48: A, Maxilla 1; B, Maxilla 2; C, Maxilliped outer plate; D, Lower lip; E, Maxilliped; F, Maxilliped inner plate; G, Right mandible; H, Mandibular Palp; I, Lower lip. J–K, paratype, female, 1.40 mm: J, Antenna 1; K, Antenna 2.

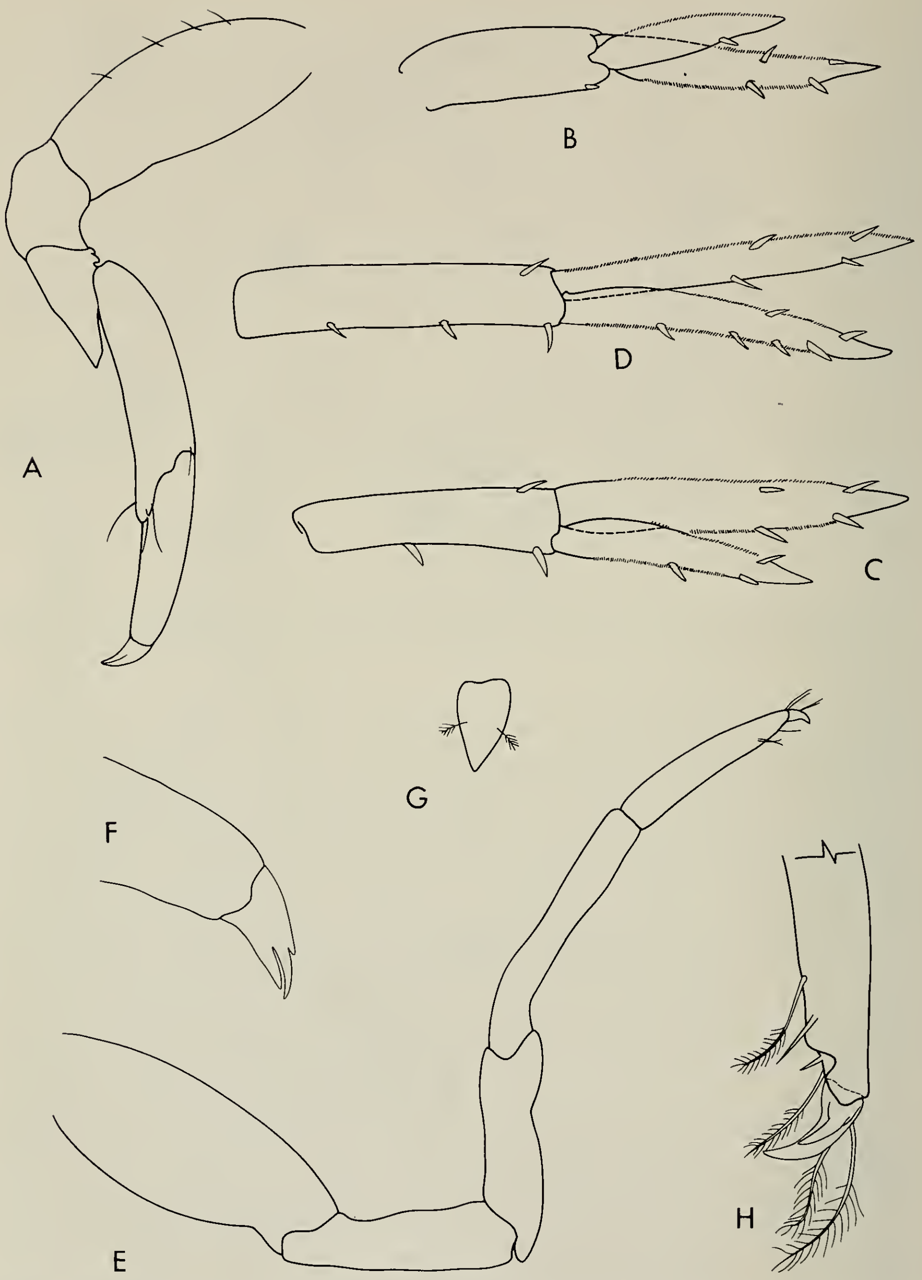


Fig. 3. *Curidia debrogania,* holotype, male, 1.59 mm, JDT Bel 48: A, Gnathopod 2; B, C, D, Uropods 3, 2, 1; E, Gnathopod 1; F, Gnathopod 2; G, Telson; H, Gnathopod 1.

with slightly rounded posterior concavity; gnathopod 1 simple, article 2 slightly inflated, articles 3 and 4 subequal and elongate, article 5 longer than 6, latter with 2 plumose setae and 2 spines near joint, dactyl with accessory process and 2 long plumose setae; gnathopod 2 basis slightly inflated, articles 3 and 4 short, subequal, article 4 extending distoventrally, article 5 elongate and distoventrally produced, article 6 elongate, shorter than 5, dactyl bifid with accessory process; pereopods 3 and 4, article 4 with anterodistal process extending approximately halfway along article 5, article 6 with several posterior spines, dactyl massive, elongate; pereopods 5–7 similar in structure to pereopods 3 and 4; pleonite 2 with obtuse middorsal hump, pleonite 3, lateral margins with strong upturned tooth; urosomite 1 elongate; uropod 1 reaching beyond uropods 2 and 3, peduncle elongate, subequal to rami, with single apicolateral spine and 3 medial marginal spines, rami lanceolate, subequal, outer ramus with 4 lateral marginal and 2 medial marginal spines, inner ramus with paired medial and lateral marginal spines, both margins of outer ramus and medial margin of inner ramus finely serrate; uropod 2 peduncle with 1 apicolateral, 1 midlateral, and 1 subapicomedial spine, outer ramus subequal to peduncle, with 2 spines on lateral margin and single distomedial spine, inner ramus 1.36 times the outer, paired spines on distolateral and distomedial margins, all margins of both rami finely serrate; uropod 3 peduncle with short subapicolateral spine, outer ramus short, with a single spine on lateral margin, inner ramus 1.43 times the outer with 2 lateral and 2 medial marginal spines, entire lateral margin of outer ramus and both margins of inner ramus finely serrate; telson entire, elongate, with 2 plumose setae.

Female.—Apart from the presence of brood plates, the only apparent differences are in antenna 1. Females of *C. debrogania* have smaller cusps and lack ventral setae on the flagellum, all setae being apical. Ovigerous specimens have been taken from Biscayne Bay, Florida, and Belize as small as 1.40 mm.

Etymology.—*Curidia debrogania* is named in honor of Debra L. Rogan, September 8, 1950 to December 25, 1981.

Types.—Deposited in the United States National Museum of Natural History collections, holotype, USNM 191041, male, 1.59 mm; paratype, USNM 191042, female, 1.40 mm.

Type-locality.—JDT Belize 48, Carrie Bow Cay, Belize, 7 June 1980, 6 m, partly cemented coral rubble in patch reef area just inside channel between Carrie Bow Cay and Water Cay, 16°48′N, 80°05′W.

Color.—White laterally, blending to translucent brown along dorsal and ventral margins of body. Pereonites 1–7, antenna 2, gnathopods, and pereopods 3–7 with distinct purple or deep maroon banding.

Distribution.—Barrier reefs of Belize, to Biscayne Bay, Florida, sublittoral, 2–20 m, usually associated with macroalgae.

Ecology.—*Curidia debrogania* is usually associated with coral reef habitats where it is found in areas of high current velocity or wave surge (i.e., lagoonal channels, or in the forereef areas). The mouthparts suggest a parasitic existence although no documentation exists to support this thesis at present. The massive dactyls on pereopods 3–7 could be used to hold on to a host in areas of high current velocities, or may aid in forcing the conical mouthparts into host tissues. The distinctive color pattern suggests that *C. debrogania* may be a mimic of some species of micromollusc. Specimens of *C. debrogania* are usually taken from rocky outcrops that have attached macroalgae.

Discussion.—While *C. debrogania* is unique among ochlesids in possessing maxilliped palps, it appears, in other external characters, closest to *Ochlesis alii* Barnard, 1970, from Hawaiian waters, and *O. innocens* Stebbing from the Australian littoral. *Curidia debrogania, O. alii,* and *O. innocens* are the only ochlesids having both antennal cusps and teeth on the posterior margin of epimeron 3. Males of *O. alii* (not at present described) should prove to have somewhat more prominent antennal cusps than females and therefore approach the condition of *C. debrogania* males. *Curidia debrogania* differs from *O. alii* in 1) the longer cusps on antennae 1 and 2; 2) the more robust palp of maxilla 1; 3) less spinose and laceolate uropods. *Ochlesis innocens* resembles *C. debrogania* in the large antennal cusps, but differs in 4) shorter peduncular article 2 and much longer flagellar article 2 of antenna 1; 5) absence of a palp on maxilla 1 (if Pirlot's identification of *O. innocens* from Isles Aru is correct, then a rudiment of a palp is present); 6) absence of a cusp on antenna 2; 7) ventral margin of coxa 1 acute versus rounded in *C. debrogania.*

Two of the four remaining species of ochlesids, *O. levetzowi* Schellenberg, 1953, and O. *eridunda* Barnard, 1972, lack antennal cusps and a tooth on epimeron 3, and in general body appearance are not as laterally flattened and dorsally acute as those species with antennal cusps and a tooth (or teeth) on epimeron 3. *Oclesis lenticulosa* K. H. Barnard, 1940, from the littoral of South Africa lacks antennal cusps, but has a tooth on epimeron 3. *Oclesis meraldi* Barnard, 1972, from the Australian littoral differs so grossly in external morphology and ornamentation from all other ochlesids that it will be used as the type-species for a new genus (Barnard, pers. comm.).

The presence of maxillipedal palps in *C. debrogania* suggests it to be more primitive (plesiomorphic) than other members of the family, all of which lack this character. This would suggest a Western Atlantic origin for the ochlesids, whereas Pacific and Indo-Pacific forms would be of more recent origin in having lost the maxillipedal palps. This hypothesis will remain unproven until additional material can be studied from wide geographical areas. *Curidia debrogania* is also the smallest representative in the Ochlesidae, with fully ovigerous females being taken at a length of 1.40 mm. Ochlesids have been overlooked by most investigators because of their minute size (most species) and cryptic habitat. Not until thorough sampling of all tropical reef areas is conducted will the zoogeograpical affinities and ecology of ochlesids be better understood.

Acknowledgments

I wish to thank Mike Carpenter of the Smithsonian Institution for tireless assistance in the field under trying conditions; Dr. J. L. Barnard of the Smithsonian Institution for critically reviewing the manuscript; the Smithsonian's Investigations of Marine Shallow Water Ecosystems (IMSWE), which is partly funded by a grant from the Exxon Corporation, for supporting the author at its field laboratory at Carrie Bow Cay, Belize. This research was funded by grants DEB 7920534 and DEB 8121128 from the National Science Foundation. This paper forms IMSWE contribution number 120.

Literature Cited

Barnard, J. L. 1970. Sublittoral Gammaridea (Amphipoda) of the Hawaiian Islands.—Smithsonian Contributions to Zoology 34:1–286, 180 figs.

———. 1972. Gammaridean Amphipoda from Australia, Part I.—Smithsonian Contributions to Zoology 103:1–333, 194 figs.

Barnard, K. H. 1940. Contributions to the crustacean fauna of South Africa, XII: Further additions to the Tanaidacea, Isopoda, and Amphipoda, together with keys for the identification of hitherto recorded marine and freshwater species.—Annals of the South African Museum 32:381–543, 35 figs.

Schellenberg, A. 1953. Ergänzungen zur Amphipoden fauna Südwest-Afrikas nebst Bemerkungen über Bratraumbildung.—Mittheilungen aus dem Zoologisch Museum in Berlin 29:107–126, 7 figs.

Stebbing, T. R. R. 1910. Crustacea. Part 5. Amphipoda. *In* Scientific Results of the Trawling Expedition H.M.C.S. Thetis.—Memoirs of the Australian Museum 4(2):565–658, pl. 47–60.

Newfound Harbor Marine Institute, Big Pine Key, Florida 33043.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 134–144

PROECHIMYS SEMISPINOSUS (RODENTIA: ECHIMYIDAE): DISTRIBUTION, TYPE LOCALITY, AND TAXONOMIC HISTORY

Alfred L. Gardner

Abstract.—The type locality of *Proechimys semispinosus* (Tomes) has been alleged to be Gualaquiza, in the lowland forests of southeastern Ecuador. A review of the travels of the collector Louis Fraser, and examination of the content of reports based on the mammals he collected, plus the comparison of the type specimen with samples representing several species of *Proechimys* from Central and South America, indicate that the type did not come from Gualaquiza. The type locality of *P. semispinosus* is corrected to Esmeraldas, on the Pacific coast of Ecuador.

The specimens on which Tomes (1860b) based the name *Echimys semispinosus* were collected by Louis Fraser in Ecuador and alleged (Allen 1916) to have come from Gualaquiza, a community on the Rio Santiago in the Province of Morona-Santiago. This site (03°24′S, 78°33′W *fide* Paynter and Traylor 1977) is east of the Andes, at 750 meters elevation, in the tropical zone of the western Amazonian forests. I have concluded, however, from my examination of the skull of the type (British Museum [Nat. Hist.] 7.1.1.173), that it is unlike skulls of any of the species of *Proechimys* known to me from South America east of the Andes. Instead, it has the cranial features that characterize populations of *Proechimys* found west of the Andes along the Pacific lowlands of Colombia and Ecuador and northward through Central America to Honduras that currently are known in the literature as either *Proechimys centralis* or *P. semispinosus*.

The present report is the result of my examination of specimens and search of the literature in an attempt to determine the provenance of the specimens that Tomes used in describing *P. semispinosus*. In addition to the examination and comparison of specimens, including types, I have explored three main sources of information: the published history of the use of the name *P. semispinosus*, accounts of Fraser's travels in Ecuador, and the content of reports on the mammals Fraser collected.

Taxonomic History

1860

Tomes described *Echimys semispinosus* based primarily on one of "three specimens . . . received in spirits, all of which were females; one of them contained two young" (1860b:267–268), and figured the skull of one of these. The specimens had been collected by Fraser at an unspecified locality in Ecuador. Tomes introduced this account by stating (p. 265), "In my first notes [Tomes 1859] on Mammals, collected by Mr. Fraser, I included the *Echimys cayennensis* from the examination of a specimen which had lost the tail, and was otherwise in an unsatisfactory condition. Other and better specimens of *Echimys* having been received, I have been able to make out clearly that they represent a new and well-marked species, and that the former specimen was similar to them."

1889
True recorded *Echinomys semispinosus* from Nicaragua and Costa Rica.

1896
Thomas described *Echinomys centralis* (type locality: San Emilio, south end of Lake Nicaragua) and said that True's (1889) report was based on the same species. Thomas also stated (p. 312), "Both in the Merida and Bogota collections there occur specimens of the genus *Echinomys* which, on account of their (in comparison with other species) 'very dark brown colour' and other characters, may fairly be assigned to *E. semispinosus,* Tomes, especially if, as seems to be the case, Tomes's woodcut of the skull is incorrect in details." Thus Thomas assigned seven specimens (p. 313) from Colombia to *E. semispinosus.*

1897
Thomas, in his description of *Echimys gymnurus* (=*Hoplomys gymnurus*), remarked (p. 551), "This handsome *Echimys* differs from Tomes's *E. semispinosus,* also from Ecuador, but without exact locality, by its richer rufous colour . . . . In all these points the Bogota *Echimys* assigned last year to *E. semispinosus* agrees much better with Tomes's description than does that [*E. gymnurus*] brought home by Mr. Rosenberg, in spite of the Ecuadoran locality of the latter."

1898
Thomas recanted his assignment of the Bogota specimens (which he here named *Echimys chrysaeolus*) to *E. semispinosus* Tomes, and decided that *E. semispinosus* was allied with the Nicaraguan specimens he had already described (1896) as *E. centralis.* This resulted from the discovery of "a dark brown *Echimys* marked, in what appears to be a hand writing similar to that on some of Fraser's labels, '*Echimys semispinosus,*' " among specimens that had been overlooked for many years in rooms of the Zoological Society. Thomas stated (p. 244), "This [specimen] so precisely agrees with Tomes's description of that animal, that there can be no reasonable doubt that it is one of the original specimens collected by Fraser and referred to in Tomes's paper." The label may have lacked notation of locality for Thomas failed to mention one.

1899
Allen proposed the name *Proechimys* (type-species, *Echimys trinitatus* Allen and Chapman) to include, among others, the species *P. semispinosus.*

1900
Thomas described *Proechimys rosa* (type locality, Santa Rosa, Prov. El Oro, Ecuador), *P. centralis panamensis* (type locality, "Savanna near Panama") and *P. centralis chiriquinus* (type locality, Bugava [=Bugaba], Prov. Chiriquí, Panama). Thomas allied *P. semispinosus* with *P. decumanus* (described by Thomas 1899, from Chongon, Prov. Guayas, Ecuador), but said that *P. rosa* was allied to the Central American species *P. centralis.*

1901
Bangs described *Proechimys burrus* (type locality, Isla San Miguel, Golfo de Panamá), which he allied with *P. centralis.*

1905
Bangs described *Proechimys gorgonae* (type locality, Isla Gorgona Colombia), which he allied with *P. centralis panamensis.*

1911
Thomas described *P. semispinosus calidior* (type locality, San Javier, Prov. Esmeraldas, Ecuador), calling it "A rufous lowland representative of true *semispinosus.*" In a footnote (p. 254), he said that the type of *P. semispinosus* was British Museum (NH) number 7.1.1.173, which means that the specimen was the 173rd cataloged on 1 January 1907.

1914
Hollister described *Proechimys rubellus* from Costa Rica. He said the type came from the Angostura Valley, but as True (1889:467) had stated earlier and as indicated on the label of the holotype, the actual collection site is Pacuare.

1914
Thomas described *P. centralis colombianus* (type locality, Condoto, Depto. Chocó, Colombia) and compared it to "*Proechimys xanthaeolus,*" apparently a *lapsus* for *P. chrysaeolus.*

1916
Allen wrote (pp. 206–207), "The type locality of *Echimys semispinosus* Tomes, according to Thomas (on the back of label), is Gualaquiza, Ecuador, this being the specimen from which the skull was figured. Three specimens of this species were received 'in spirits, all of which were females; one of them contained two young' (Tomes, P. Z. S., 1860, p. 267). Two of these specimens are now in the British Museum, 'evidently skinned out of spirit and much discolored,' as stated on the labels. I omitted to examine the type skull figured by Tomes, but from an examination of Tomes's figure it is too adult to have belonged to either of these two skins, which are only about half grown. The skin of the third specimen, doubtless the adult female mentioned by Tomes, and the one to which the figured skull belonged, has apparently been lost."

1920
Goldman arranged all of the named forms of Central American *Proechimys* as subspecies of *P. semispinosus,* except for *P. centralis chiriquinus,* which he treated as a synonym of *P. semispinosus panamensis.*

1935
Tate in his review of the taxonomy of *Proechimys,* listed *P. semispinosus* with western Amazonian species on the basis of the alleged type locality.

1937
Bole described *P. semispinosus goldmani* from Altos Cacao, Prov. Veraguas, Panama.

1940
Ellerman listed all named forms of *Proechimys semispinosus* as subspecies or synonyms of *P. cayennensis* (Desmarest), but remarked that if this be incorrect, *burrus, centralis, panamensis* (with *chiriquinus* a synonym), *rubellus, colombianus,* and *calidior* should be considered races of *P. semispinosus.*

1944
Osgood said that the type of *Proechimys semispinosus* was a skull only and that, as the type locality was in southeastern Ecuador, populations from northern Peru (Huallaga River) probably were identical or closely related. He also assigned a series of specimens from Lagunas in east central Peru to *P. semispinosus*. Osgood believed *P. semispinosus calidior* to be a ''slight subspecies of *semispinosus*'' allied with *P. rosa* and Central American forms.

1946
Kellogg described *P. semispinosus ignotus* from Isla San José, Golfo de Panamá, Panama.

1946
Goodwin treated Costa Rican *centralis, panamensis,* and *rubellus* as subspecies of *P. cayennensis*.

1948
Hershkovitz considered *P. semispinosus* a subspecies of *P. guyannensis* (E. Geoffroy), the senior synonym of *P. cayennensis* (Desmarest). He described (p. 138) *P. quadruplicatus* from Isla Llunchi, Río Napo, Ecuador, and referred to it the specimens from Lagunas, Peru, that Osgood (1944) had assumed to be representative of *P. semispinosus*. Based on the enamel patterns of the cheekteeth, he said that two kinds of *Proechimys* occur in Central America; those assignable to *P. guyannensis* as subspecies, and others (including *ignotus,* which he elevated to species rank) referable to the *P. quadruplicatus* group.

1948
Moojen treated *P. semispinosus* as a species to which he assigned all of the named forms of *Proechimys* from Central America and western Colombia and Ecuador as well as the Amazon basin populations he believed were represented by the names *gularis, hilda, kermiti, liminalis,* and *amphichoricus*. Moojen described the last two taxa as new subspecies.

1959
Hall and Kelson followed Moojen (1948) and recognized *burrus, centralis, goldmani, ignotus, panamensis* (*chiriquinus* a synonym), and *rubellus* as subspecies of *P. semispinosus*.

1961
Cabrera followed Moojen's (1948) application of *P. semispinosus* to the assignment of names to South American *Proechimys,* with the following exceptions: *colombianus, decumanus,* and *gorgonae* treated as subspecies of *P. guyannensis*; *gularis* (*sensu* Moojen 1948; not of Thomas 1911) assigned to *P. quadruplicatus* Hershkovitz.

1966
Handley considered the taxa *burrus, goldmani, ignotus,* and *panamensis* to be subspecies of Panamanian *P. semispinosus*.

1972
Patton and Gardner used the name *P. semispinosus* for Costa Rican topotypes of *P. rubellus*.

1976
Handley identified some Venezuelan populations as *P. semispinosus.*

1976
Reig and Useche used *P. centralis* for the Costa Rican *Proechimys* that Patton and Gardner (1972) had called *P. semispinosus,* stating that they preferred to follow Thomas's original application of *P. centralis* to all Central American members of the genus.

1981
Hall applied *P. semispinosus* in the same way the name was used by Hall and Kelson (1959).

Fraser's Travels in Ecuador

I have gleaned information on Louis Fraser's travels in Ecuador, from the time he arrived in Guayaquil, 20 September 1857, until he left Esmeraldas at the end of December 1859, from three reports by Tomes (1859, 1860a, b) on the mammals, several reports on the birds by Sclater (1859a, b, c, 1860a, b, c, d, e), and published extracts of letters written from Ecuador by Fraser (1858a, b, 1859a, b, c, d, 1860).

After a brief stay in Guayaquil, Fraser proceeded to Cuenca, arriving on 6 October 1857 and remaining there through November. Then he journeyed to Gualaquiza where he worked from December 1857 through February 1858, except for a two-week period in Zamora during January.

Fraser left Gualaquiza for Cuenca on 1 March (arriving 5 March) where he collected through April and May before proceeding to Riobamba. He worked in or near Riobamba during June and again in August on his return from Quito before continuing on to Pallatanga. His collections in the Pallatanga area, with trips to Chillanes, were made from the latter part of August through December 1858.

Leaving Pallatanga in mid-January 1859, Fraser collected on the slopes of Chimborazo north of Riobamba in February on his way to Quito. March, April, May, and part of June were spent in the vicinity of Quito and on the slopes of Pichincha as well as on the western slopes of the Andes northwest of Quito.

Fraser traveled southward from Quito to Babahoya where he stayed from 10 July through part of September. Then he went on to Guayaquil where, in the beginning of October, he left by ship for Esmeraldas. Fraser remained in Esmeraldas until the end of December and then left Ecuador for Guatemala.

Tomes' Reports on Fraser's Ecuadoran Mammals

Like many naturalist travellers of his day, Fraser collected a variety of vertebrates, invertebrates, and plants, but concentrated on birds. Among the several reports based wholly or in part on the mammals he collected in Ecuador are three major ones by Tomes published in the Proceedings of the Zoological Society of London (1859, 1860a, b).

In the first report, "Notes on a Collection of Mammalia made by Mr. Fraser at Gualaquiza," Tomes (1859) listed 17 taxa (some unidentified). Among these was (p. 548) "*Echimys cayenensis,* Geoff. A thickly-spined and rather large example, apparently somewhat more strongly tinged with rufous than the illustration given by Mr. Waterhouse, or than either of those given by M. Pictet.'' The list was incomplete, however, for Fraser (1858b:6158) said in a letter dated Gualaquiza, 13 February 1858, that he had ''skulls of tapir and white-lipped peccary,'' which are missing from Tomes' list. Moreover, not all of the animals that Tomes listed actually came from Gualaquiza. Fraser (1858a:5942) stated in a letter from Cuenca dated 21 October 1857 that he had ''three or four Mammalia'' on hand before he went into the southeastern lowlands of Ecuador. While at Gualaquiza, Fraser took a side trip to Zamora and collected mammals there. Nevertheless, there is no reason to question Gualaquiza as the place of origin of the rat Tomes (1859:548) reported as ''*Echimys cayenensis*.''

The next report (Tomes 1860a), ''Notes on a Second Collection of Mammalia made by Mr. Fraser in the Republic of Ecuador,'' listed 15 identified and unidentified species, two of which (*Hesperomys latimanus* and *H. minutus*) were described as new. At the end of the report, Tomes described two species (*Hesperomys bicolor* and *H. aureus*) based on specimens previously listed in his first report (Tomes 1859). With the exception of these two last named species and the *Diphylla ecaudata* (which came from ''Rio Napo'' and had been given to Fraser), the mammals of the second report were believed by Tomes (1860:211), ''to have been collected at Pallatanga on the western slope of the Cordillera: but the exact locality is not certain, from the specimens having been unfortunately mixed together.'' Tomes gave evidence that Pallatanga was the origin of some of this material. Some specimens, however, may have come from Chillanes (known to have been visited by Fraser during his stay at Pallatanga), or from the vicinity of Riobamba where Fraser worked before going to Pallatanga (but there is no record that he collected mammals there).

The final report (Tomes 1860b), ''Notes on a Third Collection of Mammalia made by Mr. Fraser in the Republic of Ecuador,'' contained 21 taxa, of which *Hesperomys caliginosus, H. albigularis,* and *Echimys semispinosus* were described as new. Pallatanga was indicated as the source of *H. albigularis,* but no locality data were given for the other two newly described species. Actually, localities were mentioned for only nine of the 21 taxa that Tomes listed. However, attention to dates, information from letters, and subsequent designations of type localities result in coastal Ecuador indicated for 1; Cuenca for 2; Gualaquiza, 3; Zamora, 2; Pallatanga, 2; Esmeraldas, 5; and unknown, 6. Of the three taxa from Gualaquiza, two are represented by the tapir and white-lipped peccary skulls first mentioned in Fraser's (1858b:6158) letter from Gualaquiza. The third is *Echimys semispinosus* represented by three specimens including the type, which Allen (1916) said, based on Thomas' determination, came from Gualaquiza.

Discussion

Fraser collected four specimens of *Proechimys*: the specimen from Gualaquiza first reported by Tomes in 1859 as *Echimys cayenensis* and three females in spirits reported without locality by Tomes in 1860. One of these three, an adult with two embryos, was the subject of the illustrations and measurements given by Tomes (1860b) in his description of *Echimys semispinosus* and to which he said the Gualaquiza specimen was ''similar.'' It is apparently this specimen that was later given British Museum (NH) catalog number 7.1.1.173, and is now labelled as the type of *Echimys semispinosus* Tomes.

The skin of the holotype now lacks a tail. The tail was present when Tomes (1860b) described *P. semispinosus* because he said it measured 5 inches, 6 lines (=139.7 mm). The skull of the holotype is in good condition. These clues confirm that the skin and skull presently labelled as the holotype of *P. semispinosus* do not represent the animal Tomes reported in 1859 from Gualaquiza, because Tomes (1860b) commented on the unsatisfactory condition of that specimen and noted that it lacked a tail.

It can be inferred from Thomas' (1896, 1897) writings that the holotype of *P. semispinosus* had been lost for some time before it was located among some specimens in rooms of the Zoological Society of London (Thomas 1898). Prior to its discovery, Thomas had assumed that material he later named *P. chrysaeolus* (Thomas, 1898) was representative of *P. semispinosus*. His confidence in that assumption was sufficiently strong for him to suggest that certain details in Tomes' figure of the skull were incorrect (Thomas 1896:312). I presume that the details Thomas was referring to included the strongly-developed parietal ridges. A single, strongly-developed ridge across the parietals is a feature characteristic of all populations of *Proechimys* found in Central America and in northern South America west of the Andes, with the exception of *P. decumanus*. Elsewhere in South America, parietal ridges, if present, are usually discontinuous, with the posterior component dorsal to and overlapping the anterior component. Specimens having a single ridge across each parietal are rare in Amazonian South America and such ridges are weakly developed, often inconspicuous.

The label on the skin of the type has the following information: *Proechimys semispinosus* Tomes; BM 7.1.1.173; Tomes collection; collector L. Fraser 1; Gualaquiza; hindfoot 46, ear 21; P. Z. S. London, 1858, p. 548 and 1860, p. 265. The catalog number indicates that this specimen was catalogued on 1 January 1907, the same date that other specimens Tomes described were catalogued (e.g., *Marmosa waterhousei*, BN 7.1.1.215; *Oryzomys albigularis*, BM 7.1.1.105; *O. caliginosus*, BM 7.1.1.128; *Thomasomys aureus*, BM 7.1.1.104). Not all of Fraser's material reported on by Tomes was catalogued on that date because the types of *Oryzomys phaeopus* Thomas, 1894 (BM 59.11.1.9), and *O. dryas* Thomas, 1898 (BM 59.11.1.11), from the same collection had been catalogued in 1859. This information suggests that the types of all of the species described by Tomes from Fraser's Ecuadoran collections were among those specimens found at the Zoological Society of London.

The label information that the skin is Fraser's number 1 is difficult to interpret. The specimen is neither the first that Fraser collected in Ecuador nor the first mammal because he said he had "three or four Mammalia" (Fraser 1858a:5942) from Cuenca where he began collecting and where *Proechimys* does not occur. One could argue that Fraser's number 1 is correct, that he used a separate series for each year, and that the holotype of *P. semispinosus* was the first prepared in 1858 and, therefore, definitely came from Gualaquiza. However, judging by Fraser's numbers for birds cited in some of Sclater's reports (1859c, 1860a, d, e) it appears that Fraser used a single series of field numbers during 1858 and 1859 and presumably from the time he began collecting in 1857. Probably all of his specimens or at least all of the vertebrates were included in the single series of numbers. Fraser's number 1705 (the holotype of *Oryzomys albigularis*) is close to Fraser's numbers that Sclater (1860a) cited for birds, also from Pallatanga. Therefore, the indication that the type of *P. semispinosus* was Fraser's first Ecuadoran mammal specimen must be incorrect.

The only *Proechimys* whose features resemble those of the type of *P. semispinosus* and may be expected to occur in the vicinity of Gualaquiza is *P. quadruplicatus* Hershkovitz, 1948. Although some features of *P. quadruplicatus* are similar to those of the type as well as to specimens identified as *P. semispinosus* by Patton and Gardner (1972) from Central America and the Pacific lowlands of Colombia and Ecuador, the skulls are clearly different. Contrasted with *P. quadruplicatus,* the skull of the type of *P. semispinosus* has a broader braincase, well-developed continuous ridges across the parietals, more posterior termination of the nasals in relation to the fronto-maxillary suture, and a less complex pattern of enamel folds on the cheek teeth ($\frac{3\text{-}3\text{-}3\text{-}4}{4\text{-}3\text{-}3\text{-}3}$ versus $\frac{4\text{-}4\text{-}4\text{-}4}{4\text{-}3\text{-}3\text{-}3}$ in *P. quadruplicatus*).

So where could Fraser have collected the type of *P. semispinosus*? *Proechimys* occurs in only four of the localities where Fraser collected: Gualaquiza, Babahoya, Guayaquil, and Esmeraldas. One of the first places where Fraser worked was Gualaquiza where he took the specimen Tomes (1859) reported as "*Echimys cayenensis.*" Tomes' (1860b) third account listed taxa from several places in Ecuador, including Gualaquiza. However, the only Gualaquizan mammals of this account were larger species; all of the small mammals Fraser collected at Gualaquiza had been covered in Tomes' first report (1859). There is no evidence that Fraser collected mammals in Babahoya or Guayaquil. Esmeraldas was the last Ecuadoran locality visited by Fraser and, in my opinion, is the most likely origin of the three specimens on which Tomes based his description of *P. semispinosus.* Furthermore, a species of *Proechimys* characterized by all of the features demonstrated by the type of *P. semispinosus* is common in the vicinity of Esmeraldas. Coincidentally, Esmeraldas was designated by Allen (1913:537) as the type locality of *Oryzomys caliginosus,* the other species Tomes (1860b) described without locality in his third report.

Conclusions

A review of Fraser's travels in Ecuador, an examination of the content of Tomes' (1859, 1860a, b) main reports on the mammals Fraser collected, and the direct comparison of the type specimen with samples of several species of *Proechimys* from Central and South America indicate that Gualaquiza is not the source of the type of *P. semispinosus.* The type locality is here corrected to Esmeraldas, Prov. Esmeraldas, on the Pacific coast of Ecuador.

Much of the confusion regarding the correct allocation of the name *P. semispinosus* resulted from the following factors: 1) The presumed loss of the type and Thomas' faith that material from "near Bogota" was representative of true *semispinosus*; 2) the belief (subsequent to the rediscovery of the type) that the type locality was Gualaquiza and, therefore, the zoogeographically-based conclusion that the name was applicable to populations east of the Andes; and 3) the obvious similarity between the type specimen and characteristics seen in populations of *Proechimys* found in Central America and the Pacific lowlands of Colombia and Ecuador.

Because of the correction of the type locality, *P. semispinosus calidior* becomes a subjective junior synonym of *P. semispinosus*. The epithets *burrus, centralis, chiriquinus, colombianus, goldmani, gorgonae, ignotus, panamensis, rosa,* and *rubellus* are available as names for populations of *P. semispinosus.* Of these, *centralis* applies to the populations in Nicaragua, Honduras, and northern Costa Rica. The southernmost population of Ecuador should be known as *P. semispinosus rosa.* Allocation of most of the remaining names awaits a taxonomic revision of the species.

Hershkovitz (1948) allied *P. ignotus* with his *P. quadruplicatus* group; however, several populations of *P. semispinosus* are superficially similar in dental structure to *P. quadruplicatus* and *ignotus* is best treated as a subspecies of *P. semispinosus.*

The Central American distribution of *P. semispinosus* extends from southeastern Honduras and eastern Nicaragua through Costa Rica and Panama including the Islas las Pearlas (see Hall 1981:873). In South America, the range is west of the Andes from the Choco of Colombia (including Isla Gorgona) to southwestern Ecuador. A record for extreme northwestern Peru (Tumbez, Rio Tumbez; see Thomas 1882:101) has not been confirmed. Those specimens may represent *P. decumanus* Thomas, 1899, which occurs in that region and is sympatric with *P. semispinosus rosa* in southwestern Ecuador (provinces of Guayas and El Oro).

Acknowledgments

I am grateful to personnel at the British Museum (Natural History), especially to Mr. J. E. Hill, for the opportunity to examine type specimens and other material in their care. D. E. Wilson and C. O. Handley, Jr., have provided valuable suggestions for improving the manuscript.

Literature Cited

Allen, J. A. 1899. The generic names *Echimys* and *Loncheres.*—Bulletin of the American Museum of Natural History 12:257–264.

———. 1913. Revision of the *Melanomys* group of American Muridae.—Bulletin of the American Museum of Natural History 32:533–555.

———. 1916. List of mammals collected in Colombia by the American Museum of Natural History Expeditions, 1910–1915.—Bulletin of the American Museum of Natural History 35:191–238.

Bangs, O. 1901. The mammals collected in San Miguel Islands, Panama, by W. W. Brown, Jr.—American Naturalist 35:631–644.

———. 1905. The Vertebrata of Gorgona Island, Colombia, III. Mammalia.—Bulletin of the Museum of Comparative Zoology 46:89–91.

Bole, B. P., Jr. 1937. Annotated list of mammals of the Mariato River District of the Azuero Peninsula.—Scientific Publications of the Cleveland Museum of Natural History 7:140–188.

Cabrera, A. 1961. Catalago de los mamiferos de America del Sur.—Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciencias Zoologicas 4(2):xxii + 309–732, frontispiece.

Ellerman, J. R. 1940. The families and genera of living rodents.—British Museum (Natural History), London 1:xxvi + 689 pp.

Fraser, L. 1858a. [Extracts from letters].—Zoologist 16:5939–5942.

———. 1858b. Mr. Louis Fraser's expedition to Ecuador and Peru [extracts from letters].—Zoologist 16:6158–6160.

———. 1859a. [Extracts from letters].—Ibis 1:113–114.

———. 1859b. [Extracts from a letter].—Ibis 1:208–209.

———. 1859c. [Extracts from a letter].—Ibis 1:332–333.

———. 1859d. [Extracts from letters].—Ibis 1:462–464.

———. 1860. [Extracts from letters].—Ibis 2:192–193.

Goldman, E. A. 1920. Mammals of Panama.—Smithsonian Miscellaneous Collections 69:1–309, 1 map.

Goodwin, G. G. 1946. Mammals of Costa Rica.—Bulletin of the American Museum of Natural History 87:271–474.

Hall, E. R. 1981. The mammals of North America, Second Ed.—T. Wiley and Sons, New York 2: 601–1181 + 90 pp.

———, and K. R. Kelson. 1959. The mammals of North America.—Ronald Press, New York 2: viii + 547–1083 + *79*.

Handley, C. O., Jr. 1966. Checklist of the mammals of Panama. Pp. 753–795 *in* R. L. Wenzel and V. J. Tipton, eds., Ectoparasites of Panama.—Field Museum of Natural History, Chicago xii + 861 pp.

———. 1976. Mammals of the Smithsonian Venezuelan Project.—Brigham Young University Science Bulletin, Biological Series 20:1–89.

Hershkovitz, P. 1948. Mammals of northern Colombia. Preliminary report no. 2: Spiny rats (Echimyidae), with supplemental notes on related forms.—Proceedings of the United States National Museum 97:125–140.

Hollister, N. 1914. Four new Neotropical rodents.—Proceedings of the Biological Society of Washington 27:57–60.

Kellogg, R. 1946. Three new mammals from the Pearl Islands, Panama.—Proceedings of the Biological Society of Washington 59:57–62.

Moojen, J. 1948. Speciation in the Brazilian spiny rats (genus Proechimys, family Echimyidae).—University of Kansas Publications, Museum of Natural History 1:301–406.

Osgood, W. H. 1944. Nine new South American rodents.—Field Museum of Natural History, Zoological Series 29:191–204.

Patton, J. A., and A. L. Gardner. 1972. Notes on the systematics of *Proechimys* (Rodentia: Echimyidae), with emphasis on Peruvian forms.—Occasional Papers of the Museum of Zoology, Louisiana State University 44:1–30.

Paynter, R. A., Jr., and M. A. Traylor, Jr. 1977. Ornithological gazetteer of Ecuador.—Harvard University, Cambridge, Massachusetts. viii + 151 pp.

Reig, O. A., and M. Useche. 1976. Diversidad cariotipica y sistematica en poblaciones Venezolanas de *Proechimys* (Rodentia, Echimyidae), con datos adicionales sobre poblaciones de Peru y Colombia.—Acta Cientifica Venezolana 27:132–140.

Sclater, P. L. 1859a. List of birds collected by Mr. Louis Fraser at Cuenca, Gualaquiza, and Zamora in the Republic of Ecuador.—Proceedings of the Zoological Society of London 1858:449–461.

———. 1859b. On the birds collected by Mr. Fraser in the vicinity of Riobamba, in the Republic of Ecuador.—Proceedings of the Zoological Society of London 1858:549–556.

———. 1859c. List of the first collection of birds made by Mr. Louis Fraser at Pallatanga, Ecuador; with notes and descriptions of new species.—Proceedings of the Zoological Society of London 1859:135–147.

———. 1860a. List of additional species of birds collected by Mr. Louis Fraser at Pallatanga, Ecuador; with notes and descriptions of new species.—Proceedings of the Zoological Society of London 1860:63–73.

———. 1860b. List of birds collected by Mr. Fraser in the vicinity of Quito and during excursions to Pichincha and Chimborazo; with notes and descriptions of new species.—Proceedings of the Zoological Society of London 1860:73–83.

———. 1860c. List of birds collected by Mr. Fraser in Ecuador, at Nanegal, Calacali, Perucho, and Puellaro; with notes and descriptions of new species.—Proceedings of the Zoological Society of London 1860:83–97.

———. 1860d. List of birds collected by Mr. Fraser at Babahoyo in Ecuador, with descriptions of new species.—Proceedings of the Zoological Society of London 1860:272–290.

———. 1860e. List of birds collected by Mr. Fraser at Esmeraldas, Ecuador, with descriptions of new species.—Proceedings of the Zoological Society of London 1860:291–298.

Tate, G. H. H. 1935. The taxonomy of the genera of Neotropical hystricoid rodents.—Bulletin of the American Museum of Natural History 68:295–448.

Thomas, O. 1882. On a collection of rodents from north Peru.—Proceedings of the Zoological Society of London 1882:98–111.

———. 1896. On new small mammals from the Neotropical region.—Annals and Magazine of Natural History (6)18:301–314.

———. 1897. Descriptions of new bats and rodents from America.—Annals and Magazine of Natural History (6)20:544–553.

———. 1898. Description of a new *Echimys* from the neighbourhood of Bogota.—Annals and Magazine of Natural History (7)1:243–245.

———. 1899. Descriptions of new Neotropical mammals.—Annals and Magazine of Natural History (7)4:278–288.

———. 1900. Descriptions of new Neotropical mammals.—Annals and Magazine of Natural History (7)5:217–222.

———. 1911. New rodents from S. America.—Annals and Magazine of Natural History (8)8:250–256.

———. 1914. New *Nasua, Lutra,* and *Proechimys* from South America.—Annals and Magazine of Natural History (8)14:57–61.

Tomes, R. F. 1859. Notes on a collection of Mammalia made by Mr. Fraser at Gualaquiza.—Proceedings of the Zoological Society of London 1858:546–549.

———. 1860a. Notes on a second collection of Mammalia made by Mr. Fraser in the Republic of Ecuador.—Proceedings of the Zoological Society of London 1860:211–221.

———. 1860b. Notes on a third collection of Mammalia made by Mr. Fraser in the Republic of Ecuador.—Proceedings of the Zoological Society of London 1860:260–268.

True, F. W. 1889. On the occurrence of *Echinomys semispinosus,* Tomes, in Nicaragua.—Proceedings of the United States National Museum 11:467–468.

U.S. Fish and Wildlife Service, National Museum of Natural History, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 145–148

THE ASSIGNMENT OF THE TEXAS TROGLOBITIC WATER SLATER *CAECIDOTEA PILUS* TO THE GENUS *LIRCEOLUS,* WITH AN EMENDED DIAGNOSIS OF THE GENUS (CRUSTACEA: ISOPODA: ASELLIDAE)

Julian J. Lewis

Abstract.—*Caecidotea pilus* is redescribed and assigned to *Lirceolus*. This genus, now containing two species, remains endemic to Texas. The addition of *C. pilus* requires emendation of *Lirceolus* to broaden the concept of the genus, especially in the characteristics of the mouthparts.

Until recently, all of the known subterranean asellid isopods of Texas were assigned to the widespread genus *Caecidotea*. In 1976 Bowman and Longley redescribed *Caecidotea smithii* from newly collected specimens from the artesian well at San Marcos, Texas. This species possessed a number of unusual morphological characters that persuaded Bowman and Longley to place it in a new genus, *Lirceolus,* so named for the similarity of the third pleopods of *Lirceus* and *Lirceolus.*

Lewis (1982) pointed out the morphological similarities of some of the other Texas asellids to *Lirceolus* and suggested the possibility that under scrutiny, additions might be made to the genus. Of the three other troglobitic asellids from Texas (all described by Steeves 1968), *Caecidotea reddelli* is clearly assigned to the correct genus. On the other hand the illustrations of *C. pilus* and *C. bisetus* by Steeves (1968) were suggestive of *Lirceolus* in the unarmed gnathopod, elongate first pleopod, and the sparsely setose exopod of the second pleopod. When examined, *C. bisetus* was found to have the usual *Caecidotea*-type transverse suture across the exopod of the third pleopod. *Caecidotea pilus* possessed not only an oblique suture, but other characteristics which necessitate its transference to *Lirceolus*. However, some of the unusual characteristics of *Lirceolus smithii* included in the diagnosis of the genus by Bowman and Longley (1976) do not apply to *L. pilus*; hence an emended diagnosis is provided here.

Several illustrations are included herein to support the placement of *L. pilus* in *Lirceolus*. Steeves (1968) illustrated the male gnathopod, pleopod 1 and pleopod 2, plus the endopod tip of the latter. Except where new details have been revealed, Steeve's drawings adequately characterize the species and are not repeated here.

Lirceolus Bowman and Longley, 1976

Diagnosis.—Eyeless, unpigmented, maximum length about 4 mm. Head without lateral incisions or rostrum. Mandible with 3-merous palp. Maxilla 1, outer lobe with 10–13 spines; inner lobe with 5–8 plumose setae. Pereopod 1 propodus palm without processes. Pleopod 1 slender, elongate, distal segment oval with sparse non-plumose setation. Pleopod 2, exopod proximal segment produced medially over distal segment; distal segment without catch lobe, with longitudinal furrow on posterior surface and 0–1 setae on distal margin. Endopod with short basal spur, basal apophysis about as long as basal spur, labial spur absent. Pleopod 3 exopod with oblique suture. Pleopods 4 and 5 with exopod and endopod partly or totally fused.

Type-species.—Asellus smithii Ulrich, 1902.

Lirceolus pilus (Steeves)
Fig. 1

Asellus pilus Steeves, 1968:188.—Reddell and Mitchell, 1969:8, 43.—Reddell, 1970:396.—Fleming, 1973:295 (in list), 297 (in key).

Conasellus pilus (Steeves).—Henry and Magniez, 1970:356.—Mitchell and Reddell, 1971:55.

Material examined.—TEXAS: Medina Co., Valdina Farms Sinkhole, 15 mi. N. Sabinal, 12 Jan 1963, leg. J. Reddell, D. McKenzie, J. Porter, holotype ♂ (USNM 119593), allotype ♀ (USNM 119594), 1 ♂, 1 ♀ paratypes (USNM 119595).

Description.—Maximum length 3.0 mm (allotype), body slender, about 4× as long as wide. Coxae visible in dorsal view. Head about 2× as wide as long. Pleotelson about 1.3× as long as wide, sides subparallel, caudomedial lobe not evident.

Antenna 1 flagellum of about 5 segments, esthetes on distal 3 segments (♂ paratype) or 1-0-1 (♀ paratype). Mandibles with 4-cuspate incisors and lacinia mobilis, palp with few plumose setae on segments 2 and 3. Maxilla 1 inner lobe with 5 plumose setae; outer lobe with 13 robust spines. Maxilliped with 3 retinacula.

Pereopod 1 propod about 3.0× as long as wide in ♂, 2.4× in ♀. Pereopod 4 sexual dimorphism slight, carpus of holotype 3.3× as long as wide, allotype 3.5×; dactyl with accessory unguis.

Pleopod 1 with 3 retinacula; exopod about 1.4× length of protopod. Pleopod 2, exopod distal segment with 1 seta; endopod tip with endopodial groove terminating in decurved beak-shaped process. Pleopod 3 as figured. Pleopods 4 and 5 exopods with single oblique suture.

Distribution.—Known only from the type-locality, Valdina Farms Sinkhole. The assignment of this species to *Lirceolus* extends the range of the genus a short distance to the west, but it remains endemic to the Balcones Fault Zone of Texas.

Relationships.—*Lirceolus pilus* is obviously closely related to *L. smithii* both morphologically and geographically. The greatest differences between the 2 species lies in the structure of their mouthparts:

	L. smithii	*L. pilus*
mandibles:		
lacinia/incisors	2-3 cuspate	4-4 cuspate
maxilla 1		
outer lobe	10 spines	13 spines
inner lobe	8 setae	5 setae

The generic relationships of *Lirceolus* remain obscure, although the addition

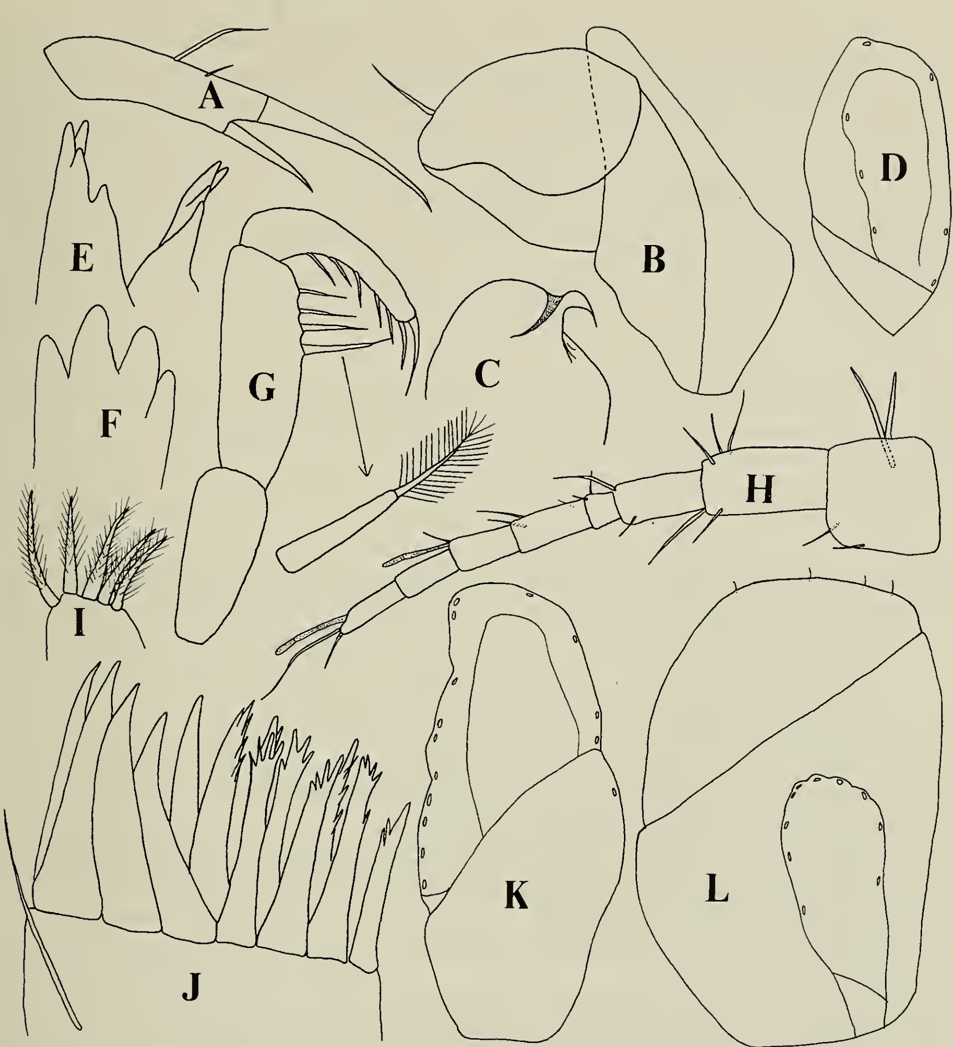


Fig. 1. *Lirceolus pilus*: A from allotype, B, C, F, G from ♂ paratype, others from ♀ paratype. A, Pereopod 4 dactyl; B, Pleopod 2, exopod; C, Same, endopod tip; D, Pleopod 5; E, Incisor and lacinia, left mandible; F, incisor, right mandible; G, Mandibular palp; H, Antenna 1; I, Maxilla 1, inner lobe; J, Same, outer lobe; K, Pleopod 4; L, Pleopod 5.

of *L. pilus* lends some insight. The mouthparts of *L. pilus* are very similar to those of troglobitic *Caecidotea* both morphologically and meristically. However, the oblique suture of pleopod 3 clearly separates *Lirceolus* from *Caecidotea*. *Lirceolus* can be separated from *Lirceus* by the lack of a rostrum and the lateral incisions of the head, present in most species of *Lirceus*. A fusion of the endopod and exopod of pleopods 4 and 5 as in *L. smithii* is unknown in both *Caecidotea* and *Lirceus*, although in *Calasellus*, pleopod 5 exopod is greatly reduced or absent (Bowman 1981).

The fusion of the pleopods reported in *L. smithii* by Bowman and Longley (1976) was difficult to ascertain in *L. pilus*. In the female paratype the pleopods appeared fused similar to those reported for *L. smithii*, but the fusion looked much less extensive in the male paratype. The unusual fleshy consistency of the pleopods in *Lirceolus pilus* (and *Lirceolus* in general) precludes an adequate description from the few specimens available. Moreover, all specimens were incomplete, lacking the flagella of the second antennae, the uropods, and most of the pereopods. Of the two males and two females in the collection, only one individual of each sex retained a single fourth pereopod to compare for sexual dimorphism.

Acknowledgments

I thank Dr. Thomas E. Bowman for the loan of specimens from the collections of the Smithsonian Institution, and for reading this manuscript. This paper is Contribution #206 (New Series) of the Department of Biology, University of Louisville.

Literature Cited

Bowman, Thomas E. 1981. *Calasellus longus*, a new genus and species of troglobitic asellid from Shaver Lake, California (Crustacea: Isopoda: Asellidae).—Proceedings of the Biological Society of Washington 94(3):866–872.

———, and Glenn Longley. 1976. Redescription and assignment to the new genus *Lirceolus* of the Texas troglobitic water slater, *Asellus smithii* (Ulrich) (Crustacea: Isopoda: Asellidae).—Proceedings of the Biological Society of Washington 88(45):489–496.

Fleming, Laurence E. 1973. The evolution of the eastern North American isopods of the genus *Asellus* (Crustacea: Asellidae). Part II.—International Journal of Speleology 5:283–310.

Henry, Jean-Paul, and Guy Magniez. 1970. Contribution à la systématique des Asellides (Crustacea Isopoda).—Annales de Spéléologie 25(2):335–367.

Lewis, Julian J. 1982. A diagnosis of the *Hobbsi* Group, with descriptions of *Caecidotea teresae*, n. sp. and *C. macropropoda* Chase and Blair (Crustacea: Isopoda: Asellidae).—Proceedings of the Biological Society of Washington 95(2):338–346.

Mitchell, Robert W., and James R. Reddell. 1971. The invertebrate fauna of Texas caves. Pp. 35–91 *in* Ernest L. Lundelius and Bob H. Slaughter, (eds.), Natural History of Texas Caves. Gulf Natural History, Dallas.

Reddell, James R. 1970. A checklist of the cave fauna of Texas. IV. Additional records of Invertebrata (exclusive of Insecta).—Texas Journal of Science 21(4):389–415.

———, and Robert W. Mitchell. 1969. A checklist and annotated bibliography of the subterranean aquatic fauna of Texas.—Texas Technological College, Water Resources Center, Special Report 24:1–48.

Steeves, Harrison R. III. 1968. Three new species of troglobitic asellids from Texas.—American Midland Naturalist 79(1):183–188.

Ulrich, Carl J. 1902. A contribution to the subterranean fauna of Texas.—Transactions of the American Microscopical Society 23:83–101.

Department of Biology and Water Resources Laboratory, University of Louisville, Louisville, Kentucky 40292.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 149–153

CAECIDOTEA FONTICULUS, THE FIRST TROGLOBITIC ASELLID FROM THE OUACHITA MOUNTAINS (CRUSTACEA: ISOPODA: ASELLIDAE)

Julian J. Lewis

Abstract.—*Caecidotea fonticulus,* a member of the *Hobbsi* Group, is the first troglobitic isopod to be described from the Ouachita Mountains. This species appears to be most closely related to two species from the Ozarks, *C. spatulata* and *C. fustis.*

The species described herein is the first troglobitic asellid to be found from the Ouachita Mountains of central Arkansas and adjacent Oklahoma. Another species occurring in the Ouachitas, *Caecidotea oculata,* has reduced eyes and pigmentation, but is reported only from epigean habitats (Mackin and Hubricht 1940). The discovery of this zoogeographically interesting new asellid was made possible by an extensive ongoing survey of Ouachita springs and their fauna by Dr. Henry W. Robison of Southern Arkansas University.

Caecidotea fonticulus, new species
Figs. 1–2

Material examined.—ARKANSAS: Polk Co., Abernathy Spring, 0.8 mi. W of Polk-Montgomery county line, on north side of Highway 8 (shown on U.S.G.S. Big Fork, Arkansas 7.5 minute quadrangle), 16 June 1979, H. W. Robison, 136 ♂♀ (USNM 191132); same locality, H. W. Robison, 21 May 1980, 16 ♂♂, 14 ♀♀ (USNM 191129); same locality, H. W. Robison, 16 Apr 1982, 29 ♂♀ (USNM 191133); same locality, Julian J. Lewis and Teresa M. Lewis, 31 May 1981, 9 ♂♂, 10 ♀♀ (USNM 191131).

A 5.0 mm ♂ from the 31 May 1981 collection is the holotype (USNM 191128), the other specimens are paratypes. All of the material examined has been deposited in the National Museum of Natural History, Smithsonian Institution.

Description.—Eyeless, unpigmented. Longest ♂ 6.0 mm, longest ♀ 5.0 mm; body slender, about 6.1× as long as wide. Head about 1.5× as wide as long, anterior margin concave, postmandibular lobes moderately produced. Pleotelson about 1.2× as long as wide, sides subparallel, caudomedial lobe produced.

Antenna 1 reaching midlength of last segment of peduncle of antenna 2, flagellum with up to 8 segments, esthete formula to 6-0, occasional segments with 2 esthetes. Mandibles with 4-cuspate incisors and lacinia mobilis; palp with plumose setae in rows on distal segments. Maxilla 1, outer lobe with 13 robust spines, inner lobe with 5 plumose setae. Maxilliped with 5–6 retinacula.

Male pereopod 1 propus about 1.4× as long as wide; palmar margin with 2 short spines proximally, high subtriangular median process separated by U-shaped cleft from similar lower distal process; dactyl flexor margin without process, undulating, with small spines. Female pereopod 1 about 2× as long as wide,

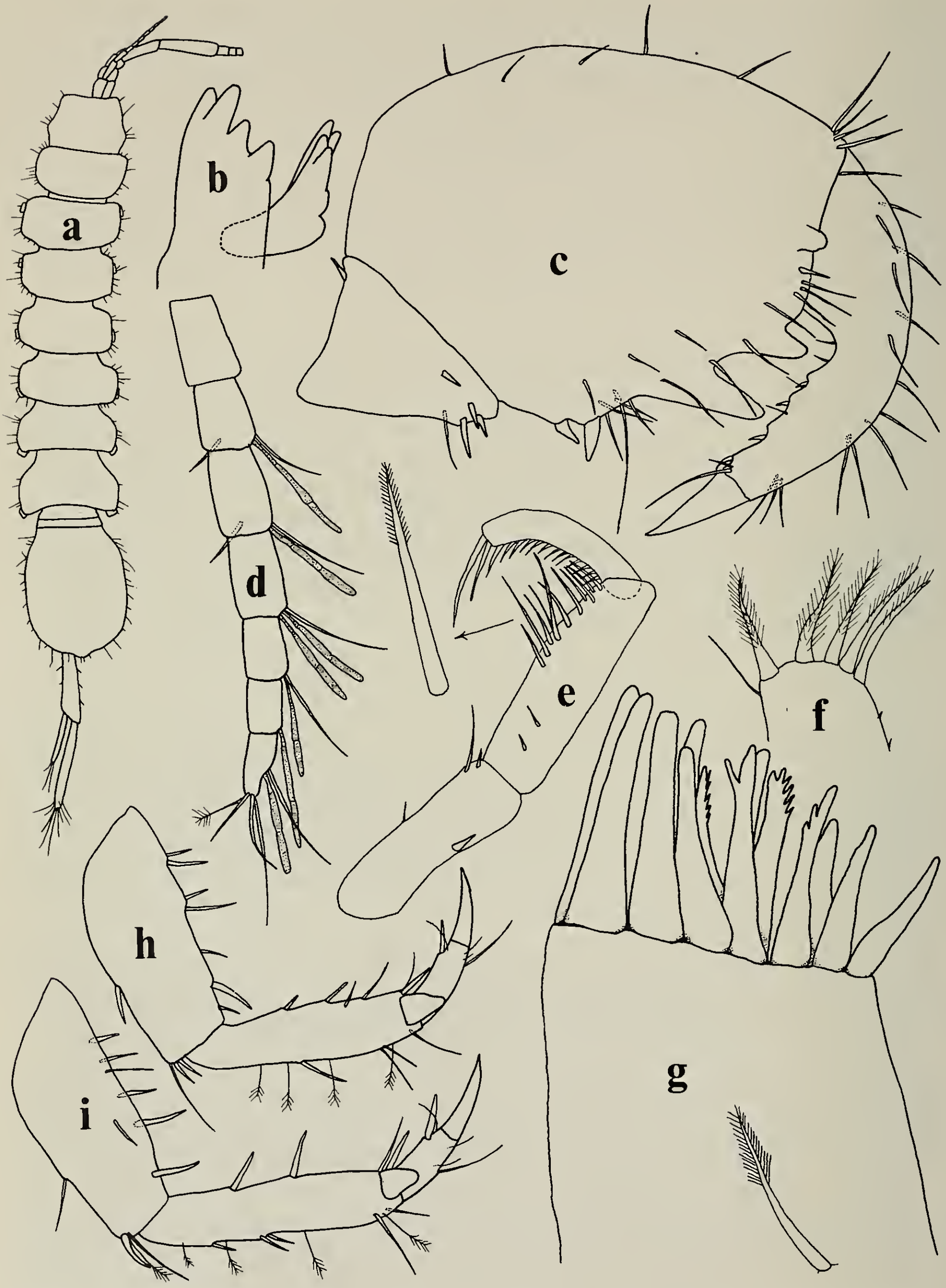


Fig. 1. *Caecidotea fonticulus*: a–h from ♂ paratypes, i from ♀ paratype: a, Habitus, dorsal; b, Incisor and lacinia, left mandible; c, Pereopod 1; d, Antenna 1, distal segments; e, Mandibular palp; f, Maxilla 1, inner lobe; g, Same, outer lobe; h, Pereopod 4, distal segments; i, Same.

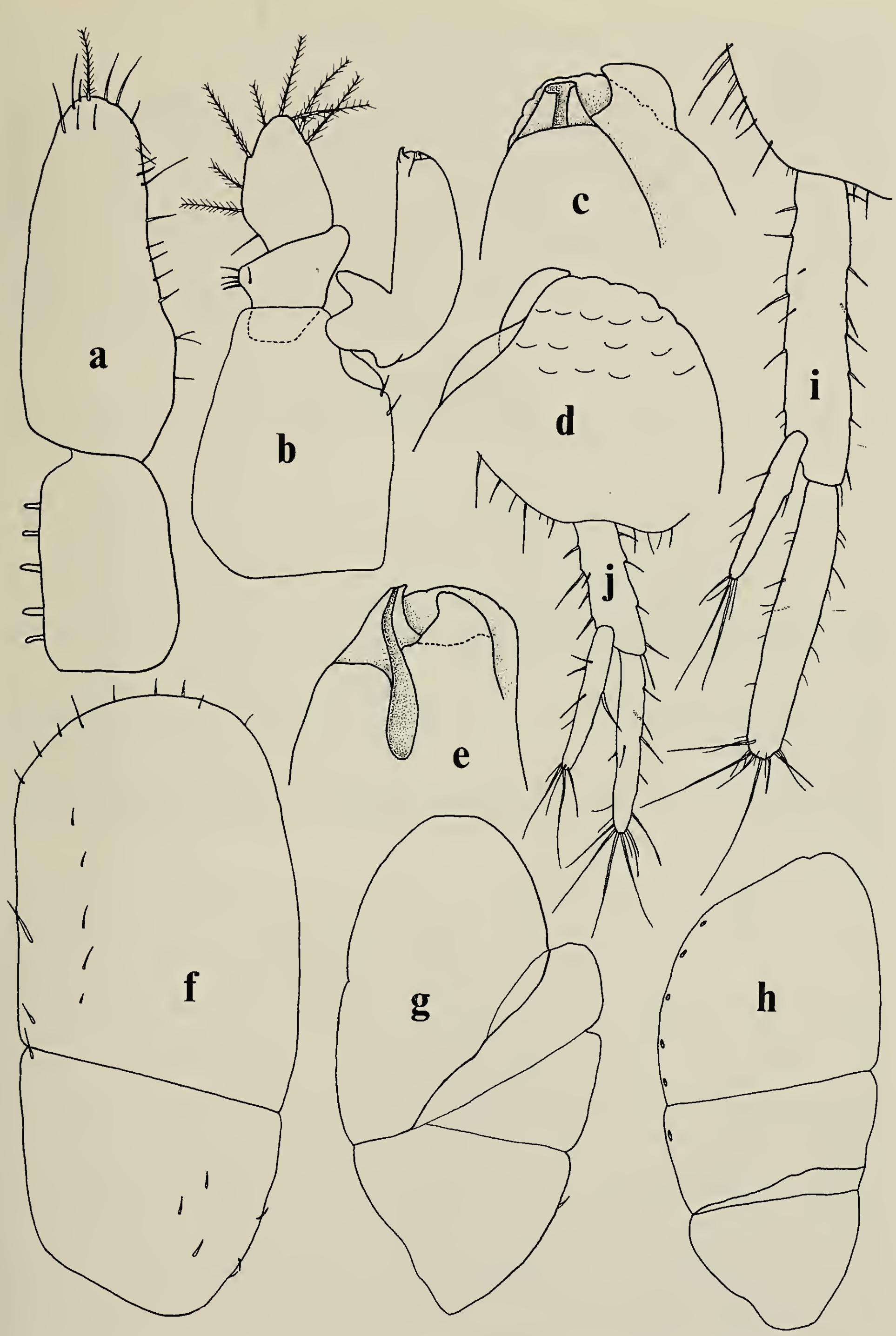


Fig. 2. *Caecidotea fonticulus*: a–i from ♂ paratypes, j from ♀ paratype: a, Pleopod 1; b, Pleopod 2; c–e, Same, endopod tip, anterior, posterior, lateral views; f, Pleopod 3; g, Pleopod 4; h, Pleopod 5; i, Uropod; j, Same.

propus without processes. Pereopod 4 of ♂ and ♀ similar, carpus about 2.4× as long as wide.

Male pleopod 1 longer than pleopod 2; protopod about 0.6× length of exopod, with 4–5 retinacula; exopod about 2.3× as long as wide, rounded distal margin with 1–2 elongate plumose setae, concave lateral margin without plumose setae. Male pleopod 2 exopod, proximal segment with 4 lateral setae, distal segment with about 8 long plumose setae along distal margin; endopod with distinct basal apophysis, tip with 4 processes: (1) caudal process broadly rounded, with scalloped surface, (2) lateral process recurved, extending slightly beyond caudal process, (3) cannula conical, truncate, directed distally, endopodial groove mostly obscured except in lateral view, and (4) mesial process low, forming a shelf across base of cannula in anterior view. Pleopod 3 exopod distal margin with sparse non-plumose setae. Pleopod 4 exopod with single sigmoid suture trifurcating to notches in lateral margin, seta present or absent, many setules present. Pleopod 5 with 2 transverse sutures. Uropods about 1.4× length of pleotelson in ♂, 0.7× in ♀.

Etymology.—The name, proposed as a noun, is derived from the Latin "fonticulus" (a little fountain or spring) in reference to the type-locality of the species.

Distribution.—Known only from the type-locality, Abernathy Spring. The spring flows from a tile pipe sunken lengthwise into the ground, giving the fountain-like appearance to which the specific name refers. After a few meters the spring stream joins another stream, Big Fork. Two species of asellids are found under rocks and in aquatic mosses in the spring stream, *C. fonticulus* and *Lirceus ouachitaensis*. This is the first record of this *Lirceus* from Arkansas, although Mackin and Hubricht (1938) reported it from the adjacent part of the Ouachitas in Oklahoma. Specimens of this asellid have also been deposited in the Smithsonian Institution (USNM 191130). The water from Abernathy Spring averages about 16°C, pH 7.0, conductivity 144 μmhos and alkalinity 70 mg/ml $CaCO_3$ (Robison, in litt.).

Relationships.—*Caecidotea fonticulus* can be readily assigned to the *Hobbsi* Group (as defined by Lewis 1982) by the following combination of male characters: pleopod 1 longer than pleopod 2, distal margin with elongate plumose setae, and pleopod 2 endopod tip with bluntly conical, distally directed cannula. Specifically, the morphology of the endopod of *C. fonticulus* resembles that of two Ozark species, *C. spatulata* and *C. fustis* (Mackin and Hubricht 1940; Lewis and Bowman 1981; Lewis 1981). All three species have in common a high, somewhat digitiform lateral process that is slightly recurved, a broad mesial process that obscures the base of the cannula, and a broad caudal process. The palmar margin of the gnathopod propus bears a triangular median process in these species, but bicuspid distal processes in *C. spatulata* and *C. fustis,* instead of the triangular distal process of *C. fonticulus*. The Ozark species are readily separated from *C. fonticulus* by their numerous elongate plumose setae along the distal margin of the third pleopod. In some populations of *C. spatulata* and *C. fustis* vestigial eyes and pigmentation are present, a characteristic not exhibited by any of the specimens of *C. fonticulus* examined.

Acknowledgments

I thank Dr. Henry W. Robison for visiting Abernathy Spring on several occasions to collect specimens, and for supplying me with detailed information on the spring. Dr. Thomas E. Bowman called my attention to the first specimens of this new species (which had been deposited in the collection of the Smithsonian Institution by Dr. Robison) and read yet another manuscript. My wife, Teresa M. Lewis, provided field assistance on a 1981 collecting trip through the Ouachitas and Ozarks, funded by a grant from the Graduate School of the University of Louisville. This paper is contribution #208 (New Series) from the Department of Biology, University of Louisville.

Literature Cited

Lewis, Julian J. 1981. *Caecidotea salemensis* and *C. fustis,* new subterranean asellids from the Salem Plateau (Crustacea: Isopoda: Asellidae).—Proceedings of the Biological Society of Washington 94(2):338–346.

———. 1982. A diagnosis of the *Hobbsi* Group, with descriptions of *Caecidotea teresae,* n. sp., and *C. macropropoda* Chase and Blair (Crustacea: Isopoda: Asellidae).—Proceedings of the Biological Society of Washington 95(2):81–94.

———, and Thomas E. Bowman. 1981. The subterranean asellids (*Caecidotea*) of Illinois (Crustacea: Isopoda: Asellidae).—Smithsonian Contributions to Zoology 335, 66 pp.

Mackin, J. G., and Leslie Hubricht. 1938. Records of distribution of species of isopods in central and southern United States, with descriptions of four new species of *Mancasellus* and *Asellus* (Asellota, Asellidae).—American Midland Naturalist 19:628–637.

———, and ———. 1940. Descriptions of seven new species of *Caecidotea* (Isopoda, Asellidae) from the central United States.—Transactions of the American Microscopical Society 59(3): 383–397.

Department of Biology and Water Resources Laboratory, University of Louisville, Louisville, Kentucky 40292.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 154–159

PSYCHRONAETES HANSENI, A NEW GENUS AND SPECIES OF ELASIPODAN SEA CUCUMBER FROM THE EASTERN CENTRAL PACIFIC (ECHINODERMATA: HOLOTHUROIDEA)

David L. Pawson

Abstract.—A new genus and species in the elasipodan family Laetmogonidae is described. Distinguishing features include large size (largest specimens probably exceed 30 cm in length), presence of a pronounced anterior "head" region with large, irregularly sized papillae, presence in the bodywall of wheels of only one type, and absence of circumoral papillae. The genus is known so far only from the eastern central Pacific. A revised key to genera in the family Laetmogonidae is presented.

During a benthic sampling and photographic survey of a large area of the eastern central Pacific, the Ocean Mineral Company collected specimens of a reasonably common, large, elasipodan holothurian, which proved to represent a new genus. Seafloor photographs of the animal *in situ* were also obtained. Specimens and photographs were entrusted to me for study.

Hansen (1975) revised the elasipodan family Laetmogonidae, and it now comprises four genera. The new genus described here is distinctive in several important respects, and appears to bear no close relationship to any other genera in the family.

Order Elasipodida Theel, 1882
Family Laetmogonidae Ekman,1926
Psychronaetes, new genus

Diagnosis.—Body fusiform, maximum length approximately 30 cm. Midventral radius naked, lateral ventral radii each with approximately 15 triangular tubefeet. Dorsal radii each with approximately 30 papillae. Dorsal papillae forming an irregular fringe around anterior dorsal end of body. Tentacles 15, no circumoral papillae. Ossicles in bodywall wheels of one type, usually 50–60 μm in diameter, usually with 9–12 spokes.

Type-species.—Psychronaetes hanseni, new species

Etymology.—The genus-name is of masculine gender, derived from Greek, *psychros* cold, and *naetes* inhabitant. The species is named in honor of Dr. Bent Hansen of the Universitetets Zoologiske Museum, Copenhagen, in acknowledgment of the valuable contributions he has made to our knowledge of the deep-sea holothurian fauna.

Remarks.—This new genus can be distinguished from others in the family Laetmogonidae as follows. The key is a modified version of that given by Hansen (1975).

Key to genera of family Laetmogonidae

1. Circumoral papillae present .... *Benthogone* Koehler, 1896
– Circumoral papillae absent 2
2. Midventral tubefeet present. Body wall ossicles wheels with marginal teeth .... *Pannychia* Theel, 1882
– Midventral tubefeet absent. Wheels lack marginal teeth 3
3. Ventrolateral papillae present, fused to form continuous brim around body .... *Apodogaster* Walsh, 1891
– Ventrolateral papillae absent. Brim, when present, composed of fused ventrolateral tubefeet 4
4. Body fusiform, up to 30 cm long, with pronounced anterior "head" region with irregular fringe of dorsal papillae .... *Psychronaetes,* new genus
– Body more or less cylindrical, usually considerably less than 20 cm long, lacking pronounced anterior "head" region.
No anterior fringe of dorsal papillae .... *Laetmogone* Theel, 1879

Psychronaetes hanseni, new species
Figs. 1, 2

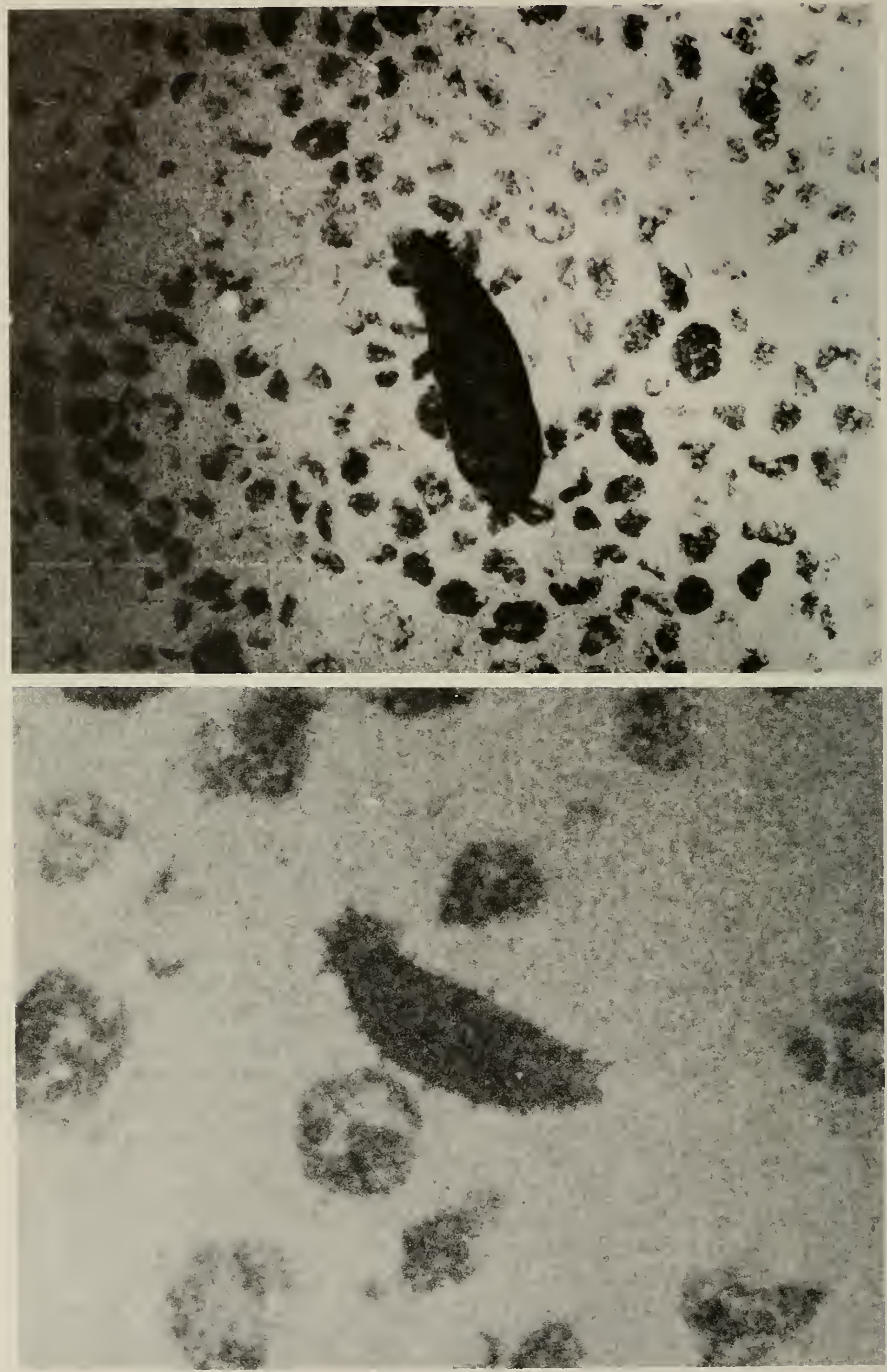
Diagnosis.—As for genus.

Material examined.—HOLOTYPE, USNM E27566, total length approximately 240 mm, greatest width approximately 60 mm; PARATYPE USNM E27567, total length approximately 70 mm, greatest width approximately 25 mm. Type-locality, eastern central Pacific, Clarion-Clipperton Fracture Zone, West of 120°W, depth 4800–5200 meters, collected by Ocean Minerals Company.

Description.—Color in alcohol variegated dark purple, lighter in smaller specimens. Body fusiform, tapering anteriorly and posteriorly (Fig. 1). Pronounced "neck" anteriorly, approximately 15% of body length from anterior end. Head region with mouth, ventrally directed, and tentacles. No circumoral papillae. Tentacles 15, with short stems and large elongate oval discs 9 × 5 mm in holotype, with long axis of disc directed towards mouth. Anus posterodorsal. Bodywall firm, leathery, not gelatinous.

Midventral radius naked. Lateral ventral radii each with 15 large and conspicuous triangular tubefeet, each approximately 10 mm long and 8 mm wide at base. Feet evenly scattered along entire lateral ventral radii. Dorsal surface with 2 poorly defined rows of numerous papillae, approximately 30 in each row, papillae apparently arising from medial side of each dorsal radius. On head region, papillae become enlarged, forming an irregular fringe around anterior dorsal end of body. Fringe contains approximately 15 papillae in larger specimens, largest papillae approximately 15 mm long and 9 mm wide at base.

Ossicles in bodywall exclusively wheels, greatly variable in size (Table 1). Wheels having smooth rim, short spokes (Table 2) and large central region; at center of wheel, raised hub made up of 4 struts. Dorsal bodywall wheels are slightly larger in average diameter and tend to have a greater number of spokes than wheels from ventral bodywall. Entire wheel strongly concave (Fig. 2a). Wheels present everywhere in bodywall, and also in tubefeet and papillae. Tentacles contain wheels, also rods (Fig. 2c) of greatly variable size (150 μm to 1



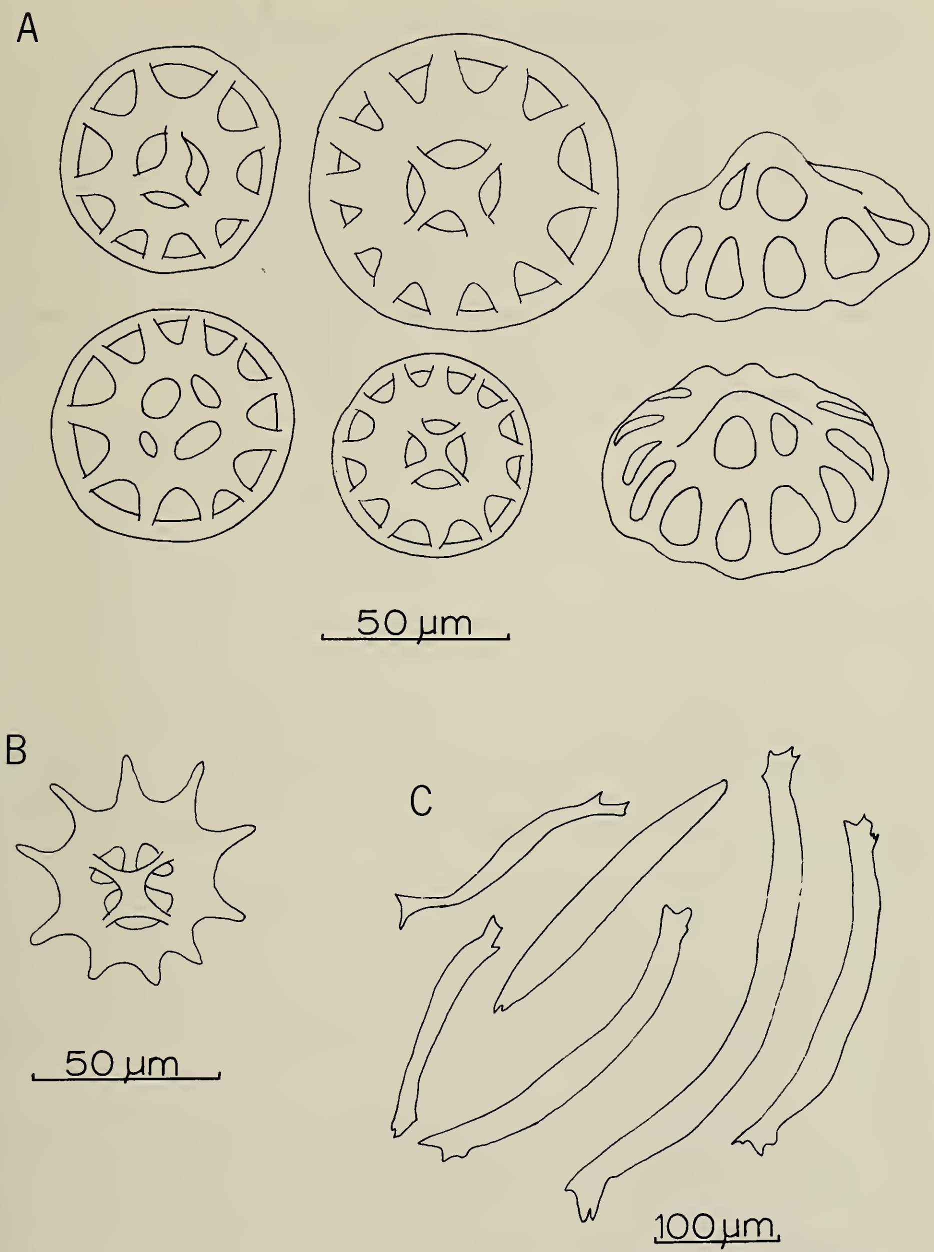


Fig. 2. *Psychronaetes hanseni,* ossicles: A, Wheels from bodywall; B, Stage in development of bodywall wheel; C, Rods from tentacles.

←

Fig. 1. Upper and lower, specimens of *Psychronaetes hanseni* on the seafloor in the vicinity of the type-locality. Dark-colored objects are manganese nodules. Each specimen is approximately 25 cm long. Note anterior "head" region with papillae, and, on upper specimen, the double row of dorsal papillae.

Table 1.—Diameter of wheel ossicles from bodywall.

Size ranges (μm)	Dorsal wheels (n = 50) Size range 51–80 μm		Ventral wheels (n = 50) Size range 48–76 μm	
46–50	0	0%	3	6%
51–55	14	28%	10	20%
56–60	18	36%	23	46%
61–65	3	6%	4	8%
66–70	9	18%	4	8%
71–75	5	10%	4	8%
76–80	1	2%	2	4%

Table 2.—Number of spokes in wheel ossicles from bodywall.

Number of spokes	Dorsal (n = 50) Number of wheels		Ventral (n = 50) Number of wheels	
8	0	0%	8	16%
9	3	6%	16	32%
10	10	20%	17	34%
11	12	24%	6	12%
12	23	46%	3	6%
13	2	4%	0	0%

mm long), usually slightly curved, often with slightly prickly ends. Developmental stages of wheels common in bodywall and tentacles (Fig. 2b). At an early stage of development, before wheel rim has formed, central 4-strut hub is underlain by tripartite piece; this piece eventually disappears, and is seldom seen in fully developed wheels.

Habitat and ecological aspects.—The sediments on which *Psychronaetes hanseni* occurs are commonly Quarternary siliceous oozes and siliceous clays consisting of clay minerals and siliceous microfossils. These sediments are fine, 65% of the material having a particle size of less than 4 μm. Preliminary analyses of seafloor photographs indicate that in three discrete sampling areas, population densities of approximately one individual of *Psychronaetes hanseni* per 1000 m^2 occur.

Remarks.—*Psychronaetes hanseni* is among the largest known elasipodan holothurians. It is surprising that this distinctive species was not encountered during the "*Albatross*" expeditions in the eastern tropical Pacific (Clark 1920). Its apparent absence from "*Challenger*" and other collections is perhaps due to its restricted distribution pattern. Certainly, this species can be identified in seafloor photographs, and no specimens representing this species have as yet been recognized in collection of several thousands of photographs from the southern Pacific and southern Atlantic Oceans examined by the author.

Acknowledgments

I am grateful to Dr. Charles Morgan of the Lockheed Ocean Laboratory for giving me access to specimens and photographs of this new holothurian, and for helping me in many other ways. Dr. Jean Nichols and Ms. Pamela Springer of

the same institution were also very helpful in providing habitat data and selected photographs.

Literature Cited

Clark, H. L. 1920. Holothurioidea.—Memoirs of the Museum of Comparative Zoology 39(4):118–154.

Hansen, B. 1975. Systematics and biology of the deep-sea holothurians. Part 1. Elasipoda.—Galathea Report 13:1–262.

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

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 160–177

LIFE DIAGRAM PATTERNS IN BENTHIC POLYCHAETES

Kristian Fauchald

Abstract.—Life diagrams in polychaetes can be grouped into three patterns. One pattern, including annual species, shows large reproductive efforts, small eggs and planktotrophic larvae. A second pattern, including the perennial species, shows low reproductive efforts, moderately large to large eggs, and non-planktotrophic development. The third pattern includes the multi-annual species, shows high reproductive effort, moderately large eggs, and non-planktotrophic development. These patterns may be in part systematically related to the environment in which the different species of polychaetes are found, but also appear related to a potential need for maintaining small cohesive reproductive units.

The study of life diagrams can be done from several points of view. A veritable jungle of modelling studies of various phases of life diagrams has been published (reviewed by Menge 1975, and Stearns 1976). General problems with modelling have been reviewed recently by Pielou (1981) and will not be considered here. It appears intuitively obvious that a certain factual base of observations must be available to model-builders so that models represent something known to occur with a frequency higher than zero in nature. Conceptual models do not necessarily have to be testable *in toto,* but at least certain facets should be available for testing. The lifespan of an individual polychaete may be as short as a few weeks (*Ophryotrocha* spp.) or last several years (*Eunice* spp.). A basic assumption of this paper is that knowledge of the lifespan of any polychaete species can be used to predict features in the life diagram of that species, and conversely, that information about certain life diagram features, such as brood size or egg size, can be used to predict general life habits and longevity of a given species.

The primary object of this study is to review the few cases for which information is available to test the assumption. A secondary purpose is to review some of the literature on the topic. Thirdly, various predictions are made about unknown features of life diagrams for selected species based on the available information, and suggestions are made as to how these predictions can be tested.

The terms *life cycle* or *life history* are usually defined as a description of the life of an individual starting at release from the parental organism and ending at death. Both terms have unfortunate implications. For example, the sequence of events is only in a formal sense cyclic since all individuals that go through the "cycle" are different (see Wiley and Brooks 1982:1–3), except perhaps in a few cloning forms and even in these, postparturition selection may "change" the clones from one release (spawning) episode to the next. The term cycle implies a static, non-evolutionary point of view. This concept can be useful, but will aid little in explaining differing powers of ecological and geographical dispersal. The term "history," as used in such combinations as natural history, implies a description of past events with little heuristic power. The term has also frequently been used to cover the first part of ontogenesis up to reproductive maturity. The information yielded by ontogenetic study of a given species has turned out to be useful as a predictor of ontogenesis in phylogenetically or ecologically related taxa. The word diagram lacks some of the problematic implications of the two other terms. It is clearly a theoretical, formal term and implies a level of abstraction useful for making testable predictive statements. The above terminological problems were first pointed out to me by Mr. Bill Kennedy.

Most studies on polychaete life diagrams have focused on a single species, or one part of the diagram has been studied for several, usually taxonomically related species (cf. papers cited in Schroder and Hermans 1975). Reviews, such as the very extensive one issued by Schroder and Hermans (1975) have usually focused on detailing the complex factual information necessary for a more theoretical approach. In the review quoted, however, the format did not allow much freedom to explore the theoretical implications.

Trendall (1982) pointed out that in mosquito fish, the different life diagram traits were not necessarily correlated from one locale to another. For this reason, life diagrams must be characterized based on a single population; possibly, for most species, differences between populations in life diagram features will be less than differences between species, but this cannot be assumed *a priori*. The path of generalizations about life diagrams leads then from a study of single populations, via comparisons of diagrams within species, to that between species and between higher taxa. In this study it is assumed that differences among populations are less than differences among species. The study is based on information about single populations, but it is assumed that the diagram found for a population is characteristic of the species as a whole.

The sequence of events in the life of a number of specimens of a single species from fertilization to death may be generalized into a *life diagram* for that species. A comparison of life diagrams for several species may be generalized into a presumably limited number of *life diagram patterns*. A life diagram pattern is thus a second-level abstraction, rather than a primary abstraction. The published literature makes it amply clear that a distinction between the two levels of abstraction has not been made. Life diagram patterns do not necessarily follow taxonomic lines, even if a primary testable prediction for any species would be that its life diagram ought to be similar to that of a related species. Life diagram patterns may follow habitat requirements and a secondary set of hypotheses for a given species might be associated with this feature. The usefulness of separating between these two levels of abstraction thus lies in the possibilities it gives for making different sets of predictions.

Any event in the life diagram of any species can only be wholly understood in connection with all other events in the life of each organism. In other words, the life diagram represents a set of co-adapted features consisting of several partially distinguishable stages or phases, where any phase may be studied separately, but where its significance may be understood only as part of the whole diagram.

Life Diagram Events

The life of any organism is a continuum. For the purposes of analysis, this continuum may be separated into a series of definable events, with the caveat that each of the defined events usually is not distinctly separable from the previous event or from the following event but forms part of the continuum. For the purpose of this discussion nine distinct life diagram events are recognized and defined. The physical location of each event is of primary importance, not least since the location is frequently associated with one or another axis of the life diagram (e.g., small egg-size is frequently correlated with pelagic early development; for example see Thorson 1950).

Spawning and fertilization.—Spawning may take place in the open water, in a burrow or tube, or into an eggmass, or the eggs may be retained in the body cavity of the female so that internal development takes place (Smith 1950). Eggs spawned inside a tube may be grouped in capsules, as in spionids (Blake 1969), or they may occur singly in a string, or stored in some other fashion (Knight-Jones *et al.* 1972). Egg sizes may vary from about 30 μm to about 2–3 mm in diameter. The eggs are usually somewhat flattened or disc-shaped. Fertilization usually appears closely associated with the spawning of the eggs and is assumed to take place when the eggs are released. The process has been poorly studied and nothing is known of the location of fertilization for most species.

Pre-release development.—The development prior to release of the larvae is usually based on energy contained within the egg-membrane, this part of the life diagram being fueled by yolk supplied by the parent. Early development usually takes place wherever fertilization took place. Several species do not have true larvae; the phase is here taken to include a shorthand description of the early development prior to the release from the egg-membrane, or to the transformation of that membrane into part of the larval or juvenile cuticle.

Larval stage.—This stage includes a number of pre-metamorphic, post-hatching developmental phases, whether they are true trochophores or not. These phases may be feeding larvae, in which case they may feed in any one of several different environments. However, most feeding polychaete larvae are planktotrophic in that they feed pelagically, usually on phytoplankton. Other larvae, such as the encapsulated spionid larvae, are adelphophagic, feeding on eggs present in the same capsule. In this particular kind of parental provisioning, a series of eggs are laid within a single capsule, but only one or a few larvae survive to hatching (Blake 1969).

Usually, but not invariably, feeding larvae are pelagic while non-feeding larvae keep close to or on the bottom (Schroder and Hermans 1975). Non-feeding larvae are usually morphologically rather different from the characteristic trochophore, but vary widely among themselves. For example, the barrel-shaped larvae in the super-family Eunicea have short apical tufts of cilia and a broad band of short cilia around the middle. At the time of release from the parental tube, they are usually poorly differentiated internally (Akesson 1967). Orbiniid larvae are completely covered with short cilia (Anderson 1959, 1961, 1966), and recognition of the prototrochal cilia can be difficult.

The length of the trochophoral stage varies tremendously. Certain spirorbids are competent to settle at the time of release (Beckwitt 1979). In contrast, certain sabellariids may remain pelagic for several months (reviewed by Mauro 1975). Perhaps the most common pattern is for the larvae to become competent to settle fairly rapidly, for example after a 10-day stay in the plankton, with the heavy settlement following after an additional 10 days in the plankton (Thorson 1946), but the larvae may be able to stay in the plankton for as much as several weeks (Wilson 1968).

Metamorphosis.—Most polychaetes undergo a gradual metamorphosis in which the posterior half of the larva elongates and becomes segmented, with setae forming in each segment (Schroder and Hermans 1975). Two to three recognizable setigers are usually formed before juveniles settle out of the plankton, but in some polychaetes, especially spionids; as many as 20 setigers may be present while juveniles are still in the plankton (Blake 1969, Hannerz 1956).

The pattern of metamorphosis is rather similar in both feeding and non-feeding larvae, but is usually less drastic in the latter since they usually do not form complex larval structures that have to be modified for adult use. In most species the start of the metamorphic events appears to be under endogenous control in that formation of segments and setae start while individuals are still in the larval habitat. The process is however frequently arrested after the first few segments are formed, and the remainder of the process appears to be triggered when the larvae contact a suitable substrate. In nearly all polychaetes the larval tissues are resorbed with no apparent discard of material at metamorphosis. Metamorphosis is discussed in detail by Schroder and Hermans (1975).

Establishment in adult habitat.—Most polychaetes appear capable of settling after the first few setigers have formed. However, some species can settle in typical larval configuration while others remain in the plankton until they have attained nearly adult configuration. The level of habitat selectivity appears to vary from species that are highly selective (Wilson 1954, 1955) to species that appear to follow the Thorsonian larval-rain model (Thorson 1950). After settlement all polychaetes will start feeding on food types, if not sizes, used by adults of the species. Species with planktotrophic larvae will at this point also shift to the adult food, which can be widely different from the phytoplankton consumed by the larvae.

Growth phase.—Little is known about the phase of life from settlement to the onset of sexual maturity. At settling most species are only a fraction of their adult length, and densities at settlement may be entirely different from adult population patterns. Density regulation in the form of post-settlement dispersal or mortality must take place. Most species are capable of moving from one location to another, even the so-called sessile taxa (see Dean 1978a, b) so the growth phase may represent a hidden small-scale dispersal phase.

Gamete maturation.—In most polychaetes early development of the sexual products takes place in gonads suspended in the coelomic cavity, with late development occurring while the sex cells are free in the coelom (Schroder and Hermans 1975). Release of sex cells from the gonads may take place as a single event, or be spread out over a longer period of time. Parallel to the late phases of gamete maturation, changes in adult morphology may also signal the onset of sexual maturity. Such changes are usually most drastic in semelparous species, but cyclic changes may also take place in interoparous forms.

Spawning.—Polychaetes may be semelparous or iteroparous. Specimens of iteroparous species may spawn repeatedly within a single spawning season, or may spawn only once within a single season. Most polychaete species appear to have protracted spawning periods, lasting for several weeks to months; a few species are known to have extremely limited, synchronized spawning, such as the palolo worm, *Palola viridis* (e.g., Hofmann 1974). While the spawning patterns of several swarming polychaetes have been well publicized, most species do not swarm, but spawn in or near the adult habitat. A number of tubicolous forms spawn within their tubes and burrowing forms may form temporary spawning burrows, leaving their spawn there.

Senescence and death.—Virtually nothing is known about typical causes of death in iteroparous polychaetes. Most semelparous forms may die upon spawning, and in the swarming forms tissues of several major organ-systems have been reported to be resorbed before the spawning takes place (Schroder and Hermans 1975). Certain semelparous forms, such as some spionids, appear to survive the spawning and remain in their tubes with the developing embryos for some period of time.

Material and Methods

The material available for study is extremely limited, in that most of the different kinds of information indicated by the listing of life diagram events must be available and studied in a single population of a species.

Hannan *et al.* (1977) in a study of life histories of benthic invertebrates of Monterey Bay included information on larval development, the size of the reproducing females and the total number of eggs present. Species studied included *Ameana occidentalis, Lumbrineris luti, Magelona sacculata, Mediomastus californiensis, Nothria elegans, Prionospio cirrifera* and *P. pygmaea.*

Emerson (1975) studied the population ecology of *Diopatra ornata* at Santa Catalina Island off southern California and included sufficient measurements to allow calculation of the necessary parameters. Beckwitt (1979) in a study of the population ecology of spirorbid polychaetes from southern California did a series of experiments on settlement and population structure allowing the inclusion of data for *Janua brasiliensis* and *Pileolaria pseudomilitaris.*

Information on the reproductive biology of onuphid polychaetes has been gathered in the vicinity of the Smithsonian Marine Station at Link Port, Florida, at Bermuda, and in Belize; the following species have been studied in some detail: *Kinbergonuphis simoni* from Florida, *Mooreonuphis jonesi* at Bermuda, and *K. pulchra* in Belize. Some information is available for additional species from Florida, and this material is used to make some testable predictions about missing data.

For each species the following information was recorded: 1. Size of the reproducing female (numbers of setigers as well as length and width measurements). 2. Average egg-size. 3. Numbers of eggs produced by a female in a single reproductive event. 4. Number and distribution of reproductive events in the life of a single individual. 5. Estimated length of life for a single individual.

Data are presented in tables and illustrations and compared to information otherwise available in the literature.

The following biological notes indicate the basic habitat and general geographical dispersal of principal species treated in this paper. Table 1 reviews some basic life diagram parameters for these species.

Amaeana occidentalis Hartman (1942) (family Terebellidae) lives in temporary burrows in sandy and muddy environments from intertidal zones to the edge of the continental shelf or a little beyond; it is known from southern and central California, but may also be present along the whole northwest Pacific coast.

Identification of species in the genus is problematic and the exact distribution is currently difficult to assess.

Diopatra ornata Moore (1910) (family Onuphidae) is tubicolous and lives at shelf and upper slope depths in sandy and muddy environment in the eastern Pacific Ocean. Emerson (1975) did a large-scale study of a single population of *D. ornata* from Santa Catalina Island.

Janua brasiliensis (Grube, 1871) (family Spirorbidae) is a small, spirally coiled worm living in a calcareous tube. It is widely dispersed in warm waters in very shallow subtidal and intertidal areas. Beckwitt (1979) examined it as part of a study of intertidal spirorbids from southern California.

Kinbergonuphis pulchra (Fauchald, 1981) (family Onuphidae) lives in relatively poorly constructed tubes in shallow subtidal areas. It is currently known only from sandy areas inside the outer edge of the barrier reef off Belize, Central America.

Kinbergonuphis simoni (Santos, Day, and Rice, 1981) (family Onuphidae) lives in poorly constructed tubes in shallow subtidal and intertidal areas in sand. It is known from both sides of peninsular Florida, and is common in bays and inlets.

Lumbrineris luti Berkeley and Berkeley (1945) (family Lumbrineridae) lives in sandy and muddy areas at shelf depths along the eastern Pacific Ocean. It does not build tubes but burrows through the substrate.

Magelona sacculata Hartman (1961) (family Magelonidae) lives in sandy substrates at shelf depths off southern and central California. It does not build a permanent tube or burrow, but appears to move through the substrate more or less continuously.

Mediomastus californiensis Hartman (1944) (family Capitellidae) was originally described from California in shallow muddy environments, but has since been reported widely from both coasts of the Americas. It builds semi-permanent burrows and appears tolerant of considerable environmental abuse in that it frequently is present in harbors and similar high-organic environments (Hannan *et al.* 1977).

Mooreonuphis jonesi Fauchald (1982) (family Onuphidae) is the only onuphid known from shallow water in Bermuda. It is common in sand and coral debris and builds tubes which are covered externally with coral and shell fragments.

Nothria elegans (Johnson, 1897) (family Onuphidae) is known from shallow subtidal to deep shelf depths off the west coast of the United States and Canada; it is tubicolous and especially common in relatively clean sandy environments.

Pileolaria pseudomilitaris (Thiriot-Quievreux, 1965) (family Spirorbidae) appears to be widespread in warm waters in intertidal and shallow subtidal areas; it is small, spirally coiled and enclosed in a calcareous tube. It was studied in southern California by Beckwitt (1979).

Prionospio cirrifera (Wiren, 1883) (family Spionidae) was originally described from shallow water in the Arctic Ocean and has since been widely reported. It is possible that material studied by Hannan *et al.* (1977) should be referred to by another name (Nancy Maciolek personal communication), but since all specimens came from a single area and were studied over a long period of time, it appears safe to assume that they represent a single species. *Prionospio cirrifera* builds a small tube which it is capable of leaving, and has been reported from a variety

Table 1.—Some ecological characteristics of polychaetes considered in the analysis. The columns are: 1. Longevity; 2. Motility pattern of adults; 3. Feeding pattern of larvae.

	1	2	3
Ameana occidentalis	annual	discretely motile	feeding
Diopatra ornata	perennial	sessile	non-feeding
Janua brasiliensis	multiannual	sessile	non-feeding
Kinbergonuphis pulchra	perennial	sessile	non-feeding
Kinbergonuphis simoni	perennial	sessile	non-feeding
Lumbrineris luti	perennial	motile	non-feeding
Magelona sacculata	annual	motile	feeding
Mediomastus californiensis	multiannual	discretely motile	non-feeding
Mooreonuphis jonesi	perennial	sessile	non-feeding
Onuphis elegans	perennial	sessile	non-feeding
Pileolaria pseudomilitaris	multiannual	sessile	non-feeding
Prionospio cirrifera	multiannual	discretely motile	feeding
Prionospio pygmaea	multiannual	discretely motile	feeding

of different environments. The particular form studied here is present along the eastern Pacific Ocean in muddy to sandy environments at shelf depths.

Prionospio pygmaea Hartman (1961) (family Spionidae) was originally described from southern California, and while the same taxonomic considerations apply to this as to the preceding species, it is more likely that it is currently referred to by its correct name. It is known from southern and central California in sandy and muddy environments at shelf and slope depths. Like its congener, it builds small, semi-permanent tubes.

Results

Table 2 shows the measured and calculated values for all species for which adequate data were available. Table 3 reviews information available for another eight species, for which some information may be missing or an inadequate number of specimens has been examined.

The lifetime reproductive effort per female varies in a systematic fashion (Fig. 1). Perennial species, defined as those that reproduce in at least two different growth seasons, have consistently low lifetime investments. For all species examined it represents less than 10% of the volume of the females and is probably overestimated since it was assumed that all individuals were in their first reproductive season and would not grow before the next reproductive event. This assumption is known to be incorrect for *Diopatra ornata* and *Mooreonuphis jonesi* (Emerson 1975; Fauchald 1982), but cannot be corrected without knowledge of the exact age of all females examined.

The two annual species examined have considerably higher lifetime reproductive efforts, representing more than 20% of the volume of the reproducing females. The reproductive effort is underestimated in that it has been assumed that females of both species reproduce only once and die after reproduction. Some annual species are known to partition their spawning into several shorter bursts, with regeneration of the coelomic oocytes between events (Schroder and Hermans 1975). The available data did not make it possible to estimate whether or not either species shows such patterns.

Table 2.—Life diagram characteristics for the species of polychaetes considered in the analysis. The columns are: 1. Total number of setigers; 2. Total length in mm; 3. Maximal width in mm; 4. Largest egg-diameter in micrometer; 5. Smallest egg-diameter in micrometer; 6. Volume of a single egg in 10^6 cubicmicrometers; 7. Numbers of eggs in a single spawn; 8. Volume of eggs in a single spawn in 10^6 micrometers; 9. Numbers of spawning events per female per lifetime; 10. Lifetime volume of eggs per female in 10^6 cubicmicrometers; 11. Volume of adult female in 10^6 cubicmicrometers; 12. Fecundity per female per lifetime, measured as the relative volume of eggs per female per lifetime, in parts per hundred.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Amaena occidentalis	—	100	4.5	210	158	2.77	14,000	38,792.39	1	38,792.39	159,043.13	24.39	Central California
Diopatra ornata	380	500	3.0	235	176	3.90	900	3510.00	4	14,040.00	3,534,291.74	.40	Southern California
Janua brasiliensis	—	—	—	—	—	10.00	15	150.00	24	3649.50	3000.00	121.65	Southern California
Kinbergonuphis pulchra	191	67.41	.95	331	248	10.67	74	789.59	3	2368.76	47,781.68	4.96	Belize
Kinbergonuphis simoni	167	56.22	.90	356	267	13.34	46	613.44	3	1840.33	35,765.62	5.15	Florida
Lumbrineris luti	—	200	2.36	100	75	.29	500	145.30	2	290.60	10,618.58	2.74	Central California
Magelona sacculata	—	30	.60	130	98	.65	3000	1951.16	1	1951.16	8482.30	23.00	Central California
Mediomastus californiensis	—	15	.50	80	60	.15	1500	226.19	1	226.19	294.52	76.80	Central California
Mooreonuphis jonesi	122	35.40	.87	164	123	1.29	22	28.81	3	86.42	21,044.16	.41	Bermuda
Onuphis elegans	—	300	2.94	240	180	4.07	789	3212.42	4	12,849.67	2,036,600.27	.63	Central California
Pileolaria pseudomilitaris	—	—	—	—	—	15.0	—	220.00	24	4866.6	5000.00	97.33	Southern California
Prionospio cirrifera	—	13	.50	30	22	.01	500	3.89	1	3.89	255.25	1.49	Central California
Prionospio pygmaea	—	11	.50	60	45	.06	500	31.10	1	31.10	215.98	14.40	Central California

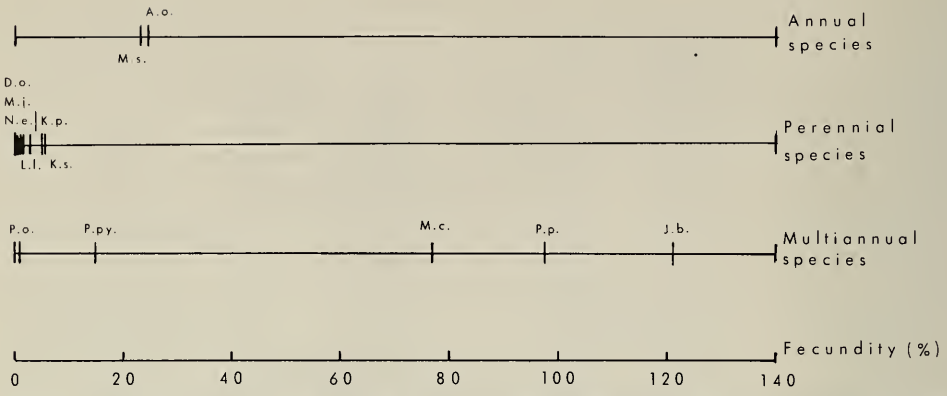


Fig. 1. Diagram showing the relative fertility of annual, perennial and multiannual species. The fecundity measure is in per cent of the total volume of the female. The species are: A.o., *Ameana occidentalis*; D.o., *Diopatra ornata*; J.b., *Janua brasiliensis*; K.p., *Kinbergonuphis pulchra*; K.s., *K. simoni*; L.l., *Lumbrineris luti*; M.s., *Magelona sacculata*; M.c., *Mediomastus californiensis*; M.j., *Mooreonuphis jonesi*; N.e., *Onuphis elegans*; P.p., *Pileolaria pseudomilitaris*; P.o., *Prionospio cirrifera*; P. py., *Prionospio pygmaea.*

Multiannual species, defined as those species that go through two or more generations in a single growth season, show a great deal of variability. Three taxa, a capitellid and two spirorbids, a have extremely high lifetime reproductive efforts, above 75% in all three cases; two spionids show low to moderate reproductive efforts. In the case of the two spirorbids, it is known that a single individual may produce up to 24 batches of eggs in a lifetime (Beckwitt personal communication). Spirorbids live in an unstable environment, so at least some of these egg-batches probably remain unrealized in the life of any given female. The resulting reduction in reproductive effort could be considerable, but even if one half of the possible egg-batches were skipped, the lifetime reproductive effort would still be more than twice that for any annual or perennial species. It was assumed that the two spionids breed only once, as the most conservative estimate possible. If in fact each female breeds twice, the reproductive effort per female will increase above the level of the annual species and be close to the level of the two spirorbids.

Comparing information in Tables 1 and 2 leads to some interesting conclusions. Three major life diagram patterns appear to be present. One, represented by annual species, shows large reproductive efforts, moderately large eggs, and planktotrophic larvae. The second pattern, represented by perennial species, shows low reproductive efforts, moderately large to large eggs and a non-planktotrophic development. The third pattern, represented by the multiannual forms, shows a (probable) high reproductive effort, relatively small eggs, and a non-planktotrophic development. These patterns are indicated in Figure 2 as Pattern I and Patterns IIa and IIb. The two latter patterns appear related in that both include forms that lack planktotrophic larvae and any organized larval or adult dispersal phase.

Another interesting point is that both perennial and multi-annual forms are relatively sedentary as adults. Onuphids, which make up the bulk of the perennial

Table 3.—Life diagram features for selected species of polychaetes for which inadequate data are available for complete determination of life diagram pattern. The columns are: 1, Total number of setigers; 2, Total length in millimeters; 3, Maximum width in millimeters; 4, Greatest egg diameter in micrometers; 5, Smallest egg diameter in micrometers; 6, Volume of a single egg in 10^6 cubicmicrometer; 7, Numbers of eggs in a single spawning event; 8, Volume of eggs in a single spawning event in 10^6 cubicmicrometer; 9, Numbers of spawning events in the life of a female; 10, Life-time volume of eggs for a single female in 10^6 cubicmicrometers; 11, Total volume of the females in 10^6 cubicmicrometers; 12, Lifetime fecundity for each female in %; 13, Locality from which the sampled specimens were taken, comments.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Axiothella sp. specimen 1.	13	54.0	1.5	185	138	1.85	500	927.37	1	927.37	—	—	Florida, incomplete
Specimen 2	16	58.0	1.0	243	183	4.22	500	2110.15	1	2110.15	—	—	Florida, incomplete
Specimen 3	17	50.56	1.6	270	202	5.78	480	2775.75	1	2775.75	101,656.91	2.73	Florida
Specimen 4	16	53.60	1.6	226	169	3.57	500	1785.12	1	1785.12	—	—	Florida, incomplete
Capitella capitata sp. 1	15	4.32	.32	120	90	—	—	—	—	—	—	—	Florida, incomplete
Diopatra cuprea specimen 1	83	48.0	2.0	183	137	1.81	3182	5760.14	4	23,040.58	—	—	Florida, incomplete
Specimen 2	148	67.0	2.0	197	147	2.26	1600	3616.00	4	14,464.00	210,486.71	6.87	Florida
Eteone lactea specimen 1	107	33.60	.80	95	72	.26	1200	306.21	1	306.21	16,919.36	1.81	Florida
Specimen 2	187	40.80	1.12	98	73	.28	1300	362.82	1	362.82	40,196.30	.90	Florida
Glycinde solitaria sp. 1	190	16.80	.96	87	65	.23	900	208.46	1	208.46	1158.12	18.00	Florida
Haploscoloplos fragilis													
Specimen 1	127	52.5	2.5	150	112	.99	1800	1781.28	1	1781.28	257,217.90	.69	Florida
Specimen 2	80	18.72	1.12	135	101	.72	400	286.28	1	286.28	18,443.01	1.55	Florida
Magelona sp. specimen 1	70	25.6	1.92	140	105	.81	1750	1414.31	1	1414.31	74,119.47	1.91	Florida, in reg.
Onuphis eremita oculata													
Specimen 1	—	32.96	1.60	211	158	2.45	—	—	4	—	—	—	Florida
Ophelina sp. specimen 1	50	36.5	1.5	96	72	—	—	—	—	—	—	—	Florida
Owenia fusiformis													
Specimen 1	18	24.80	1.12	105	79	.34	2500	844.75	1	844.75	24,433.05	3.46	Florida
Streblosoma crassibranchia													
Specimen 1	70	49.60	2.40	221	166	3.16	4000	126,020.41	1	12,620.41	224,385.11	5.62	Florida
Specimen 2	52	32.80	2.72	173	130	1.41	—	—	—	—	—	—	Florida, incomplete
Specimen 3	57	61.44	2.40	184	138	1.83	4000	—	—	—	—	—	Florida, incomplete
Specimen 4	53	48.96	2.88	196	147	2.20	—	—	—	—	—	—	Florida, incomplete

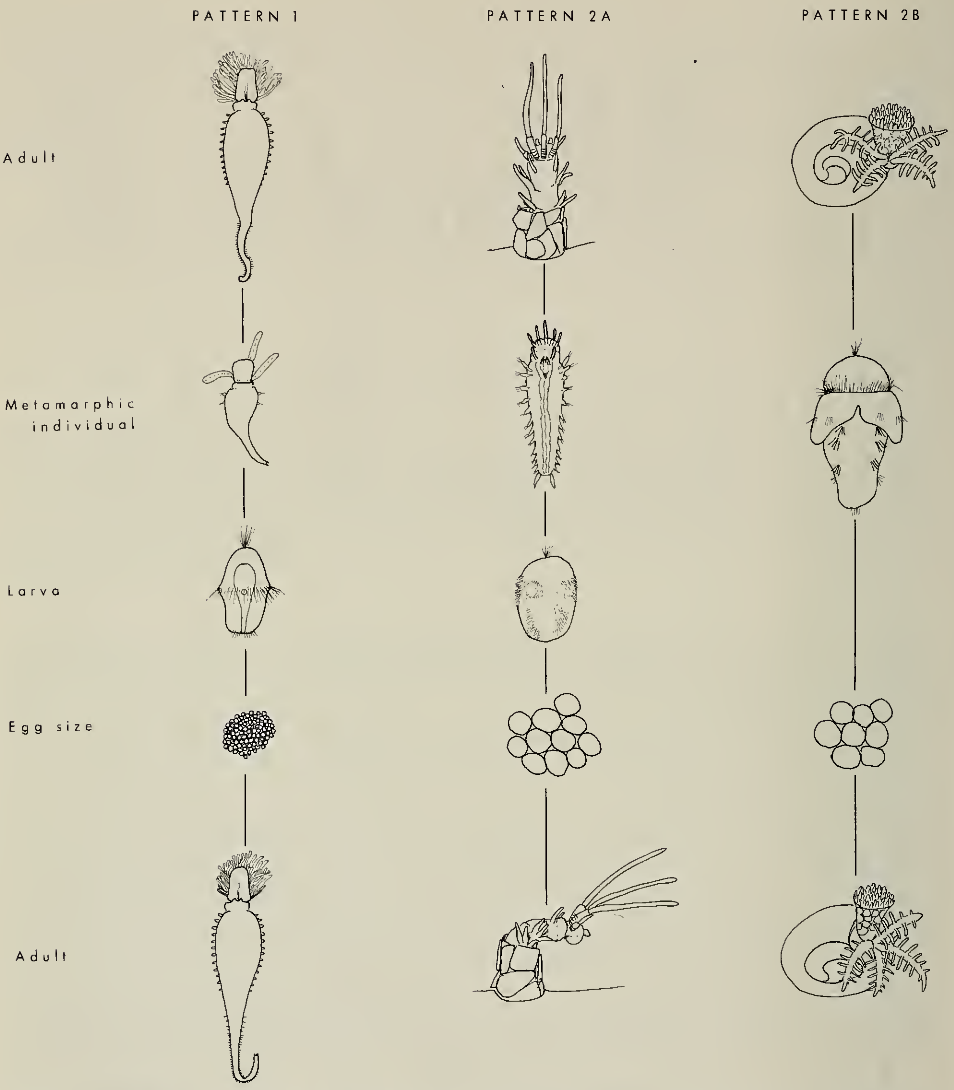


Fig. 2. Life diagram patterns for 3 selected species of polychaetes. The species are from left to right: *Amaeana occidentalis*, *Kinbergonuphis simoni* and *Pileolaria pseudomilitaris*. The patterns are discussed further in the text.

species examined, are all tubicolous. These species also appear to have lost the pelagic dispersal stage in that they have non-feeding, benthic larvae that are capable of settling immediately upon release (Emerson 1975; Fauchald personal observations). *Kinbergonuphis simoni* and *Mooreonuphis jonesi* both brood their young and release them from the parental tube at the 10- (or more) setiger stage (Fauchald 1982 and personal observations). Beckwitt (1979) demonstrated that specimens of the two spirorbid species were capable of settling immediately upon release from the parental tube.

Discussion

The benthopelagic life-cycles of marine invertebrates are usually discussed in terms of fitness of the species, expressed as the number of offspring of each female (cf. Caswell 1980, 1981). The reduction in length of the pelagic phase of the life diagram was considered an exceptional, relatively rare phenomenon by Caswell (1981) who demonstrated under what conditions selection for a reduced larval life might take place. In fact, a variety of marine invertebrates including prosobranch snails, all benthic peracarid crustaceans, and various polychaetes show a loss of the pelagic life-phase, so the pattern can hardly be considered exceptional. Furthermore, among the polychaetes a variety of otherwise unrelated groups show a reduction in the length of larval life; presumably this loss has occurred independently in each of these groups.

The life-diagram patterns of polychaetes identified above appear difficult to fit with the fitness theory for a variety of reasons. First, the large, perennial forms among the polychaetes usually show reduced motility as adults (Fauchald and Jumars 1979); second, these same species also show reduced motility as larvae and appear to lack a dispersal phase altogether. In contrast, annual forms, which also include a number of large species, are frequently highly motile both as larvae and as adults. The multiannual forms probably show the high reproductive effort expected by theory (the Pianka version of McArthur and Wilson's r- and K-selection theory, Pianka 1970), but do not agree with that theory in that neither larvae nor adults have high dispersal abilities and the reproductive effort is channeled into a few highly developed larvae rather than into the numerous broadcast offspring predicted by the theory.

Shields (1982) in a discussion of the maintenance of sexual reproduction, stated that most life-diagram theory is based on the assumption that most species have large, panmictic populations and that in such populations the maintenance of sex leads to what Williams (1975) referred to as the cost of meiosis. A highly fit genotype that arises through sexual reproduction will very probably be lost to the next generation through well documented genetic processes. According to Shields (1982) asexual reproduction, which would inititally keep the highly fit genotype intact, eventually would lead to a ratcheting of mutations, spreading them through the population. Shields pointed out that in relatively small populations of related organisms, sexual reproduction will stabilize a successful genome and will tend to weed out deleterious mutations. Thus maintenance of sex in these forms, while of long-term importance in evolution, is basically a conservative feature allowing a small, successful population to maintain itself while conditions remain reasonably stable (in ecological time) but to retain the evolutionary flexibility that sexual reproduction implies in evolutionary time.

The explanation for the loss of a larval dispersal phase in the perennial sessile polychaetes appears to involve a Shieldian inbreeding: the loss of a dispersal phase simply is a means of maintaining a cohesive, small interbreeding population so that a successful genome can be maintained. The loss of larval life then does not involve individual fitness *per se*; Caswell's fitness argument presumably works for relationships within each population, but the overriding feature, the maintenance of a small interbreeding population, has been the determining factor in losing the dispersal phase.

The loss of dispersal in multi-annual forms may be related to the habitat these forms usually occupy. These forms usually occur in relatively ephemeral environments. Clearly, disturbed patches are distributed in a statistically predictable fashion. For example, soft muddy and sandy bottoms in middle-shelf environments are usually stable, and few disturbances occur. However, one or a few major storm-systems will sweep over most coastlines from time to time and the waves from these systems will disturb bottom sediments in water deeper than that reached by normal wave-trains. An interrupted band of disturbed soft sediments is thus created along many coast-lines, but it is impossible to predict exactly where the disturbance will come in a given year: we know that the disturbance will come, in a statistical sense, but cannot predict exactly where nor when. Most of the multi-annual forms are small, and may themselves be moved around with the disturbed sediments. Further, if the "life-expectancy" of a disturbed patch is longer than the life-expectancy of specimens of the species occupying the patch, then it is clearly to the advantage of the occupying species to see to it that its offspring do not get dispersed much beyond the outlines of the patch. The net effect of this ecological determinant will be exactly the same as for the perennial species in that each actually interbreeding population will remain small, and specimens found close to each other have a high probability of being closely related as well.

The annual species have retained large numbers of small offspring and the larvae may spend a long time in the plankton. It is possible that these taxa have very large, panmictic populations and thus fulfill the criteria for maintenance of sex indicated by Williams (1975); however, there may also be valid ecological reasons why large numbers of larvae are maintained among these taxa. Provided that adults die after breeding, each population of larvae that settle will have to settle in an environment where the presence of adults of the same species cannot be used as a cue in settlement. However, Wilson (1954, 1955) demonstrated that the larvae of *Ophelia bicornis* are attracted to sand where adults have been present, reducing the chance-settlement in this particular species. It is also possible that taxa in this category are unspecific in their ecological requirements and may be presently found in extensive environments, such as sandy and muddy bottoms with variable grain size, organic content, and depth. Under these circumstances, it would be to the advantage of the species to spread its larvae as widely as possible and thus to maintain maximum genetic flexibility.

The result of this study points out, that while the life-diagram theory as it has developed probably is correct, other features must be taken into account, and that the extremely heavy focus of the life-diagram theory on fitness and with the hidden assumption of large, panmictic populations, has made the investigators overlook the consequences of the fact that many animals occur in small, isolated or partially isolated populations in which a successful genome is being maintained by a loss of dispersal mechanisms. The pattern developed here is not universal: a great number of polychaetes do in fact disperse over wide areas and do have larvae that live for a long period of time in the plankton (Wilson 1968; Scheltema 1974), but a surprisingly large number of species appear to shorten the larval life, either by spawning into an egg-mass (lumbrinerids, maldanids, terebellids), by brooding (onuphids, serpulids, spionids) or even by direct development (nereidids). In these cases, I believe the best interpretation of the curtailment of long larval life lies in the attempt at maintaining small breeding populations, rather than in any optimization of fitness in terms of numbers of offspring. A second interpretation might be that the curtailment of larval life reduces larval wastage if the adult environment is hard to find and patchy. Note that these two explanations may simultaneously be correct. I believe that the fitness theory as currently conceived might have great value in explaining differences between individual organisms within a confined environment.

The reduction in lifetime reproductive effort in the perennial species indicates that for these species, most of which are large (for polychaetes) a larger fraction of the energy consumed has been shifted to growth rather than to reproduction. This is especially striking when comparing the lifetime reproductive effort of similar sized onuphids which are perennial, with the annual terebellids.

The findings of this study are consistent with the review by Schaffer and Gadgil (1975) of higher plants. In some respects the coincidence may be fortuitous since the present emphasis has been on the role of reduced larval dispersal in maintaining a cohesive genetic structure in the population, rather than on the selection for an optimal life diagram emphasized by Schaffer and Gadgil (1975). It may be competitively of so great importance for a population to maintain genetic cohesiveness that selection for other features in the short term becomes trivial.

As indicated by Trendall (1982) different life diagram traits may not at all be closely correlated to each other. The idea of a life diagram for all populations of species may be spurious: each population, with the constraints built into the basic morphology and development of the taxon, may adapt the life diagrams to the local conditions under which the population survives. Despite this caveat, it appears that the polychaetes investigated so far can be fitted into the three patterns described above.

Very few of the 15,000+ known species of polychaetes were taken into account in erecting this system of life diagram patterns. An attempt was made at having as many and as varied morphological forms represented as possible, but inevitably, the few species examined represent a biased sample including species for which data could be easily gathered or were already present in the literature. The detailed structure of the life diagram patterns for polychaetes may change, but the basic outline will probably remain similar to the one detailed above.

Some Predictions

For the last several years I have been following the reproductive activity of selected species of polychaetes in the vicinity of the Smithsonian Marine Station at Link Port, Florida. For some species I have gathered sufficient information to include them among the species listed above. However, for most of them I have either inadequate numbers of specimens or some pieces of information cannot be gathered with the techniques I am using.

Table 3 reviews information for these taxa. Based on life-diagram patterns I outlined above, I believe the following statements will, when tested, describe the situation for these species.

Two of the species for which I have been gathering data are onuphids, *Onuphis eremita oculata* Hartman (1951) and *Diopatra cuprea* (Bosc, 1802). For both species I lack crucial data, but the average egg-sizes for both indicate that the life diagram for each should be similar to that found for other onuphids, with low reproductive effort, small numbers of eggs and lack of pelagic larvae, or at least tube-brooding until larvae are competent to settle.

Axiothella sp., a maldanid, is known to discharge eggs into an eggmass; the egg-size and average numbers of eggs per batch indicate a reduced larval development, without a feeding larval stage. The reproductive effort of the only complete female sampled indicates that the species should live for at least two seasons.

Glycinde sp., a goniadid, has a relatively high reproductive effort combined with small eggs; it is suspected that this species may be annual and have a pelagic, planktotrophic larva.

Streblosoma sp. of the family Terebellidae, has relatively large eggs, and moderately high reproductive effort. Related species are known to spawn into a loosely organized egg-mass, which deteriorates rapidly and releases larvae, which, while they may be planktotrophic, are capable of settling shortly after release from the egg mass. Based on the available information, it appears that *Streblosoma* will show a similar pattern. The species may be an annual.

The capitellids studied by Grassle and Grassle (1974, 1976) show a bewildering array of different life-diagrams. Some taxa have planktotrophic larvae, others have a reduced larval life or direct development, the average egg-diameters appear well correlated with the developmental pattern exhibited (see also Schroder and Hermans 1975, and Hermans 1979). The consequences in terms of life-diagrams are that the forms with a planktonic larva are capable of dispersing rapidly and widely, whereas the forms without such larvae are capable of building up larger populations once a suitable habitat has been located. The only specimen of *Capitella* measured in the current study had large eggs and thus should belong to the taxa with a reduced larval development. The different recruitment strategies of the capitellids may well determine longevity and thus differential resource utilization by each species, and may thus explain why the Grassles found more than a single species in a sample in certain areas off Massachusetts.

Two specimens of *Haploscoloplos fragilis* measured during the current study show egg sizes similar to those measured for *Scoloplos armiger,* another orbiniid, by Anderson (1959). The reproductive effort is very low and very few segments contained eggs in both specimens. It is suggested that this orbiniid shows a mixed strategy: the larvae are planktotrophic, but the individual specimens live for at least two seasons or alternatively, are capable of spawning more than once, each well separated out in the life of the female. The two individuals, both complete, are very different in size, indicating that perhaps the latter alternative may be the correct one.

A single specimen of a species of *Ophelina* was measured. The egg diameters are similar to those measured for *Armandia bioculata* by Hermans (1979) and it is predicted that the life diagram will be characteristic of an annual species, with high reproductive effort, small, planktotrophic larvae and relatively lengthy planktonic life.

Another interesting prediction is related to the structure of the deep sea benthos. The dominating benthic forms at least among the polychaetes in deep water are all forms that fit with the pattern found above for multi-annual forms (see Hartman 1965, Hartman and Fauchald, 1971). The shallow water multi-annual forms are associated with areas of randomly disturbed sediments or other unstable, unpredictable environments. The dominance of species with a similar life diagram in the deep sea benthos indicates that a similar disturbance pattern may be present in the apparently stable deep sea benthos. As indicated by Dayton and Hessler (1972) this disturbance is very probably biological in nature.

Acknowledgments

This study started with a lecture I gave during the class in polychaete biology at Catalina Marine Science Center, University of Southern California, in 1979. Bill Kennedy and Fred Piltz, the assistants in that class, and also the students encouraged me to develop the topic further; particularly Bill Kennedy was instrumental in getting me started. The reaction to a paper I gave at the annual meeting of American Society of Zoologists in Tampa indicated that the material would create a great deal of interest, if not agreement. Various versions of the paper have been read by Meredith L. Jones, Mary E. Rice, Peter A. Jumars, Kirk Fitzhugh, and David E. Russell, all of whom gave their candid opinions but should not be held responsible for its content.

This is contribution #116 from the Smithsonian Marine Station at Link Port, Florida.

Literature Cited

Akesson, B. 1967. The embryology of the polychaete *Eunice kobiensis*.—Acta Zoologica 48:141–192, 22 figs.

Anderson, D. T. 1959. The embryology of the polychaete *Scoloplos armiger*.—Quarterly Journal of Microscopical Science 100:89–166.

———. 1961. The development of the polychaete *Haploscoloplos fragilis*.—Quarterly Journal of Microscopical Science 102:257–272.

———. 1966. The comparative embryology of the Polychaeta.—Acta Zoologica 47:1–42.

Beckwitt, R. D. 1979. Genetic structure of *Pileolaria pseudomilitaris* (Polychaeta: Spirorbidae) in southern California.—Dissertation, University of Southern California, Los Angeles, 126 pp., 11 figs., 13 tbs.

Blake, J. A. 1969. Reproduction and larval development of *Polydora* from northern New England (Polychaeta: Spionidae).—Ophelia 7:1–63.

Caswell, H. 1980. On the equivalence of maximising reproductive value and maximising fitness.—Ecology 61(1):19–24, 1 tb.

———. 1981. The evolution of "mixed" life histories in marine invertebrates and elsewhere.—American Naturalist 117(4):529–536, 1 fig.

Dayton, P. K., and R. R. Hessler. 1972. Role of biological disturbance in maintaining diversity in the deep sea.—Deep-Sea Research 19:199–208.

Dean, D. 1978a. Migration of the sandworm, *Nereis virens*, during winter nights.—Marine Biology 45:165–173.

———. 1978b. The swimming of bloodworms (*Glycera* spp.) at night, with comments on other species.—Marine Biology 48:99–104.

Eckelbarger, K. J. 1980. An ultrastructural study of oogenesis in *Streblospio benedicti* (Spionidae), with remarks on diversity of vitellogenic mechanisms in Polychaeta.—Zoomorphologie 94:241–263, 32 figs.

Emerson, R. R. 1975. The biology of a population of *Diopatra ornata* at Santa Catalina Island, California.—Dissertation, University of Southern California, Los Angeles, 325 pp., 30 figs., 27 tbs.

Fauchald, K. 1982. Description of *Mooreonuphis jonesi*, a new species of onuphid polychaete from shallow water in Bermuda, with comments on variability and population ecology.—Proceedings of the Biological Society of Washington, 94(4):807–825.

———, and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds.—Oceanography and Marine Biology, An Annual Review 17:193–284, 23 figs., 33 tbs.

Grassle, J. F., and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes.—Journal of Marine Research 32(2):253–284, 11 figs., 2 tbs.

Grassle, J. P., and J. F. Grassle. 1976. Sibling species in the marine pollution indicator *Capitella* (Polychaeta).—Science 192(4239):567–569.

Hannan, C. A., L. W. Hulberg, K. M. Mawn, and J. W. Nybakken. 1977. A study to develop standard procedures for life history analysis of benthic invertebrates for biological monitoring in marine and estuarine environments.—Moss Landing Marine Laboratories, California State University Consortium, Moss Landing, California, 217 pp.

Hannerz, L. 1956. Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil and Poecilochaetidae n. fam. in the Gullmar Fjord (Sweden).—Zoologiska Bidrag fran Uppsala 31:1–204, 57 figs.

Hartman, O. 1965. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas.—Allan Hancock Foundation Publications, Occasional Paper 28:1–378, 52 pls.

———, and K. Fauchald. 1971. Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas Part II.—Allan Hancock Monographs in Marine Biology 6:1–327, 34 pls.

Hermans, C. O. 1979. Polychaete egg sizes, life histories and phylogeny. *In* S. E. Stancyk, ed. Reproductive ecology of marine invertebrates.—The Belle W. Baruch Library in Marine Science 9:1–9, 1 fig., 3 tbs.

Hofmann, D. K. 1974. Maturation, epitoky and regeneration in the polychaete *Eunice siciliensis* under field and laboratory conditions.—Marine Biology 25:149–161.

Knight-Jones, E. W., P. Knight-Jones, and P. J. Vine. 1972. Anchorage of embryos in Spirorbinae (Polychaeta).—Marine Biology 12:289–294, 2 figs.

Mauro, N. A. 1975. The premetamorphic developmental rate of *Phragmatopoma lapidosa* Kinberg 1867, compared with that in temperate sabellariids (Polychaeta, Sabellariidae).—Bulletin of Marine Science 25(3):387–392.

Menge, B. A. 1975. Brood or broadcast? The adaptive significance of different reproductive strategies in the two intertidal sea stars *Leptasterias hexactis* and *Pisaster ochraceus*.—Marine Biology 31:87–100.

Palmer, A. R., and R. R. Strathmann. 1981. Scale of dispersal in varying environments and its implication for life histories of marine invertebrates.—Oecologia 48:308–318, 8 figs., 2 tbs.

Pianka, E. On *r*- and *K*-selection.—American Naturalist 104:592–597.

Pielou, E. C. 1981. The usefulness of ecological models: a stock-taking.—Quarterly Review of Biology 56:17–31.

Schaffer, W. M., and M. D. Gadgil. 1975. Selection for Optimal life histories in plants. Pp. 142–157 *in* M. L. Cody and J. M. Diamond (eds.). Ecology and evolution of communities.—The Belknap Press of Harvard University Press. 5 figs., 2 tbs.

Scheltema, R. S. 1974. Relationship of dispersal to geographical distribution and morphological variation in the polychaete family Chaetopteridae.—Thalassia Jugoslavica 10(1/2):297–312.

Schroder, P. C., and C. O. Hermans. 1975. Annelida: Polychaeta. *In* A. C. Giese and J. S. Pearse (eds.). Reproduction of marine Invertebrates. III, Annelids and Echiurans, Chapter 1:1–213.

Shields, W. M. 1982. Inbreeding and the paradox of sex: a resolution?—Evolutionary Theory 5(5): 245–279, 4 figs., 5 tbs.

Smith, R. I. 1950. Embryonic development in the viviparous polychaete *Neanthes lighti*.—Journal of Morphology 87:417–466.

Stearns, S. C. 1976. Life-history tactics: a review of ideas.—Quarterly Review of Biology 51:3–47.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Oresund).—Meddelelser fra Kommissionen for Danmarks Fiskeri- og Havundersogelser, serie plankton 4(1):1–523, 199 figs.

———. 1950. Reproductive and larval ecology of marine bottom invertebrates.—Biological Reviews, Cambridge 25:1–45.

Trendall, J. T. 1982. Covariation of life history traits in the mosquitofish, *Gambusia affinis*.—American Naturalist 119(6):774–783, 4 tbs.

Wiley, E. O., and D. R. Brooks. 1982. Victims of history—a nonequilibrium approach to evolution.—Systematic Zoology 31(1):1–24, 7 figs., 2 tbs.

Williams, G. C. 1975. Sex and evolution.—Princeton University Press Monographs in Population Biology 8:1–200, 17 figs.

Wilson, D. P. 1954. The attractive factor in the settlement of *Ophelia bicornis* Savigny.—Journal of the Marine Biological Association of the United Kingdom 34:361–380.

———. 1955. The role of micro-organisms in the settlement of *Ophelia bicornis* Savigny.—Journal of the Marine Biological Association of the United Kingdom 34:531–543.

———. 1968. The settlement behaviour of the larvae of *Sabellaria alveolata* (L.)—Journal of the Marine Biological Association of the United Kingdom 48:387–435.

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

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 178–180

ARGYROTHECA ARGUTA, A NEW SPECIES OF BRACHIOPOD FROM THE MARSHALL ISLANDS, WESTERN PACIFIC

Richard E. Grant

Abstract.—*Argyrotheca arguta* is characterized by small size (maximum width 2.8 mm), white, clear or translucent shell, and weak to absent costae. It occupies cryptic habitats under coral fronds or in recesses, and has been found on the sea side and the lagoon side of the reefs at Enewetak and Bikini atolls.

A book on the natural history of Enewetak is in preparation under the auspices of the Mid Pacific Research Laboratory at Enewetak. I was invited to write up the brachiopods, based upon my observations of them there and the collections in the National Museum. Only three species have been found at Enewetak, yet despite all the work that has been done, there remains unnamed a species of *Argyrotheca*. This has been a mild inconvenience for years (e.g., Cooper 1954) but previously the collection was too small to allow a confident decision as to whether these small shells represent a new species or merely babies of a described form. Now enough material is at hand to reveal features other than mere size that indicate that the Enewetak form is a distinct species, apparently endemic to the Marshall Islands.

The editors of the book on Enewetak wish to avoid the introduction of new taxa, hence this short note to describe *Argyrotheca arguta*, new species.

Phylum Brachiopoda Dumeril
Class Articulata Huxley
Order Terebratulida Waagen
Superfamily Terebratellacea King
Family Megathyrididae Dall
Genus *Argyrotheca* Dall
Argyrotheca arguta, new species
Fig. 1

Diagnosis.—Shell small; known width less than 3 mm; outline heart-shaped with slightly emarginate anterior margin; profile biconvex with inflated dorsal valve and rather flat ventral valve; color white to light tan or clear, translucent; some shells with low and indistinct costae, most lacking costae.

Ventral valve with open triangular pedicle foramen flanked by strong divergent hinge teeth extending nearly to anterior margin. Dorsal valve with deep hinge sockets formed between valve edge and socket plates; loop short, simple, with 2 descending branches circling laterally and converging on median septum; some adults with serrate anterior margins.

Holotype.—USNM 265875: the largest shell in the collection with width 2.8 mm.

Etymology.—From the Latin "argutus" = "clear," referring to the translucent shell.

Comparison.—This species is characterized by small size and translucent shell

Fig. 1. *Argyrotheca arguta*: 11 shells attached to underside of coral frond from USNM loc. 32014 on the lagoon side of Igurin Island, Enewetak Atoll, depth 14 m. The long arrow points to the holotype, the short arrows to other specimens (×4).

that lacks the reddish color or stripes that typify other species of *Argyrotheca*, and lacks the radial costae that most species show. It was recognized long ago that these shells did not fit easily into any of the described species (Cooper 1954) but they were not described for fear that they were merely juveniles. The present sample is larger than any studied previously and it contains very small shells as well as a majority that seem to have ceased growth at a width between 2 and 3 mm. The species is currently known only from Enewetak and Bikini, but further exploration probably will reveal it throughout the Marshall Islands. It is associated with the small cemented brachiopod *Thecidellina congregata* Cooper at both atolls.

Species of *Argyrotheca* in the Caribbean Sea are larger than *A. arguta* and have costae and red stripes. Two species in the Pacific, *A. australis* and *A. mayi* from Australia and Tasmania, also differ from *A. arguta* by larger size, strong costation, and colored radial stripes.

Habitat.—*Argyrotheca arguta* was found in two abundant patches at Enewetak, both on the ceilings of recesses in the reef. The samples were obtained by divers who observed the habitat. The sample at Bikini was obtained by dredge, so the habitat was not seen. One Enewetak sample is from the sea side of the reef at Rigili Island at a depth of about 30 m; the other is from the lagoon side of Igurin at 14 m. The dredged sample from Bikini was taken from about 100 m depth on the south side of the atoll (Cooper 1954).

Literature Cited

Cooper, G. A. 1954. Recent brachiopods. Bikini and nearby atolls, Part 2. Oceanography (biologic).—U.S. Geological Survey Professional Paper 260-G:315–318, pl. 80–81.

Department of Paleobiology, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
96(1), 1983, pp. 181–188

HARBANSUS SLATTERYI, A NEW SPECIES OF MYODOCOPINE OSTRACODE FROM THE GREAT BARRIER REEF OF AUSTRALIA (PHILOMEDIDAE)

Louis S. Kornicker

Abstract.—*Harbansus slatteryi,* new species, is described and illustrated. The specimens were collected from the Lizard Island Group, Great Barrier Reef, Australia. The genus had not previously been recorded from Australia.

The genus *Harbansus* Kornicker, 1978, was proposed for numerous species collected in the Atlantic Ocean, and also in the Pacific Ocean as far west as Hawaii. The present report extends the range farther west and south to the Great Barrier Reef in the Coral Sea off Queensland, Australia.

Harbansus Kornicker, 1978

Type-species.—*Harbansus bradmyersi* Kornicker, 1978.

Harbansus slatteryi, new species

Figs. 1–4

Etymology.—The species is named for Peter N. Slattery who collected some of the specimens.

Material.—Palfrey Island, Lizard Island Group, Great Barrier Reef, Queensland, Australia. Collected by Peter N. Slattery, Sept–Oct 1977: core sample, water depth 12 m, quartz sand substrate, 1 adult female, USNM 157790, holotype; station 8, at far edge of reef flat adjacent to coral head at edge of coral reef, probably exposed only twice a year at extreme low tides, fine to medium fine sand, 5 large cores (each 0.0176 m^2) sieved through 500 μ mesh, 1 adult female, USNM 158490, paratype. West of Lizard Island Research Station, off Casuarina Beach, station AC-4A, 27 May 1980, 200–300 yards offshore of sandy beach, small sand patch between coral heads in patch reef near edge, about 2 m deep, 3 adult males, USNM 158491, paratypes, collected by Anne C. Cohen. Lagoon south of Lizard Island, between Lizard Island and Palfrey Island, station AC-6, 28 May 1980, off sandy beach with 1 palm tree, about 200–300 yards from shore, sparse *Thalassia* bed in very silty sand, about 2 m deep, collected by Anne C. Cohen, paratypes: 1 adult male, USNM 158492; 1 adult male, USNM 158627; 1 adult female, USNM 159092; 1 adult male, USNM 159093.

Description of adult female (Figs. 1–3).—Carapace elongate with long narrow rostrum and caudal process (Figs. 1, 2). Ornamentation (Fig. 1): Each valve with 3 horizontal ribs and additional smaller rib near and parallel to anterodorsal margin; on some specimens, anterior end of rib dorsal to adductor muscle attachment area joining anterior end of anterodorsal rib to form small process extending very slightly past anterior end of rostrum (Fig. 1); on other specimens, anterodorsal

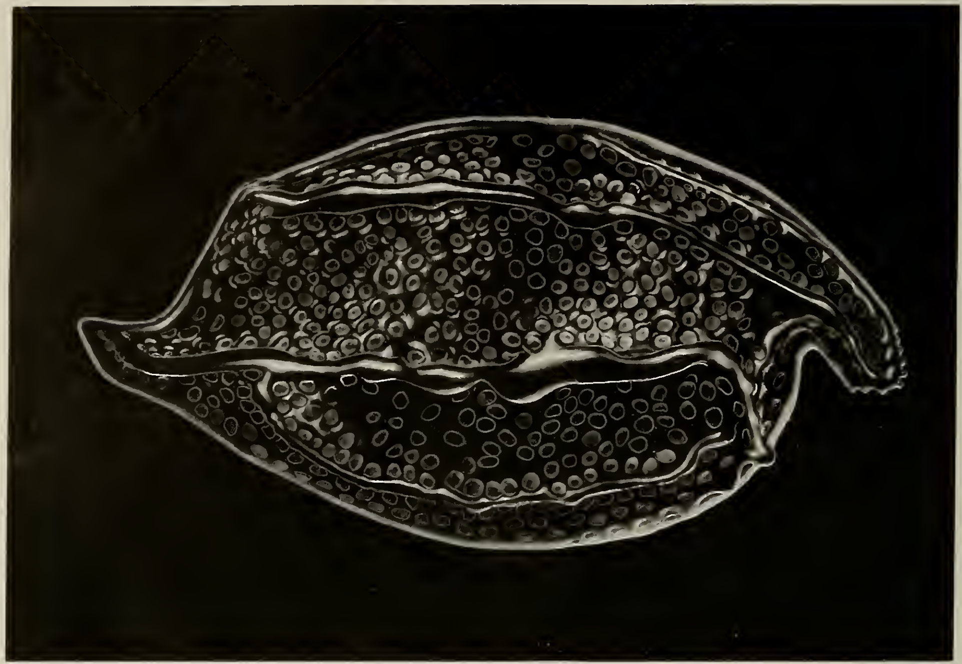


Fig. 1. *Harbanus slatteryi*, adult female, holotype, USNM 157790, lateral view of complete specimen, length 1.00 mm.

rib not reaching anterior margin; midrib passing through area of central adductor muscle attachments; its anterior end bending ventrally to join with anterior end of ventral rib to form small process extending slightly past anteroventral margin of valve; low vertical rib connecting anterior ends of rib dorsal to adductor muscle attachments and midrib. Surface of valves with abundant oval fossae (Fig. 1). Long bristles forming row near distal end of caudal process (Fig. 2c), along ventral margin of each valve, and sparsely distributed over valve surface (these bristles not shown in illustrations).

Infold (Fig. 2): Infold of rostrum with 4 long bristles forming row (Fig. 2a, b); 2 bristles present at inner end of incisure; anteroventral infold with 1 short bristle ventral to inner end of incisure and with ridges paralleling valve margin; inner edge of infold anterior to caudal process with about 6 small bristles; ridge forming anterior end of pocket in caudal process with 6 frondlike bristles forming row (Fig. 2c); 2 minute bristles along posterior edge of caudal process.

Selvage (Fig. 2b): Narrow lamella with short marginal fringe present along dorsal and anterior edges of rostrum (Fig. 2b) and becoming wider along ventral margin of rostrum; narrow lamella with short marginal fringe present along anteroventral edge of valve becoming wider in vicinity of incisure; ventral lamella wide with long marginal fringe; narrow lamella with short fringe present along posterior margin of valve; lamella apparently absent along posterior edge of caudal process.

Size: USNM 157790, length 1.00 mm, height 0.53 mm; USNM 158490, length 1.07 mm, height 0.60 mm; USNM 159092, length 1.08 mm, height 0.57 mm.

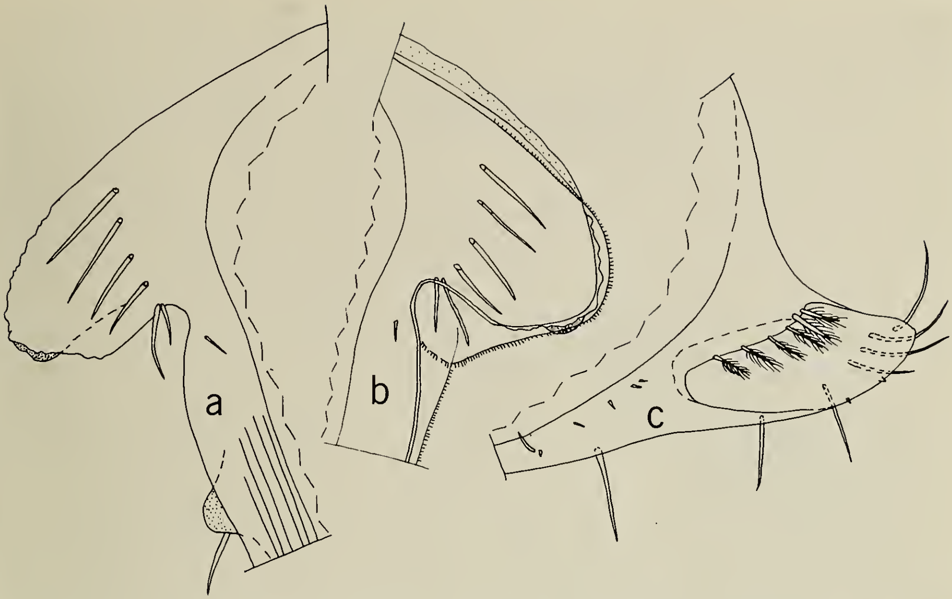


Fig. 2. *Harbanus slatteryi,* adult female, holotype, USNM 157790: a, Anterior of right valve, inside view; b, Rostrum and incisure of left valve, including selvage, inside view; c, Caudal process of right valve, inside view.

First antenna (Fig. 3a): Joints 1–4 with surface spines forming rows. 2nd joint with 1 dorsal bristle. 3rd joint short, with 3 bristles, 1 ventral, 2 dorsal. 4th joint elongate, with terminal bristles, 2 ventral, 1 dorsal. 5th joint elongate; sensory bristle with 2 short proximal filaments, 3 longer distal filaments, and 2 minute spines at tip. 6th joint fused with 5th, with 1 small medial bristle. 7th joint: a-bristle about twice length of bristle of 6th joint; b-bristle about twice length of a-bristle, shorter than sensory bristle of 5th joint, with 1 distal marginal filament, and tip with 2 minute spines; c-bristle with 1 short proximal filament and 1 short and 2 long distal filaments. Eighth joint: d- and e-bristles about same length as sensory bristle, bare with blunt tips; f- and g-bristles about same length as sensory bristle; f-bristle with 1 short proximal filament and 3 longer distal filaments, and with 2 minute spines at tip; g-bristle with 1 short proximal filament and 2 longer distal filaments, and with 2 minute spines at tip; all filaments on bristles of joints 5, 7, 8 with spine at tip.

Second antenna (Fig. 3b): Protopodite with few faint spines forming rows on medial and lateral surfaces near dorsal margin. Endopodite 2-jointed: 1st joint with 2 short proximal anterior bristles; 2nd joint elongate with bare rounded or tapering tip and 1 long spinous ventral bristle. Exopodite: Elongate 1st joint with 1 minute terminal medial bristle; bristle of 2nd joint reaching past 9th joint, with about 10 stout ventral spines followed by numerous slender ventral spines; bristles of joints 3–7 with few long proximal dorsal hairs; bristles of joints 3–8 with stout proximal ventral spines followed by long natatory hairs on both margins; 9th joint with minute lateral tooth and 3 bristles: 1 long with stout proximal ventral spines and distal natatory hairs, 1 medium with short marginal spines, 1 short and either bare or with few faint spines; joints 3–8 with basal spines (spines slightly larger on some distal joints); basal spine of 8th joint about one-half length of 9th joint; joints 2–8 with minute spines forming row along distal margin.

Mandible (Fig. 3c): Coxale endite hirsute and spinous, without small bristle near base. Basale: dorsal margin with 3 bristles (1 near middle, 2 subterminal; ventral margin with 1 terminal bristle with short marginal spines; medial surface spinous, with 4 bristles near ventral margin (3 proximal, 1 near middle) (2 dashed bristles broken off illustrated limb but present on right limb); lateral surface with 2 bristles with long spines near ventral margin. Exopodite about three-fourths length of dorsal margin of 1st endopodial joint, with 2 subterminal bristles (lateral and proximal of these much longer than other and spinous). 1st endopodial joint with medial spines and 3 spinous ventral bristles. 2nd endopodial joint: dorsal margin with proximal spines and 6 bristles near middle forming 2 groups (1 bristle in proximal group, 5 in distal group); ventral margin with 4 bristles forming 2 distal groups (2 bristles in each group); medial surface with spines forming rows. End joint with 2 long claws with faint ventral spines, and 3 slender bristles.

Maxilla (Fig. 3d, e): Precoxale and coxale with dorsal fringe of long hairs. Dorsal margin of coxale with hirsute dorsal bristle. Endite I wider than endites II and III, with 6 bristles; endite II also with 6 bristles; endite III with about 7 distal bristles and 1 proximal lateral bristle. Basale with 3 bristles along distal margin. Exopodite small, with 3 bristles (2 long, 1 short) (Fig. 3e). Endopodite: 1st joint with 1 spinous alpha-bristle and 2 beta-bristles (beta-bristles obscure and number approximate); end joint with about 7 claws and bristles.

Fifth limb (Fig. 3f–h): Endite I with 1 bristle; endite II with about 5 bristles; endite III with 6 or more bristles. Exopodite: 1st joint with main tooth consisting of 3 bilobed teeth and 2 pointed smooth peglike teeth, 1 at each end of the bilobed teeth (Fig. 3f, g); 1 small spinous bristle proximal to inner peglike tooth; additional bristles on 1st joint obscure; large tooth of 2nd joint triangular with large node near middle of inner margin (Fig. 3h); bristles of 2nd joint obscure; 3rd joint with 2 bristles on outer lobe and 3 on inner lobe; 4th and 5th joints fused, hirsute, with total of 6 bristles.

Sixth limb (Fig. 3i): 1 short spinous bristle in place of epipodial appendage; endite I small, with 2 short spinous bristles; endite II narrow, with 3 spinous terminal bristles; endite III broad with 6 spinous terminal bristles; endite IV broad with 5 spinous terminal bristles; end joint not prolonged posteriorly, with 5 or 6 bristles (3 or 4 anterior bristles spinous, 2 posterior bristles hirsute); limb hirsute.

Seventh limb (Fig. 3j): Each limb with 6 bristles (2 proximal, 4 terminal), each bristle with marginal spines and 1–4 bells; terminal comb with about 5 recurved teeth; 4 or 5 short pegs present opposite comb.

Furca (Fig. 3k): Each lamella with 6 claws; claws 1, 2, 4 stout, claw 3 and claws following claw 4 slender. Claw 1 with teeth along posterior edge and also with fairly large medial teeth forming row; distal medial tooth especially prominent; remaining main claws with teeth along posterior edge; edge of lamella following claw 6 hirsute.

Bellonci organ (Fig. 3l): Elongate with rounded tip and 2 or 3 weak proximal sutures.

Eyes (Fig. 3l): Medial eye with light brown pigment. Lateral eye small, unpigmented, with 2 light-amber ommatidia.

Fig. 3. *Harbanus slatteryi,* adult female, holotype, USNM 157790: a, Left 1st antenna, medial view; b, Endopodite and distal part of protopodite of left 2nd antenna, lateral view; c, Left mandible, medial view; d, Right maxilla, medial view; e, Exopodite of right maxilla, medial view as seen through limb shown in "d"; f, Distal part of left fifth limb, anterior view; g, Detail of tooth of 1st expodal joint of 5th limb shown in "f"; h, Distal part of right 5th limb, tooth of 1st exopodal joint not shown (posterior view); i, 6th limb; j, 7th limb; k, Posterior of body showing right lamella of furca, right genitalia, right Y-sclerite, right segment of girdle; l, Anterior of body showing left lateral eye, medial eye and bellonci organ, and upper lip.

Upper lip (Fig. 3l): Consisting of single lobe.

Genitalia (Fig. 3k): Consisting of sclerotized ring on each side of body, each with attached spermatophore.

Y-sclerite (Fig. 3k): Typical for genus.

Eggs: USNM 157790 with 3 eggs in marsupium; USNM 158490 with 2 eggs.

Description of adult male (Fig. 4).—Except for having a slightly broader ros-

Fig. 4. *Harbanus slatteryi*, a, b, adult male paratype, USNM 158492, length 0.95 mm; a, Lateral view of complete specimen showing left valve with outline of ribs and 11 typical fossae, position of central adductor muscle attachments (dashed circle), position of left lateral eye (stippled), left lamella of furca, and left copulatory organ; b, Anterior of body showing left lateral eye with few ommatidia along dorsal margin, medial eye and bellonci organ, and upper lip. c–i, Adult male paratype, USNM 158627, length 0.97 mm: c, Left 1st antenna, medial view; d, Endopodite, distal part of protopodite, 1st joint of exopodite of left 2nd antenna, medial view; e, Left mandible, medial view; f, Maxilla; g, Distal part of 5th limb; h, 6th limb; i, 7th limb.

trum and caudal process, carapace of male similar in shape and ornamentation to that of adult female (Fig. 4a).

Infold: Infold of rostrum with 4 long bristles; 2 bristles present at inner end of incisure; anteroventral infold with 1 short bristle ventral to inner end of incisure and with ridges paralleling valve margin; inner edge of infold anterior to caudal process with about 4 small bristles; ridge forming anterior edge of pocket in caudal process with 5 or 6 frondlike bristles forming row; 2 or 3 minute bristles forming row along posterior edge of caudal process.

Selvage: Similar to that of female.

Size: USNM 158492, length 0.95 mm, height 0.46 mm; USNM 158491, 3 specimens, length 0.98 mm, height 0.48 mm, length 0.94 mm, height 0.45 mm, length 0.95 mm, height 0.48 mm; USNM 158627, length 0.97 mm, height 0.47 mm.

First antenna (Fig. 4c): 1st joint with medial spines forming rows. 2nd joint with few lateral spines and 1 dorsal bristle with long marginal hairs. 3rd joint short with small medial spines and 3 bristles (2 dorsal, 1 medial near ventral margin); 4th joint with 1 bare dorsal terminal bristle. 5th joint small, wedged ventrally between 4th and 6th joints; sensory bristle with bulbous proximal part with abundant filaments (filaments not shown on illustrated limb), and stem with 3 filaments near middle and 2 minute spines at tip (only proximal part of stem shown on illustrated limb). 6th joint with bare medial bristle. 7th joint: a-bristle spinous, longer than bristle of 6th joint; b-bristle about twice length of a-bristle, with 2 filaments near middle and bifurcate tip; c-bristle longer than sensory bristle of 5th joint, with 7 or 8 marginal filaments and bifurcate tip. 8th joint: d- and e-bristles slightly shorter than c-bristle, bare with blunt tips (bristles not shown on illustrated limb); f-bristle slightly shorter than c-bristle, with 6 marginal filaments and bifurcate tip; g-bristle same length as c-bristle, with 5 marginal filaments and 2 spines at tip (bristle not shown on illustrated limb).

Second antenna (Fig. 4d): Protopodite bare. Endopodite 3-jointed: 1st joint short with 4 short anterior bristles; 2nd joint elongate with 2 long proximal bristles; 3rd joint elongate, reflexed, with 2 small bristles near sclerotized beaklike tip, and minute processes along inner margin. Exopodite: 1st joint elongate with minute terminal medial bristle; 2nd joint slightly longer than 3rd joint; bristle of 2nd joint with 3 or 4 long proximal hairs on dorsal margin and about 6 proximal hairs on ventral margin; hairs on ventral margin of bristle followed by 3 stout spines; both margins of bristle distal to spines with natatory hairs; bristles of joints 3–8 longer than bristle of 2nd joint, with natatory hairs but no spines; 9th joint with 3 bristles (1 long, stout, with natatory hairs; 1 medium with few ventral spines in addition to natatory hairs; 1 short with natatory hairs); joints 2–8 with slender spines forming row along distal margin; basal spine observed on 8th joint only.

Mandible (Fig. 4e): Coxale endite represented by faint minute spine. Basale: medial surface with 4 short bristles near ventral margin (3 proximal, 1 near middle); ventral margin with 3 long spinous bristles (2 proximal of these with bases on lateral surface slightly inward from ventral margin); dorsal margin with 3 long bristles, 1 near middle, 2 terminal. Exopodite spinous, reaching past middle of dorsal margin of 1st endopodial joint, with 1 long and 1 short bristle. 1st endopodial joint with few medial spines and 3 ventral bristles (2 long, 1 short). 2nd endopodial joint: medial surface with spines forming rows; ventral margin with bristles forming 2 distal groups, each with 2 bristles; middle of dorsal margin with 6 bristles. End joint with 2 stout claws and 3 bristles (1 dorsal, lateral; 2 ventral).

Maxilla (Fig. 4f): Limb reduced and with weakly developed bristles.

Fifth limb (Fig. 4g): Epipodial appendage with 35 bristles. Endites weakly developed with few bristles. Exopodite: 3rd joint with 2 ringed outer bristles, inner bristles obscure; remaining joints obscure, with total of about 5 bristles.

Sixth limb (Fig. 4h): A single spinous bristle in place of epipodial bristle. Endite I with 3 bristles; endite 2 with 3 terminal bristles; endite III with 5 or 6 bristles;

endite IV with 4 or 5 bristles. End joint not prolonged posteriorly, with 6 or 7 bristles (4 or 5 anterior bristles either spinous, hirsute, or with long proximal hairs and short distal spines; 2 posterior bristles stout, hirsute); limb hirsute.

Seventh limb (Fig. 4i): 4 bristles in terminal group, 2 on each side, each with 4 bells; some bristles with few faint, distal, marginal spines; proximal bristles absent. Terminus with comb of 3 teeth, each lateral tooth with long proximal spines; surface opposite comb without pegs.

Furca (Fig. 4a): Similar to that of female except claw 1 without stout, distal, medial tooth present on female.

Bellonci organ (Fig. 4b): Elongate with round tip and about 4 proximal sutures.

Eyes (Fig. 4b): Medial eye bare with reddish brown and black pigment. Lateral eye about same size as medial eye or slightly larger, with about 7 ommatidia but difficult to count because of black pigment.

Upper lip (Fig. 4b): Consisting of single lobe.

Genitalia (Fig. 4a): Each copulatory limb elongate, lobate, with terminal process with marginal teeth.

Y-sclerite: Similar to that of female.

Comparisons.—Previously described species of *Harbansus* having lateral ribs on the carapace are *H. paucichelatus* (Kornicker, 1958:233), *H. bradmyersi* Kornicker (1978:24), and *Harbansus* species B (Kornicker, 1978:49). The adult females of the last two species differ from the new species *H. slatteryi* in not having natatory hairs on the exopodal bristles of the 2nd antenna. The adult female mandible of *H. slatteryi* differs from all previously described species of the genus in having only two claws instead of three on the end joint of the mandible. The adult female of *H. slatteryi* bears four or five (usually five) pegs on the tip of the 7th limb compared to only two or three pegs on *H. paucichelatus*.

Acknowledgments

My thanks to the following individuals for their help: Peter N. Slattery, Moss Marine Laboratory, Moss Island, California, and Anne C. Cohen, Department of Invertebrate Zoology, Smithsonian Institution, for collecting specimens studied herein; to Carolyn Bartlett Gast, Smithsonian Institution, for the shaded rendering of the carapace, and to Thomas E. Bowman, Smithsonian Institution, for commenting on the manuscript.

Literature Cited

Kornicker, Louis S. 1958. Ecology and taxonomy of Recent marine ostracodes in the Bimini area, Great Bahama Bank.—Publications of the Institute of Marine Science (The University of Texas) 5:194–300.

———. 1978. *Harbansus*, a new genus of marine Ostracoda, and a revision of the Philomedidae (Myodocopina).—Smithsonian Contributions to Zoology 270, 75 pp.

Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560.

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings* of the Biological Society of Washington contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers will be published in English (except for Latin diagnosis/description of plant taxa which should not be duplicated by an English translation), with a summary in an alternate language when appropriate.

Publication Charges.—Authors will be asked to assume publication costs of page-charges, tabular material, and figures, at the lowest possible rates.

Submission of manuscripts.—Manuscripts should be sent to the Editor, *Proceedings* of the Biological Society of Washington, National Museum of Natural History, 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 will be reviewed in order of receipt by a board of associate editors and appropriate referees.

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. Synonymy of abbreviated style (author, date, page) (except in botanical papers), with full citations of journals and books (no abbreviations) in the Literature Cited is required.

The establishment of new taxa must conform with the requirements of the appropriate international codes of nomenclature. Authors are expected to be familiar with these codes and to comply with them. New species-group accounts must designate a type-specimen deposited in an institutional collection.

The sequence of material should be: Title, Author(s), Abstract, Text, Acknowledgments, Literature Cited, Author's (s') Address(es), Appendix, List of Figures (entire figure legends), Figures (each numbered and identified), Tables (each table numbered with an Arabic numeral and heading provided).

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 a facsimile with the original, and retain an author's copy. Pages must be numbered on top. One manuscript page = approximately 0.5 printed page. Underline singly scientific names of genera and lower categories; leave other indications to the editor.

Figures and tables with their legends and headings should be self-explanatory, not requiring reference to the text. Indicate their approximate placement by a pencil mark in the margin of the manuscript.

Illustrations should be planned in proportions that will efficiently use space on the type bed of the *Proceedings* (12.5 × 20 cm) and should not exceed 24 × 15 inches. Figures requiring solid black backgrounds should be indicated as such, but not masked.

Art work will be returned only on request.

Proofs.—Galley proofs will be submitted to authors for correction and approval. Reprint orders will be taken with returned proof.

Costs.—Page charges @ $60.00, figures @ $10.00, tabular material $3.00 per printed inch.

All authors are expected to pay the charges for figures, tables, changes at proof stage, and reprints. Payment of full costs will probably facilitate speedy publication.

CONTENTS

(ISSN 0006-324X)

Proceedings
of the
BIOLOGICAL SOCIETY
of
WASHINGTON

Volume 96 7 July 1983 Number 2

THE BIOLOGICAL SOCIETY OF WASHINGTON

1983–1984

Officers

PROCEEDINGS

Membership in the Society is open to anyone who wishes to join. There are no prerequisites. Annual dues of $15.00 include subscription to the *Proceedings of the Biological Society of Washington. Library subscriptions to the Proceedings are: $18.00 within the U.S.A., $23.00 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 Instutution, 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.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 189–201

THREE NEW SPECIES OF *COLOBOMATUS* (COPEPODA: PHILICHTHYIDAE) PARASITIC IN THE MANDIBULAR CANALS OF HAEMULID FISHES

Roger F. Cressey and Marilyn Schotte

Abstract.—Three new species of *Colobomatus* are described from the mandibular canals of three genera of American haemulid fishes. These are the first species of *Colobomatus* reported from the Haemulidae and are the first described with abdominal processes in the female. Males of two of the new species are described. One of the species (*C. quadrifarius*) is restricted to the Eastern Pacific and the other two (*C. caribbei* and *C. belizensis*) to the western Atlantic. Data are presented to suggest that an optimum host size exists for parasite infestation, accompanied by diminishing infestations in smaller and larger size groups.

During an examination of fishes in Belize for a study of host-parasite relationships, a new copepod belonging to the genus *Colobomatus* was discovered in the mandibular canals of its host fish, *Haemulon sciurus* (Shaw). Subsequent examination of 475 tropical and subtropical haemulid fishes (three genera and 32 species) yielded two additional new species from the same site on the hosts. Twenty of the 32 fish species examined were infested with one of the three new species.

Since Hesse's designation of the genus in 1873, 34 species of *Colobomatus* have been reported. They are members of the poecilostomatoid family Philichthyidae and are known only from the mucous and sensory canal systems of marine fishes. The females are typically highly modified with a variety of appendages and processes thought to be useful in maintaining position in the lateral-line canals (Izawa 1974). The males are much less modified and are smaller. Males of only nine species have been described thus far.

Sekerak (1970) published the first report of *Colobomatus* found in the "dentary canals" of host fish. Essafi and Raibaut (1980) described a closely related genus *Colobomatoides* from the pre-opercular cephalic system. All of the copepods in the present study were located in the mandibular canals of the hosts.

Methods and Materials

Fresh and alcohol-preserved fish were examined by removing the skin of the ventral portions of the lower jaws and exposing the mandibular canals. Figure 1 shows the typical position of the parasite in one of the chambers of the canal. In total, 238 copepods were recovered, 181 ♀ and 1 ♂ of *Colobomatus belizensis*, 47 ♀ and 2 ♂ of *C. quadrifarius* and 7 ♀ of *C. caribbei*. Numbers preceding host names in Materials Examined sections indicate the number of infested fish. Table 2 indicates numbers of fish examined. The abbreviation USNM refers to Smithsonian Institution and SOSC to Smithsonian Oceanographic Sorting Center specimens now in the general collections of the Division of Fishes, Smithsonian Institution. Drawings were prepared with the aid of a Wild M20 compound microscope with drawing tube.

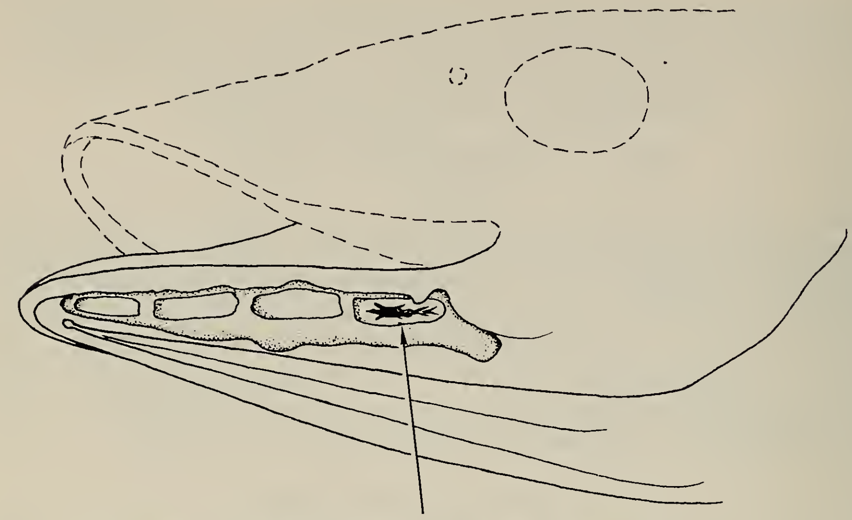


Fig. 1. Ventrolateral view of *Haemulon* mandibular canal showing position of *Colobomatus in situ.*

Colobomatus quadrifarius, new species
Figs. 2C–4E

Material examined.—Holotype ♀ (USNM 190517), allotype ♂ (USNM 190518), paratypes 15 ♀ (USNM 190519–22) from the mandibular canals of 17 *Orthopristis reddingi* Jordan and Richardson (USNM 43247, 167149, 167570 and 176154) from Baja California and Bay of Guaymas, Mexico. Additional material.—4 ♀ from 3 *Anisotremus davidsoni* (Steindachner) (USNM acc. no. 294075 and SOSC Ref. nos. 290 and 586) from Sonora, Mexico; 7 ♀ from 5 *A. dovii* (Gunter) (USNM 144347–8 and USNM acc. no. 294075) from Colombia and Panama (both Pacific); 6 ♀ from 3 *A. interruptus* (Gill) (USNM 181330) from Nayarit, Mexico; 3 ♀ and 1 ♂ from 2 *A. pacifici* (Gunther) (USNM 114476, 220731) from El Salvador and Guatemala; 5 ♀ from 4 *Haemulon flaviguttatum* Gill (USNM 50426, 80548, 176149) from Panama and Baja California; 4 ♀ from 3 *H. steindachneri* (Jordan and Gilbert) (USNM 19632, 19879) from Colima and Cape St. Lucas, Mexico; 2 ♀ from 1 *Orthopristis chalceus* (Gunther) (USNM 41389) from Galapagos.

Description.—Female: Body form as in Fig. 2C. Length of body: 4.73–7.58 mm based on 3 specimens. Pre-oral cephalic process bifurcate. Body constricted be-

Table 1.—Rate of infestation by *Colobomatus belizensis* in mandibular canals of 91 specimens of *Haemulon sciurus* related to size of fish.

Host SL (mm)	<80	80–109	110–139	140–169	170–199	200–229	>230
Negative fish	13	7	2	0	2	2	1
One *Colobomatus*	2	5	2	2	7	3	—
Two *Colobomatus*	1	1	10	12	15	3	—
Three *Colobomatus*	0	0	0	1	0	0	—
% Infestation	19%	46%	86%	100%	92%	75%	—

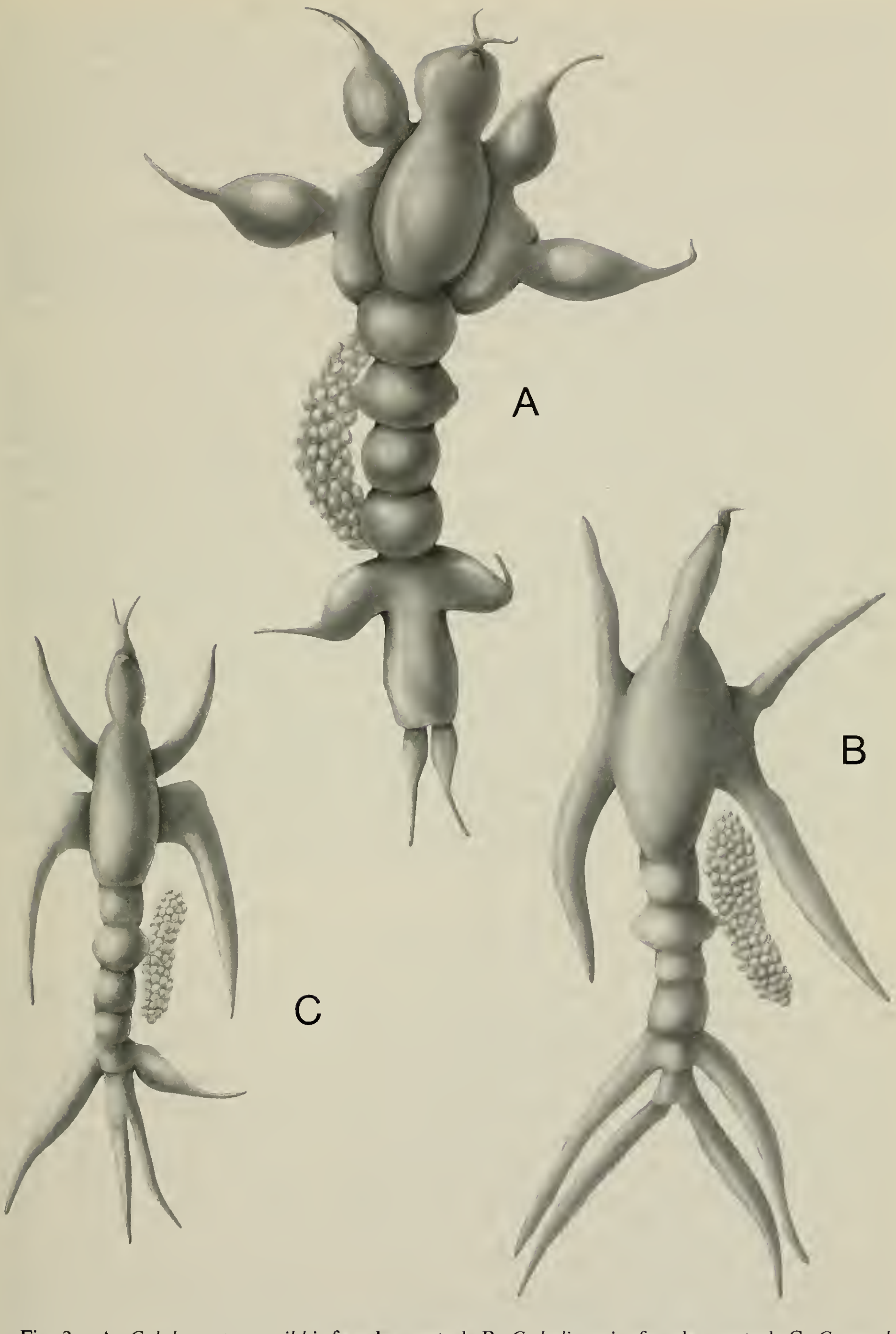


Fig. 2. A, *Colobomatus caribbi*, female, ventral; B, *C. belizensis*, female, ventral; C, *C. quadrifarius*, female, ventral.

tween thoracic segments 3 and 4. Thoracic segments 4 and 5 fused, bearing 2 anteriorly directed and 2 posteriorly directed processes. In lateral aspect, processes usually extend from raised shoulders except in specimens from *H. steindachneri*. Sixth thoracic segment and genital segment (seventh according to Kabata 1979) each clearly separated. Four abdominal segments clearly separate, third bearing 2 conspicuous lateral processes. Caudal rami fused with last abdominal segment, about 8 times longer than wide.

Male: Body form as in Figs. 3A and 3B. First antenna 6-segmented with setae as indicated in Fig. 3C. First 3 segments subequal in length, last three becoming progressively shorter. Second antenna (Fig. 3D) 5-segmented, first and second segments each with short spine, large recurved spines on each of last 3 segments and additional spine on terminal segment.

Legs 1 and 2 biramous; rami somewhat overlapping. Leg 1 basipod with spine on outer distal corner; exopod (Fig. 4A) first segment with fringe on outer margin and stout pectinate spine on outer distal corner, last segment with 4 pectinate spines on outer margin and 3 inner plumose setae; endopod (Fig. 4B) first segment with inner plumose setae, last segment with 2 stout pectinate spines on outer distal margin and 4 inner plumose setae. Leg 2 exopod (Fig. 4C) first segment as in leg 1, last segment with 2 pectinate spines, distal fringed spine, and 2 inner plumose setae; endopod (Fig. 4D) as in leg 1 except outer margin of first segment with row of long hairs and only 3 plumose setae on inner margin of last segment. Leg 3 (Fig. 4E) represented by 5 setae, innermost 2 pectinate.

Etymology.—The specific name (*quadrifarius*) is Latin meaning "four-fold" and refers to the four abdominal processes in the female.

Remarks.—The female of *C. quadrifarius* is distinguished from its congeners by the presence of the long lateral processes on the third abdominal segment. None of the previously described species of *Colobomatus* has abdominal processes in addition to the caudal rami, although they are present in a closely related genus, *Colobomatoides,* described by Essafi and Raibaut (1980).

Colobomatus belizensis, new species

Figs. 2B, 4A–D, 6B–E, 7A–C

Material examined.—Holotype ♀ (USNM 190523) collected by the first author from mandibular canals of *Haemulon sciurus* (Shaw) 21 April 1981 at Carrie Bow Cay, Belize; allotype ♂ (USNM 190524) from the same host (USNM 167633) from Florida and 91 paratype ♀ (USNM 190525–42) from the same host (USNM 15815, 53293, 74404, 83798, 143731, 167610, 167633, 170872) from Florida (all locations in the Florida Keys, including Dry Tortugas except one from Pensacola); Belize (USNM 198808 and hosts examined at Carrie Bow Cay); Mexico (USNM 37089 Cozumel, 192263 Yucatan); West Indies (USNM 34948, 38666, 38739); Cuba (USNM 192263). Additional material.—12 ♀ from 7 *Haemulon aurolineatum* Cuvier (USNM acc. no. 261501, USNM 17716, 2 uncatalogued specimens) from South Carolina, Florida, and Brazil; 5 ♀ from 2 *H. carbonarium* Poey (USNM 80586, USNM acc. no. 249542) from Dominica and Panama; 15 ♀ from 8 *H. chrysarygyreum* Günther (USNM 6940, 35149–50, 35093, 41314) from Key West, Barbados, Abaco, and St. Lucia; 1 ♀ from 1 *H. macrostomum* Günther (USNM 80589) from Panama; 6 ♀ from 4 *H. melanurum* (Linnaeus) (USNM 3118, 10511,

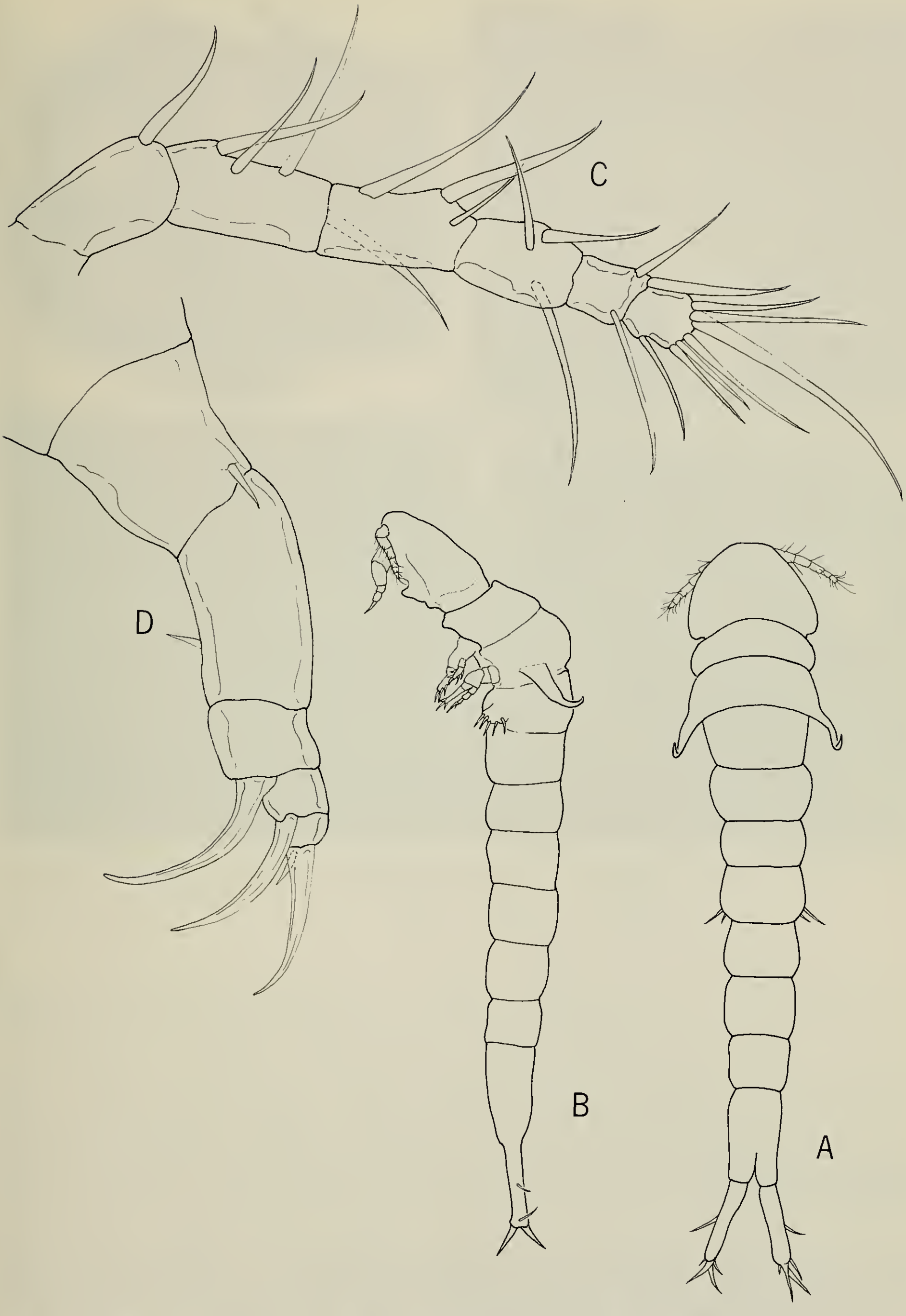


Fig. 3. *Colobomatus quadrifarius,* male: A, Dorsal; B, Lateral; C, First antenna; D, Second antenna.

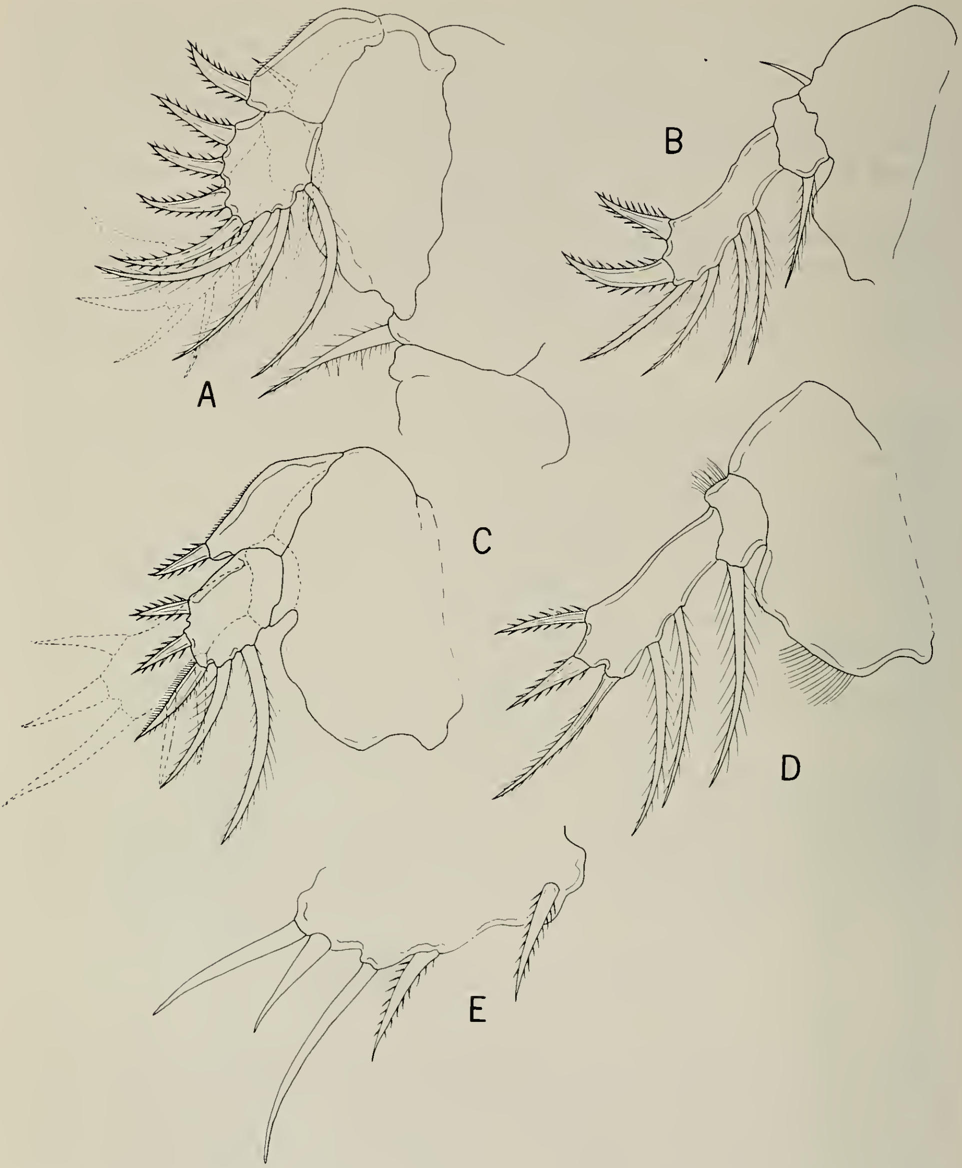


Fig. 4. *Colobomatus quadrifarius,* male: A, Leg 1; B, Leg 1, endopod; C, Leg 2; D, Leg 2, endopod; E, Leg 3.

38479, 39808) from Bahamas, West Indies and Guyana; 2 ♀ from 1 *H. parrai* (Desmarest) (USNM 81097) from Toro Point, Panama; 20 ♀ from 12 *H. plumieri* (Lacépède) (USNM 37088, 82448, 142536, acc. no. 294075) from Cuba, Virgin Islands, Colombia (Caribbean) and Cozumel, Mexico; 16 ♀ from 10 *H. steindachneri* (Jordan and Gilbert) (USNM 10265, acc. no. 278057, *Oregon* stations 5654, 10536, 17628–9) from Caribbean coast of South America (Colombia to Brazil); 9 ♀ from 9 *Orthopristis chrysopterus* (Linnaeus) (USNM 35205, 163701)

Fig. 5. *Colobomatus belizensis*, female, SEM photos: A, Oral area; B, Labrum; C, Tip of second maxilla; D, Second maxilla *in situ* within oral cone (lower fringe-labium?).

North Carolina and Louisiana; 3 ♀ from 2 *O. ruber* (Cuvier and Valenciennes) (USNM 123123, 278057) from Venezuela and Guyana.

Description.—Female: Body form as in Fig. 2B. Length of body: 4.13–9.38 mm, based on 3 specimens. Single, simple cephalic lobe, acute at tip, extending above buccal cone. Degree of segmentation at base of third segment (''neck'') variable. Four long, slender processes, 2 anterior and 2 posterior, simple and usually rounded at tip. Genital segment (seventh thoracic segment) with small lateral lobes. Egg sacs often as long as abdomen, easily broken when copepod is handled. Four abdominal segments more or less definite; penultimate segment with 2 lateral processes. Caudal rami well-developed and similar to those processes described above.

First antenna very small, placed dorsolaterally near insertion of buccal cone. Oral area typical of genus (see SEM photos, Figs. 5A–D). Labrum modified as forked, posteriorly directed process between mandibles. Mandibles with small ventral process; first maxilla bifid. Second maxilla considerably larger, bifid, terminal segments with numerous large spinose processes. Maxillipeds absent.

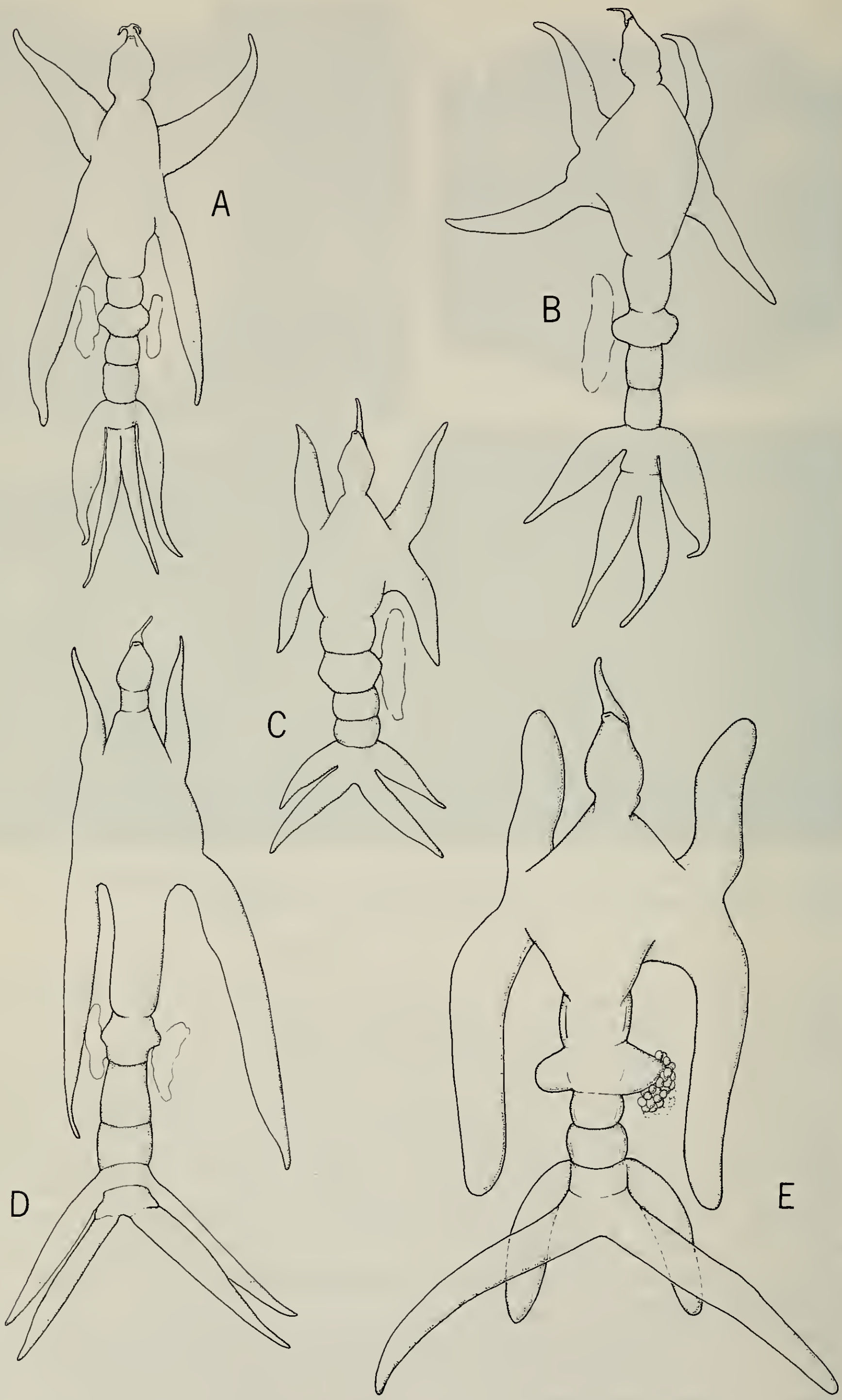


Fig. 6. *Colobomatus quadrifarius*, female: A, ventral; *C. belizensis*: B–E, Ventral.

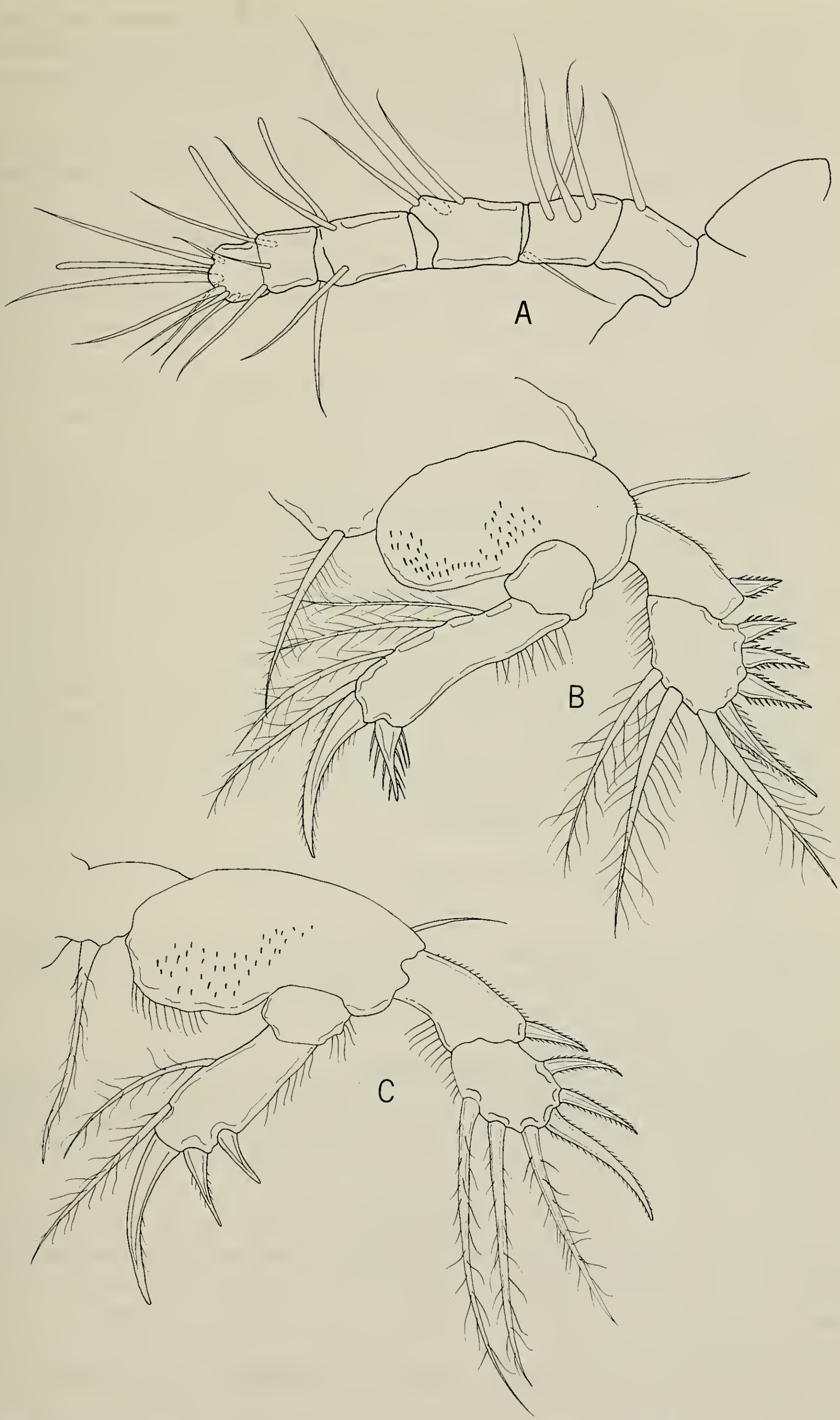


Fig. 7. *Colobomatus belizensis*, male: A, First antenna; B, Leg 1; C, Leg 2.

Male: Total length 1.94 mm. Width of cephalon 0.36 mm. General body form typical of genus with wide cephalon, body tapering gradually to end of abdomen bearing elongate, caudal rami. Third thoracic segment with 2 dorsolateral processes directed posteriorly with tips curving away from body.

First antenna (Fig. 7A) 6-segmented with one aesthete on each of last 3 segments; first 4 subequal in length. Second antenna similar to that of *C. quadrifarius* (Fig. 3B).

Legs 1 and 2 biramous (Figs. 7B and 7C) with patch of spinules on basipods. The 2-segmented exopod of leg 1 with one stout spine on first segment and 4 on the second, all with numerous spinules along both margins. Second segment bearing 3 long plumose setae; setae also found on interior margins of both segments.

Short first segment of endopod unarmed; second segment, 2.5 times as long, bearing 2 strongly sclerotized spines, innermost twice as long as outermost, each bearing spinules on margins.

Leg 2 with one less spine on exopod than leg 1. Endopod with 2 setae and 3 spines. Leg 3 reduced to 5 setae, similar to that of *C. quadrifarius* (Fig. 4E). Fifth thoracic segment bearing 2 lateral setae. Each caudal ramus bearing one lateral seta and 4 terminal setae.

Etymology.—The specific name, *belizensis,* is derived from the type-locality.

Remarks.—The female of *C. belizensis* is similar in body form to *C. quadrifarius* and like it and the other new species, *C. caribbei,* can be differentiated from others in the genus by the presence of two long lateral processes extending from the penultimate abdominal segment. The present species has a single, simple, cephalic projection anterior to the oral cone in contrast to the bifurcate process of *C. quadrifarius.* The thoracic processes appear to be more dorsally placed as well as raised in *C. quadrifarius.*

Colobomatus caribbei, new species
Fig. 2A

Material examined.—Holotype ♀ (USNM 190543) from mandibular canal of *Anisotremus surinamensis* (Bloch) (USNM 123121) from Venezuela, paratypes 6 ♀ (USNM 190544–46) from the same host (USNM 30878, 80533, 123121) from Florida, Panama, and Venezuela.

Description.—Female: Body form as in Fig. 2A. Body length: 4.95–12.23 mm based on 5 specimens. Anterior cephalic process bifid. Head and first 3 thoracic segments fused. Thoracic segments 4 and 5 separated from anterior segments by constriction and bearing 2 anteriorly directed processes and 2 laterally directed processes; processes bulbous in basal half and attenuated in distal half. In dorsal aspect, the processes appear to be borne on raised shoulders. Thoracic segments 6 and 7 (genital segment) distinct. First 2 abdominal segments distinct. Abdominal segments 3 and 4 fused; segment 3 with 2 lateral processes. Caudal rami attenuated in distal half.

Male: Unknown.

Etymology.—The specific name, *caribbei,* is derived from the type-locality in the Caribbean Sea.

Remarks.—As in the two previous species, this species is characterized by the

Table 2.—Synopsis of hosts examined and *Colobomatus* infestations of each (A = Atlantic, P = Pacific).

Fish species	No. of fish examined	No. of fish infested	% infested	*Colobomatus* spp.
Anisotremus caesius (P)	4	0	0	neg
A. davidsoni (P)	4	3	75	*quadrifarius*
A. dovii (P)	8	5	60	*quadrifarius*
A. interruptus (P)	10	3	33	*quadrifarius*
A. pacifici (P)	12	2	17	*quadrifarius*
A. surinamensis (A)	9	4	44	*caribbei*
A. virginicus (A)	15	0	0	neg
Haemulon album (A)	11	0	0	neg
H. aurolineatum (A)	14	7	50	*belizensis*
H. bonariense (A)	17	0	0	neg
H. boschmae (A)	26	0	0	neg
H. carbonarium (A)	13	2	15	*belizensis*
H. chrysargyreum (A)	9	8	89	*belizensis*
H. flaviguttatum (P)	13	4	31	*quadrifarius*
H. flavolineatum (A)	15	0	0	neg
H. macrostomum (A)	13	1	8	*belizensis*
H. maculicauda (P)	16	0	0	neg
H. melanurum (A)	10	4	40	*belizensis*
H. parrai (A)	13	1	8	*belizensis*
H. plumieri (A)	13	12	92	*belizensis*
H. sciurus (A)	91	64	70	*belizensis*
H. scudderi (P)	14	0	0	neg
H. sexfasciatum (P)	10	0	0	neg
H. steindachneri (A)	21	10	45	*belizensis*
H. steindachneri (P)	16	3	19	*quadrifarius*
H. striatum (A)	16	0	0	neg
Orthopristis brevipinnis (P)	3	0	0	neg
O. chalceus (P)	12	1	8	*quadrifarius*
O. chrysopterus (A)	6	5	83	*belizensis*
O. forbesi (P)	2	0	0	neg
O. reddingi (P)	30	17	56	*quadrifarius*
O. ruber (A)	9	2	22	*belizensis*

presence of lateral processes on the penultimate segment. The bifid cephalic lobe distinguishes the present species from *C. belizensis*, and the bulbous nature of the appendages as well as the fused abdominal segments separate it from *C. quadrifarius* and *C. belizensis*.

Discussion

The three new species of *Colobomatus* described here appear to be closely related on the basis of the presence of the two lateral processes on the third abdominal segment of each. Essafi and Raibaut (1980) described a new genus *Colobomatoides* based in part on the presence of abdominal processes in the female. Although the three species described here possess abdominal processes, we feel that sufficient differences exist between *Colobomatoides* and these new species to warrant including the three new ones in the genus *Colobomatus*. These

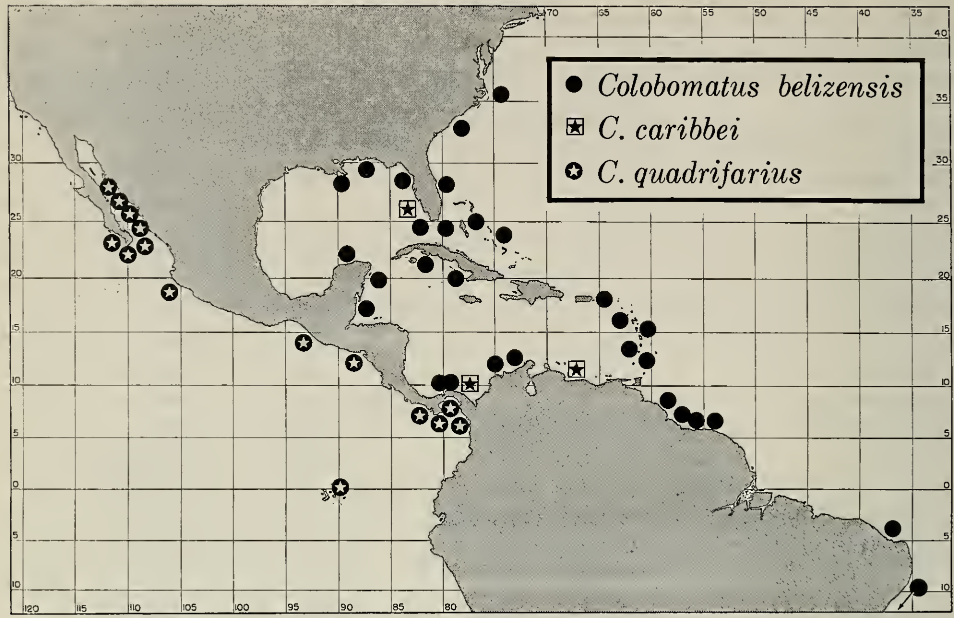


Fig. 8. Distribution of three new species of *Colobomatus*.

new species, however, are the first *Colobomatus* species with this character to be described.

The generic diagnosis of *Colobomatus* should be amended to state that the female may or may not possess abdominal processes and the key to philichthyid genera provided by Essafi and Raibaut (1980) modified.

Effect of Host Size

Table 1 suggests that an optimum size host is preferred by the parasite. All 15 specimens of *Haemulon sciurus* between 140–169 mm SL were infested. The rate of infestation diminishes in smaller and larger size groups.

Host Specificity and Biogeography

The present work includes species of hosts from three haemulid genera present in the tropical and semitropical western Atlantic and eastern Pacific (see Table 2). Figure 8 shows the distribution of each of the species. *Colobomatus quadrifarius* infests species of three genera (*Haemulon, Orthopristis,* and *Anisotremus*) in the eastern Pacific with little host specificity indicated beyond a possible restriction to haemulid fishes. The two Atlantic *Colobomatus* species, however, do show some degree of host specificity as *C. caribbei* is known thus far only from *Anisotremus*, and *C. belizensis* from *Haemulon* and *Orthopristis*.

Acknowledgments

The work in Belize was facilitated by Dr. Klaus Ruetzler (Smithsonian Institution), director of the Investigations of Marine Shallow Water Ecosystems project at Carrie Bow Cay, Belize. This paper is contribution number 119 of the Investigations of Shallow Water Ecosystems Project, supported in part by the Exxon Corporation.

Literature Cited

Essafi, K., and A. Raibaut. 1980. *Colobomatoides splendidus n.g., n.sp.*, (Copepoda, Philichthyidae) parasite de poissons téléostéens du genre *Sparus* (Sparidae) des côtes de Tunisie.—Extrait des Archives de l'Institut Pasteur de Tunis 57(4):355–361.

Izawa, K. 1974. On three new species of *Colobomatus* (Cyclopoida: Philichthyidae) parasitic on Japanese fishes.—Publications of the Seto Marine Laboratory 21:335–343.

Kabata, Z. 1979. Parasitic copepods of British fishes. 468 pp. London: The Ray Society.

Sekerak, A. 1970. Parasitic copepods of *Sebastes alutus* including *Chondracanthus triventricosus sp. nov.* and *Colobomatus kyphosus sp. nov.*—Journal Fisheries Board of Canada 27 (11): 1943–1959.

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

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 202–224

NOTES ON THE BIOLOGY OF SOME SEAGRASS-DWELLING CRUSTACEANS (STOMATOPODA AND DECAPODA) FROM CARIBBEAN PANAMA

Loren D. Coen and Kenneth L. Heck, Jr.

Abstract.—A year-long sampling program in seagrass meadows along the Caribbean coast of Panama yielded two stomatopod and 58 decapod species in 45 genera and 22 families, a number of which was previously unreported from Panamanian waters. Though not complete, this annotated list provides information on size, seasonality, reproductive state, and presence of parasites. High species affinities with recent collections from Bermuda and the Carolinas exist. Specifically, 59% of the species treated here are reported from the Carolinas and 64% from Bermuda; however, no regional endemics were found. Range extensions are made for several species. Recent literature and taxonomy are reviewed for most species discussed.

Abele, in a symposium volume on the Panamic biota in 1972, pointed out that almost no information was available at that time on the crustaceans of Panama. In recent years there have been publications on the brachyuran fauna of the Bahamas (Garth 1978) and the north coast of Colombia (Lemaitre 1981), and on the decapod fauna of Bermuda (Markham and McDermott 1981). Yet, with the exception of Gore and Abele's (1976) publication on the porcellanid crabs of Panama, and Gore's (1982) recent study on the Porcellanidae of Central America, our knowledge of the Panamanian crustacean fauna, especially on the Caribbean coast, remains nearly as limited as when Abele made his comments ten years ago.

Here we provide new information on a number of poorly known decapod and stomatopod crustaceans found primarily in seagrass habitats along the Caribbean coast of Panama. Included are data on size, reproductive condition, habitat, and other observations on the natural history of the 60 species treated here. This is clearly a small percentage of the total decapod and stomatopod fauna of the Caribbean coast of Panama and our list is in no way comprehensive. However, we believe that it does provide an indication of the species commonly found in subtidal seagrass habitats along the Caribbean Panamanian coast. Other information on the species treated here has been previously published by Heck (1977, 1979) and Heck and Wetstone (1977).

Study Sites

Sites consisted of vegetated subtidal meadows within 30 m of the shore. Study areas were located 20 km to the northeast of the Caribbean end of the Panama Canal (Fig. 1). Detailed descriptions of our stations 1–4 are provided by Heck (1977) and Weinstein and Heck (1979). Station 1 was seaward of a thick mangrove shoreline (*Rhizophora mangle* (L.)) and contained thick growths of *Thalassia*

Fig. 1. Location of collection sites along the Caribbean coast of Panama.

testudinum (König) and *Halimeda opuntia* (L.) with lesser amounts of *Syringodium filiforme* (Kützing), *Udotea flabellum* (F.) (Ellis and Solander) and *Penicillus capitatus* (Lamarck). Sediments were mostly fine muds, and the site was protected from wave shock by a small patch reef. Station 2 was exposed to the most severe wave shock of our 5 study areas. Dominant vegetation included *T. testudinum* and *S. filiforme*. Sediments were calcareous sand with some larger coral and *Halimeda* fragments. Station 3 received the least wave shock among our 5 sites. *Thalassia testudinum* was the dominant plant, although *H. opuntia* and *H. incrassata* (Ellis) were also present. Sediments were coarse with many coral and *Halimeda* fragments. Station 4 was surrounded by reefs and located in the lee of two small islands. *Thalassia testudinum* was the dominant plant although *S. filiforme* was also present. Sediments were coarse with many coral fragments. Station 5 was located in a small cove lined with red mangroves (*R. mangle*). Vegetation was sparse, with some *T. testudinum* and *S. filiforme* present.

Salinities ranged from nearly 0‰ during heavy rains to nearly 38‰ during the dry season, although values were most often similar to open sea salinities (~38‰). Water temperatures ranged from about 27–31°C (see Glynn 1972, for additional information on the physical regime). Although the stations were subtidal, water depth rarely exceeded 2 m or became shallower than 1 m during any one tidal cycle.

Methods

Samples were collected by a 4.87 m otter trawl, with 19 mm stretch mesh wings and a 6.3 mm liner. Monthly samples (station 1–4) were taken during the period of July 1974–May 1975, according to the schedule described by Heck (1977). Station 5 was only sampled during July, August, and September. Samples were taken diurnally, except for one set of night samples in May 1975 at stations 1, 2 and 3 (an average of 4 trawls per station). All samples were preserved in 10% formalin and later transferred to 70% isopropanol before identifications were made. All available specimens were identified, sex determined and measured to gather information on size at sexual maturity. By our criteria male shrimps were mature if the appendix masculina on the second pleopod was apparent (with a few exceptions, e.g., *Synalpheus* in which the appendix masculina is absent). Female shrimps were only separated into ovigerous and non-ovigerous categories. Maturity of anomuran and brachyuran crabs follows Abele and Blum's (1977) criteria. Male crabs were considered mature with the development of gonopods; females if the abdomen was covered by the sternum.

Most measurements are given for carapace length (cl), measured by dial caliper to the nearest 0.1 mm from posterior margin of the carapace to the postorbital margin. For crabs, carapace width (cw) includes the greatest width measured including spines. For hermit crabs, shield length (sl) was measured as in Provenzano (1959). Descriptions were not considered necessary but recent faunal summaries and classic monographs where these may be found are summarized (Table 1) as an aid to future works in the zoogeographical areas. The classification and nomenclature scheme used here has been adopted from The Biology of Crustacea (1982; L. G. Abele, pers. comm.) and Abele and Felgenhauer (1982).

Part of the collection was lost or badly damaged in transport from Panama, and resulting deficiencies are noted where appropriate in the text. Thus, many of the preliminary identifications (Heck 1977) done by authorities in the field are retained, though the specimens could not be measured or sexed.

ANNOTATED SPECIES LIST

SUPERORDER HOPLOCARIDEA

ORDER STOMATOPODA

Family Gonodactylidae

Gonodactylus lacunatus Mannins, 1966

Material.—Station 5; Sept; 1 male.

Measurements.—cl 5.4 mm.

Distribution.—From the western Atlantic, the Caribbean Sea, Yucatan, Nicaragua and Colombia; sublittoral to 50 m, though usually in shallower waters.

Family Pseudosquillidae

Pseudosquilla ciliata (Fabricius, 1787)

Material.—Stations 1, 3 and 4; Aug, Sept, Oct, Feb and Apr; 7 individuals.

Measurements.—Males, 4.3 to 7.9 mm cl; females, 5.0 to 7.3; juveniles, 3.4 to 3.5.

Habitat.—Shelly-sand, coralline algae, coral, though most often seagrasses.

Distribution.—From tropical oceans in the Indo-West Pacific, the western Atlantic, Bermuda, the Bahamas, Florida and western Africa; to 110 m, though primarily in shallower waters.

Table 1.—Brief summary of the carcinological literature (Decapoda) relating to the faunal area.*

Author(s)	# of species treated†	Taxonomic group discussed	Comments‡
FAUNAL SUMMARIES			
Abele 1970	154	Decapoda of northwestern Gulf of Mexico	a, k
Abele 1972a,b	485	Pacific and Caribbean Decapods of Panama	a
Felder 1973	143	Crabs and lobsters of the northwest Gulf of Mexico	a, k
Garth 1978	53	Brachyura of the Bahamas	a
Heck 1977	65	Decapoda, Caribbean Panama	f
Lamaitre 1981	96	Shallow-water Brachyura of Colombia	a
Markham and McDermott 1981	276	Decapoda of Bermuda	f
Park 1969	15	Portunidae of Biscayne Bay	a
Powers 1977	352	Crabs of the Gulf of Mexico	a
Rouse 1970	103	Littoral Crustacea of southwest Florida	a, k
Wass 1955	113	Decapoda of northwest Florida	a, k
Williams 1965	220	Decapoda of the Carolinas	a, k
TAXONOMIC WORKS (including monographs)			
Camp 1973	28	Stomatopoda of Florida (Hourglass Cruises)	a, k
Chace 1972	218	Shrimps of the Smithsonian-Bredin Expedition (Caribbean and West Indies)	a, k
Coutière 1909	45	American *Synalpheus* species	a, k
Gore and Abele 1976	43	Pacific Panama and adjacent Caribbean, Procellanidae	a, k
Gore and Scotto 1979	22	Western Atlantic Parthenopidae	a, k
Haig 1960	85	Eastern Pacific Porcellanidae	a, k
Holthuis 1958	5	Calappidae of the West Indies	a, k
Holthuis 1959	121	Decapoda of Suriname (Dutch Guiana)	a, k
Lemaitre *et al.* 1982	12	Provenzanoi group of pagurid crabs	a, k
Lyons 1970	6	Scyllaridae of Florida (Hourglass Cruises)	a, k
Manning 1961	2	Genus *Leander*	a, k
Manning 1969	62	Stomatopoda of the western Atlantic	a, k
Manning and Chace 1971	11	Processidae of the northwestern Atlantic	a, k
Perez Farfante 1969	8	Genus *Penaeus*	a, k
Perez Farfante 1971	5	Genus *Metapenaeopsis*	a, k
Provenzano 1959	23	Shallow-water hermit crabs of Florida	a, k
Rathbun 1918	238	Grapsoid crabs of America	a, k
Rathbun 1925	273	Spider crabs of America	a, k
Rathbun 1930	349	Cancroid crabs of America	a, k
Rathbun 1937	127	Oxystomatous crabs and allied groups	a, k
Williams 1974b	14	Genus *Callinectes*	a, k

* NOTE: This is not meant to be exhaustive, but rather a guide to the most accessible literature; earlier references may be omitted if they are covered within the scope of another, more recent treatment. Totals may be approximate to account for supergenera, subspecies, etc.

† Total number of species addressed (includes subspecies and those reviewed from adjacent waters).

‡ Key to contents of papers: a, annotated list; f, faunal list without additional information; k, keys included (or new descriptions).

ORDER DECAPODA
SUBORDER DENDROBRANCHIATA
SUPERFAMILY PENAEOIDEA
Family Penaeidae

Metapenaeopsis martinella Perez Farfante, 1971

Material.—Stations 1, 2, 3 and 5; Sept and May; 10 individuals.

Measurements.—One juvenile male, 10 mm cl; mature females, 9.8 to 12.6.

Habitat.—Chace (1972) reported specimens from coral reefs, shelly bottoms and calcareous algae.

Remarks.—This species was identified in Heck (1977) as *Trachypenaeus restrictus* but reexamination allowed the identification to be corrected. Most individuals from night samples, stations 2 and 3. The species known from Cuba, Brazil, and the western Caribbean; 4 to 137 m. Genus reviewed by Perez Farfante (1971).

Penaeus (*Melicertus*) *duorarum notialis* Perez Farfante, 1967

Material.—Stations 1–5; present in all sampled months; 300 individuals.

Measurements.—Males, 3.9 to 6.3 mm cl; females, 4.5 to 20.6.

Habitat.—On muds, sand and sand within rocky patches.

Remarks.—Specimens taken primarily in day trawls (cf. Greening and Livingston 1982); most were immature. Over 80% from station 1. Subspecies ranges from Cuba to the Virgin Islands, Mexico, the Caribbean Sea to Brazil and the western coast of Africa; to 732 m, though generally to 65 m. Genus reviewed by Perez Farfante (1969).

Family Sicyonidae

Sicyonia laevigata Stimpson, 1871

Material.—Stations 1, 2 and 3; May only; 16 individuals.

Measurements.—Males (two), 7.4 mm cl; mature females, 7.2 to 11.1.

Habitat.—Common in areas with abundant shell cover and among rocks; also in *Thalassia*.

Remarks.—All but two (87%) collected in night samples. Williams (1965) noted sexually mature individuals as small as 18 mm total length. Greening and Livingston (1982) reported *S. laevisata* in their nighttime seagrass samples. Species ranges from North Carolina to northwestern Florida, the West Indies, Colombia and the Pacific coast of Panama; to 90 m.

SUBORDER PLEOCYMATA
INFRAORDER STENOPODIDEA
Family Stenopodidae

Stenopus hispidus (Oliver, 1811)

Material.—Station 3; Sept and May (night); 2 individuals.

Measurements.—Both males, 6.2 and 7.6 mm cl.

Habitat.—Grass flats and areas with coral rubble (Chace 1972).

Distribution.—Widely ranging from Bermuda, central eastern Florida and south Florida to the West Indian region, Surinam, the Red Sea, Japan, southeast Africa, and Hawaii; to 210 m.

INFRAORDER CARIDEA
SUPERFAMILY PALAEMONIDEA
Family Palaemonidae

Leander tenuicornis (Say, 1818)

Material.—Stations 1–3; April and May; 24 individuals.

Measurements.—Males, 4.9 to 5.1 mm cl; ovigerous females, 6.3 to 8.4.

Habitat.—Most often associated with vegetation, *Sargassum, Thalassia* and mangroves (Ledoyer 1969; Chace 1972).

Remarks.—Most individuals from station 1. It is distributed in shallow or pelagic waters of all tropical and subtropical seas except those in the extreme eastern Pacific. Only 2 species known in American waters. See Manning (1961) for a comparison of this species with *L. paulensis* (Ortmann).

Periclimenes americanus (Kingsley, 1878)

Material.—Majority at station 1; collections scattered throughout sampling period; 19 individuals.

Measurements.—Males, 2.3 to 3.5 mm cl; ovigerous females, 2.7 to 3.3.

Habitat.—Associated with coral reefs, on mud and sand flats, submerged structures and especially in seagrass and mangrove habitats (Chace 1972).

Distribution.—Species ranges from Bermuda, North Carolina to northwest Florida, Yucatan Peninsula, and West Indies; to 73 m.

Family Gnathophyllidae

Gnathophylloides mineri Schmitt, 1933

Material.—One ovigerous female; data lost.

Measurements.—2.2 mm cl.

Habitat.—Among sea urchin spines, rocks, and coral rubble (Chace 1972).

Distribution.—From Bermuda, southeastern Florida, Yucatan Peninsula and the Caribbean Sea; littoral and sublittoral.

SUPERFAMILY ALPHEOIDEA
Family Processidae

Ambidexter symmetricus Manning and Chace, 1971

Material.—Stations 1, 2 and 3; May; 7 individuals.

Measurements.—Males, 3.4 to 4.3 mm cl; ovigerous females, 3.4 to 5.2.

Habitat.—Common on vegetated bottoms, especially seagrasses.

Remarks.—One individual (5.8 mm cl) was infested with a bopyrid isopod (branchial; Table 2). Processid shrimp are a common seagrass-inhabiting group, being taken especially at night (Ledoyer 1969; Manning and Chace 1971; Greening and Livingston 1982; personal observations). This species is noted from the western Atlantic, including eastern and western Florida (Gulf of Mexico), Puerto Rico and Trinidad; to 6 m. This is the first report of *A. symmetricus* from Panama.

Processa fimbriata Manning and Chace, 1971

Material.—Most from stations 1 and 2; Apr and May; 55 individuals.

Measurements.—Males, 2.9 to 4.2 mm cl; ovigerous females, 5.4 to 5.6.

Habitat.—Areas of broken shell, coral rubble, sponges and *Thalassia.*

Remarks.—The majority of the individuals collected at night (93%). Reported from North Carolina to Brazil, including south Florida, the Bahamas and Puerto Rico; sublittoral to 37 m. This constitutes a new record for Panama.

Family Alpheidae

Alpheus armillatus H. Milne Edwards, 1837

Material.—Stations 1, 2 and 3; May only; 16 individuals.

Measurements.—Males, 5.3 to 9.2 mm cl; one non-ovigerous female, 11.7; ovigerous females, 5.3 to 11.7.

Habitat.—In oyster bars, coral rubble, rocks and *Thalassia* beds (Chace 1972).

Distribution.—Bermuda, North Carolina to the Gulf of Mexico and Brazil; sublittoral.

Alpheus floridanus Kingsley, 1878

Material.—Stations 1 and 2; Oct, Dec and Jan; 8 individuals.

Measurements.—Males, 4.3 to 8.8 mm cl; ovigerous females, 6.4 to 19.8.

Habitat.—Soft-sediments.

Distribution.—From Bermuda, the southeastern United States to the Gulf of Mexico, Brazil, Guyana and the Congo (eastern Atlantic); to 37 m.

Alpheus formosus Gibbes, 1850

Material.—Stations 1 and 3; Aug and Mar; 2 females.

Measurements.—3.6 and 5.5 mm cl.

Habitat.—On sand and mud flats, rocks, oyster bars and coral rubble.

Distribution.—From Bermuda, North Carolina and throughout the West Indies to Brazil; to 42 m.

Alpheus normanni Kingsley, 1878

Material.—Stations 1 and 5; Oct and May; 4 individuals.

Measurements.—Males, 4.1 to 5.4 mm cl; one ovigerous female, 6.3.

Habitat.—In *Thalassia,* sponges and coral rubble (especially *Porites*); also among ascidians (Abele 1970).

Remarks.—All 3 males were found associated with a sponge (Station 5). Wass (1955) found this shrimp to be common in the northeast Gulf of Mexico, and Greening and Livingston (1982) collected this species mostly at night. Found from Bermuda, Virginia to the Gulf of Mexico, throughout the West Indies to Tobago and in the Pacific in the Gulf of California; littoral to 73 m.

Synalpheus fritzmuelleri Coutière, 1909

Material.—Stations 1 and 2; Aug, Feb and May; 6 individuals.

Measurements.—Ovigerous females (two), 3.2 and 5.0 mm cl; remaining specimens, 2.9 to 3.8.

Habitat.—Commonly collected in sponges (Abele 1970) and in grass flats, as well as among mangrove roots (Chace 1972).

Remarks.—Both ovigerous females collected from sponges. *S. fritzmuelleri* recorded from Bermuda, North Carolina to the Gulf of Mexico and the West Indies to Brazil; in the eastern Pacific from Baja, California; littoral to 50 m.

Synalpheus goodei Coutière, 1909

Material.—Station 2; Oct; 19 individuals.

Measurements.—Ovigerous females (13), 4.6 to 6.1 mm cl.

Habitats.—Associated with rocky intertidal areas encrusted with corals; Gore (pers. comm.) found it living on or near a large keratose sponge.

Remarks.—Six of the 19 specimens lost in transit. Species known from Bermuda, central east Florida Gore (pers. comm.), the Gulf of Mexico and Curaçao; to 60 m.

Synalpheus pandionis Coutière, 1909

Material.—Stations 1 and 2; Aug and Feb; 3 individuals.

Measurements.—Ovigerous females (three), 4.9 to 5.5 mm cl.

Habitat.—Collected from *Thalassia* with clumps of *Porites* rubble and algae (Chace 1972).

Distribution.—This rare species reported from the Gulf of Mexico, Barbados and Curaçao; to 60 m.

Synalpheus townsendi Coutière, 1909

Material.—Station 2; Aug and Feb; 4 individuals.

Measurements.—One ovigerous female, 4.0 mm cl; the remaining specimens, 1.9 to 3.9.

Habitat.—Common in sponges (Abele 1970) and *Thalassia* beds with clumps of *Porites* (Chace 1972). Gore (1981) recorded it from a deep reef in the Florida Keys.

Remarks.—Chace (pers. comm.) suggests that references to associations with *Pocillopora* are in error, referring probably to growth forms of *Porites*. Species occurs from Bermuda and North Carolina, southwest through the Gulf of Mexico and the West Indies to Brazil; to 102 m.

Family Hippolytidae

Hippolyte zostericola (Smith, 1873)

Material.—Stations 2 and 3; Sept and May; 4 individuals.

Measurements.—Four ovigerous females, 1.7 to 2.6 mm cl.

Habitat.—Usually common in submerged vegetation (Chace 1972; Greening and Livingston 1982).

Remarks.—From Bermuda and Massachusetts to the Yucatan Peninsula, Trinidad and Curaçao; in shallow waters. See Williams (1965) and Chace (1972) for a discussion of its taxonomic difficulties.

Latreutes fucorum (Fabricius, 1798)

Material.—Stations 1 and 2; Apr and May; 15 individuals.

Measurements.—Ovigerous females, 2.3 to 3.5 mm cl; a single non-ovigerous female, 2.2.

Habitat.—Most often associated with floating and submerged vegetation (Wass 1955; Abele 1970; Chace 1972).

Distribution.—Ranges from Newfoundland to the Gulf of Mexico, Bermuda and Puerto Rico; pelagic (in vegetation) and sublittoral.

Thor manningi Chace, 1972

Material.—Stations 1, 2 and 5; Aug and May; 12 individuals.

Measurements.—Single male, 2.3 mm cl; ovigerous females, 1.9 to 3.7; females (non-ovigerous), 1.8 to 2.6.

Habitat.—Common in grass flats.

Remarks.—Most specimens were taken in night samples. Recorded from Bermuda, North Carolina to Tobago, Curaçao and in the eastern Pacific; to 4 m. Chace (1972) suggested that this hippolytid may be a sequential (protandric) hermaphrodite.

Tozeuma carolinense Kinglsey, 1878

Material.—Stations 1–5; all months sampled; 1068 individuals.

Measurements.—Males (mature), 3.5 to 6.7 mm cl; ovigerous females, 5.1 to 10.8; non-ovigerous females, 5.2 to 9.4. Several males less than 3.5 mm cl were collected, each with a developing appendix masculina.

Habitat.—Common in vegetation, with color being highly variable (Abele 1970; Greening and Livingston 1982; pers. obs.).

Remarks.—*T. carolinense* dominated with decapoda fauna (ranked by abundance) at all stations. Ovigerous females were found throughout the year, with ovigery in a given collection always greater than 65%. Previous studies on this species have been primarily concerned with its larval development (Bryce 1961; Ewald 1969), although Voss (1956) briefly discussed its natural history. Found from Bermuda and Massachusetts to Panama; littoral to 75 m.

Trachycaris restrictus (A. Milne Edwards, 1878)

Material.—Stations 2, 3 and 5; Aug, Mar, Apr and May; 13 individuals.

Measurements.—Ovigerous females (13), 5.0 to 6.8 mm cl.

Remarks.—Genus with one species. This rare and curious looking hippolytid has been recorded from Bermuda to Brazil and in the eastern Atlantic from Canary Islands to Saint Helena Island (Holthuis 1949); to 100 m. This is probably the first record of this species from Panama.

INFRAORDER PALINURA
SUPERFAMILY PALINUROIDEA
Family Scyllaridae

Scyllarus Fabricius, 1775

Remarks.—Two individuals were collected; however, both were lost in transit. See Williams (1965) and Lyons (1970) for a review of this group.

Family Palinuridae

Palinurus argus (Latreille, 1804)

Material.—Stations 1, 2 and 5; Aug, Oct, Mar, Apr and May; 27 juvenile individuals.

Measurements.—Specimens ranged from 11.2 to 37.4 mm cl.

Habitat.—Spiny lobsters commonly found around rocky and coral reef areas; generally in areas offering concealment (Khandler 1964; Davis 1971, 1981; Berrill 1975).

Remarks.—Juveniles were taken primarily at Station 1, possibly associated with the nearby red mangroves, where dense prop roots offer areas of concealment (Heck 1977). *P. arsus* has been recorded from Bermuda, North Carolina to the Gulf of Mexico, the West Indies and Brazil; to 100 m. Williams (1965) gives a general overview of this species' ecology.

INFRAORDER ANOMURA
SUPERFAMILY COENOBITOIDEA

(Note: hermit crabs were tentatively identified in Panama by one of us (KLH); however, most were damaged during extraction. Though intact specimens were originally verified, measurements and sexing for most specimens were impossible).

Family Diogenidae

Calcinus tibicen (Herbst, 1791)

Material.—Stations 2, 3 and 5; Sept and May night; 3 individuals.

Measurements.—One specimen measured, 4.4 mm sl.

Habitat.—Common in rocky shores.

Remarks.—Found in Bermuda, the West Indies, Florida and Brazil; intertidal to 32 m. See Provenzano (1959) for further information.

Clibanarius antillensis Stimpson, 1862

Material.—Stations 1–5; all sampled months; 91 individuals.

Measurements.—Measurable specimens from 1.6 to 4.7 mm sl.

Remarks.—Ovigerous females were present in August and September. Over 68% of the specimens from station 2. Known from Bermuda, south Florida, the West Indies, Curaçao and Brazil; in shallow waters. See Provanzano (1959) for additional information.

Dardanus venosus (H. Milne Edwards, 1848)

Material.—Stations 2, 3 and 5; Aug, Apr and May; 3 individuals.

Measurements.—One male, 6.4 mm sl; two females, 8.3 and 16.1.

Habitat.—Found in grassbeds (Williams 1965).

Remarks.—Bright red transverse bands on walking less and chela make this species quite distinctive, even after alcohol preservation. Found from North Carolina to the West Indies, including Surinam, Brazil and Bermuda. Found nearshore to 91 m, but has been collected to 366 m. Biffar and Provenzano (1972) treat this species in their review of the genus.

Paguristes limonensis McLaughlin and Provenzano, 1974

Material.—Stations 1–5; all sampling months; 166 individuals.

Measurements.—Males, 3.3 to 3.6 mm sl; measured females (all ovigerous), 3.6 to 5.9.

Remarks.—Over 77% of these hermit crabs were collected at night. The majority of individuals were badly damaged during extraction from the shell. Ovigerous females were taken in July, August, September, November, January, March, April and May. This recently described species ranges from the west coast of Florida, Panama and Colombia; to 234 m. See McLaughlin and Provanzano (1974) for a more detailed taxonomic discussion.

SUPERFAMILY PAGUROIDEA

Family Paguridae

Pagurus bonairensis Schmitt, 1936

Material.—Stations 1–5; all months sampled; 190 individuals.

Measurements.—Ovigerous females, 3.1 to 4.8 mm sl.; remaining specimens, 2.4 to 5.2.

Habitat.—Common in seagrass (*Thalassia*) beds (in the northeastern Gulf of Mexico, Abele 1970; Greening and Livingston 1982; personal obs.).

Remarks.—Most individuals collected at station 4; over 26% were collected in May night trawls. Ovigerous months included July, August, September, November, March and May. This abundant species was previously misidentified as *P. annulipes* (see Rouse 1970) by Provenzano (1959). Occurs in Florida, Cuba and Puerto Rico, although in the northern part of its range this species is often confused with *P. annulipes* (Rouse 1970; Gárcia-Gómez 1982). Garciá-Gómez (1982) provides further clarification.

Pagurus brevidactylus (Stimpson, 1858)

Material.—Stations 1–5; all sampling months; 50 individuals.

Measurements.—Ovigerous females, 3.9 to 5.4 mm sl; remaining intact specimens, 3.6 to 4.1.

Habitat.—Provenzano (1959) suggests that this species is most often taken on hard bottoms to 229 m; we collected our samples in sandy-vegetated areas less than 2 m.

Remarks.—Ovigerous months included August, September and February to May. This species has been noted from Bermuda, Florida, the Caribbean and northeast Gulf of Mexico; intertidal to 50 m. See McLaughlin (1975) and Lemaitre *et al.* (1982) for a reclarification of this species.

SUPERFAMILY GALATHEOIDEA

Family Porcellanidae

Megalobrachium mortenseni Haig, 1962

Material.—One individual; all additional data lost.

Measurements.—Male, 4.0 mm cw.

Habitat.—In sandy areas with calcareous algae (Brazil), coarse sediments (gravel) and among rocks.

Remarks.—Haig (1962) discussed the close resemblance of *M. mortensi* to *M. erosum,* the latter occurring in the Gulf of California. Gore and Abele (1976) considered the two to be geminate species. Reported from the Virgin Islands southward to Brazil; to 27 m. This is a new record for Caribbean Panama.

Petrolisthes armatus (Gibbes, 1850)

Material.—Stations 1, 2 and 3; Aug to Mar; 38 individuals.

Measurements.—Male, 3.8 to 7.4 mm cw; ovigerous females, 3.0 to 6.3; non-ovigerous females, 3.1 to 4.3.

Habitat.—Found in oyster and mussel bars, coral rubble, mangroves and around pilings (Haig 1960). Gore and Abele (1976) found this species abundant in rocky coralline intertidal on both sides of the Panamanian isthmus.

Remarks.—Ovigerous females found in all collecting months. Haig (1960) reports ovigerous females also throughout the year among material examined from intertidal and subtidal habitats. This porcellanid crab is reported from Bermuda, Georgia and central eastern Gulf coast of Florida to Brazil; western Africa and eastern Pacific (Gulf of California to Peru); to 20 m.

Petrolisthes galanthinus (Bosc, 1802)

Material.—Stations 1, 2, 3 and 5; July to May; 44 individuals.

Measurements.—Males, 3.6 to 7.0 mm cw; ovigerous females, 4.4 to 8.8; a single non-ovigerous female, 4.1.

Habitat.—Under rocks, coral rubble and on shell and sand bottoms. Also associated with sponges, coral and anenomes (Haig 1960; Gore and Abele 1976).

Remarks.—Ovigerous females were taken July, August, February and March (September and October were the only other months when females were taken at all). Haig (1960) found ovigerous females in January, February and March; southwest Caribbean, ovigery from January to August (Gore and Abele 1976). Species common in the Atlantic from North Carolina to Brazil, including the Caribbean area and Surinam. In the Pacific, Haig (1960) reported it only from Panama, but Gore and Abele (1976) noted its occurrence from Ecuador and Costa Rica also.

INFRAORDER BRACHYURA
SECTION DROMIACEA
SUPERFAMILY DROMIOIDEA
Family Dromiidae

Dromidia antillensis Stimpson, 1858

Material.—Station 3; Apr; 2 individuals.

Measurements.—Males (two), 17.8 and 18.8 mm cw.

Habitat.—Most often on rocky substrates.

Remarks.—These crabs typically carry sponges or tunicates with their fifth leg, modified for grasping the dorsal covering; both specimens had sponges. Found from Bermuda and North Carolina to the Gulf of Mexico, the West Indies, Colombia and Surinam to Brazil; littoral to 300 m. See Powers (1977) for an excellent summary of this group.

SECTION OXYSTOMATA
SUPERFAMILY LEUCOSIOIDEA
Family Calappidae

Calappa angusta H. Milne Edwards, 1880

Material.—Stations 1 and 2; Aug, Nov, Mar and May; 4 individuals.

Measurements.—Males (four), 6.3 to 45.1 mm cw (45.1 mm, mature).

Habitat.—From coral, sand, shell and gravel substrates.

Distribution.—From Bermuda and North Carolina to Brazil, including the West Indies and the Gulf of Mexico; to 200 m.

Calappa ocellata Holthuis, 1958

Material.—Stations 1 and 2; both were lost in transit; 2 individuals.

Habitat.—Among corals and on sandy bottoms.

Remarks.—This and the previous calappid species possess a large, toothed dactyl used to open gastropod shells (often with hermits inside, Vermeij 1982). Shoup (1968) discusses this unique predatory behavior. *C. ocellata* ranges from Bermuda and North Carolina to Brazil; to 52 m, though common in shallower waters (see Holthuis 1958).

Hepatus pudibundis (Herbst, 1785)

Material.—Station 1; specimens lost; 2 individuals.

Habitat.—On sand, mud and shelly bottoms (Holthuis 1959).

Remarks.—The low abundance of this and the previous two calappid species is surely a result of their habit of remaining partially buried much of the time (Pearse, Humm and Wharton 1942), thus escaping collection by trawling. This species has been reported from North Carolina to Brazil, including Louisiana and Texas in the Gulf of Mexico and from western Africa; intertidal to 49 m.

SECTION OXYRHYNCHA
SUPERFAMILY MAJOIDEA
Family Majidae

Chorinus heros (Herbst, 1790)

Material.—Stations 1, 2 and 3; May night; 6 individuals.

Measurements.—One male, 11.3 mm cw; females, 10.7 to 17.0.

Habitat.—Found on rocks, broken shell, coarse sand, sponges, and sabellarid reefs (Gore, pers. comm.).

Distribution.—From Bermuda and central eastern Florida to Cuba and Brazil; shallow to 48 m.

Macrocoeloma diplacanthum (Stimpson, 1860)

Material.—Stations 1–5; all collecting months; 33 individuals.

Measurements.—Males from 7.4 to 31.8 mm cw (including lateral spines); non-ovigerous females, 16.9 to 28.7; ovigerous females, 21.8 to 28.4.

Habitat.—Near shallow reefs and on sandy substrates.

Remarks.—All individuals were collected in day sampling. Ovigerous females found in July, August, November and April. Animals were always encrusted with numerous sponges, algae and debris. Rathbun (1925) reported individuals from Jamaica and Cuba with rhizocephalan infestations, but none were found infested here. Species ranges from Key West, Florida to Colombia, including the Bahamas and the Caribbean Sea; in shallow water to 24 m.

Microphrys bicornutus (Latrielle, 1825)

Material.—Stations 1–5; all months sampled; 195 individuals.

Measurements.—Mature males, 5.1 to 23.3 mm cw (including lateral spines); immature males, 8.8 to 8.9; mature females, 6.2 to 17.6; immature females, 6.3 to 8.9; ovigerous females, 11.6 to 21.1.

Habitat.—On reefs, seagrasses, sponges, and a variety of substrates such as shell, rock, sand and mud.

Remarks.—This majid ranked third in overall species abundance. It was most common at stations 1 and 2. Twenty-six ovigerous females were collected (in all months but March). These "decorator crabs" covered with a variety of algae, sponges and other sessile invertebrates. *M. bicornutus* occurs from North Carolina to Brazil, including the Bahamas, the Florida Keys, St. Croix (pers. obs.), Colombia and Bermuda; to 30 m. Powers (1977) provides an excellent review of this species. Williams (1965) summarizes its known parasites and Hazlett (1979 and included references), the behavioral literature on this species. This is one of the few species dealt with here, whose biology has been studied in some detail.

Mithrax (Mithraculus) forceps (A. Milne Edwards, 1875)

Material.—Stations 1–5; in all sampling months; 88 individuals.

Measurements.—Males, 4.9 to 21.2 mm cw; ovigerous females (17), 6.8 to 16.4; non-ovigerous females, 6.8 to 16.4.

Habitat.—Under coral rubble, in sponges, *Thalassia* beds, and several coarse substrates (coral, shell, and rock).

Remarks.—Most (87%) were collected during daytime trawls. Ovigerous females were found from July to October, January and March to May (all months within which females were collected). Abele (1970) noted that this brick red crab commonly preyed on barnacles. Recorded from Bermuda, North Carolina to the Gulf of Mexico, Trinidad and Colombia; intertidal to 90 m. See Powers (1977) for a brief introduction to this species' biology.

Mithrax (Mithraculus) ruber (Stimpson, 1871)

Material.—Station 4; data lost; 1 individual.

Habitat.—From sand, coral and mud substrates, with sponges and in seagrasses near reefs.

Distribution.—Puerto Rico, Cuba, St. Thomas, Barbados, Curaçao and Colombia; to 153 m, though usually shallower.

Pitho Bell, 1835

Remarks.—A total of 148 individuals belonging to this genus were collected over the course of this study. Over 70% were from May night trawls. In daytime sampling, most (70%) individuals at station 1; for night samples, the majority (60%) at station 3 (May). No *Pitho* spp. were taken at station 2 (daytime), yet 19 individuals (most *P. lherminieri*) were collected at night (May).

The following account by species, for the genus *Pitho* is tentative. We found, and others have noted (Abele 1970 and pers. comm.), a great deal of variation (especially with size and sex) regarding the lateral teeth of the carapace. Rathbun's (1925) key to the species employs these teeth as major diagnostic characters. Based on our observations of over 140 individuals, other criteria must be used to sort out specimens to species, particularly when several are sympatric. Rathbun (1925) has some excellent figures (fig. 116 and 117) of both male abdominal segments and antennal articles, but caution should be exercised when crabs are immature or adults are larger than average-sized. Note: totals below may be different than original species counts (Heck 1977); some specimens were lost.

Pitho aculeata (Gibbes, 1850)

Material.—Stations 1 and 3; Aug, Sept and Mar to May; 9 individuals (tentatively identified).

Measurements.—Mature males, 10.6 to 24.6 mm cw; juvenile males, 12.1 to 14.4; one ovigerous female, 19.3; mature females (non-ovigerous), 20.6 to 22.4; one juvenile female, 12.9.

Habitat.—Sand, shell and mud bottoms with corals; algae (e.g. *Sargassum*) and seagrass.

Remarks.—All were collected in daytime sampling. Reported from the Bahamas, Florida (west and Keys) to the West Indies and the northern coast of South America; in shallow water.

Pitho anisodon (von Martens, 1872)

Material.—Stations, 1–4; Sept, Oct and May; 62 individuals originally identified.

Measurements.—Mature males, 18.1 to 25.3 mm cw; one immature male, 12.4 (May); ovigerous females, 23.7 to 26.8 (all May); one immature female, 10.1 (May); one non-ovigerous female, 26.3 (May).

Habitat.—Found in rocks, sand, grassbeds, mud and coral bottoms.

Remarks.—This species was the most abundant *Pitho* spp. Collected in greatest numbers in September, October and May, with the majority (81%) taken at night in May (37 of 50 at station 3 for all night samples). The species occurs in the Bahamas, Florida, Cuba, Jamaica and Curaçao; to 22 m.

Pitho lherminieri (Schramm, 1867)

Material.—Stations 1–4; all months sampled; 59 individuals originally identified.

Measurements.—Mature males, 12.3 to 22.9 mm cw; juvenile males, 10.5 to 13.5; ovigerous females (two), 16.8 and 18.3 (station 3, May night); non-ovigerous females (mature), 18.3 to 24.9; immature females, 9.5 to 9.8 (September and May).

Habitat.—Found on most coarse bottoms and with seagrasses (Lemaitre 1981); infrequently on mud.

Remarks.—Majority of individuals collected at night in May (63%). Noted from North Carolina to west Florida, the West Indies to Brazil; to 221 m, though usually to 51 m.

Pitho quadridentata (Miers, 1879)

Materials.—Stations 1–4; most in Sept and May; 24 individuals originally identified.

Measurements.—Mature males, 11.5 to 25.0 mm cw; one immature male, 13.0 (May); 4 ovigerous females (Sept and May night), 20.2 to 26.2; juvenile females, 9.5 to 9.8 (Sept and May night).

Remarks.—Most individuals from station 1 (62%). Rathbun (1925) discussed its resemblance to *P. anisodon*. Previously reported only from Jamaica. This probably constitutes the first record for Panama and Central America.

Pitho sexdentata Bell, 1835

Material.—Station 2 night; May; 2 individuals.

Remarks.—Two specimens originally recorded by Heck (1977). This species has previously been collected in the Pacific only (Rathbun 1925; Garth 1958). Unfortunately, these specimens could not be relocated.

Podochela gracilipes Stimpson, 1871

Material.—Stations 1, 3 and 5; May; 3 males.

Measurements.—Males, 3.3 to 4.5 mm cw.

Habitat.—Associated with rocks, gravel, sand, shell and coral.

Distribution.—From North Carolina to the Gulf of Mexico, the Caribbean Sea, including Colombia, Surinam and Brazil; to 220 m, although we collected from depths less than 2 m.

Podochela riisei Stimpson, 1860

Material.—Stations 1 and 3; Aug, Oct and Apr; 4 individuals.

Measurements.—Males, 4.8 to 6.4 mm cw; a single ovigerous female, 9.7 (Apr).

Habitat.—Found on most coarse substrates, though often with algae (e.g. *Sarsassum*) and *Thalassia* (Wass 1955; Greening and Livingston 1982).

Remarks.—Abele (1970) found this species often covered with bryozoans. It is reported from Bermuda and North Carolina to Mexico and Brazil; shallow to 90 m.

Podochela sidneyi Rathbun, 1924

Material.—Station 1; Aug, Feb and May; 3 badly damaged individuals.

Distribution.—North Carolina, east and west Florida, Texas, Yucatan Peninsula and Cuba; to 186 m.

[Note: these 3 *Podochela* spp. are very similar and the identifications are all tentative; dactyls of the last 3 legs missing). Wass (1955) suggests that *P. sidneyi*'s sternal plates are flatter than those of *P. riisei.*]

Stenorhynchus seticornis (Herbst, 1788)

Materials.—Stations 3, 4 and 5; Aug to Nov; 9 individuals.

Measurements.—Males, 9.8 to 18.7 mm cw; two ovigerous females (September), 10.0 and 10.7; non-ovigerous females, 7.7 to 9.7.

Habitats.—On coarse bottoms such as rock, gravel, sand, shell and coral rubble.

Remarks.—Found from Bermuda, North Carolina to Brazil, including Colombia; to 1487 m, though more often in shallower waters. Yang (1967) recognized three distinct species in the Atlantic. Previous accounts of *S. seticornis* from the eastern Atlantic (West Africa) are incorrect. Manning and Holthuis (1981:304) review the current status of this genus in the Atlantic. Powers (1977) briefly lists references on the biology of this interesting crab. See Schnever (1978) for some recent work on this species.

SUPERFAMILY PARTHENOPOIDEA

Family Parthenopidae

Heterocrypta granulata (Gibbes, 1850)

Material.—Station 4; August; one individual.

Measurements.—Male, 12.8 mm cw.

Habitat.—Found on shelly, mud, sand, gravel, rock and coral bottoms; also collected in *Thalassia* (Lemaitre 1981).

Remarks.—This parthenopid crab has been reported from Massachusetts to Georgia, the Gulf of Mexico, and the West Indies to Brazil; generally less than 50 m. Gore and Scotto (1979) provide an excellent review of the family.

SECTION BRACHYRHYNCHA
SUPERFAMILY PORTUNOIDEA
Family Portunidae

Callinectes danae Smith, 1869

Material.—Stations 1–5; all sampling months; 66 individuals.

Measurements.—Mature males, 58.3 to 105.4 mm cw (including lateral spines); juvenile males, 20.4 to 69.4; ovigerous females (two), 76.4 and 99.2; females (mature), 61.9 to 103.6; juvenile females, 20.9 to 60.3.

Habitat.—Common in muddy estuaries, in mangroves, algae, and shelly bottoms; from nearly fresh to full strength seawater (Williams 1974b).

Remarks.—Ovigerous females taken in August and October. Miles (1951) reported ovigerous females beginning at 67 mm cw. Rathbun (1930) found *C. danae* along high energy sandy beaches and Park (1969) noted its occurrence on the seaward sides of islands in Biscayne Bay, Florida. Over 38% of the crabs maintained a rhizocephalan infection (Table 2). This species noted from Bermuda, Central Florida and the Yucatan Peninsula to Brazil; to 75 m. Williams (1974b) reviews this genus.

Cronius tumidulus (Stimpson, 1871)

Material.—Stations 1, 2, 3 and 4; 93% in May (night); 59 individuals.

Measurements.—Mature males, 15.0 to 35.2 mm cw (including lateral spines); juvenile males, 9.0 to 15.5 (May); two ovigerous females (Station 2 and 3, May night); mature females, 16.1 to 34.2 (Sept and May); juvenile females, 9.3 to 14.0 (May only).

Habitat.—Coral, sand and rocky bottoms and in *Sargassum* and *Thalassia.*

Remarks.—This species has often been reported from *Thalassia* beds (Rathbun 1930; Garth 1978); in fact, Park (1969) found it exclusively there. Several crabs had rhizocephalans (see Table 2). Noted from Bermuda, the central east and west coasts of Florida, the Florida Keys and the Bahamas; 73 m.

Lupella forceps (Fabricius, 1793)

Material.—Station 3; Dec; one individual.

Measurements.—One immature male, 30.5 mm cw (including lateral spines).

Habitat.—Common offshore on muddy bottoms and in vegetated areas (Park 1969).

Distribution.—Found in the West Indies, Colombia and Surinam; Parks (1969) collected one individual in Biscayne Bay, Florida; to 15 m.

Portunus ordwayi (Stimpson, 1860)

Material.—Stations 1 and 2; May night; 10 individuals.

Measurements.—Males, 42.8 to 48.8 mm cw (including lateral spines), ovigerous females (two; station 1 May night), 40.7 and 46.0; females (non-ovigerous), 40.6 to 45.4.

Habitat.—On sand, gravel, shell and coral rubble bottoms.

Distribution.—From Massachusetts, Bermuda and North Carolina to the Gulf of Mexico, the Caribbean Sea and southward to Brazil; to 106 m.

SUPERFAMILY XANTHOIDEA

Family Goneplacidae

Cyrtoplax spinidentata (Benedict, 1892)

Material.—Stations 1 and 3; Dec, Jan and May; 3 individuals.

Measurements.—Males (three), 9.9 to 16.8 mm cw.

Habitat.—With sponges and algae.

Remarks.—This monospecific genus previously known from the West Indies (Jamaica, Puerto Rico, St. Thomas and Trinidad); in shallow water. This constitutes the first record for Panama and Central America.

Family Xanthidae

Panopeus occidentalis Saussure, 1857

Material.—Stations 1–5; all months sampled; 96 individuals.

Measurements.—Males, 4.0 to 30.5 mm cw; females, 6.0 to 28.8.

Habitats.—On sand, shell, rock and gravel bottoms, around sponges, mangrove roots, pilings; in *Thalassia* (and algae) in the Bahamas (Garty 1978) and Colombia (Lemaitre 1981).

Remarks.—Most specimens from station 1 (65%) in day trawls 88%; see also observations by Oliveira (1940). Ovigerous females in July, September, and October. This abundant xanthid ranges from Bermuda, North Carolina to Brazil including the West Indies; intertidal to 18 m. Williams (1965) provides a synopsis on the biology of this species.

Pilumnus dasypodus Kingsley, 1879

Material.—Station 5; Aug; one individual.

Measurements.—One ovigerous female, 7.5 mm cw.

Habitat.—Reported on sponges from pilings, jetties and buoys (Abele 1970).

Remarks.—Ranges from North Carolina to the Gulf of Mexico, and the West Indies to Brazil including Colombia; to 29 m. Williams (1965) has summarized the ecology of this species. (Note: two other *Pilumnus* were originally identified [KLH] in Panama as *P. reticulatus* Stimpson [2 specimens] and *P. pannosus* Rathbun [9 specimens]; however, these were lost in transport).

Discussion

Of the 58 decapod species discussed here, five or 8.6% represent new records for Caribbean Panama and of these, one (*Cyrtoplax spinidentata*), represents a new record for Central America. Both of the two stomatopod species were previously known from Central American waters. No endemics were found.

Although our collection is only a small percentage of the total decapod fauna of Panama (estimated to be 1400 species by Abele [1972]), we believe that we have good coverage of the grassbed fauna. Those species missed will be mostly infaunal, such as alpheids and stomatopods, or rare species, especially those active at night.

The species treated here show close affinities with the Carolinian fauna treated by Williams (1965). For example 34 (59%) of the species collected in Panama

Table 2.—Summary of parasitic infestations during 1974–75 sampling period.

Species infested	# of individuals*	Pertinent data
Ambidexter symmetricus	1	1 ♀, 5.8 mm cl; Station 1 May
Callinectes sapidus	17	17 ♀, 53.9–91.8 mm cw Aug, Sept, Oct, Dec, Feb Mar, Apr, May; Stations 1, 2, 3, & 5
Cronius tumidulus	2	1 ♂, 1 ♀, 15.8, 18.2 mm cw Aug and May; Stations 1 and 2
Microphrys bicornutus	3	2 ♂, 1 ♀, 8.3–9.1 mm cw Oct, Mar and May; Stations 1, 2 & 3
Panopeus occidentalis	1	1 ♀, 8.8 mm cw Aug, Station 1

* Note: Rhizocephalan occurrences for all species except *A. symmetricus*. One processid with bopyrid isopod (branchial).

grassbeds are also found off the Carolinas (Williams 1965). Thirty-seven (64%) of our species are known from Bermuda (Markham and McDermott 1981). Most of our species are, however, restricted to tropical, subtropical and warm temperate waters. This is exemplified by the fact that only two of our species (3.4%) show up on Williams (1974*a*) check list of the decapods of the northeastern United States (New Jersey to Maine). In addition 14 species (24%) are shared with the results of Heck's (1979) trawling study in turtlegrass beds of the northwestern Gulf of Mexico, while only two species (3.4%) are shared with the decapods collected in a similar trawling study in eelgrass beds of the lower Chesapeake Bay (Heck and Orth 1980).

Acknowledgments

We thank L. G. Abele, R. H. Gore, and F. A. Chace, Jr. for their constructive criticisms of earlier drafts of the paper. Species identifications were gladly given by Drs. Lawrence G. Abele, Florida State University (Decapods) and Patsy McLaughlin, Florida International University (hermit crabs). Support for this work was provided by the Department of Biological Science (Florida State University), the Department of Zoology (University of Maryland), by a Smithsonian Predoctoral Fellowship to one of us (KLH) and by the Division of Environmental Research, Academy of Natural Sciences of Philadelphia.

Literature Cited

Abele, L. G. 1970. The marine decapod (Crustacea of the northwestern Gulf of Mexico.—M.S. thesis, Florida State University, Tallahassee, 137 pp.

———. 1972a. Comparative habitat diversity and faunal relationships between the Pacific and Caribbean decapod Crustacea of Panama.—Ph.D. dissertation, University of Miami, Florida 124 pp.

———. 1972b. Comparative habitat diversity and faunal relationships between the Pacific and Caribbean Panamanian decapod Crustacea: a preliminary report with some remarks on the crustacean fauna of Panama.—Bulletin of the Biological Society of Washington 2:125–138.

———, and N. Blum. 1977. Ecological aspects of the freshwater decapod crustaceans of the Perlas Archipelago, Panamá.—Biotropica 9:239–252.

———, and B. E. Felgenhauer. 1982. Decapoda.—*In:* S. P. Parker, ed., Synopsis and classification of living organisms, Volume 2, pp. 296–326. McGraw-Hill, New York.

Berrill, M. 1975. Gregarious behavior of the spiny lobster, *Panulirus argus* (Crustacea, Decapoda).—Bulletin of Marine Science 25:515–522.

Biffar, T. A., and A. J. Provenzano, Jr. 1972. Biological results of the University of Miami Deep-Sea expeditions. 94. A reexamination of *Dardanus venosus* (H. Milne Edwards) and *D. imperator* (Miers), with a description of a new species of *Dardanus* from the western Atlantic (Crustacea, Decapoda, Diogenidae).—Bulletin of Marine Science 22:775–805.

Bowman, T. E., and L. G. Abele. 1982. Classification of the recent Crustacea.—*In:* L. G. Abele (ed.) The Biology of Crustacea, pp. 1–28, Academic Press, New York.

Bryce, G. W., Jr. 1961. Larval development of *Tozeuma carolinense* Kingsley, including ecological notes on adults.—M.S. thesis, University of North Carolina, Chapel Hill, North Carolina 59 pp.

Camp, D. K. 1973. Stomatopod Crustacea.—Memoirs of the Hourglass Cruises, Marine Research Laboratory, Florida Department of Natural Resources, St. Petersburg, Florida 3(2), 100 pp.

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).—Smithsonianian Contributions to Zoology 98, 179 pp.

Coutière, H. 1909. The American species of snapping shrimps of the genus *Synalpheus*.—Proceedings of the U.S. National Museum 36:1–93.

Davis, G. E. 1971. Aggregations of spiny sea urchins, *Diadema antillarum*, as shelter for young spiny lobsters, *Panulirus argus*.—Transactions of the American Fisheries Society 100:586–587.

———. 1981. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management.—Fishery Bulletin 78:979.

Ewald, J. J. 1969. Observations on the biology of *Tozeuma carolinense* (Decapoda, Hippolytidae) from Florida, with special reference to larval development.—Bulletin of Marine Science 19: 510–549.

Felder, D. L. 1973. An annotated key to crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico.—Publication No. LSU-56-73-02 of the Center for Wetland Resources, L.S.U., Baton Rouge, Louisiana. 103 pp.

Gárcia-Gómez, J. 1982. The Provenzanoi group of hermit crabs (Crustacea, Decapoda, Paguridae) in the western Atlantic Part I. *Pagurus maclaughlinae*, a new species.—Bulletin of Marine Science 32:647–655.

Garth, J. S. 1948. The Brachyura of the "Askoy" Expedition with remarks on carcinological collecting in the Panama Bight.—Bulletin of the American Museum of Natural History 92(1): 1–66.

———. 1958. Brachyura of the Pacific coast of America, Oxyrhyncha.—Allan Hancock Pacific Expeditions. 21(1):1–499.

———. 1978. Marine biological investigations in the Bahamas. 19. Decapoda Brachyura.—Sarsia 63:317–333.

Glynn, P. W. 1972. Observations on the ecology of the Caribbean and Pacific coasts of Panama.—Bulletin of the Biological Society of Washington 2:13–30.

Gore, R. H. 1981. Three new shrimps, and some interesting new records of decapod Crustacea from a deep-water coral reef in the Florida Keys.—Proceedings of the Biological Society of Washington 94(1):135–162.

———. 1982. Porcellanid crabs from the coasts of Mexico and Central America (Crustacea: Decapoda: Anomura).—Smithsonian Contributions to Zoology 363:1–34.

———, and L. G. Abele. 1976. Shallow water porcelain crabs from the Pacific and adjacent Caribbean waters (Crustacea: Anomura: Porcellanidae).—Smithsonian Contributions to Zoology 237, 30 pp.

———, and L. E. Scotto. 1979. Crabs of the family Parthenopidae (Crustacea: Brachyura: Oxyrhyncha) with notes on specimens from the Indian River region of Florida.—Memoirs of the Hourglass Cruises, Marine Research Laboratory, Florida Department of Natural Resources, St. Petersburg, Florida 3(6):98 pp.

Greening, H. S., and R. J. Livingston. 1982. Diel variation in the structure of seagrass-associated epibenthic macroinvertebrate communities.—Marine Ecology Progress Series 7:137–156.

Haig, J. 1960. The Porcellanidae (Crustacea, Anomura) of the eastern Pacific.—Allan Hancock Pacific Expeditions 24:1–440.

———. 1962. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916 LXXIX: Porcellanid crabs from Eastern and Western America.—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbehavn 124:171–192.

Hazlett, B. A. 1979. Individual distance in Crustacea, III. The spider crab *Microphrys bicornutus*.—Zeitschrift fur Tierpsychologie 49:65–70.

Heck, K. L., Jr. 1977. Comparative species richness, composition, and abundance of invertebrates in Caribbean seagrass (*Thalassia testudinum*) meadows (Panama).—Marine Biology 41:335–348.

———. 1979. Some determinants of the composition and abundance of motile macroinvertebrate species in tropical and temperate turtlegrass (*Thalassia testudinim*) meadows.—Journal of Biogeography 6:183–200.

———, and G. S. Wetstone. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows.—Journal of Biogeography 4:135–142.

———, and R. J. Orth. 1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay—decapod Crustacea.—Estuaries 3:289–295.

Holthuis, L. B. 1958. West Indian crabs of the genus *Calappa*, with a description of three new species.—Studies of the Fauna of Curacao and other Caribbean Islands 8:146–180.

———. 1949. The caridean Crustacea of the Canary Islands.—Zoologische Mededelingen 30:227–255.

———. 1959. The Crustacea Decapoda of Suriname (Dutch Guiana).—Zoologische Verhandelingen 44:1–296.

Rhandler, N. A. 1964. Sponge as a shelter for young spiny lobsters.—Transactions of the American Fisheries Society 93:204.

Ledoyer, M. 1959. Les Caridea de la frondaison des herbiers de phanérogames de la région de Tuléar.—Recueil des Travaux de la Station Marine d'Endoume (Supplement) 8:63–123.

Lemaitre, R. 1981. Shallow-water crabs (Decapoda, Brachyura) collected in the southern Caribbean near Cartagena, Colombia.—Bulletin of Marine Science 31:234–266.

———, P. A. McLaughlin, and J. Gárcia-Gómez. 1982. The Provenzanoi group of hermit crabs (Crustacea, Decapoda, Paguridae) in the western Atlantic. Part IV. A review of the group, with notes on variations and abnormalities.—Bulletin of Marine Science 32:670–701.

Lyons, W. G. 1970. Scyllarid lobsters (Crustacea, Decapoda).—Memoirs of the Hourglass Cruises, Marine Research Laboratory, Florida Department of Natural Resources, St. Petersburg, Florida 1(4):74 pp.

McLaughlin, P. A. 1975. On the identify of *Pagurus brevidactylus* (Stimpson) (Decapoda: Paguridae), with the description of a new species of *Pagurus* from the western Atlantic.—Bulletin of Marine Science 25:359–376.

———, and A. J. Provenzano, Jr. 1974. Hermit crabs of the genus *Paguristes* (Crustacea: Decapoda: Diogenidae) from the western Atlantic. Part. II. Descriptions of six new species.—Bulletin of Marine Science 25:359–376.

Manning, R. B. 1961. A redescription of the Palaemonid shrimp, *Leander paulensis* Ortmann, based on material from Florida.—Bulletin of Marine Science 11:525–536.

———. 1969. Stomatopod Crustacea of the western Atlantic.—Studies in Tropical Oceanography 8:1–380.

———, and F. A. Chace, Jr. 1971. Shrimps of the family Processidae (Crustacea, Decapoda, Caridea) from the northwestern Atlantic.—Smithsonian Contributions to Zoology 89, 41 pp.

———, and L. B. Holthuis. 1981. West African brachyuran crabs (Crustacea: Decapoda).—Smithsonian Contributions to Zoology 306, 379 pp.

Markham, J. C., and J. J. McDermott. 1981. A tabulation of the Crustacea decapoda of Bermuda.—Proceedings of the Biological Society of Washington 93:1266–1276.

Miles, R. M. 1951. An analysis of "trashfish" of shrimp trawlers operating in Apalachicola Bay and adjacent Gulf of Mexico.—M.S. thesis, Florida State University, Tallahassee, 45 pp.

Oliveira, L. P. H. de. 1940. Observações preliminares sobre a biologia dos Crustaceos do genero *Panopeus* Milne Edwards, 1834.—Memorias do Instituto Oswaldo Cruz, Rio de Janeiro 35:153–171.

Park, J. R. 1969. A preliminary study of portunid crabs in Biscayne Bay.—Quarterly Journal of the Florida Academy of Science 32:12–20.

Pearse, A. S., J. J. Humm, and G. W. Wharton. 1942. Ecology of sand beaches at Beaufort, NC.—Ecological Monographs 12:135–190.

Perez Farfante, I. 1969. Western Atlantic shrimps of the genus *Penaeus*.—Fishery Bulletin 67:461–591.

———. 1971. Western Atlantic shrimps of the genus *Metapenaeopsis*, with descriptions of three new species (Crustacea: Decapoda: Penaeidae).—Smithsonian Contributions to Zoology 79, 37 pp.

Powers, L. W. 1977. A catalogue and bibliography to the crabs of the Gulf of Mexico.—University of Texas Marine Science Institute, Contribution to Marine Science Supplement No. 20, 190 pp.

Provenzano, A. J., Jr. 1959. The shallow-water hermit crabs of Florida.—Bulletin of Marine Science 9:349–420.

Rathbun, M. J. 1918. The grapsoid crabs of America.—Bulletin of the U.S. National Museum 97: 1–461.

———. 1925. The spider crabs of America.—Bulletin of the U.S. National Museum 152:1–613.

———. 1930. The candroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae.—Bulletin of the U.S. National Museum 152:1–609.

———. 1937. The oxystomatous and allied crabs of America.—Bulletin of the U.S. National Museum 166:1–278.

Rouse, W. L. 1970. Littoral Crustacea from southwest Florida.—Quarterly Journal of the Florida Academy of Science 32:127–152.

Schnever, G. 1978. *In situ* observations on the behaviour of and biology of the tropical spider crab *Stenorhynchus seticornis* Herbst (Crustacea, Decapoda, Brachyura).—*In:* D. S. McLusky and A. J. Berry (eds.), Physiology and behaviour of marine organisms, pp. 297–302, Pergammon Press, New York.

Shoup, J. B. 1968. Shell opening by crabs of the genus *Calappa*.—Science 160:887–888.

Vermeij, G. J. 1982. Gastropod shell form, breakage and repair in relation to predation by the crab *Calappa*.—Malacologia 23:1–12.

Voss, G. L. 1956. Protective coloration and habitat of the shrimp *Tozeuma carolinensis* Kingsley, (Caridea: Hippolytidae).—Bulletin of Marine Science 6:359–363.

Wass, M. L. 1955. The decapod crustaceans of Alligator Harbor and adjacent inshore water of northwestern Florida.—Quarterly Journal of the Florida Academy of Science 18:129–176.

Weinstein, M. P., and K. L. Heck, Jr. 1979. Ichthyofauna of seagrass Meadows along the Caribbean coast of Panama and in the Gulf of Mexico: composition, structure and community ecology.—Marine Biology 50:97–107.

Williams, A. B. 1965. Marine decapod crustaceans of the Carolinas.—Fishery Bulletin 65:1–298.

———. 1974a. Marine flora and fauna of the northeastern United States: Crustacea: Decapoda.—NOAA Technical Report NMFS Circ-389, 50 pp.

———. 1974b. The swimming crabs of the genus *Callinectes* (Decapoda: Portunidae).—Fishery Bulletin 72:685–798.

Yang, W. T. 1967. A study of zoeal, megalopal and early crab stages of some oxyrhynchous crabs (Crustacea: Decapoda).—Ph.D. diss., Univ. of Miami, Florida. 459 pp.

(LDC) Department of Zoology, University of Maryland, College Park, Maryland 20742; (KLH) Division of Environmental Research, The Academy of Natural Sciences of Philadelphia, 19th and the Parkway, Philadelphia, Pennsylvania 19103.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 225–237

STUDIES OF NEOTROPICAL CADDISFLIES, XXXIV: THE GENUS *PLECTROMACRONEMA* (TRICHOPTERA: HYDROPSYCHIDAE)

Oliver S. Flint, Jr.

Abstract.—The new species, *P. lisae*, is described from Mexico and also recorded from Costa Rica. The distributions of the three known species are reviewed and figures of wings and male genitalia given. The larva and pupa of *P. lisae* are described and figured. They inhabit long, silk and sand tubes attached to rocks in the bottom gravel in lotic situations and appear to be strongly predatory. No traces of any capture net were found. A key is presented to the larvae of the six Neotropical Macronematinae genera in which this stage is known.

Plectromacronema was established in 1906 by Georg Ulmer for the new species *comptum*, taken at Santarem, Brazil. Subsequently the species was recorded from Venezuela (Navás 1924), Guyana (Mosely 1931), and Suriname (Flint 1974). Nathan Banks (1920) described the new genus and species *Podomacronema subfuscum* from northeastern Argentina. I synonymized this genus in 1967 with *Plectromacronema*, but recognized the distinctness of the two species. The genus has contained until now these two species, one from northern South America, the other from northeastern Argentina.

In the summer of 1966, when on a field trip to Mexico and Guatemala, my daughter Elizabeth (familiarly Lisa) called my attention one dusk to a swarm of large, dark caddisflies active over a pool on a small stream in the coastal mountains of Chiapas, Mexico. As soon as one was caught, it was obvious to me that these must be a species of *Plectromacronema*, but far from the known range of the genus. A good series was obtained on this occasion, and the next summer a single example was beaten from a riverside tree in Costa Rica. Attempts on several occasions to find the immature stages of the genus at the Chiapas site were unsuccessful.

In May of 1981, Dr. Paul J. Spangler, my wife and I travelled to Mexico, where, at the invitation of Dr. Joaquin Bueno S., we helped with a field course in aquatic insects, then all travelled into southern Chiapas, collecting there. At the Río Lacanja, 22 km east of Ocosingo on the road to Palenque, we discovered some interesting long, silken caddisfly tubes attached to large stones in the river bottom. Many of them still contained hydropsychid larvae, and a few mature pupae. That night many females (and a teneral male) of the new species of *Plectromacronema* came to our lights. Study of the metamorphotypes in Washington proved that at long last the larvae and pupae, previously unknown, of this genus were firmly associated with the adults.

Plectromacronema Ulmer

The three species of the genus fall into two well defined groups based on leg structures. *Plectromacronema comptum* is alone in having a spur count of 1,4,3

Figs. 1–3. Wings: 1, *Plectromacronema comptum*; 2, *P. subfuscum*; 3, *P. lisae*.

(Ulmer claimed a second spur on the foreleg, but I can not see anything macroscopic), and in having the basitarsus of the foreleg elongate and nearly cylindrical. The other two species have a spur count of 2,4,4, and the basitarsus of the foreleg elongate, but at midlength greatly widened and flattened. However, the general appearance and uniformity of the male genitalia in all three species precludes the restoration of two genera for the two species groups.

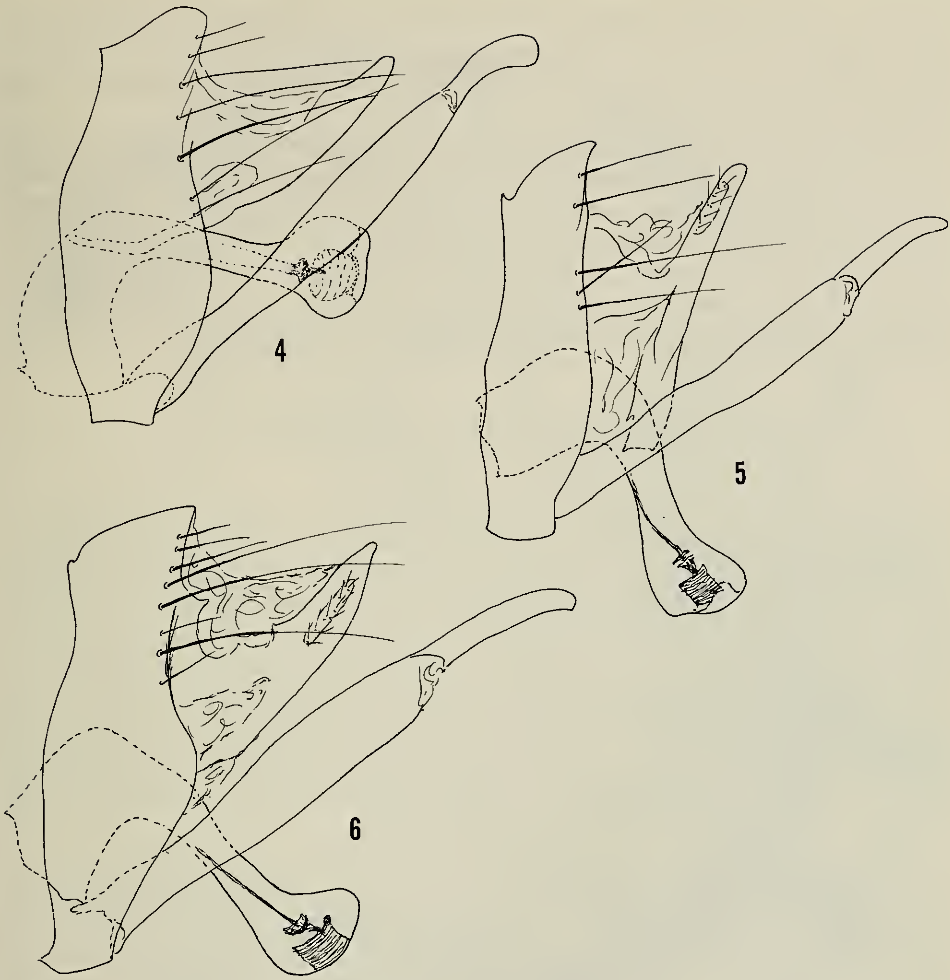
The three species are easily distinguished by the color patterns of the forewings, even though there is considerable variation in the exact numbers and placement of the spots. Male genitalia differ very slightly between the three species, with the tip of the aedeagus offering the best characters.

Plectromacronema comptum Ulmer
Figs. 1, 4

Plectromacronema comptum Ulmer, 1906:63–65.—Fischer, 1963:163–164.—Flint, 1974:114–115; 1978:395, 403.

This species is easily recognized by the coloration which shows three clusters of pale marks on the front margin of the forewing. Posteriad of these pale marks are many scattered, small, variable, pale spots.

Biology.—The immature stages of this species are unknown. My few experiences with adults, as well as collection records, indicate that the species inhabits large rivers. Three collection records (Flint 1974) contain the note "on water surface," in the evening, or during rainfall.



Figs. 4–6. Male genitalia, lateral: 4, *Plectromacronema comptum*; 5, *P. subfuscum*; 6, *P. lisae*.

Distribution.—In the literature the species is recorded from Brazil, Guyana, Surinam, and Venezuela. The following records either add new countries or major political subdivisions. French Guiana, 60 mi up Maroni River, Wm. Schaus, 1 ♀. Venezuela, Edo. Bolivar, Anacoco (6°5′N, 61°8′W), 60 m, 10–30 Aug 1979, 3 ♀ (IZAM); Río Cuyuni, El Dorado, 10 Feb 1976, C.M. & O.S. Flint, Jr., 1 ♀.

Plectromacronema subfuscum (Banks)
Figs. 2, 5

Plectromacronema comptum Ulmer.—Ulmer, 1913:392–393 (Misidentification).
Podomacronema subfuscum Banks 1920:356.—Fischer, 1963:164.
Plectromacronema subfuscum (Banks).—Flint, 1967:12.

In coloration this species has a rather dark anterior margin of the forewing, with several distinct, white spots in the apical fourth. The pale marks on the basal three-fourths of the wing have a distinctive, blurred appearance.

Biology.—The immature stages of this species are also unknown. I have taken adults at lights near small- to medium-sized watercourses, generally with alternating riffles and pools. Collections at light are almost exclusively females, rarely with teneral males appearing.

Distribution.—This species is found well to the south of the ranges of the other two species. It has only been recorded from the Province of Misiones in Argentina, where I have also made several collections. The following are new country records: Brazil, Edo. Santa Catarina, Nova Teutonia (27°11′S, 52°23′W), 28 Oct–2 Nov 1939, F. Plaumann, 1 ♂, 12 ♀ (MCZ, USNM); same, but 7 Jan 1964, 1 ♂. Uruguay, Dpto. Artigas, San Gregorio, 29 Nov 1959, C. S. Carbonell, 4 ♂, 10 ♀ (FHCU, USNM). Dpto. Paysandú, Puerto Pepe-Ají, 1 Dec 1959, C. S. Carbonell, 11 ♀ (FHCU, USNM).

Plectromacronema lisae, new species
Figs. 3, 6–23

This species is most closely related to *P. subfuscum,* with which it shares a similar spur count and structure of the foreleg, but from which it is easily distinguished by coloration. The pale spots are clear and distinct, and there is a regular series of pale marks along the costal margin which are not aggregated into three large marks as they are in *P. comptum,* nor limited to three large spots in the apical fourth as they are in *P. subfuscum.* Differences in the male genitalia between the three species are minute and seem to be primarily in the shape of the apex of the aedeagus. In *P. comptum* the tip is more rounded both above and below the stem; in the other species the tip is more enlarged above the stem than below. In *P. lisae* this enlargement is rather abrupt and almost as high as long, but in *P. subfuscum* it is distinctly longer than high.

Adult.—Length of forewing, ♂ 14–18 mm, ♀ 13–16 mm. Color fuscous; antennae basally golden yellow, legs stramineous, basitarsus of foreleg infuscate; forewing fuscous marked with small hyaline spots, those of costal margin being considerably enlarged. Fifth abdominal sternum anterolaterally with oval, clear, raised boss. Male genitalia: Ninth segment annular, slightly produced dorsomesally. Tenth tergum elongate, with membranous areas dorsomesally and laterobasally; apices pointed, deeply divided dorsomesally. Clasper elongate, slender, basal segment nearly parallel-sided; apical segment terete, clearly separated from basal segment. Aedeagus with erect, broad, basal section, stem at right angles to base; apex with ventral margin confluent with base of stem, dorsal margin produced dorsad, about as high as long; internally with single duct with distinct collar subapically, and ending in cylindrical cavity extending inward from center of posterior surface.

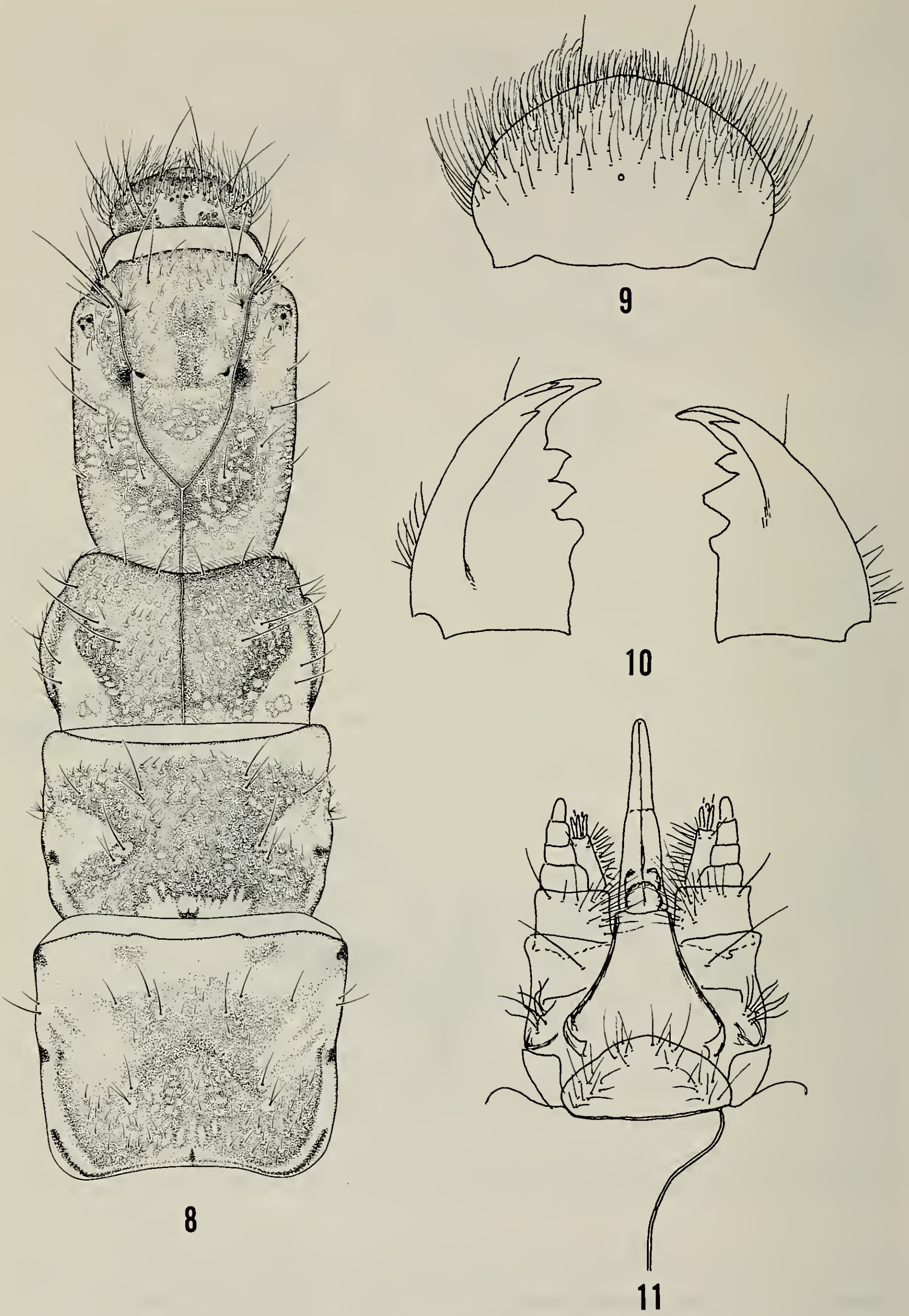
Larvae.—Length to 16 mm, width to 3 mm. Sclerites yellow with fuscous markings.

Head.—Elongate, about 1½ times as long as broad. Color basically yellow, infuscate dorsally with distinct, pale, muscle scars. Frontoclypeus with anterior margin convex; anterior fourth with small accessory setae, with anterolateral palmate hairs. Gena with surface smooth, with few small setae; ventrally lacking stridulatory grooves, with row of stout, spicate setae along each side; ventral ecdysal line lacking on one side of anterior apotome. Labrum rounded anteriorly,

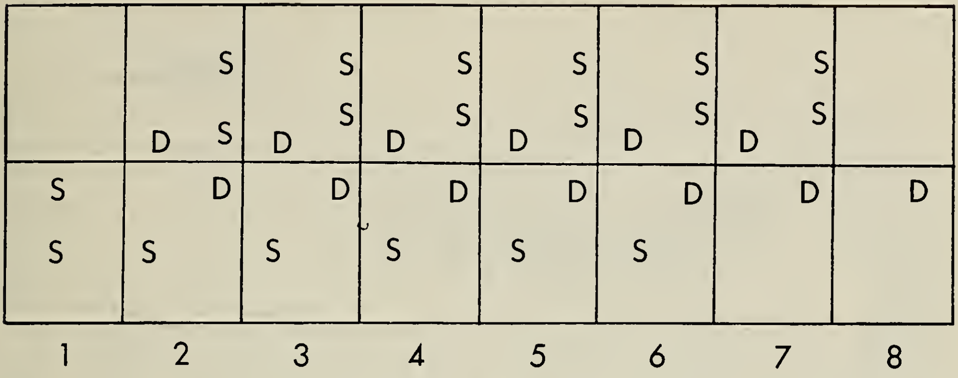
Fig. 7. *Plectromacronema lisae*, larva, lateral.

almost semicircular in outline; anterior half hairy with anterior margin very hairy. Mandibles with strong mesal teeth and multiple, sharp, apical teeth; no mesal brushes. Submentum evenly convex anteriorly; setate laterad. Labium very long, slender, sclerotized.

Thorax.—Pronotum dark mesally with pale muscle scars, paler laterad; meso- and metanota darkest mesally, paler laterally. Pronotum with anterior margin bearing fringe of slender, short hairs; surfaces of all nota smooth, with scattered



Figs. 8–11. *Plectromacronema lisae*, larva: 8, head and thoracic nota, dorsal; 9, labrum, dorsal; 10, mandibles, dorsal; 11, maxillolabium and anterior margin of genae, ventral.



1	2	3	4	5	6	7	8
	S D S	S D S	S D S	S D S	S D S	S D S	
S S	D S	D S	D S	D S	D S	D	D

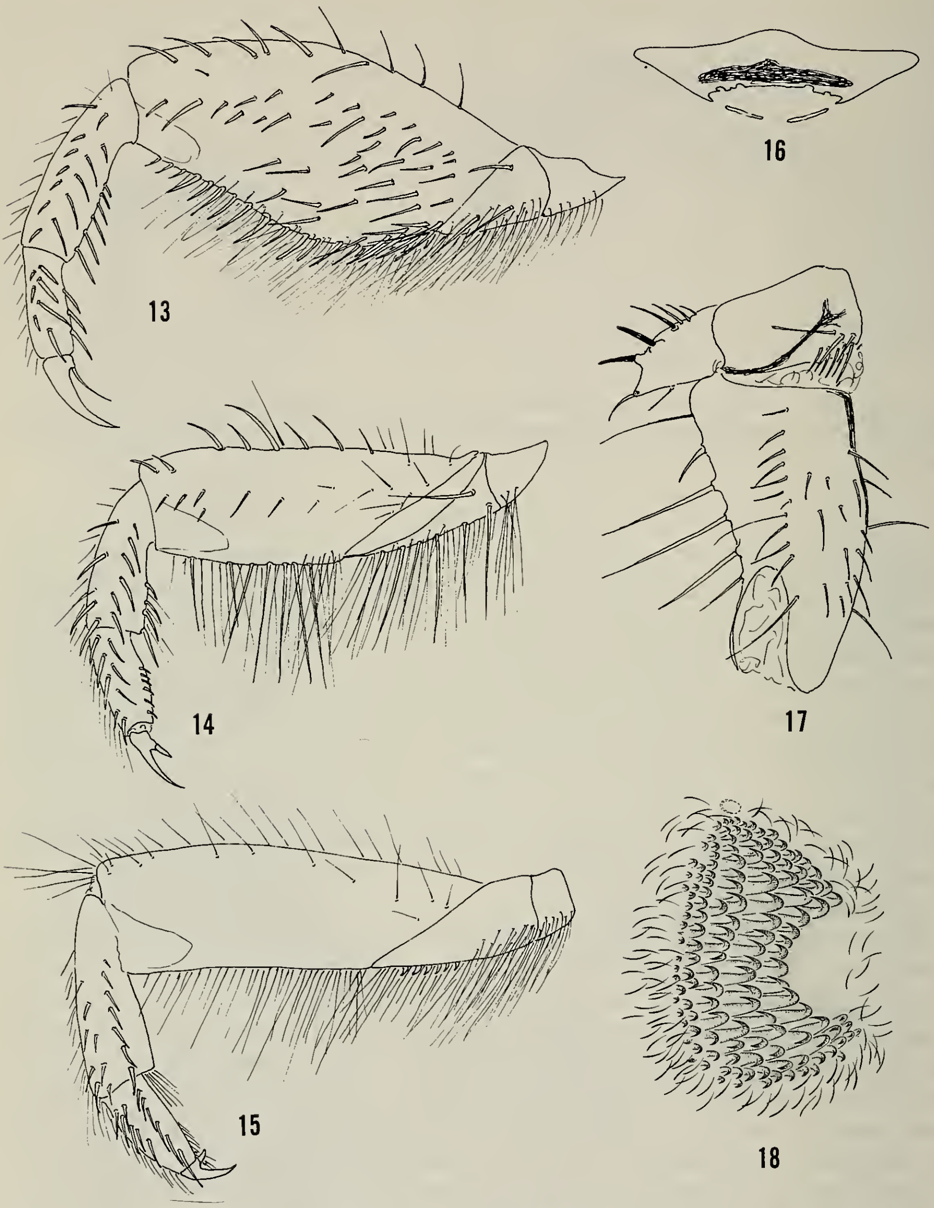
Fig. 12. *Plectromacronema lisae,* schematic gill diagram of lateral aspect of first 8 abdominal segments. S = a single, long, central stalk with lateral filaments; D = 2 S-type gills with adjacent bases.

small, decumbent hairs and few erect setae. Prosternite transverse, narrow, with dark central mark; meso- and metasterna unornamented. Foretrochantin broad, tapering to blunt point apically, with 3 or 4 large, bladelike setae dorsally, arising from large bases. All legs nearly equal in length, forefemur distinctly widened. Foreleg with inner face of femur, tibia and tarsus with rows of enlarged, bladelike setae; ventral margin of femur with fringe of long hairs and row of short, bladelike setae. Midleg with inner face of tibia and tarsus with rows of enlarged, bladelike setae; ventral margin of femur with fringe of long hairs, dorsal margin with scattered spinous setae. Hindleg with inner face of tibia and tarsus bearing rows of short, bladelike setae; ventral margin of femur with sparse fringe of long hairs; ventral margin of trochanter with row of very short, enlarged setae in fringe of long hairs. No thoracic gills.

Abdomen.—Gills consisting of central stem bearing many lateral filaments; placed as in Fig. 12; double gills above lateral line often with bases separated, very small posteriad and virtually lost in lateral line. Lateral line lacking on segments 1–3; very long and dense on segments 4–7, curving ventrad anteriorly on segment 8, with complete fringes over dorsum along posterior of segments 4 and 5. Integument with many, darkened, decumbent setae, and few, scattered, erect setae. Segments 2–8 with paired, ventrolateral pockets (generally appearing to be slightly invaginated with posterior face partially folded over opening, occasional examples appear to have pockets everted and almost proleg-like with covering of crotchets), bearing dense rows of spines whose tips are hooked anteriad. Sternum 9 bearing pair of ovoid sclerites, with posteriorly directed, bladelike setae on basal ¾, posterior fourth with long setae; ventrolaterally with long setae. Anal gills, if present, not showing. Anal proleg with scattered setae; anal brush reduced to 4 long setae; anal claw sharply angled ventrad, ventral sole plate with dense brush of dark setae.

Pupa.—Length to 16 mm, width to 3 mm.

Head.—Labrum semicircular with rounded basolateral lobes; basolateral lobe with 5–6 setae, anterolateral margin with 7–10 setae each side. Mandibles scler-



Figs. 13–18. *Plectromacronema lisae,* larva: 13, foreleg, inner face; 14, midleg, inner face; 15, hindleg, inner face; 16, prosternite; 17, propleuron and coxa, lateral; 18, abdominal hook-pocket, anterior to left.

otized, elongate, almost parallel-sided, inner margin coarsely serrate; basolateral surface with brush of setae. Face with scattered setae; vertex with brush of about 12 setae; basal antennal segment with brush of about 10 setae.

Thorax.—Meso- and metanota with 2 pairs of short, submesal setae, one pair near anterior margin, other at midlength. Coxae of all legs with apical tuft of dark setae. Midleg with tibia and tarsus flattened and broadened; tarsus with short, but dense, lateral fringe.

Abdomen.—Segments 2–7 bearing lateral gills, those on 4–7 being somewhat united basally; with ventral gills on 2–7. Hook plates anteriorly on segments 3–8, becoming progressively more erect posteriad; posterior plate on segment 3. All segments with few erect setae posteriad; segments 3–7 with band of scattered, posteriorly-directed, spinous setae along posterior. Eighth sternum with pair of oval sclerites bearing many, posteriorly-directed, bladelike setae. Apical processes elongate, slightly arcuate, rugose, apex broad with thin plate dorsally; with scattered setae.

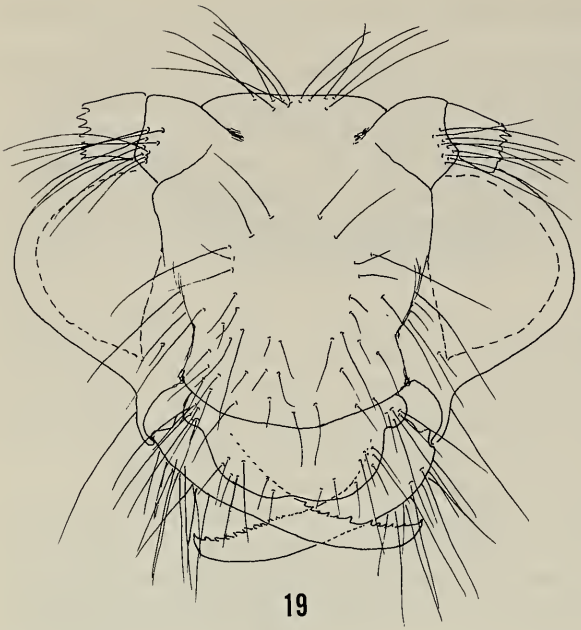
Material.—Holotype, male: Mexico, Edo. Chiapas, rt. 185 km 35 [12 km north Arriaga], 7–8 July 1966, Flint & Ortiz. USNM Type 100590. Paratypes: same data, 19 ♂; Río Lacanja, 22 km north Ocosingo, 19 May 1981, C.M. & O.S. Flint, Jr., 1 ♂, 21 ♀; same, but J. Bueno & H. Velasco, 3 ♂, 8 ♀ (IBUNAM). Costa Rica, [Pcia. Guanacaste], Río Corobici, [3.4 mi north] Las Canas, 15 June 1967, Flint & Ortiz, 1 ♂. Other: Río Lacanja site, 20 larvae, 7 pupae.

Biology.—The three collections of this species all were made at fast-flowing, clear, cool streams of apparent good water quality with bottom of sand, gravel, large stones and boulders. In size they varied greatly; the stream at the type-locality is barely half a meter wide by a few decimeters deep, the Río Lacanja is about 10 meters wide by half a meter deep, and the Río Corobici perhaps about 15 meters wide.

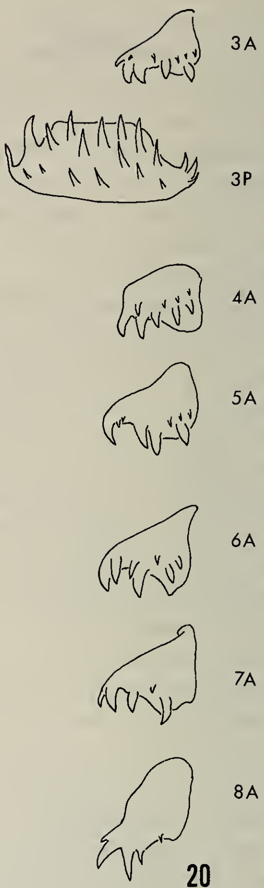
The adult males of the type collection were taken just before dusk, flying in a swarm up to a meter or so above the water surface over a small, sand-bottomed pool. The Costa Rican male was beaten from a low branch of a riverside tree, and the Río Lacanja adults all came to an ultraviolet light after dark.

The larvae were found in the Río Lacanja inhabiting long silken tubes incorporating sand grains and small pebbles which were partially attached to large rocks resting in the bottom sand and gravel. They were most frequently found where the current was the strongest, flowing between contiguous rocks in a rather coarse sand mixture. The tubes did not extend noticeably above the level of the sand, and their posterior ends were usually free of the rock, although for most of their length they were attached to the rock. When removed from the water many larvae crawled from their tubes, as did some of the mature pupae from the bottoms of their tubes.

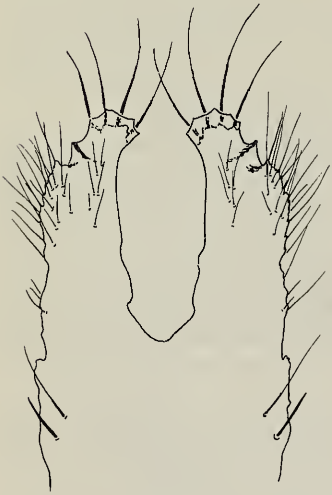
In the laboratory, the long tubes proved to be difficult to interpret, there being no way to be absolutely certain as to which was anterior or posterior, nor if the whole tube was present. The longest tube was 70 mm long and from 5–10 mm in diameter. The inner surface was formed of a dense mat of silk to the outside of which was cemented sand grains. Some parts were only silken, but gave the appearance of having been attached to a smooth object, probably the host rock or a large pebble. The inner diameter of the tube appears to be slightly larger than the diameter of the larva. Several tubes showed a flared, silk-lined opening at one end, which I interpret to be the upper end. In no tube could I find any type of structured catching net. The pupae inhabit tubes appearing identical to those of the larvae. In only one of five tubes still containing pupae did I find a mass of debris behind the pupa with admixed larval sclerites; in all the other tubes this region was open and the sclerites gone. Those tubes that appeared



19



20



21

22

Figs. 19–22. *Plectromacronema lisae*: 19, pupal head, anterior; 20, pupal hook plates, with abdominal segment number and anterior or posterior position; 21, pupal apical appendages, dorsal; 22, larval anal proleg, lateral.

Fig. 23. *Plectromacronema lisae*, habitat, Río Lacanja.

nearly complete contained the pupa near the posterior end (to judge from the orientation of the pupa). There was no solid anterior closure, but the anterior portion was loosely clogged with sand and debris, sometimes with a loose mesh of silken strands at the bottom of this sand. Below this, there was a long portion of the tube, one to three times the length of the pupa, that was clean and in which the pupa apparently moved.

Four larval guts were cut open and the contents examined. One was mostly empty, but did contain the recognizable remains of a small larva of a polycentropodid caddisfly and a chironomid head capsule, plus a quantity of an amorphous blackish material. A second was filled with the blackish material, recognizable sclerites of small arthropods, and apparently large pieces of arthropod cuticle. The third contained only a very small amount of fine blackish matter, and the fourth, larger quantities of the same. In conjunction with the strongly spined legs, rows of spines on the venter of the head, and sharply pointed mandibles, it seems probable that the larvae are strongly predatory, but the brushes on the labrum and femora suggest that they may also brush fine particulate organic matter from the substrate. Perhaps they utilize the silken lining of the tube to strain fine particulate organic matter from the water, in a manner similar to that of the Philopotamidae (Wallace and Malas 1976).

Neotropical Macronematine Larvae

With the discovery and description of the larvae of *Plectromacronema,* only the immature stages of *Centromacronema, Pseudomacronema,* and *Neoleptonema* remain undescribed of the nine Neotropical genera of Macronematinae. It is quite probable that the larvae of *Neoleptonema* will key to *Leptonema,* as the genera are very similar and probably not distinct. It is more difficult to speculate on the appearance of the other two genera. They may well run to couplet 5, or *Centromacronema* may approach the appearance of *Macronema* in couplet 3.

In order to aid in the recognition of the larvae of the Neotropical macronematine genera, I offer the following provisional key which incorporates references to recent descriptions and name changes.

1. Foretrochantin very broad, almost rectangular; forefemur broad and truncate apically; head and thoracic nota very long and slender (Roback 1966, as Hydropsychidae sp.1) .... *Synoestropsis*
– Foretrochantin pointed anteriad; apex of forefemur not broad and truncate; head and thorax not disproportionately elongate 2
2. Abdominal sterna 2–7 with paired, ventrolateral pockets bearing recurved hooks .... *Plectromacronema*
– Abdominal sterna lacking such structures 3
3. Anal proleg very long and slender, jointed in the middle (Flint and Bueno 1982) .... *Macronema*
– Anal prolegs neither exceedingly long nor jointed 4
4. Head without a carina on genae (Flint and Wallace 1980) ..... *Leptonema*
– Head with a carina on genae 5
5. Carinae of genal halves meeting at posterior of frontoclypeus, encircling the frontal area of the head (Wiggins 1977, as *Macronema*) ..... *Macrostemum*
– Carinae on genal halves not meeting on midline of head, frontal area of head open to the posterior (Flint and Wallace 1980) .... *Blepharopus*

Acknowledgments

The species is dedicated with pleasure to my daughter, Mrs. Elizabeth A. Mattingly, whose sharp eyes were instrumental in the initial discovery of this species. The excellent habitus drawings (Figs. 7, 8, 18) were prepared by the departmental staff artist, Mr. Young T. Sohn. The wing photographs are the fine work of Mr. Victor E. Krantz of the National Museum of Natural History.

Material was supplied by: Ing. C. S. Carbonell, Facultad de Humanidades y Ciencias (Departmento de Artropodos), Universidad de la República, Montevideo, Uruguay (FHCU); Dr. Joaquin Bueno Soria, Instituto de Biologia, Universidad Nacional Autonoma de Mexico, Mexico City, Mexico (IBUNAM); Ing. C. J. Rosales, Instituto de Zoologia Agrícola, Facultad de Agronomia, Maracay, Venezuela (IZAM); and Ms. M. Thayer, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ).

Literature Cited

Banks, N. 1920. New neuropteroid insects.—Bulletin of the Museum of Comparative Zoology 64: 299–362.

Fischer, F. C. J. 1963. Hydropsychidae, Arctopsychidae.—Trichopterorum Catalogus IV:1–172.

Flint, O. S., Jr. 1967. Studies of neotropical caddis flies, V: Types of the species described by Banks and Hagen.—Proceedings of the United States National Museum 123(3619):1–37.

———. 1974. Studies of neotropical caddisflies, XV: The Trichoptera of Surinam.—Studies on the Fauna of Suriname and Other Guianas 14(55):1–151.

———. 1978. Studies of neotropical caddisflies, XXII: Hydropsychidae of the Amazon Basin.—Amazoniana 3:373–421.

———, and J. Bueno S. 1982. Studies of neotropical caddisflies, XXXII: The immature stages of *Macronema variipenne* Flint & Bueno, with the division of *Macronema* by the resurrection of *Macrostemum* (Trichoptera: Hydropsychidae).—Proceedings of the Biological Society of Washington, 95:358–370.

———, and J. B. Wallace. 1980. Studies of neotropical caddisflies, XXV: The immature stages of *Blepharopus diaphanus* and *Leptonema columbianum* (Trichoptera: Hydropsychidae).—Proceedings of the Biological Society of Washington 93:178–193.

Mosely, M. E. 1931. Trichoptera and Ephemeroptera of British Guiana, with special reference to the Oxford expedition to British Guiana, 1929.—The Entomologist 64:169–170.

Navás, L. 1924. Quelques insectes de l'Amérique méridionale.—Annales de la Société Scientifique de Bruxelles, Documents et Comptes Rendus 43:249–254.

Roback, S. S. 1966. The Catherwood Foundation Peruvian-Amazon expedition, XI—The Trichoptera larvae and pupae.—Monographs of the Academy of Natural Sciences of Philadelphia 14: 235–303.

Ulmer, G. 1906. Neuer beitrag zur kenntnis aussereuropaeischer Trichopteren.—Notes from the Leyden Museum 28:1–116.

———. 1913. Verzeichnis der südamerikanischen Trichopteren, mit Bemerkungen über einzelne Arten.—Deutsche Entomologische Zeitschrift 1913:383–414.

Wallace, J. B., and D. Malas. 1976. The fine structure of capture nets of larval Philopotamidae (Trichoptera), with special emphasis on *Dolophilodes distinctus*.—Canadian Journal of Zoology 54:1788–1802.

Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera).—University of Toronto Press, Toronto and Buffalo. 401 pp.

Department of Entomology, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 238–249

A REVISION OF THE BOGUEIDAE HARTMAN AND FAUCHALD, 1971, AND ITS REDUCTION TO BOGUEINAE, A SUBFAMILY OF MALDANIDAE (POLYCHAETA)

Paul S. Wolf

Abstract.—*Boguea enigmatica* Hartman, 1945, is redescribed and its known range extended. Notes on its larval development are presented. The description of *Boguella ornata* Hartman and Fauchald, 1971, is emended. Based on these revisions, the family Bogueidae is reduced to Bogueinae, a subfamily of Maldanidae based on morphological and ontogenetic criteria. Keys to the subfamilies of Maldanidae, modified from Fauchald (1977), and to the genera of Bogueinae are given.

Hartman (1945) first described *Boguea enigmatica* from Bogue Sound, North Carolina, as a member of the Oweniidae. Hartman and Fauchald (1971) later described *Boguella ornata* from deep waters off the coast of New England, at which time they also erected the family Bogueidae with *Boguea* as the type-genus. *Boguea enigmatica* and *Boguella ornata* have not been recorded outside of their type-localities.

Superficially the Bogueidae are unique among the polychaetes in possessing avicular (terebelloid) uncini and yet lacking the head modifications typical of other families with avicular uncini (e.g., Terebellidae, Ampharetidae, Sabellidae, and Pectinariidae). However, the following redescription of *Boguea enigmatica* and emended description of *Boguella ornata* show that the Bogueidae share many morphological and ontogenetic characters with the Maldanidae; therefore, Bogueidae is reduced to a subfamily of the Maldanidae.

Due to the apparent disagreements in definitions of life stages (see Bookhout and Horn 1949, and Hermans 1979, for example), it is necessary to define the criteria used in this paper for separating larvae, juveniles, and adults. Specimens are considered larvae if they still contain some yolk material. Depending upon the stage of development, larvae may or may not possess rostrate uncini. Larvae examined range from 2 to about 16 setigers long. Ciliated bands were not seen on any of the larvae examined. Specimens are considered juveniles if they lack yolk material, yet still possess the rostrate uncini in the anterior setigers. Juveniles range from about 15–23 setigers. Adults are those individuals lacking rostrate uncini (except perhaps in far posterior setigers), and ranging from about 23–30 setigers. It should be noted that the above life-stage distinctions pertain only to *Boguea enigmatica* as it is described in this paper.

Bogueinae, new rank

Oweniidae (in part).—Hartman, 1945:42.

Bogueidae.—Hartman and Fauchald, 1971:148.—Fauchald, 1977:135.—Hobson and Banse, 1981:20.

Diagnosis.—Cephalic plaque absent; cephalic keel and ciliated nuchal slits present. Segmental collars absent. Notopodial spines may be present in far posterior setigers. Neurosetae as avicular (terebelloid) uncini, arranged in single or double rows. Pygidium simple or adorned with papillae; anus terminal, without a ventral valve.

Boguea Hartman, 1945

Diagnosis.—Cephalic keel distinct. Body composed of three well defined regions. Uncini from setiger 5, in single rows to setiger 9, then in double rows except in far posterior setigers. Notopodial spines present in far posterior setigers. Pygidium simple, without papillae.

Boguea enigmatica Hartman, 1945

Boguea enigmatica Hartman, 1945:42, pl. 7, figs. 4–6.—Hartman and Fauchald, 1971:148, pl. 23, figs. h–i.

Material examined.—NORTH CAROLINA: Bogue Sound, Summer, 1940, 6–10 ft., sand overlaid with shell fragments, holotype (AHF Poly 0391) and 35 paratypes (AHF Poly 0392); 6 Aug 1962, 2–3 m, sand and shell (primarily *Crassostrea virginica*), 15 specimens (ZMC); 10 May 1972, *ca* 2.5 m, sand and shell, 2 specimens (both gravid, 1 with brood) (ZMC). SOUTH CAROLINA: Sta. 0797(4B), 25 Aug 1977, 31°53′N, 80°46′W, 13 m, sand, 1 juvenile (USNM 059817), 1 juvenile (Texas Instruments collection). GEORGIA: Sta. 0220(5C), 25 Feb 1977, 31°08′N, 80°50′W, 19 m, sand, 1 specimen (Texas Instruments collection); Sta. 0513(5B), 16 May 1977, 31°12′N, 81°08′W, 11 m, sand, 1 specimen (Texas Instruments collection); Sta. 0517(5C), 16 May 1977, 31°08′N, 80°50′W, 14 m, sand, 2 specimens (USNM 059823); 1 juvenile (USNM 059815); 2 specimens (Texas Instruments collection); Sta. 0828(5C), 31 Aug 1977, 31°08′N, 80°50′W, 14 m, sand, 1 juvenile (USNM 059816); Sta. 1263(5B), 31°12′N, 81°08′W, 11 m, sand, 1 specimen (USNM 059822). FLORIDA, Northeast: Sta. 0877(6F), 9 Jan 1977, 30°23′N, 80°18′W, 43 m, sand, 1 juvenile (Texas Instruments collection); Sta. 0862(6B), 31 Aug 1977, 30°23′N, 81°15′W, 15 m, sand, 2 specimens (USNM 059820 and 059821). Tampa Bay: Interstate Electronics Corp. 713TB, Sta. 003, 11 Oct 1979, 27°37.1′N, 82°54.0′W, 12 m, sand-gravel, 10 specimens (2 females); Sta. 004, 11 Oct 1979, 27°37.1′N, 82°55.1′W, 10 m, sand, 4 specimens; Sta. 013, 11 Oct 1979, 27°37.6′N, 82°54.5′W, sand-gravel, 3 specimens; 723TB, Sta. 001, Jan 1980, 27°37.6′N, 82°54.5′W, 13 m, sand, 1 specimen; Sta. 003, Jan 1980, 27°37.1′N, 82°54.0′W, 12 m, sand-gravel, 3 specimens; Sta. 004, Jan 1980, 27°37.1′N, 82°55.1′W, 10 m, sand, 1 specimen; Sta. 006, Jan 1980, 27°36.5′N, 82°53.4′W, 12 m, sand-gravel, 2 specimens. FLORIDA, Southwest: BLM, Sta. 24C, Nov 1980, 25°16.90′N, 83°43.18′W, 88.4 m, medium sand, 1 specimen; Sta. 2101H (MAFLA), Feb 1978, 26°24′59.6″N, 82°15′08.9″W, 11 m, sand, 1 specimen. Pensacola: Interstate Electronics Corportion, 732MO, Sta. 012, June 1980, 30°17.2′N, 87°18.5′W, 6 m, sand, 1 juvenile. ALABAMA: Mobile Bay (Mobil Oil Corporation), Sta. 053, July 1978, 30°15′13″N, 88°03′08″W, 6 m, sand, 1 specimen. MISSISSIPPI: Horn Island, Corps of Engin-ers, Sta. 023, 7 Nov 1980, 30°15.05′N, 88°49.78′W, 5.5 m, sand, 33 specimens (including 1 female with brood of 31 larvae); 3 Apr 1981, 44 specimens (including 3 females, 1 ripe male, 20 juveniles, 9 larvae). Petit Bois Island, Corps of Engineers, Sta. 038, 22 Oct 1980, 30°13.91′N, 88°32.48′W, 3.8 m, sand 1 specimen; 3 Apr 1981, 167 specimens (including 12 females, 4 ripe males, 39 juveniles, 66 larvae). TEXAS: East Flower Garden Reef, U.S. National Marine Fisheries Service, Sta. EFG-IV-6-3, 22 Oct 1981, 27°53.63′N, 93°39.10′W, 102 m, silty sand, 2 specimens; Sta. EFG-IV-7-4, 26 Oct 1981, 27°55.38′N, 93°38.96′W, 101 m, silty sand, 1 juvenile.

Redescription.—Length to about 10.0 mm, width to about 0.5 mm. Adults to about 30 setigers. Glandular areas present, accentuated by methyl green staining. Midventral glandular streak present along entire length of worm from posterior rim of mouth.

Body (Fig. 1a) divided into 3 regions marked by degree of segmentation, types and number of notosetae, number of rows of uncini as well as relative number of individual uncini in each row, and development and distribution of glandular areas.

Anterior region.—Comprises prostomium, peristomium, and setigers 1–8. Prostomium (Fig. 1a–b) rounded and slightly flattened anteriorly, arched dorsally due to presence of cephalic keel; cephalic plaque absent; curved, ciliated nuchal slits located laterally. Cilia present around ventral perimeter of prostomium, in addition ciliated areas present at least laterally on prostomium and peristomium. Exact location and amount of cilia indeterminable due to poor condition of specimens.

Prostomium and peristomium fused; peristomium with large rounded mouth ventrally. Margin of peristomium and setiger 1 indistinct except for slight lateral indentations.

Segmentation of anterior region distinct from setiger 2. Setigers 2–8 campanulate when contracted, each widest anteriorly; when extended, each setiger longer than wide, with rounded margins. Collars absent; junction of setigers 8–9 indistinct.

Notopodia with simple setae only, emerging from small conical projections near middle of each setiger. Setae smooth basally, finely hispid along most of length (Fig. 1c). Up to 8 setae per fascicle arranged in 2 rows of 4 each; occasionally with 1–2 additional small, thin capillary setae.

Neuropodia present from setiger 5 as small, slightly elevated tori, each with single row of avicular uncini. Each uncinus with about 15 teeth arranged in 3 crescentic rows surmounting large, anteriorly directed main fang (Fig. 1d–e). Uncini numbering 5–9 on setiger 5, gradually increasing to 7–11 on setiger 8.

Glandular areas of anterior region are shown in Fig. 1a, after staining with methyl green (Banse 1970). Prostomium and peristomium with scattered cells, saddled area at cephalic keel, and narrow belt at frontal margin of prostomium. Glandular cells of setiger 1 scattered throughout with additional encircling band of cells anterior to notopodia. This band is interrupted by the midventral glandular streak. Glandular areas of setigers 2–8 completely encircle the body.

Middle region.—Comprises setigers 9–14. Segmentation indistinct; setigers longer than wide; notopodia and neuropodia as in anterior region.

Notosetae (Fig. 1f) similar to those in anterior region but about half as wide and numbering only 4 per fascicle arranged in 2 rows of 2 each.

Uncini in double rows from setiger 9. Anterior row with 2–5 uncini, their main

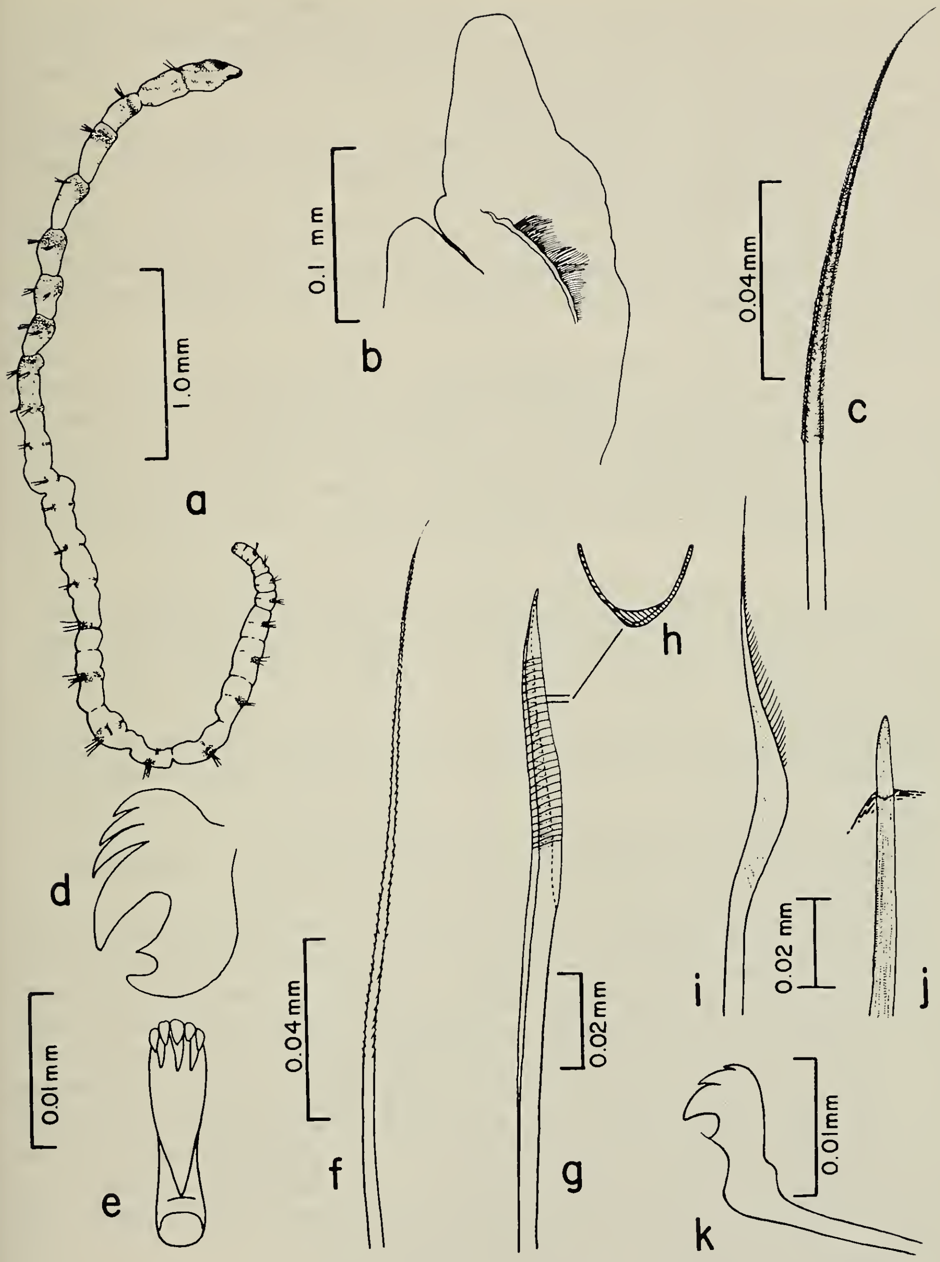


Fig. 1. *Boguea enigmatica*: a, Whole worm showing staining pattern, lateral view; b, Prostomium, lateral view; c, Hispid notoseta from setiger 2; d, Avicular uncinus from setiger 7, lateral view; e, Same, edge-on view; f, Notoseta from setiger 11; g, Channelled notoseta from setiger 16; h, Same, diagrammatic cross section; i, Serrate notoseta from setiger 16; j, Notopodial spine from setiger 16; k, Juvenile rostrate uncinus from setiger 2.

fangs directed posteriorly. Posterior row with 8–14 uncini, their main fangs directed anteriorly. About 4 uncini added to anterior row by setiger 14 while number of uncini in posterior row remains constant or randomly varies by 1–2. Shape and dentition of uncini as in anterior region.

Glandular regions (after methyl green staining) restricted to small areas around notopodia and posterior to neuropodial tori; some specimens may also have scattered cells dorsally on setiger 9 (Fig. 1a).

Posterior region.—Comprises remainder of body from setiger 15 to pygidium. Segmentation indistinct (except in far posterior setigers) (Fig. 1a). Setigers gradually decreasing in length and width posteriorly; noto- and neuropodia as in previous body regions.

Notopodia each with 2 rows of simple setae: anterior row of about 6 setae which, viewed laterally, appear unilimbate (Fig. 1g); edge-on view reveals 2 margins forming U-shaped channel (Fig. 1h). Posterior row of about 6 serrate simple setae (Fig. 1i), each alternating with channelled setae and strongly curved towards anterior end of worm. Notosetae decreasing in number and gradually replaced by narrow capillary setae and 1–4 acicular spines (Fig. 1j) in 3–7 posteriormost setigers.

At setiger 15, number of uncini in posterior row abruptly decreases ($\bar{x} = 4.8$, $n = 6$); anterior row retains nearly same number of uncini as in preceding setigers. Farther back number of uncini in both rows gradually decreases with anterior row decreasing more rapidly than posterior row; last 1–2 setigers sometimes devoid of uncini.

Glandular areas of some specimens located only at neuropodial tori. In others, even from same locality, cells also present at notopodia and coalesce across dorsum.

Pygidium simple with terminal anus; ventral valve absent.

Distribution.—Atlantic, North Carolina to northwest Florida; Gulf of Mexico, southern Florida to Texas; 2–102 m; primarily sand substrata.

Notes on larval development.—*Boguea enigmatica* broods its young. Gravid females were found in clear tubes together with eggs and variously developed larvae. The broods were found in abandoned serpulid polychaete tubes, but more often, the boguein tube was cemented to the concave side of empty bivalve shells (e.g., *Spisula soldissima* and indeterminable venerids in the Mississippi Sound area, and *Crassostrea virginica* in Bogue Sound, North Carolina). Developing larvae were found between the body of the mother and the interior wall of the tube. Other eggs remained inside the mother's body. The brood sometimes revealed all stages of larval development from egg to advanced larval stage (14–16 setigers). Eggs of one female *B. enigmatica* measured about 220 μm. There were approximately 75 eggs within the female's body cavity.

Of the setigerous larvae examined, none has less than 2 pairs of notosetal bundles. It appears then, following the reasoning of Bookhout and Horn (1949), that the first 2 pairs of bundles appear simultaneously even though the notopodia of the first setiger may each contain 2 notosetae while the notopodia of the second setiger each contain only 1 seta. All notosetae are very thin, without discernible limbate margins or pinnae as in the adult. The mouth begins forming at the 3-setiger stage. Rostrate uncini (Fig. 1k) begin developing at the 4-setiger stage (Fig. 2a). At the 6-setiger stage (Fig. 2b), nuchal slits are apparent for the first time although they do not appear ciliated.

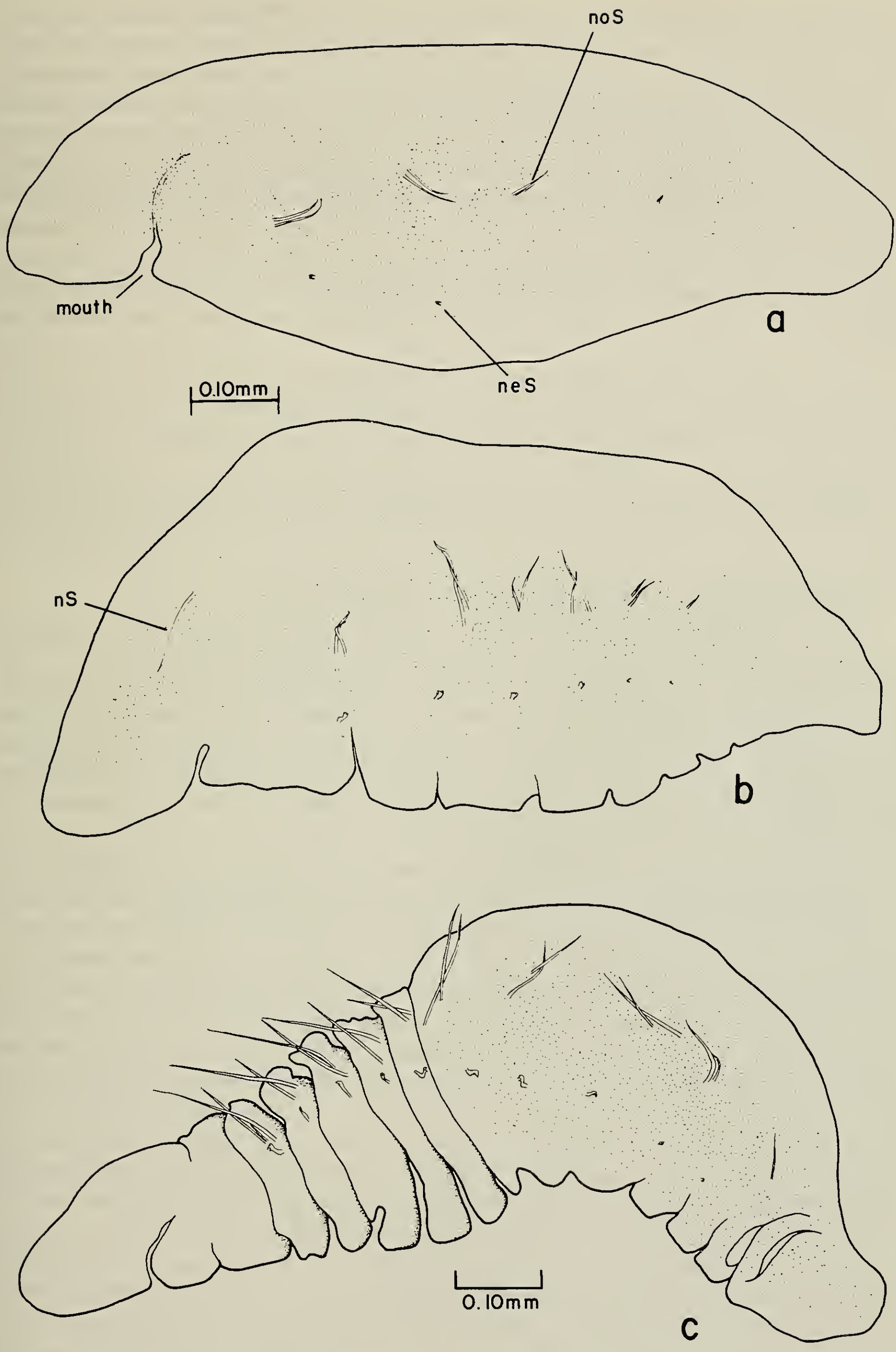


Fig. 2. *Boguea enigmatica* larvae: a, 4-setiger stage; b, 6-setiger stage; c, 10-setiger stage. nS, nuchal slit; neS, neuroseta; noS, notosetae; stippling indicates yolk.

At the 10-setiger stage (Fig. 2c), a pharynx is visible, segmentation of setigers 1–5 is distinct, yolk remains posterior to setiger 6, and rostrate uncini are well developed anteriorly. Also at the 10-setiger stage, the anus becomes apparent.

At the 12-setiger stage, the first avicular uncinus appears, developing below the rostrate uncinus of setiger 5. At the 15- to 16-setiger stage, the anterior row of avicular uncini on setiger 9 is developing and notopodial spines are present in the last 1–2 setigers. The adult distribution and types of notosetae are still not apparent. All yolk material has been absorbed and segmentation is distinct throughout. Fecal pellets are present in some specimens.

The smallest specimen of *B. enigmatica* not found with other larvae is 16 setigers long. This is about the stage at which larvae emerge from the parent tube.

At the 17-setiger stage, some anterior notosetae are limbate and have distal pinnae as in the adult. At the 19-setiger stage, the channelled notosetae as well as the serrate notosetae of the posterior region are seen developing for the first time.

In general, development of all morphological characters proceeds from the anterior to the posterior end. The development of notosetae always precedes that of the neurosetae. In contrast, at the 11-setiger stage of *Axiothella mucosa,* uncini develop before the notosetae (Bookhout and Horn 1949).

Juvenile specimens (about 16–23 setigers) are morphologically identical to adults except that the juveniles have 2 types of neurosetae. The rostrate uncini (Fig. 1k) are present, 1 per fascicle, from setiger 1. Beginning at setiger 5, the rostrate uncinus is always located in the superior part of the neuropodial fascicle. As the worm matures, the rostrate uncini are lost randomly along the body, usually occurring first in the anterior setigers. The specimens are thus left in the typical adult condition of having only avicular uncini, except in some far posterior setigers where occasionally a rostrate uncinus is present.

The loss of the rostrate uncini gives a clue to setal formation and migration, i.e., setae form ventrally in the fascicle and migrate dorsally where they are lost. Further evidence for this process is found in observing where the smallest avicular uncinus occurs in the fascicle. In developing worms, the smallest uncinus is always located dorsally with consecutively larger uncini being formed ventrally. This sequence is consistent with that found by Pilgrim (1977) for *Clymenella torquata* (Leidy, 1855) and *Euclymene modesta* (Quatrefages, 1865). Bookhout and Horn (1949, fig. 11) show a rostrate uncinus for larval *Axiothella mucosa* that is quite different from the adult uncinus (Andrews 1891, fig. 35). Day (1967: 616) states that the first uncini in maldanids appear as "S-shaped hooks," although he does not give specific examples or pertinent citations. Larval uncini are reported for members of other families as well, e.g., Sabellidae (*Euchone*) by Banse (1970) and Ampharetidae (*Hobsonia florida*) by Zottoli (1974).

That larval uncini can be lost and not replaced, as is the case in the first four setigers of *B. enigmatica,* may not be uncommon. I have observed that juvenile specimens of *Asychis elongata* (Verrill, 1873) collected in Mississippi Sound have a pair of rostrate uncini in setiger 1. As the worm matures, the uncini are lost leaving the adult arrangement, i.e., uncini absent in setiger 1.

Remarks.—The staining technique used here was described by Banse (1970). The stain delineates, presumably, the mucus-secreting cells. Before staining, glandular cells appear only as thickened, granular regions limited to setigers 2–8. Methyl green staining reveals glandular cells as described above and shown in Figure 1a. Larvae and juveniles were not stained.

This redescription of *Boguea enigmatica* differs considerably from the original. The most noteworthy discrepancy is that uncini begin on setiger 5 instead of 4 as stated by Hartman (1945). Among the paratypes and other specimens examined are individuals with uncini beginning on setiger 4. This is, however, due to regeneration of the anterior end.

As in other maldanids, *Boguea enigmatica* has a large, sac-like proboscis indicating that it is a deposit feeder. Cursory gut analysis revealed tests of diatoms and protozoans such as Radiolaria.

Boguella Hartman and Fauchald, 1971, emended

Diagnosis.—Cephalic keel and nuchal slits poorly defined. Uncini from setiger 4, in double rows except in far posterior setigers. Both *Rhodine*-type and avicular (terebelloid) uncini present in most setigers. Plumose notosetae present medially. Notopodial spines absent. Pygidium papillate.

Boguella ornata Hartman and Fauchald, 1971, emended

Boguella ornata Hartman and Fauchald, 1971:149, pl. 23, figs. a–g.

Material examined.—NEW ENGLAND: Bermuda rise, Sta. A119, 19 Aug 1966, 32°15.8′ to 32°16.1′N, 64°31.6′ to 64°32.6′W, 2095–2223 m, pteropod ooze, holotype (AHF Poly 0927), and 16 paratypes (AHF Poly 0928).

Description.—Length to about 7.0 mm, width to about 0.6 mm. Largest specimen (holotype) with 25 setigers. Prostomium globular and rounded anteriorly. Cephalic keel and nuchal slits poorly defined (Fig. 3a). Prostomium and peristomium fused; peristomium with small crescentic mouth. Entire head granular in appearance (Fig. 3a). Peristomium followed by 1–2 long asetigerous segments.

Segmentation distinct throughout; anterior margins of some anterior setigers sometimes collar-like depending upon state of contraction.

Notosetae of setigers 1–6 of 2 types (Fig. 3b) arranged in 2 rows per fascicle. Setae of anterior row stout, abruptly tapering, pubescent; setae of posterior row smooth basally, with fine pinnae distally. Notosetae of setigers 7 or 8 through 15–17 include thin, minutely hispid simple setae and 1–4 long, plumose setae (Fig. 3c); thereafter notosetae as in setigers 1–6.

Uncini avicular, beginning on setiger 4 in double rows (Fig. 3d); anterior row of 22-setiger paratype composed of smaller, *Rhodine*-type uncini (Fig. 3e), posterior row composed of larger terebelloid uncini (Fig. 3f). Uncini of both anterior and posterior rows similar in size and terebelloid in shape on setiger 11. Anterior row with larger, terebelloid uncini and posterior row with smaller, *Rhodine*-type uncini from setiger 12 to about 17. Posterior row of uncini absent from setiger 18; all uncini absent from setiger 19. Pygidium as described by Hartman and Fauchald (1971:151, pl. 23, fig. c).

Remarks.—The emended description differs considerably from the original given by Hartman and Fauchald (1971:149). One noteworthy discrepancy is the setiger on which the uncini are first present. On the holotype and 14 of the 16

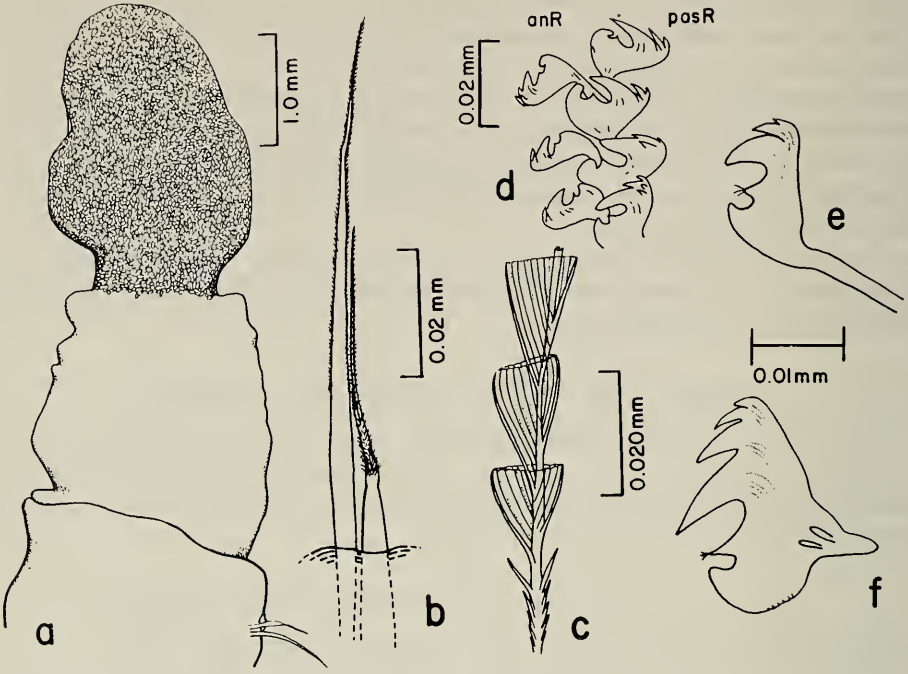


Fig. 3. *Boguella ornata*: a, Anterior end, lateral view; b, Notosetae from setiger 4; c, Part of plumose notoseta from setiger 12; d, Neuropodial uncini from setiger 4; e, *Rhodine*-type uncinus from setiger 9, lateral view; f, Avicular uncinus from same, lateral view. anR, anterior row; poR, posterior row.

paratypes, the uncini begin on setiger 4; however, on two of the paratypes, the uncini begin on setiger 5. On those two specimens, another setiger has been added anteriorly, thereby not affecting setal arrangements of posterior setigers, e.g., plumose setae still beginning on setiger 7. No specimens contained anterior setigers with just one row of uncini as originally described. Because of the poor condition of all type-material, the distribution of glandular areas could not be determined with certainty. It does appear, however, that the heaviest concentration of gland cells is in setigers 1–8; in some specimens these areas retained a brown pigment. In addition, the prostomium may be completely covered with gland cells due to the dense granular appearance of the epidermis (Fig. 3a). In some specimens, dorsolateral nuchal slits could be seen under low magnification; however, these structures could not be seen on slide-mounted specimens.

Boguella ornata is known only from its original discovery (Hartman and Fauchald 1971:151).

Discussion.—During examination of specimens of *Boguea enigmatica*, including type-material, it became apparent that this species has many characters in common with the Maldanidae. These are: 1) presence of a cephalic keel as in the Lumbriclymeninae and Rhodininae; 2) presence of ciliated nuchal slits apparently identical to those of the Lumbriclymeninae; 3) presence of a large ventral mouth cavity; 4) fused prostomium and peristomium; 5) distinctly segmented anterior body region of 8 setigers; 6) fused junction of setigers 8 and 9; 7) indistinctly segmented posterior body region; 8) unadorned pygidium as in the Lumbriclymeninae and Rhodininae; 9) presence of capillary notosetae arranged in 2 rows per fascicle as described for *Euclymene oerstedi* and *Clymenella torquata* (Pilgrim 1977); 10) presence of fine pinnae on the notosetae; 11) change in the type of notosetae posteriorly; 12) presence of distinct glandular regions, which are more pronounced anteriorly and diffuse posteriorly; 13) presence of uncini in double rows, facing in opposite directions in some setigers, as in the Rhodininae; 14) uncini beginning on setiger 5 as in some species of Rhodininae; 15) presence of rostrate larval uncini that are very similar to typical maldanid uncini and to rostrate uncini of larval *Axiothella mucosa* (Bookhout and Horn 1949); 16) ventral formation and dorsal migration and loss of noto- and neurosetae as in *Euclymene oerstedi* and *Clymenella torquata.*

Boguella ornata, in addition to most of the characters above, shares at least two additional characters with the Maldanidae: plumose setae, similar to those shown for *Asychis elongata* by Light (1974, fig. 1c); and *Rhodine*-type uncini.

Boguea enigmatica differs from maldanids, as currently described, in having: 1) three constant and well defined body regions; 2) notopodial spines in posterior setigers; 3) true avicular uncini; and 4) uncini beginning in single rows, changing to double rows, and then back to single rows posteriorly. *Boguella ornata* additionally differs from maldanids in having a unique papillated pygidium, and abruptly tapering, pubescent notosetae.

Some maldanids may actually have three well defined body regions. Most present descriptions allude to the presence of at least two body regions based primarily on degree of segmentation. Pilgrim (1977) described three body regions for *Euclymene oerstedi* and *Clymenella torquata* based on changes and patterns in the relative numbers of neurosetae from one region to the next. The body regions would be defined differently in these two species if degree of segmentation was used. Maldanid body regions cannot be defined until very detailed morphological comparisons are made. Included in this review should be a variety of morphological features such as the degree of segmentation; the number, type, and distribution of notosetae and neurosetae; the distribution of glandular regions; and perhaps even certain internal structures such as the alimentary canal and nephridia (Pilgrim 1965, 1977).

Notopodial spines are presently unknown among the maldanids. True avicular uncini like those of terebellids are also absent among maldanids; however, the uncinus of the Rhodininae resembles the avicular uncini. The *Rhodine*-type uncinus has a prominent posterior process which is lacking in the avicular uncinus. It is particularly noteworthy that *Boguella ornata* has *both* types of uncini. *Boguella,* then, may be the phylogenetic "link" between the Rhodininae and newly proposed Bogueinae.

In considering the above discussion, it is concluded that *Boguea enigmatica* and *Boguella ornata* possess characters which would place them in the Maldanidae. However, no existing subfamily can contain them primarily because of the type and distribution of their uncini. It is for this reason that I propose to reduce the family Bogueidae to the subfamily Bogueinae within the Maldanidae.

Key to the Subfamilies of Maldanidae
(Modified from Fauchald 1977)

1. Both cephalic and anal plaques absent 2
– At least anal plaque present 4
2. Avicular uncini present .... Bogueinae
– Avicular uncini absent, only rostrate uncini present 3
3. Rostrate uncini in double rows, posterior segments with encircling collars .... Rhodininae
– Rostrate uncini in single rows, posterior segments not collared .... Lumbriclymeninae
4. Cephalic plaque absent, anal plaque present .... Nicomachinae
– Both cephalic and anal plaques present 5
5. Anus dorsal .... Maldaninae
– Anus terminal .... Euclymeninae

Key to the Bogueinae Genera

1. Uncini present from setiger 4, plumose notosetae (Fig. 3c) present in middle setigers .... *Boguella*
– Uncini present from setiger 5, plumose notosetae absent .... *Boguea*

Acknowledgments

The author wishes to thank the following people for loan of material: Dr. Meredith Jones, Smithsonian Institution (USNM); Dr. Mary E. Petersen, Zoological Museum, Copenhagen (ZMC); Ms. Susan Williams, Allan Hancock Foundation (AHF); and Mr. Peter Miller, Texas Instruments, Inc. The following people reviewed all or parts of the manuscript and offered much appreciated advice and encouragement: Drs. Mary E. Petersen (ZMC); Kristian Fauchald (USNM); William Light, University of Wisconsin—Madison; and Kevin Eckelbarger, Harbor Branch Foundation.

Colleagues at Barry A. Vittor and Associates, Inc., contributed greatly to the completion of this paper: Messrs. Michael Ewing, Gary Goeke, Jerry Gathof, and Ms. Joan Uebelacker assisted through review and valuable discussions; Ms. Dorothy Cotton typed correspondence and parts of the manuscript; and Mr. Ben Jordan prepared the final figures for publication.

Much of the material examined was collected during work performed under contract numbers AA550-CT7-2 (U.S. Bureau of Land Management to Texas Instruments, Inc.), 68-01-4610 (Environmental Protection Agency to Interstate Electronics Corp.), NA80-GA-C-0075 Work Unit B-2 (U.S. Department of Commerce, National Marine Fisheries Service to TerEco, Inc.), and a contract from Mobil Oil Corp. to TechCon, Inc.

Drs. Andrew Lissner (Interstate Electronics Corp.) and E. A. Kennedy (TerEco, Inc.) provided collections for some material examined.

Barry A. Vittor and Associates, Inc., provided material and partial monetary support for this research.

Literature Cited

Andrews, E. A. 1891. Report upon the Annelida Polychaeta of Beaufort, North Carolina.—Proceedings of the United States National Museum 14(852):277–302.

Banse, K. 1970. The small species of *Euchone* Malmgren (Sabellidae, Polychaeta).—Proceedings of the Biological Society of Washington 83(35):387–408.

Bookhout, C. G., and E. C. Horn. 1949. The development of *Axiothella mucosa* (Andrews).—Journal of Morphology 84:145–183.

Day, J. H. 1967. A monograph on the Polychaeta of Southern Africa.—British Museum of Natural History Publication 656:1–878.

Fauchald, K. 1977. The polychaete worms. Definitions and keys to the orders, families and genera.—Natural History Museum of Los Angeles County, Science Series 28:1–190.

Hartman, O. 1945. The marine annelids of North Carolina.—Bulletin of Duke University Marine Station 2:1–54.

———, and K. Fauchald. 1971. Deep water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas, Part 2.—Allan Hancock Monographs in Marine Biology 6:1–327.

Hermans, C. O. 1979. Polychaete egg sizes, life histories and phylogeny. *In:* S. E. Stancyk (Ed.), Reproductive ecology of marine invertebrates.—The Belle W. Baruch Library in Marine Science 9:1–9.

Hobson, K. D., and K. Banse. 1981. Sedentariate and archiannelid polychaetes of British Columbia and Washington.—Canadian Bulletin of Fisheries and Aquatic Sciences 209:1–144.

Leidy, J. 1855. Contributions towards a knowledge of the marine invertebrates of the coasts of Rhode Island and New Jersey.—Journal of the Academy of Natural Sciences of Philadelphia 3:135–158.

Light, W. J. 1974. Occurrence of the Atlantic maldanid *Asychis elongata* (Annelida, Polychaeta) in San Francisco Bay, with comments on its synonymy.—Proceedings of the Biological Society of Washington 87(17):175–184.

Pilgrim, M. 1965. The functional anatomy and histology of the alimentary canal of the maldanid polychaetes *Clymenella torquata* and *Euclymene oerstedi.*—Journal of Zoology 147:387–405.

———. 1977. The functional morphology and possible taxonomic significance of the parapodia of the maldanid polychaetes *Clymenella torquata* and *Euclymene oerstedi.*—Journal of Morphology 152(3):281–302.

Quatrefages, A. de. 1865. Histoire naturelle des Annéles marina et d'eau douce. Annélides et Gephyriens 1:1–588. Paris: Librarie Encyclopédique de Rôret.

Verrill, A. E. 1873. Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region.—U.S. Fish Commission Report for 1871–72:295–778.

Zottoli, R. A. 1974. Reproduction and larval development of the ampharetid polychaete *Amphicteis floridus.*—Transactions of the American Microscopical Society 93(1):78–89.

Barry A. Vittor and Associates, Inc., 8100 Cottage Hill Rd., Mobile, Alabama 36609.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 250–252

A NEW SPECIES OF *CANCELLARIA* (MOLLUSCA: CANCELLARIIDAE) FROM THE NORTHERN GULF OF MEXICO

Richard E. Petit

Abstract.—A previously unknown species of Cancellariidae, *Cancellaria rosewateri*, is described. This new species, from the northern Gulf of Mexico, is unlike any previously known from the Caribbean, and subgeneric placement is not possible as there are no closely related species with which it may be grouped. Comparisons are made with a species from the Miocene of California and with the Indo-Pacific genus *Merica*.

During examination of material dredged by the R/V *Oregon* in 1962, two specimens of a unique new deep-water cancellariid were discovered. Subgeneric placement of this new species, *Cancellaria rosewateri*, is not attempted as there seem to be no closely related species. Comparison with the Indo-Pacific taxon *Merica* is made under the discussion below. The R/V *Oregon* also obtained at a nearby station a specimen of *Gerdiella cingulata* Olsson & Bayer, 1972. *Gerdiella* is unknown in the Tertiary of the Caribbean and Panamic areas, but is very similar to, if not the same as, *Mericella* Thiele, 1929, from the western Indian Ocean.

Class Gastropoda
Order Caenogastropoda
Superfamily Cancellariacea Ponder
Family Cancellariidae Forbes & Hanley
Cancellaria Lamarck

Cancellaria Lamarck, 1799: 71.

Type-species.—*Voluta reticulata* Linné, 1767, by monotypy.

Cancellaria rosewateri, new species
Fig. 1

Material examined.—Holotype: Length 29.3 mm, width 18.6 mm, R/V *Oregon* Station 4156, depth, 200 fathoms, 90 miles SSE of Pascagoula, Mississippi, 29°08′N, 88°18′W, 19 December 1962, USNM 811465. Paratype: Length 30.4 mm, width 18.8 mm, R/V *Oregon* Station 4154, 200 fathoms, 95 miles SSE of Mobile, Alabama, 29°17′N, 87°39′W, 18 December 1962, USNM 811464.

Shell description.—Nucleus eroded but apparently smooth, naticoid, of about 1½ whorls. Postnuclear whorls, about 5 in number, rounded, with small but distinct shoulder behind which lies a sutural channel. Shell thin but solid, slightly translucent, with sculpture of evenly spaced smooth spiral cords, about 16 on body whorl with about 8 visible on penultimate whorl and spire whorls. Both spiral cords and their interspaces devoid of axial sculpture except for fine growth lines. Aperture ovate. Columella concave with 3 almost equal folds, anterior one forming edge of short, shallow anterior canal. Inside of aperture lirate, lirations

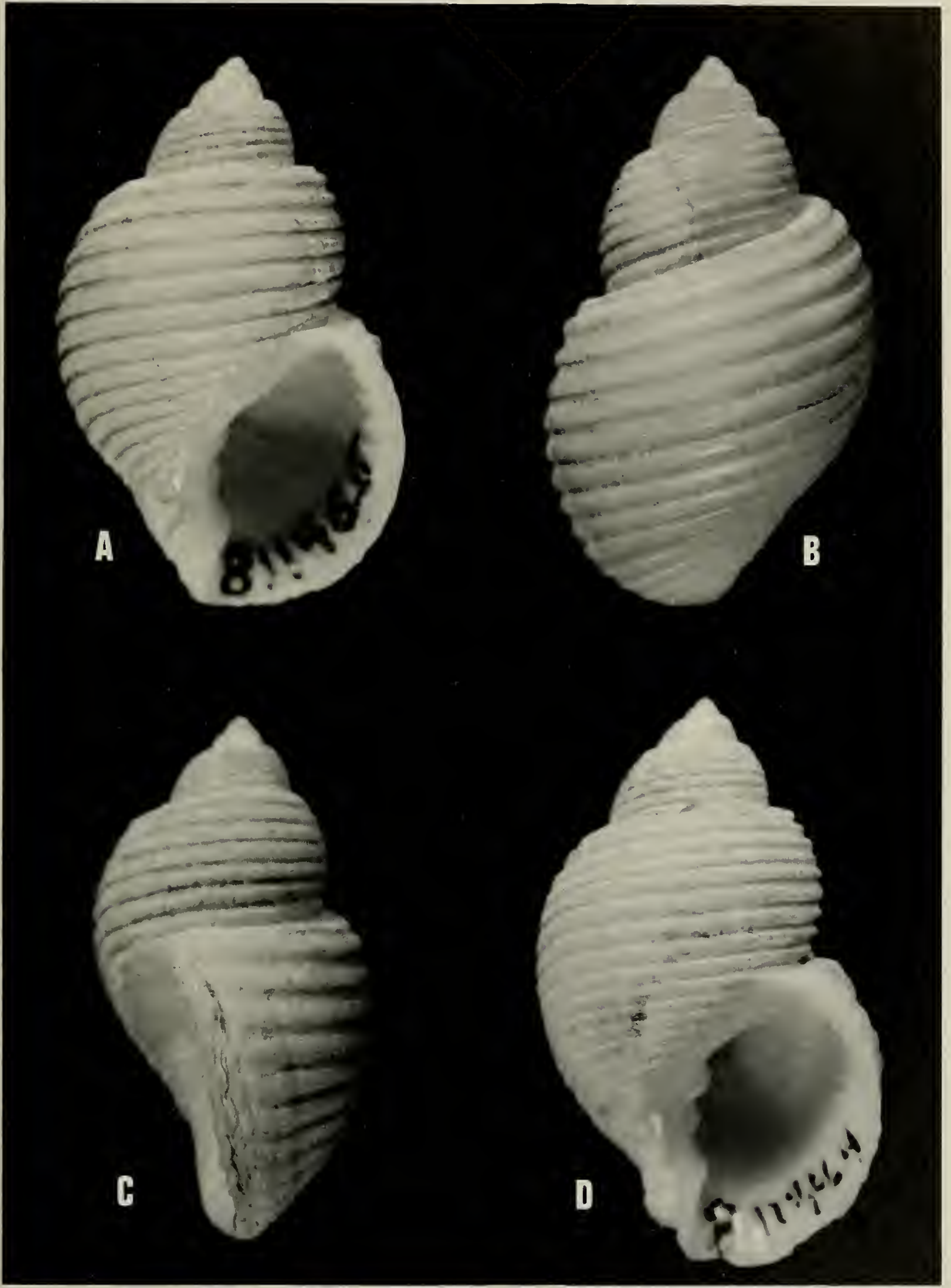


Fig. 1. *Cancellaria rosewateri*: A, B, C, Holotype (USNM 811465), 29.3 × 18.6 mm; D, Paratype (USNM 811464), 30.4 × 18.8 mm.

seeming to match external spiral cords, and extending well into aperture. Shell horn-colored, suffused with light brown arranged in 2 indistinct spiral bands, the widest occupying posterior half of body whorl, and the other the center third of anterior half. Periostracum brown, but not describable from remaining traces.

Type-locality.—200 fathoms, 90 miles SSE of Pascagoula, Mississippi (R/V *Oregon* Station 4156)

Distribution.—At present known only from the type-locality and nearby R/V *Oregon* Station 4154.

Etymology.—Named for Dr. Joseph Rosewater, Curator, Division of Mollusks, National Museum of Natural History, Smithsonian Institution, in recognition of his contributions to malacology and in appreciation of the assistance he has given me over a period of many years. Dr. Rosewater was also the first to recognize this species as new and kindly made the specimens available for study and description.

Discussion.—Comparison of *Cancellaria rosewateri* with Caribbean and Panamic species is difficult as there are no known species, Recent or Tertiary, which are similar. *Cancellaria obtusa* Deshayes, 1830, of the Panamic-Pacific Province, has similar sculpture but has a straighter columella with unequal plications. *Cancellaria darwini* Petit, 1970, from the Galapagos Islands, has sculpture that is primarily spiral but possesses a straight columella. The shape of the aperture and the columella of *Cancellaria rosewateri* closely resemble those features in species of the Indo-Pacific genus *Merica*. Species of *Merica* also have spiral sculpture, but not in the form of smooth bands as on *C. rosewateri.* Also, the outer lip of *Merica* is markedly prosocline with a distinct stromboid notch. In *C. rosewateri* the outer lip is only slightly prosocline and lacks any evidence of a stromboid notch. *Cancellaria rosewateri* has many characters in common with *C. dalli* (Anderson & Martin, 1914) as figured by Addicott (1970:117, pl. 15, figs. 11–13, 23, 27), but that species is described as having two columellar folds. Some European Tertiary cancellariids have been placed in *Merica* by various authors but it is doubtful that any of these are congeneric with the Indo-Pacific type.

Literature Cited

Addicott, W. O. 1970. Miocene gastropods and biostratigraphy of the Kern River Area, California.—United States Geological Survey Professional Paper 642:1–174, pls. 1–21.

Deshayes, G. P. 1830. Encyclopédie Méthodique. Histoire naturelle des vers 2(1):1–256. Paris.

Lamarck, J. B. P. A. 1799. Prodrome d'une nouvelle classification des coquilles. . . .—Société d'Histoire Naturelle de Paris, Mémoires:63–91.

Linné, C. von. 1767. Systema naturae per regna tria naturae . . . . edition duodecimo reformata. Vol. 1, pt. 2. Stockholm.

Olsson A. A., and F. M. Bayer. 1972. *Gerdiella*, a new genus of deep-water cancellariids.—Bulletin of Marine Science 22(4):875–880.

Petit, R. E. 1970. Notes on Cancellariidae (Mollusca: Gastropoda)—II.—Tulane Studies in Geology and Paleontology 8(2):83–88, pl. 1.

Ponder, W. F. 1973. The origin and evolution of the Neogastropoda.—Malacologia 12(2):295–338.

Thiele, J. 1929. Handbuch der systematischen Weichtierkunde.—Jena, Gustav Fischer, 1929–1935. 1154 pp.

Research Associate, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. Mailing address: P.O. Box 30, North Myrtle Beach, South Carolina 29582.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 253–269

A NEW SPECIES OF POLYMORPHIC FISH, *CICHLASOMA MINCKLEYI*, FROM CUATRO CIÉNEGAS, MEXICO (TELEOSTEI: CICHLIDAE)

Irv Kornfield and Jeffrey N. Taylor

Abstract.—*Cichlasoma minckleyi* is described from the Cuatro Ciénegas basin, Coahuila, Mexico. Discrete morphological variants occurring sympatrically within this taxon incorporate differences normally separating distinct congeners. Variation is partitioned into two non-overlapping body forms (deep-bodied and slender-bodied) within which occur two distinct pharyngeal morphs (papilliform and molariform), each maintained at high frequencies in natural populations. Field observations of matings both between morphs and between forms have established conspecificity of morphological variants. The dichotomous intraspecific variation presented by *C. minckleyi* suggests that phenetic characterization alone may be insufficient to delineate biological species within some members of the Cichlidae.

An unusual neotropical cichlid has received considerable attention from evolutionary biologists because of discrete, pronounced morphological and trophic variation. The specific status of this fish had been unresolved because the magnitude of morphological variation suggested the existence of at least three closely related taxa (LaBounty 1974), while biochemical analysis strongly supported the existence of a single polymorphic species (Sage and Selander 1975). Recent field studies (Kornfield *et al.* 1982) have confirmed the biochemical analyses and established conspecificity among morphological variants. Described here is *Cichlasoma minckleyi*, a new species of polymorphic cichlid endemic to the Cuatro Ciénegas basin, Coahuila, Mexico.

Methods

Standard counts and measurements were recorded following the procedures of Taylor and Miller (1980). Measurements and qualitative shape descriptions of pharyngeal jaws were taken from Barel *et al.* (1977) with the following additions: mid-pharyngeal jaw width (MPW) is the distance between the margins of the dentigerous area of the lower pharyngeal jaw at the midpoint of lower pharyngeal length parallel to the line of measured lower pharyngeal width; pharyngeal jaw horn width (PHW) is the maximum distance across one horn (ramus) of the lower pharyngeal jaw. Head width (HW) is the maximum distance between opercula measured over the body (with no caliper compression) at the central, fullest portion of the operculum.

Specimens are deposited in the Museum of Zoology, the University of Michigan (UMMZ) and the National Museum of Natural History, Washington, D.C. (USNM).

Cichlasoma minckleyi, new species
Figs. 1–9, Tables 1–3

Cichlasoma cf. *cyanoguttatum* Hubbs and Miller, 1965:52.

Cichlasoma sp. Taylor and Minckley, 1966:19–21 (including radiographs of trophic morphs).—Taylor, 1966:161–162, pl. 8, fig. 2; pl. 9, figs. 1–2.—Miller, 1968: 6.—Minckley, 1969:44–45.—Kornfield and Koehn, 1975:427–437.—Sage and Selander, 1975:4669–4673.—Hoogerhoud and Barel, 1978:52–56.—Hutchinson, 1978:180–181, fig. 113.—Kornfield, 1978:336.—Minckley, 1978:394–397, 399–401.—Vermeij and Covich, 1978:836–837.—Deacon *et al.*, 1979:42.—Liem, 1979: 121.—Thompson, 1979:680–681, fig. 9e.—Graves and Rosenblatt, 1980:243.—Turner and Grosse, 1980:259,269.—Jimenez *et al.*, 1981:409–411.—Kornfield *et al.*, 1982:658–664.

Parapetenia sp. LaBounty, 1974:5, 46, 54–64, 73, 99, figs. 7–9, 11, 15, 23, 25, 33, 34, tables 1, 3, 5–8.

Cichlasoma minckleyi Kornfield, 1981:96–97 (nomen nudum).

Diagnosis.—A polymorphic species endemic to the Cuatro Ciénegas basin in Coahuila, Mexico, placed tentatively in the *Parapetenia* group (Regan 1906–08) and distinguished from other members of the group by the sympatric occurrence of individuals of two discretely-variant body forms (deep-bodied and slender-bodied) within each of which two distinct pharyngeal morphs (papilliform and molariform) are represented. In addition, there are typically XVI, 10–11 dorsal ray elements, V, 8–9 anal fin elements, 14 pectoral fin rays, 11–12 gill rakers, and 29 vertebrae. The caudal peduncle is relatively slender with the length equal to or (usually) greater than the least depth. Sexual dichromatism, as developed in breeding adults, is uniquely diagnostic for this species: males are dark-green to black with the body and fins peppered with pale bluish spots, while females are snowy-white with distinctly contrasting black markings along the flank.

Holotype.—UMMZ 209434, 93.4 mm SL male, deep-bodied form, papilliform morph, Posos de la Becerra, 15.7 km by road SSW of Cuatro Ciénegas de Carranza, Coahuila, Mexico, R. R. Miller and family, C. L. Hubbs, W. L. Minckley, D. R. Tindall, and J. E. Craddock, 6 Apr 1961.

Paratypes.—(all from Coahuila, Mexico): UMMZ 130385 (9), 20–54 mm, and UMMZ 130395 (19), 18–70 mm, Cuatro Ciénegas, E. G. Marsh, Jr., 18 Sept 1939; UMMZ 179180 (2), 69 and 84 mm, Escobeda, hot spring 10.1 km S of Cuatro Ciénegas, W. L. Minckley and J. E. Craddock, 17 Aug 1960; UMMZ 179184 (1), 28 mm, irrigation ditch (La Angostura) from El Garabatal River, 2.6 km S of Cuatro Ciénegas, Minckley and Craddock, 18 Aug 1960; UMMZ 179194 (148), 14–34 mm, ditch (La Angostura canal) from El Garabatal, 6.6 km WSW of Cuatro Ciénegas, Minckley, Craddock, and others, 19 Aug 1960; UMMZ 179200 (9), 14–74 mm, Laguna San Marcos at San Marcos, 24.2 km by road SSW of Cuatro Ciénegas, Minckley, Craddock, and others, 20 Aug 1960; UMMZ 179216 (5), 9–144 mm, Rio Mesquites, 9.0 km S of Cuatro Ciénegas, Minckley, Craddock, and others, 21–22 Aug 1960; UMMZ 179224 (12), 15–31 mm, Altamira (6.4 km ENE of El Candido), 16 km S and 4.8 km E of Cuatro Ciénegas, Minckley and Craddock, 23 Aug 1960; UMMZ 179832 and USNM 229347 (155), 25–135 mm, collected with holotype; UMMZ 179838 (25), 28–114 mm, Puente Colorado, 10.2 km S of Cuatro Ciénegas, Miller, Hubbs, Minckley, and Tindall, 6 Apr 1961;

Table 1.—Measurements of *Cichlasoma minckleyi* in thousandths of the standard length (holotype UMMZ 209434; others from UMMZ 179832, 179838, and 198947). Figures in parentheses are means.

		Deep-bodied form		Slender-bodied form	
Measurement	Holotype	Papilliform morph (n= 7)	Molariform morph (n= 7)	Papilliform morph (n =11)	Molariform morph (n= 4)
Standard length, mm	93.4	52.4–96.7 (83.2)	50.7–86.6 (70.4)	54.3–110.4 (72.6)	67.1–144.7 (92.1)
Predorsal length	440	421–459 (452)	434–467 (446)	414–449 (433)	411–445 (428)
Preanal length	696	694–724 (709)	677–707 (695)	676–709 (695)	706–735 (721)
Prepelvic length	411	406–426 (417)	416–448 (431)	421–451 (442)	455–490 (470)
Body depth	433	412–448 (426)	396–448 (423)	355–388 (376)	356–380 (368)
Head length	357	361–375 (368)	361–386 (374)	366–393 (383)	369–386 (381)
Postorbital length	142	132–141 (138)	138–144 (141)	135–146 (142)	134–145 (140)
Snout length	142	135–155 (148)	138–163 (150)	134–161 (147)	140–166 (156)
Preorbital depth	97	73–107 (95)	79–103 (91)	89–109 (96)	97–115 (103)
Interorbital body width	95	92–104 (100)	85–103 (95)	75–103 (87)	82–136 (98)
Orbit diameter	87	84–113 (98)	97–108 (103)	92–116 (107)	80–109 (98)
Cheek depth	150	122–146 (140)	126–154 (139)	128–149 (138)	136–151 (142)
Mandible length	138	131–147 (140)	126–149 (139)	159–188 (175)	171–184 (177)
Upper-jaw length	112	105–126 (117)	105–129 (117)	113–141 (128)	129–137 (132)
Caudal-peduncle length	164	141–156 (148)	142–153 (149)	147–165 (155)	155–170 (161)
least depth	139	134–146 (139)	133–140 (136)	129–141 (134)	133–137 (135)
Dorsal-base length	542	525–553 (537)	522–548 (533)	488–534 (512)	486–516 (504)
Longest (=last) dorsal spine length	149	149–181 (167)	144–182 (164)	149–198 (158)	142–173 (161)
Anal-base length	217	189–213 (206)	199–219 (209)	188–227 (210)	198–218 (208)
Pectoral length	234	243–262 (253)	235–273 (257)	228–260 (243)	236–254 (246)
Pelvic length	236	236–271 (245)	227–258 (246)	223–263 (243)	245–284 (260)
Gut length	2141	1551–3403 (2715)	1155–2170 (1725)	1283–2000 (1645)	1242–1341 (1302)
Width of pharyngeal plate (dentigerous portion)	118	120–133 (128)	134–169 (147)	116–126 (121)	109–126 (119)
Width of last, medial pharyngeal tooth	3.2	2.7–4.8 (3.9)	9.9–18.5 (14.8)	2.8–4.5 (3.5)	4.5–8.9 (7.3)

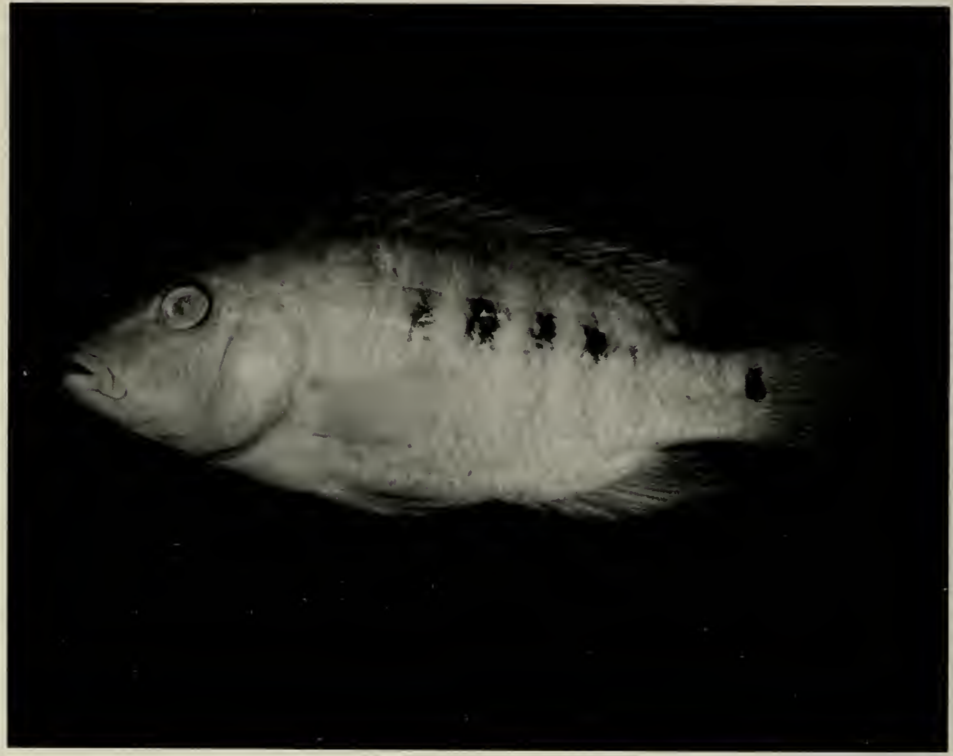


Fig. 1. *Cichlasoma minckleyi*, new species, UMMZ 209434, male, 93.4 mm SL, holotype, deep-bodied form, papilliform pharyngeal morph, Posos de la Becerra, Cuatro Ciénegas de Carranza, Coahuila, Mexico, 1961.

UMMZ 179859 (74), 25–164 mm, Tierra Blanca, 10.2 km WSW of Cuatro Ciénegas, Miller, Hubbs, Minckley, and P. Lugo, 8 Apr 1961; UMMZ 179877 (2), 20 and 25 mm, Puente Chiquito, 6.7 km S of Cuatro Ciénegas, Miller, Hubbs, and Minckley, 10 Apr 1961; UMMZ 179881 (27), 10–91 mm, Laguna Churince, 21.6 km by road SSW of Cuatro Ciénegas, Miller family, Hubbs, Minckley, and Tindall, 10 Apr 1961; UMMZ 180465 (one skeleton), 169 mm, pools along La Angostura canal near Garabatal River, *ca.* 8 km WNW of tip of San Marcos Mt., Cuatro Ciénegas basin, W. L. and B. A. Minckley and P. Lugo, 18 Apr 1963; UMMZ 198937 (28 preserved and 3 skeletons), 28–149 mm, Río Mesquites at Los Corrales, Cuatro Ciénegas basin, G. R. Smith, J. N. Taylor, and P. Yant, 25 Mar 1975; UMMZ 198942 (1), 39 mm, small tributary to Río Mesquites at Los Corrales, Cuatro Ciénegas basin, Smith and Yant, 26 Mar 1975; UMMZ 198947 (89 preserved and 36 skeletons), 18–98 mm, lagunas at El Mojarral, 8.7 km SW of Cuatro Ciénegas, Smith, Taylor, and Yant, 26 Mar 1975; USNM 231944 (3), 123–140 mm, lagunas at El Mojarral, I. L. Kornfield and D. C. Smith, 29 July 1979; USNM 231945 (126), 54–77 mm, Posos de la Becerra, Kornfield and Smith, 12 Aug 1979; USNM 231946 (38), 23–51, lagunas at El Mojarral, D. C. Smith, 7–12 July 1980; USNM 231947 (2 skeletons), 120 mm, lagunas at El Mojarral, Kornfield, 16 July 1981.

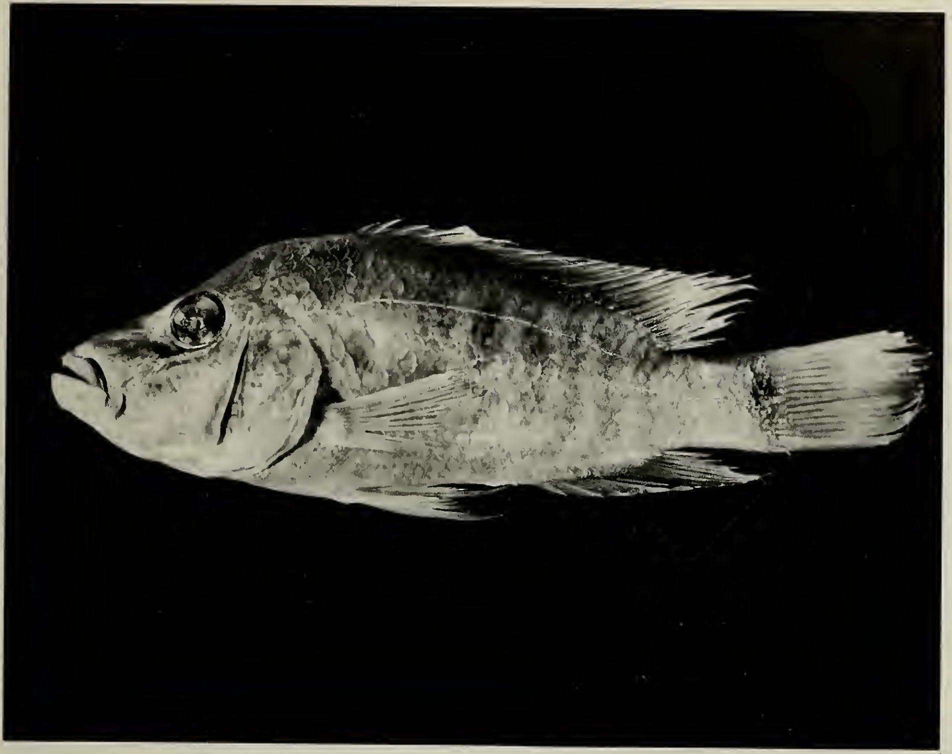


Fig. 2. *Cichlasoma minckleyi,* new species, UMMZ 179832 (ID #122.1), male, 93.5 mm SL, paratype, slender-bodied form, papilliform pharyngeal morph, Posos de la Becerra, Cuatro Ciénegas de Carranza, Coahuila, Mexico, 1961.

Description.—Body forms and color pattern are shown in Figs. 1–2. Proportional measurements are given in Table 1, and meristic data appear below (no significant differences in counts exist between either body forms or pharyngeal morphs).

Dorsal spines, XV(7), XVI(66), XVII(1); dorsal soft rays, 9(3), 10(24), 11(43), 12(4); anal spines, IV(1), V(68), VI(5); anal soft rays, 7(4), 8(55), 9(15); pectoral rays (both fins counted in 25 specimens), 13(3), 14(38), 15(9).

Scales: lateral series, 28(2), 29(1), 30(5), 31(14), 32(1); upper lateral line, 17(1), 18(2), 19(7), 20(7), 21(5), 22(1), and lower lateral line, 10(3), 11(6), 12(8), 13(6); scale-row overlap of upper lateral line on lower, −1(3), 0(4), 1(9), 2(5), 3(2); transverse scales, 17(6), 18(14), 19(2); upper lateral line to soft dorsal origin (not including scales on scaly sheath along fin base), 3(20), 3½(3); upper lateral line to origin of anal fin, 11(20), 12(3); rows around caudal peduncle, 17(1), 18(3), 19(12), 20(3); rows on cheek, 5(4), 6(14), 7(3).

Gill rakers on first arch (total including all anterior rudiments): upper limb, 3(30), 4(40); lower limb, 7(5), 8(46), 9(19); total, 11(25), 12(36), 13(9).

Vertebrae: precaudal, 13(21), 14(17); caudal, 15(23), 16(15); total, 28(7), 29(30), 30(1).

Deep-bodied form (Fig. 1): Body relatively stout, depth 2.2–2.5 in SL; head

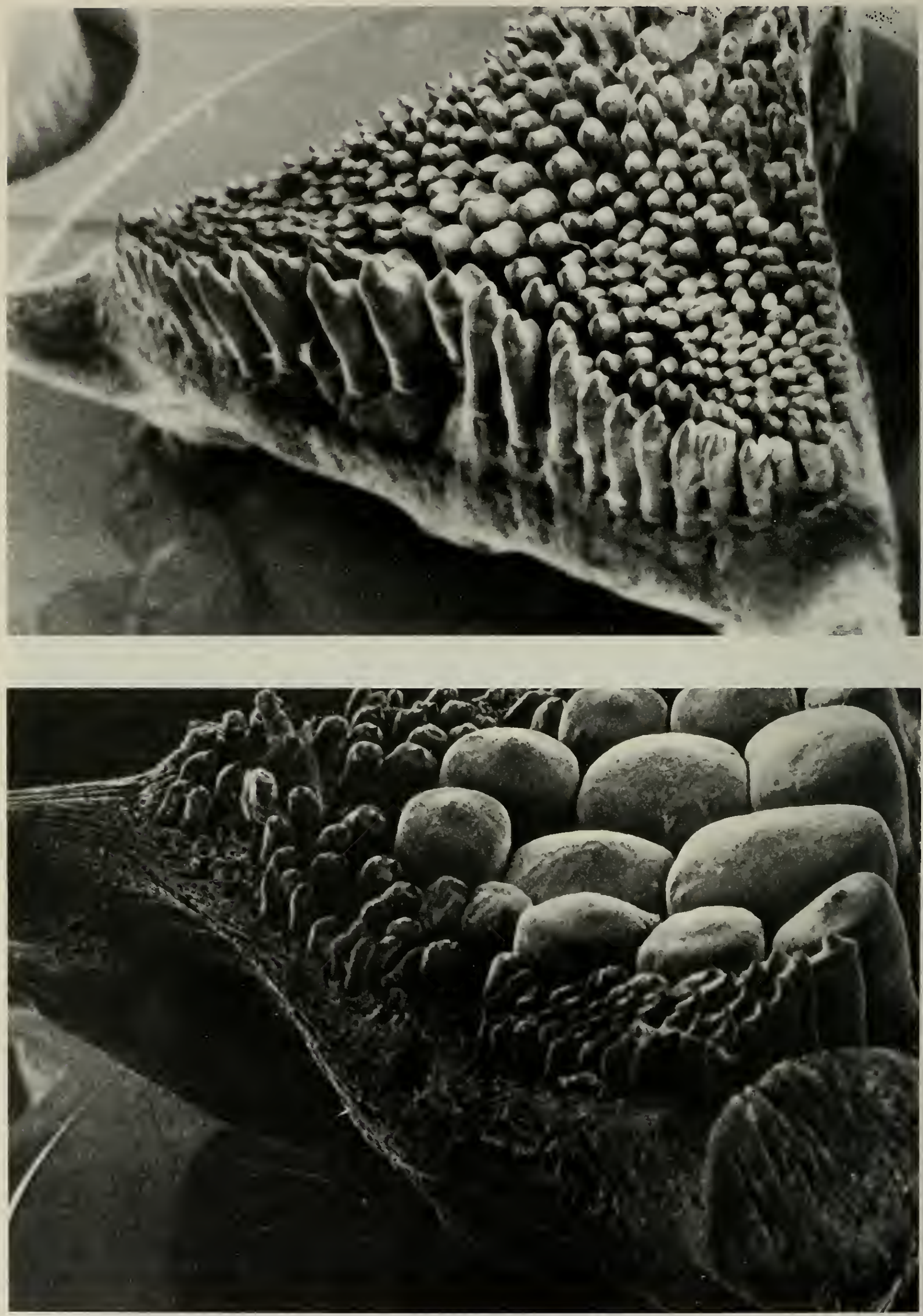


Fig. 3. Lower pharyngeal jaws defining papilliform pharyngeal morph (above) and molariform pharyngeal morph (below). Both specimens 120 mm SL, male, USNM 231947.

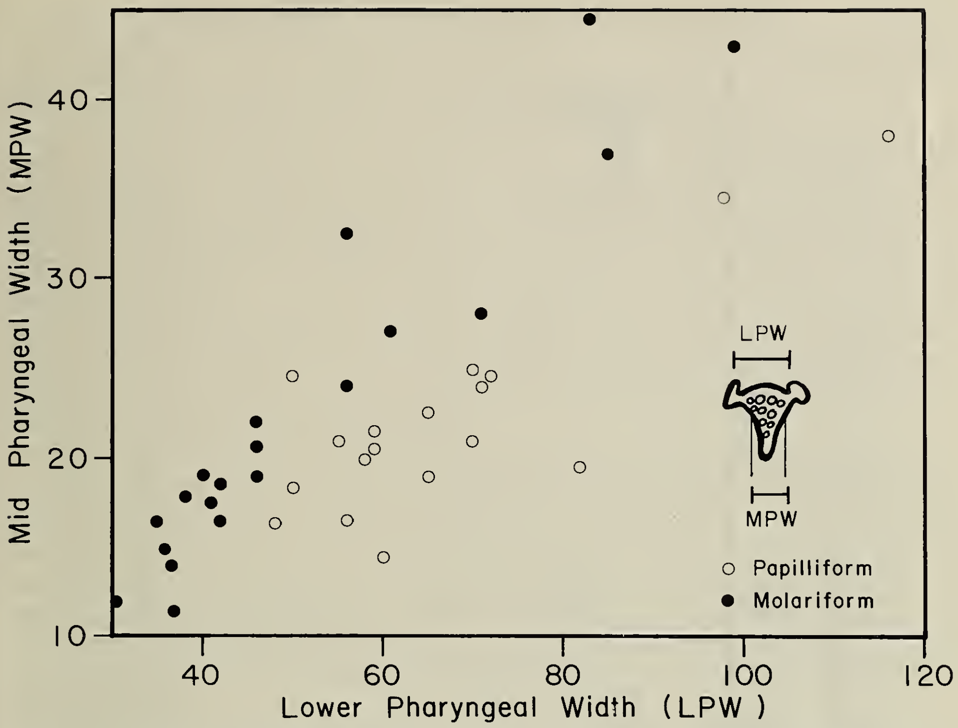


Fig. 4. Regression of mid-pharyngeal width (MPW) on maximum width of lower pharyngeal (LPW) for papilliform and molariform pharyngeal jaw morphs.

short, length much less than body depth over pelvic base; predorsal contour smoothly convex in subadults, becoming straighter and steeper with age (large adult males often develop a pronounced nuchal hump, producing a concavity over the orbit); prepelvic contour approximately straight, not so steep as predorsal; greatest body depth at or near origin of dorsal. Mouth relatively small, horizontal to slightly oblique; jaws approximately equal anteriorly. Ascending process of premaxillary extending to above anterior margin of orbit. Frenum along margin of lower lip generally weak or absent. Gill rakers well-spaced, short and stout.

Dorsal base of moderate length, originating above or slightly behind insertion of pectoral fin; dorsal spines increasing rapidly in length to fifth or sixth, then more gradually to last, which is approximately 0.45 head length in individuals over 70 mm SL. Soft rays of dorsal fin when relaxed not reaching beyond anterior third of caudal fin (except when prolonged in adults). Pectoral fin rounded, asymmetric, equal to approximately two-thirds head length, rarely extending to anal fin origin. Pelvic fin usually extending to vent or beyond. Caudal fin rounded; peduncle length equal to or greater than least depth.

Dental arcade rounded, jaw teeth unicuspid, widely and regularly set, implanted erect in few bands with outer row prominent. Anterior pair in outer row of upper jaw largest, conical and acutely pointed, with tips slightly to strongly recurved

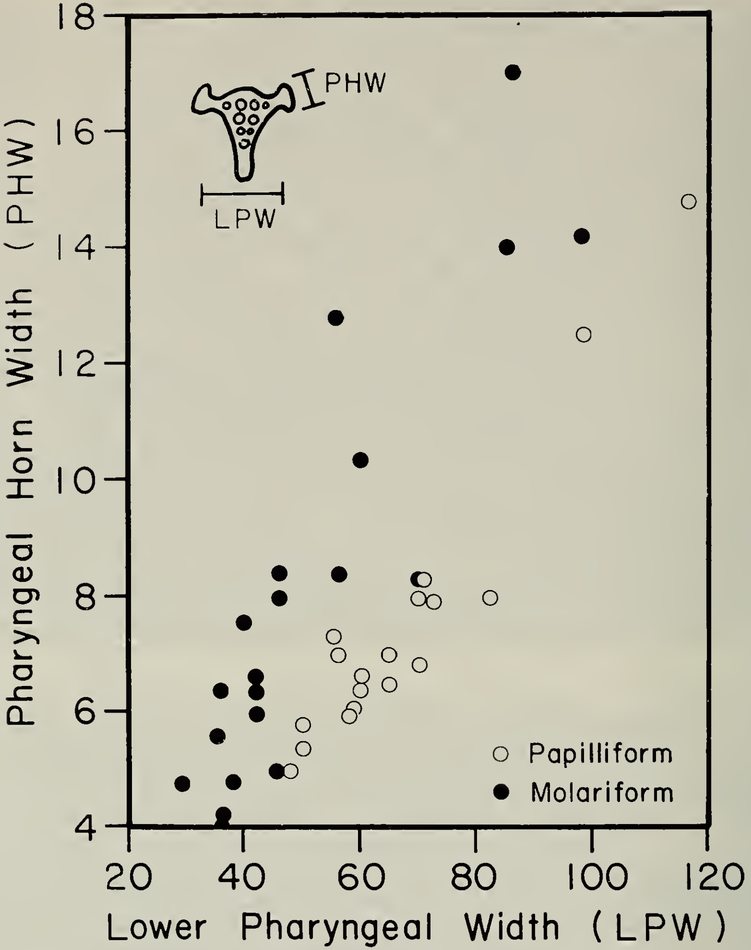


Fig. 5. Regression of pharyngeal jaw horn width (PHW) on maximum width of lower pharyngeal jaw (LPW) for papilliform and molariform pharyngeal jaw morphs.

(often worn in large specimens), usually lacking posterior cusp. Flanking teeth in upper jaw less recurved, gradually decreasing in size laterally. Anterior pair of teeth in lower jaw similar in shape but smaller than central pair in upper, equivalent to flanking teeth which gradually decrease in size.

Occlusal surface of lower pharyngeal jaw with dentigerous portion 1.1 to 1.3 times broader than long (in 20 individuals 51–121 mm SL). Pharyngeal dentition dimorphic, with molars in central rows either well-developed (=molariform morph) or lacking (=papilliform morph; see Fig. 3). Dentition in papilliform morphs with numerous slender unicuspid teeth arranged in irregular rows; dentition in molariform morphs with 4–8 massive molars in each of two median rows, decreasing in size anteriorly, increasing in number with SL, flanked laterally by 1–2 irregular rows of smaller molars, with small papilliform teeth distributed irregularly over remaining occlusal surface. Lower pharyngeal of papilliform morph with narrower mid-occlusal width and narrower rami (Figs. 4–5).

Slender-bodied form (Fig. 2): Body elongate, depth 2.6–2.8 in SL (n = 15, 54.3–144.7 mm SL); head relatively long, length equal to or greater than body depth over pelvic base. Mouth relatively large, oblique; lower jaw projecting beyond upper. Caudal peduncle slender, length greater than least depth.

Coloration.—Basal color (in preservation) variable, ranging from tan to dark brown or black; a series of 4–7 black rectangular blotches centered between the upper lateral line and anterior extension of the lower lateral line (Fig. 1), the first typically originating above midpoint of pectoral fin and the last under the posterior soft dorsal. Blotches often overlie fainter crossbars, most conspicuous in subadults but frequently obscured by dark basal coloration in adult males. Caudal spot, centered above lower lateral line at peduncle base, present in subadults, but often faint or lacking in dark-colored adults. Adults also occasionally develop diffuse black speckling over the flanks and lighter, irregular spotting on the unpaired fins. Paired fins dusky or hyaline.

In life, basal color in nonreproductive individuals varies from light grey or tan through yellowish-green to dark green or grey, while markings on the flank are black; both ground color and development of flank pattern are subject to rapid alterations in particular individuals. Sexual dichromatism in breeding adults is marked. Adult males are dark-green to black (often with the flank pattern completely obscured) with light blue spots distributed over much of the head, flanks, and vertical fins. In spectacular contrast, the ground color in breeding females is an intense, snowy white; the black flank markings are conspicuous, but blue spotting is absent.

Comparisons.—Characters that distinguish *C. minckleyi* from other *Cichlasoma* species are summarized in the diagnosis above. Though its origins are obscure, *C. minckleyi* appears to be more closely related to endemic cichlids of the Río Pánuco drainage, the first major river south of the Rio Grande, than to *C. cyanoguttatum,* which ranges northward into Texas and has recently gained access to the Cuatro Ciénegas basin via newly constructed irrigation systems. This hypothesis of relationships is supported by association of both the Pánuco species—specifically, *C. labridens* (Pellegrin), *C. bartoni* (Bean), and *C. steindachneri* Jordan and Snyder—and *C. minckleyi* with the *Parapetenia* group within *Cichlasoma* (Regan 1906–08; LaBounty 1974; Taylor and Miller, in press), while *C. cyanoguttatum* is a member of the *Herichthys* group (recognized as a genus by Regan 1906–08, but placed in *Cichlasoma* by Meek 1904, and most subsequent authors). These two groupings have traditionally been distinguished on the basis of jaw dentition; *Parapetenia* species have fewer, more widely-spaced, conical teeth, with one or more anterior pairs in each jaw enlarged to form canines, while the teeth in *Herichthys* species are more numerous, closely-spaced, compressed and incisor-like distally. Unfortunately, such a distinction is not as clear-cut as originally formulated. Several so-called *Parapetenia* species, including *C. minckleyi* and *C. labridens,* have only weakly enlarged anterior teeth at best, providing intermediate dentitional types between *Parapetenia* and *Theraps,* a third grouping within *Cichlasoma* characterized by generalized conical jaw teeth but no canines (Regan 1906–08). Further, variability in jaw dentition within populations of *C. cyanoguttatum* can be extensive and include relatively noncompressed, conical patterns; indeed, *C. pavonaceum* (Garman), a species recently placed in the synonymy of *C. cyanoguttatum* (Taylor and Miller, in press) was included in the *Theraps* group by Regan (1906–08). Clarification of supraspecific relationships

Fig. 6. Pharyngobranchial apophysis from molariform pharyngeal jaw morph (right) and papilliform jaw morph (left). Both specimens 120 mm SL, male, USNM 231947.

among these species awaits renewed phylogenetic study of subgroupings within the genus *Cichlasoma*.

Intraspecific variation observed in *Cichlasoma minckleyi* mimics morphological diversity encountered among other species within *Cichlasoma*. In *C. minckleyi,* variation related to both pharyngeal architecture and body shape is present. In

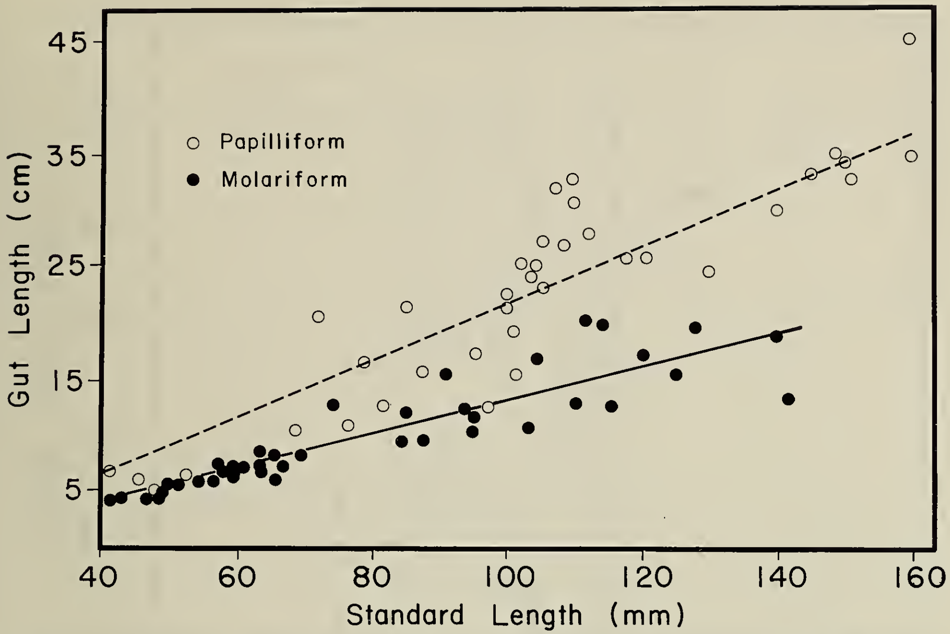


Fig. 7. Regression of gut length on standard length for papilliform and molariform pharyngeal jaw morphs.

the deep-bodied form (Fig. 1), two suites of integrated morphological characters accompany the dichotomy in pharyngeal dentition (Table 2). The lower pharyngeal jaw in papilliform morphs is more delicate, possessing a significantly narrower outline (Fig. 4) with smaller horns (Fig. 5) than the molariform morph. The size and position of branchial musculature differs conspicuously between morphs. The molariform pharyngeal apparatus is characterized by general hypertrophy with marked enlargement of the levator externis, levator posterior and retractor dorsalis muscles (Hoogerhoud and Barel 1978). Differences in neurocranial articulation of the upper pharyngeal jaw are dramatic, with dorsal support in the molariform morph provided by a massive pharyngobranchial apophysis (Fig. 6). Correlated with the pharyngeal modifications in deep-bodied forms is a dimorphism in intestinal length; gut length in the molariform morph is significantly less than that in the papilliform morph (Fig. 7). A degree of trophic (dietary) specialization occurs between pharyngeal morphs (Taylor and Minckley 1966; LaBounty 1974; Sage and Selander 1975), but is not as pronounced as originally believed (Smith 1982). Gut content analysis indicates that gastropods occur in molariform morphs but are usually, though not invariably, absent from guts of papilliform morphs. However, gastropods form only a minor component of all food items and dietary overlap between morphs is relatively great, particularly in juvenile and subadult fishes.

In addition to these internal characters, pharyngeal morphs of deep-bodied forms can be distinguished externally by a significant difference in head width (Fig. 8; C. D. N. Barel, pers. comm.) caused by the massiveness of pharyngeal and associated musculature in the molariform morph. In the field, this difference

Table 2.—Morphometric dichotomy between papilliform and molariform morphs of deep-bodied *Cichlasoma minckleyi* analyzed by linear regression.

	Test for equality of slope		Regression equations	
Character	df	F	Papilliform morph	Molariform morph
Mid-pharyngeal width (MPW)	1,34	12.30**	MPW = 3.49 + 0.28 LPW	MPW = −2.12 + 0.49 LPW
Pharyngeal horn width (PHW)[a]	1,35	36.46**	PHW = −1.53 + 0.14 LPW	PHW = −0.62 + 0.17 LPW
Gut length (GL)	1,34	10.58**	GL = −8.74 + 0.30 SL	GL = −2.30 + 0.19 SL
Head width (HW)	1,28	34.93***	HW = 10.74 + 0.26 HL	HW = −1.08 + 0.55 HL

** $P < 0.01$; *** $P < 0.001$.

[a] Slopes are statistically homogeneous; comparison of Y-intercepts by covariation analysis is presented.

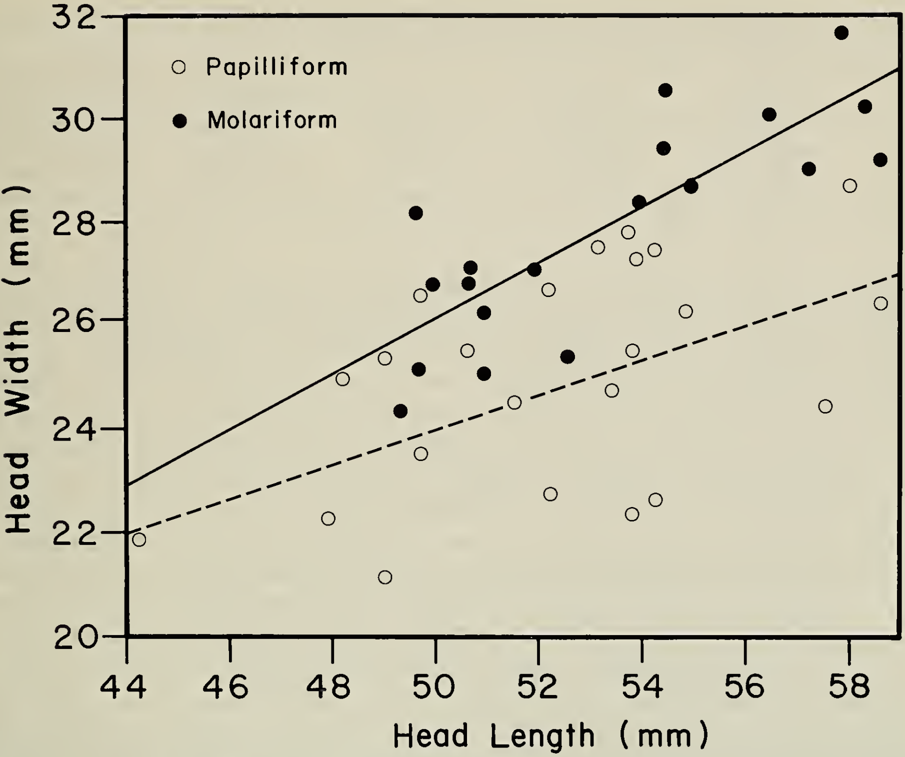


Fig. 8. Regression of head width (HW) on standard length for papilliform and molariform pharyngeal jaw morphs.

is not apparent to the human observer, but may perhaps be perceptible by the fish, particularly since opercular extension is a frequent element of territorial behavior in this and allied species (Baerends and Baerends-Van Roon 1950; pers. observ.). If perceptible, head width dimorphism could provide a convenient signal potentially preadapting pharyngeal morphs for assortative mating.

Morphological diversity encountered between deep-bodied and slender-bodied forms is pronounced. The streamlined form (Fig. 2) is characterized by differences in a number of external characters (Table 1) that become more marked with age. Though the differences may not be apparent in small fish, no adults with completely intermediate morphology have been recognized. Gut analysis of slender-bodied forms suggests that they principally consume other fishes (Taylor and Minckley 1966; LaBounty 1974; Sage and Selander 1975), a rare food item in the diet of deep-bodied forms; correspondingly, gut length in slender-bodied forms is usually shorter than that seen in deep-bodied individuals (Table 1). The external shape and dietary dichotomy between body forms does not involve pharyngeal morphology; both papilliform and molariform dentitions have been observed among slender-bodied individuals (LaBounty 1974).

Sympatric representation of dichotomous morphologies with respect to pharyngeal dentition and body form has provided a compelling basis to recognize multiple taxa within the Cuatro Ciénegas basin (Taylor and Minckley 1966;

Table 3.—Relative frequency of the molariform phenotype, by sex, in deep-bodied forms from five localities in the Cuatro Ciénegas basin. Sample size in parentheses.

	Laguna El Mojarral	Rancho Orozco	Escobeda	Posos de la Becerra	Laguna Churince
♂♂	0.583 (26)	0.500 (16)	0.462 (13)	0.384 (86)	0.375 (24)
♀♀	0.400 (35)	0.294 (17)	0.111 (9)	0.122 (156)	0.250 (28)

Minckley 1969; LaBounty 1974; Kornfield and Koehn 1975). The diversity seen within *C. minckleyi* is precisely the kind which characterizes differences among distinct biological species within the genus *Cichlasoma*, as illustrated, for example, by the endemic cichlid fauna of the Río Pánuco basin (Taylor and Miller, in press). In the Río Verde, a sympatric pair of deep-bodied species, *Cichlasoma bartoni* and *C. labridens*, exhibits a comparable dichotomy in pharyngeal dentition, while in the Río Gallinas system, *C. labridens* and *C. steindachneri* differ in both body form and pharyngeal dentition. Unlike the Cuatro Ciénegas situation, however, the Río Pánuco species can also be distinguished on the basis of breeding coloration, electrophoretic comparisons, and a number of meristic characteristics. Nevertheless, conventional morphological treatment of *C. minckleyi* concluded that the taxa consisted of at least three species within the Cuatro Ciénegas basin. However, biochemical studies demonstrating parallel variation in isozyme frequencies between pharyngeal morphs among isolated localities strongly supported a single-species hypothesis (Sage and Selander 1975). This systematic problem has been resolved by field observations of reproductive behavior. Successful matings both between deep-bodied fish of different pharyngeal morphs (Kornfield *et al.* 1982) and between different body forms (Taylor, unpubl.) convincingly established conspecificity. As a corollary, this finding emphasizes the potential insufficiency of phenetic (=morphological) criteria in delimiting species within the family Cichlidae.

The relative contributions of genetic and environmental factors to total phenotypic variation within *C. minckleyi* are unclear. While most deep-bodied specimens can be easily assigned to a specific pharyngeal morph, a small percentage of fish (<5%) exhibit intermediate pharyngeal morphologies and gut lengths. The genetic basis for intermediacy is unknown, but cannot be due to hybridization in the conventional sense. Proportions of the two pharyngeal morphs vary in different size-classes and also can differ considerably among localities. However, within localities, the proportion of individuals with molariform dentition is substantially greater in males than in females (Table 3). While such a difference might reflect differential selective pressures, its consistency across localities suggests a simple model for the inheritance of alternate pharyngeal states. Assuming that pharyngeal phenotype is regulated by a single diallelic locus with a recessive molariform allele, the difference in the relative proportion of the two types between males and females is consistent with sex linkage (Fig. 9). However, accurate recognition of control over dentition and body form will require further studies of formal inheritance.

Distribution.—Cichlasoma minckleyi is known only from the Cuatro Ciénegas basin, Coahuila, Mexico. Within the basin it is common and widely distributed in most streams, ponds and lagunas. At a few localities, in the southeastern part

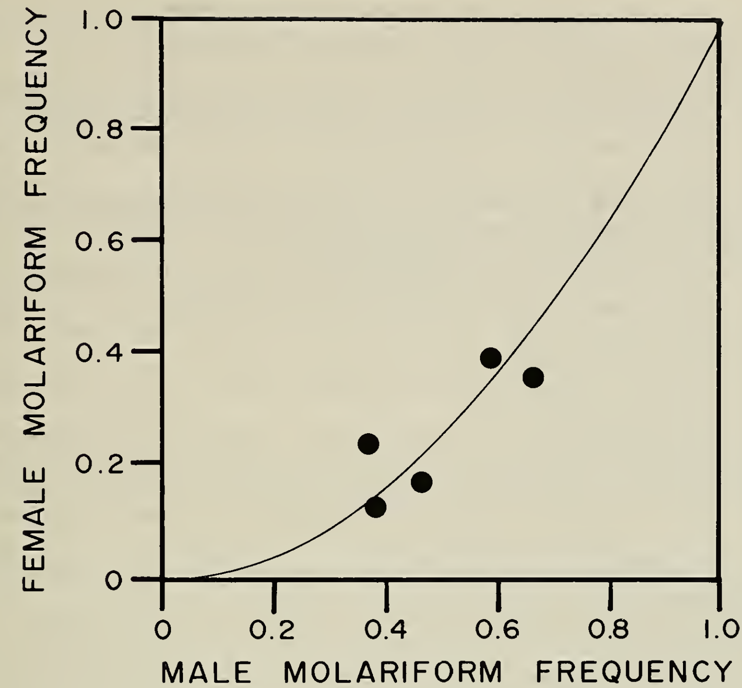


Fig. 9. Observed relative frequencies of molariform pharyngeal jaw phenotype in males and females from five localities in the Cuatro Ciénegas basin. Curve represents expected relationship when molariform phenotype is recessive and sex-linked.

of the basin, including Laguna Santa Tecla, it occurs sympatrically with the recent colonist, *C. cyanoguttatum*. The associated fish fauna of the basin has been described by Minckley (1969, 1978).

Etymology.—The species is named after Dr. W. L. Minckley of Arizona State University who has investigated the biota of Cuatro Ciénegas for many years.

Acknowledgments

We sincerely appreciate the guidance of C. D. N. Barel in our morphological analyses. Invaluable assistance was provided by David C. Smith. Our thanks to Hugh DeWitt for reading the manuscript; E. C. Theriot and W. N. Watkins prepared Figures 1 and 2, respectively. We gratefully acknowledge the cooperation of Carlos Tovar Flores, Of. Coordinadora de Investigaciones Pesqueras Externas, Direccion General del Instituto Nacional de la Pesca, for permitting our field work in Cuatro Ciénegas. This research was supported by NSF grant DEB 78-24074 (IK), the Migratory Fish Research Institute, Faculty Research Fund, University of Maine, and Earthwatch, The Center for Field Research, Belmont, Massachusetts.

Literature Cited

Baerends, G. P., and J. M. Baerends-Van Roon. 1950. An introduction to the study of the ethology of cichlid fishes.—Behaviour, Supplement number 1:1–243.

Barel, C. D. N., M. J. P. van Oijen, F. Witte, and E. L. M. Witte-Maas. 1977. An introduction to the taxonomy and morphology of the haplochromine Cichlidae from Lake Victoria.—Netherlands Journal of Zoology 27:333–389.

Deacon, J. E., G. Kobetich, J. D. Williams, S. Contreras, and others. 1979. Fishes of North America—endangered, threatened, or of special concern: 1979.—Fisheries 4:29–44.

Graves, J. E., and R. H. Rosenblatt. 1980. Genetic relationships of the color morphs of the serranid fish *Hypoplectrus unicolor*.—Evolution 34:240–245.

Hoogerhoud, R. J. C., and C. D. N. Barel. 1978. Integrated morphological adaptations in piscivorous and mollusc-crushing *Haplochromis* species.—Proceedings of the Zodiac Symposium on Adaptation (Pudoc Wageningen, the Netherlands):52–56.

Hubbs, C. L., and R. R. Miller. 1965. Studies of cyprinodont fishes. XXII. Variation in *Lucania parva*, its establishment in western United States, and description of a new species from an interior basin in Coahuila, Mexico.—Miscellaneous Publications of the Museum of Zoology, University of Michigan 127:1–111.

Hutchinson, G. E. 1978. An introduction to population ecology.—Yale University Press, New Haven, Connecticut, 260 pp.

Jimenez, G. F., G. Guajardo M., and C. H. Briseno. 1981. Trematodos de peces dulceacuicolas de Coahuila, Mexico. I. *Quadripaludis luistoddi* gen. et sp. nov. (Trematoda: Hemiuridae) parasitos de ciclidos endemicos de Cuatro Ciénegas.—Southwestern Naturalist 26:409–413.

Kornfield, I. L. 1978. Evidence for rapid speciation in African cichlid fishes.—Experientia 34:335–336.

———. 1981. Biological status of the cichlid fishes of Cuatro Ciénegas.—Proceedings of the Desert Fishes Council 12:96–97.

———, and R. K. Koehn. 1975. Genetic variation and speciation in New World cichlids.—Evolution 94:427–437.

———, D. C. Smith, P. S. Gagnon, and J. N. Taylor. 1982. The cichlid fish of Cuatro Ciénegas, Mexico: direct evidence of conspecificity among distinct trophic morphs.—Evolution 36:658–664.

LaBounty, J. F. 1974. Materials for the revision of cichlids from northern Mexico and southern Texas, U.S.A.—Unpublished Ph.D. dissertation, Arizona State University, Tempe, Arizona, 121 pp.

Liem, K. F. 1979. Modulatory multiplicity in the feeding mechanism in cichlid fishes, as exemplified by the invertebrate pickers of Lake Tanganyika.—Journal of Zoology 189:93–125.

Meek, S. E. 1904. The fresh-water fishes of Mexico north of the Isthmus of Tehuantepec.—Field Columbia Museum Publication 93 (Zoology Series, 5):1–252.

Miller, R. R. 1968. Two new species of the genus *Cyprinodon* from the Cuatro Ciénegas basin, Coahuila, Mexico.—Occasional Papers of the Museum of Zoology, University of Michigan 659:1–15.

Minckley, W. L. 1969. Environments of the bolson of Cuatro Ciénegas, Coahuila, Mexico, with special reference to the aquatic biota.—Texas Western Press, University of Texas, El Paso, Texas, Science Series 2:1–63.

———. 1978. Endemic fishes of the Cuatro Ciénegas Basin, Northern Coahuila, Mexico. Pp. 383–404 *In:* R. H. Wauer and D. Riskind, eds., Trans. Symp. Biol. Resources of the Chihuahuan Desert Region, U.S. and Mexico.—Transactions and Proceedings of the U.S. National Parks Service. Ser. 3. York.

Regan, C. T. 1906–08. Pisces. *In:* Biologia Centrali-Americana 8:1–203.

Sage, R. D., and R. K. Selander. 1975. Trophic radiation through polymorphism in cichlid fishes.—Proceedings of the National Academy of Sciences 72:4669–4673.

Smith, D. C. 1982. Trophic ecology of the cichlid morphs of Cuatro Ciénegas, Mexico.—Unpublished M.S. thesis, University of Maine, Orono, Maine, 45 pp.

Taylor, D. W. 1966. A remarkable snail fauna from Coahuila, Mexico.—The Veliger 9:152–228.

———, and W. L. Minckley. 1966. New World for biologists.—Pacific Discovery 19:18–22.

Taylor, J. N., and R. R. Miller. 1980. Two new cichlid fishes, genus *Cichlasoma*, from Chiapas, Mexico.—Occasional Papers of the Museum of Zoology, University of Michigan 693:1–16.

———, and ———. (In press). Cichlid fishes (genus *Cichlasoma*) of the Río Pánuco basin, eastern Mexico, with description of a new species.—Occasional Papers of the Museum of Natural History, University of Kansas.

Thompson, K. W. 1979. Cytotaxonomy of 41 species of neotropical Cichlidae.—Copeia 1979:679–691.

Turner, B. J., and D. J. Grosse. 1980. Trophic differentiation in *Ilyodon,* a genus of stream-dwelling goodeid fishes: speciation versus ecological polymorphism.—Evolution 34:259–270.

Vermeij, G. J., and A. P. Covich. 1978. Coevolution of freshwater gastropods and their predators.—American Naturalist 112:833–843.

(IK) Department of Zoology and Migratory Fish Research Institute, University of Maine, Orono, Maine 04469; (JNT) Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida 33432.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 270–272

CLARIFICATION OF THE NAMES *RANA MYSTACEA* SPIX, 1824, *LEPTODACTYLUS AMAZONICUS* HEYER, 1978 AND A DESCRIPTION OF A NEW SPECIES, *LEPTODACTYLUS SPIXI* (AMPHIBIA: LEPTODACTYLIDAE)

W. Ronald Heyer

Abstract.—Méhelÿ in 1904 proposed a lectotype designation for *Rana mystacea* Spix, 1824, that differs from Heyer's lectotype designation of 1978. *Leptodactylus amazonicus* Heyer, 1978, is a synonym of *Rana mystacea* Spix, 1824, and a new species is proposed to solve the remaining consequent nomenclatural problem.

Dr. Marinus Hoogmoed brought to my attention a paper by Méhelÿ (1904) which I had overlooked in my review of the *Leptodactylus fuscus* species group (Heyer 1978). Méhelÿ (1904: 219) designated a lectotype for *Rana mystacea* Spix, 1824, which differs from and obviously predates my designation for the species (Heyer 1978:30). To summarize briefly, Spix based his new species, *mystacea,* on two Brazilian specimens (since destroyed), a male from ''Bahia'' (Spix 1824, plate 3, figure 3) and a female from ''Solimoens'' (=Rio Solimões) (Spix 1824, plate 3, figure 1). Méhelÿ (1904:219) considered the Bahia specimen to belong to the species *Rana typhonia* Daudin [=*Leptodactylus fuscus* (Schneider, 1799)] and chose the Rio Solimões specimen as represented in figure 1, plate 3 of Spix to be the name-bearer of *mystacea.* I considered the Bahia and Solimões specimens to represent two distinct members of the *mystaceus* complex and chose the figure of the Bahia specimen as the name bearer of *mystacea* and described a new species, *amazonicus,* for the species represented by the figured specimen from the Rio Solimões. As Méhelÿ's action takes precedence, the consequences are: (1) *Leptodactylus amazonicus* Heyer, 1978, becomes a synonym of *Rana mystacea* Spix, 1824; (2) the species of the *mystaceus* complex from the northern Atlantic forests of Brazil lacks a name, as no other name has been proposed for the species involved. Consequently, the following name is proposed for the species referred to as *Leptodactylus mystaceus* in the 1978 paper.

Leptodactylus spixi, new species

Holotype.—USNM 96409, an adult male from Brazil: Rio de Janeiro; Saco de São Francisco, Niteroi. Collector unknown, collected on 13 Oct 1923.

Paratopotypes.—USNM 96407–8, 96410–11.

Referred specimens.—Other specimens as indicated under distribution section for *Leptodactylus mystaceus* in Heyer, 1978 (p. 65).

Diagnosis.—Most individual *spixi* have a combination of a distinct light stripe on the posterior surface of the thigh and distinct white tubercles on the surfaces of the posterior tarsus and sole of foot; these states are shared with *albilabris*

(Günther), 1859; *elenae* Heyer, 1978; *fragilis* (Brocchi), 1877; and *latinasus* (Espada), 1875. *Leptodactylus spixi* has distinct dorsolateral folds (at least indicated by color pattern), *fragilis* and *latinasus* lack distinct dorsolateral folds. *Leptodactylus spixi* has white tubercles on the dorsal surface of the tibia; the tibia is smooth in *elenae*. *Leptodactylus spixi* is found in east coastal Brazil, *albilabris* occurs in the West Indies.

Some individuals of *L. spixi* lack the white tubercles on the tarsus and sole of foot (light thigh stripe present). These states are shared with at least some individuals of *furnarius* Sazima & Bokermann, 1978 (=*laurae* Heyer, 1978), *fuscus* (Schneider), 1799, *geminus* Barrio, 1973, *gracilis* (Duméril & Bibron), 1841, *longirostris* Boulenger, 1882, *notoaktites* Heyer, 1978, and *poecilochilus* (Cope), 1862. The tubercles on the dorsal surface of the tibia distinguish *L. spixi* from all these species.

Description of holotype.—Snout shape subelliptical from above, rounded with protruding ridge from side; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum large, distinct, diameter about ¾ eye diameter; well developed vocal slits present; slight external lateral vocal fold present, not developed into well developed sac; vomerine teeth in two long angulate, arched series almost in medial contact posterior to choanae; first finger much longer than second; fingers I and IV free, fingers II and III with slight lateral ridges; thumb lacking asperities; dorsum smooth; a pair of well developed dorsolateral folds from behind eye to hind leg; distinct supratympanic fold, from eye to shoulder; belly smooth, ventral disk distinct; toes free, tips not expanded; subarticular tubercles moderately developed; metatarsal ridge barely indicated; tarsal fold extending about ⅞ length tarsus; upper tibia scattered with white-tipped tubercles; posterior surface of tarsus and sole of foot with many white-tipped tubercles.

SVL 43.0 mm, head length 19.8 mm, head width 14.5 mm, interorbital distance 3.2 mm, eye-nostril distance 4.2 mm, femur 16.4 mm, tibia 21.5 mm, foot 24.7 mm.

Dorsum with irregular darker brown markings on lighter brown background including irregular interorbital triangle with apex directed posteriorly and chevron in suprascapular region; dorsolateral folds barely highlighted by darker brown color; dark canthal stripe from nostril to tympanum, interrupted by eye; distinct light stripe from tip of snout, running below dark canthal stripe, under eye and tympanum to angle of jaw; upper lip with slightly darker shading below light stripe; limbs barred above; venter immaculate; posterior surface of thigh almost uniform tan dorsally, bordered below by distinct light stripe highlighted by dark brown above and below.

Etymology.—Named for J. B. Spix, who was not to blame for the confusion that his figures have caused subsequent generations of herpetologists.

Distribution:—To my knowledge, no additional specimens have been documented from east coastal Brazil than those listed previously (Heyer 1978:65, and fig. 61).

Acknowledgments

Dr. Marinus Hoogmoed (Rijksmuseum van Natuurlijke Historie, Leiden) not only pointed out the Méhelÿ paper I had overlooked, but analyzed the nomenclatural situation in consultation with his colleague, Dr. Holthius, and suggested that I should propose a new species to solve the situation.

Ronald I. Crombie and George R. Zug (Smithsonian Institution, USNM) kindly reviewed this paper.

Literature Cited

Heyer, W. R. 1978. Systematics of the *fuscus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae).—Science Bulletin of the Natural History Museum of Los Angeles County 29:1–85.

Méhelÿ, L. 1904. Investigations on Paraguayan batrachians.—Annales Historico-Naturales Musei Nationalis Hungarici 2:207–232 + Plate XIII.

Spix, J. B. 1824. Animalia nova sive species novae Testudineum et Ranarum, quas in itenere per Brasiliam, annis 1817–1820. Monaco. 53 pp. + 22 plates.

Department of Vertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 273–275

A NEW BATHYAL SPECIES OF *CORALLIODRILUS* (OLIGOCHAETA: TUBIFICIDAE) FROM THE SOUTHEAST ATLANTIC

Christer Erséus

Abstract.—*Coralliodrilus longiductus,* n. sp. (subfamily Phallodrilinae) is described from the continental slope west of Angola. It is the first species of *Coralliodrilus* from bathyal waters, and it is distinguished from its congeners by its slender, bipartite, and heavily muscular atria.

The genus *Coralliodrilus* was established by Erséus (1979) for *C. leviatriatus* from coral reef sands at Bermuda. Subsequently, seven additional species, four from the Great Barrier Reef (Erséus 1981), and three from Italy (Erséus, in press), have been described.

While examining a collection of oligochaetes from the "Atlantis II-42" cruise undertaken by the Woods Hole Oceanographic Institution in Walvis Bay (SE Atlantic), a new species closely related to the shallow-water species of *Coralliodrilus* was encountered. This note provides the description of this species.

The specimens were all stained in paracarmine and mounted whole in Canada balsam. The type-material has been deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Coralliodrilus longiductus, new species
Fig. 1

Holotype.—USNM 74635

Type-locality.—Continental slope west of Luanda, Angola, 09°05′S, 12°17′E to 08°56′S, 12°15′E, 1427–1643 m (AII-42 Sta. No. 202).

Paratypes.—USNM 74636–74639, 4 whole-mounted specimens from the type-locality.

Other material examined (author's collection).—Three whole-mounted specimens from the type-locality.

Description.—Length (2 complete, fixed specimens) 2.8–3.1 mm, 33–34 segments. Diameter at clitellum (slightly compressed worms), 0.14–0.18 mm. Prostomium small. Clitellum extending over ½X–XII. Somatic setae (Fig. 1A) bifid, with upper tooth thinner and shorter than lower. Bifids slender, 32–44 μm long, about 1 μm thick, 3 per bundle anteriorly, 2–3(4) per bundle in post-clitellar segments. Ventral setae of XI modified into penial bundles (Fig. 1B, ps), each of which contains 5–7 (generally 6) straight setae, 25–33 μm long, about 1.5 μm thick. Ectal tips of penial setae very narrow, single-pointed and curved, protruding into male invaginations. Male pores as paired invaginations (Fig. 1B, mi), located in line with ventral somatic setae, in posterior part of XI. Spermathecal pores paired in lateral lines, in anterior part of X.

Pharyngeal glands extending into VI. Male genitalia (all structures paired) (Fig. 1B): whole vas deferens not observed in available material, but appears shorter

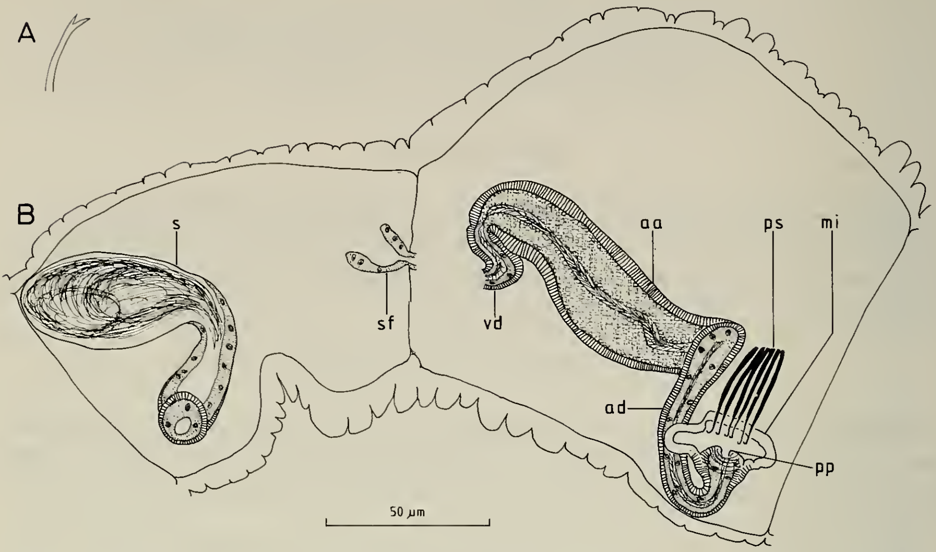


Fig. 1. *Coralliodrilus longiductus*: A, Free-hand drawing of somatic seta; B, Lateral view of spermatheca and male genitalia in segments X–XI. aa, atrial ampulla; ad, atrial duct; mi, male invagination; pp, pseudopenis; ps, penial setae; s, spermatheca; sf, sperm funnel; vd, vas deferens.

than atrium and is, ectally at least, muscular; vs entering apical, ental end of atrium; atrial ampulla, 90–115 μm long, 22–32 μm wide, with 3–4 μm thick outer lining of longitudinal muscles, and ciliated, granulated inner epithelium; atrial duct, up to 80 μm long, about 10 μm wide, muscular, terminating in small, muscular, protrusible pseudopenis in lateral wall of male invagination; prostate glands absent. Spermathecae (Fig. 1B, s) with ducts, 40–55 μm long, 13–25 μm wide, and very thin-walled ampullae, 50–85 μm long, 25–45 μm wide; sperm in random masses.

Remarks.—This new species shares the feature of bipartite atria with the Australian *C. atriobifidus* and *C. oviatriatus* (both described by Erséus 1981), and one of the new species from Italy (Erséus, in press). However, *C. longiductus*, n. sp. is distinguished from the other three by (1) its heavily muscular atria (atrial musculature thin in *atriobifidus* and *oviatriatus*, distinct but of varying thickness in the Italian species), and (2) its slender spermathecal ducts (these ducts are elaborate and longer than the spermathecal ampullae in *C. atriobifidus*, short and inconspicuous in *C. oviatriatus* and the Italian species).

Acknowledgments

I am indebted to Drs. H. L. Sanders, F. J. Grassle, and G. R. Sampson (WHOI), for placing the material at my disposal.

Literature Cited

Erséus, C. 1979. *Coralliodrilus leviatriatus* gen. et sp.n., a marine tubificid (Oligochaeta) from Bermuda.—Sarsia 64:179–182.

———. 1981. Taxonomic studies of Phallodrilinae (Oligochaeta, Tubificidae) from the Great Barrier Reef and the Comoro Islands with descriptions of ten new species and one new genus.—Zoologica Scripta 10:15–31.

———. (In press). Three new species of the marine genus *Coralliodrilus* (Oligochaeta, Tubificidae) from Italy.—Bolletino di Zoologia.

Swedish Museum of Natural History, Stockholm, and Department of Zoology, University of Gothenburg; postal address: Department of Zoology, Box 25059, S-400 31 Gothenburg, Sweden.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 276–290

NEW SPECIES OF *FABRICIOLA* AND *FABRICIA* (POLYCHAETA: SABELLIDAE) FROM BELIZE

Kirk Fitzhugh

Abstract.—Two new species of sabellid polychaetes, *Fabriciola trilobata* and *Fabricia infratorquata*, are described from Belize. Methyl green staining patterns of epithelial mucous gland cells are also described. Setal and collar segment characteristics are discussed.

An analysis of benthic samples from Twin Cays, Belize, revealed the presence of two numerically dominant undescribed species belonging to the genera *Fabriciola* Friedrich, 1939, and *Fabricia* Blainville, 1828. These species are described in the present paper. I also give the first report of methyl green staining and its variability in these genera. Staining in sabellids has been reported by Banse (1970, 1972, 1979) for a few genera, but not in *Fabriciola* or *Fabricia*. In his work on species of *Euchone*, Banse (1970) suggested the importance of this technique in providing additional diagnostic characters.

The present descriptions and references to other species follow the pattern established by Banse (1956), according to whom the development of the collar dorsally and ventrally is the primary character distinguishing the two genera. This pattern was continued by Banse (1957) and Hartmann-Schroeder (1971). In the species key provided by Friedrich (1939), shaft length of abdominal uncini was used as a main diagnostic feature. Diagnoses given by Day (1967) included collar characteristics plus uncini shaft length and condition of palps (filamentous or not); the two latter characters appeared to be given greater weight. Fauchald (1977) restated Day's diagnoses. In Fauchald's key, genera were separated on the basis of possession of long- or short-handled abdominal uncini. The two genera cannot be separated based on shaft length since both long and short forms occur in both genera. Collar development as put forth by Banse (1956) is thus suggested as a more useful and consistent character by which to distinguish the genera *Fabriciola* and *Fabricia*.

Fabriciola trilobata, new species

Figs. 1–2, 3a–c; Table 1

Material examined.—West Bay, Twin Cays, Belize; 30 cm depth; mat of *Caulerpa verticillata* on rootmat of *Rhizophora mangle*, some organic debris and fragments of *Halimeda*; 7 Apr 1982 (Array F202), 9 Apr 1982 (Array F203), 11 Apr 1982 (Array F204); coll. K. Fauchald. Holotype: F204 A-4 (USNM 74679). Paratypes: F204 A-1, 4 specimens (USNM 74680); F204 A-2, 6 specimens (USNM 74681); F204 A-3, 9 specimens (USNM 74682); F204 A-4, 13 specimens (UNSM 74683); F204 A-5, 5 specimens (UNSM 74684); F204 B-1, 11 specimens (USNM 74685); F204 B-2, 16 specimens (USNM 74686); F204 B-3, 7 specimens (USNM 74687); F204 B-4, 8 specimens (USNM 74688); F204 B-5, 6 specimens (USNM 74689); F204 C-1, 1 specimen (USNM 74690); F204 C-2, 11 specimens (USNM

74691); F204 C-3, 6 specimens (USNM 74692); F204 C-4, 2 specimens (USNM 74693); F204 C-5, 7 specimens (USNM 74694); F204 D-1, 2 specimens (USNM 74695); F204 D-2, 1 specimen (USNM 74696); F204 D-3, 9 specimens (USNM 74697); F204 D-4, 10 specimens (USNM 74698); F204 D-5, 8 specimens (USNM 74699). Additional material: F202 A-1, 4 specimens (USNM 74700); F202 A-3, 1 specimen (USNM 74701); F202 A-4, 4 specimens (USNM 74702); F202 A-5, 4 specimens (USNM 74703); F202 B-1, 4 specimens (USNM 74704); F202 B-2, 1 specimen (USNM 74705); F202 B-4, 8 specimens (USNM 74706); F202 C-1, 3 specimens (USNM 74707); F202 C-2, 6 specimens (USNM 74708); F202 C-3, 3 specimens (USNM 74709); F202 C-4, 1 specimen (USNM 74710); F202 C-5, 4 specimens (USNM 74711); F202 D-1, 1 specimen (USNM 74712); F202 D-2, 5 specimens (USNM 74713); F202 D-3, 4 specimens (USNM 74714); F202 D-5, 1 specimen (USNM 74715); F203 A-1, 2 specimens (USNM 74716); F203 A-2, 2 specimens (USNM 74717); F203 A-3, 1 specimen (USNM 74718); F203 A-4, 4 specimens (USNM 74719); F203 A-5, 4 specimens (USNM 74720); F203 B-1, 2 specimens (USNM 74721); F203 B-2, 1 specimen (USNM 74722); F203 B-3, 4 specimens (USNM 74723); F203 B-4, 1 specimen (USNM 74724); F203 B-5, 2 specimens (USNM 74725); F203 C-1, 1 specimen (USNM 74726): F203 C-2, 2 specimens (USNM 74727); F203 C-3, 1 specimen (USNM 74728); F203 C-4, 6 specimens (USNM 74729); F203 C-5, 2 specimens (USNM 74730); F203 D-1, 2 specimens (USNM 74731); F203 D-2, 6 specimens (USNM 74732); F203 D-3, 2 specimens (USNM 74733); F203 D-4, 6 specimens (USNM 74734); F203 D-5, 2 specimens (USNM 74735).

Diagnosis.—*Fabriciola* with filiform palps of variable length. Peristomium restricted to dorsal half of anterior end; visible ventrally and laterally, fused dorsolaterally to collar segment; anterior ventral margin expanded into shelf-like process. Ventral collar smooth, fused dorsolaterally to collar segment. Dorsal collar higher, divided by middorsal longitudinal groove. Anterior groove margin extended as triangular lobe, overlapped posteriorly by pair of collar lobes. Thoracic uncini with main fang surmounted by large offset tooth and 2 smaller teeth, crested by 4 rows of smaller teeth. Short-handled abdominal uncini with rows of teeth increasing in number with successive setigers: 7, 7–8 and 9 rows of teeth in setigers 9, 10 and 11, respectively. Abdominal neurosetae include 1–2 superior minute limbate setae and 2–3 inferior long, narrow limbate setae.

Description.—The holotype is a complete specimen with 9 thoracic and 3 abdominal setigers. Length 4.04 mm (0.78 mm comprising branchial crown) and width 0.19 mm.

Attached to the peristomium are a pair of semicircular branchial lobes, each with a large branchial heart located dorsally (Fig. 1a). Three radioles are attached to each branchial lobe; they are unbranched and rounded externally. Usually 7 pairs of ciliated pinnules extend from the inner side of each radiole. The proximal pair are longest, with more distal pinnules becoming shorter, such that all extend to about the same height; nearly ¾ the radiole length. Distal ends of the radioles are drawn out as very fine filaments. In the holotype the filamentous end contributes about ¼ of the radiole length, but in paratypes examined the end may be as much as ½ the radiole length. A pair of filiform palps are present, each originating from the inner side of each branchial lobe, adjacent to the middle radiole. Palps are distally blunt, and, in the holotype are about ¾ the radiole

Table 1.—Comparison of selected species of *Fabriciola*.

Species	Peristomium	Collar	Thoracic notosetae
trilobata	Visible laterally and ventrally; limited to dorsal half of anterior end.	Smooth, even ventrally; higher dorsally, middorsal margin trilobate.	Setiger 1–8: 4–5 long limbates. Setiger 3–8: 1–2 spatulates.
capensis	Visible dorsally, ventrally and laterally.	Smooth, even ventrally; dorsally same height as ventrum, middorsal margin trilobate.	Long bilimbate setae.

length. In paratypes, palp length is variable, ranging from ¼ to ¾ the radiole length. Internally, the length of the palps is almost completely occupied by a convoluted vessel, representing an extension of either the circulatory system or coelom.

The peristomium is visible ventrally and laterally (Fig. 1b, c), limited to the dorsal half of the anterior end. The ventral anterior margin is complete and slightly expanded, forming a rounded shelf-like process. Dorsolaterally, the peristomium fuses with the collar segment.

A distinct collar is present. Ventrally it is entire, even, and with rounded edges. Dorsolaterally, it fuses with the collar segment. Dorsally the collar extends slightly further anteriorly than it does ventrally. A middorsal longitudinal groove splits the anterior ⅓ of the collar segment into right and left halves. A small triangular lobe extends from the anterior end of the groove and is partly overlapped posteriorly by a pair of lateral lobes, each of which is slightly larger than the median lobe.

The collar segment is basically cylindrical, becoming only slightly wider posteriorly. The intersegmental groove between the collar segment and setiger 1 is only distinct ventrally. Just anterior to the groove is a partial annulation, complete ventrally and disappearing laterally. It is assumed this does not denote an additional achaetous segment.

Thoracic setigers are cylindrical with distinct segmentation. Setiger 1 is shortest, about ½ the length of the collar segment, and slightly wider than long. Each subsequent thoracic setiger is longer than the previous. Setiger 2 is as long as wide, setiger 5 is about twice as long as wide, and setiger 8 about 2.5 times as long as wide.

The abdominal setigers (9–11) become progressively shorter (Fig. 2a). Setigers 9–10 are cylindrical, 11 is dorsoventrally flattened. Setiger 9 is ⅔ as long as setiger 8 and 1.5 times longer than wide. Setiger 10 is as long as wide and setiger 11 is wider than long. Setigers 9–10 are the same width as thoracic segments, with setiger 11 abruptly narrower. Segmentation is distinct. Swollen, pad-like glandular areas are present just posterior to notopodial tori of setiger 9–10 and at anterior lateral margins of setiger 11.

Thoracic noto- and neuropodial tori are represented only by a slight swelling. Notopodia of setiger 1 are situated dorso-laterally; neuropodia are absent. No-

Table 1.—Continued.

Thoracic neurosetae	Abdominal notosetae	Abdominal neurosetae
5–7 uncini. Main fang + 1 large and 2 smaller teeth + 4 arcs of smaller teeth.	Short-handled uncini. Setiger 9: 25 uncini; 7 rows of teeth. Setiger 10: 28 uncini; 7–8 rows of teeth. Setiger 11: 18 uncini; 9 rows of teeth.	1–2 superior minute, narrow limbates; 2–3 inferior long, narrow limbates.
Uncini with main fang + 1–2 large teeth + 1 arc of 12–14 smaller teeth.	Long-handled uncini with 18 rows of teeth.	Slender capillaries.

topodia of subsequent thoracic setigers are lateral. Neuropodia are ventral to and slightly posterior to notopodia. Notosetae in setiger 1 include 4–5 long superior and 1 shorter inferior limbate setae. Superior notosetae in setigers 2–8 are long limbates similar to those of setiger 1, numbering 4–5 (Fig. 2d). Setigers 3–8 also possess 1–2 inferior short spatulate setae (Fig. 2b). Thoracic neurosetae are gently curved acicular uncini; 5–7 per fascicle, in a single vertical row (Fig. 2g). In lateral view, the distal ends of uncini have a large main fang surmounted obliquely by a large tooth followed by 4 smaller teeth. In frontal view, the large tooth above the main fang is clearly offset and accompanied by 2 smaller teeth (Fig. 2h). Teeth above this first row form a series of concentric arcs. Proximal to the distal end is a slight swelling of the shaft, which tapers proximally to a rounded end.

Abdominal notosetae occur on distinct lateral tori located on the posterior ¼ of the setiger, and are the same length as thoracic neuropodia. The number of uncini varies in that setiger 9 has 25, setiger 10 has 28 and setiger 11 has 18 uncini. Uncini are short-handled with a slight constriction below the proximal-most tooth row, followed by a slight swelling and a truncate base (Fig. 2i). Uncini of setiger 9 have 7 rows of teeth; the number of teeth per row from proximal to distal as follows: 1+2+3+3+4+6+5. Setiger 10 uncini have 7–8 tooth rows, those with 8 rows having the formula: 1+2+3+3+4+4+4+4. Setiger 11 uncini possess 9 tooth rows with the formula: 1+2+4+3+4+3+4+4+4. Abdominal neurosetae originate just ventral to notopodial tori. No neuropodial tori could be discerned. Neurosetae are of 2 types: 1–2 very minute superior limbate setae with a narrow limbation (Fig. 2c) and 2–3 inferior limbate setae with very long, slender shafts and a very narrow limbation extending about ¾ the length of the shaft (Fig. 2e–f). Neurosetae are directed dorsally.

The pygidium is roughly triangular and dorsoventrally flattened (Fig. 2a). Anteriorly it is the same width as the adjacent segment, narrowing and becoming rounded posteriorly. A V-shaped glandular zone extends along the outer margin, the arms of the V becoming wider posteriorly. The anus is a depressed, midventral longitudinal slit.

A pair of dark crescentic-shaped eyes (dorsal view) are in the collar segment on either side of the middorsal groove. A pair of smaller, circular eyes are located laterally in the posterior ¼ of the pygidium. No otocysts could be found.

The holotype (in alcohol) is opaque and cream colored. The palps of some

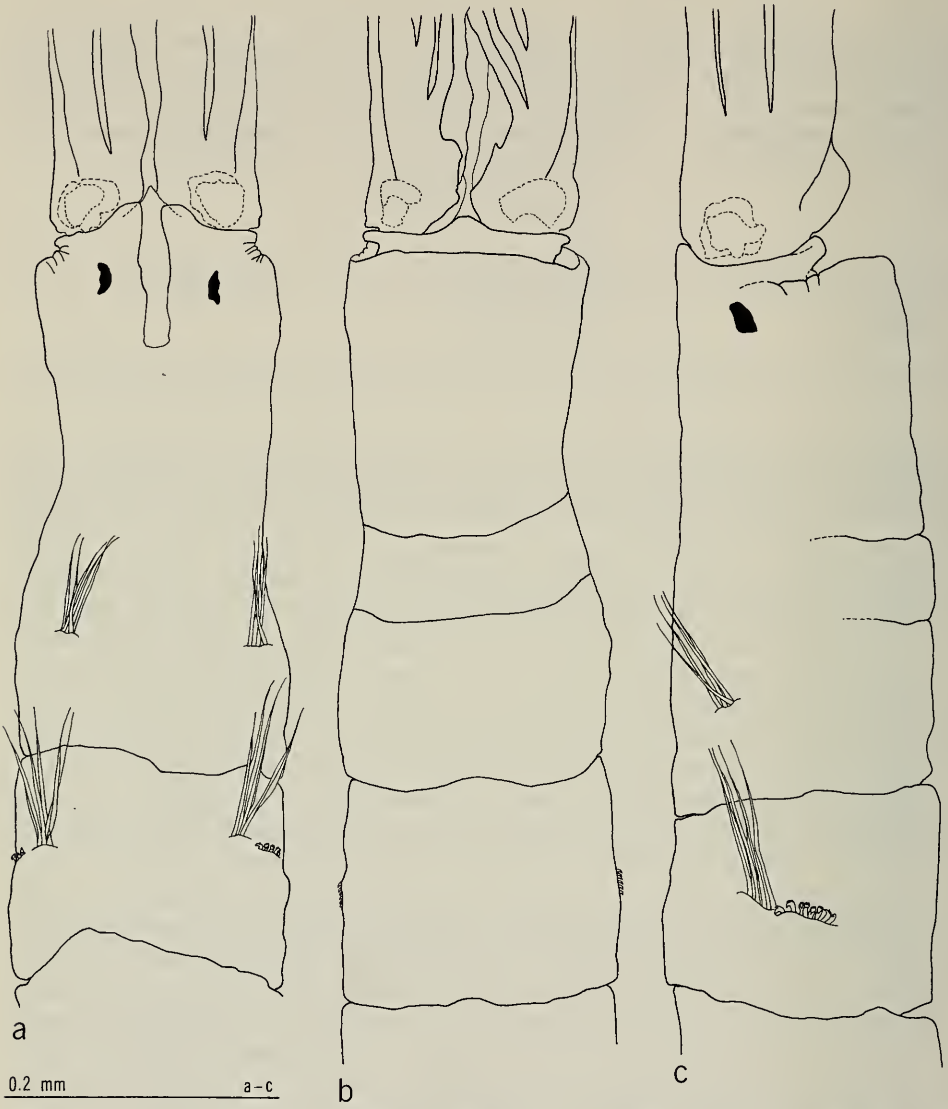


Fig. 1. *Fabriciola trilobata* (holotype, USNM 74679): a–c, Dorsal, ventral and lateral views of anterior end.

individuals examined were dull orange or yellow, sometimes with a corresponding lighter coloration in the radioles. Some individuals contained dark brown pigmentation extending dorsally on the branchial lobes, ventral peristomial margin, and along the anterior margin of the ventral collar. The middorsal groove, adjacent posterior region and lateral lobes showed similar pigmentation.

Tubes are thick, about 2–2.5 times as wide as the individual, constructed with loosely bound plant and detrital material. The central space within the tube is very narrow, such that nearly the entire length of the worm is in contact with the tube wall.

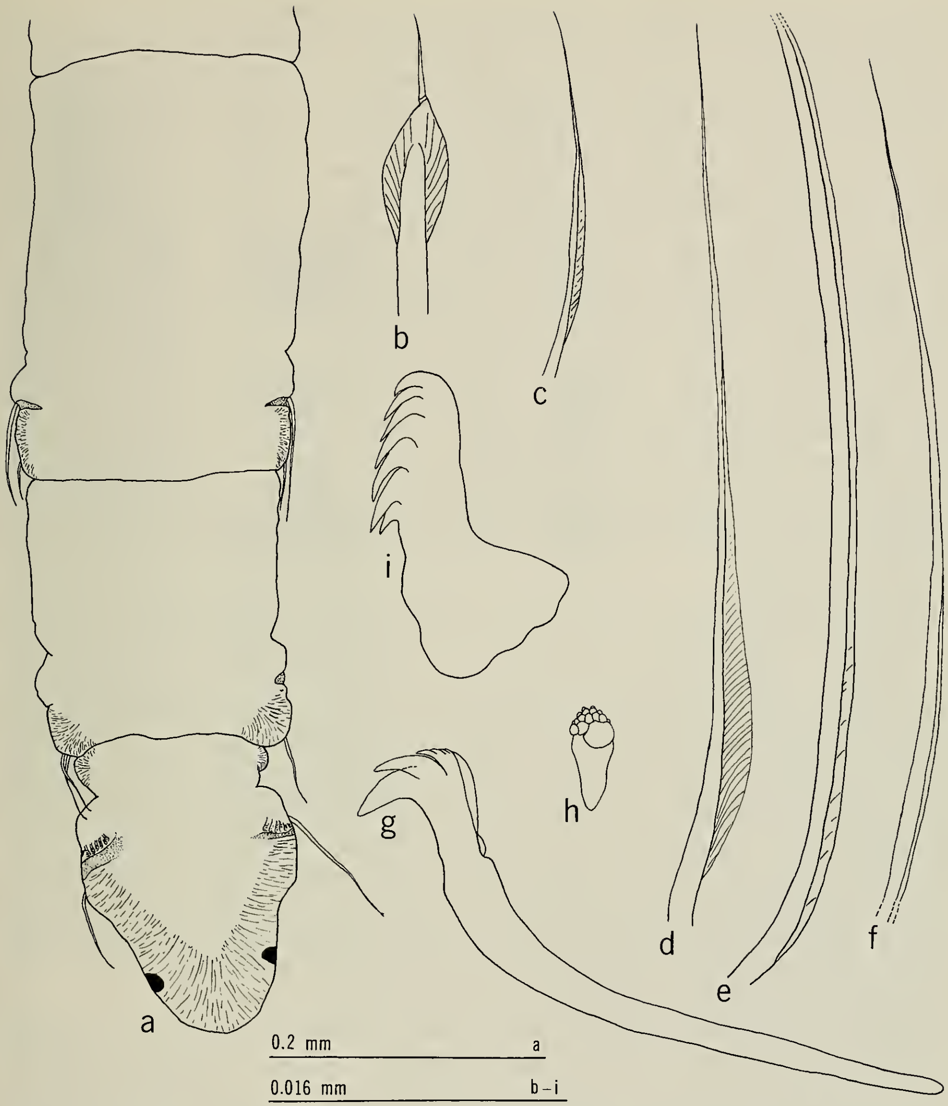


Fig. 2. *Fabriciola trilobata* (a from holotype; b–i from paratype, USNM 74683): a, Posterior end, dorsal view; b, Thoracic spatulate seta from setiger 3; c, Superior abdominal neuroseta from setiger 10; d, Thoracic notoseta from setiger 3; e–f, Proximal and distal portions of inferior abdominal neuroseta from setiger 10; g–h, Lateral view of thoracic neuropodial uncinus and frontal view of tooth arrangement, both from setiger 5; i, Abdominal notopodial uncinus from setiger 9.

The holotype and some paratypes were stained with a dark solution of methyl green in ethanol. Specimens were placed in the solution for 30 minutes, allowed to destain in ethanol for 10 minutes and observed. Uptake of stain differed considerably from holotype and paratypes; thus both patterns will be described.

In the holotype the collar segment only stained ventrally, extending from just posterior to the collar margin to the posterior segment margin, becoming darker posteriorly (Fig. 3a). Setiger 1 stained darkest ventrally along the anterior margin, extending posteriorly as a triangular pattern to the near the ventral midpoint. Remainder of the ventrum was more lightly stained, fading laterally and dorsally. Notopodial tori did not stain. On setiger 2 a broad midventral strip was darkest, with less staining to either side, fading laterally and dorsally. Noto- and neuropodial tori of this and following thoracic and abdominal setigers did not stain. Setiger 3 stained evenly ventrally, with lateral and dorsal staining as in previous setigers. The ventral anterior half of setiger 4 was well stained, becoming lighter posteriorly, laterally and dorsally. Setigers 5–7 had fewer, but larger, stain-accepting cells ventrally and laterally, thus imparting a light green hue. The anterior margin of setiger 8 was stained as in adjacent setigers, becoming darker posteriorly. Setigers 9–10 were darker and evenly stained on both sides of the segments with large staining cells. Setiger 11 was similar to 9–10 but darker. Glandular areas on abdominal setigers stained darker than the rest of the corresponding segment. The pygidium stained very deeply, especially the glandular area. The fecal groove was non-staining, extending from the anterior margin of the anus along the ventral midline of setigers 11–10. On setiger 9 it extends diagonally to the left to near the dorsal midline of the anterior margin, continuing anteriorly to the collar segment.

In paratypes examined, the anterior portion of the collar segment accepted stain only in a well defined lateral area just posterior to the eyes, extending to near the dorsal midline posteriorly (Fig. 3b–c). Much of this area was characterized by large, dark staining cells. The posterior region of the collar segment was uniformly stained ventrally and ventrolaterally. Setiger 1 showed a dense staining region along the midventral anterior margin, with the remainder of the ventrum lightly stained. Laterally, a green hue was present in addition to some large stain-accepting cells. The anterior and posterior midventral margins of setiger 2 were densely stained, in addition to large staining cells interspersed between the two areas. The remaining ventral and lateral areas were lightly stained. The ventral anterior margin of setiger 3 was darkly stained, becoming lighter posteriorly with some large staining cells. Lateral staining was similar to anterior setigers. The remaining segments and pygidium stained similar to the holotype.

Remarks.—*Fabriciola trilobata* shows some similarity to *F. capensis* (Monro 1937:366; see also Day 1955:447). Table 1 compares the two species. Both exhibit a trilobate middorsal collar margin formed by the presence of a middorsal groove. The body of both species is elongate, but *F. capensis* possesses much longer segments. The two species differ in that in *F. trilobata* the dorsal side of the collar is higher than the ventral, while in *F. capensis* it is even; also, all thoracic notosetae in the latter species are bilimbate and no spatulate setae have been reported. Abdominal uncini of the two species differ in number of tooth rows (7–9 in *F. trilobata* and 18 in *F. capensis*).

In addition to the above characters, the tooth arrangement above the main fang of thoracic uncini, increasing number of tooth rows in uncini of successive abdominal setigers, and the presence of minute superior limbate setae in abdominal neuropodia have not been described in any other *Fabriciola* species. Banse (1957) reported the presence of minute "needle-like" setae in thoracic notopodia of *Oriopsis rivularis* (Annenkova 1929), and Banse (1959) noted a similar setal type

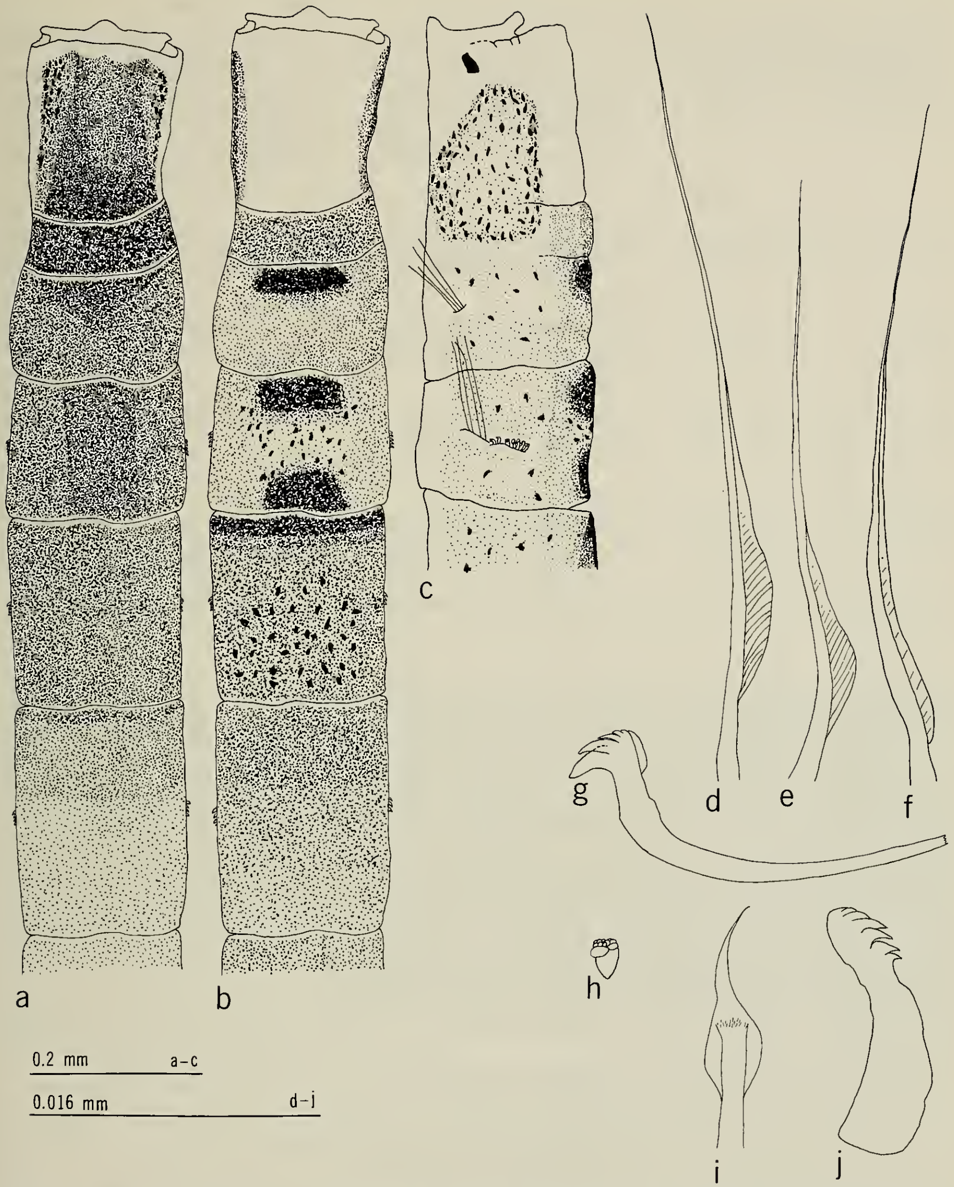


Fig. 3. *Fabriciola trilobata:* a, Staining pattern of anterior end of holotype, ventral view; b–c, Staining pattern of anterior end of paratype (USNM 74685), ventral and lateral views. *Fabricia infratorquata* (all from paratypes, USNM 74658): d–e, Superior and inferior thoracic notosetae from setiger 6; f, Abdominal neuroseta from setiger 9; g–h, Lateral view of thoracic neuropodial uncinus and frontal view of tooth arrangement, both from setiger 6; i, Thoracic spatulate seta from setiger 3; j, Abdominal notopodial uncinus from setiger 9.

Table 2.—Comparison of selected species of *Fabricia*.

Species	Palps	Collar	Thoracic notosetae
infratorquata	Absent	Indistinct dorsally, split by middorsal groove; large triangular lobe ventrally.	Setiger 1–8: 3–4 long limbates. Setiger 2,6–8: 1 short limbate. Setiger 3–5: 1–2 spatulates.
bansei	Absent	Indistinct dorsally, large triangular lobe ventrally.	Setiger 1–8: 4–5 limbates. Setiger 2–8: 2–3 spatulates.
brunnea	Absent	Pair semicircular lobes dorsally; elongate lobe ventrally.	Setiger 1: pointed setae. Setiger 2–8: 3 limbates, 1 spatulate.
gerdi	Absent	Indistinct dorsally, large rounded lobe ventrally.	4–6 long limbates, 1–2 short limbates.
sabella	Present	Indistinct dorsally, triangular lobe ventrally.	Setiger 1: 3–6 long, 2–3 short limbates. Setiger 2–8: 5–6 long limbates. Setiger 3–7: 2 spatulates.

in thoracic notopodia of *Fabriciola acuseta.* It is likely that small setal forms have been overlooked in thoracic and abdominal setigers of *Fabriciola.*

The distinct difference between the staining pattern of the holotype in comparison to paratypes might suggest sexual dimorphism. An alternative explanation might be changes in gland cell distribution in relation to size or age of individuals. The latter suggestion is unlikely since both large and small individuals stained similarly. Only Banse (1970) has examined staining variability using *Euchone incolor* Hartman, 1965, from different localities. He only noted staining differences which were probably attributable to geographic variation, making no mention of noticeable differences within a single locality.

Etymology.—The specific epithet refers to the three lobes at the anterior middorsal collar margin.

Distribution.—*Fabriciola trilobata* is known only from the type-locality.

Fabricia infratorquata, new species

Figs. 3d–j, 4; Table 2

Material examined.—West Bay, Twin Cays, Belize; 30 cm depth; mat of *Caulerpa verticillata* on rootmat of *Rhizophora mangle,* some organic debris and fragments of *Halimeda*; 7 Apr 1982 (Array F202), 9 Apr 1982 (Array F203), 11 Apr 1982 (Array F204); coll. K. Fauchald. Holotype: F204 D-4 (USNM 74644). Paratypes: F204 A-1, 1 specimen (USNM 74645); F204 A-2, 7 specimens (USNM 74646); F204 A-3, 3 specimens (USNM 74647); F204 A-4, 2 specimens (USNM 74648); F204 A-5, 1 specimen (USNM 74649); F204 B-1, 4 specimens (USNM 74650); F204 B-2, 4 specimens (USNM 74651); F204 B-3, 2 specimens (USNM 74652); F204 B-4, 1 specimen (USNM 74653); F204 B-5, 1 specimen (USNM 74654); F204 C-2, 3 specimens (USNM 74655); F204 C-4, 1 specimen (USNM

Table 2—(Continued).

Thoracic neurosetae	Abdominal notosetae	Abdominal neurosetae
Setiger 2–5: 6–8 uncini in double rows. Setiger 6–8: 5–6 uncini in single rows. Main fang + 1 large and 1 small tooth + 3 rows of smaller teeth.	11–14 long-handled uncini; 7 rows of teeth; 1–5 teeth per row.	1–2 long, narrow limbates.
6–12 uncini. Main fang + 1 large tooth + arc of smaller teeth.	14 long-handled uncini; 5–6 rows of teeth; 1–2 teeth per row.	2–4 narrow limbates.
8–9 uncini in partial double rows. Main fang + 3 rows of smaller teeth.	Long-handled uncini; 6–7 rows of teeth; 2–3 teeth per row.	?
12–14 uncini in double rows. Main fang + 1 large tooth + 1 small tooth + arc of 9 smaller teeth.	16–21 short-handled uncini; 9 rows of teeth; 1–3 teeth per row.	3–4 narrow limbates.
9–12 uncini. Main fang + 4 rows of smaller teeth.	30 long-handled uncini; 9 rows of teeth.	2–3 long and 1–2 short narrow limbates.

74656); F204 D-3, 4 specimens (USNM 74657); F204 D-4, 9 specimens (USNM 74658); F204 D-5, 1 specimen (USNM 74659). Additional material: F202 A-1, 2 specimens (USNM 74660); F202 B-1, 2 specimens (USNM 74661); F202 B-4, 1 specimen (USNM 74662); F202 C-2, 3 specimens (USNM 74663); F202 C-4, 1 specimen (USNM 74664); F202 D-2, 1 specimen (USNM 74665); F202 D-3, 5 specimens (USNM 74666); F203 A-1, 1 specimen (USNM 74667); F203 A-5, 3 specimens (USNM 74668); F203 B-3, 1 specimen (USNM 74669); F203 B-5, 1 specimen (USNM 74670); F203 C-1, 1 specimen (USNM 74671); F203 C-2, 2 specimens (USNM 74672); F203 C-4, 2 specimens (USNM 74673); F203 C-5, 1 specimen (USNM 74674); F203 D-1, 1 specimen (USNM 74675); F203 D-2, 1 specimen (USNM 74676); F203 D-4, 2 specimens (USNM 74677); F203 D-5, 1 specimen (USNM 74678).

Diagnosis.—Small species of *Fabricia* without palps. Peristomium concealed by collar segment. Ventral collar a distinct, anteriorly rounded triangular lobe. Dorsal and lateral parts of collar low, indistinct. Dorsal, longitudinal midline of collar segment occupied by broad groove. Collar segment divided into anterior and posterior parts by distinct annulation. Thoracic neuropodial uncini of setigers 2–5 in irregular double rows, continuing as single rows in setigers 6–8; with 2 unequal teeth above main fang, followed by series of smaller teeth. Abdominal uncini long-handled, with 7 rows of teeth.

Description.—The holotype is a complete specimen with 8 thoracic and 3 abdominal setigers. Length 1.60 mm (0.56 mm comprising the branchial crown) and width 0.21 mm.

A pair of semicircular branchial lobes are attached anteriorly, each with a large branchial heart situated dorsally (Fig. 4a). Three radioles are attached to each branchial lobe; they are unbranched and rounded externally. Four to 5 pairs of

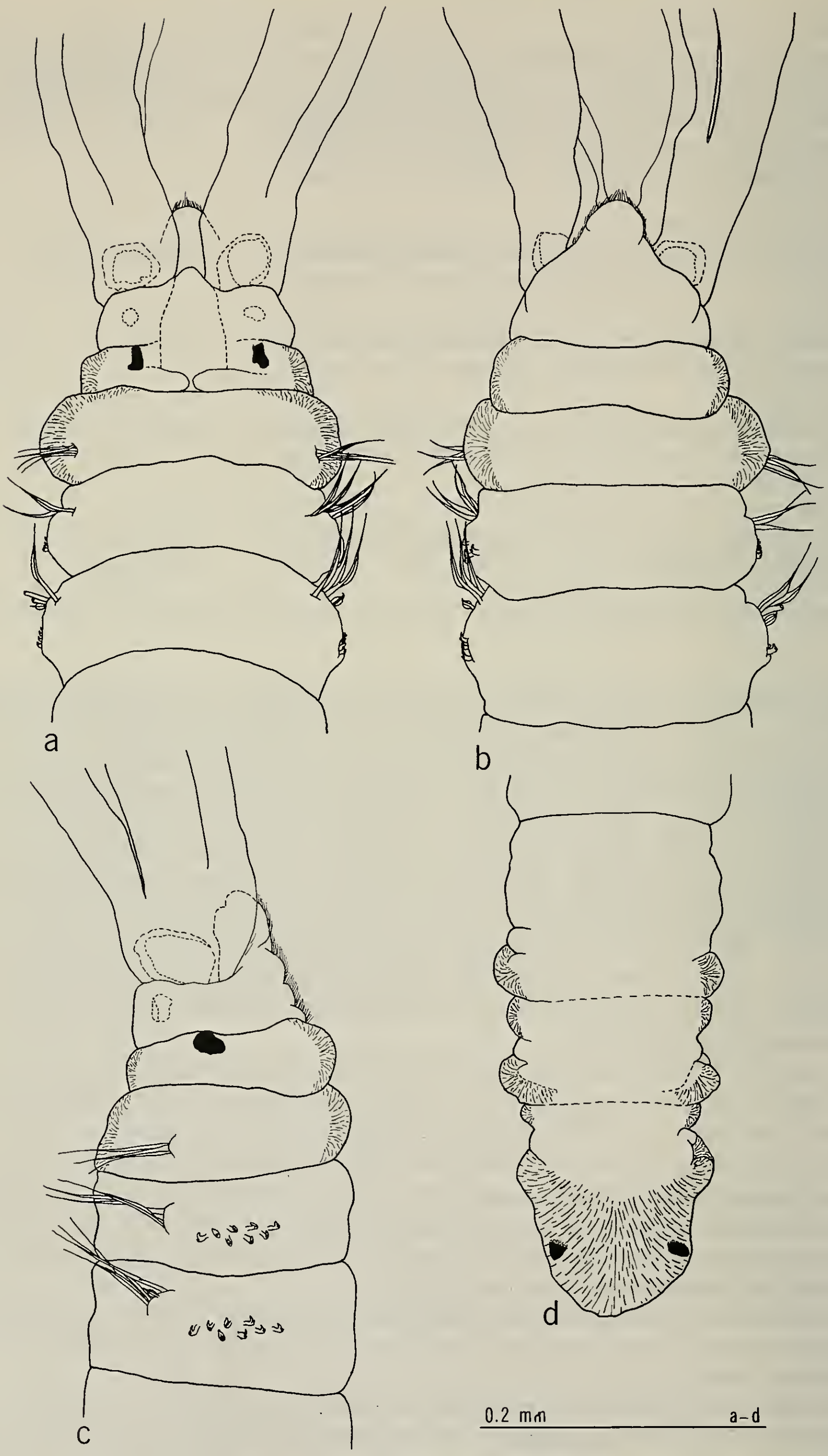


Fig. 4. *Fabricia infratorquata* (paratype, USNM 74658): a–c, Dorsal ventral and lateral views of anterior end; d, Posterior end, dorsal view.

ciliated pinnules extend from the inner side of each radiole. The proximal pair are longest, with successive pairs becoming shorter so that all terminate near the distal end of the radiole. Distal ends of the radioles are blunt. Palps are absent.

The collar segment completely conceals the peristomium. Ventrally, the collar is distinct, forming a thick, large triangular lobe which is rounded anteriorly (Fig. 4b–c). The ventral surface of the ventral collar is heavily ciliated. Laterally and dorsally the collar is low and indistinct. The dorsal collar is divided by a longitudinal middorsal groove which extends from the anterior margin of the collar segment as a slight protrusion to near the segment's posterior margin, and occupies the middorsal ⅓ of the collar segment width. Adjacent to the posterior margin of the groove are a pair of indistinct narrow ridges, situated perpendicular to the groove and directed middorsally, with a narrow gap between the 2 ridges. The collar segment is separated into anterior and posterior halves by an annulation which is distinct ventrally and laterally, disappearing dorsally as it nears the middorsal groove. The anterior part of the collar segment is slightly longer than the posterior part, but the latter is wider. Ventrally, the posterior part is slightly inflated, overlapping the anterior portion of setiger 1. The ventral half of the ventral collar and the epidermis of the posterior part of the collar segment contain a large number of glandular cells.

All thoracic setigers are cylindrical, constricted at intersegmental grooves. Transition from the collar segment to setiger 1 is denoted by an abrupt increase in segment width. Setiger 1 is the shortest thoracic segment, about ⅔ the length of the collar segment. All subsequent thoracic setigers become longer. Setigers 1–4 are widest, about ¼ wider than the collar segment, and are wider than long. Setigers 5–8 only decrease slightly in width, but are longer than wide. The epidermis of setiger 1 is composed of glandular cells of about the same thickness as in the posterior portion of the collar segment.

Abdominal setigers become successively shorter, with setiger 9 about ½ the length of setiger 8 (Fig. 4d). All are wider than long, becoming slightly narrower posteriorly. Setigers 9–10 are cylindrical and setiger 11 is slightly dorsoventrally flattened. Separation between thorax and abdomen is distinct. Intersegmental grooves are indistinct on abdomen. Pad-like, swollen glandular areas occur laterally behind notopodial tori of setigers 9–10, and at the anterior lateral margins of setigers 10–11.

Noto- and neuropodial thoracic tori are only slight swellings. Notopodia are located dorsolaterally in all segments. Neuropodia, absent from setiger 1, are situated ventral to and slightly posterior to notopodia of remaining setigers. Notosetae in setigers 1–8 include 3–4 superior long, nearly straight, limbate setae (Fig. 3d). Setigers 2 and 6–8 also have 1 inferior shorter limbate seta with a curved shaft (Fig. 3e). Setigers 3–5 also possess 1–2 inferior short spatulate setae (Fig. 3i). Notosetal fascicles are inserted obliquely. Thoracic neurosetae are gently curved acicular uncini (Fig. 3g). Uncini of setigers 2–5 occur in vertical, irregular double rows; the anterior row being slightly dorsal to the posterior row. Each row within a torus contains 3–4 uncini. Neurosetae in setigers 6–8 are in a single row of 5–6 uncini in each setiger. In lateral view, the distal end appears to have a main fang surmounted obliquely by a large tooth, followed by 3 smaller teeth. In frontal view, the main fang is surmounted by 2 pair of unequal teeth (Fig. 3h). Above the large tooth are 3 smaller teeth; proximal to this are two concentric arcs of teeth. Proximal to the distal end the shaft is slightly swollen, then tapers to a rounded end.

Abdominal notopodia are distinct lateral tori on the posterior ¼ of the segments, and of the same length as thoracic neuropodia. Notosetae are long-handled uncini, numbering 14 in setigers 9–10 and 11 uncini in setiger 11 (Fig. 3j). All uncini have 7 rows of teeth; the number of teeth per row as follows (proximal to distal): 1+2+3+4+5+4+3. Proximal to the teeth the shaft is slightly constricted, then inflated proximally and terminated in a truncate base. Neurosetae originate just ventral to notopodia. No neuropodial tori are visible. All neurosetae are of one type: 1–2 subequal, long-shafted limbate setae with a narrow limbation, and are directed dorsally (Fig. 3f).

The pygidium is not clearly delimited from setiger 11, thus is assumed to begin just posterior to the notopodial tori. Anteriorly, the pygidium is of the same width as the adjacent segment, narrowing slightly posteriorly to a rounded end. It is dorsoventrally flattened. Except for the anterior margin, the entire pygidium surface is glandular. The anus is a slightly depressed, longitudinal, midventral slit.

A pair of large roughly crescentic eyes (dorsal view) are visible just posterior to the intrasegmental annulation of the collar segment, on either side of the middorsal groove. A pair of smaller, circular eyes are located laterally in the pygidium. A pair of translucent otocysts, slightly smaller than the anterior pair of eyes, are located dorsally in the anterior part of the collar segment on either side of the middorsal groove.

The holotype and other large individuals are opaque and cream colored in alcohol. Small individuals tend to be more translucent.

Individuals occupy soft, thick tubes (about 2–2.5 times as thick as the worm), constructed with plant and detrital material. The inner tube diameter is only slightly greater than the width of the worm, such that nearly the entire length of the individual is in contact with the tube.

The holotype and some paratypes were stained with methyl green by the method described above. In the holotype, the posterior portion of the collar segment and setiger 1 were uniformly stained dark green except for the fecal groove and tori, neither staining in any segment. Setigers 2–8 were uniformly stained lightly, giving a green hue. Setigers 9–11 stained much darker than adjacent setigers due to large stain-accepting cells and glandular areas. The pygidium was darkly stained as in other glandular areas. Paratypes stained similar to the holotype. Some specimens did show a greater degree of staining in setigers 5–8, resembling that of abdominal setigers. The ventral collar of one specimen did stain lightly, but otherwise it was similar to other individuals.

Remarks.—Fabricia infratorquata is one of a group of *Fabricia* which possess a distinct, triangular ventral collar. Table 2 compares these species. *Fabricia infratorquata* is readily distinguished from *F. sabella* (Ehrenberg, 1836; see Hartmann-Schroeder 1971:513) in that the latter possesses palps and all thoracic uncini occur in single rows. *Fabricia bansei* Day (1961:543) differs from *F. infratorquata* in the arrangement and number of teeth on thoracic and abdominal uncini. *Fabricia infratorquata* closely resembles *F. brunnea* Hartman (1969:693) in that both have at least some thoracic uncini in double rows; the species differ in that the dorsal collar of the latter has a pair of small semicircular lobes and abdominal uncini have 2–3 teeth per row (1–5 teeth per row in *F. infratorquata*). *Fabricia* *gerdi* Hartmann-Schroeder (1974:199) is also very similar to the new species in relation to the collar and occurrence of thoracic uncini in double rows; they differ in the arrangement of teeth on the thoracic and abdominal uncini.

Etymology.—The specific epithet refers to the large, triangular ventral collar.

Distribution.—*Fabricia infratorquata* is known only from the type locality.

Discussion

Fabriciola trilobata and *Fabricia infratorquata* both possess a character which has not been described in these genera: the asymmetrical arrangement of teeth above the main fang of thoracic uncini. Examination of uncini in a frontal view has not been common, probably due to difficulty in manipulating setae for observation at such an angle. As a result a possible diagnostic character has been overlooked.

Another setal characteristic of both species not commonly described is the number of teeth per row in abdominal uncini. Most species in which this has been described display a rather uniform number of teeth in each row, except in some cases of variation at extreme proximal and distal tooth rows. In the species described herein this pattern did not occur. In *F. trilobata* the number of teeth per row gradually increased in a proximal-distal direction, except for uncini from setiger 11, in which median tooth rows alternated with 3 and 4 per row. *Fabricia infratorquata* displayed an increasing number of teeth from proximal to distal, with a slight decrease in the 2 distal-most rows. A similar pattern was noted by Friedrich (1939) for *Fabriciola baltica*, with the arrangement: 3+4+5+6+6+6+6+4+4. This pattern of variation is probably common in other species of both genera, but has yet to be examined.

The majority of *Fabriciola* and *Fabricia* descriptions pay little attention to abdominal neurosetae; most reports refer to them as fine capillaries or ignore their presence. Closer attention should be given to these setae since size and structural differences, as seen in *F. trilobata*, could be of taxonomic use.

The presence of an annulation on the collar segment of *F. trilobata* and *F. infratorquata* suggests the presence of an additional achaetous segment. Figures of *Fabriciola limnicola* given by Hartman (1951) depict an annulation very similar to that on *F. trilobata*. Annulations have also been illustrated by Day (1955) for *F. capensis*, by Day (1957) for *F. mossambica*, and by Friedrich (1939) for *F. baltica*. Figures of *Fabricia* show a similar annulation but it is situated further anteriorly, suggesting that it is simply a demarcation of the collar from the collar segment. In *F. infratorquata* this does not occur; the annulation is distinctly posterior to the collar, suggesting that the collar "segment" is composed of two segments. At this time it can only be suggested that this feature be noted in future descriptions until such time as sectioning determines if it is an actual segment boundary.

Acknowledgments

I gratefully acknowledge Dr. Kristian Fauchald for his constant assistance, for providing space at the National Museum of Natural History, and making available the benthic samples from which the present species were described. His critical review of the manuscript is greatly appreciated.

Funding for this research was provided in part by Smithsonian Institution contract #SF2062530000.

Literature Cited

Banse, K. 1956. Beiträge zur Kenntnis der Gattungen *Fabricia, Manayunkia* und *Fabriciola* (Sabellidae, Polychaeta).—Zoologische Jahrbucher, 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, Kobenhaven 119:67–105.

———. 1959. *Fabricia acuseta* n. sp., *Fabriciola ghardaqa* n. sp. und *Oriopsis armandi* (Claparede) aus dem Roten Meer (Sabellidae, Polychaeta).—Kieler Meeresforschungen 15:113–116.

———. 1970. The small species of *Euchone* Malmgren (Sabellidae, Polychaeta).—Proceedings of the Biological Society of Washington 83:387–408.

———. 1972. Redescription of some species of *Chone* Kroyer and *Euchone* Malmgren, and three new species (Sabellidae, Polychaeta).—Fishery Bulletin 70:459–495.

———. 1979. Sabellidae (Polychaeta) principally from the northwest Pacific Ocean.—Journal of the Fisheries Research Board of Canada 36:869–882.

Day, J. H. 1955. The Polychaeta of South Africa. Part 3: Sedentary species from Cape shores and estuaries.—Journal of the Linnean Society of London 42:407–452.

———. 1957. The polychaete fauna of South Africa. Part 4: New species from Natal and Moçambique.—Annals of the Natal Museum 14:59–129.

———. 1961. The polychaete fauna of South Africa. Part 6: Sedentary species dredged off Cape coasts with a few new records from the shore.—Journal of the Linnean Society of London 44: 463–560.

———. 1967. A monograph on the Polychaeta of southern Africa. Part 2: Sedentaria.—British Museum of Natural History Publications 656:459–878.

Fauchald, K. 1977. The polychaete worms. Definitions and keys to the orders, families and genera.—Natural History Museum of Los Angeles County, Science Series 28:1–190.

Friedrich, H. 1939. Polychaeten—Studien. V–X. Zur Kenntnis einiger wenig bekannter odor neuer Polychaeten aus der westlichen Ostsee.—Kieler Meeresforschungen 3:362–373.

Hartman, O. 1951. Fabricinae (feather-duster polychaetous annelids) in the Pacific.—Pacific Science 5:379–391.

———. 1969. Atlas of sedentariate polychaetous annelids from California.—Allan Hancock Foundation, University of Southern California, Los Angeles, 812 pp.

Hartmann-Schroeder, G. 1971. Annelida, Borstenwurmer, Polychaeta.—Die Tierwelt Deutschlands 58:1–594.

———. 1974. Teil II. Die Polychaeten des Untersuchungsgebietes. *In* G. Hartmann und G. Hartmann-Schroeder, Zur Kenntnis des Eulitorals der afrikanischen Westkuste Zwischen Angola und Kap der Guten Hoffnung und der afrikanischen Ostkuste von Südafrika und Moçambique unter besonderer Berucksichtigung der Polychaeten und Ostracoden.—Mitteilungen des Hamburger Zoologisches Museum und Institüt, Erganzungsband 69:95–228.

Monro, C. C. A. 1937. Notes on a collection of Polychaeta from South Africa, with the description of a new species belonging to the family Sabellidae.—Annals and Magazine of Natural History (Series 10) 19:366–370.

Division of Worms, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Current address: Texas A&M University, Building 311, Fort Crockett, Galveston, Texas 77550.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 291–300

BERMUDALANA ARUBOIDES, A NEW GENUS AND SPECIES OF TROGLOBITIC ISOPODA (CIROLANIDAE) FROM MARINE CAVES ON BERMUDA

Thomas E. Bowman and Thomas M. Iliffe

Abstract.—*Bermudalana aruboides*, a blind unpigmented cirolanid isopod representing a new genus, is described from inland marine caves on Bermuda. It is the first hypogean cirolanid known from Bermuda. The close resemblance between *Bermudalana* and *Arubolana*, known from brackish groundwater on Aruba, Netherlands Antilles, suggests that both were derived from a common marine ancestor.

The inland marine caves of Bermuda contain a rich and diverse invertebrate fauna (Sket and Iliffe 1980). The extensive nature of the underwater portions of these limestone caves, some being more than 1.5 km in length (Iliffe 1980), and the presence of strong tidal currents passing through them have resulted in the establishment of a considerable range of biotopes. In coastal cave entrances and those cave passages with strong tidal currents, sponges, bryozoans, hydroids, and other encrusting organisms literally cover all rock surfaces. Deeper into the caves, where tidal currents become more diffuse, sponges and other associated fauna become far less numerous. In the deepest inland caves most remote from the sea, the walls are totally barren of encrusting organisms and only specially adapted troglobitic species are present. This zonation approximately corresponds to that recognized in terrestrial caves (Poulson and White 1969): a twilight zone near the entrance, a middle zone of complete darkness and variable temperature, and a zone of complete darkness and constant temperature in the deep interior. In marine caves as well as in terrestrial caves, the twilight (coastal entrance) zone has the largest and most diverse fauna; the middle zone has some species which may commute to the surface (bats and crickets in terrestrial caves; lobsters in marine caves). The deep interior cave, while being the most depauperate, possesses environmental and faunal aspects unique to caves.

The existence of marine troglobites is a relatively new discovery. As recently as 1965, Vandel stated that "animals (from marine caves) have not usually undergone noticeable modification" and thus "marine caves . . . have but a slight interest to the biospeleologist" (1965:8). In our faunal survey of Bermuda's marine caves, the following troglobitic species have so far been described: *Atlantasellus cavernicolus*, an isopod representing a new family (Sket 1979); *Somersiella sterreri* and *Typhlatya iliffei*, two new species of caridean shrimp (Hart and Manning 1981); and *Mesonerilla propsera*, a new archiannelid polychaete (Sterrer and Iliffe 1982). Additional new species described from Bermuda's caves which may or may not be troglobitic include *Miostephos leamingtonensis*, a new calanoid copepod (Yeatman 1980); and *Apseudes bermudeus*, a new hermaphroditic tanaidacean (Băcescu 1980). We here describe a new genus and species of troglobitic cirolanid isopod from deep interior marine caves on Bermuda.

Fig. 1. Church Cave, Bermuda, seen from entrance.

Bermudalana, new genus

Diagnosis.—Eyes absent. Without pigment except brown incisors of mandibles. Pleonites all free, all reaching lateral margin of pleon. Frontal lamina with keel. Clypeus produced ventrally into slender conical process. Peduncles of antenna 1 and 2 3- and 5-segmented; flagella with relatively few segments. Maxilla 2 reduced, palp and exopod lacking, endopod with only a few distal setae. Maxilliped with sparse setation, palp 4-segmented, endite with 1 retinaculum. Pereopods 1–3 prehensile; pereopods 4–7 slender, ambulatory. Pleopods 1–2 with undivided setose rami. Pleopods 3–5 with 2-segmented setose exopods and undivided endopods; endopods of pleopods 3–4 with a few apical setae, endopod of pleopod 5 without setae. Appendix masculina inserted subterminally. Penes well developed, narrowly cylindrical, separated at base.

Type species.—Bermudalana aruboides, new species.

Etymology.—From the locality, Bermuda, plus (*Ciro*)*lana*. Gender feminine.

Bermudalana aruboides, new species

Figs. 2–4

Material.—Bermuda: Church Cave (also known as Paynter's Vale Cave), Hamilton Parish, 11 July 1982, leg. T. M. Iliffe, 4 ♂ (3.9, 3.8, 3.6, 3.1 mm) and 2 ♀ (4.1, 3.3 mm) were collected from 7 to 10 m water depths with scuba using a suction bottle. Wonderland Cave (also known as Whitby Cave), Hamilton Parish, 19 May 1982, leg. T. M. Iliffe, 2 ♂ (3.7, 3.4 mm) and 3 ♀ (4.0, 4.0, ? mm) were collected from 10 to 15 m depths with scuba using a suction bottle. The 3.9 mm ♂ from Church Cave is the holotype (USNM 195020); the other specimens are paratypes (Church Cave specimens USNM 195021, Wonderland Cave specimens USNM 195022).

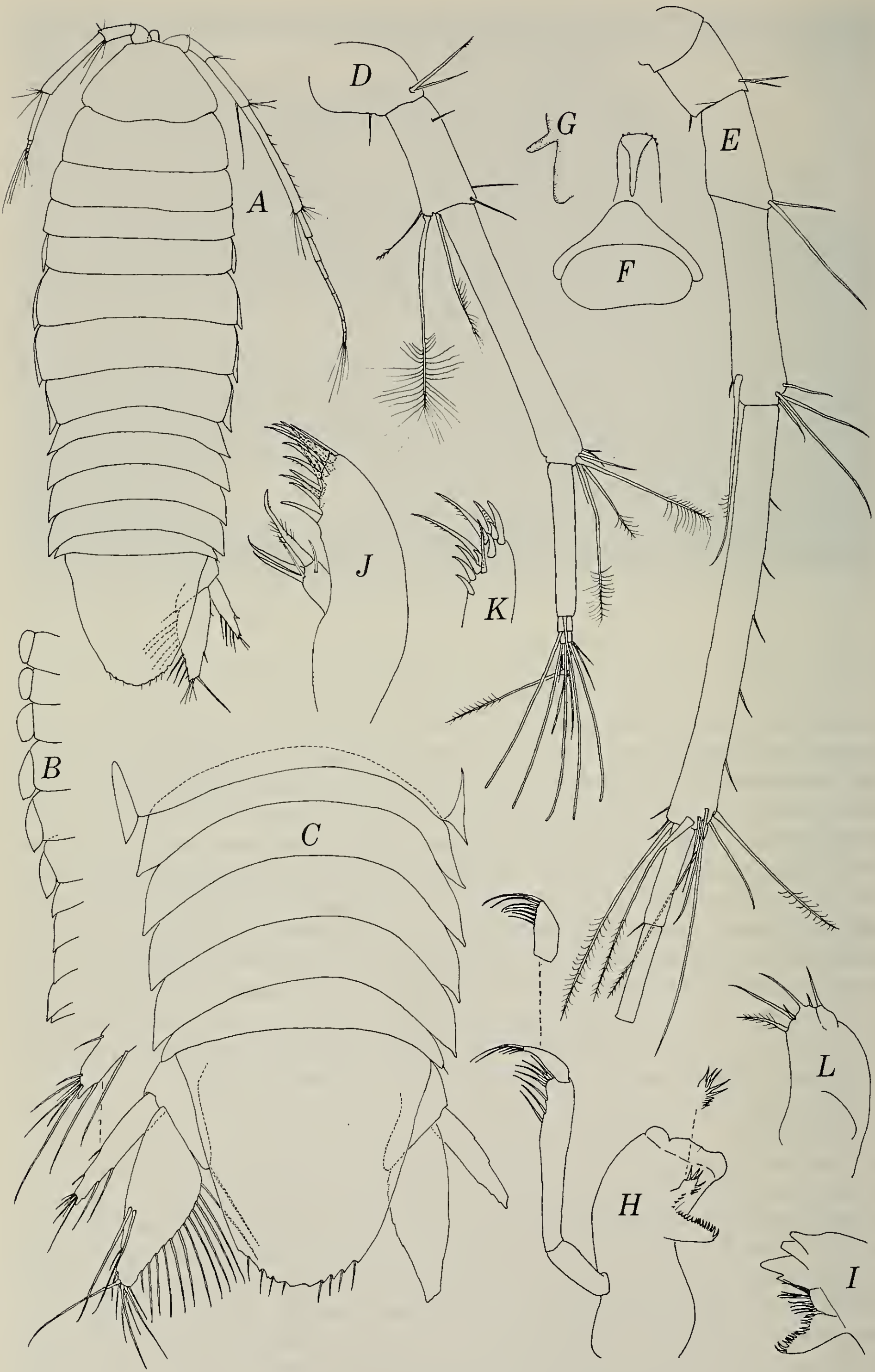
Distribution.—Known only from the anchialine habitats of Church and Wonderland Caves, Bermuda.

Habitat.—The Bermuda islands consist of a mid-ocean volcanic seamount capped with Pleistocene and Recent, marine and eolian limestones. Bermuda is one of the world's most geographically isolated islands, located 1000 km east of the North American continent in the section of the North Atlantic known as the Sargasso Sea. Bermuda has never been part of a continental land mass. The island's limestone caves were formed during low stands of sea level corresponding to periods of Pleistocene glaciation (Bretz 1960; Palmer *et al.* 1977; Iliffe 1981). As postglacial sea levels rose, much of the former extent of the caves was flooded by sea water. Approximately 200 inland caves are known from Bermuda, over half of which contain tidal, sea level pools.

Church Cave is located on the grounds of the Castle Harbour Hotel about 250 m linear distance from Castle Harbour, the nearest body of open salt water. The main entrance is about 26 m above sea level and consists of an opening 25 m wide by 15 m high in a collapse sink 25 m in diameter. Inside this entrance, a long steep breakdown slope descends to a sea level lake 35 m wide by 35 m across (Fig. 1). A small amount of sunlight from the entrance can reach one corner of the lake, but the rest remains in total darkness. The tides in this lake have an average range of 40% that of the open sea and have a lag time of about 107 minutes. Surface salinity is between 15.5 and 22.8‰, probably varying with rainfall, while at 1, 10, and 20 m depths, salinities are about 27, 34.5, and 35.3‰ respectively. Surface temperatures seasonally range from about 16 to 19°C, but temperatures in deeper waters (20.3°C at 20 m) remain nearly constant year round. The natural geothermal gradient has been proposed as a possible explanation for this anomalous temperature increase with depth (Iliffe *et al.* 1983). The sides of the lake are undercut, with the bottom being 20 m at the deepest point and floored with breakdown blocks of considerable size, but little fine sediments. The underwater parts of the cave are abundantly decorated with delicate speleothems, including "soda straws" and helectites, all perfectly preserved despite their long submersion. The presence of such speleothems, which only form in air, in all explored parts of the underwater caves indicates that the caves were dry during the prolonged periods of Pleistocene glaciation when sea levels were 80 to 100 m lower than today. Only one underwater cave passage has been found extending away from the lake and this ends after 45 m in a flowstone plug.

Wonderland Cave is located 2 km northwest of Church Cave and is 420 m from Castle Harbour. It was once operated as a commercial cave, but has not been used for such purposes since the 1940s. A steep set of 89 steps descends from the small entrance building located at an elevation of 24 m to a large room developed along a linear inclined fissure. The room contains a sea level lake 60 m long by as much as 12 m wide. This lake is 18 m at the deepest point and floored by large slabs of breakdown. A 50 m long underwater passage extends from the far side of the lake to re-emerge in an air-filled breakdown room. No other underwater passages have been found. As in Church Cave, many large stalactites and stalagmites are present even in the deepest parts of the lake.

All specimens of *Bermudalana* were taken from open waters of the lakes by


A
B
C
D
E
F
G
H
I
J
K
L

cave divers as the animals were observed swimming several meters above the bottom. Divers used a bright underwater light to scan the very clear cave waters. Any animals or particles in the water would flash as the light beam passed across them, effectively locating them. The swimming behavior of *Bermudalana* is most likely a result of the animal's food locating actions and not an escape reaction. No specimens were ever observed crawling over the substrate. The lack of any encrusting organisms with only planktonic or nektonic species being observed also supports the idea that *Bermudalana* is a predator, capturing its food from open waters. Other animals collected or observed from Church and Wonderland Caves include a halocyprid ostracod now under study, a peracarid representing a new order (Bowman and Iliffe, in preparation), and a caridean shrimp, probably *Typhlatya iliffei*. Copepods are probably also present as they have been found in nearly every marine cave studied in Bermuda. It is likely that *Bermudalana* will also be found in other far inland caves of Bermuda as they are investigated.

Description.—Body moderately slender, slightly more than 3× as long as wide, length about 4 mm. Anterior margin of head slightly concave on either side of minute rostrum, about 1.7× as wide as long. Frontal lamina visible in dorsal view, about a third longer than wide, ventral surface produced into carina. Clypeus in lateral view produced into rather slender cylindrical process.

Pereonites 1 and 5–7 subequal in length, distinctly longer than the subequal pereonites 2–4; all pereonites with rounded posteroventral corners. Posteroventral corners of coxae 2–4 rounded, of 5–7 with small points. Pleon (excluding telson) about half length of pereon; pleonites 1–4 subequal in length, pleonite 5 shorter and slightly narrower, epimera all ending in small points. Telson linguiform, slightly shorter than width at base, posterior sixth with 4 setae on each side set in marginal notches; marginal spines absent.

Antenna 1 reaching slightly beyond posterior margin of pereonite 1; peduncle segment 3 very long, peduncle segments 2–3 with long plumose distal setae; flagellum 5-segmented, 1st segment nearly 3× as long as remaining segments combined, all segments with long esthetes. Antenna 2 reaching posterior margin of pereonite 6; segments of peduncle successively longer; flagellum 8-segmented.

Incisors of mandibles with 3 cusps, cusps more deeply separated in right mandible; left lacinia with 10 spines, right lacinia with 9 spines; molar with 14 spines; segment 2 of palp about 2.5× as long as segment 1, with about 7 marginal setae on distal fifth; segment 3 slightly shorter than segment 1, with about 7 setae.

Maxilla 1 exopod apex with 10 spines, 2 much longer than others, and a central seta; endopod with 3 apical spines and 2 subterminal setae. Maxilla 2 reduced to single ramus armed apically with 4 long and 2 short setae. Maxilliped endite with 2 apical plumose setae.

Pereopods 1–3 subchelate, dactyl closing against palm of expanded propus; palm bearing distally a spine with posterior setule, 3–5 thickset spines, and 8–15

⟵

Fig. 2. *Bermudalana aruboides*: A, Habitus, dorsal; B, Coxae and epimera, lateral; C, Pleon and telson, dorsal; D, Antenna 1; E, Antenna 2 peduncle; F, Frontal process, clypeus, and labrum; G, Clypeus, lateral; H, Left mandible; I, Incisor, lacinia, and molar of right mandible; J, Maxilla 1; K, Maxilla 1 exopod, apex; L, Maxilla 2.

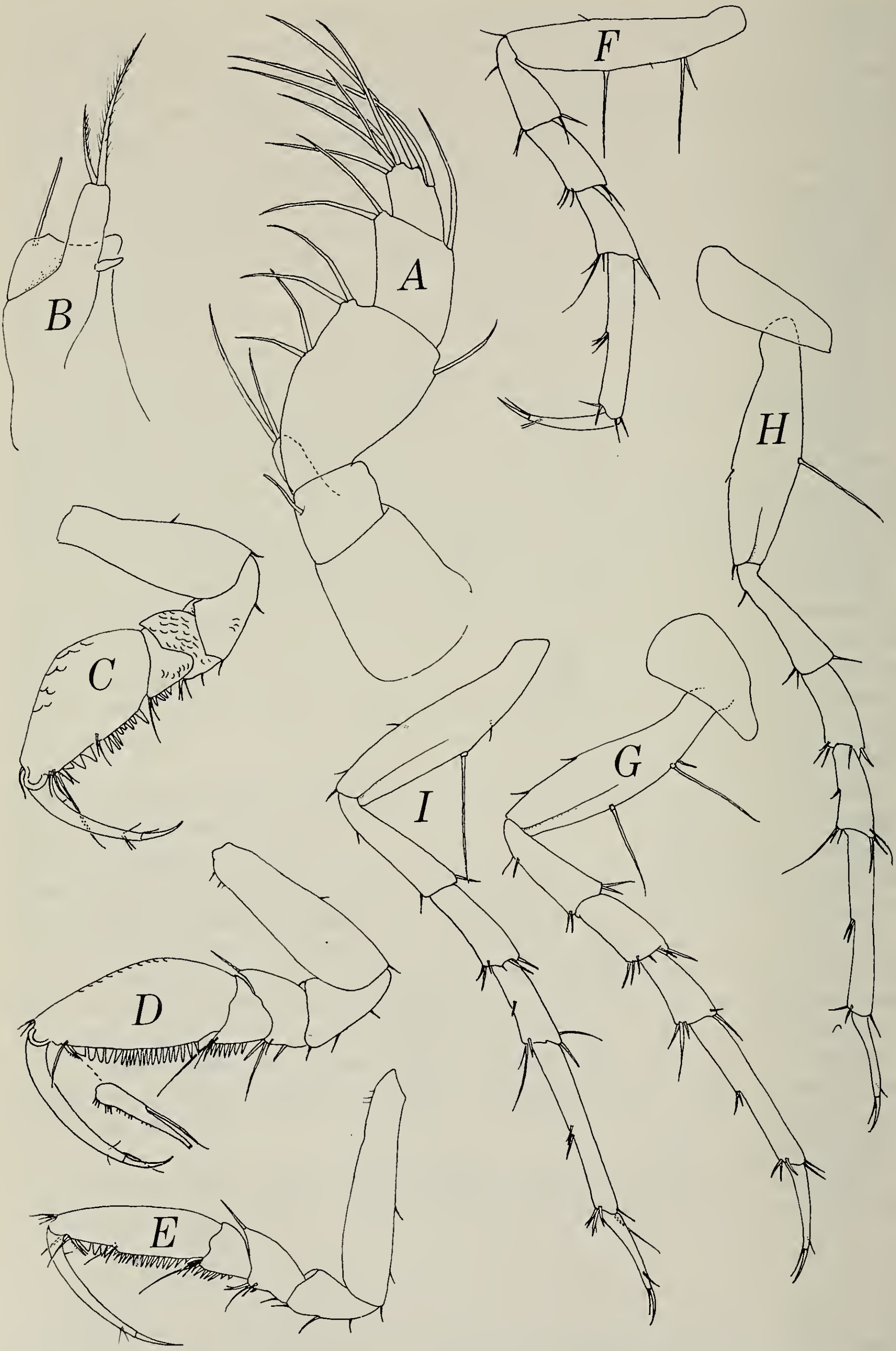


Fig. 3. *Bermudalana aruboides*: A, Maxilliped; B, Maxilliped endite; C–I, Pereopods 1–7.

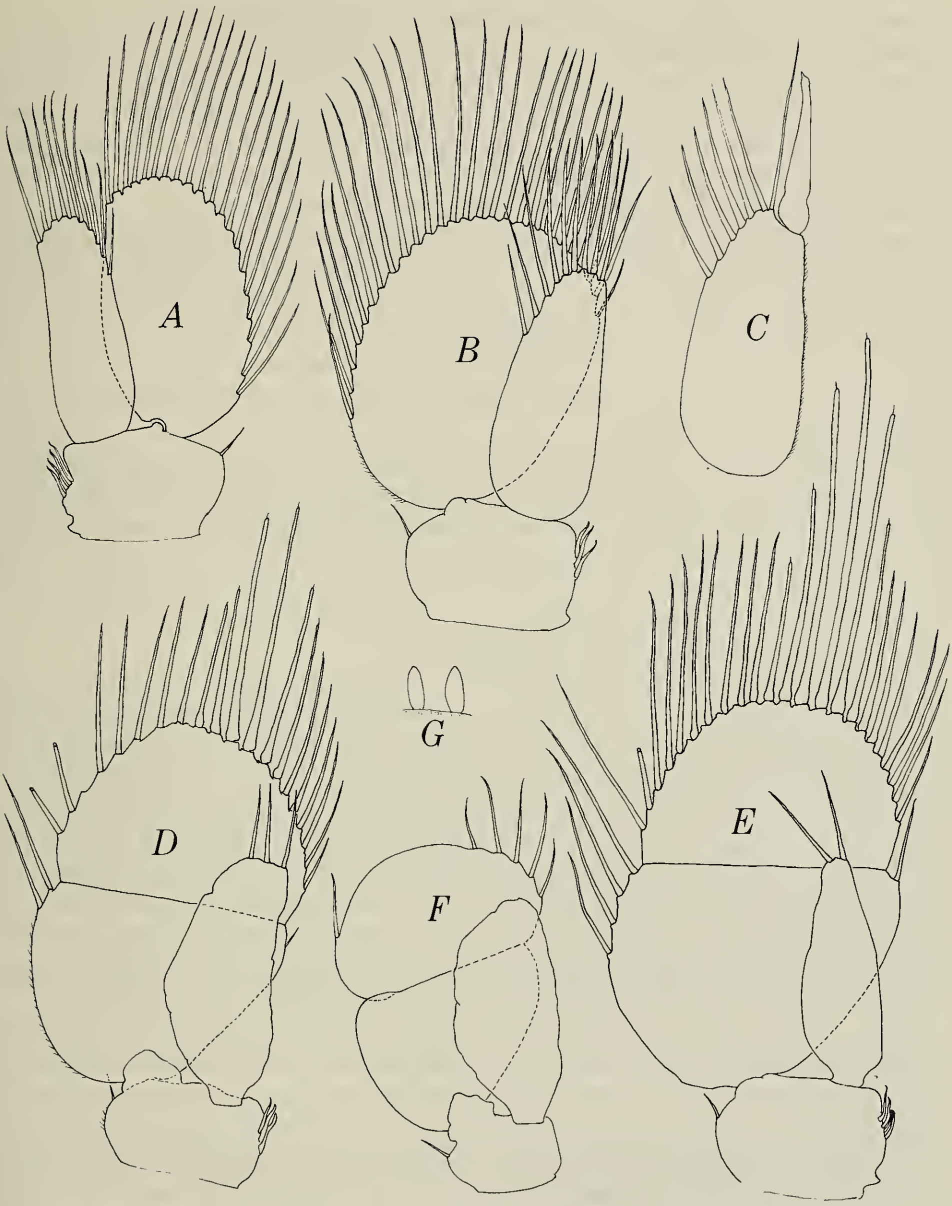


Fig. 4. *Bermudalana aruboides*: A–B, Pleopods 1–2, ♀; C, Pleopod 2 endopod, ♂; D–F, Pleopods 3–5, ♀; G, Penes, ♂.

more slender spines; posterior margin of carpus with 4–7 slender spines. Propus of pereopod 2 slightly less expanded but longer than that of pereopod 1; propus of pereopod 3 slender. Pereopods 4–7 slender, sparsely armed with spines, mostly at distal ends of segments; basipods with long setae on posterior margins, 2 on pereopods 4–5, 1 on pereopods 6–7.

Exopods of pleopods 1–4 with long marginal setae, some of those on apex of pleopods 3–4 longer, thicker, and ending in terminal setule. Exopod of pleopod 5 with 4 medial and 1 lateral setae on distal segment; apex without setae. Endopods of pleopods 3–4 much narrower than very broad exopods, armed with 2 apical setae in pleopod 3, 3 in pleopod 4; endopod of pleopod 5 without setae. Appendix masculina of ♂ pleopod 2 about 0.6× as long as endopod, with constriction near base, curving slightly laterally and ending acutely.

Uropod endopod pyriform, about a third longer and 3× as wide as sublinear exopod; medial margin and apex armed with long setae, lateral margin with 2 short setae in distal part and 2 long setae set in from margin slightly distal to midlength. Exopod with 2 long medial setae, 2 short lateral setae, and cluster of setae lateral to apex, medial part of which is produced into narrow process.

Etymology.—The specific name refers to the important similarities between *Bermudalana* and *Arubolana*.

Relationships.—The combination of five pleonites reaching the lateral margin of the pleon and pereopods 1–3 prehensile is found in two genera of Cirolanidae, *Bahalana* Carpenter, 1981, with one species from Lighthouse Cave, San Salvadore Island, Bahamas, and *Sphaeromides* Dollfus, 1897, with three species from caves adjacent to the Mediterranean. These genera differ from *Bermudalana* in having a normally developed maxilla 2, a 5-segmented palp on the maxilliped, and a basally inserted appendix masculina.

The closest relative of *Bermudalana* is *Arubolana* Botosaneanu and Stock, 1979, represented by a single species, *A. imula* Botosaneanu and Stock, from brackish groundwater in Aruba, Netherlands Antilles. The two genera have in common reduced segmentation of antennae 1 and 2, a greatly reduced maxilla 2, a maxilliped with a 4-segmented palp, an appendix masculina inserted subterminally, and interrupted marginal setae on the exopod of pleopod 5. *Arubolana* differs in having pleonite 5 overlapped laterally by pleonite 4 and only pereopods 1–2 prehensile. These differences are usually believed to be of generic value in the Cirolanidae, hence we have proposed a new genus for the Bermuda cirolanid. We realize, however, that a plausible case could be made for assigning the latter to *Arubolana* or for recognizing *Bermudalana* as a subgenus of *Arubolana*.

Origin.—The common possession by *Arubolana* and *Bermudalana* of several specialized character-states not found elsewhere in the Cirolanidae can be explained best by their evolution from a common ancestor. Convergent evolution could be evoked for a single character-state but is highly unlikely for such a combination of several character-states. Aruba and Bermuda are separated by about 1400 miles (2250 km) and water of abyssal depths; dispersal from one of these islands to the other by a small troglobitic isopod would seem to be a remote possibility. Rafting on floating objects carried from Aruba to Bermuda via the Gulf Stream cannot be disproven, but we do not consider it a serious possibility. The origin of the two species from a common marine ancestral species is a more believable alternative, but two difficulties must be faced. 1. Cirolanids are rarely found at the abyssal depths (>2000 m) of most of the Atlantic between Aruba and Bermuda. Depths recorded for three blind deep-sea species of *Cirolana* are *C. caeca* Dollfus, 1903, 1200–2500 m; *C. anocula* Kensley, in press, 750 m; *C. californiensis* Schultz, 1966, 700–2000 m (Brusca and Ninos 1978). 2. Prehensile pereopods in the Cirolanidae are known only in hypogean species. The reason for this is not known, but might be related to a shift in feeding from scavenging to predation in cave cirolanids. Carpenter (1981) reports that *Bahalana geracei* holds its prey firmly with prehensile pereopods 1–3 and bites off small pieces with its mandibles.

Nevertheless, Aruba and Bermuda have never been connected by land and if *Arubolana* and *Bermudalana* had a common ancestor, as we firmly believe, it must have been a marine cirolanid. It is possible that the ancestral cirolanid lacked prehensile pereopods and that the latter evolved independently in the two genera after reaching their present localities.

Acknowledgments

This study was supported by a National Science Foundation Grant (DEB-8001836) to Thomas M. Iliffe. We thank Drs. C. W. Hart, Jr., and R. B. Manning for their reviews of the manuscript. Cave diving equipment and techniques used to conduct this study met standards of the National Speleological Society. This paper is Contribution No. 939 from the Bermuda Biological Station for Research, Inc.

Literature Cited

Băcescu, M. 1980. *Apseudes bermudeus* n. sp. from caves around the Bermuda Islands.—Acta Adriatica 21:401–407.

Botosaneanu, L., and J. H. Stock. 1979. *Arubolana imula*, n. gen., n. sp., the first hypogean cirolanid isopod found in the Lesser Antilles.—Bijdragen tot de Dierkunde 49(2):227–233.

Bretz, J. H. 1960. Bermuda: A partially drowned, late mature, Pleistocene karst.—Bulletin of the Geological Society of America 71:1729–1754.

Brusca, R. C., and M. Ninos. 1978. The status of *Cirolana californiensis* Shultz, and *C. deminuta* Menzies and George, with a key to the California species of *Cirolana* (Isopoda: Cirolanidae).—Proceedings of the Biological Society of Washington 91(2):379–385.

Carpenter, J. H. 1981. *Bahalana geracei* n. gen., n. sp., a troglobitic marine cirolanid isopod from Lighthouse Cave, San Salvador Island, Bahamas.—Bijdragen tot de Dierkunde 51(2):259–267.

Dollfus, A. 1897. Sur deux types nouveaux de Crustacés Isopodes appartenant à la faune souterraine des Cevennes.—Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris 125:130–131.

———. 1903. Note préliminaire sur les espèces de genre *Cirolana* recuillies pendent les campagnes de 'l'Hirondelle' et de la 'Princesse Alice'.—Bulletin de la Société Zoologique de France 28(2): 5–10.

Hart, C. W., Jr., and R. B. Manning. 1981. The cavernicolous caridean shrimps of Bermuda (Alpheidae, Hippolytidae, and Atyidae).—Journal of Crustacean Biology 1(3):441–456.

Iliffe, T. M. 1980. Mid-ocean cave diving.—Underwater Speleology 7(4):46–48.

———. 1981. The submarine caves of Bermuda.—Proceedings of the Eighth International Congress of Speleology, Bowling Green, Kentucky, U.S.A., pp. 161–163.

———, C. W. Hart, Jr., and R. B. Manning. 1983. Biogeography and the caves of Bermuda.—Nature 302:141–142.

Kensley, B. In press. The South African Museum's *Meiring Naude* cruises. Marine Isopoda of the 1977, 1978 and 1979 Cruises.—Annals of the South African Museum.

Palmer, A. N., M. V. Palmer, and J. M. Queen. 1977. Geology and origin of the caves of Bermuda.—Proceedings of the Seventh International Congress of Speleology, Sheffield, U.K., pp. 336–339.

Poulson, T. L., and W. B. White. 1969. The cave environment.—Science 165:971–981.

Sket, B. 1979. *Atlantasellus cavernicolus* n. gen., n. sp. (Isopoda Asellota, Atlantasellidae n. fam.) from Bermuda.—Bioloski Vestnik (Ljubljana) 27(2):175–183.

———, and T. M. Iliffe. 1980. Cave fauna of Bermuda.—Internationale Revue der gesamten Hydrobiologie 65(6):871–882.

Sterrer, W., and T. M. Iliffe. 1982. *Mesonerilla prospera*, a new archiannelid from marine caves on Bermuda.—Proceedings of the Biological Society of Washington 95(3):509–514.

Vandel, A. 1965. Biospeleology: The biology of cavernicolous animals.—Pergamon Press, Oxford, U.K., 524 pp.

Yeatman, H. C. 1980. *Miostephos leamingtonensis*, a new species of copepod from Bermuda. – Journal of the Tennessee Academy of Science 55(1):20–21.

(TEB) Department of Invertebrate Zoology (Crustacea), NHB 163, Smithsonian Institution, Washington, D.C. 20560; (TMI) Bermuda Biological Station for Research, Ferry Reach 1–15, Bermuda.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 301–306

VARICHAETADRILUS, A NEW NAME FOR *VARICHAETA* BRINKHURST, 1981, *NON* SPEISER, 1903, (DIPTERA) WITH A DESCRIPTION OF A NEW SPECIES *V. FULLERI*

Ralph O. Brinkhurst and R. Deedee Kathman

Abstract.—The genus *Varichaeta* Brinkhurst, 1981, is renamed *Varichaetadrilus. Varichaetadrilus fulleri,* new species, is described from material collected in Kentucky. The species has distinctive penes and lacks dorsal hair and pectinate setae; all setae are bifid. The *bifidus* form of *V. pacificus* is described. It differs from the typical form by the lack of hair and pectinate setae.

The genus *Varichaeta* Brinkhurst, 1981, was erected because a clear distinction could be made between the male ducts of this genus and those of *Isochaetides* Hrabě, 1966 (Brinkhurst 1981). Two of the previous *Varichaeta* species had been assigned to *Isochaetides* (or its precursor *Isochaeta* Pointner, 1911; see Brinkhurst 1981 for clarification) as all of the species involved have very long, tubular male ducts. In *Isochaetides* the vasa deferentia are very long and the atria are quite short, but in *Varichaeta* the atria are at least as long as the vasa deferentia. The penes in *Varichaeta* are unusually large, erectile, and have short cuticular sheaths at the distal end only. The *Isochaeta–Isochaetides* complex belongs to those few genera in which all the species lack dorsal hair and pectinate setae (i.e., *Clitellio* Savigny, 1820, and *Limnodrilus* Claparède, 1862) which is the basis for the name. Other genera (*Potamothrix* Vejdovský and Mrázek, *Aulodrilus* Bretscher for example), contain species with hair and pectinate setae and others that lack them, but there has never been any suggestion of splitting these genera on the basis of setal pattern. In fact, this degree of variation is given only subspecific or varietal status by several authors in the absence of any other significant differences in the taxa concerned (see *Tubifex tubifex* (Müller, 1774); *Ilyodrilus frantzi* Brinkhurst, 1965; *Potamothrix prespaensis* (Hrabě, 1931)—all in Brinkhurst 1971).

While the male ducts of *V. nevadana* (Brinkhurst, 1965) and *V. israelis* (Brinkhurst, 1971) were thought to be of the form found in *Isochaeta–Isochaetides*, the inclusion of both species in that complex was therefore acceptable despite the presence of hair and pectinate setae. Once the male ducts of these two plus *V. pacifica* Brinkhurst, 1981, could be recognized as distinctive, the genera were separated by Brinkhurst (1981). The name *Varichaeta* was used to indicate the presence of hair and pectinate setae in contrast to *Isochaeta.* As the name *Varichaeta* proves to be preoccupied (*Varichaeta* Speiser, 1903–Diptera) we now propose the name *Varichaetadrilus* for the three known species, *Varichaetadrilus pacificus* (Brinkhurst, 1981) new combination (type-species), *Varichaetadrilus nevadana* (Brinkhurst, 1965) new combination, and *Varichaetadrilus israelis* (Brinkhurst, 1971) new combination.

In addition, specimens collected by S. L. H. Fuller (Academy of Natural Sciences, Philadelphia) in Kentucky prove to belong to this genus, and these will now be described.

Varichaetadrilus fulleri, new species
Fig. 1

Diagnosis.—Worms up to 50 mm long, about 1 mm wide anteriorly, more than 200 segments. Prostomium small, pharynx large and eversible, septa in anterior segments very thick, muscular. Setae bifid, 2–3 or up to 5 per bundle anteriorly, 1, sometimes 2 from behind the clitellum; upper teeth shorter than the lower in 1 or 2 anterior segments, longer than the lower in most preclitellar bundles (or worn and broken to appear shorter); upper teeth shorter and thinner than the lower posteriorly. No genital setae. Spermathecal pores in position of missing ventral setae of X, male pores slightly median to line of (missing) ventral setae of XI, female pores in the same line in 11/12. Spermathecae voluminous with elongate spermatozeugma; ducts wide, capacious with folded walls and cervix-like plugs between ampullae and ducts. Male ducts exceedingly long, both vasa deferentia and atria elongate; prostate glands small, attached to atria close to union with vasa deferentia; penes very large, erectile, with cuticular sheaths on distal ends only; terminal parts of ejaculatory ducts make S-bends before entering penes.

Material examined.—Holotype: USNM 79466, 1 dissected mature specimen on 2 slides, Canada Balsam preparation. Type-locality: 3.2 miles WNW of Birk City, Daviess Co., Kentucky, 11 July 1981. Paratypes: 2 mature specimens, Academy of Natural Sciences, Philadelphia, coll. 3.2 miles WNW of Birk City, Davies Co., 30 July 1981; USNM 79467–79475, 8 mature and 6 immature specimens on 12 slides; Brinkhurst collection: 1 mature specimen on 1 slide; Kathman collection: 1 mature specimen on 1 slide; localities as above plus other localities near Birk City and Green River 3.5 miles SE of Calhoun, McLean County, Kentucky, all coll. S. L. H. Fuller, May–July 1981.

Etymology.—"*fulleri*"—for S. L. H. Fuller, the collector.

Remarks.—The enormously elongate male ducts are impossible to illustrate in their entirety as they cannot be dissected out in one piece or seen in whole mounts with ease, but they resemble those of the other species in the genus. The relative length of each vas deferens cannot be determined but the recognition of several fragments of the vas suggests it may be as long as the atrium. The penes are erectile and are seen in various degrees of retraction in the material available. The setae are all bifid, unlike those of the other species in the genus, but this does not exclude this new species as other well-established genera share this variation (see above for some of many examples). The large size of these worms may be a product of local environment, as specimens of *Limnodrilus hoffmeisteri* Clap., from the same localities are unusually large. A total of 67 samples which contained oligochaetes were examined in this survey, executed in three searches in 1981 (May–June, July–August, and October). The new species was found in association with other tubificids (*Limnodrilus hoffmeisteri* 18 samples, *L. maumeensis* 12, *L. udekemianus* 9, *L. cervix* 2, *Branchiura sowerbyi* 15) and on one occasion, with another unidentifiable large tubificid with bifid setae. Other tubificids were found in samples not containing *Varichaetadrilus* (*Limnodrilus claparedeianus, L. angustipenis, Aulodrilus pigueti*) and it was not associated with

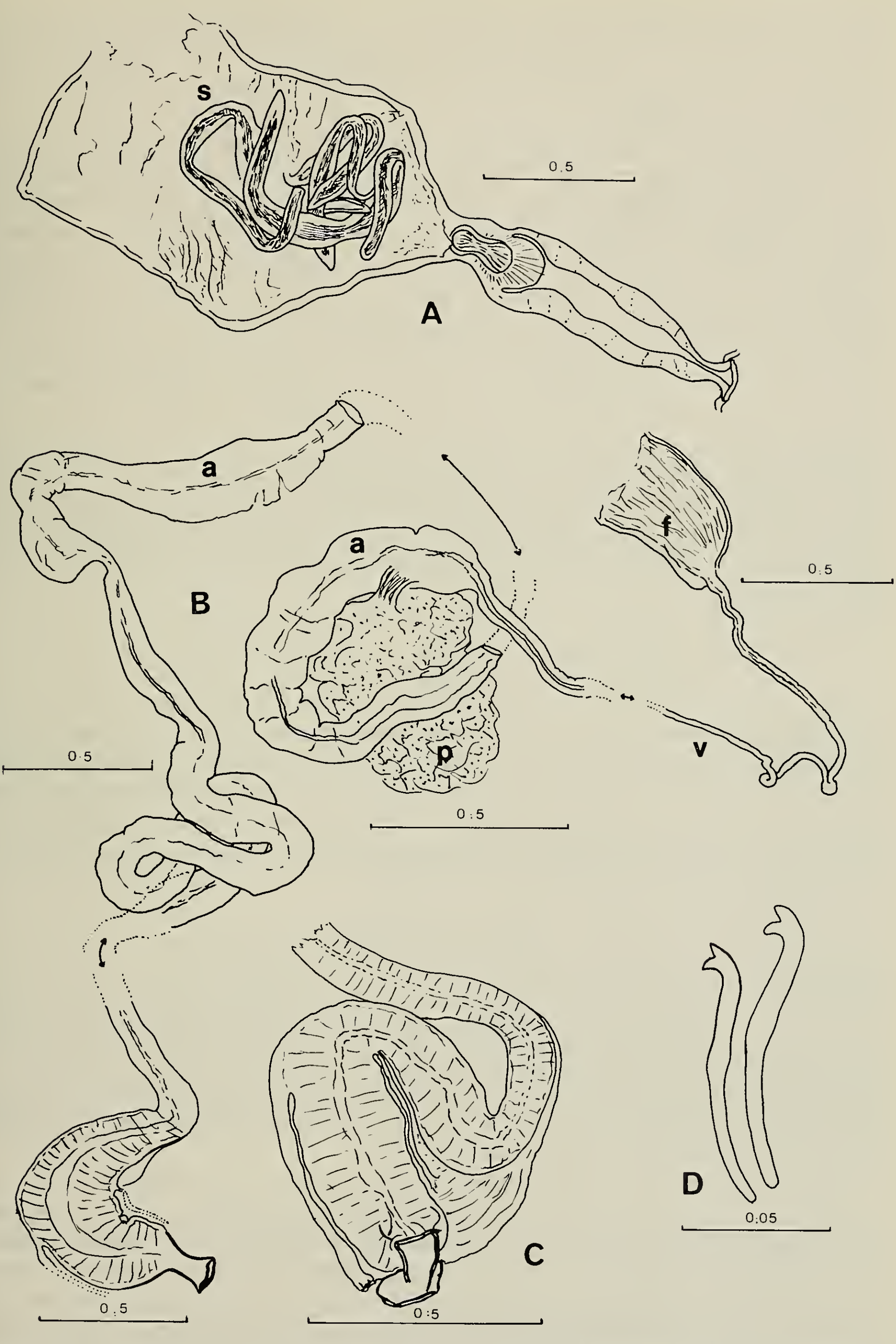


Fig. 1. *Varichaetadrilus fulleri* (from type-series): A, Spermatheca showing valve at union of duct with ampulla (s = spermatozeugma); B, Four pieces of male duct (a = atrium, f = funnel, p = prostate, v = vas deferens); C, Penis in sigmoid form of the in situ condition (teased apart in B); D, setae.

the naidids *Dero digitata, Nais variabilis, N. pardalis, N. bretscheri* and *Haemonais waldvogeli* or the large worm *Sparganophilus eiseni*. The new species appears to be very tolerant of organic pollution, being found in association with an indicator assemblage.

Other collections made by the authors from the Green River and its tributaries in the Mammoth Cave system (well upstream of the localities cited here) failed to reveal this new species, and so the discovery of *V. fulleri* in the Green River does not appear to be due to downward migration from a refuge cave environment. As we know of no unique characteristic of the Green River, we can only assume that *V. fulleri* has been overlooked or mistaken for a *Limnodrilus* species until now, and that it is, in fact, widely distributed. However, the senior author failed to find it in his examination of all of the collections of the Academy of Natural Sciences, Philadelphia, from the rivers along the southeast seaboard of the U.S.A. up to 1962, and the junior author has similarly identified material from detailed studies in Tennessee, Alabama, Georgia, and some sites in South Carolina without seeing it, and it has not been reported by scientists actively working with oligochaetes in Louisiana. It is possible that it forms part of a lower Mississippi fauna, a suggestion confirmed by the recent independent discovery of the species by C. R. Bingham (personal communication), who will describe that material elsewhere.

Varichaetadrilus pacificus (Brinkhurst, 1981)
Fig. 2

Seven specimens of this species were found in the Columbia River at Snag Island (lower elevation, samples A and E, August 1980, Miller Sands area) by Dr. R. J. Diaz from samples collected by the U.S. Corps of Engineers. All seven lack hair and pectinate setae, and are therefore termed the *bifidus* form of the species. One other fragment has a few sparse hair setae and may also belong to this species, but that could not be determined.

This finding further substantiates the belief that the presence of hair and pectinate setae can probably be affected by environmental conditions. This site is subjected to occasional intrusions of salt water. The senior author has also seen specimens of the *bergi* and *blanchardi* forms of *T. tubifex* from springs 70 km from Tripoli, Libya (Dr. C. S. Woods, personal communication), but the *bergi* forms had hair setae in postclitellar bundles only. Such sites are well known to have elevated conductivity levels in the water. The *blanchardi* form was recently reported from France by Giani and Martinez-Ansemil (1981), in the Eau Salée, which descriptive name alone makes the point.

Poddubnaya (1980) obtained new material of the *bergi* form from the type-locality (Lake Issyk-Kul). She stated that the presence of the typical form and the variant form in the same locality precludes the possibility of regarding these as subspecies, as discussed earlier by Brinkhurst (1971) who reduced these variants to "forms" and who has subsequently used this terminology consistently for this same setal variation where other characteristics do not differ. Poddubnaya presents measurements of 14 characteristics of the male ducts and spermathecae, giving error terms (the number of specimens measured is 100 or more of each

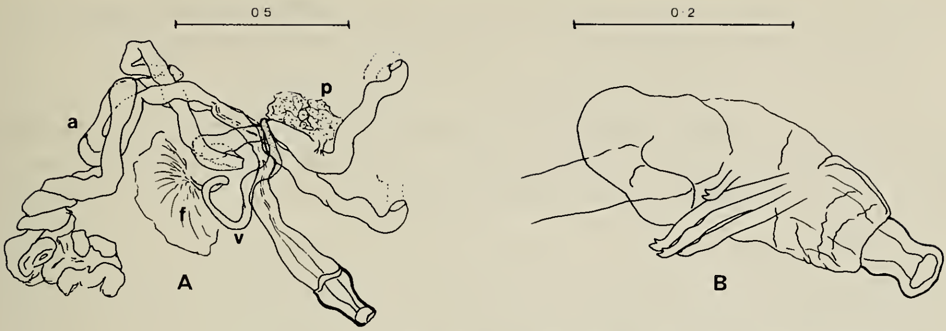


Fig. 2. *Varichaetadrilus pacificus,* bifidus form: A, Male duct from funnel to penis, fragmented; B, Penis with penial setae.

form). These values establish the fact that the size of these parts may be smaller (vas deferens parameters) or larger (atrial parameters) in the *bergi* form in comparison to the *tubifex* form, but the form of the parts is quite similar. The only major distinction (in our opinion) may be the gradual transition between the narrow and wide parts of the longer vas deferens in *tubifex* as opposed to the gradual transition in *bergi,* though Poddubnaya also describes differences in the positions of pharyngeal glands and postseptale of the anterior nephridia, characters that are difficult to evaluate as they are so seldom described.

The final resolution of this problem of potential setal variation within a species will, of course, only be solved if the *bergi* and *blanchardi* forms of *T. tubifex* (or one of the other species showing this same set of variations) can be produced by culturing experiments.

The reference to setae in the generic definition should be omitted. This characteristic should only be used in those genera in which the hair setae are characteristically absent.

Acknowledgments

We wish to acknowledge Mr. S. L. H. Fuller and the Academy of Natural Sciences, Philadelphia, for permission to publish this description.

The senior author is indebted to R. W. Huddleson (Chevron Oil Field Research Co.) for noting the nomenclatural problem in his assiduous monitoring of the literature, and to the late H. R. Baker for assistance. The manuscript was prepared by M. Stone.

Literature Cited

Brinkhurst, R. O. 1971. *In* Brinkhurst, R. O., and B. G. M. Jamieson. Aquatic oligochaeta of the world.—Oliver and Boyd, Edinburgh, xi + 806 pp. Part 2. Systematics. 8. Family Tubificidae, pp. 444–625.

———. 1981. A contribution to the taxonomy of the Tubificinae (Oligochaeta: Tubificidae).—Proceedings of the Biological Society of Washington 94:1048–1067.

Giani, N., and E. Martinez-Ansemil. 1981. Contribution à la connaissance des oligochaetes aquatiques du bassin de l'Argens (Var, France).—Annales de Limnologie 17:121–141.

Poddubnaya, T. L. 1980. Independence of the species *Tubifex bergi* (Hrabě) (Oligochaeta, Tubificidae) from Lake Issyk-Kul.—Trudy Instituta Biologii Vnutrennikh vod Akademii Nauk SSSR 41:41–52.

(ROB) Ocean Ecology Laboratory, Institute of Ocean Sciences, P.O. Box 6000, Sidney, British Columbia V8L 4B2, Canada. (RDK) E.V.S. Consultants Ltd., Box 8, Marine Technology Center, Sidney, British Columbia V8L 3S1, Canada.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 307–308

BIOLUMINESCENCE IN THE MARINE OSTRACOD *CYPRIDINA AMERICANA* (MÜLLER, 1890) OFF MANZANILLO, MEXICO (MYODOCOPA: CYPRIDININAE)

David Lapota

Abstract.—A myodocopid ostracod, *Cypridina americana* (Müller, 1890), found in coastal waters off Manzanillo, Mexico, was observed to be bioluminescent. Collection of this ostracod extends the known geographic distribution of this little-studied species and documents the only observation of bioluminescence in a species of *Cypridina* found in Eastern Pacific coastal waters.

Marine ostracods create spectacular bioluminescent displays in the world's oceans (Haneda 1940; Harvey 1952; Turner 1965; Tett and Kelly 1973). Specifically, luminescence has been observed in five species of *Vargula* (Kornicker and King 1965; Seliger and McElroy 1965; Shimomura *et al.* 1969; Raymond and DeVries 1976; Kornicker and Baker 1977; Morin and Bermingham 1980), one species of *Pyrocypris* (Tett and Kelly 1973), 22 species of *Conchoecia* (Rudjakov 1967; Angel 1968), and two species of *Cypridina* (Haneda 1940, 1953; Tsuji *et al.* 1970).

During the Varifront III cruise (16 Nov to 16 Dec 1981) into the Gulf of California, a third species of *Cypridina* was observed to be bioluminescent. The details of this observation are reported herein.

A plankton net (35 μm mesh, 1 m long) was towed at the sea surface from the USNS *DeSteiguer* at approximately two knots for 15 minutes on 27 November, 1800 hrs (GMT 331, 0100 hrs) at 19°23.8′N, 105°18.9′W, one hour prior to sunset. The sample was diluted with freshly filtered (0.45 μm) seawater for isolation of organisms and subsequent observation of bioluminescence. Only two ostracods, both actively swimming, were found within the entire collection. After several washings, each was placed into an individual vial. One of the two specimens, an adult male, was identified as *Cypridina americana* (Müller, 1890) by Dr. Louis S. Kornicker and Anne C. Cohen of the Smithsonian Institution and is deposited in the U.S. National Museum (USNM 159080).

Three hours following isolation of the ostracods, the vials were inadvertently jarred and a point of blue light was immediately observed within each ostracod. A second jarring of the vials produced an intense and persistent blue luminous cloud from each. Within the clouds were points of light that persisted for at least one minute. Subsequent jarring of the ostracods produced only brief and sometimes delayed flashes observable for only several seconds. The source of the discharged luminous clouds from these ostracods was not investigated although the mechanism for light production in the ostracod *Vargula hilgendorfii* (Müller, 1890) has been well documented (Harvey 1916, 1952).

Müller (1890) described *Cypridina americana* from specimens collected off the west coast of Colombia and Ecuador at 5°N 82°W, 3°N 85°W, and 3°S 81°W. *Cypridina americana* was reportedly found off Hawaii (Sharpe 1908) but Müller

(1912) identified the specimen as *Cypridina sharpei.* Other than Müller's (1890) description of *C. americana,* no other reports were found in the literature (personal communication, L. S. Kornicker). Collection of this ostracod off Manzanillo, Mexico extends the known geographic distribution of this little studied species and also documents the only observation of bioluminescence in a species of *Cypridina* in Eastern Pacific coastal waters.

Acknowledgments

I am indebted to Dr. Louis C. Kornicker and Anne C. Cohen, National Museum of Natural History, Smithsonian Institution, for identification of the luminous ostracod, for making available to me Müller's collection data of the known distribution of *C. americana,* and drawing my attention to Morin and Bermingham's observations on *V. bullae.* I am also grateful for comments and suggestions from Drs. Kornicker and Richard V. Lynch, III (Naval Research Laboratory, Washington, D.C.). Financial support is gratefully acknowledged from the Naval Ocean Systems Center Independent Research Program.

Literature Cited

Angel, M. V. 1968. Bioluminescence in planktonic halocyprid ostracods.—Journal of the Marine Biological Association, United Kingdom 48:255–257.

Haneda, Y. 1940. Phenomenon of bioluminescence.—Seirigaku-Shidoshu 5:18–31.

———. 1953. Observation on some marine luminous organisms of Hachijo Island, Japan.—Recent Oceanographic Works of Japan 1:103–108.

Harvey, E. N. 1916. The mechanism of light production in animals.—Science 44:208–209.

———. 1952. Bioluminescence. Academic Press, New York, 649 pp.

Kornicker, L. S., and C. E. King. 1965. A new species of luminescent Ostracoda from Jamaica, West Indies.—Micropaleontology 11(1):105–110.

———, and J. H. Baker. 1977. *Vargula tsujii,* a new species of Ostracoda from Lower and southern California (Myodocopa: Cypridininae) .—Proceedings of the Biological Society of Washington 90(2):218–231.

Morin, J. G., and E. L. Bermingham. 1980. Bioluminescent patterns in a tropical ostracod.—American Zoologist 20:851 (Abstract).

Müller, G. W. 1890. Neue Cypridiniden.—Zoologische Jahrbücher, Abteilungen für Systematik 5(2): 211–252.

———. 1912. Ostracoda.—Das Tierreich 31:1–434.

Raymond, J. A., and A. L. DeVries. 1976. Bioluminescence in McMurdo Sound, Antarctica.—Limnology and Oceanography 21:599–602.

Rudjakov, J. A. 1967. The study of the luminescence of pelagic ostracoda. Pp. 52–62, *in:* Bioenergetics and biological spectrophotometry.—Moscow: Nauka.

Seliger, H. H., and W. D. McElroy. 1965. Light: Physical and biological action.—Academic Press, New York, 417 pp.

Sharpe, R. W. 1908. A further report on the Ostracoda of the United States National Museum.—Proceedings of the U.S. National Museum 35 (1651):399–430.

Shimomura, O., F. H. Johnson, and T. Masugi. 1969. *Cypridina* bioluminescence: Light emitting oxyluciferin-luciferase complex.—Science 164:1299–1300.

Tett, P. B., and M. G. Kelly. 1973. Marine bioluminescence.—Oceanography and Marine Biology Annual Review 11:89–173.

Tsuji, F. I., R. V. Lynch, III, and Y. Haneda. 1970. Studies on the bioluminescence of the marine ostracod crustacean *Cypridina serrata.*—Biological Bulletin 139:386–401.

Turner, R. J. 1965. Notes on the nature and occurrence of marine bioluminescent phenomena.—N.I.O. Internal Report, No. 134, 30 pp.

Radiation Physics Division, Code 534, Naval Ocean Systems Center, San Diego, California 92152.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 309–316

ESCHMEYER NEXUS, A NEW GENUS AND SPECIES OF SCORPAENID FISH FROM FIJI

Stuart G. Poss and Victor G. Springer

Abstract.—*Eschmeyer nexus* is described from a single mature female 41.3 mm in SL, taken in 27–43 m from Ono-i-lau in the Lau Islands, Fiji. It can be distinguished from other scorpaenids by the following combination of characters: 8 short dorsal-fin spines, 3 spines and 8 segmented rays in the anal fin; 19 or 20 pectoral-fin rays; 1 spine and 3 segmented rays in the pelvic fin; only unbranched rays in fins; no scales (except in lateral line); branchiostegal membranes not fused to isthmus; no preorbital spines; and no slit behind posteriormost hemibranch.

A distinctive new genus and species of scorpaenid fish was collected from Ono-i-lau, Lau Islands, Fiji. The new form emphasizes the problems inherent in the most comprehensive and widely used classification of the scorpaenoids (Matsubara 1943a, b). It exhibits a number of advanced and primitive character-states not previously observed in combination in scorpaenoids, further obscuring the limits of several traditionally recognized but inadequately defined family-group taxa. The purpose of this paper is to make a name available for this species, deferring discussion of its relationships until the morphology of other presumably related scorpaenids can be more thoroughly studied. Assignment of this new species to the Scorpaenidae anticipates conclusions reached in studies now in progress by the first author.

Methods of taking counts and measurements follow those of Eschmeyer (1969) as modified by Poss and Eschmeyer (1978).

The right side of the holotype was dissected to reveal the configuration of the swimbladder musculature and to expose the dorsal bony elements of the first gill arch which were stained with alizarin but not removed.

Eschmeyer, new genus

Type-species.—*Eschmeyer nexus.*

Diagnosis.—A scorpaenid fish with: dorsal fin VIII, 13; anal fin III, 8; pelvic fin I, 3; 19 or 20 pectoral-fin rays; extremely short anterior dorsal-fin spines; only unbranched rays in fins; frontal and parietal bones strongly ossified; no preorbital spines; no scales (except for lateral line); branchiostegal membranes not fused to isthmus; and no slit behind posteriormost hemibranch.

Description.—Head large, slightly compressed (Figs. 1 and 2), with posterior half of frontal and parietal bones strongly ossified, rugose. Lacrimal (infraorbital 1) immovable, with posteroventral border tapering to a small point. Nasal bone tubular, without spine. Mouth upturned. Teeth on vomer; none on palatines. No slit behind posteriormost hemibranch. Three infrapharyngobranchial tooth plates. Epibranchial of first gill arch with elongate uncinate process diverging from ramus of bone at angle of about 45° (Fig. 3; presence of interarcual cartilage uncertain). No cirri on lower jaw. Branchiostegal rays 7. Branchiostegal membranes of each side not fused to isthmus. Isthmus with fleshy extension posteriorly. Ventral surface of urohyal with broad transverse flange. Body compressed, oblong; skin slightly granular, scaleless, except for lateral line. Swimbladder absent. Swimbladder musculature present, originating from cranium and cleithrum and inserting on parapophyses of vertebrae 6–10 (Fig. 4). Baudelot's ligament attached to first vertebra. Neural spines of vertebrae 6–9 thin, almost hair-like (Fig. 5). Proximal dorsal-fin pterygiophores (except anteriormost 2) interdigitating without interruption between successive neural arches of precaudal vertebrae. Caudal skeleton with parhypural and hypurals 1 and 2 fused into single autogenous plate, hypurals 3 and 4 fused and forming autogenous plate (slightly fused to urostyle?); hypural 5 autogenous; haemal spines of second and third preural centra autogenous; neural spine of second preural centrum short, 3 epurals; 2(1?) pairs of uroneurals; hypurapophysis absent.

Etymology.—Named for Dr. William N. Eschmeyer in recognition of his contributions to the study of scorpaenoid fishes; gender is masculine.

Eschmeyer nexus, new species

Figs. 1–5

Holotype.—USNM 233855, 41.3 mm in standard length (SL). Fiji Is., Ono-i-lau I., outside of barrier reef on NW side of island 21°38′S, 178°45′W, 27–43 m, V. G. Springer party, Sta. VGS-82-14, 1 May 1982, 0705–1000 hrs. Mature female.

Description.—Dorsal VIII, 13 (posteriormost ray split to base, counted as one); anal III, 8 (posteriormost split); pectoral 19 (left), 20 (right); pelvic I, 3; vertebrae 10 + 15 = 25.

Anterior profile of head inclined about 39° from horizontal. Skin over lower part of head somewhat loose, wrinkled, and slightly granular in texture. Four infraorbital bones; second deep, with large subocular shelf on dorsomedial border (widest posteriorly). Third infraorbital bone deep, without spine, with shelf on dorsomedial border continuous with that on second infraorbital bone. Interorbit broad. Interorbital ridges weak, widely spaced, converging slightly but not meeting over midorbit. Supraorbital ridge vaguely defined, better ossified posteriorly. Anterior nostril prominent, pore situated before orbit, bordered anteroventrally by smaller pore of infraorbital sensory canal and anterodorsally by pore of supraorbital canal. Laterosensory pores of head distinct, moderately sized, with slightly raised margins. Preopercle with 5 short, blunt spines, uppermost (first) most pungent, second largest, fifth a weak point. Pores of preopercular sensory canal with notably raised margins. Opercle strongly ossified, with 2 large, blunt spines on posterodorsal margin, smaller ventral spine more pungent; dorsal margin inclined dorsoposteriorly about 5° above horizontal axis of body. Interopercle without spine. Parietal with broad low ridge. Pterotic with low ridge. Posttemporal emarginate anteriorly, not forked; with strong spine. Supracleithrum bearing small, strong spine. Cleithral spine present. Ventral margin of dentary not strongly directed medially; no symphyseal knob. Mandibular pores 5 on each side, anteriormost 2 pores near symphysis arranged one behind the other. Anguloarticular bone not projecting strongly posteroventrally, inclined ventromedially at angle of about 45°. Maxilla without cirrus, extending to below middle of pupil. Gill rakers short, 14 total, 4 on upper arch, 10 on lower arch. Pseudobranch with 11 filaments.

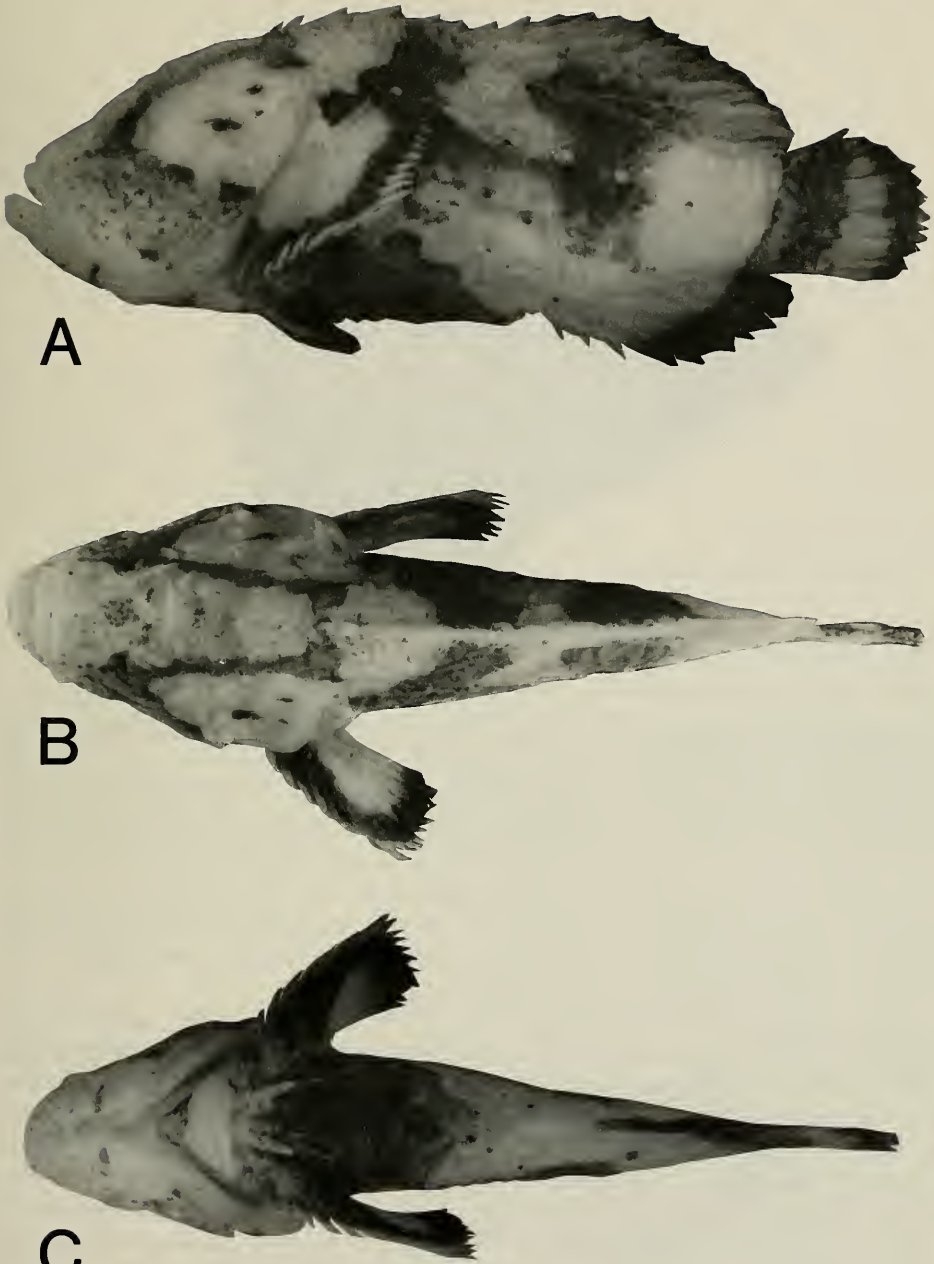


Fig. 1. Holotype of *Eschmeyer nexus*, USNM 233855, 41.3 mm SL. A, Lateral view; B, Dorsal view; C, Ventral view.

Fig. 2. Holotype of *Eschmeyer nexus*, USNM 233855.

Lateral line not high on body, with 10 tubed scales, posteriormost on base of caudal fin. Lateral line scales without spinous projections.

Dorsal fin originating over middle of operculum, spine in anterior part of fin extremely short, stout, and pungent. Dorsal-fin membrane weakly incised between spines 3 and 4. Longest pectoral-fin rays (9–11 from dorsalmost) not reaching anus. Pelvic-fin insertion at base of pectoral fin. Pelvic-fin membrane adnate to body, fused to membrane of opposite side (see *Comparisons* below). Caudal fin stubby, rounded, with 18 total fin-ray elements (2 procurrent and 8 segmented dorsally, 7 segmented and 2 procurrent ventrally).

Color in life unknown. Color pattern in 70% ethanol as in Fig. 1. Body color pale yellowish brown, covered by several broad dark-brown to brownish-black bars or patches. Two large saddle-shaped, somewhat irregular bars on upper two-thirds of body and dorsal-fin base; bars diffusely connected by narrower band just below lateral line; anterior bar below dorsal spines 5–8, posterior bar below segmented dorsal rays 2–9. Broad, dark greyish-brown patch on belly and lower part of pectoral-fin base, continuous with broad, nearly black, mostly submarginal band on lateral and medial surfaces of pectoral fins. Pale transverse band extending across breast, just anterior to pectoral fins. Broad, uninterrupted brownish-black oblique band extending across caudal-fin base and distal part of segmented anal-fin rays. Narrower, but similarly colored, subterminal bar on caudal fin. Head with two brown bars radiating from eye; lower bar much broader, extending posteroventrally across cheek, over preopercle and lower half of opercle; upper bar narrower, directed dorsomedially and fused to slightly broader, small saddle-shaped bar extending transversely over dorsal-fin origin. Few irregular dark-brown spots over anteroventral part of body and dorsal part of opercle. Few dark scattered specks in interorbit and over lower jaw.

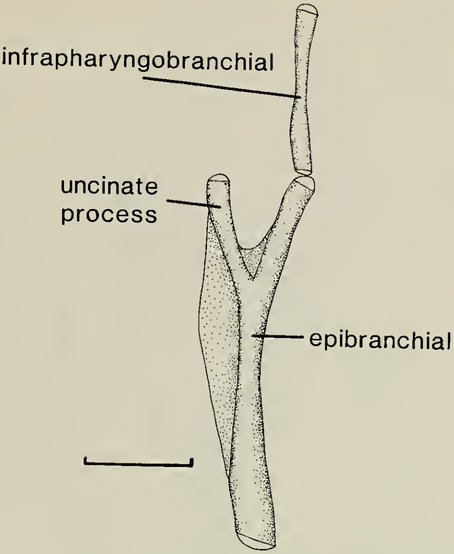


Fig. 3. Dorsolateral view of upper elements of right first gill arch in *Eschmeyer nexus*. Bar represents 1 mm.

Measurements for holotype (percent SL in parentheses): Head length 16.7(40); snout length 4.1(10); orbit diameter 3.9(9); interorbital width 3.2(8); upper jaw length 8.5(21); length of postorbital part of head 8.7(21); greatest body depth 15.2(37); anal-fin length (base of first spine to end of longest ray) 13.9(34); caudal-fin length 9.0(22); pectoral-fin length 8.7(21); pelvic-fin length 7.3(18). Dorsal-

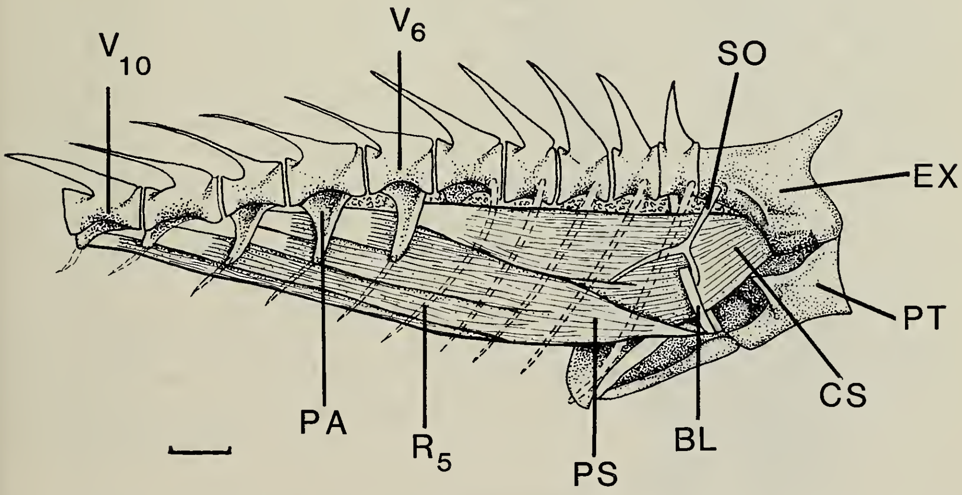


Fig. 4. Dorsal (slightly oblique) view of *Eschmeyer nexus* swimbladder muscle and associated bony elements. Ribs, indicated by dashed line, lie dorsal to swimbladder muscle. BL, Baudelot's ligament. CS, cranial slip of swimbladder muscle. EX, exoccipital. PA, vertebral parapophysis. PS, pectoral girdle slip of swimbladder muscle. PT, posttemporal. R_5, rib associated with 5th vertebral centrum. SO, spinooccipital nerve. $V_{6,10}$, 6th, 10th vertebral centrum. Bar represents 1 mm.

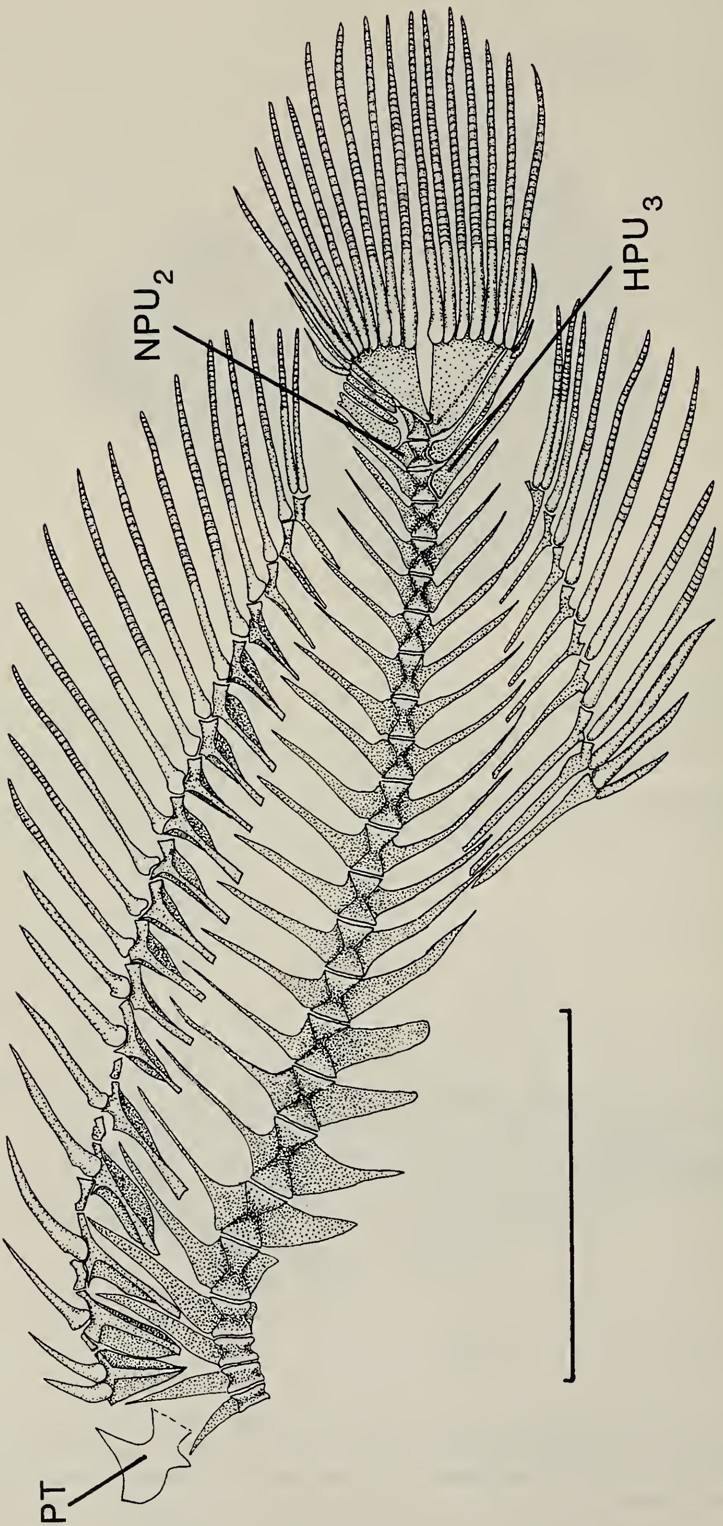


Fig. 5. Postcranial axial skeleton and posttemporal of *Eschmeyer nexus* (based on radiograph; for relation of ribs see Fig. 4). HPU_3, haemal spine of third preural centrum. NPU_2, neural spine of second preural centrum. PT, posttemporal. Bar represents 1 cm.

spine lengths: first 1.5(4); second 1.9(5); third 3.2(8); fourth 3.9(9); fifth 3.5(8); penultimate 3.6(9); last 4.4(11). Anal-spine lengths: first 2.3(6); second 3.2(8); third 4.7(11). Distance between interorbital ridges 2.2(5); least depth of caudal peduncle 6.0(14). Distance from snout tip to: [base of] first dorsal spine (predorsal length) 15.1(37); second dorsal spine 16.2(39); third dorsal spine 17.5(42); fourth dorsal spine 19.9(48); fifth dorsal spine 21.8(53); pelvic-fin insertion 14.2(34). Transverse width of first dorsal spine at midlength 0.2(0.5); deepest incision of fin membrane between third and fourth dorsal spines (from tip of fourth spine to membrane) 1.0(2); length of dorsalmost preopercular spine 1.4(3). Distance between: tip of opercle and dorsal-fin base 5.2(13); first and fifth dorsal spines 6.1(15); fifth and last dorsal spines 4.8(12); last dorsal spine and last dorsal ray 6.2(15); anal-fin origin and last anal ray 10.7(26); pelvic-fin insertion and anal-fin origin 16.8(41); first dorsal spine and pelvic-fin insertion 14.0(34); first dorsal spine and anal-fin origin 21.2(51); fifth dorsal spine and pelvic-fin insertion 15.9(38); last dorsal spine and pelvic-fin insertion 17.5(42); last dorsal spine and last anal ray 19.2(46); last dorsal ray and anal-fin origin 13.7(33); last dorsal spine and anal-fin origin 13.8(33).

Etymology.—From the Latin *nectere* (to tie or connect) in reference to features of the species that, in combination, suggest a close relationship to several groups of scorpaenoids. Here treated as a noun in apposition.

Remarks.—The holotype was captured by use of SCUBA and rotenone in an area usually having strong wave action. Especially calm weather made diving at this locality possible. Rotenone was placed in a large gently downsloping channel in the reef slope at a depth of about 27 m and on the steep sloping face of the reef at about 36 m. Dead fishes of a number of species were picked up to a depth of about 43 m, but most were obtained from the channel at the shallowest depth.

Comparisons.—*Eschmeyer* can be differentiated from all other scorpaenid fishes by the combination of characters given in the diagnosis. Among scorpaenids only *Minous* Cuvier (Scorpaenidae: Minoinae) has as few as 8 dorsal spines (7–12). *Eschmeyer* differs conspicuously from *Minous* in having 3 rather than 5 segmented rays in the pelvic fin and in lacking a detached ray in the pectoral fin, branchiostegal membranes that are fused to the isthmus, preorbital spines, and a movable lacrimal. Among scorpaenoids, *Eschmeyer* is perhaps most similar to *Peristrominous* Whitley (Aploactinidae) in overall appearance but can be distinguished readily in having 8 dorsal-fin spines (12 or 13 in *Peristrominous*), 19 or 20 pectoral-fin rays (14 or 15 in *Peristrominous*), 3 anal-fin spines (1 in *Peristrominous*), and in lacking a fleshy extension at the anteriormost part of the isthmus.

Among other scorpaenids, fusion of the pelvic-fin membranes to each other is an atypical condition known to occur only rarely in some specimens of *Gymnapistes marmoratus* (Cuvier) and *Vespicula dracaena* (Cuvier), both currently assigned to the Tetraroginae. Whether the holotype of *Eschmeyer nexus* is such a variant is unknown.

Acknowledgments

Funds for support of the fieldwork resulting in the collection of *Eschmeyer nexus* and publication of this study were derived from grants made to V. G. Springer by the Smithsonian Scholarly Studies Program and the Max and Victoria

Dreyfus Foundation. We thank Dr. William Smith-Vaniz for reviewing this manuscript.

Literature Cited

Eschmeyer, W. N. 1969. A systematic review of the scorpionfishes of the Atlantic ocean (Pisces: Scorpaenidae).—Occasional Papers of the California Academy of Sciences 79:1–143, figs. 1–13.

Matsubara, K. 1943a. Studies on the scorpaenoid fishes of Japan. Anatomy, phylogeny and taxonomy (I).—Transactions of the Sigenkagaku Kenkyusyo 1:1–170, figs. 1–66.

———. 1943b. Studies on the scorpaenoid fishes of Japan. Anatomy, phylogeny and taxonomy (II).—Transactions of the Sigenkagaku Kenkyusyo 2:171–486, figs. 67–156, 4 plates.

Poss, S. G., and W. N. Eschmeyer. 1978. Two new Australian velvetfishes, genus *Paraploactis* (Scorpaeniformes: Aploactinidae), with a revision of the genus and comments on the genera and species of the Aploactinidae.—Proceedings of the California Academy of Sciences 41(18): 401–426, fig. 1–14, 6 tbs.

(SGP) Department of Ichthyology, The Academy of Natural Sciences of Philadelphia, Nineteenth and the Parkway, Philadelphia, Pennsylvania 19103. (VGS) Division of Fishes, National Museum of Natural History, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 317–322

FENNEROSQUILLA, A NEW GENUS OF STOMATOPOD CRUSTACEAN FROM THE NORTHWESTERN ATLANTIC

Raymond B. Manning and David K. Camp

Abstract.—A new genus, *Fennerosquilla*, is recognized for *Chloridella heptacantha* Chace, 1939, a species previously assigned to the genus *Squilla*. This new genus can be distinguished from *Squilla* by the presence of seven teeth on the dactylus of the claw and by the strongly bilobed lateral process of the sixth thoracic somite.

The unusual morphological features of the northwestern Atlantic *Chloridella heptacantha* Chace (1939:52), subsequently assigned to the genus *Squilla* Fabricius, 1787, have been recognized for some time (Manning 1969:147; 1978b:40). It is the only species now assigned to *Squilla* with seven teeth on the dactylus of the claw and a strongly bilobed lateral process of the sixth thoracic somite. Recent collections of this species (Camp 1983) led us to reevaluate its generic status. We believe that it is sufficiently distinct from other species assigned to *Squilla* to warrant the recognition of a new, monotypic genus. Descriptors used to indicate body size and eye size follow definitions given by Manning (1978b:2).

Fennerosquilla, new genus
Fig. 1

Definition.—Size moderate, total lengths of adults less than 100 mm. Body generally smooth, surface slightly punctate; carinae well developed, sides eroded. Anterior margin of ophthalmic somite rounded or faintly emarginate, unarmed. Eye small to very small, cornea bilobed, set obliquely on stalk. Ocular scales subquadrate to emarginate, separate. Rostral plate elongate, triangular, with median carina. Carapace with normal complement of carinae (median, intermediates, laterals, reflected marginals), median with well-developed anterior bifurcation. Mandibular palp present. Four epipods present. Dactylus of claw with 7 teeth. Lateral process of fifth thoracic somite a single broad lobe, directed laterally. Lateral process of sixth thoracic somite strongly bilobed, subtriangular anterior lobe almost as large as posterior. Lateral process of seventh thoracic somite bilobed, triangular anterior lobe smaller than posterior. Abdomen with 8 carinae (paired submedians, intermediates, laterals, and marginals) on each of anterior 5 somites, intermediates and laterals strongly developed. Telson inflated basally, dorsal surface with median carina and carinae of marginal teeth, lacking supplementary dorsal carinae or tubercles; 3 pairs of marginal teeth present, submedians with fixed apices; prelateral lobes present. Basal prolongation of uropod produced into 2 strong spines, inner longer; inner margin crenulate, unarmed.

Type-species.—*Chloridella heptacantha* Chace, 1939, herein designated. The genus is monotypic.

Etymology.—We believe it is appropriate to dedicate this genus to Fenner A. Chace, Jr., who originally described the type-species. The gender is feminine.

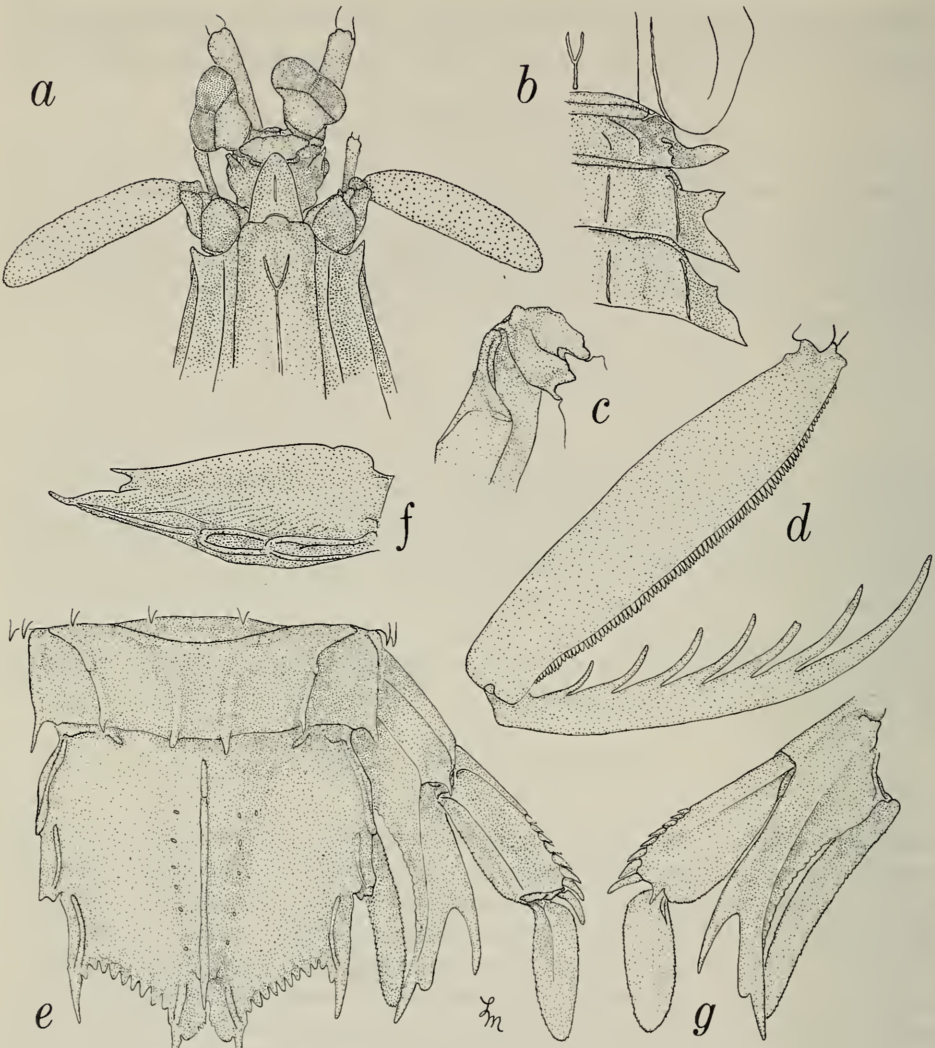


Fig. 1. *Fennerosquilla heptacantha*, female, total length 74.5 mm, USNM 126025. a, Head and anterior part of carapace; b, Exposed thoracic somites 5–7; c, Carpus of raptorial claw; d, Propodus and dactylus of raptorial claw; e, Sixth abdominal somite, telson and right uropod, dorsal view; f, Telson, right lateral view; g, Right uropod, ventral view.

Remarks.—Until now, 25 genera had been recognized in the family Squillidae (see Manning 1980:367 for a list of 24 of these genera and original references, and Manning and Lewinsohn 1982:352), most having been separated from the genus *Squilla* in the last two decades (Manning 1968, 1972, 1976, 1977, 1978a, b). Of the 26 genera now assigned to the Squillidae, eleven are distinguished by the presence of movable apices on the submedian teeth of the telson in adults; in the remaining 15 genera (including *Fennerosquilla*), the apices of the submedian teeth are fixed in adults, although they may be movable in postlarvae and early juvenile stages. Of these latter 15 genera, only five have single lateral processes on the fifth thoracic somite: *Anchisquilla*, *Lenisquilla*, *Squilloides*, *Squilla*, and *Fennersoquilla*. The first two of these genera completely lack the median carina of the carapace. *Squilloides* lacks a mandibular palp and has but four teeth on the dactylus of the claw. Thus, *Fennerosquilla* might be confused only with members of the genus *Squilla*.

Fennerosquilla can be readily distinguished from *Squilla* by the following distinctive features: elongate, triangular rostral plate; seven teeth on the claw; reduction of number of epipods to four; and large anterior lobe of the sixth thoracic somite. Other features characteristic of *Fennerosquilla heptacantha* serving to distinguish it from *Squilla* include: long, slender antennular peduncles, longer than the carapace and rostral plate combined; extremely narrow, elongate carapace, with the anterior width less than half the median length; long, slender propodus of the raptorial claw (the claw, when folded, exceeds the anterior margin of the ophthalmic somite); strongly flattened, strongly carinate abdomen; basally inflated telson, with the median carina appearing convex anteriorly, concave posteriorly in lateral view; and relatively large rounded lobe on the outer margin of the inner spine of the basal prolongation of the uropod. Finally, the eyes are small relative to body size (Table 1); eyes of the smallest *F. heptacantha* are similar in relative size to those of the largest specimens of *Squilla* (except possibly *S. surinamica*, a much smaller species than *F. heptacantha* and most other species of *Squilla*).

We suspect that the presence of a strongly bilobed lateral process of the sixth thoracic somite in *F. heptacantha* is not an indication of affinity with Indo-West Pacific stocks of squillids, most of which share this feature, but is an independent development. *Fennerosquilla* may represent an offshoot of the genus *Squilla*.

The importance of shape of lateral processes of the exposed thoracic somites in distinguishing groups of species within the Squillidae has been recognized since Kemp (1913:20, 21) divided the long-recognized, heterogeneous *Squilla* into two broad groups based solely on shape of the lateral process of the fifth thoracic somite. In a later revision of the Squillidae (see Manning 1968), the nature of differences in shape of the lateral process of the fifth thoracic somite among various squillid species was thoroughly discussed. At that time, two basic forms of the lateral process were recognized, and the difference between them was believed to indicate a fundamental difference between two stocks within the family. One form was expressed as a bilobed process of the fifth thoracic somite; the two lobes were either on the same horizontal plane, as in *Alima*, or almost so, and consequently there was no ventral spine on that somite. In the second form, the anterior lobe had rotated ventrally in relation to the posterior lobe, was no longer basally connected with the posterior lobe, and formed a separate ventral spine. Thus, the posterior lobe projected laterally or anterolaterally from the body, but the anterior lobe projected more ventrally and often was obscured from dorsal view because of its position on the body. Based on this fundamental difference, as well as other considerations, several new genera were erected to contain species formerly assigned to *Squilla* and having a bilobed lateral process of the fifth thoracic somite. Species retained in *Squilla* had a ventral spine and a single-lobed lateral process of the fifth thoracic somite. One of the genera then recognized, *Oratosquilla* Manning, 1968, received the greatest number of species

Table 1.—Representative corneal indices (CI = carapace length divided by cornea width, multiplied by 100) of several species of *Squilla* compared with those of *F. heptacantha.*

Species	Known range of CI
Squilla lijdingi Holthuis, 1959	260–363
S. rugosa Bigelow, 1893	270–424
S. empusa Say, 1818	296–491
S. deceptrix Manning, 1969	311–446
S. caribaea Manning, 1969	315–405
S. intermedia Bigelow, 1893	316–400
S. chydaea Manning, 1962	328–413
S. edentata edentata (Lunz, 1937)	338–492
S. obtusa Holthuis, 1959	350–421
S. cadenati Manning, 1970	352–468
S. brasiliensis Calman, 1917	354–492
S. discors Manning, 1962	361–439
S. neglecta Gibbes, 1850	369–498
S. edentata australis Manning, 1969	370–447
S. mantis (Linnaeus, 1758)	381–433
Fennerosquilla heptacantha (Chace, 1939)	412–576
S. surinamica Holthuis, 1959	441–469

having a bilobed process. Species of *Squilla* sensu stricto were then restricted to the Atlanto-East Pacific, whereas species of *Oratosquilla* were confined almost exclusively to the Indo-West Pacific region [except *O. massavensis* (Kossmann, 1880), an immigrant to the eastern Mediterranean Sea through the Suez Canal (Lewinsohn and Manning 1980:11)].

Differences in shape of the lateral processes of the sixth and seventh thoracic somites were not stressed in the 1968 revision of the Squillidae, although it was suggested that those features "may prove to be of some importance in classification at the generic level" (Manning 1968:118). All of the species transferred to *Oratosquilla* in 1968 share a strongly bilobed lateral process of the sixth thoracic somite, whereas only one of the species then retained in *Squilla*, *S. heptacantha,* has a strongly bilobed process on that somite (Manning 1969: fig. 47*d*; Fig. 1b, herein). In that species, the anterior lobe of the process of the sixth thoracic somite is almost as large as the posterior lobe. In other species retained in *Squilla,* the lateral process of the sixth thoracic somite is either a single lobe, or the anterior lobe is distinctly smaller than the posterior one. Further, most species transferred to *Oratosquilla* in 1968 have a bilobed lateral process of the seventh thoracic somite as well, and the anterior lobe of that process is relatively large. Species retained in *Squilla* have either a simple process of the seventh thoracic somite or a bilobed process with the anterior lobe greatly reduced.

After the 1968 revision of the Squillidae and a subsequent monograph of the West Atlantic species were completed (Manning 1969), more detailed studies were begun on species of *Oratosquilla*, and the genus was found to comprise several morphologically heterogeneous groups of species (Manning 1971). As more specimens became available and additional information on their morphology was obtained, several new genera were recognized for species previously assigned to *Oratosquilla*. In some of these genera, basic distinctions from *Oratosquilla* included different configurations of the lateral processes of the exposed thoracic somites and different numbers of teeth on the dactylus of the claw. For example, *Busquilla* Manning, 1978a, was erected for *O. quadraticauda* (Fukuda, 1911) (not seen by Manning in 1968) and another, previously undescribed species. The lateral process of the fifth thoracic somite in these species, although appearing in dorsal view to be bilobed with both lobes in almost the same plane, is actually somewhat similar to the lateral process found in species of *Squilla*; the two lobes are separate and in different planes as well. Furthermore, in *Busquilla* species the anterior lobes of the lateral processes of the sixth and seventh somites are proportionally smaller than those seen in most species of *Oratosquilla*, and their claws have five rather than six teeth on the dactylus.

Later, *Kempina* Manning, 1978b, was erected for *O. mikado* (Kemp and Chopra, 1921) and two other species having lateral processes with separated lobes in different planes on the fifth thoracic somite and strongly bilobed processes on the sixth and seventh somites. Like species of *Oratosquilla*, species of *Kempina* have six teeth on the dactylus of the claw. *Natosquilla* Manning, 1978b, erected for *O. investigatoris* (Lloyd, 1907), also has separate lobes in different planes on the fifth somite, but the anterior lobes of the lateral processes of the following two somites are reduced in size. *Natosquilla* further differs from *Oratosquilla* in having 10–18 rather than six teeth on the dactylus of the claw.

These findings have clarified the usefulness of shapes of lateral thoracic processes as generic characters. First, the concept that two distinct stocks within the Squillidae can be distinguished by the shape of the lateral process of the fifth thoracic somite is still valid but requires modification. The principally Indo-West Pacific stock, plus the wide-ranging *Alima*, can no longer be characterized as having both lobes of the lateral process of the fifth thoracic somite basally connected and in the same or almost the same horizontal plane. However, this stock can be differentiated from the principally Atlanto-East Pacific stock, comprising *Squilla* and its allies, by whether or not the two lobes are visible in dorsal view. In the latter group, the posterior lobe always obscures the ventrally rotated anterior lobe, whereas in the former group, even though the anterior lobe may be ventrally rotated, it is still visible in dorsal view. Second, as demonstrated by *Busquilla* and *Fennerosquilla*, shape of the lateral process of the sixth thoracic somite may be an important generic character (in combination with other characters), as suggested in 1968. Finally, shape of the process of the seventh somite alone is not necessarily important at the generic level, as shown by some species of *Oratosquilla*. In *O. asiatica* Manning, 1978, *O. pentadactyla* Manning, 1978, *O. quinquedentata* (Brooks, 1886), and *O. woodmasoni* (Kemp, 1911), the anterior lobe of the lateral process of the seventh thoracic somite is proportionally much smaller than in other species of the genus.

Since 1968, when *Squilla* was restricted to its Atlanto-East Pacific components, several other features have emerged as important characters at the generic level within the Squillidae, including number of epipods, presence or absence of the mandibular palp, and number of teeth on the dactylus of the claw. As a general rule, these features are constant at the generic level. One possible exception occurs among species assigned to *Clorida*, where, so far as is known, all of these features vary. That genus, however, also requires revision.

We plan to reevaluate these characters in species now assigned to *Squilla*, in which two species (*S. neglecta* Gibbes, 1850, and *S. parva* Bigelow, 1891) lack the mandibular palp, three species (*S. aculeata* Bigelow, 1893, *S. prasinolineata* Dana, 1852, and *S. grenadensis* Manning, 1969) have four rather than five epipods, and another species (*S. decimdentata* Manning, 1970) has 10 rather than six teeth on the claw. Two of these species, *S. neglecta* and *S. prasinolineata*, have but five teeth on the claw.

Acknowledgments

We thank Lilly King Manning for preparing the illustrations, and W. G. Lyons, J. F. Quinn, Jr., and E. W. Truby of the Florida Department of Natural Resources, Marine Research Laboratory, for their comments on the manuscript.

Literature Cited

Camp, D. K. 1983. Occurrence of *Squilla heptacantha* (Chace, 1939) (Crustacea: Stomatopoda: Squillidae) in the northeastern Gulf of Mexico.—Northeast Gulf Science 6(1):55–57.

Chace, F. A., Jr. 1939. Preliminary descriptions of one new genus and seventeen new species of decapod and stomatopod Crustacea. Reports on the scientific results of the first Atlantis expedition to the West Indies, under the joint auspices of the University of Havana and Harvard University.—Memorias de la Sociedad Cubana de Historia Natural 13(1):31–54.

Kemp, S. 1913. An account of the Crustacea Stomatopoda of the Indo-Pacific region, based on the collection in the Indian Museum.—Memoirs of the Indian Museum 4:1–217.

Lewinsohn, Ch., and R. B. Manning. 1980. Stomatopod Crustacea from the eastern Mediterranean.—Smithsonian Contributions to Zoology 305:1–22.

Manning, R. B. 1968. A revision of the family Squillidae (Crustacea, Stomatopoda), with the description of eight new genera.—Bulletin of Marine Science 18(1):105–142.

———. 1969. Stomatopod Crustacea of the western Atlantic.—Studies in Tropical Oceanography 8:viii + 380 pp.

———. 1971. Keys to the species of *Oratosquilla* (Crustacea: Stomatopoda), with descriptions of two new species.—Smithsonian Contributions to Zoology 71:1–16.

———. 1972. Notes on some stomatopod crustaceans from Peru.—Proceedings of the Biological Society of Washington 85:297–307.

———. 1976. Redescriptions of *Oratosquilla indica* (Hansen) and *Clorida verrucosa* (Hansen), with accounts of a new genus and two new species (Crustacea, Stomatopoda).— Beaufortia 25(318): 1–13.

———. 1977. Preliminary accounts of five new genera of stomatopod crustaceans.—Proceedings of the Biological Society of Washington 90:420–423.

———. 1978a. New and rare stomatopod Crustacea from the Indo-West-Pacific region.—Smithsonian Contributions to Zoology 264:1–36.

———. 1978b. Further observations on *Oratosquilla*, with accounts of two new genera and nine new species (Crustacea: Stomatopoda: Squillidae).—Smithsonian Contributions to Zoology 272:1–44.

———. 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.

———, and Ch. Lewinsohn. 1982. *Rissoides*, a new genus of stomatopod crustacean from the East Atlantic and South Africa.—Proceedings of the Biological Society of Washington 95:352–353.

(RBM) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (DKC) Florida Department of Natural Resources, Marine Research Laboratory, 100 Eighth Avenue S.E., St. Petersburg, Florida 33701.

PROC. BIOL. SOC. WASH.
96(2). 1983, pp. 323–332

PROCAMBARUS (ORTMANNICUS) LEITHEUSERI, NEW SPECIES, ANOTHER TROGLOBITIC CRAYFISH (DECAPODA: CAMBARIDAE) FROM PENINSULAR FLORIDA

Richard Franz and Horton H. Hobbs, Jr.

Abstract.—A new troglobitic crayfish, *Procambarus (Ortmannicus) leitheuseri*, is described from six localities in Hernando and Pasco counties, Florida. Its closest affinities seem to be with the two subspecies of *P. (O.) lucifugus*. It may be distinguished from the nominate subspecies by the presence of pigment in the eye, and from *P. (O.) l. alachua* by features of the first pleopod of the male, among which is the absence of a caudal process.

Twelve troglobitic crayfishes belonging to three genera are now known to inhabit the subterranean waters of Florida. Except for *Procambarus (Ortmannicus) franzi* Hobbs and Lee (1976) and the new species described herein, all were included in a review of the American troglobitic decapods (Hobbs et al., 1977). These two crayfishes not reported there occur in the peninsular section of the state: *P. (O.) franzi*, known only from the type-locality, Orange Lake Cave (Sec. 33/34, T. 12S, R. 21E) and Hell Hole (Sec. 6, T. 14S, R. 21E), Marion County, and *P. (O.) leitheuseri*, new species, from six localities in Hernando and Pasco counties. The latter records mark the southwestern limits of the known range of the troglobitic members of the subgenus *Ortmannicus* in peninsular Florida. A key to the albinistic crayfishes of the subgenus is appended to the description that follows.

We are pleased to name this crayfish for its discoverer Arthur T. Leitheuser, who has added much to our knowledge of the distribution of the troglobitic crayfishes of Florida.

Procambarus (Ortmannicus) leitheuseri, new species
Fig. 1

Diagnosis.—Albinistic, eyes without facets but provided with small pigment spot. Rostrum with marginal spines; median carina absent. Carapace with cervical spine cephaloventral to row of small spines or tubercles flanking caudal margin of cervical groove. Aerola 6.3 to 10.4 times as long as broad and constituting 32.9 to 38.2% of total length of carapace (43.8 to 49.7% of postorbital carapace length). Suborbital angle absent. Postorbital ridge with cephalic spine and with or without 2 to several more posterior spines or tubercles. Hepatic area with many small tubercles, some spiniform. Antennal scale about twice as long as wide, broadest slightly distal to midlength. Ischia of third and fourth pereiopods of first form male with simple hooks, that on third overreaching basioischial articulation and that on fourth highly arched, almost reaching basioischial articulation but lacking opposing tubercle on basis; coxa of fourth pereiopod with prominent oblique boss. First pleopod of first form male reaching coxa of third pereiopod, asymmetrical, provided with subapical setae; distal extremity bearing subspiculiform mesial process directed caudally at approximately 75 degree angle to shaft of appendage and curved somewhat laterally; cephalic process acute, somewhat hooding central projection cephalically, and directed caudodistally; caudal element lacking caudal knob but represented by prominent, corneous adventitious process caudomesially, latter rounded distally, convex mesially, and somewhat concave laterally; and corneous beaklike central projection, most conspicuous of terminal elements, directed caudodistally subparallel to cephalic process. Annulus ventralis freely movable, subrhomboidal, about twice as broad as long, and completely exposed, not partly hidden by projections from sternum immediately cephalic to it; cephalic area with convex, elevated marginal area bearing submedian, oblique furrow; sinus originating in furrow and following sigmoid curve, terminating almost on median line slightly posterior to midlength of annulus. Postannular sclerite slightly more than half as wide and about half as long as annulus with cephalomedian area somewhat inflated. First pleopod in female moderately well developed.

Holotypic male, form I.—Cephalothorax (Fig. 1*a, k*) subcylindrical. Abdomen narrower than thorax (8.4 and 10.0 mm). Greatest width of carapace greater than height at caudodorsal margin of cervical groove. Areola 8.4 times as long as wide with 1 or 2 punctations across narrowest part. Cephalic section of carapace approximately 1.6 times as long as areola, length of latter 38.2% of entire length of carapace (48.0% of postorbital carapace length). Rostrum with margins subparallel along caudal half and gently convergent to base of acumen where provided with small slightly divergent marginal spines. Acumen reaching base of distal fourth of ultimate segment of antennular peduncle; dorsal surface excavate and punctate. Subrostral ridge weak and evident in dorsal aspect along caudal seventh of rostrum. Postorbital ridges well developed, grooved dorsolaterally, and terminating cephalically in small corneous spine; posteriormost part of right ridge with 3 minute corneous subacute tubercles, left with 5, two of which somewhat lateral to axis of ridge. Dorsolateral part of cervical groove flanked caudally by row of spiniform tubercles, ventralmost member of row (cervical spine) larger than others. Suborbital angle obsolete. Branchiostegal spine moderately strong and acute. Except for anterior parts of orbital, antennal, and mandibular areas, entire dorsolateral and lateral surfaces of carapace studded with tubercles, some of which spiniform.

Abdomen slightly longer than carapace (23.5 and 22.0 mm). Pleura of third through fifth abdominal segments rounded anteroventrally and angular caudoventrally. Cephalic section of telson with 2 spines in each caudolateral corner, more mesial one in each movable. Cephalic lobe of epistome (Fig. 1*j*) cordiform, with cephalolateral margins slightly elevated (ventrally); main body with anteriorly flared depression but lacking distinct fovea; epistomal zygoma broadly arched. Ventral surface of proximal podomere of antennular peduncle with spine slightly distal to midlength. Antenna with prominent spine on lateral surface of basis and another on ventral surface of ischium; flagellum extending caudally beyond telson by almost 4 times length of latter. Antennal scale (Fig. 1*i*) about twice as long as broad, widest slightly distal to midlength, and lamellar area about 3 times as wide as thickened lateral part.

Third maxilliped overreaching rostrum by length of ultimate podomere; ischium with distolateral margin subserrate, ending in acute prominence, and lateral half

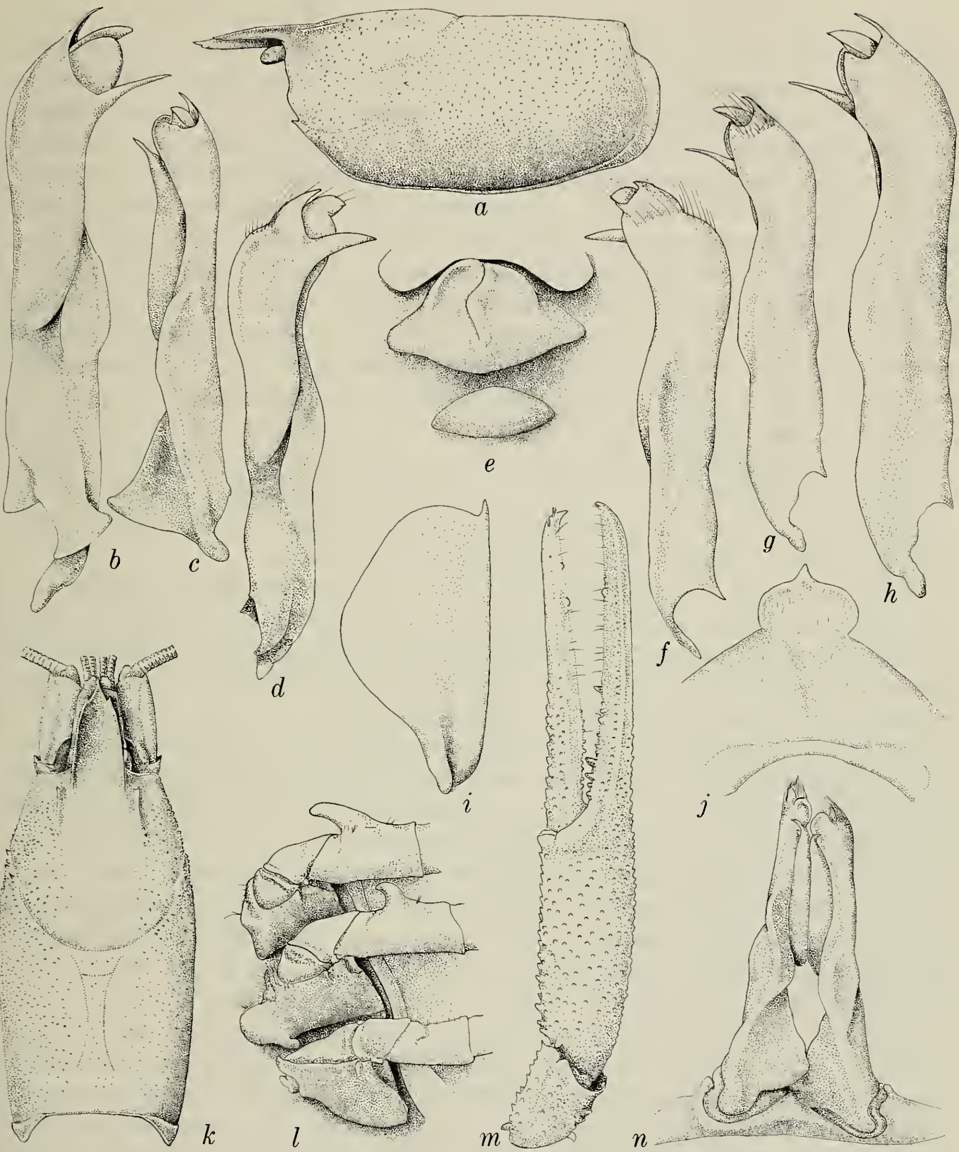


Fig. 1. *Procambarus (O.) leitheuseri* (all illustrations from holotype except *d, f,* from morphotype, and *e* from allotype): *a,* Lateral view of carapace; *b, d,* Mesial view of first pleopod; *c,* Caudolateral view of first pleopod; *e,* Annulus ventralis; *f-h,* Lateral view of first pleopod; *i,* Antennal scale; *j,* Epistome; *k,* Dorsal view of carapace; *l,* Proximal podomeres of third, fourth, and fifth pereiopods; *m,* Dorsal view of distal podomeres of cheliped; *n,* Caudal view of first pleopods.

of ventral surface with scattered short setiferous punctations; exopod reaching almost to end of merus.

Right chela (Fig. 1*m*) subovate in cross section, not strongly depressed. Mesial surface of palm with several irregular rows of 12 to 14 strongly elevated tubercles;

remainder of palm strongly tuberculate. Both fingers with well defined submedian longitudinal ridge flanked proximally by tubercles and more distally by setiferous punctations. Opposable margin of fixed finger with row of 9 tubercles along proximal half of finger, fourth from base largest, and with single, large, more ventrally situated one slightly proximal to midlength; row of minute denticles extending between and ventral to row of tubercles from base of finger almost to corneous tip. Lateral surface of fixed finger with tubercles, decreasing in size distally, along proximal half followed by row of setiferous punctations, latter reaching corneous tip of finger. Opposable margin of dactyl with row of 11 corneous tubercles, sixth from base largest, along proximal two-fifths of finger; minute denticles between tubercles and forming broad band immediately distal to last tubercle of row, band continuing to base of corneous tip of finger. Mesial surface of dactyl similar to lateral surface of fixed finger; tubercles, diminishing in size distally, reaching almost midlength of finger.

Carpus of cheliped longer than broad, tuberculate on all surfaces although sparsely so ventrally; 3 most prominent tubercles spiniform, one situated on dorsodistal angle and 2 on ventrodistal margin. Shallow oblique sulcus on dorsal surface flanked by small subsquamous tubercles.

Merus of cheliped strongly tuberculate except for proximal parts of mesial and lateral surfaces. Dorsal surface with sublinear series of tubercles; those on ventral surface not limited to usual 2 rows; rows poorly defined but mesial one consisting of about 25, more distal members of lateral row larger and corneous. Ischium with irregular row of 5 tubercles along mesial margin.

Hooks on ischia of third and fourth pereiopods (Fig. 1*l*) as described in *Diagnosis*. Coxa of fourth pereiopod with prominent oblique (almost vertically disposed), somewhat inflated boss, its ventral border turned mesially; boss on coxa of fifth pereiopod much smaller and tuberculiform.

Sternum between third and fourth pereiopods rather deep with conspicuous mat of plumose setae extending mesially from ventrolateral margins. First pleopods (Fig. 1*b, c, g, h, n*) as described in *Diagnosis*. Uropods with both lobes of basal podomere bearing spines, that on mesial lobe very strong; distomedian spine on mesial ramus far removed from distal margin of ramus.

Allotypic female.—Differing from holotype in following respects: areola 9 times as long as wide; cephalic section of carapace 1.8 times length of areola, latter only 35.2% of entire length of carapace, 45.3% of postorbital carapace length; acumen with accessory spine on dextral side at base of corneous tip, latter slightly overreaching peduncle of antennule; posterior tubercles of postorbital ridges weak and none corneous; posteroventral extremities of third and fourth abdominal segments not distinctly angular; epistome with paired marginal angles flanking anteromedian projection; antennal flagellum slightly shorter than in holotype; serrations on lateral margin of ischium of third maxilliped less well developed than in holotype; opposable margin of fixed finger of chela with row of 15 tubercles along proximal fourth, third from base largest; tubercles on lateral margin of finger very poorly developed; opposable margin of dactyl with row of 8 tubercles, fifth from base largest; irregular mesial and lateral rows of tubercles on ventral surface of merus consisting of about 16 and 18, respectively.

Annulus ventralis (Fig. 1*e*) only moderately deeply located on sternum (see

Diagnosis). First pleopod reaching cephalic margin of annulus when abdomen flexed. (See *Measurements*.)

Morphotypic male, form II.—Differing from the holotype, except in secondary sexual characters, in only few respects: spines and tubercles almost everywhere decidedly more prominent, but little different in number or distribution; pigment spot in eye larger and pigment more concentrated; acumen overreaching antennular peduncle by about one-third of its length; subrostral ridges evident dorsally along almost basal half of rostrum; 4 well developed spines along posterior part of postorbital ridge, left with 3; hooks on ischia of third and fourth pereiopods much less well developed, and bosses on coxae of fourth and fifth pereiopods not nearly so prominent.

First pleopods (Fig. 1*d, f*) only slightly asymmetrical and with distinct hump on preapical cephalic surface. Mesial and cephalic processes strong, and central projection less prominent than in first form male; all disposed much as in holotype, but more distinctly caudally; caudal element not clearly defined.

Type-locality.—"Eagle's Nest" (= Lost Sink, Eagle Hole), 5.4 km northwest of the junction of U.S. Highway 19 and State Road 50 (NE¼, NE¼, SW¼, Sec. 21, T. 22S, R. 17E), Hernando County, Florida. This is a flooded cave system that opens to the surface in the bottom of a sinkhole pond 76 meters in diameter, in the Chassahowitzka Swamp. The entrance consists of a series of vertical shafts, most of which are either too small to permit access or are blocked by rocks. The largest shaft, 2 by 2 meters in diameter, opens into the top of a very large bell-shaped gallery at a water depth of 21 meters. The room is roughly oval in shape with the long axis oriented in an east–west direction. Tunnels lead out on the east and west sides, and water flow is from east to west, although some divers have reported observing occasional reversals in this pattern. The highest part of the room's floor is at a water depth of 38 meters, but the floor quickly drops away on all sides to depths of as much as 61 meters. The floors of the room and tunnels are composed of coarse sand and, in places, of large blocks of breakdown. Easily disturbed organic silt, sometimes in thick layers, covers the floor under the entrance shafts and in less traveled, deeper sections of the cave. It is present in cracks and crevices in the ceiling of the room. Divers have explored both the upstream and downstream passages to depths in excess of 91 meters and distances in excess of 300 meters.

Disposition of types.—The holotype, allotype, and morphotype are deposited in the National Museum of Natural History (Smithsonian Institution), numbers 178361, 178362, and 178585, respectively, as are paratypes consisting of two second form males (maintained alive) and a dry female. The remaining paratypes (see specimens examined) are deposited in the Florida State Museum.

Size.—The largest of the available specimens is a female from Die Polder 3 which has a carapace length of 27.4 (postorbital carapace length, 20.8) mm. Corresponding lengths of the largest male (form II, from Arch Sink) are 24.4 and 18.6 mm. The holotype is the only first form male available (see Tab. 1 for measurements).

Range and specimens examined.—*Procambarus (O.) leitheuseri* has been collected in only six localities, all in Hernando and Pasco counties, Florida: HERNANDO COUNTY—(1) the type-locality, 1 ♂I, the holotype, A. T. Leitheuser and L. F. Collins, coll.; (2) Die Polder 2, 3.6 km ENE of junction of U.S. Hwy.

Table 1.—Measurements (mm) of *Procambarus (O.) leitheuseri.*

	Holotype	Allotype	Morphotype
Carapace			
Height	8.9	7.3	10.0
Width	10.0	8.0	11.1
Total length	22.0	17.9	24.4
Postorbital length	17.5	13.9	18.6
Areola			
Width	1.0	0.7	1.2
Length	8.4	6.3	8.8
Rostrum			
Width	3.2	2.4	3.2
Length	5.7	4.9	6.6
Right Chela			
Length, palm mesial margin	7.7	4.2	6.1
Palm width	3.7	2.4	3.6
Length, lateral margin	22.1	12.8	17.9
Dactyl length	12.8	7.5	10.8
Abdomen			
Width	8.4	6.7	9.3
Length	23.5	19.1	24.8

19 and State Rte. 50 (Weekiwachee Springs) (NW¼, NE¼, NE¼, Sec. 5, T. 22S, R. 18E), depth about 60 m, near bottom of shaft, 1 ♀, 24 February 1980, A. T. Leitheuser and J. Bentz, coll.; (3) Die Polder 3, 4.2 km E of junction of U.S. Hwy. 19 and State Rte. 50 (Weekiwachee Springs) (NW¼, SE¼, NW¼, Sec. 5, T.23S, R.18E), 1 ♀, 5 September 1982, W. K. Fehring, S. Fehring, coll.; 4 ♀, 9 October 1982, WKF, SF and P. Heinerth, coll. PASCO COUNTY—(4) Black Hole, 4.0 km S of Aripeka (SW¼, NE¼, Sec. 14, T. 24S, R. 16E), 1 ♀, PH, coll.; (5) Arch Sink, 6.3 km E of U.S. Hwy. 19 at junction of Kelly Rd. and Aubrey Rd., (NW¼, NE¼, SW¼, Sec. 2, T. 24E, R. 17E), 2 ♂ II, 1 j♀, 11 January 1983, ATL, PH, coll.; (6) Nexus Sink in Beacon Woods System, 2.5 km E of junction of U.S. Hwy. 19 and State Rte. 52 (Bayonet Point) (NE¼, SE¼, SE¼, Sec. 3, T. 25S, R. 16E), 1 ♂ II, 1 ♀, 11 January 1983, ATL, PH, coll. Two males, form II, with carapace lengths of about 25 mm, are being maintained alive at the Smithsonian Institution, and two others at the Florida State Museum, anticipating their molt to form I.

In addition, crayfish presumably belonging to this species were observed by A. T. Leitheuser, W. K. Fehring, P. Heinerth and other divers in at least two other sinks: HERNANDO COUNTY—(1) Little Springs (=Double D's Sink, Twin D's), 1.0 km SW of junction of U.S. Hwy. 19 and State Rte. 50 (Weekiwachee Springs) (NE¼, NW¼, SW¼, Sec. 2, T. 23S, R. 17E); (2) Little Salt Spring, 6.0 km NW of Weekiwachee Springs on State Rte. 50 (NW¼, NE¼, NE¼, Sec. 29, T. 22S, R. 17E).

All of the known localities for *P. (O.) leitheuseri,* including those sight records of cave divers, occur within a karst area in the Gulf Coastal Lowlands region (as defined by White 1970), in southwestern Hernando and northwestern Pasco counties. The range of the species is thought to extend from the salt water of the Gulf of Mexico on the west to the Brooksville Ridge on the east. The northern and southern limits are currently undefined, but presumably they lie between the Withlacoochee River and Tampa Bay. The Brooksville Ridge appears to form an effective barrier to the eastern expansion of the species. It may also separate *P. (O.) leitheuseri* from the closely related *P. (O.) lucifugus lucifugus* (Hobbs, 1940) which occurs on the other side of the ridge near Floral City, in southeastern Citrus County. This "ridge" actually consists of a series of north-south trending ridges that reach elevations in excess of 60 meters. Their surfaces are covered with sand, which, in turn, is underlain with clastic sediments of the Bone Valley and Alachua formations (White 1970). Thick deposits of white sand, thought to be old stabilized dunes, occur along the western margins of the ridge complex. Franz and Lee (1982) proposed that when moderate to heavy accumulations of unconsolidated sediments cover underlying limestones, they disrupt the flow of organic detritus into the aquifer and produce a severely energy-limited system that excludes troglobitic crayfishes.

Variations.—The tubercles, and especially the spines, ornamenting the specimens from Arch and Nexus sinks are much more prominent than in those from the other localities; however, their numbers and disposition do not vary conspicuously. Too, the pigment in the eyes of these specimens is much denser and covers a larger area than that in specimens from other localities. Among the 13 specimens for which measurements are available, there seems to be no correlation between size of the crayfish and the ratio of the length of the areola to its width. None of the males has ratios of areola length to carapace length of less than 35.3, but of the eight females, in only two is the ratio greater: 35.7 and 37.2, while in only two of the five males is the ratio greater than 37.2. As for the ratio of areola length to postorbital carapace length, there seems to be no correlation with carapace length.

Relationships.—Procambarus (Ortmannicus) leitheuseri has its closest affinities with *P. (O.) lucifugus* and its allies and, perhaps surprisingly, shares more in common with *P. (O.) lucifugus alachua* (Hobbs, 1940) than with the geographically more proximate nominate subspecies. In addition to possessing a black pigment spot in the eye, the rostral margins are usually tapering anteriorly, at most weakly biconvex; the postorbital ridges are provided with tubercles or spines in addition to that capping the anterior extremity, and the areola is comparatively broad, all characters shared with *P. (O.) lucifugus alachua* rather than with the nominate subspecies. It differs from the former chiefly in features of the first pleopod of the first form male: the caudal process is obsolete; the hump, which is present at the cephalic base of the cephalic process in *P. (O.) lucifugus alachua* is less prominent and bent mesially; and the cephalic process is proportionately longer. In addition, the areola is also broader, more so than in most of the Floridian troglobitic members of the subgenus.

Ecological notes.—Procambarus (O.) leitheuseri has been found in flooded caves at water depths between 16.7 and 69.9 meters. These caves are developed in the upper Eocene limestones of the Ocala Group and are apparently integral parts of a major conduit system that carries fresh water toward the Gulf of Mexico. Vertical shafts formed in the Suwannee Limestone (Oligocene age) connect caves with the surface. Shafts typically open in the bottom of water-filled sinkhole depressions. Some of these depressions show daily fluctuations in their water levels that may be related to tidal activity on the Gulf. Tides may also account for the observed flow reversals encountered at Eagle's Nest. According to W. K. Fehring, there is a salt water layer at a depth of 27.4 meters in the Beacon Woods system, particularly at Nexus Sink, in Pasco County. Crayfish have been observed only in the freshwater zone above the halocline. Fehring and his associates are studying the waters in the cave systems along the Gulf coast.

Divers report that a rain of silt passes through the vertical shafts from the surface and is deposited in thick layers on cave floors. The silt either accumulates under the shafts or disperses into the cave, depending on the amount of water movement in the system. Crayfishes are usually associated with the silt. None has been seen in the surface ponds or in the shafts. It is believed that the organic fraction of the silt is generated from biotic production in the surface ponds.

All of the known localities for *P. (O.) leitheuseri* lie within 11.6 km of the Gulf of Mexico. Black Hole and Eagle's Nest occur 1.2 and 1.5 km, respectively, from the Gulf, and their surface ponds are near sea level. Both ponds receive drainage from adjacent wetlands. At Black Hole, the water in the pond and in the cave is usually nearly black in color (hence the name) due to continual drainage of acidic water from surrounding red bay (*Persea borbonia*) dominated bayheads. Die Polder 2 and 3 and Beacon Woods sinks occur near the 12.1 meter contour, and are located in sandhills near the base of the Brooksville Ridge in a longleaf pine-turkey oak-wire grass association.

At Eagle's Nest, *P. (O.) leitheuseri* was collected with *Troglocambarus maclanei* Hobbs, and the troglobitic amphipods *Crangonyx grandimanus* Bousfield and *C. hobbsi* Shoemaker.

Key to Troglobitic Members of Subgenus *Ortmannicus*
(Modified from Hobbs *et al.* and Daniel 1977:26–27

1 Eyes with pigment 2

— Eyes without pigment 5

2(1) Pigment in eyes red 3

2′ Pigment in eyes black 4

3(2) Several cervical spines present; postorbital ridge with spines caudally; male with hook on ischium of fourth pereiopod opposed by tubercle on basis; cephalic process of first pleopod of male situated lateral to central projection. Female with caudally directed tuberculiform processes on caudal margin of sternum immediately anterior to annulus ventralis .... *orcinus* Hobbs and Means, 1972

3′ Only 1 cervical spine present; postorbital ridge without spines caudally; male with hook on ischium of fourth pereiopod not opposed by tubercle on basis; cephalic process of first pleopod of male situated anterior to central projection. Female lacking caudally directed tuberculiform processes on caudal margin of sternum immediately anterior to annulus ventralis .... *erythrops* Relyea and Sutton, 1975

4(2′) Areola more than 10 times as long as wide; first pleopod of male, form I, with caudal process and with hump at cephalic base of cephalic process. (The eyes of about 50% of the intergrade population in Marion County, Florida, lack pigment.) ...... *lucifugus alachua* (Hobbs, 1940)

4′ Areola less than 10 times as long as wide; first pleopod of male, form I, with caudal process obsolete and lacking hump at cephalic base of cephalic process .... *leitheuseri*, new species

5(1′) Male with hook on ischium of fourth pereiopod distinctly overreaching basioischial articulation; female with multituberculate sternum immediately anterior to annulus ventralis 6

5′ Male with hook on ischium of fourth pereiopod not overreaching basioischial articulation; female without tubercles on sternum immediately anterior to annulus 7

6(5) Postorbital ridge with spines or tubercles caudally; areola less than 20 times as long as broad. Male with cephalic process of first pleopod situated lateral to central projection .... *horsti* Hobbs and Means, 1972

6′ Postorbital ridge without caudally situated spines or tubercles; areola more than 20 times as long as broad. Male with cephalic process of first pleopod situated cephalic to central projection .... *pallidus* (Hobbs, 1940)

7(5′) Rostrum narrower at base than over eye; areola more than 20 times as long as wide; first pleopod of male with preapical curvature of at least 80 degrees (see note concerning eye pigment in couplet 4) .... *lucifugus lucifugus* (Hobbs, 1940)

7′ Rostrum tapering from base; areola less than 20 times as long as wide; first pleopod of male with preapical curvature of no more than 60 degrees .... *franzi* Hobbs and Lee, 1976

Acknowledgments

For collecting the specimens on which this description is based and for furnishing us data concerning the habitats occupied by them, we extend our thanks to D. Basile, J. Bentz, G. S. Brkich, L. Collins, W. K. Fehring, S. Fehring, T. Gien, P. Heinerth, J. Kasserman, A. T. Leitheuser, D. P. Manor, P. C. Meng, J. Stone, and C. Vilece. We are also grateful to T. A. Bowman and to J. F. Fitzpatrick, Jr., for their criticisms of the manuscript.

Literature Cited

Franz, Richard, and David S. Lee. 1982. Distribution and evolution of Florida's troglobitic crayfishes.—Bulletin of the Florida State Museum, Biological Sciences 28(3):53–78, 9 figs.

Hobbs, Horton H., Jr. 1940. Seven new crayfishes of the genus *Cambarus* from Florida, with notes on other species.—Proceedings of the United States National Museum 89(3097):387–423, figs. 14–22.

———, H. H. Hobbs III, and Margaret A. Daniel. 1977. A review of the troglobitic decapod crustaceans of the Americas.—Smithsonian Contributions to Zoology 244:v + 183 pp., 70 figs.

———, and David S. Lee. 1976. A new troglobitic crayfish (Decapoda, Cambaridae) from peninsular Florida.—Proceedings of the Biological Society of Washington 89(32):383–391, 1 fig.

———, and D. Bruce Means. 1972. Two new troglobitic crayfishes (Decapoda, Astacidae) from Florida.—Proceedings of the Biological Society of Washington 84(46):393–409, 2 fig.

White, W. A. 1970. The geomorphology of the Florida peninsula.—Florida Bureau of Geology, Bulletin 51, 164 pp.

(RF) Florida State Museum, University of Florida, Gainesville, Florida 32611; (HHH) Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
96(2), 1983, pp. 333–338

ATYA ABELEI, A NEW ATYID SHRIMP (CRUSTACEA, DECAPODA, ATYIDAE) FROM THE PACIFIC SLOPE OF PANAMA

Bruce E. Felgenhauer and Joel W. Martin

Abstract.—*Atya abelei* is described from a single male collected from the Pacific drainage of Panama. It is easily distinguished from its sympatric congeners by having acute rostral prominences, no comb setae on pereopods 1 and 2, and three transverse white bands on the dorsum.

The genus *Atya* Leach, 1815, has recently been reviewed by Hobbs and Hart (1982). These authors include the American and West African representatives of the genus which currently includes 11 species.

Six of the 11 species have been reported from Panama in Central America (Abele 1975; Hobbs and Hart 1982): *Atya scabra* (Leach, 1815); *A. innocous* (Herbst, 1764) [a senior synonym of *Atya tenella*]; *A. margaritacea* (A. Milne Edwards, 1864) [a senior synonym of *Atya rivalis*]; *A. dressleri* Abele, 1975; and *A. crassa* Smith, 1871. As a result of investigations of the biology of Panamanian atyids (Felgenhauer and Abele, in press) an apparently new species of *Atya* was found in the Pacific drainage. The specimen had been maintained in an aquarium for one and one-half years and we were alerted to the possibility that it was unique by its color pattern, method of feeding, and size. Below we describe the specimen and provide notes on its feeding behavior and color.

Atya abelei, new species
Figs. 1–4

Material.—Holotype, ♂ USNM 195335, 8.1 mm cl, 49 mm tl. Type locality: Panama, El Valle, Cocle Province, unnamed tributary of Rio Anton, 600 m elevation, 17 Oct 1980; coll. B. E. Felgenhauer, N. H. Williams.

Description.—Rostrum (Fig. 3A–B) short with distinct dorsal carina extending to sharply acute tip; latter projecting just beyond basal antennal segment. Lateral prominences acute. Dorsal and ventral carinae lacking teeth. Ventral carina armed with several rows of long plumose setae. Carapace (Fig. 3A–B) smooth, lacking pubescence. Antennal spine and sharply acute pterygostomial spine present. Distinct doublure lacking pubescence. First 4 abdominal pleura (Figs. 1, 3G) broadly rounded posteroventrally; ventral margins of third and fourth pleura armed with several long simple setae. Fifth and sixth pleura slightly angled and blunt, with prominent strong setae present on ventral margin of fifth. Telson (Fig. 3D) armed on each side of midline with row of 7 strong spines; each row beginning about ⅓ distance from anterior margin of telson and terminating in single additional spine at each posterolateral margin. Posterior margin with 2 strong spines located above one another just anterior to posterior margin, and 12 long plumose setae. Eyes well developed and pigmented. Preanal carina (Fig. 3F, H) long, terminating in bifid tooth. Antennule (Fig. 3A–B) bearing single row of 5 or 6

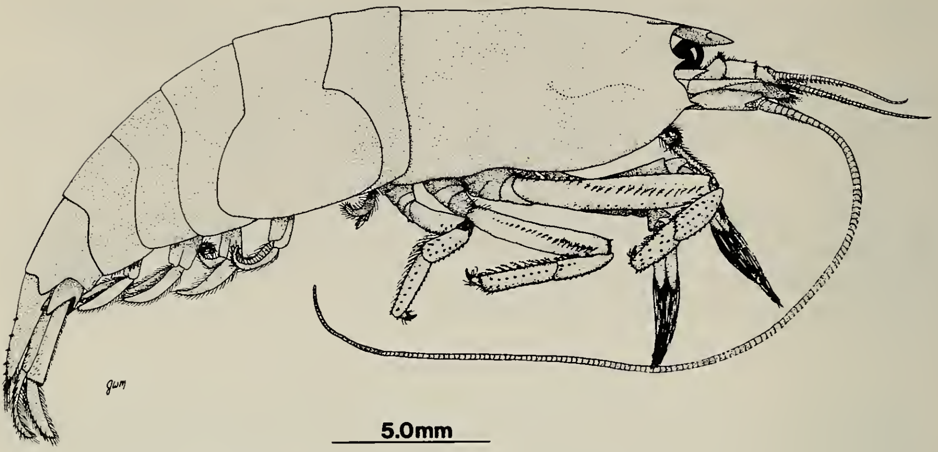


Fig. 1. *Atya abelei,* male holotype, lateral view.

dark spines on distal margin of basal segment; this segment with longitudinal rows of simple setae on dorsal surface. Second segment about twice length of proximal segment and bearing single medial dark spine dorsally; distal margin armed with 7 or 8 such spines. Dorsum of third segment with 6 or 10 dark spines on distal margin. Antennae extending about ⅔ length of body. Scaphocerite reaching just beyond antennular peduncle. Third maxilliped pediform, extending slightly beyond antennular peduncle. Fused propodus-dactylus with several rows of strong serrate setae. First 2 pereopods typical for genus and similar. Propodus and dactylus armed with long setae modified for filtering. No serrate or comb setae present. Third pereopod (Fig. 3C) swollen and armed with single row of

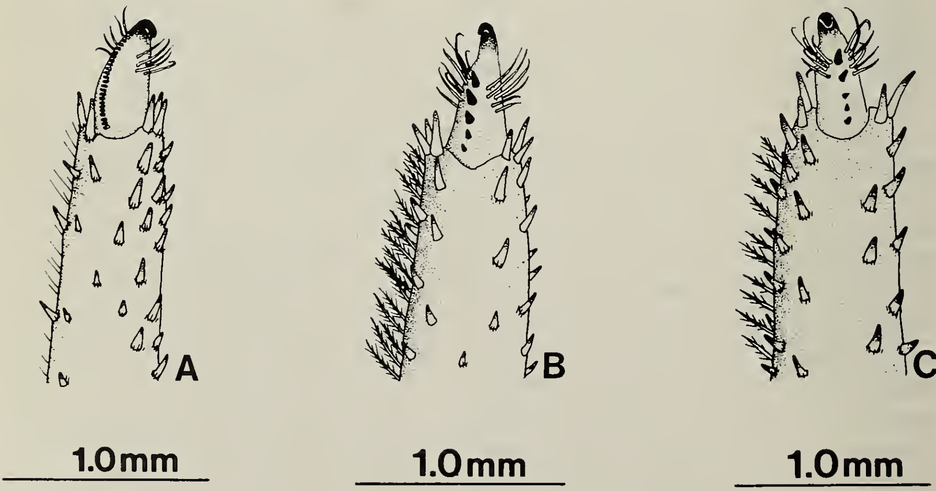


Fig. 2. *Atya abelei,* male holotype, dactylus and distal parts of propodus of pereopods 3 through 5. A, pereopod 5; B, pereopod 4; C, pereopod 3.

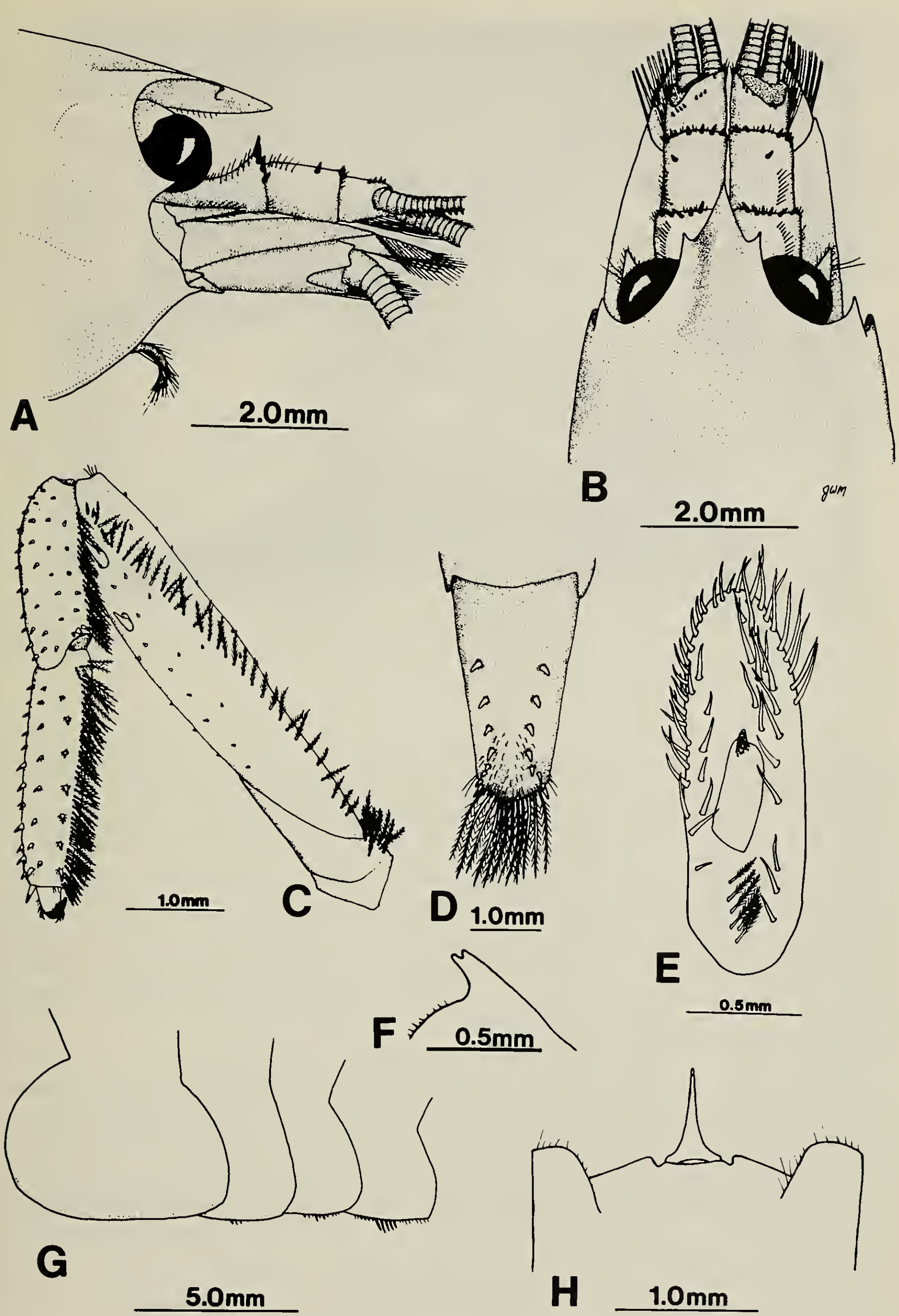


Fig. 3. *Atya abelei*, male holotype. A, anterior region, lateral view; B, anterior region, dorsal view; C, pereopod 3; D, telson, dorsal view; E, appendices masculina and interna; F, preanal carina, lateral view; G, Second through fifth abdominal pleura; H, Sternum of sixth abdominal segment and preanal carina.

Fig. 4. Color patterns of Panamanian atyids. White arrow indicates *Atya abelei*. Black on white arrow points to *A. innocous*. Shrimp feeding in center is *A. margaritacea*. The larger shrimp feeding at bottom left is another individual of *A. innocous*.

densely plumose setae originating on lateral surface of merus and continuing to tip of propodus. Merus with 2 strong movable spines on ventromesial side. Short sclerotized spines present on dorsal surface of merus, carpus, and propodus. Merus approximately 6 times as long as wide, about 3 times length of carpus, slightly more than twice length of propodus, and about 7 times length of dactylus. Flexor surface of dactylus (Fig. 2C) bearing single row of 5 blunt spines; distal part narrow and acute. Fourth pereopod similar to third but less swollen. Merus with 2 movable spines on ventrolateral margin and 3 sharp spines on corresponding part of carpus. Dactylus (Fig. 2B) bearing row of 5 strong spines on flexor surface; distal part narrow and acute.

Fifth pereopod similar to fourth with single short sharp spine on ventrolateral margin of ischium-basis. Merus armed with 3 sharp movable spines on ventromesial margin. Carpus with 1 large sharp movable spine on corresponding surface. Dactylus (Fig. 2A) armed differently from that in other pereopods, bearing single row of approximately 25 serrate denticles on lateral flexor margin; tip sharp and acute. Endopod of first male pleopod broadly ovate, subequal in length to exopod, with scattered short curved spines on anterior surface. Appendix masculina (Fig. 3E) slightly more than 3 times as long as wide. Margins with long curved spines, mesial surface bearing scattered long spines. Proximal region armed with several long plumose setae.

Color.—The color pattern described below is from the single live male kept in an aquarium at Florida State University. The ground color of the ventral half of the body is light grey and the upper half rust brown. The intensity of the brown dorsum increases anteriorly. Light yellow specks are present on all parts of the body. The light brown carapace is marked with a prominent transverse band distinctly bordered posteriorly by black. On the upper posterior surface of the carapace there is a black band that decreases in width ventrally.

The first abdominal segment has a white transverse band covering much of the segment. The third and fourth abdominal segments are light brown. The fifth segment has a small white band on its dorsal surface, and the sixth is entirely white. The proximal region of the uropods is also white and in the distal region blending to yellowish brown. The antennular peduncle and antenna are concolorous light brown. The pereopods and pleopods are all translucent brown.

Etymology.—This new species is named in honor of Lawrence G. Abele for his many contributions to crustacean biology.

Habitat.—*Atya abelei* inhabits rock rubble in water flowing at a velocity of 1.5–2.0 m/sec. *Atya abelei* and *A. margaritacea* occur in the same microhabitat with *A. innocous,* primarily found clinging to vascular plants at the stream edge (Felgenhauer and Abele, in review).

Feeding Behavior.—*Atya abelei* feeds primarily by passive filtration. Careful observations of this shrimp in aquaria for over a year revealed little evidence for scraping the substrate for food as is common for many atyids. The absence of scraping setae on the chelate pereopods would inhibit the shrimp's ability to remove material effectively from the substrate and probably accounts for the minimum amount of scraping in this species.

Discussion.—*Atya abelei* appears most closely related to *Atya innocous* which occurs in both the Atlantic and Pacific drainages of Panama and the West Indies (Abele and Blum 1977; Chace and Hobbs 1969). The species can easily be distinguished in that *A. abelei* does not have scraping denticles on the terminal brushes of the first and second pereopods. In addition, the angle of the lateral prominences of the rostrum is acute in *A. abelei* and the preanal carina terminates in a bifid tooth; these conditions are never present in specimens of *A. innocous* (Hobbs and Hart 1982). Other features that serve to separate the two species include the following: the ventral margin of the second through the fifth abdominal pleura in some populations of *A. innocous* is armed with sclerotized denticles on the ventral margins (Hobbs and Hart 1982), whereas *A. abelei* lacks these denticles and instead exhibits long simple setae in this region; the merus of the third pereopod of *A. innocous* is unarmed while the merus of *A. abelei* has two strong movable spines on the inner margin. In addition to the above characters, the species can be distinguished in the field by its color (Fig. 4). *Atya innocous* exhibits a longitudinal stripe extending from the base of the rostrum to the anterior margin of the telson. *Atya abelei* has large white transverse bands bordered anteriorly or posteriorly in black on the dorsum of the carapace, first abdominal segment, and fifth abdominal segment.

Acknowledgments

We wish to thank Dr. N. H. Williams for assistance in the field. Special thanks must be given Dr. Robert Dressler and the Smithsonian Tropical Research Institute for their kind hospitality and use of facilities in Panama. We are extremely grateful to Drs. Horton H. Hobbs, Jr., and C. W. Hart, Jr., for allowing us to see a manuscript xerox copy of their monograph on the genus *Atya*. Lastly, we must thank Dr. Horton H. Hobbs, Jr., for critically commenting on an early draft of the manuscript. Funds were provided by the National Science Foundation (Doctoral Improvement Grant) NSF No. DEB-801835.

Literature Cited

Abele, L. G. 1975. A new species of freshwater shrimp (genus *Atya*) from the Pacific drainages of Panama.—Proceedings of the Biological Society of Washington 88:51–58.

———, and N. Blum. 1977. Ecological aspects of the freshwater decapod crustaceans of the Perlas Archipelago, Panama.—Biotropica 9:239–252.

Chace, F. A., Jr., and H. H. Hobbs, Jr. 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica.—Bulletin of the United States National Museum 292:1–258.

Felgenhauer, B. E., and L. G. Abele. (In press). Aspects of mating in the tropical freshwater shrimp *Atya innocous* (Herbst).—Biotropica.

———, and ———. Ultrastructure and ecological morphology of the feeding and associated appendages of the tropical tropical freshwater shrimp *Atya innocous* (Herbst). (In review).

Hobbs, H. H., Jr., and C. W. Hart, Jr. 1982. The shrimp genus *Atya* (Decapoda: Atyidae). Smithsonian Contributions to Zoology 364: iii + 143 pp.

Department of Biological Science, Florida State University, Tallahassee, Florida 32306.

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings* of the Biological Society of Washington contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers will be published in English (except for Latin diagnosis/description of plant taxa which should not be duplicated by an English translation), with a summary in an alternate language when appropriate.

Publication Charges.—Authors will be asked to assume publication costs of page-charges, tabular material, and figures, at the lowest possible rates.

Submission of manuscripts.—Manuscripts should be sent to the Editor, *Proceedings* of the Biological Society of Washington, National Museum of Natural History, 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 will be reviewed in order of receipt by a board of associate editors and appropriate referees.

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. Synonymy of abbreviated style (author, date, page) (except in botanical papers), with full citations of journals and books (no abbreviations) in the Literature Cited is required.

The establishment of new taxa must conform with the requirements of the appropriate international codes of nomenclature. Authors are expected to be familiar with these codes and to comply with them. New species-group accounts must designate a type-specimen deposited in an institutional collection.

The sequence of material should be: Title, Author(s), Abstract, Text, Acknowledgments, Literature Cited, Author's (s') Address(es), Appendix, List of Figures (entire figure legends), Figures (each numbered and identified), Tables (each table numbered with an Arabic numeral and heading provided).

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 a facsimile with the original, and retain an author's copy. Pages must be numbered on top. One manuscript page = approximately 0.5 printed page. Underline singly scientific names of genera and lower categories; leave other indications to the editor.

Figures and tables with their legends and headings should be self-explanatory, not requiring reference to the text. Indicate their approximate placement by a pencil mark in the margin of the manuscript.

Illustrations should be planned in proportions that will efficiently use space on the type bed of the *Proceedings* (12.5 × 20 cm) and should not exceed 24 × 15 inches. Figures requiring solid black backgrounds should be indicated as such, but not masked.

Art work will be returned only on request.

Proofs.—Galley proofs will be submitted to authors for correction and approval. Reprint orders will be taken with returned proof.

Costs.—Page charges @ $60.00, figures @ $10.00, tabular material $3.00 per printed inch.

All authors are expected to pay the charges for figures, tables, changes at proof stage, and reprints. Payment of full costs will probably facilitate speedy publication.

CONTENTS

(ISSN 0006-324X)

Proceedings
of the
BIOLOGICAL SOCIETY
of
WASHINGTON

Volume 96 31 October 1983 Number 3

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 include subscription to the *Proceedings of the Biological Society of Washington. Library subscriptions to the Proceedings are: $18.00 within the U.S.A., $23.00 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 Instutution, 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.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 339–348

NECTOCARMEN ANTONIOI, A NEW PRAYINAE, CALYCOPHORAE, SIPHONOPHORA FROM CALIFORNIA

Angeles Alvariño

Abstract.—*Nectocarmen antonioi* n. gen., n. sp. was found 13 April 1981 at 33°36.7′N, 118°18.4′W, off California, at a depth of less than 70 m. The siphonophore was complete, with nectophores, gastrozooids, tentacles, palpons, tentilla, bracts, and gonophores. It differs from other genera (*Rosacea, Nectodroma* or *Praya, Prayoides, Lilyopsis, Desmophyes, Stephanophyes*) in the subfamily Prayinae in the characteristics of its nectophores, bracts, and gonophores, but constitutes a morphological link among them.

Nectocarmen, new genus

Diagnosis.—A member of the subfamily Prayinae, which includes the genera *Rosacea* (2 species), *Nectodroma* or *Praya* (2 species), *Lilyopsis* (2 species), and *Prayoides, Desmophyes,* and *Stephanophyes* (1 species each). The principal characteristics of these genera and of *Nectocarmen* are given in Table 1.

Type-species.—*Nectocarmen antonioi,* new species.

Etymology.—*Necto* (''swimming,'' Greek) + *Carmen,* my mother's name (Latin for poetry, song, and garden).

Nectocarmen antonioi, new species
Figs. 1–5

Material.—Off California, San Pedro Channel, 33°36.7′N, 118°18.4′W, R/V *David Starr Jordan* sta 88.3 *33,* cruise 8104, 13 April 1981, vertical tow from about 70 m to surface: Holotype, complete colony, USNM 60895; paratype, eudoxids, USNM 60896.

Etymology.—Named for my father, Antonio.

Description.—The subfamily Prayinae of the suborder Calycophorae are large prayids with pulsating nectophores and a heavy stem. The bracts are composed of a large amount of mesoglea, which aids the flotation of the whole animal. Prayids lack the apical gas-filled float of the Physonectidae, and are propelled by the nectophores at the upper part of the stem, which also supports the large bracts, gastrozooids, palpons, tentacles, tentilla, and gonophores.

The holotype is based on a polygastric specimen with a pair of small nectophores at the top of the stem, and well-developed eudoxids hanging from the stem, along with bracts, gastrozooids, tentacles, palpons, tentilla, gonophores, and free cormidia. The details of the siphonophore observed have been carefully reproduced, and the whole animal represented in detail in Fig. 1. Drawings give a more reliable representation of specimens than photographs.

Polygastric phase: In the polygastric phase, *Nectocarmen antonioi* exhibits 2 transparent kidney-shaped cylindrical nectophores, one slightly larger than the

Table 1.—Principal differential characteristics of the genera in the subfamily Prayinae, and the new genus.

Genera character	*Rosacea* Bigelow, 1911	*Praya* Quoy & Gaimard, 1833 = *Nectodroma* Bigelow, 1911	*Prayoides* Leloup, 1934	*Lilyopsis* Chun, 1885	*Desmophyes* Haeckel, 1888	*Stephanophyes* Chun, 1888	*Nectocarmen* n. gen.
Nectophores	Large flat smooth cylinders. Large hydroecium.	Round large pair with multi-form (branched) radial subumbral canals. Large hydroecium.	Round large pair, deep hydroecium.	3 equal size wedge-shaped.	Biserial lateral view wedge-shaped soft and transparent.	Distributed in corona.	Soft, transparent kidney shape. Hydroecium small deep groove.
Somatocyst	Does not lie as a free canal in mesoglea, but forms the pallial canal on dorsal wall of hydroecium.	Branched system of canals.	Unbranched short upper branch, or short descent branch and a short thick upper one.	Simple thin tube, lying obliquely in mesoglea.	Simple club ended, lying obliquely in mesoglea.	Complex asymmetrically rebranching up to ten times. Tips of branchlets pigmented.	Single, pear-shaped, lying vertically in mesoglea.
Nectosac	Small, about 1/4 of length of nectophore. Sinuous meandering lateral canals.	Small, ¼–½ of length of nectophore. Canals multi-branched or in network.	Short, branched canals, up to 15 branches.	Large, with meandering radial canals. Ostial tubercles or pigmented spots.	Small. Lateral radial canals straight. Ring of minute pigment flecks and tubercles around the ostium.	Occupying great part of nectophore. Ostium nearly parallel with long axis. Some small red tubercles on ventral side of ostium.	Large, occupying most of nectophore. Anterior and posterior canals straight, lateral canals reach up close to top of nectosac bending down to ring canal. No tubercles or pigmented spots on ostium.

Table 1.—Continued.

Genera character	*Rosacea* Bigelow, 1911	*Praya* Quoy & Gaimard, 1833 = *Nectodroma* Bigelow, 1911	*Prayoides* Leloup, 1934	*Lilyopsis* Chun, 1885	*Desmophyes* Haeckel, 1888	*Stephanophyes* Chun, 1888	*Nectocarmen* n. gen.
Bract	Oval, with central organ. Left and right hydroecian canal of different size (one less than ¼ of other) Dorsal bracteal canal short, extends to anterior part. Ventral bracteal canal short.	Flattened semicircular. No median central organ. Dorsal bracteal canal recurved. Ventral bracteal canal long. Both bracteal canals may have small branches. Hydroecial canals of almost equal length.		6 bracteal canals. No central organ.	Kidney shape, round above. With median pear-shaped vesicle (central organ). 4 main bracteal canals.	Bracteal canal system similar to previous genera.	Transparent, oval, flat. Bracteal canals almost straight. One hydroecial canal larger and more curved than the other.
Gonophore	Well-developed medusoids. No asexual eudoxid nectophore.	Medusoids with well developed radial and ring canals. ♀ larger than ♂. Pedicular canal trifid branched. Female with 4–6 large ova.		Large asexual eudoxid nectophores. Radial canals in 2 pairs from pedicular canal. Unisexual gonophores with reduced umbrella. Females and males on same stem.	Large asexual eudoxid nectophores, and groups of unisexual reduced gonophores. Eudoxids of both sexes on same stem.	Large asexual eudoxid nectophores, with meandering canals. The 4 radial canals do not branch together from pedicel. Small red tubercles. Bunch of reduced medusoid gonophores, canals in zigzag branching laterally. 2–3 female alternating with 2–3 male cormidia.	No asexual eudoxid nectophores. Gonophores laterally flat hemispheres, with 4 straight radial canals together from pedicel to ring canal. Pedicular canal trifid branched. Ovaries with small ova. No tubercles or pigmented spots on edge of umbrella.

Fig. 1. *Nectocarmen antonioi,* complete specimen, about 200 mm long.

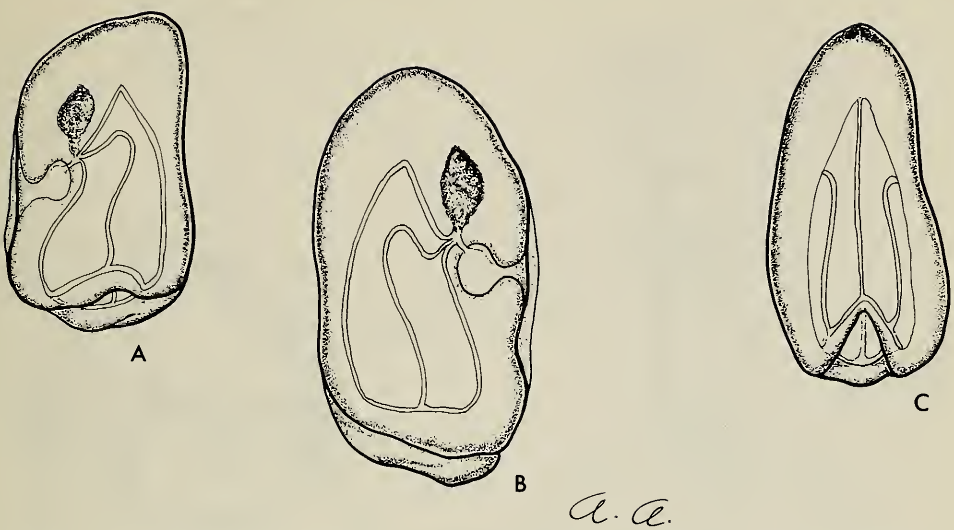


Fig. 2. Pair of nectophores of *Nectocarmen antonioi* (3–4 mm long): A, Small nectophore; B, Large nectophore; C, Dorsal view of either nectophore. Hydroecium, nectosac, radial and circular canals, and somatocyst can easily be observed.

other, with a large nectosac reaching nearly to the top of the nectophore. The nectophores are 3–4 mm long and about 2.5 mm wide. The hydroecium is only ⅓ the width of the nectophore, and does not run its entire length; it forms a deep groove, with rounded lobes (superior and inferior) closing the entrance, and this whole structure is covered by the flaps of the nectophore walls.

The pair of nectophores are bound together by the hydroecium, embracing each other by this structure (Fig. 2).

The nectosac is large, similar to that of *Stephanophyes superba* Chun, 1885 (1891) but with differences in the hydroecium, somatocyst, and radial canals. The pallial canal extends slightly up the nectosac, forming the radial canals. The anterior and posterior radial canals are straight, and the lateral canals bend upward to a position close to the top of the nectosac, then turn straight down to the ring or circular canal. The velar end of the nectosac, the ostium, is large, extending upward at the dorsal side. No ring of minute pigment flecks or tubercles is observed on the ostium.

The somatcyst is pear-shaped, and lies vertically in the mesoglea, extending slightly above the top of the nectosac.

Gastrozooids retain the larval tentacle, modified to form a series of tentilla. The base of the gastrozooids is enlarged into the nematocyst-producing area, the basigaster.

Palpons of reduced gastrozooids, with simple tentacles or palpacles, serve as feelers or testers.

The tentilla, with the subterminal battery of nematocysts, are spirally twisted filaments, with cnidobands (sabre-shaped nematocysts) forming the chief part of the stinging organs.

Gastrozooids, tentacles, palpons and tentilla lie under the bracts, and are shown in Fig. 1, and in detail in Fig. 3.

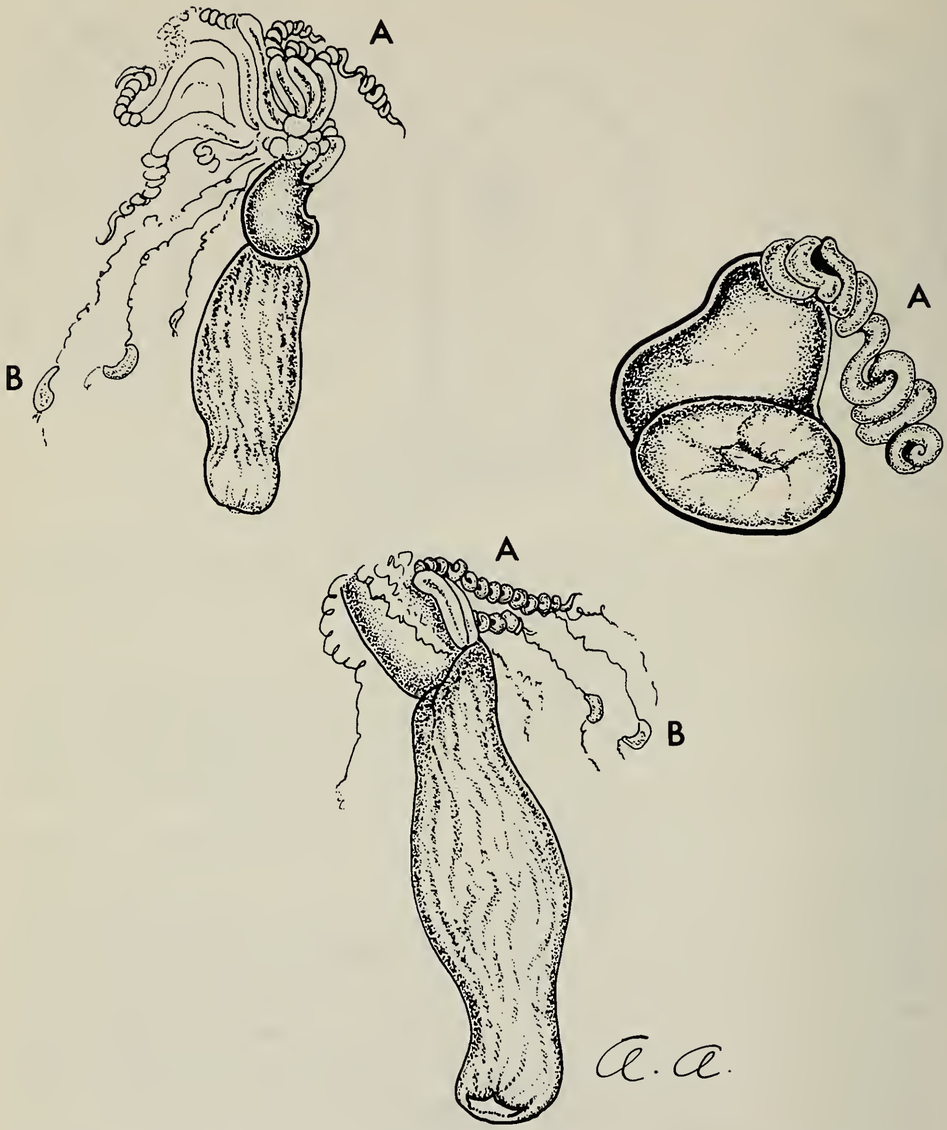


Fig. 3. Gastrozooids of *Nectocarmen antonioi* (2–3 mm long): A, Tentacles; B, Tentilla.

Eudoxid phase: The eudoxid phase has no asexual nectophore.

The bracts, which reach a maximum length of 10–12 mm, are oval, kidney-shaped, laterally flattened masses of mesoglea, the inferior part of which is concave and the upper part convex. They are divided into 2 lobes, with a third lobe on the concave distal side forming part of the hydroecial cavity of the bract. Unlike *Desmophyes,* no central organ (pear-shaped vesicle) is present at the junction of the main bracteal canals.

The bracts contain 4 large canals. The dorsal bracteal canal, which is slightly curved, ends in an ampullar dilatation, as does the nearly straight ventral bracteal canal; left and right hydroecial canals also end in ampullar dilatations. The right

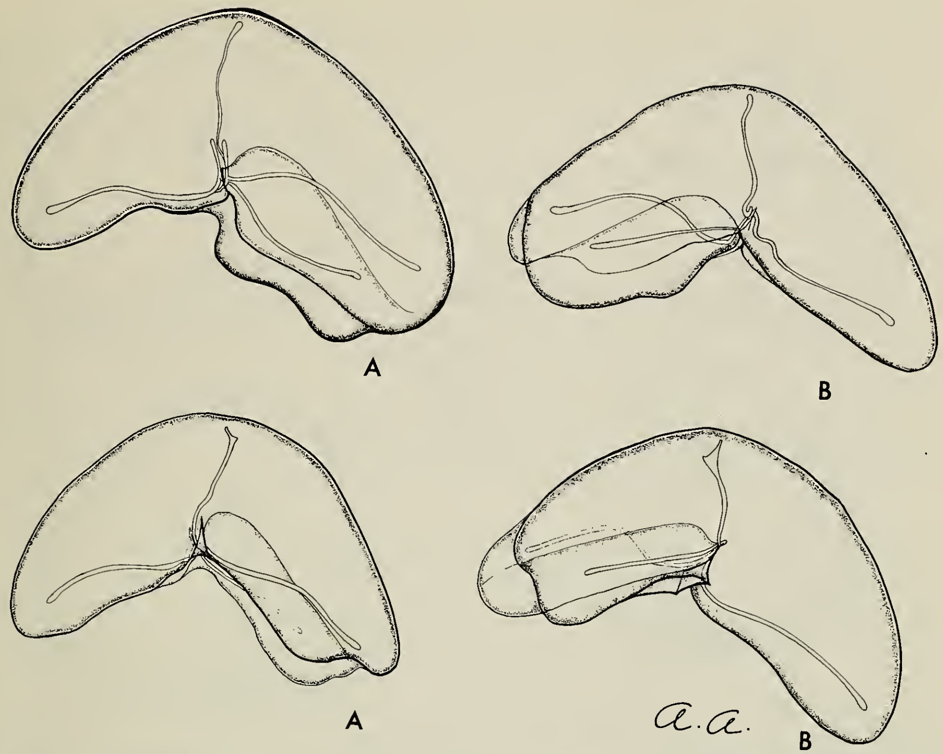


Fig. 4. Bracts of *Nectocarmen antonioi* (10–12 mm longest axis): A, Lateral right view of two bracts; B, Lateral left view of two bracts.

hydroecial canal is longer than the left. The former curves upwards and then extends down, and the latter bends down and then up. Usually, the left canal is straighter than the right. Neither the bracteal nor the hydroecial canals branch into small branchlets or spurs (Fig. 4).

The bracts, with gastrozooids, tentacles, palpons, tentilla and gonophores, may detach from the stem and swim freely in the ocean.

The sexual gonophores are large and hemispherical in shape, laterally flattened, retaining the medusoid characteristics, but without marginal tentacles. Female and male gonads occupy the mouthless manubrium. The gonophores pulsate intermittently, and are capable of propelling the cormidia in the water.

The gonophores are budded at the stem, below the base of the gastrozooids. They are, as explained, large bells, laterally compressed, with 4 straight radial canals ending at the ring canal. The bells hang from the bract by the pedicular canal, and the four radial canals run from the pedicel to the circular canal. Near the top of the umbrella, the pedicel has trifid branches embedded in the mesoglea, as is seen in *Nectodroma (Praya) reticulata* (Bigelow, 1931). The large, pear-shaped vesicles inside are the female gonads, containing numerous small ova. Male gonads are small, pointed, sausage-shaped vesicles (Fig. 5).

Male and female eudoxids may be found on the same stem.

It is probable that each cormidium includes either male or female gonophores, providing a sexual separation when male cormidia and female cormidia swim

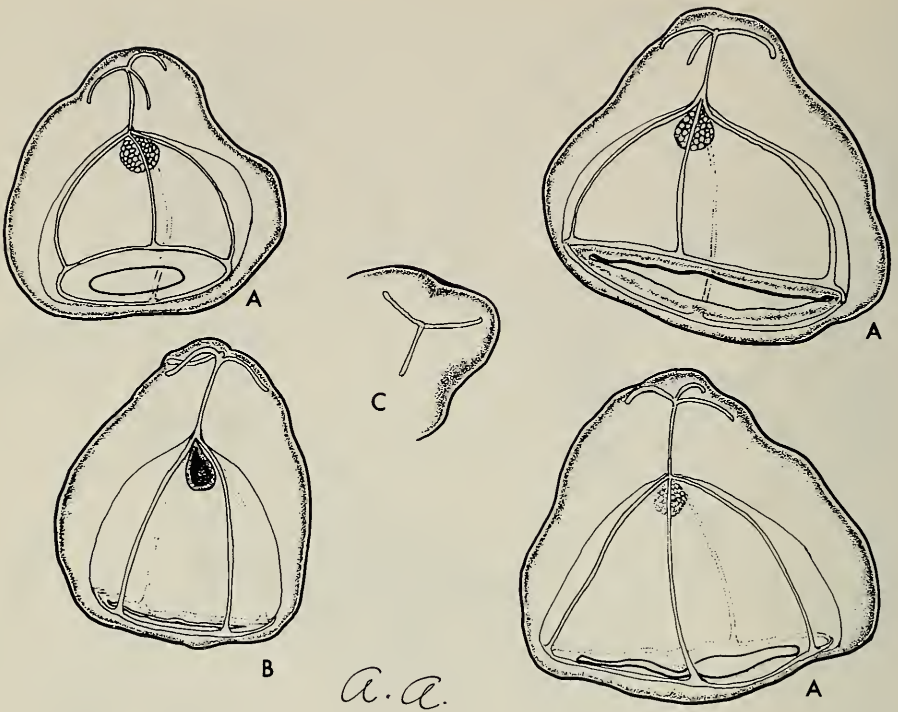


Fig. 5. Gonophores of *Nectocarmen antonioi* (3–4 mm high): A, Female gonophores; B, Male gonophore; C, Upper view of gonophore to show the trifid branching pedicel.

freely in the ocean. Some of the cormidia were detached, but obviously belonged to the same whole animal.

The nectophores, bracts, and gonophores are transparent; gastrozooids, palpons, and tentacles range in color from bright reddish to faded pink or rose.

The nectophores function in propulsion; the bracts are composed of enlarged masses of mesoglea and act as protection for gastrozooids and gonozoids or gonophores, as well as contributing to the buoyancy of the animal. The stem contracts and expands, and the gonophores also perform active pulsations, contributing to the propulsion of the siphonophores; by spreading the stem into loops they also amplify the potential field of the tentacles and the fishing predatory capacity of the siphonophore.

Discussion.—The principal differential characteristics of the genera in the subfamily Prayinae are presented in Table 1, together with those for *Nectocarmen* n. gen.

The general shape of the nectophores is similar to that of the other genera in the subfamily, especially *Rosacea* Bigelow, 1911, and *Desmophyes* Haeckel, 1888, also described by Kawamura (1915). However, the hydroecium is smaller than that of *Rosacea,* or *Desmophyes,* and similar to that of *Stephanophyes.* The nectosac is large, as in *Stephanophyes* and *Lilyopsis* (Alvariño 1981; Chun 1885, 1891), but the radial canals do not display the meandering pattern observed in *Stephanophyes* and *Lilyopsis.* The somatocyst of *Nectocarmen* is different from that of other Prayinae genera, including *Prayoides intermedia* Leloup, 1934.

The bracts resemble in general outline those of *Nectodroma (Praya)*, but differ in the detail of the shape and pattern of the canals, as can be observed by comparing present illustrations with those by Alvariño (1981), Bigelow (1911), and Totton and Bargmann (1965). Bracts in *Nectocarmen antonioi* do not have the vesicular organ of *Desmophyes*.

The eudoxids of the new siphonophore do not have the large asexual eudoxid nectophore that is found in *Lilyopsis, Desmophyes,* and *Stephanophyes*. The gonophores are similar to those of *Nectodroma (Praya)*; however, sexual nectophores are pear-shaped in *Nectodroma,* and hemispherical in *Nectocarmen*. Both *Nectodroma (Praya)* and *Nectocarmen* present the trifid branched pedicular canal, but the gonads of the former include 4–6 large ova (Bigelow 1931), while in the latter the ova are small and numerous. In *Nectocarmen* the four radial canals of the gonophore converge at the pedicel, and run straight to the circular canal, characteristics different from the other genera in the subfamily, though similar to *Nectodroma (Praya)*. No tubercles or pigmented spots appear on the margin of the gonophoral umbrella, whereas in the other species of the subfamily those structures are present.

Species of the following Prayinae have been observed in California waters (Alvariño 1967, 1971): *Nectodroma dubia* (Quoy and Gaimard, 1833), *N. reticulata* (Bigelow, 1911), *Rosacea plicata* Bigelow, 1911. Bigelow and Leslie (1930) reported *N. reticulata* from Monterey, but Totton and Bargmann (1965) indicate it was probably *N. dubia*.

There is a peculiar phenomenon common to Siphonophorae and Medusae, in that most of the species present an erratic distribution (Alvariño 1977, 1981; Sears 1953). Sears (1953:11) says: ''There appears to be a tendency among coelenterates for a seemingly good species to appear in a particular locality, often in considerable numbers, and after a time to disappear, never to be seen again.'' This must be related to the peculiarity in patchiness and irregular aggregational distribution characteristics of siphonophores and other coelenterate populations, and the ineffectiveness of the plankton sampling gear in capturing these organisms (Biggs, Bidigare, and Smith 1981; Hamner *et al.* 1975). Because of their swimming behavior and speed, and their life cycle characteristics, siphonophores are capable of avoiding capture by plankton nets (Biggs 1977).

Acknowledgments

I would like to express my appreciation to Drs. Izadore Barrett, Frank Ferrari, John R. Hunter, and Reuben Lasker for reading the manuscript, and to Dr. Thomas E. Bowman and Ms. Martha Brown for their careful editing of the paper. My thanks are also due to Esperanza Manaligod for typing the table included in this work.

Literature Cited

Alvariño, A. 1967. Bathymetric distribution of Chaetognatha, Siphonophorae, Medusae and Ctenophora off San Diego, California.—Pacific Science 21:473–485.

———. 1971. Siphonophores of the Pacific, with a review of the world distribution.—Bulletin Scripps Institution of Oceanography, University of California San Diego, La Jolla, California 16:1–432.

———. 1977. Indicadores planctonicos: Distribucion batimetrica de algunas Medusas (Planktonic indicators: Bathymetric distribution of some Medusae).—Memorias II Simposio Latinoamericano sobre Oceanografia Biologica, Venezuela 1975 1:161–190.

———. 1981. Siphonophorae. Atlas del Zooplancton del Atlantico Sud-occidental.—Publication Instituto Nacional de Investigación y Desarrollo Pesquero [INIPED], Ministerio de Comercio e Intereses Marítimos, Subsecretaria de Intereses Marítimos, Argentina, pp. 383–441.

Bigelow, H. B. 1911. Siphonophorae. ALBATROSS expedition to the eastern tropical Pacific.—Memoirs of the Museum of Comparative Zoology at Harvard College 38(2):173–401.

———. 1931. Siphonophorae from the ARCTURUS oceanographic expedition.—Zoological Scientific Contribution, New York Zoological Society 8(11):525–592.

———, and M. Leslie. 1930. Reconnaissance of the waters and plankton of Monterey Bay, 1928.—Bulletin of the Museum of Comparative Zoology at Harvard College 70:492–581.

Biggs, D. C. 1977. Field studies of fishing, feeding and digestion in Siphonophores.—Marine Behaviour and Physiology 4(4):261–274.

———, R. R. Bidigare, and D. E. Smith. 1981. Population density of gelatinous macrozooplankton: *In situ* estimation in oceanic surface waters.—Biological Oceanography 1(2):157–173.

Chun, C. 1885. Ueber die cyclische Entwickelung der Siphonophores.—Sitzungsberichte der königlich Preussischen Akademie der Wissenschaften zu Berlin 1885:511–529.

———. 1891. Die Canarischen Siphonophores in monographischen Darstellungen I. *Stephanophyes superba* und die familie der Stephanophyiden.—Abhandlungen senckenbergische naturforschende Gesellschaft 16:553–627.

Haeckel, E. 1888. Report on the Siphonophorae.—Report on the Scientific Research Expedition, H.M.S. CHALLENGER, Zoology 21:1–380.

Hamner, W. M., L. P. Madin, A. L. Alldredge, R. W. Gilmer, and P. O. Hamner. 1975. Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior.—Limnology and Oceanography 20(6):907–917.

Kawamura, T. 1915. Calycophorae, II.—Zoological Magazine, Tokyo 27:317–324.

Leloup, E. 1934. Siphonophores de l'Ocean Atlantique tropical et austral.—Bulletin Muséum Royal Histoire Naturelle de Belgique 10(6):1–87.

Sears, M. 1953. Notes on Siphonophores. 2. A revision of the Abylinae.—Bulletin of the Museum of Comparative Zoology at Harvard College 109(1):1–119.

Totton, A. K., and H. E. Bargmann. 1965. A synopsis of the Siphonophora.—British Museum, Natural History, pp. 1–230.

National Marine Fisheries Service, NOAA, Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 349–354

A NEW *STROMBINA* SPECIES (GASTROPODA: PROSOBRANCHIA) FROM THE TROPICAL WESTERN ATLANTIC

Richard S. Houbrick

Abstract.—*Strombina* (*Cotonopsis*) *argentea* is the fourth living *Strombina* species and the first *Cotonopsis* taxon described from the tropical western Atlantic. It has the most northern distribution of any western Atlantic *Strombina* species and occurs in deep water. This species is the largest of the four Atlantic taxa, and morphologically resembles the eastern Pacific *Strombina* (*Cotonopsis*) *deroyae* Emerson and D'Attilio, 1969. There is considerable intraspecific variation in axial sculpture. The radula is typically columbellid in form.

While processing material dredged by the National Marine Fisheries ship R/V *Oregon* in deep water near Silver Bank off the north coast of the Dominican Republic, ten specimens of a new, remarkably large *Strombina* species were recognized. Two were live-collected and contained dried animals, allowing examination of the operculum and radula.

The genus *Strombina* was widespread in the Caribbean during the Miocene, but the diversity of this taxon decreased in the Pliocene. Although there are many species living in the eastern Pacific today, only three Recent species were previously known from the western Atlantic, all from the southern Caribbean, and referred to the subgenus *Strombina* s.s. This paper describes a fourth *Strombina* species that is allocated to the subgenus *Cotonopsis* Olsson, a group previously known only from the Neogene of Central America and the Recent eastern Pacific fauna. The presence of a large, distinctive *Strombina* living in deep water to the north of the Greater Antilles and Caribbean Sea adds significant dimension to the composition and distribution of this lineage in the western Atlantic.

Description

Family Columbellidae
Strombina Mörch, 1852
Subgenus *Cotonopsis* Olsson, 1942
Strombina (*Cotonopsis*) *argentea*, new species
Figs. 1–2

Shell (Table 1).—Shell large and slender, fusiform, with elongate tapering spire comprising 10 weakly inflated whorls and ranging in length from 30–43 mm. Whorls sculptured with 19–28 weak slightly curved axial ribs extending length of whorl. Some shells nearly smooth but early whorls of teloconch sculptured with distinct axial ribs. Protoconch large, bulbous, smooth, about 1½ whorls. Body whorl large, nearly smooth, round in cross section, slightly angulate at periphery, about one-half shell length. Axial ribs present on anterior of body whorl but fading out near lip. Thick varix just above edge of outer lip. Siphonal constriction of body

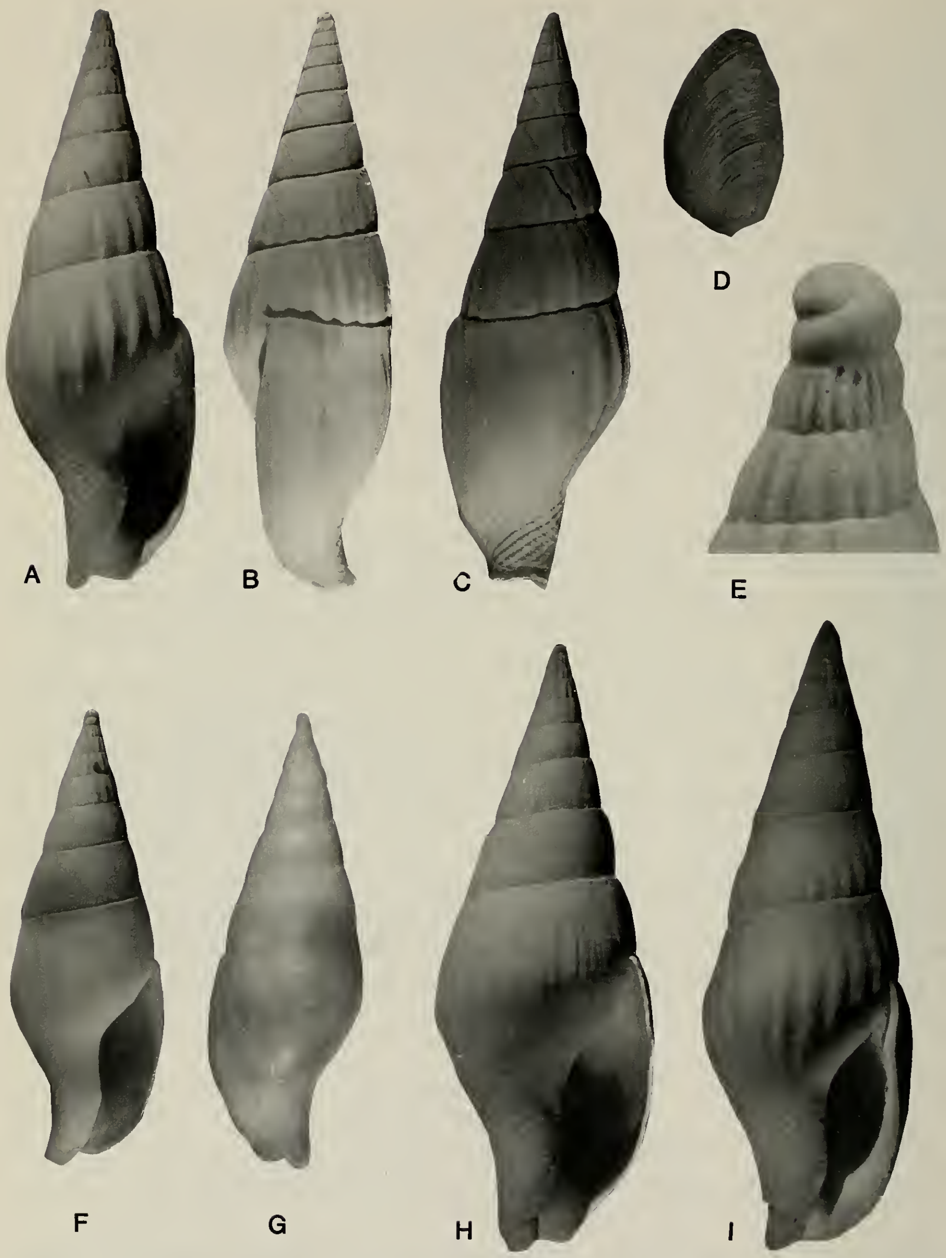


Fig. 1. *Strombina* (*Cotonopsis*) *argentea* (all specimens whitened with ammonium chloride to enhance sculptural details—Fig. G is natural; A, B, C, Apertural, side and dorsal views of holotype, USNM 810345, 39 mm; D, Operculum of holotype, 6 mm long; E, Detail of protoconch and sculpture of early whorls, USNM 821851, 22.5×; F, Paratype, showing protoconch, USNM 821851, 31 mm; G, Dorsal view, same as F, but natural to show glossy shell and light tan color pattern; H, Weakly sculptured specimen, paratype USNM 821851, 43 mm; I, Specimen with strong axial sculpture, paratype, USNM 821851, 41 mm.

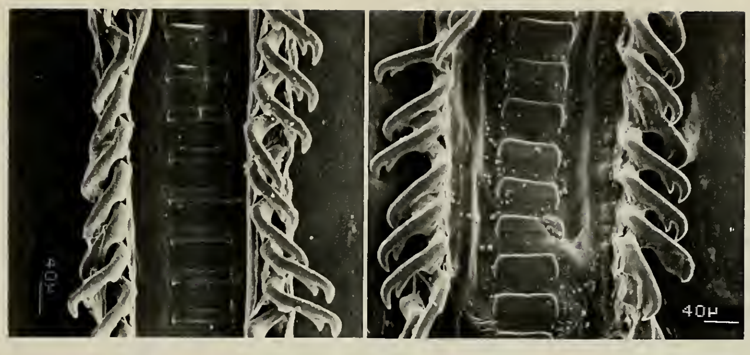


Fig. 2. Scanning electron micrographs of radula of *Strombina* (*Cotonopsis*) *argentea*. Lateral teeth spread back to show weak rachidian teeth. Note large interspaces on radular membrane between rachidian and lateral teeth.

whorl sculptured with fine spiral striae. Suture straight, slightly impressed. Aperture little less than one-half shell length, narrow, lunate, sinuous. Anterior siphonal canal long, curved to left, slightly reflected dorsally. Anal canal short, deeply incised. Parietal area somewhat thickened. Columella concave, sinuous and twisted at canal constriction. Slight columellar wash present. Outer lip smooth with thickened sinus at anal canal and slight posterior extension onto body whorl. Inner lip with tiny denticles and 1 to 2 larger teeth adjacent to anal canal. Denticles not extending into aperture. Shell color white with 2 broad bands of faded, yellowish-tan zigzag markings.

Operculum (Fig. 1, D).—Operculum thin, corneous, lenticular with terminal nucleus at edge.

Radula (Fig. 2, Table 2).—Radular ribbon rachiglossate (1+1+1), typically columbellid in form, narrow, relatively long, little over one-fourth shell length, comprising about 245 rows of teeth. Rachidian tooth a weak, narrow, nearly rectangular plate with rounded dorsal edges, pointed where joined to basal membrane. Wide interspace between rachidian tooth and lateral teeth. Lateral tooth comprising a shaft with peg-like base, 2 hooked cusps at tip, single blunt hook on mid shaft of tooth.

Animal.—Preserved, dried animals, when rehydrated, appeared to be unpigmented and had a large foot, and a smooth mantle edge with a muscular, well-developed anterior siphon. Head small, with short tentacles each with a small basal eye. Proboscis pleurembolic, long, containing large buccal mass and long radular ribbon. The poor state of preservation did not allow detailed anatomical studies.

Table 1.—Shell measurements of *Strombina argentea* (all measurements in mm).

Statistic (n = 10)	$\bar{x}$	SD	Var.	Range
Length	38.83	3.57	11.45	30–43
Width	12.97	1.26	1.42	10.3–14.6
Length of aperture	18.05	1.95	3.43	14–20.6
Width of aperture	5.21	0.58	0.31	4.1–6.2
No. of whorls	10.1	0.32	0.09	10–11

Table 2.—Radular measurements (all measurements in mm).

Character (n = 2)	Radula length	Rows of teeth	Shell length	Shell length / Radula length
Mean	10.2	244.8	39.5	4.07

Type-locality.—384–430 m, 20°48′N, 70°46′W, near Silver Bank, 60 miles NE of Luperon, Dominican Republic; NMFS, R/V *Oregon*, Station 5432.

Holotype (Fig. 1, A–B).—USNM 810345; length 39 mm, width 13.1 mm. 9 paratypes, USNM 821851 (for measurements see Table 1).

Etymology.—From the Latin adjective *argenteus*, "silver," in reference to the Silver Bank area, where the specimens were taken.

Remarks

Specimens of this species were dredged in depths of 210–235 fms (384–430 m) in the Silver Bank Passage between Mouchoir Bank and Silver Bank. The shell form and axial sculpture are adapted to a sandy bottom habitat and all dead shells had drill holes indicative of predation by naticid snails. Several shells showed repair marks due to crab attacks. Two specimens were collected alive. Within the rectum of one of these were the remains of a sipunculan worm of the genus *Aspidosiphon*.

The degree of axial sculpture shows considerable intraspecific variation. Some shells are nearly devoid of axial ribs while in others they may be pronounced. Axial sculpture is strongest on the early, post-nuclear whorls and on the penultimate and body whorls, and is most pronounced on the anterior portion of each whorl, adjacent to the suture. When axial ribbing is strong, the suture appears wavy.

Among the Recent Panamic fauna, *Strombina deroyae* Emerson and d'Attilio, 1969, from the Galapagos, assigned by Keen (1971) to *Cotonopsis*, is morphologically close to the western Atlantic *Strombina argentea* although the color pattern of the latter is weaker. *Strombina argentea* also resembles *Strombina fusinoidea* Dall, 1916, in general form, but that taxon is a *Strombina* s.s., and differs accordingly.

Strombina argentea has a shell remarkably convergent with that of *Cyomesus chaunax* (Bayer, 1971), a totally unrelated turbinellid species. The latter differs chiefly in having strong columellar plications.

Strombina is not a common taxon in the Recent Caribbean fauna. Olsson and Harbison (1953:230) pointed out that *Strombina* is characteristically Panamic in the Recent fauna, but in the Miocene and Pliocene it was well represented in an extended Caribbean province by a number of species. It also occurred in north Florida (Petuch 1982:304). Petuch (1980:86) noted that there are only three living species in the western Atlantic, while Keen (1971) recorded 25 species living in the eastern Pacific. Weisbord (1962:327–328) listed about 25 fossil species from the Caribbean and as many as 40 species are named from Neogene deposits in tropical America (Woodring 1964:252). J. and W. Gibson-Smith (1974), in an extensive overview of this group in the Caribbean, estimated about 60 fossil taxa occurred in that province during Miocene and Pliocene times.

Three subgenera of *Strombina* have been proposed: *Strombina* s.s., *Cotonopsis* Olsson, 1942, and *Sincola* Olsson and Harbison, 1953. Although most western Atlantic living and fossil species are allocated to *Strombina* s.s., J. and W. Gibson-Smith (1974:51) pointed out several Caribbean fossil taxa which do not fit the limits of these subgenera and suggested that the entire group was in need of revision.

The three living Caribbean species, *Strombina pumilio* (Reeve, 1859), *S. caboblanquensis* Weisbord, 1962, and *S. francisiae* J. and W. Gibson-Smith, 1974, are all assigned to *Strombina* s.s. None of these taxa bears any resemblance to the much larger *Strombina argentea*, which falls within the limits of the subgenus *Cotonopsis*. *Cotonopsis* differs from *Strombina* s.s. in lacking a thickening or hump on the back of the body whorl, by the circular section of the body whorl, a less thickened lip that is not strongly denticulate within, and in the more strongly recurved anterior canal. *Cotonopsis* was originally based on two fossil species in the Tertiary beds of the Burica Peninsula, Panama. Keen (1971) has assigned four living eastern Pacific species to *Cotonopsis*. The subgenus *Cotonopsis* was previously unrecorded in the Recent or fossil fauna from the western Atlantic. A review of the Caribbean fossils depicted in the literature revealed nothing similar to *Strombina argentea*; moreover, none of the fossils from the Dominican Republic shown by Maury (1917, pl. 15) and Pilsbry (1921) or those of Jamaica (Woodring 1928) are similar to this species. Exclusive of *S. argentea*, all Recent and most fossil species from the western Atlantic belong to *Strombina* s.s. The type-species of *Cotonopsis*, *Strombina panacostaricensis* Olsson, 1942, has axial ribs on each whorl and the spiral striae on the body whorl constriction seen in *S. argentea*, but lacks the long twisted anterior canal of the latter.

Acknowledgments

I wish to thank Dr. M. J. Harasewych for his help with photography and for critically reading the manuscript. My thanks to Ms. J. Piraino for taking the SEM micrographs and to Mrs. June Jones for typing the drafts of this paper. Dr. Mary Rice identified the sipunculan remains. This is contribution No. 115 of the Smithsonian Marine Station, Ft. Pierce, Florida.

Literature Cited

Bayer, F. M. 1971. New and unusual mollusks collected by R/V John Elliott Pillsbury and R/V Gerda in the tropical western Atlantic.—Bulletin of Marine Science 21(1):111–236.

Emerson, W. K., and A. D'Attilio. 1969. A new species of *Strombina* from the Galapagos Islands.—Veliger 11(3):195–197, pl. 39.

Gibson-Smith, J., and W. Gibson-Smith. 1974. The genus *Strombina* (Mollusca: Gastropoda) in Venezuela, with descriptions of a new Recent and some fossil species.—Boletin Informatino. Associacion Venezolana de Geologia, Mineria y Petroleo 17(4,5,6):49–70, pls. 1–4.

Keen, M. A. 1971. Sea shells of tropical west America, 2nd Ed. Stanford. 1064 pp., 22 pls.

Maury, C. J. 1917. Santo Domingo type sections and fossils.—Bulletins of American Paleontology 5(29):1–249, 39 pls.

Olsson, A. A., and A. Harbison. 1953. Pliocene mollusca of southern Florida.—The Academy of Natural Sciences of Philadelphia, Monograph No. 8, 456 pp., 65 pls.

Petuch, E. J. 1980. A reanalysis of Neogene Caribbean provinciality with reference to the discovery of a relict Caenogastropod fauna off northern South America. Unpublished Ph.D. Dissertation, University of Miami, 163 pp.

———. 1982. Geographical heterochrony: contemporaneous coexistence of Neogene and Recent molluscan faunas in the Americas.—Palaeogeography, Palaeoclimatology, Palaeoecology 37: 277–312.

Pilsbry, H. A. 1921. A review of W. M. Gabb's Tertiary Mollusca of Santo Domingo.—Proceedings of the Philadelphia Academy of Natural Sciences 73(2):305–428, pls. 16–47.

Weisbord, N. E. 1962. Late Cenozoic gastropods from northern Venezuela.—Bulletins of American Paleontology 42(193):1–672, 48 pls.

Woodring, W. P. 1928. Miocene mollusks from Bowden Jamaica. Part 2, Gastropods and discussion of results.—Carnegie Institution of Washington, No. 385: vii + 564 pp., 39 pls.

———. 1964. Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (Gastropods: Columbellidae to Volutidae).—U.S. Geological Survey Professional Paper 306-C:241–297, pls. 39–47.

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

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 355–364

CARENZIA, A NEW GENUS OF SEGUENZIACEA (GASTROPODA: PROSOBRANCHIA) WITH THE DESCRIPTION OF A NEW SPECIES

James F. Quinn, Jr.

Abstract.—*Carenzia* is proposed for three species of seguenziacean gastropods, with *Seguenzia carinata* Jeffreys, 1877, as type-species. *Carenzia carinata* and *C. trispinosa* (Watson, 1879) are redescribed and illustrated with photomacrographs and scanning electron micrographs; *C. inermis* is described as new and illustrated with photomacrographs. *Carenzia carinata* is known from both sides of the North Atlantic Ocean in depths of 1000–2000 m; *C. trispinosa* occurs in similar depths but is restricted to the western side of the North Atlantic; *C. inermis* is reported from off Oregon in depths of about 2000 m.

Several species-groups within the genus *Seguenzia* Jeffreys, 1876, which were informally recognized by Quinn (in press), should be accorded generic rank. Diagnoses of these new genera were to be published as part of a systematic review of the western Atlantic species of Seguenziacea (Quinn, in preparation). However, in a monograph of New Zealand seguenziaceans Marshall (in press) is providing diagnoses for at least two of these genera, leaving only the *Seguenzia carinata* group to be diagnosed among western Atlantic *Seguenzia*. Publication of this paper prior to a full review is prompted by discovery of a new species of the *S. carinata* group from off Oregon which is to be included in a monograph of northeastern Pacific archaeogastropods (McLean, personal communication). *Carenzia,* new genus, is herewith diagnosed, and the two western Atlantic species, *C. carinata* (Jeffreys, 1877) and *C. trispinosa* (Watson, 1879), are redescribed and illustrated. *Carenzia inermis,* new species, is described from the northeastern Pacific. Two New Zealand species of *Carenzia* will be described by Marshall (in press).

Institutional abbreviations used in this paper are: BM(NH), British Museum (Natural History); LACM, Los Angeles County Museum of Natural History; UMML, Rosenstiel School of Marine and Atmospheric Science (RSMAS), University of Miami; USNM, U.S. National Museum of Natural History.

Carenzia, new genus

Seguenzia.—Auct. (partim).

Type-species.—*Seguenzia carinata* Jeffreys, 1877; herein designated.

Diagnosis.—Shell small, trochoid, peripherally carinate, nacreous under a porcelaneous layer; spire evenly conical to turreted, with mid-whorl carina at least on early whorls; base convex, usually with deep, wide umbilicus, occasionally with spiral threads; aperture rhomboidal; outer lip with shallow, V-shaped sinus at suture, and another in peripheral part of base; columella strongly arched, with or without distinct tooth; protoconch smooth or with spiral ridges, terminal varix low; animal, operculum and radula as yet undescribed.

Remarks.—*Carenzia* differs from *Seguenzia* in the more conical shape of the shell, lack of strong axial and spiral sculpture on the later whorls, V-shaped anal sinus, and lack of a distinct sinus in the periphery. From the genus which includes *Fluxina discula* Dall, 1889 (to be described by Marshall, in press), *Carenzia* differs in the much more elevated shell, prominent protoconch, and presence of a mid-whorl carination in addition to the peripheral carina. Although animals of this genus are undescribed, Bouchet and Warén (personal communication) have material of *C. carinata* (Jeffreys, 1877) from which they will prepare an anatomical discussion of the species. Marshall (in press) will present illustrations of the radula of at least one of his new species. *Carenzia* is known from the Atlantic and northeastern Pacific oceans, and New Zealand waters (Marshall, in press).

Etymology.—From the Latin *carina,* a keel, and *Seguenzia*; gender feminine.

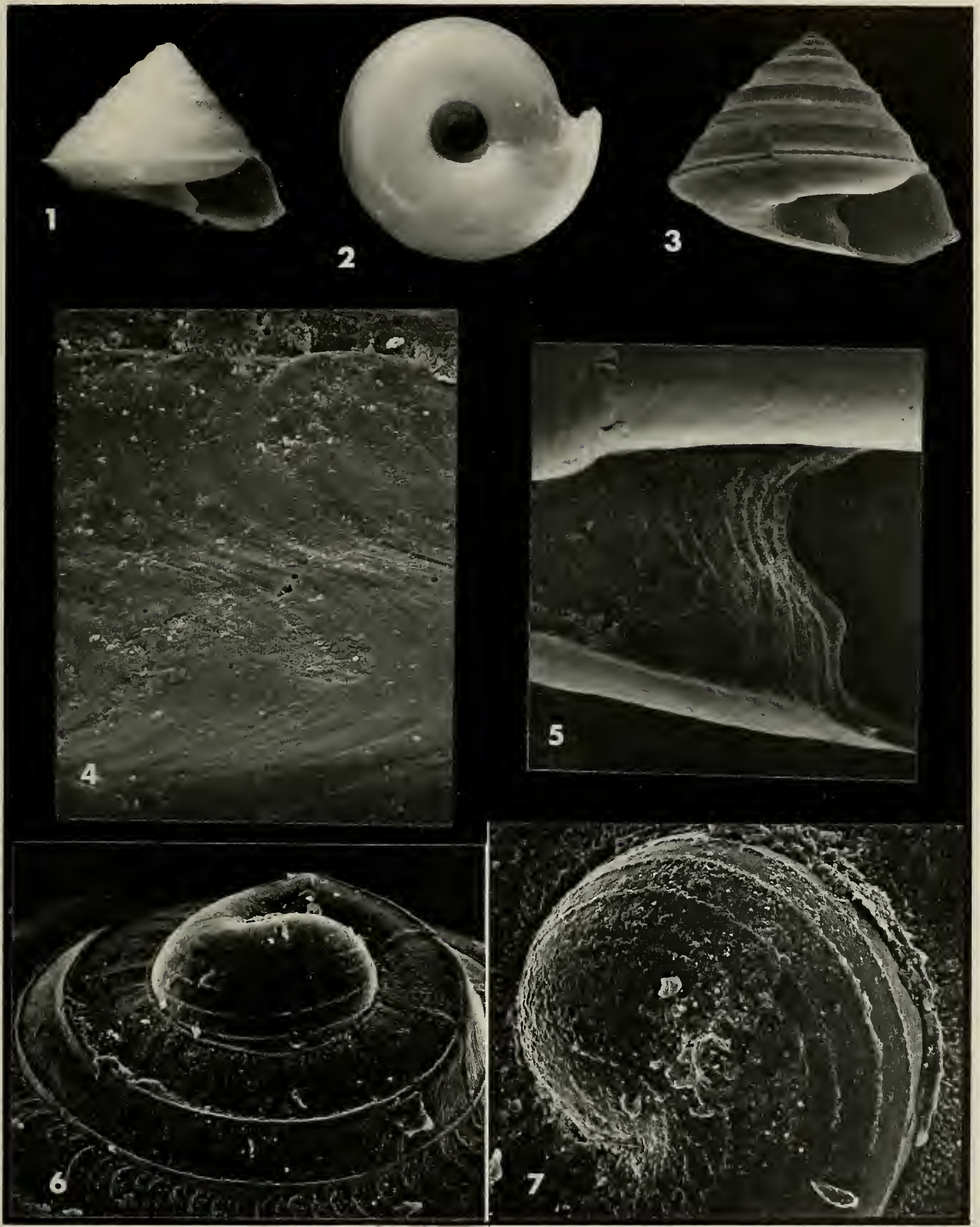
Carenzia carinata (Jeffreys, 1877)
Figs. 1–7

Seguenzia carinata Jeffreys, 1876:201 (nomen nudum); 1877:320; 1879:606; 1885: 43, pl. 5, figs. 3, 3a.—Kobelt, 1878:163; 1888:256.—Watson, 1879:590; 1886: 108, pl. 7, fig. 2.—Nobre, 1884:50; 1932:182; 1936:130; 1938—40:339, 341.—Tryon, 1887:47, pl. 8, figs. 81–83.—Dall, 1889a:383; 1889b:142.—Dautzenberg, 1889:55; 1927:144.—Dautzenberg and Fischer, 1897:162; 1906:54.—Locard, 1898:68.—Johnson, 1934:74.—? Clarke, 1961:350, pl. 4, fig. 6; 1962:11 (partim ?).—Nordsieck, 1968:20, pl. 4, fig. 09.73.—Abbott, 1974:38.—Laubier and Bouchet, 1976:470–472.—Warén, 1980:15.

Seguenzia carinata var. *attenuata* Locard, 1898:68.

Material examined.—1 specimen, USNM 181657 (lectotype, herein designated); 1 specimen, USNM 821198 (paralectotype); *Valorous* station 13, 56°01′N, 34°42′W, 1263 m; 20 August 1875.—1 specimen, USNM 181658 (paralectotype); *Porcupine* station 22, 56°08′N, 13°34′W, 2311 m; July 1870.—1 specimen, USNM 181659; *Talisman* station, off Azores, 1246 m.—1 specimen, BM(NH) 1887.2.9.374a; *Challenger* station 73, 38°30′N, 31°14′W, 1829 m; 30 June 1873.—1 specimen, BM(NH) 1887.2.9.375a; *Challenger* station 78, 37°26′N, 25°13′W, 1829 m; 10 July 1873.—3 specimens, BM(NH) 1887.2.9.376–379; *Challenger* station 85, 28°42′N, 18°06′W, 2059 m; 19 July 1873.—6 specimens, UMML 30.8021; *Gerda* station G-1111, 23°51.9′N, 80°42.7′W, 1080–1089 m; 10′ otter trawl; 30 April 1969.—3 specimens, UMML 30.8020; *Gerda* station G-1106, 24°02′N, 81°30′W, 1706–1723 m; 10′ otter trawl; 29 April 1969.—8 specimens, USNM 94307; *Blake* station 34, 23°52′N, 88°56′W, 732–1098 m.—1 specimen, UMML 30.8288; *John Elliott Pillsbury* station P-604, 18°58′N, 87°28′W, 970–988 m; box dredge; 17 March 1968.—4 specimens, BM(NH) 1887.2.9.380; *Challenger* station 120, 8°37′S, 34°28′W, 1115 m; 9 September 1873.

Description.—Shell small, conical, whorls about 5, weakly inflated, strongly carinate peripherally, polished, white, iridescent under porcelaneous layer. Protoconch small, about 275 μm in diameter, prominent, glassy, with minute spiral ridges, set off from teleoconch by fine growth discontinuity visible only under high magnification. Spire whorls carinated by sharp spiral angulation at or slightly above mid-whorl, flat above, slightly concave below angulation, smooth, sometimes with obscure, slightly flexuous, axial lirae near the suture lines; suture



Figs. 1–7. *Carenzia carinata*. 1, Lectotype, USNM 181657, height 2.7 mm, width 4.4 mm; 2, Same, basal view; 3, SEM micrograph of specimen from *Gerda* station G-1111, UMML 30.8021, apertural view, 13.4×; 4, Same, close-up of whorl surface, growth lines trace outline of anal sinus, 335×, s = suture line; 5, Same, oblique basal view, 67×; 6, same, oblique view of protoconch, 134×; 7, Specimen from *Blake* station 34, USNM 94307, vertical view of protoconch, 268×.

indistinct. Periphery marked by strong, obscurely crenulate carina, visible only on last whorl. Base smooth, convex to flat proximally, concave under periphery. Umbilicus wide, approximately 25% width of shell, bounded peripherally by spiral thread; ridge behind columella not developed. Aperture rhomboidal; outer lip bisinuate; sinuses broadly V-shaped, with rounded apices, shallow; anal sinus on whorl shoulder, apex just above mid-whorl carina; basal sinus in outer ⅓ of basal lip, edge very weakly flared; columella arcuate, terminating in weak, obtuse denticle. Animal undescribed.

Measurements.—Lectotype: 2.7 mm high, 4.4 mm wide, 5+ whorls.

Type-locality.—*Valorous* station 13, 56°01′N, 34°42′W, 1263 m (herein designated).

Remarks.—The simple, unornamented or obscurely crenulated mid-whorl carina, lack of subsutural carina and spiral threads on the base, smaller protoconch with spiral ridges, and weaker columellar tooth distinguish *C. carinata from C. trispinosa* (Watson, 1879), the only other species of *Carenzia* known from the North Atlantic Ocean. From *C. inermis*, new species, *C. carinata* differs in being smaller, having a more conical shell outline, stronger mid-whorl and peripheral carinae, flatter base, much wider umbilicus, and distinct columellar tooth. The mid-whorl carina of *C. carinata* is rather variable: always sharp and strong on the early teleoconch whorls, but in many specimens becoming weak, or even disappearing on later whorls. This latter condition prompted Locard (1898) to establish the varietal name *attenuata*; however, both forms may be found in the same lot of specimens, so no distinction of morphotypes is warranted.

The occurrence of *C. carinata* is somewhat more widespread than would be expected from experience with species in other seguenziacean genera. *Carenzia carinata* is amphi-Atlantic in distribution, extending from the northern end of the Mid-Atlantic Ridge (56°01′N) to the Canary Islands (28°42′N) in the east, and to off the northeastern bulge of Brazil (8°37′S) in the west. Most other seguenziaceans in the Atlantic Ocean are more provincial in distribution, occurring on only one side of the ocean, often in or along the edges of only one or two basins (unpublished data). A record for the southeastern Altantic (Clarke 1961) is of questionable validity. As noted by Laubier and Bouchet (1976), the photographed specimen does not appear to be *C. carinata.* Since I have not examined the specimens, I am here including Clarke's report in the synonymy with a query. *Carenzia carinata* is known principally from depths of 1000–2000 m, but has been recorded from as shallow as 732 m and as deep as 2311 m. Although rare in collections from the western Atlantic, *C. carinata* is rather common in depths of about 2000 m in the Bay of Biscay (Laubier and Bouchet 1976; Bouchet, personal communication).

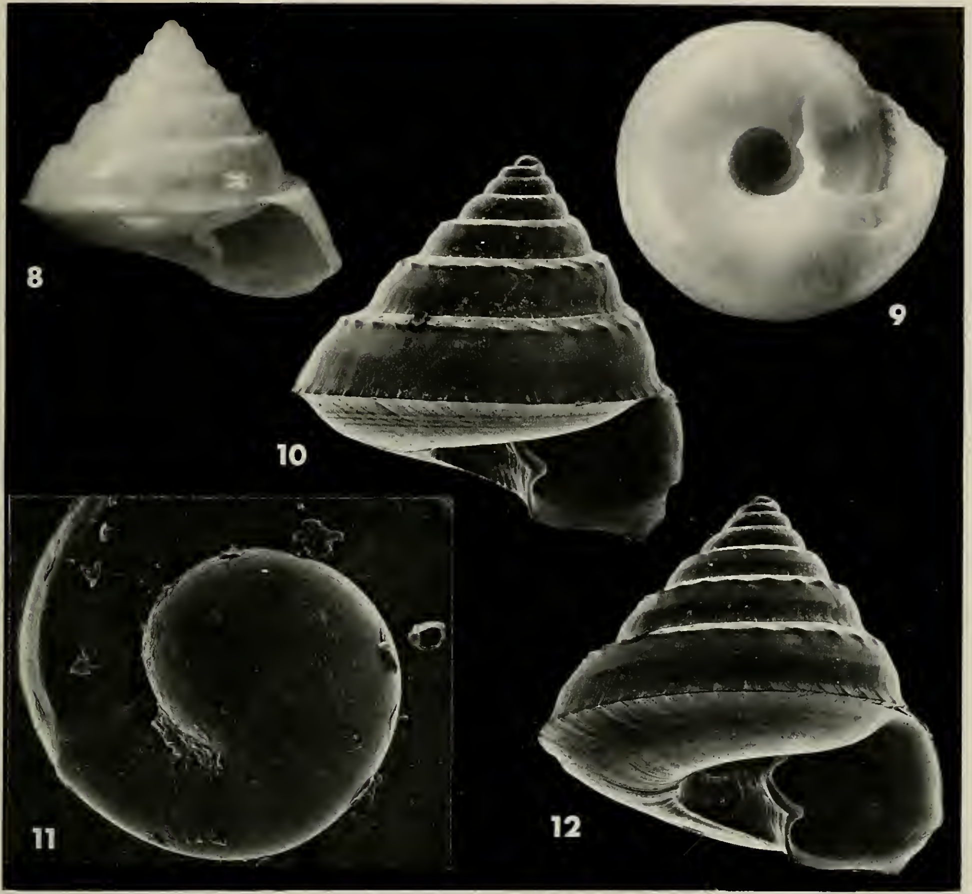
As noted by Warén (1980), the name *carinata* dates from 1877, not 1876. Jeffreys' (1876) listing included no figure, and his description consisted only of the phrase "base perforated or umbilicated," certainly not adequate to make the name available under the current rules governing zoological nomenclature.

Carenzia trispinosa (Watson, 1879)

Figs. 8–12

Seguenzia trispinosa Watson, 1879:591; 1886:110, pl. 7, fig. 4.—Tryon, 1887:47, pl. 8, figs. 79, 80.—Dall, 1889a:268; 1889b:142; 1890:335.—Maury, 1922:90.—Johnson, 1934:74.—Pulley, 1952:170.—Clarke, 1962:11.—Abbott, 1974:38.

Material examined.—1 specimen, USNM 94912; *Albatross* station, south of Cape Hatteras.—1 specimen, UMML 30.8289; *Columbus Iselin* station CI-356,



Figs. 8–12. *Carenzia trispinosa*. 8, Lectotype, BM(NH) 1887.2.9.381, height 3.35 mm, width 3.9 mm; 9, Same, basal view; 10, SEM micrograph of specimen from *Albatross* station 2751, USNM 614078, apertural view, 13.4×; 11, Same, vertical view of protoconch, 134×; 12, same, oblique basal view, 13.4×.

24°21.8′N, 77°24.8′W, 1561–1547 m; 41′ otter trawl; 20 August 1975.—3 specimens, UMML 30.8016; *Gerda* station G-368, 24°03′N, 81°10′W, 961–1016 m; 16′ otter trawl; 15 September 1964.—1 specimen, UMML 30.8292; *Gerda* station G-370, 23°54′N, 81°19′W, 1281 m; 16′ otter trawl; 16 September 1964.—4 specimens, UMML 30.7745; *Gerda* station G-964, 23°46′N, 81°51′W, 1390–1414 m; 10′ otter trawl; 1 February 1968.—5 specimens, UMML 30.7758; *Gerda* station G-965, 23°45′N, 81°49′W, 1394–1399 m; 10′ otter trawl; 1 February 1968.—2 specimens, UMML 30.8023; *Gerda* station G-1112, 23°44′N, 81°14′W, 2276–2360 m; 10′ otter trawl; 30 April 1969.—1 specimen, UMML 30.8015; *Gerda* station G-214, 23°43′N, 82°49′W, 1354–1620 m; 6′ Isaacs-Kidd midwater trawl; 20 January 1964.—2 specimens, UMML 30.8290; *Gerda* station G-960, 23°30′N, 82°26′W, 1692–1697 m; 10′ otter trawl; 31 January 1968.—6 specimens, UMML 30.8017; *Gerda* station G-959, 23°25′N, 82°35′W, 1830 m; 10′ otter trawl; 31 January 1968.—1 specimen, USNM 821199; *Blake* station 34, 23°52′N, 88°56′W, 732–1098 m.—

6 specimens, USNM 94306; *Blake* station, Yucatan Strait.—5 specimens, USNM 96575; 4 specimens, USNM 97111; 28 specimens, USNM 330745; *Albatross* station 2751, 16°54′N, 63°12′W, 1257 m; large beam trawl; 28 November 1887.—1 specimen, *Albatross* station 2117, 15°24′40″N, 63°31′30″W, 1250 m; large beam trawl; 27 January 1887.—23 specimens, USNM 96603; 1 specimen, USNM 406699; *Albatross* station 2760, 12°07′N, 37°17′W, 1865 m; large beam trawl; 18 December 1887.—49 specimens, USNM 96878; *Albatross* station 2754, 11°40′N, 58°33′W, 1609 m; large beam trawl; 5 December 1887.—1 specimen, UMML 30.8291; *John Elliott Pillsbury* station P-754, 11°36.9′N, 68°42.0′W, 684–1574 m; 10′ otter trawl; 26 July 1968.—1 specimen, BM(NH) 1887.2.9.381 (lectotype, herein designated); 3 specimens, BM(NH) 1887.2.9.382–384 (paralectotypes); *Challenger* station 120, 8°37′S, 34°28′W, 1115 m; 9 September 1873.—44 specimens, USNM 330854; *Albatross* station 2764, 36°42′S, 56°23′W, 21 m; large beam trawl; 12 January 1888.

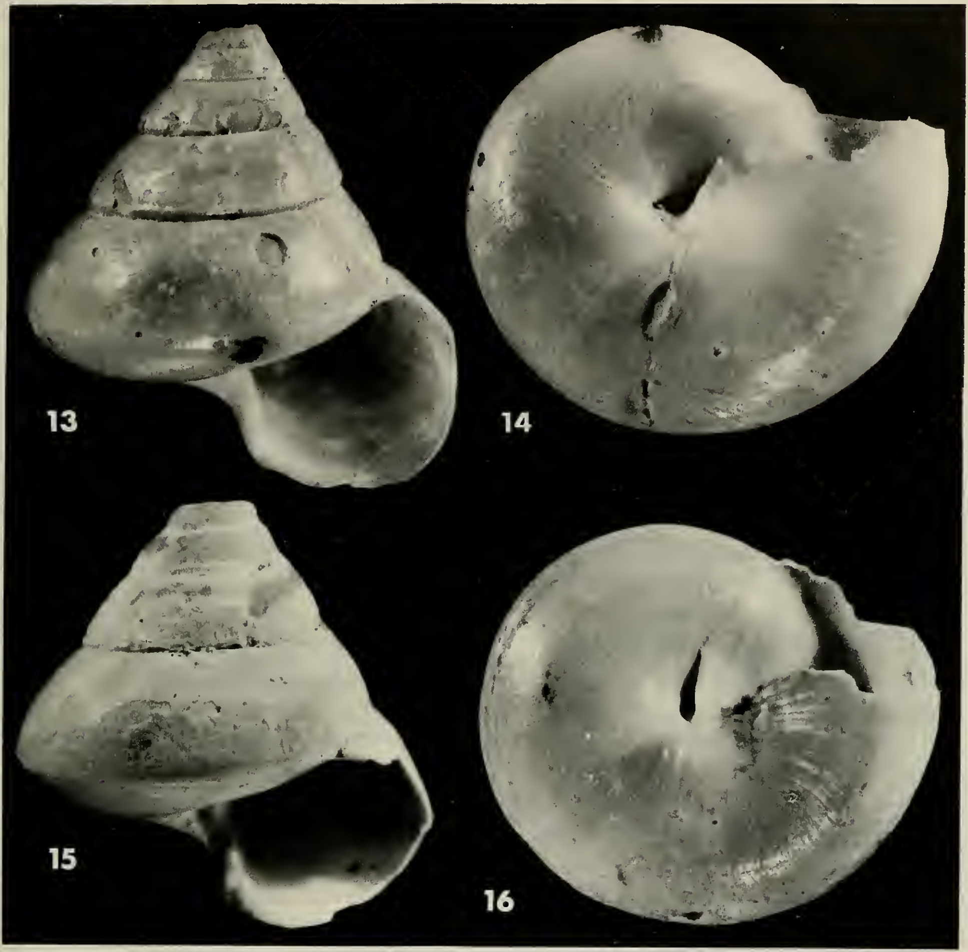
Description.—Shell small, conical, polished, white, iridescent under porcelaneous layer; whorls 6, strongly shouldered near suture, weakly to strongly carinate at mid-whorl, strongly carinate at periphery. Protoconch rather large, about 380 μm in diameter, glassy, prominent. First 2 teleoconch whorls with sharp mid-whorl angulation which may become obsolete or strongly tuberculate on later whorls. All whorls subsequent to second with strong subsutural carina forming narrow, horizontal subsutural shelf; carina usually strongly tuberculate, often with fine spiral thread running across tops of tubercles. Periphery marked by strong, sharp, obscurely crenulate to tuberculate carina, visible only on last whorl. Base with narrow concave zone peripherally and broad convex inner area separated by weak, sharp spiral angulation or thread; inner area smooth and polished, with fine spiral striae, or with distinct spiral cords. Umbilicus wide, approximately 25% width of shell, bounded peripherally by spiral cord and shallow groove; walls convex above and below strong spiral groove corresponding to columellar tooth. Aperture rhomboidal; outer lip bisinuate; sinuses broadly V-shaped, with rounded apices, shallow; anal sinus on whorl shoulder, apex about midway between subsutural and mid-whorl carinae; basal sinus slightly peripheral to middle of basal lip; columella strongly arcuate, terminating in rather strong, narrow, blunt tooth. Animal unknown.

Measurements.—Lectotype: 3.35 mm high (measured from tip of protoconch to tip of columellar tooth), 3.9 mm wide, 5½ whorls. Largest specimen: 4.6 mm high (overall), 4.8 mm wide, 6½ whorls.

Type-locality.—*Challenger* station 120, 8°37′S, 34°28′W, 1115 m.

Remarks.—This species is the most highly sculptured of any described species of *Carenzia*. The tuberculate subsutural, mid-whorl and peripheral carinae, and striate base immediately distinguish *C. trispinosa* from *C. carinata* and *C. inermis*. As in *C. carinata, C. trispinosa* has a variable expression of sculptural elements: the tubercles on the carinae may be strong, sharp and closely spaced, or rather weak, blunt and widely spaced; the mid-whorl carina may become very reduced or absent after the first 2 or 3 teleoconch whorls; the base may be completely smooth, have fine impressed striae or distinct cords. All variations may be found in a lot with numerous specimens.

Carenzia trispinosa has been reported only from the western Atlantic Ocean from off North Carolina south to off Argentina (36°42′S). Bathymetric occurrence of *C. trispinosa* is similar to that of *C. carinata*, having been reported from 684–



Figs. 13–16. *Carenzia inermis*. 13, Holotype, LACM 1806, height 6.8 mm, width 6.4 mm; 14, Same, basal view; 15, Paratype, USNM 784742, height 6.3 mm, width 6.3 mm; 16, Same, basal view.

2360 m, principally between 1000 and 2000 m. The depth record of 21 m (*Albatross* station 2764, off Rio de la Plata, Argentina) is certainly a mistake. *Calliotropis actinophora* (Dall, 1890) was also collected at this station, and, like *C. trispinosa*, rarely occurs shallower than 1000 m (Quinn 1979). Since the other stations off the Rio de la Plata are in depths comparable to 2764, the specimens were probably mislabelled as to station number. Two stations may be possibilities: *Albatross* 2763 (24°17′S, 42°48′30″W, off Rio de Janeiro, Brasil, 1228 m) and *Albatross* 2754 (11°40′N, 58°33′W, SE of Barbados, 1610 m). Both stations are within the normal depth range of *C. trispinosa* and simple transcription errors could change either to 2764. *Albatross* 2754 is more likely the correct station since it was near other stations from which *C. trispinosa* had been collected. The 30° latitudinal gap between the most southern undisputed localities of this species reflects the woeful lack of collecting effort along the northeastern coast of South America.

Carenzia inermis, new species
Figs. 13–16

Material examined.—1 specimen, LACM 1806; R/V *Cayuse* station BmT-331, 44°33.0′N, 128°20.2′W, 2820 m; 3 November 1973 (holotype).—1 specimen, USNM 784742; R/V *Yaquina* station OTB-186, 44°39.4′N, 125°36.3′W, 2800 m; 26 July 1967 (paratype).

Description.—Shell small, conical, whorls 5+, inflated, weakly carinate, iridescent under porcelaneous layer. Protoconch and one or more teleoconch whorls missing from both specimens. Early remaining whorls with faint, regularly spaced, flexuous axial plicae above and below suture; mid-whorl area smooth except for obscure spiral angulation visible only with oblique lighting and high magnification; later whorls almost smooth, with only collabral growth lines and evanescent spiral threads. Periphery weakly carinated by single spiral thread, slightly overhanging succeeding whorl, giving slightly channeled look to suture; last ¼ whorl without peripheral thread, slightly flattened between anal sinus and periphery. Base convex, well-rounded, smooth except for two or three obscure spiral threads near peripheral thread, collabral growth lines, and some spiral threads similar to those above periphery. Umbilicus narrow, edge defined by strong, rounded ridge, internally constricted by broad spiral ridge, with narrow channel formed between circumumbilical and internal ridges. Aperture roughly quadrate; outer lip thin, bisinuate; sinuses (reconstructed from growth lines) shallow, broadly V-shaped, with rounded apices; anal sinus on whorl shoulder; basal sinus just peripheral to middle of base; columella broadly arcuate, without tooth, melding smoothly with outer lip, buttressed by intraumbilical ridge. Animal unknown.

Measurements.—Holotype: 6.8 mm high, 6.4 mm wide, 5 whorls. Paratype: 6.3 mm high, 6.3 mm wide, 4 whorls. Both specimens missing apex.

Type-locality.—R/V *Cayuse* station BmT-331, off Oregon, 44°33.0′N, 128°20.2′W, 2820 m.

Remarks.—The relatively large, smooth shell with very weak peripheral carina and narrow umbilicus readily distinguishes *C. inermis* from *C. carinata* and *C. trispinosa*. *Carenzia inermis* is known only from the two types, so no discussion of variation, areal distribution, or bathymetry is possible at this time.

Acknowledgments

James H. McLean (LACM) brought the new species to my attention and kindly allowed me to include it in this report. In addition, he has provided a great deal of information without which our current understanding of the Seguenziacea would be considerably diminished. Bruce A. Marshall (National Museum of New Zealand) provided photographs of several of his new species and generously deferred description of *Carenzia* to me. I am grateful to the following for the opportunity to examine specimens in their care: Joseph Rosewater and Richard S. Houbrick, USNM; Kathie Way, BM(NH); and Gilbert L. Voss, RSMAS. Some of the specimens examined for this report were collected during the National Geographic-University of Miami Deep-Sea Expeditions. W. G. Lyons, D. Crewz, and J. Darovec (Florida Department of Natural Resources) read and commented on this paper. Lana Tester (Florida Department of Natural Resources) supplied the SEM micrographs. Sally D. Kaicher provided photomacrographs of all type material. This report constitutes a scientific contribution from the University of Miami.

Literature Cited

Abbott, R. T. 1974. American seashells. 2nd Ed.—Van Nostrand Reinhold, New York, 663 pp.

Clarke, A. H. 1961. Abyssal mollusks from the South Atlantic Ocean.—Bulletin of the Museum of Comparative Zoology 125(12):345–387.

———. 1962. Annotated list and bibliography of the abyssal marine molluscs of the world.—National Museum of Canada, Bulletin 181:vi + 114 pp.

Dall, W. H. 1889a. Report on the Mollusca. Part II. Gastropoda and Scaphopoda. Reports on the results of dredging . . . in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey steamer "Blake" . . . .—Bulletin of the Museum of Comparative Zoology 18:1–492.

———. 1889b. A preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the southeastern coast of the United States.—Bulletin of the United States National Museum 37:1–221.

———. 1890. Preliminary report on the collection of Mollusca and Brachiopoda obtained in 1887–88. Scientific results of explorations by the U.S. Fish Commission steamer "Albatross." No. VII.—Proceedings of the United States National Museum 12:219–362.

Dautzenberg, P. 1889. Contribution à la faune malacologique des Iles Açores.—Résultats des Campagnes Scientifiques accomplies sur son yacht par le Prince Albert I^{er}, Prince de Monaco 1:1–112.

———. 1927. Mollusques provenant des campagnes scientifiques du Prince Albert I^{er} de Monaco dans l'Océan Atlantique et dans le Golfe de Gascogne.—Résultats des Campagnes Scientifiques accomplies sur son yacht par le Prince Albert I^{er}, Prince de Monaco 72:1–400.

———, and H. Fischer. 1897. Campagnes scientifiques de S. A. le Prince Albert I^{er} de Monaco. Dragages effectués par l'*Hirondelle* et par la *Princesse Alice,* 1888–1896.—Mémoires de la Société Zoologique de France 10:139–234.

———, and ———. 1906. Mollusques provenant des dragages effectués à l'ouest de l'Afrique pendant les campagnes scientifiques de S. A. S. le Prince de Monaco.—Résultats des Campagnes Scientifiques accomplies sur son yacht par le Prince Albert I^{er}, Prince de Monaco 32: 1–125.

Jeffreys, J. G. 1876. Preliminary report of the biological results of a cruise in H.M.S. 'Valorous' to Davis Strait in 1875.—Proceedings of the Royal Society of London 25:177–230.

———. 1877. New and peculiar Mollusca of the Eulimidae and other families of Gastropoda, as well as of the Pteropoda, procured in the 'Valorous' Expedition.—Annals and Magazine of Natural History (4)19:317–339.

———. 1879. Notes as to the position of the genus *Seguenzia* among the Gastropoda.—Journal of the Linnean Society of London, Zoology 14:605–606.

———. 1885. On the Mollusca procured during the 'Lightning' and 'Porcupine' Expeditions, 1868–70. (Part 9).—Proceedings of the Zoological Society of London for 1885:27–63.

Johnson, C. W. 1934. List of marine Mollusca of the Atlantic coast from Laborador to Texas.—Proceedings of the Boston Society of Natural History 40(1):1–204.

Kobelt, W. 1878. Illustrirtes Conchylienbuch. Nürnberg, xvi + 331 pp.

———. 1886–1888. Prodromus faunae molluscorum testaceorum maria Europaea inhabitantium.—Nürnberg, iv + 550 pp.

Laubier, L., and P. Bouchet. 1976. Un nouveau copépode parasite de la cavité palléale d'un gastéropode bathyal dans le Golfe de Gascogne *Myzotheridion seguenziae* gen. sp. nov.—Archives Zoologie Expérimentale et Général 117(4):469–484.

Locard, A. 1898. Expéditions scientifiques du "Travailleur" et du "Talisman" pendant les années 1880, 1881, 1882, 1883. Mollusques testacés. II.—Paris, 515 pp.

Marshall, B. A. In press. Recent and Tertiary Seguenziidae (Mollusca: Gastropoda) from the New Zealand region.—Records of the National Museum of New Zealand.

Maury, C. J. 1922. Recent Mollusca of the Gulf of Mexico and Pleistocene and Pliocene species from the Gulf States. Part 2: Scaphopoda, Gastropoda, Amphineura, Cephalopoda.— Bulletins of American Paleontology 9(38):34–142.

Nobre, A. 1884. Moluscos marinhos do Noroeste de Portugal. Porto.

———. 1932. Moluscos marinhos de Portugal. Vol. 1.—Porto, 466 pp.

———. 1936. Moluscos marinhos de Portugal. Vol. 2.—Porto, 381 pp.

———. 1938–1940. Fauna malacologica de Portugal: I. Moluscos marinhos e das águas salobras.—Porto, xxxii + 807 pp.

Nordsieck, F. 1968. Die Europäischen Meeres—Gehauseschnecken (Prosobranchia) vom Eismeer bis Kapverden und Mittelmeer.—Gustav Fischer, Stuttgart, viii + 273 pp.

Pulley, T. E. 1952. An illustrated check list of the marine mollusks of Texas.—Texas Journal of Science 2:167–199.

Quinn, J. F., Jr. 1979. Biological results of the University of Miami Deep-Sea Expeditions. 130. The systematics and zoogeography of the gastropod family Trochidae collected in the Straits of Florida and its approaches.—Malacologia 19(1):1–62.

———. In press. A revision of the Seguenziacea Verrill, 1884 (Gastropoda:Prosobranchia). I. Summary and evaluation of the superfamily.—Proceedings of the Biological Society of Washington.

———. In preparation. A revision of the Seguenziacea Verrill, 1884 (Gastropoda: Prosobranchia). II. Systematics of the western Atlantic species.

Tryon, G. W. 1887. Manual of Conchology. Vol. 9. Solariidae, Ianthinidae, Trichotropidae, Scalariidae, Cerithiidae, Rissoidae, Littorinidae.—Philadelphia, 488 pp.

Warén, A. 1980. Marine Mollusca described by John Gwyn Jeffreys, with the location of the type material.—Conchological Society of Great Britain and Ireland, Special Publication 1:1–60.

Watson, R. B. 1879. Mollusca of H.M.S. Challenger Expedition. III. Trochidae, viz. the genera *Seguenzia, Basilissa, Gaza* and *Bembix*.—Journal of the Linnean Society of London 14:586–605.

———. 1886. Report on the Scaphopoda and Gasteropoda collected by H.M.S. Challenger during the Years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger, 1873–1876, Zoology 15:1–680.

Florida Department of Natural Resources Marine Research Laboratory, 100 Eighth Avenue SE, St. Petersburg, Florida 33701.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 365–369

THE LYCOTEUTHID GENUS *OREGONIATEUTHIS* VOSS, 1956, A SYNONYM OF *LYCOTEUTHIS* PFEFFER, 1900 (CEPHALOPODA: TEUTHOIDEA)

Ronald B. Toll

Abstract.—Oregoniateuthis Voss, 1956 is placed in the synonymy of *Lycoteuthis* Pfeffer, 1900. Based on new records, *Oregoniateuthis springeri* Voss, 1956 is shown to be conspecific with *Lycoteuthis diadema* (Chun, 1900) and is placed in synonymy. The type of *Lycoteuthis lorigera* (Steenstrup, 1875) is shown to be a male. Sexual dimorphism in the family Lycoteuthidae is discussed.

Voss (1962) erected a new genus and species, *Oregoniateuthis springeri,* for a single male specimen of a small lycoteuthid squid taken from the stomach of a shark from the Gulf of Mexico. Voss (1962) expanded the description of *O. springeri* based on the holotype (USNM 575090) and a second trawl-collected male (UMML 31.376) from near the type-locality. He also redescribed *Onychoteuthis* (??) *lorigera* Steenstrup, 1875, known only from the type taken from the stomach of a sperm whale from the South Pacific, and placed this species into *Oregoniateuthis.* Voss (1962) considered the possibility that *O. springeri* might be the male of some previously described species; however, the type of *O. lorigera,* reported to be a female, served to validate the genus by sharing with *O. springeri* elongate dorsolateral arms.

Present findings based on new records include an undescribed photophore in female *Lycoteuthis diadema* and show that *O. springeri,* known previously only from males, is conspecific with *L. diadema,* known previously only from females.

A reexamination of the type of *O. lorigera* shows it to be a male and further demonstrates that *Oregoniateuthis* can no longer be retained as a separate genus.

The following abbreviations are used: USNM—National Museum of Natural History, formerly United States National Museum, Smithsonian Institution; UMML—Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami; SAM—South African Museum; ORE—M/V *Oregon*; ORE II—M/V *Oregon* II; CI—R/V *Columbus Iselin*; SIL BAY—M/V *Silver Bay*; IKMT—Issacs-Kidd midwater trawl; FT—flat trawl; ST—shrimp trawl; PT—pelagic trawl; ML—mantle length; GL—gladius length; F(F)—female(s); M(M)—male(s).

Lycoteuthis Pfeffer, 1900

Lycoteuthis Pfeffer, 1900:156.
Thamatolampus Chun, 1903:67.
Asthenoteuthion Pfeffer, 1912:172.
Leptodontoteuthis Robson, 1926:2.
Oregoniateuthis Voss, 1956:120.

Diagnosis.—Lycoteuthids with single large photophore embedded in musculature of fin/mantle complex near apex of fins, with 7 additional serially arranged, rod-like photophores in elongate posterior projection of mantle of males (unknown in *L. lorigera*); dorsolateral arms elongate in males.

Lycoteuthis diadema (Chun, 1900)

Enoploteuthis diadema Chun, 1900:532.
Lycoteuthis diadema Chun, 1903:569.
Oregoniateuthis springeri Voss, 1956:120; 1962:283.
(for a more detailed synonymy consult Voss 1962:275).

Material examined.—Holotype of *Oregoniateuthis springeri* Voss, M, ML = 80 mm, ORE 382, 29°11.30′N, 88°07.30′W, 200 fms, 21 June 1951, 100′ FT, USNM 575090. Other material:—1F, ML = 125 mm (approx.) (GL = 132 mm), CI-256, 23°37′N, 77°06′W to 23°39′N, 77°07′W, 1360 m, in stomach of *Synaphobranchus brevidorsalis,* 1 Nov 1974, UMML 31.1735.—6FF, ML = 91–88 mm (GL = 96.2–93.5 mm), 35 miles from Port Elizabeth, South Africa, over 100 fms, in stomach of yellowfin tuna, 23 April 1974, S 38, SAM.—13FF, ML = 89–73 mm (GL = 88.0–69.2 mm), ORE II 10906, 29°17′N, 86°36′W, 0–200 fms, 70′ ST, 8 Feb 1970, USNM 730614.—1F, ML = 79 mm (GL = 85.3 mm), between Lamberts Bay and Vandeling Island, in stomach of *Merluccius capensis,* ?May 1974, S 599, SAM.—3FF, ML = 91–73 mm (GL = 85.2–71.3 mm), ORE II 10907, 28°36′N, 86°15′W, 0–200 fms, 191′ ST, 9 Feb 1970, USNM 730615.—1F, ML = 82 mm (GL = 82.5 mm), 25°09′N, 80°34′W, in stomach of *Merluccius albidus,* 19 Aug 1931, USNM 576949.—1M, ML = 98 mm (GL = 73.8 mm), ORE II 11150, 24°17′N, 87°41′W, 0–305 fms, 71′ ST, 14 Aug 1970, USNM 730611.—1M, ML = 93.7 mm (GL = 70 mm approx.), ORE 3296, 28°36′N, 89°48′W, 244–520 fms, 21 Aug 1961, UMML 31.376.—3MM, ML = 95–91 mm (GL = 69.5–62.9 mm), ORE II 10907 (sta. data above), USNM 730612.—4MM, ML = 88–85 mm (GL = 69.2–62.8 mm), ORE II 10906 (sta. data above), USNM 730613.—2MM, ML = 86–85 mm (GL = 65.8–64.2 mm), ORE II 11186, 27°49′N, 85°12′W, 0–250 fms, 120′ PT, 27 Aug 1970, USNM 730610.—2FF, ML = 56–46 mm (GL = 59.6–47.4 mm), SIL BAY 1198, 24°11′N, 83°31′W, 200 fms, 9 June 1959, UMML 31.228.—1F, ML = 53 mm (GL = 54.5 mm), west and north of Cape Point, South Africa, in stomach of *Thunnus alalunga*?, 16 Mar 1962, A 30612, SAM.—1F, ML = 9 mm (GL = 9 mm), ALBATROSS, 32°18′N, 63°30′W, Ocean Acre 7-13-N, 0–1500 m, 3 m IKMT, 8 Sept 1969, USNM 726955.

Partial redescription.—In females the posterior tip of the mantle is drawn out into a short tail that is longitudinally cleft ventrally. A single large photophore lies in a pocket in the musculature at the apex of the fins. It is located slightly dorsoposteriorly to the convex surface of the conus of the gladius. The photophore is laterally compressed, convex dorsally and flat to slightly concave ventrally. A layer of densely placed, large, dark reddish-brown chromatophores surrounds it. The opening in the musculature dorsal to the photophore is covered by translucent connective tissue that forms a dorsally directed window for the emission of light.

See Voss (1962) for a more complete description of this and the following species.

Lycoteuthis lorigera (Steenstrup, 1875)

Onychoteuthis (??) *lorigera* Steenstrup, 1875:473.
Oregoniateuthis lorigera.—Voss, 1962:288.

Material examined.—Holotype, M, ML = 180 mm, fraen Kaskelotmave, Sydhavet, Mus. Zool. Skibslaege. Moller. Zoologisk Museum, København.

Partial redescription.—The badly damaged male reproductive organs are small. The remains of 1 to 3 ruptured spermatophores were found in Needham's sac. Only a single set of reproductive organs was found, located on the left side of the animal; however, the poor condition of the visceral complex does not preclude the possibility of paired organs.

The posterior part of the gladius (conus) is now missing.

Discussion.—Two fortuitous discoveries by the writer during investigations of gladius morphology, namely the proper determination of the gender of the type of Steenstrup's *O. lorigera* and the identification of a previously undescribed photophore in females of *Lycoteuthis diadema*, prompted a review of the generic relationships of *Oregoniateuthis*.

Knowledge of the correct sex of the type of *Lycoteuthis lorigera* nullified the single substantial factor that previously substantiated *Oregoniateuthis*; a nominal species diagnosed by elongate dorsolateral arms in the female, a character of males attributable to *O. springeri*.

The photophore at the base of the short posterior mantle projection found in females of *L. diadema* appears to be homologous to the most proximal of the 8 serially arranged photophores found within the much longer mantle projection of males attributable to *O. springeri*. No other lycoteuthids, with the possible exception of *L. lorigera*, have internal photophores similarly located.

A review of capture data revealed that each of 2 sequential net hauls (ORE II 10906 and 10907) contained both a large number of reproductively mature (gravid) females attributable to *L. diadema* (USNM 730614, 67FF and 730615, 15FF) and similarly developed (spermatophores present) males attributable to *O. springeri* (USNM 730612, 4MM and 730613, 13 MM). These capture records suggest a large mating aggregation.

In 5 previous reports that indicate the gender of specimens attributed to either *L. diadema* or *O. springeri* (Chun 1910; Voss 1956, 1962, 1962a, 1967) all *L. diadema* are females, all *O. springeri*, males. Examination of the holdings of the USNM and the UMML also revealed only females of *L. diadema* and males of *O. springeri* (total of over 150 animals).

These combined lines of evidence based on anatomical, behavioral, occurrence and distributional data provide ample grounds to place *O. springeri* in the synonymy of *L. diadema*. Retention of these as separate taxa would require that the males of one and the females of the other have yet to be reported. In light of the distribution and ecology of these animals and the extensive collecting that has been conducted, particularly in the Gulf of Mexico and western Atlantic Ocean, this possibility is untenable.

High levels of sexual dimorphism are known to exist in the Lycoteuthidae based on *Selenoteuthis scintillans*, albeit not as great as now recognized in *Lycoteuthis*. Several important parallels in sex-linked character expression exist between *Se-*

lenoteuthis and *Lycoteuthis*. Only the males of both genera possess brachial photophores. These are located at the arm tips in *S. scintillans* and along the aboral surface of the arms in *L. diadema*. The terminal mantle photophore in male *S. scintillans* is proportionally nearly twice the size of that found in conspecific females (compare Figs. 12b and 13a in Voss 1962). In *L. diadema* the posterior mantle (tail) photophores are more numerous in males (8) than females (1). Toll (1982) showed that *L. diadema* and *S. scintillans* share sex-linked character expression in 3 gladius indices. Females of both species have greater anterior gladius width and anterior vane length indices while males have a greater free rachis length index.

Sexual dimorphism is well known in other teuthoid families. The males of both *Alloteuthis* and *Uroteuthis* (family Loliginidae) have a more elongate posterior projection of the mantle than do conspecific females. This is similar to the condition now recognized in *Lycoteuthis diadema*. Males of *Berryteuthis anonychus* (family Gonatidae) lack hooks on the arms while conspecific females bear hooks on the basal portions of arms I–III (Roper, Young and Voss 1969). In 6 genera of cranchiids only the females possess brachial end organs (N. Voss 1980). Among non-teuthoid cephalopods, only males of *Sepia confusa* possess a tail-like elongation of the fins (Massy and Robson 1923). Males of *S. incerta* and *S. burnupi* possess specially modified arms (Roeleveld 1972). Sexual dimorphism in the class reaches its greatest expression in the pelagic octopods *Argonauta* and *Tremoctopus* in which the females reach a size in excess of 20 times that of the diminutive males.

Imber (1975) suggested that *O. springeri* (=*L. diadema*) may be conspecific with *L. lorigera* and tentatively placed it in synonymy. This is rejected in light of the significant difference in size at maturity. Imber's use of *longimanus* as the correct senior synonym of *lorigera* is seen as based on circumstantial evidence and is not followed here.

Unfortunately, over a century after Steenstrup described *L. lorigera* it remains known from only the type. Further evaluation of its taxonomic affinities must await additional material. Some records of females of *L. diadema* from southern latitudes may be pertinent to future consideration of *L. lorigera*.

Acknowledgments

Dr. J. Knudsen loaned the type of *Onychoteuthis lorigera*. Ms. M. Roeleveld provided specimens from South African waters. Mr. S. Hess assisted in the verification of spermatophore remains. Drs. C. Roper, J. Rosewater and G. Voss and Ms. N. Voss read the manuscript and made many constructive suggestions. Mr. M. Sweeney assisted the writer during three visits to the Smithsonian Institution, loaned material and read the manuscript. Juel Rembert typed the final manuscript.

This work was supported in part by a Doctoral Dissertation Improvement Grant from the National Science Foundation (DEB-8012544) and a Predoctoral Appointment to the Division of Mollusks from the Smithsonian Institution Fellowship Program. I gratefully acknowledge this support.

Literature Cited

Chun, C. 1900. Aus den Tiefen des Weltmeeres.—Gustav Fischer, Jena, viii + 549 pp., 390 figs., 46 pls.

———. 1903. Aus den Tiefen des Weltmeeres. Zweite Auflage.—Gustav Fischer, Jena, x + 592 pp., 482 figs., 46 pls.

———. 1910. Die Cephalopoden. 1. Teil: Oegopsida.—Wissenschaftliche Ergebnisse VALDIVIA 18(1): 1–401, atlas of 61 pls.

Imber, M. J. 1975. Lycoteuthid squids as prey of petrels in New Zealand seas.—New Zealand Journal of Marine and Freshwater Research 9(4):483–492.

Massy, A. L., and G. C. Robson. 1923. On a remarkable case of sex-dimorphism in the genus *Sepia*.—Annals and Magazine of Natural History (9)12:435–442.

Pfeffer, G. 1900. Synopsis der oegopsiden Cephalopoden.—Mitteilungen aus dem Naturhistorischen Museum 17 (Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 17):145–198.

———. 1912. Die Cephalopoden des Plankton Expedition.—Ergebnisse Plankton Expedition der Humboldt-Stiftung 2: 1–815, atlas of 48 pls.

Robson, G. C. 1926. The Cephalopoda obtained by the S. S. PICKLE. Supplementary Report.—Report of the Fisheries and Marine Biological Survey, Union of South Africa 4(8):1–6, 1 pl.

Roeleveld, M. A. 1972. A review of the Sepiidae (Cephalopoda) of southern Africa.—Annals of the South African Museum 59(10):193–313, 11 pls., 20 figs.

Roper, C. F. E., R. E. Young, and G. L. Voss. 1969. An illustrated key to the families of the order Teuthoidea (Cephalopoda).—Smithsonian Contributions to Zoology 13, 32 pp., 16 pls.

Steenstrup, J. 1875. *Hemisepius*, en ny slaegt of *Sepia*-blaekspruttemes familie, med bemaerkninger om *Sepia*-formerne i almindelighed.—Kongelige Danske Videnskabernes Selskabs Skrifter 5(10):465–482, 2 pls.

Toll, R. B. 1982. The comparative morphology of the gladius in the order Teuthoidea (Mollusca: Cephalopoda) in relation to systematics and phylogeny.—Doctoral Dissertation, University of Miami, 390 pp., 41 pls., 12 figs.

Voss, G. L. 1956. A review of the cephalopods of the Gulf of Mexico.—Bulletin of Marine Science of the Gulf and Caribbean 6(2):85–178.

———. 1962. A monograph of the Cephalopoda of the North Atlantic I. The family Lycoteuthidae.—Bulletin of Marine Science of the Gulf and Caribbean 12(2):264–305.

———. 1962a. South African cephalopods.—Transactions of the Royal Society of South Africa 36(4):245–272, 1 pl.

———. 1967. Some bathypelagic cephalopods from South African waters.—Annals of the South African Museum 50(5):61–88, 9 pls.

Voss, N. A. 1980. A generic revision of the Cranchiidae (Cephalopoda; Oegopsida).—Bulletin of Marine Science 30(3):365–412, 13 figs.

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Present Address: Department of Biology, University of the South, Sewanee, Tennessee 37375.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 370–378

PARANDALIA BENNEI (PILARGIDAE) AND *SPIOPHANES LOWAI* (SPIONIDAE), NEW SPECIES OF POLYCHAETOUS ANNELIDS FROM MAZATLAN BAY, PACIFIC COAST OF MEXICO

Vivianne Solís-Weiss

Abstract.—Two new species of polychaetes from the Pacific coast of Mexico are described: *Parandalia bennei* and *Spiophanes lowai.* Both are from shallow sandy bottoms.

During a recent survey of the benthic fauna of Mazatlan Bay, a number of polychaetous annelids new to science were encountered. Two of them are described below.

The study area is the bay of Mazatlan, a shallow zone, between 3.5 and 25 meters with active sediment transport and predominately sandy bottoms.

The generic definitions follow Fauchald (1977).

The types of the new species are deposited in the following institutions: National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), Allan Hancock Foundation (AHF), and Instituto de Ciencias del Mar y Limnología, Universidad Nactional Autónoma de México (ICML).

Family Pilargidae

Parandalia Emerson and Fauchald, 1971

The genus *Parandalia* was separated from *Loandalia* Monro, 1936, as emended by Hartman (1947:505) (see also Thomas 1963:29, and Pettibone 1966:195) chiefly on the basis of the presence of emergent notopodial spines or acicula in *Parandalia* and their absence on *Loandalia.*

Parandalia bennei, new species

Figs. 1A–D, 2 A–E

Material examined.—Mazatlan Bay, Mexico, 23°11′55″N, 106°25′20″W, 22 Aug. 1979, holotype ICML-1011; 2 paratypes, ICML 1011-1, ICML 1011-2; one paratype, USNM 073015, one paratype AHF-1345.

Description.—The holotype is complete with 59 setigers. The four complete paratypes have 53, 59, 66 and 68 setigers respectively.

The body is long and slender, 46 mm long and 0.9 mm wide, including the setae. It is anteriorly inflated and rounded in cross section; the middle and posterior part of the body is somewhat flattened dorsoventrally. The color of the preserved specimens is light brown to yellowish. The parapodia are all biramous. The body, after the first 7 setigers, becomes somewhat flattened dorsoventrally. The segmentation is rather indistinct in the anterior region, becoming very con-

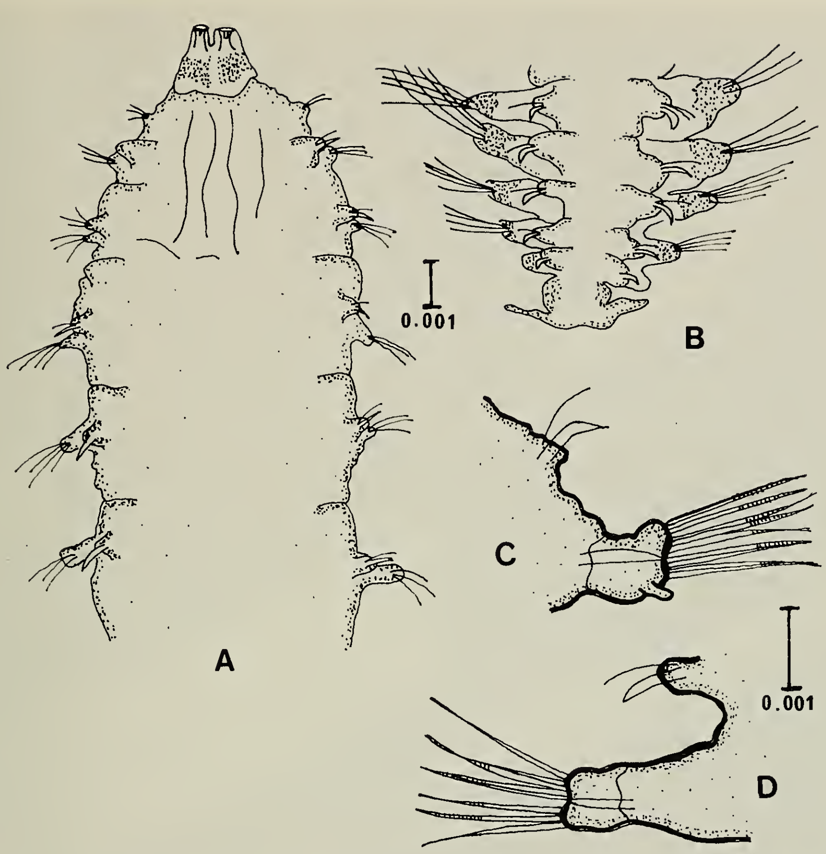


Fig. 1. *Parandalia bennei* (holotype): A, Anterior end, dorsal view; B, Posterior end, dorsal view; C, Parapodium from right setiger 36, posterior view; D, Left parapodium from setiger 50, anterior view. Scales in mm.

spicuous posteriorly. The segments are hexagonal in shape and the septal regions are narrowed.

The prostomium is less than half as wide as the first setiger, with a longitudinal cleft between the bases of the palpophores. Distally on each of the well developed palpophores are located two short and retractile rodlike palpostyles (Fig. 1A). The proboscis was not everted in any of the specimens; however, one can see through the body wall that there are no jaws associated with the large mouth. The peristomium is not clearly distinguished from the prostomium and bears no tentacular cirri or any other structure.

The parapodia are poorly developed on the first 7 setigers. The first parapodium bears only the neuropodium. The acicular spine protrudes from notopodium on all setigers starting at setiger 6.

The neuropodia increase in size from setiger 7 to about 10 segments from the posterior end from which they decrease gradually.

The notopodia are similar in size all along the body, each bearing a single thick

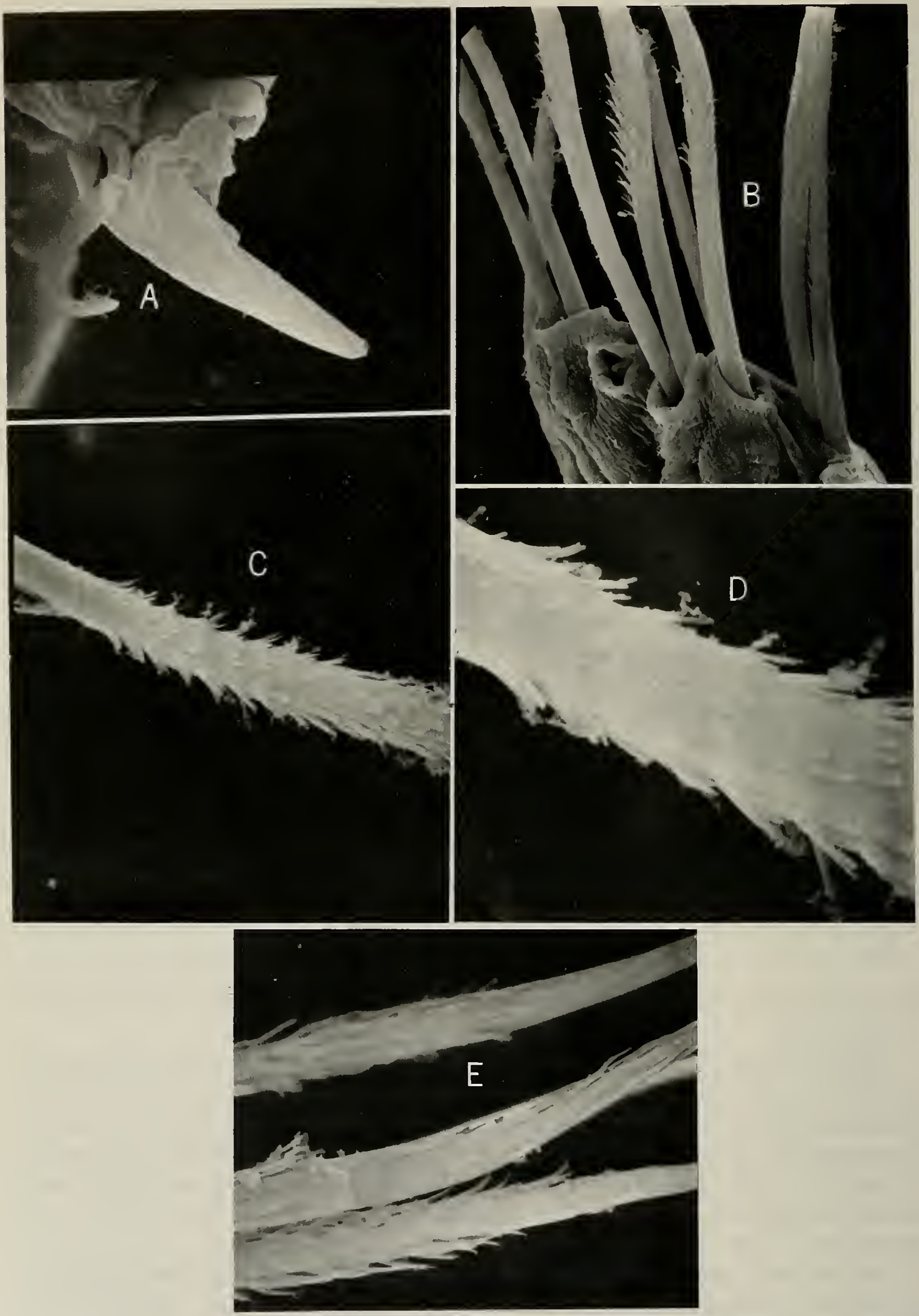


Fig. 2. *Parandalia bennei* (holotype): A, Notopodium showing spine and notoseta from middle setiger (×2600); B, Posterior neuropodium showing bases of neurosetae (×1000); C, Base of neuroseta from middle setiger (×1100); D, Middle portion of same (×2400); E, Distal ends of neurosetae (×2200). Scanning electron microscope (SEM).

colorless emergent spine or aciculum which is short and pointed distally. In addition, 1 or 2 simple slender capillary notosetae are present and there is no dorsal cirrus (Figs. 1C, D, 2A).

The neuropodia bear simple capillary setae in numbers varying from 6 (anteriorly) to 12 posteriorly (Fig. 1C, D). Where 12 setae are present, they emerge from the neuropodium in pairs (Fig. 2B).

The neuropodium bears a single stout colorless aciculum which is thicker than the neurosetae. It reaches the distal edge of the neuropodium and may protrude slightly in some parapodia. The neurosetae are long and slender, sometimes showing double curvatures. The basal third of the neuroseta is smooth; the middle third has groups of fibers which fan out and sometimes show an irregular spiral pattern (Fig. 2C, D); in the distal third the fibers become parallel to the axis of the neuroseta (Fig. 2E).

In the posterior region, the parapodia become more elongated with brown pigmented patches on the distal tips of the neuropodia (Fig. 1D). The last few segments decrease in size towards the pygidium and lose their hexagonal shapes. The posteriormost segment bears no setae.

The pygidium has 3 anal cirri (Fig. 1B) including a pair of lateral long cirri and a shorter midventral one. The anal aperture is ventrally located but rather inconspicuous.

Remarks.—The different species of *Parandalia* closely resemble each other externally. *Parandalia bennei* is closest to *P. fragilis,* Hartmann-Schröder, 1959, referred to *Loandalia fauveli* by Pettibone, 1966. Based on Hartmann-Schröder's description, the main differences between the two species are the following:

—A pair of palpostyles are present in each palpophore in *P. bennei* and only a single palpostyle per palpophore in *P. fragilis* (and other *Parandalia* spp.).
—Palpostyles are round and papilliform in *P. fragilis,* rodlike in *P. bennei.*
—There is no anterior asetigerous segment present in *P. bennei* as there is in *P. fragilis.*
—First parapodium is uniramous in *P. bennei* and biramous in *P. fragilis.*
—The pygidium constitutes the most conspicuous way to separate *P. bennei* from other species: in *P. fragilis* the pygidium forms a pigmented, well developed disc with small cirri. In *P. bennei,* the lateral cirri are large, the anal plate is reduced, never concave, and there is no pigmentation.

Etymology.—The specific name is a free derivation of the name of my husband, to whom this species is dedicated.

Distribution.—*Parandalia bennei* was found in shallow bottom areas in three different stations in Mazatlan Bay. There is a predominance of fine sands in two stations and coarse sands in one station.

Family Spionidae
Spiophanes Grube, 1860
Spiophanes lowai, new species
Figs. 3A–D, 4A–G, 5A–C

Material examined.—Mazatlan Bay, Mexico, 23°11′55″N, 106°25′20″W, 9 m, 25 May 1979 (holotype ICML-1012). Sinaloa coast south of Mazatlan, Mexico,

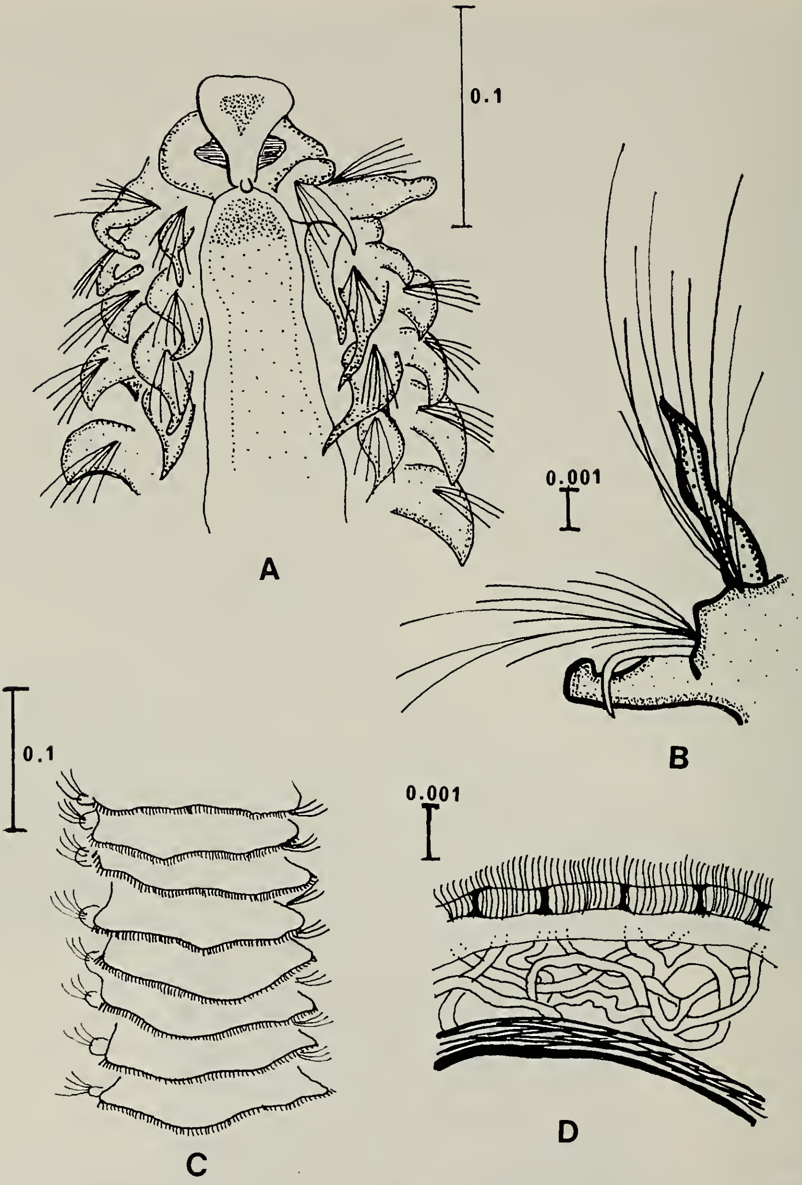


Fig. 3. *Spiophanes lowai* (holotype): A, Anterior end, dorsal view; B, Right parapodium, setiger 1; C, Dorsal view of the ciliated ridges from middle part of body; D, enlargement of part of a dorsal ridge. Scales in mm.

23°38′5″N, 106°55′6″W, 37 m, 23 August 1981 (2 paratypes, USNM 80179, 80467). The holotype is incomplete with 49 setigers, 15 mm long and 23 mm wide including the setae. Color (preserved) is white with dark brown parapodial glands in setigers 10 to 15.

The prostomium is subtriangular with very poorly developed frontal horns; it tapers posteriorly and extends to the level of setiger 1, with a small occipital antenna.

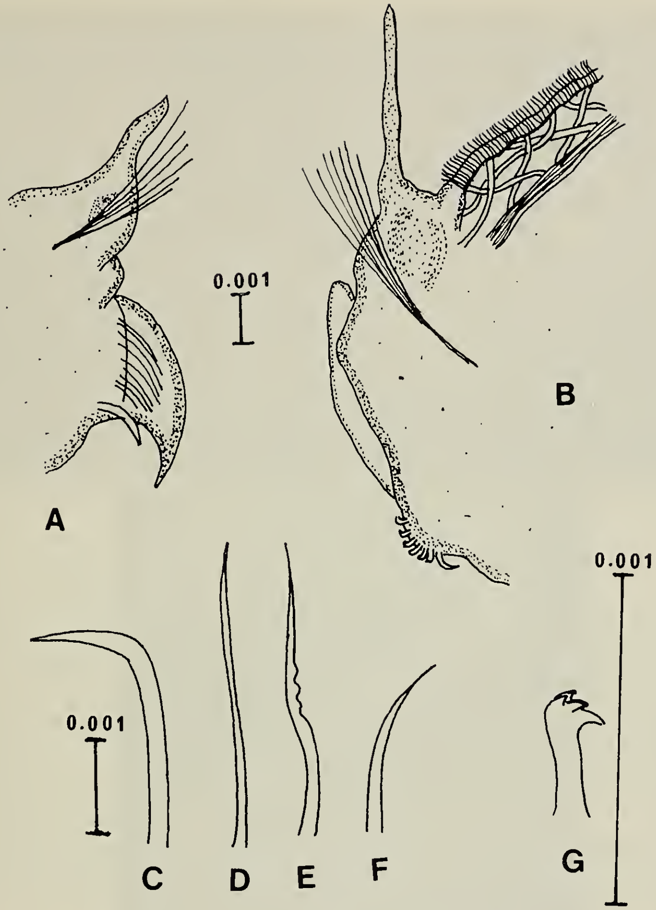


Fig. 4. *Spiophanes lowai* (holotype): A, Left parapodium of setiger 8; B, Right parapodium of setiger 43, anterior view; C, Neuropodial spine of first setiger; D, Capillary notoseta; E, Indented setae of setigers 8 and 9; F, Sabre setae; G, Neuropodial hook. Scales in mm.

There are large pigmented areas on the dorsal part of the prostomium and at the level of the first 2 setigers (Fig. 3A). The palps are missing. The enlarged peristomium forms a conspicuous lateral collar. Nuchal organs are poorly developed, appearing as thin bands extending to setiger 2. The neuropodia of the first setiger bear a long smooth spine, curved at right angles as is characteristic for *Spiophanes* (Figs. 3B, 4C). The first notopodial lamellae are cirriform (Fig. 3A, B). From setiger 2 to 4, the notopodial lamellae increase in size and become foliose in shape (Fig. 3A). More posteriorly, the notopodial lamellae become reduced, retaining a broad base and a slender cirrus (Fig. 4B). Neuropodial lamellae are similar in shape and size through the first 17 setigers (Figs. 3B, 4A). More posteriorly, the lamellae become smaller and remain uniform in shape and size through the rest of the body (Fig. 4B).

Most notopodial setae are capillary, unilimbate and smooth (Fig. 4D). The setae of setigers 2 to 4 are longer than those of the rest of the body. In the notopodia

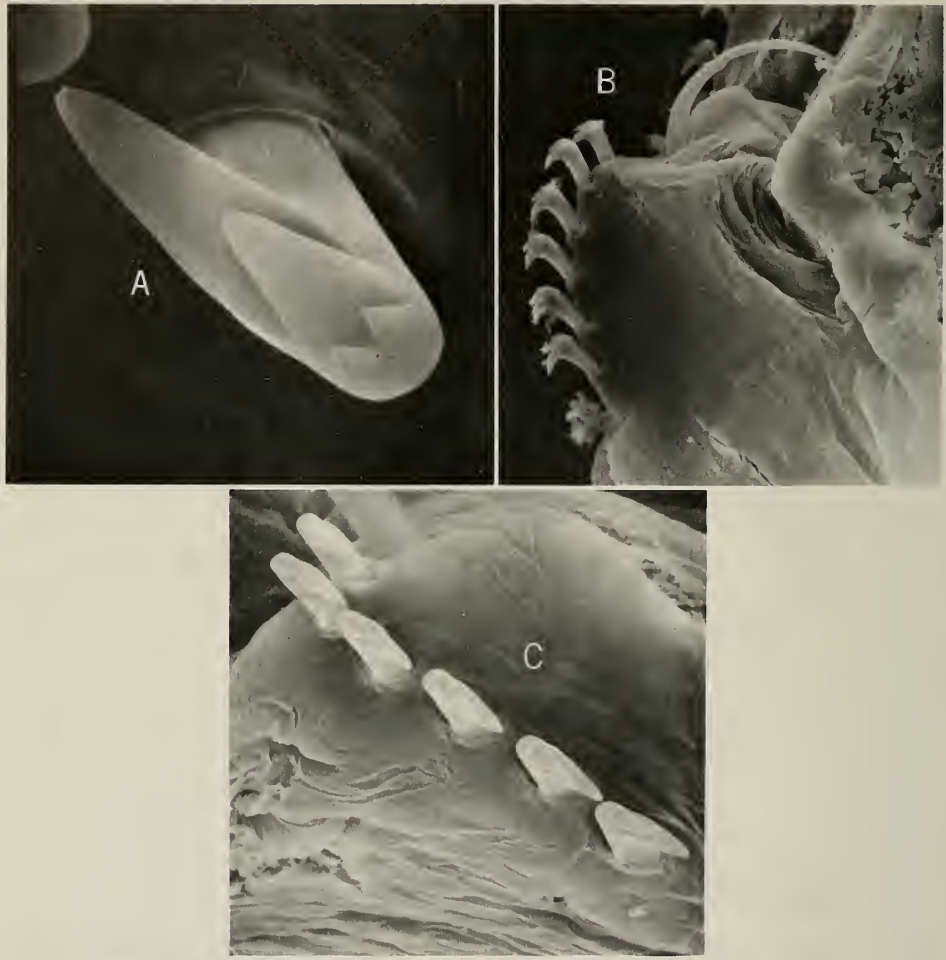


Fig. 5. *Spiophanes lowai:* A, Frontal view of neuropodial hook (×4400); B, Neuropodium of setiger 47, showing hooks and sabre setae (×440); C, Same showing basal parts of hooks (×940). Scanning electron microscope (SEM).

of setigers 7 and 8 there are indented setae of the same size as the accompanying notosetae. Bacillary setae are present from setiger 5; each seta is long, slender, unsheathed and with frayed appearance. Thread glands are inconspicuous.

Lower smooth neuropodial sabre setae first appear on setiger 5 and continue posteriorly, one per ramus.

The dark colored parapodial glands are located in setigers 10 to 15. Neuropodial hooks first appear in setiger 15, posterior to the parapodial glands, usually six hooks per ramus. Each hook is straight, lacks a hood and bears 4 teeth, the lowermost tooth being much larger than the other 3 (Figs. 4G, 5A–C). Five hooks are arranged in a vertical row with the sixth hook posterior to the lower hook and anterior to the sabre setae (Fig. 5C).

Transverse dorsal ridges connecting the dorsal lamellae of the notopodia begin on setiger 17 and continue posteriorly to the end of the fragment. They are well developed, overlapping on the following segment, highly vascularized and ciliated (Fig. 3C, D). The first ridge is lower than the rest.

Transparent and delicate genital pouches begin at setiger 15. The pygidium is unknown.

The tube of the paratype is mucous, transparent, and covered with fine sand.

Remarks.—Examination of specimens of *S. kroeyeri* Grube, 1860, and *S. berkeleyorum* Pettibone, 1962, in the collection of the USNM, show that *S. lowai* can be differentiated from these two species as follows:

1) The peristomium in *S. lowai* is broad and well developed as in *S. berkeleyorum*; it is reduced in *S. kroeyeri.*
2) Nuchal organs are poorly developed in *S. lowai.* In *S. berkeleyorum* and in *S. kroeyeri* they are very well developed (Light 1978, and examination of type-material in USNM).
3) Prostomium and anterior dorsum are pigmented in *S. lowai.* Pigmentation is absent in *S. kroeyeri* and *S. berkeleyorum.*
4) Parapodial glands are present from setiger 6 to 12 in *S. kroeyeri* and 10 to 15 in *S. lowai.*
5) Inferior sabre setae are first present on setiger 5 in *S. lowai* and on setiger 4 in *S. kroeyeri* and *S. berkeleyorum.*
6) Notopodial lamellae are similar in *S. kroeyeri* and *S. berkeleyorum* in that 1 to 4 are digitiform, and 5 to 15 are low, rounded and semicircular according to Light (1978). Posteriorly they have wide obcordate bases and digitiform tips. In *S. lowai* the first lamella is digitiform, 2 to 4 increase in size and are foliose, and posteriorly each lamella has a wide base and digitiform tip.
7) The dorsal transverse ridges are much more developed in *S. lowai* than in the other two species.
8) The indented setae were not found in specimens of *S. berkeleyorum* and *S. kroeyeri* examined, including the types of *S. berkeleyorum.*

However, in material of *S. kroeyeri* in the USNM collections, the specimens from British Columbia (Cat. No. 53249) agree with *S. lowai*; other specimens identified as *S. kroeyeri* lack indented setae and the high overlapping dorsal ridges.

Spiophanes kroeyeri is a cosmopolitan species reported from widely differing areas, and probably examination of further material will show that there are in fact more than one species involved in what is now called *S. kroeyeri* Grube.

Etymology.—The specific name is a derivation of the name Lowa Weiss to whom this species is dedicated.

Distribution.—The species was collected in shallow sandy bottoms in the bay of Mazatlan and the Sinaloa coast, south of Mazatlan.

Acknowledgments

I am deeply indebted to Dr. Kristian Fauchald for all the guidance provided in every step of this work, and without whom this work could not have been accomplished. I wish to thank also Dr. Meredith Jones for his help during my stay in his laboratory. I am grateful to Biol. Yolanda H. de Uribe for the work done at the SEM (model JOEL, JSM35), to Drs. M. Hendrickx and A. Van der Heiden for inviting me to participate in this project and to the Instituto de Ciencias del Mar y Limnología for providing the support to complete this work.

Literature Cited

Emerson, R. R., and K. Fauchald. 1971. A revision of the genus *Loandalia,* Monro with description of a new genus and species of pilargid polychaete.—Bulletin of the Southern California Academy of Science 70:18–22.

Fauchald, K. 1977. The polychaete worms. Definitions and keys to the orders, families and genera.—Natural History Museum of Los Angeles County Science Series 28:1–190.

Foster, N. M. 1971. Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea.—Studies on the fauna of Curaçao and Caribbean Islands 36:1–183.

Grube, A. E. 1860. Beschreibung neuer oder wenig bekannter Anneliden. Beitrag: Zahlreiche Gattungen.—Archiv für Naturgeschichte (Berlin) 26:71–118.

Hartman, O. 1947. Polychaetous annelids. Part VIII. Pilargiidae.—Allan Hancock Pacific Expeditions 10:483–522.

Hartmann-Schröder, G. 1959. Zur Ökologie der Polychaeten des Mangrove-Estero-Gebietes von El Salvador.—Beitrage zur Neotropischen Fauna 1:69–183.

Light, W. J. 1977. Spionidae (Annelida: Polychaeta) from San Francisco Bay, California: A revised list with nomenclatural changes, new records and comments on related species from the northeastern Pacific Ocean.—Proceedings of the Biological Society of Washington 90:66–88.

———. 1978. Spionidae (Polychaeta, Annelida) invertebrates of the San Francisco Bay estuaries system.—The Boxwood Press, Pacific Grove. xii + 211 pp.

Monro, C. C. A. 1936. Polychaete worms. II.—Discovery Reports 12:59–198.

Pettibone, M. H. 1962. New species of polychaete worms (Spionidae: *Spiophanes*) from the east and west coast of North America.—Proceedings of the Biological Society of Washington 75: 77–88.

———. 1966. Revision of the Pilargidae (Annelida: Polychaeta) including descriptions of new species and redescription of the pelagic *Podarmus ploa,* Chamberlin (Polynoidae).—Proceedings of the United States National Museum 118 (3525):155–208.

Thomas, J. 1963. Polychaetous worms from the Arabian Sea. I. A new species of the genus *Loandalia,* Monro.—Bulletin of the Department of Marine Biology and Oceanography University of Kerala 1:29–34.

Instituto de Ciencias del Mar y Limnología, Laboratorio de Ecología Costera, Apartado Postal 70-305, Universidad Nacional Autónoma de México, México, D.F. 04510.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 379–391

AMPHISAMYTHA GALAPAGENSIS, A NEW SPECIES OF AMPHARETID POLYCHAETE FROM THE VICINITY OF ABYSSAL HYDROTHERMAL VENTS IN THE GALAPAGOS RIFT, AND THE ROLE OF THIS SPECIES IN RIFT ECOSYSTEMS[1]

Robert Zottoli

Abstract.—Amphisamytha galapagensis, a new polychaete species of the family Ampharetidae, is described from hydrothermal vents of the Galapagos Rift. The placement of *A. galapagensis* in the genus *Amphisamytha* and its relationship with the other two species in the genus are discussed. The developmental biology and ecology of *A. galapagensis* in hydrothermal vent ecosystems are described.

Recently, I examined a collection of ampharetid polychaetes collected by the DSRV/*Alvin* from the Galapagos Rift, situated about 330 km northeast of the Galapagos Islands, and 640 km west of Ecuador. The Rift is part of the world-wide mid-oceanic ridge system where, in certain locales, warm water issues from hydrothermal vents. Crane and Ballard (1980) give a physical description of the Galapagos hydrothermal fields. Such areas often support dense communities of benthic animals, dominated by large vesicomyid bivalve molluscs or by mussels. Other organisms associated with vents include long, tube dwelling, vestimentiferan worms, brachyuran and galatheid crabs, dense aggregations of serpulid polychaetes, eel-like fish, and many other less abundant forms (Galapagos Biology Expedition Participants 1979; RISE Project Group 1980). Free-living chemoautotrophic bacteria, which use energy derived from oxidation of hydrogen sulfide to convert carbon dioxide to organic carbon, most likely serve as the food base for such communities. Bacteria living in trophosomal tissue of the vestimentiferan tube worm, *Riftia pachyptila* Jones, most likely provide nutrients to their host by means of a similar chemoautotrophic process (Cavanaugh *et al.* 1981; Felbeck 1981; Felbeck *et al.* 1981; Jones 1981; Southward *et al.* 1981).

The ampharetid *Amphisamytha galapagensis*, described here for the first time, is a detritivore. The external anatomy, larval development, and the role of this species in hydrothermal vent ecosystems are discussed.

Materials and Methods

Specimens were collected by the submersible DSRV/*Alvin* as follows: 1. Specimens, vacuumed from masses of mussel shells and the bases of vestimentiferan tubes with a "slurp gun," were preserved, and later examined at the surface; 2. Mussel clumps were removed from the bottom with a clam rake and placed in

---

[1] Contribution No. 34 of the Galapagos Rift Biology Expedition, supported by the National Science Foundation.

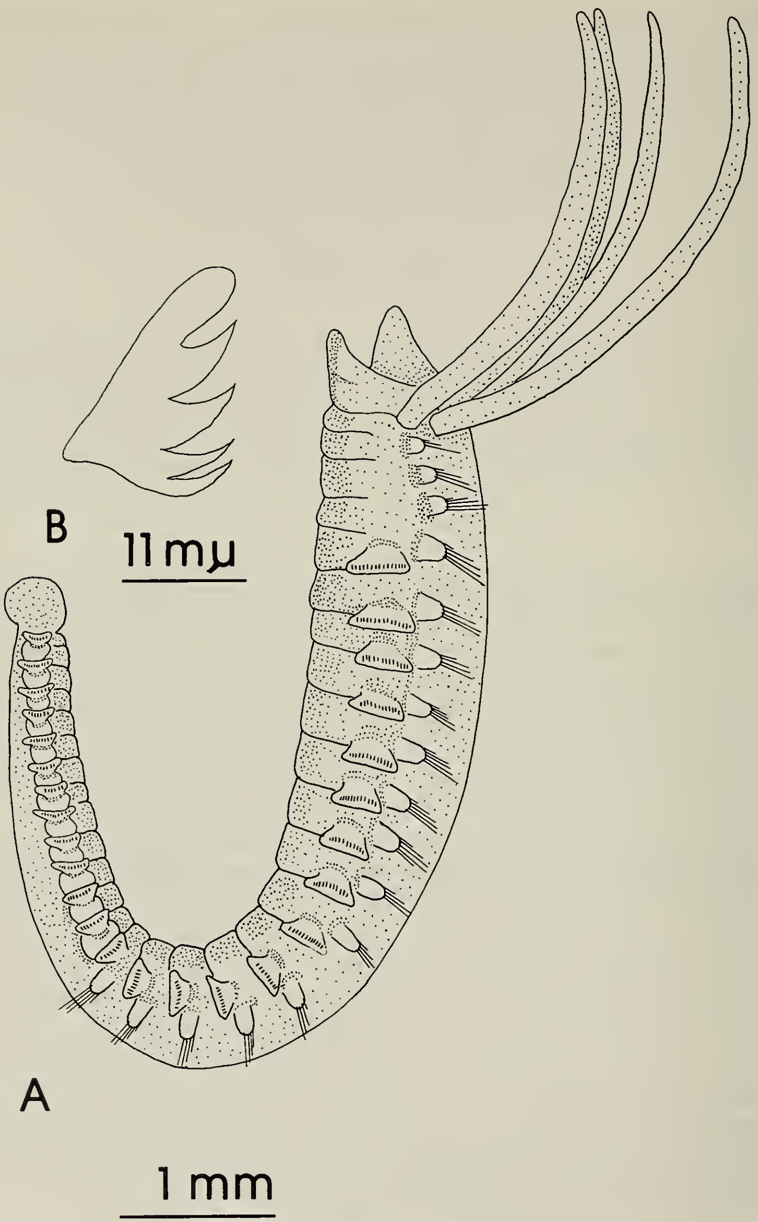


Fig. 1. *Amphisamytha galapagensis*: A, Lateral view of entire worm. Setae start on segment 4. In younger specimens setae may be found on segment 3; B, Mid-thoracic uncinus, lateral view.

an insulated bucket attached to *Alvin*'s basket; at the surface, mussels were rinsed over sieves with mesh openings of 0.297 and 0.88 mm; water left in the insulated bucket was filtered through the same sieves; animals retained on the sieves were preserved and examined at a later time; 3. Vestimentiferan tubes and galatheid crabs were treated in the same manner as mussel clumps.

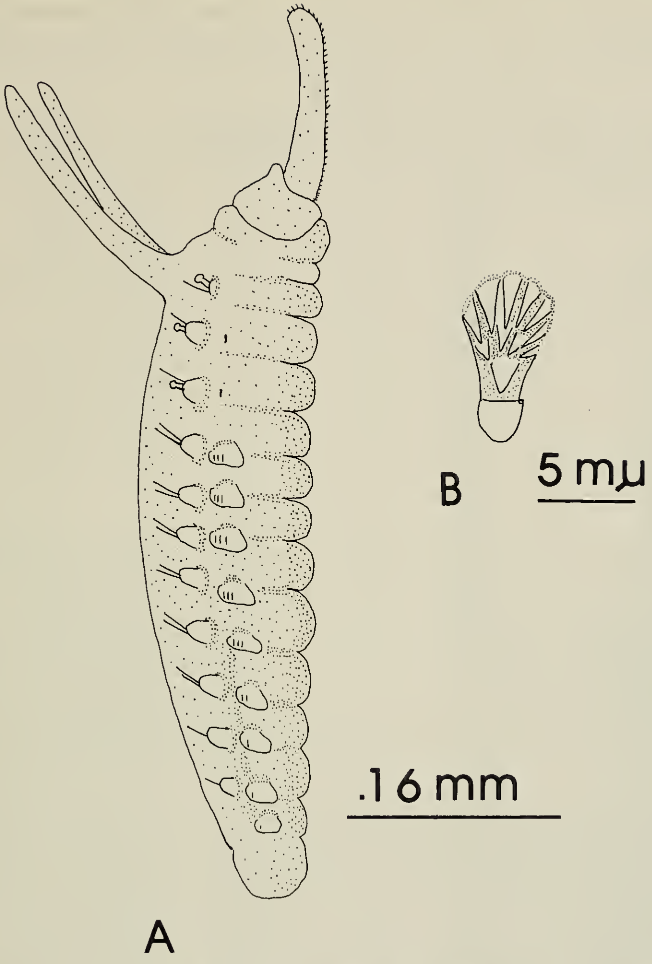


Fig. 2. *Amphisamytha galapagensis*: A, 11-setiger larva, lateral view; B, Larval uncinus, frontal view.

The mechanical devices used to collect vent organisms are described by Galapagos Biology Expedition Participants (1979).

Systematics

Ampharetid polychaetes, for the most part, are wide anteriorly and taper gradually towards the posterior end (Fig. 1A). The prostomium is trilobed. Segments 1 and 2, which lie immediately behind the prostomium, are fused in most species and, ventrally, form the lower lip. Segment 3 is either achaetous or bears two lateral bundles of setae (paleae or winged capillary). Malmgren (1865–1866) and Fauvel (1927) recognized two segments in front of the paleal, making it the third; while Nilsson (1912), Hessle (1917), and Uschakov (1957) recognized one biannular segment, making the paleal segment the second. The former numbering system is used here.

Table 1.—Location, number of juveniles and adults, and source of *Amphisamytha galapagensis* examined in this study.

Alvin dive and vent area	Date	Number of specimens[1]		Maximum depth (m)	Source
		A	J		
878: Search for Clambake	11/19/79	0	1	2725	With galatheid crab
879: Mussel Bed	1/20/79	1	2	2495	Mussel washings
880: Mussel Bed	1/21/79	7	18	2493	Mussel washings
883: Garden of Eden	1/25/79	0	6	2493	Slurp gun in mussel area
884a: Garden of Eden	1/25/79	0	11	2482	Clam bucket mussel washings
884b: Garden of Eden	1/25/79	12	3	2482	Rubble residue from mussel area
887: Mussel Bed	2/12/79	3	21	2488	Mussel Bed
888a: Mussel Bed	2/13/79	6	51	2483	Galatheid washings
888b: Mussel Bed	2/13/79	3	7	2483	Galatheid washings
890: Rose Garden	2/15/79	0	9	2447	In jar with two galatheid crabs
891: Garden of Eden	2/16/79	23	24	2488	Rock scrapings
892: Rose Garden	2/17/79	2	9	2454	Residue from cooler
894a: Rose Garden	2/19/79	0	36	2457	—
894b: Rose Garden	2/19/79	1	8	2457	From amphipod trap?
896-22: Rose Garden	2/21/79	26	72	2460	Instant ocean washings
N983: Rose Garden	11/30/79	1	1	2457	Vestimentifera tube washings
N98335: Rose Garden	11/30/79	0	1	2457	Vestimentifera tube washings
N98336: Rose Garden	11/30/79	0	11	2457	Vestimentifera tube washings
N983112: Rose Garden	11/30/79	14	75	2457	Vestimentifera tube washings
N9846: Rose Garden	12/ 1/79	0	4	2451	Vestimentifera tube washings
N9846c: Rose Garden	12/ 1/79	3	6	2451	Vestimentifera tube washings
N9847: Rose Garden	12/ 1/79	0	2	2451	Vestimentifera tube washings
N989: Mussel Bed	12/ 6/79	3	8	2482	Bottle rack washings
N99011: Rose Garden	12/ 7/79	0	1	2451	Vestimentifera tube washings
N99013: Rose Garden	12/ 7/79	1	0	2451	Vestimentifera tube washings
N99014: Rose Garden	12/ 7/79	0	2	2451	Vestimentifera tube washings
N99019: Rose Garden	12/ 7/79	1	1	2451	Vestimentifera tube washings
N99040: Rose Garden	12/ 7/79	0	1	2451	Vestimentifera tube washings
N99041: Rose Garden	12/ 7/79	16	11	2451	Vestimentifera tube washings
N9931: Garden of Eden	12/10/79	7	6	2518	Vestimentifera tube washings
N9932: Garden of Eden	12/10/79	2	0	2518	Vestimentifera tube washings
N9934: Garden of Eden	12/10/79	5	0	2518	Vestimentifera tube washings

Vent area	Coordinates
Search for Clambake	00°47.92′N, 86°13.5′W
Mussel Bed	00°47.89′N, 86°09.21′W
Garden of Eden	00°47.69′N, 86°07.74′W
Rose Garden	00°48.25′N, 86°13.48′W

[1] A = adult, J = juvenile.

Amphisamytha galapagensis, new species

Figs. 1A, B, 2A, B

Material examined.—See Table 1. Holotype, USNM 81288; 13 Paratypes, USNM 81289.

Description.—Holotype, gravid female, 9.6 mm long, 1.2 mm wide, with 30 setigerous segments. Other specimens up to 10.2 mm long and 1.5 mm wide with 32 setigerous segments. Sexually mature worms as small as 3.6 mm in length. Worms longer than this considered adults. About 300 elliptical eggs, 40–150 μm at their widest point, in body cavity of one 9-mm-long female; 60 eggs at maximum

Table 2.—Number of smooth winged capillary setae per notopodium on "setigerous" segments of the 11- to 18-setiger stages of *Amphisamytha galapagensis*.

Segment	Setiger	Setiger stage						
		11a	11b	14	18a	18b	18c	18d
3	1	3	2	3	2	1	1	0
4	2	3	3	3	3	4	2	5
5	3	3	4	3	4	5	4	6
6	4	3	5	3	5	5	5	6
7	5	3	4	4	4	5	4	6
8	6	3	3	5	6	5	5	6
9	7	3	3	3	6	4	5	6
10	8	3	3	3	3	4	5	7
11	9	3	2	2	4	4	4	7
12	10	2	2	2	5	4	5	7
13	11	1	1	2	4	4	4	7
14	12			1	4	4	4	7
15	13			1	4	3	4	6
16	14			1	4	3	4	7
17	15				4	2	3	7
18	16				2	2	3	7
19	17				2	2	3	6
20	18				2	2	2	5

11a = 0.5 × 0.14 mm
11b = 0.7 × 0.18 mm
14 = 0.8 × 0.18 mm
18a = 1.05 × 0.25 mm
18b = 1.5 × 0.35 mm
18c = 1.75 × 0.4 mm
18d = 8.0 × 1.2 mm

diameter. Color of adult in alcohol white to pale orange. Prostomium indistinctly trilobed, lacking glandular ridges. About 25 smooth, ventrally grooved oral tentacles. Segments 1 and 2 fused, with ventral part forming lower lip. Segment 3 lacking paleae. Minute notopodial lobes with 2–3 short winged capillary setae on segment 3 in juveniles and smaller adults. Each seta approximately 0.25 mm long, 5 μm wide basally, and 6 μm wide across the blade. Four pairs of smooth branchiae about ⅓ of body length, individually inserted, across dorsal surface of segments 3–5. Origin of branchial pairs described in larval development section. Wide gap between branchial groups. Notopodial lobes bearing 6–10 smooth winged capillary setae from segment 4 to end of thorax. Each seta about 0.75 mm long, 10 μm wide basally and 13 μm wide across blade. Notopodia of segments 4 and 5 raised dorsally; notopodia of segment 4 smaller than others. 17 thoracic setigerous segments. Neuropodial lobes (uncinigerous pinnules) each with single row of toothed uncini from segment 7 to end of abdomen. 14 uncinigerous thoracic and 12–15 uncinigerous abdominal segments. Thoracic and abdominal uncini in single transverse rows with, respectively, about 20 and 15 per row in larger specimens. Thoracic and abdominal uncini with 4 teeth in single row above rounded basal prow (Fig. 1B). Larval uncini may be found in juveniles and young adults (Fig. 2B). No notopodial, neuropodial, or anal cirri. Notopodia absent from abdominal segments. Thickened glandular pads above uncinigerous pinnules on most abdominal segments. Pygidium bilobed.

Remarks.—The genus *Amphisamytha* was created by Hessle (1917) to include ampharetids with four pairs of smooth branchiae, no setae on segment 3, no glandular ridges on the prostomium, 14 thoracic uncinigerous segments and notopodia on abdominal segments.

Day (1964) considered *Amphisamytha* Hessle (1917) and *Hypaniola* Annekova (1928) to be synonyms of *Lysippides* Hessle (1917). He expanded this genus to include those with or without setae on segment 3. Admittedly the three genera are closely allied; however, the complete lack of setae on segment 3 in larger specimens, I feel, justifies the separation of *Amphisamytha* from these closely related genera.

Amphisamytha galapagensis is distinguished from the other two members of the genus, *A. bioculata* (Moore) and *A. japonica* (Hessle), by the complete lack of anal cirri and by the possession of thick glandular pads above uncinigerous pinnules in most abdominal segments.

Etymology.—Specific name refers to geographic area where specimens were collected.

Feeding

Amphisamytha galapagensis lives in mucus-lined tubes covered by detritus and small chips of volcanic glass, which resemble tubes of the brackish water ampharetids *Hypania invalida* (Grube) and *Hypaniola kowalewskii* (Grimm) (Manoleli 1977). The tubes are attached to solid surfaces such as lava or clam shells.

The morphology of the feeding apparatus of *A. galapagensis* is remarkably similar to that described for the majority of ampharetid species. This suggests a similarity in feeding behavior. Below is a description of feeding behavior, from the sources noted, for *Asabellides oculata* (Webster) and *Hobsonia* (*Amphicteis*) *floridus* (Hartman) (Fauchald and Jumars 1979; personal observations); *Hypania invalida* (Grube) (Manoleli 1975); and *Melinna palmata* (Grube) (Dragoli 1961). In general ampharetids feed by extending tentacles from the tube and over the sediment surface. Mucus, secreted in the ventral part of each tentacle, traps detritus which is carried by ciliary action along the ventral tentacular groove to the mouth. Manoleli (1975) noted that the tentacles are suddenly extended to about three-fourths of the body length from the tube onto the sediment surface; then, laden with detritus, they are gradually retracted towards the mouth, sometimes independently of one another. Similar feeding behavior was noted by the author for *A. oculata* (Webster) and by Dragoli (1961) for *M. palmata* (Grube). Although most ampharetids are considered to be detritus feeders, Manoleli (1975) suggested that *H. invalida* (Grube) and *H. kowalewskii* (Grimm) are suspension feeders since phytoplankton is common in gut cavities.

The presence of detritus and bacteria in digestive tracts of juvenile and adult *A. galapagensis* lends support to the idea that mainly they consume particulate matter that settles on solid surfaces; however, suspension feeding cannot be ruled out. The bulk of their food most likely consists of chemoautotrophic bacteria and fecal pellets from other organisms.

Reproduction and Larval Development

Sexually mature worms range from 3.6 to 10.2 mm long and from 0.75 to 1.5 mm wide. Based on observations on other ampharetid species, eggs probably

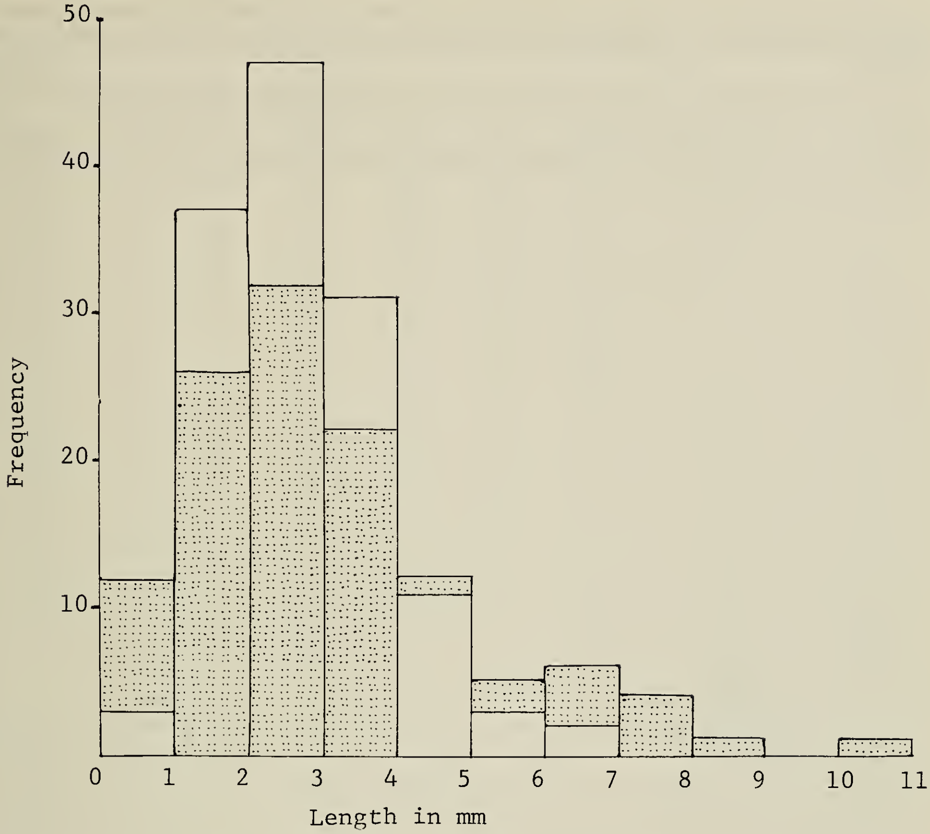


Fig. 3. Frequency histogram for length of a collection of *Amphisamytha galapagensis* from the Rose Garden on *Alvin* dives 890, 892, 894, 896 (clear portion); 983, 894 and 990 (shaded portion). Refer to systematics section for dive locations.

pass singly through nephridia and nephridiopores into the anterior part of the tube where they are fertilized by sperm released by males in the same fashion. Gametes of the ampharetid *Melinna cristata* (Sars) are ejected in two streams from the anterior end of the tube (Nyholm 1950) while Fauvel (1897) indicated that *Ampharete grubei* (Malmgren) and *Amphicteis gunneri* (Sars) shed eggs singly into the water column through two nephridia on the fourth setigerous segment.

Unfertilized eggs, between 40–150 μm maximum width, are irregularly elliptical with a large germinal vesicle. Developing larvae beyond the fertilized egg and prior to the 10-setiger stage were not found. Larval stages in this paper are named on the basis of the number of segments (setigers) bearing capillary setae. In an adult, however, setiger refers to any segment bearing setae of the capillary or uncinate type.

The 11-setiger stage, illustrated in Fig. 2A, is described below. Larval ciliary bands (prototroch, metatrochs or telotroch) were not evident. They disappear at about the 6-setiger stage in *H. floridus* (Hartman), which has similar larval development (Zottoli 1974). There is a single, median, ventrally grooved and ciliated tentacle protruding from the mouth. In the 8-setiger stage of *H. floridus* (Hartman)

Table 3.—Number of larval uncini per uncinigerous pinnule on "setigerous" and "post-setigerous" segments of the 11- to 18-setiger stages of *Amphisamytha galapagensis*. Larval sizes are listed in Table 2.

		Setiger stage						
Segment	Setiger	11a	11b	14	18a	18b	18c	18d
3	1	0	0	0	0	0	0	0
4	2	1	0	0	0	0	0	0
5	3	1	1	0	0	0	0	0
6	4	3	1	1	0	0	0	0
7	5	3	1	1	5	2	7	0
8	6	3	2	4	5	3	7	0
9	7	3	2	4	4	3	6	0
10	8	2	2	3	4	3	4	0
11	9	2	2	3	4	2	3	0
12	10	1	1	2	4	2	3	0
13	11	1	1	2	3	3	3	0
14	12	1	1	2	3	3	3	0
15	13	1	1	1	3	3	3	0
16	14			1	3	3	3	0
17	15			1	3	2	3	0
18	16			1	3	2	3	0
19	17				2	3	3	0
20	18				2	3	3	0
	"Post-setiger" (abdomen)							
21	1				2	6	5	0
22	2				2	5	5	0
23	3					5	4	0
24	4					4	4	0
25	5					3	2	0
26	6					2	1	0
27	7					1	1	0
28	8							0
29	9							0
30	10							14
31	11							10
32	12							6
33	13							6

this tentacle is used in feeding, and detrital particles, bound in mucus secreted at the tentacle tip, are transported by ciliary action along the ventral groove to the mouth. Prostomial eyespots are lacking and fused segments 1 and 2 lie immediately behind prostomium. Segments 3–5 bear small notopodia, each with one spatulate and one smooth winged capillary seta. Spatulate setae are larval structures formed only in notopodia of the first three setigers. They disappear in later stages. Similar setae were described by Wilson (1928) on the first 11 setigers of the terebellid polychaete *Loimia medusa* (Savigny). One uncinus is embedded in the epidermis on each side of segments 4 and 5 below the notopodia. Each uncinus bears about 6–10 teeth above a single tooth and rounded basal part (Fig. 2B). Segments 6–13 each bear a pair of notopodia bearing smooth, winged capillary setae (Table 2). Uncinigerous pinnules, each have larval uncini on segments 7–

Table 4.—Number of adult uncini per uncinigerous pinnule on ''setigerous'' and ''post-setigerous'' segments of the 11- to 18-setiger stages of *Amphisamytha galapagensis*. Larval sizes are listed in Table 2.

		Setiger stage						
Segment	Setiger	11a	11b	14	18a	18b	18c	18d
3	1	0	0	0	0	0	0	0
4	2	0	0	0	0	0	0	0
5	3	0	0	0	0	0	0	0
6	4	0	0	0	0	0	0	0
7	5	0	0	0	0	5	1	18
8	6	0	0	0	0	6	1	18
9	7	0	0	0	0	4	2	22
10	8	0	0	0	0	4	3	25
11	9	0	0	0	0	3	2	23
12	10	0	0	0	0	3	3	20
13	11	0	0	0	0	3	3	17
14	12			0	0	2	3	20
15	13			0	0	2	2	19
16	14			0	0	2	2	19
17	15				0	2	2	18
18	16				0	3	2	17
19	17				0	1	2	15
20	18				0	1	1	14
	''Post-setiger'' (abdomen)							
21	1					0	0	15
22	2					0	0	14
23	3					0	0	15
24	4					0	0	15
25	5					0	0	13
26	6					0	0	14
27	7					0	0	14
28	8							14
29	9							15
30	10							2
31	11							0
32	12							0
33	13							0

13 (Fig. 2A, Table 3). First and only pair of branchiae originate from dorsal surface of segment 3. As growth continues the uncini disappear from segments 4 and 5.

In the 14-setiger stage, the second pair of branchiae arise behind the first on dorsal surface of segment 4; larval uncini disappear from segment 6.

The following changes take place between the stages above and adult worms: 1) Smooth winged capillary setae on segment 3 are lost. This suggests that possession of setae on segment 3 is a primitive character in the family Ampharetidae. 2) Abdominal segments increase in number to 12–15. 3) Larval spatulate setae are lost. 4) Uncini change in number and structure: a) There is an increase in number of adult uncini per uncinigerous pinnule (Fig. 1B, Table 4) coinciding with a decrease in number of larval uncini (Fig. 2B, Table 4). Uncini are first formed in the dorsal part of each pinnule. b) As new uncini are formed, older ones are pushed ventrally. Usually, one developing uncinus is visible in each abdominal uncinigerous pinnule of young worms. Uncini of the maldanid polychaetes *Clymenella torquata* (Leidy) and *Euclymene oerstedi* (Claparede) are formed ventrally rather than dorsally as above (Pilgrim 1977). This character may aid in determining general evolutionary relationships between polychaete families. Length of individual *A. galapagensis* uncini in each row increases slightly from ventral to dorsal supporting the idea that uncini move along the row. Pilgrim (1977:294) made the point that in maldanids, "the difference in length between ventral and dorsal chaetae *in older worms* becomes an indicator of their rate of progress along the row, and presumably of the growth rate of the whole body, the greater difference in length, the lower the growth rate." As uncini of *A. galapagensis* differ slightly in length along each row, a rapid growth rate is suggested. Larval uncini are still present in the ventral part of adult posterior abdominal uncinigerous pinnules. Since newly formed uncini are of the adult type, the presence of larval uncini suggests that once a particular size is reached, growth slows. This would allow food reserves to be used for gamete production and development, rather than growth, thus enhancing the reproductive potential of the population. 5) A fourth pair of branchiae appears on dorsal surface of segment 5. 6) Up to 25 smooth, ventrally grooved and ciliated, oral tentacles are developed.

Development of this species is similar to that of the ampharetids *A. grubei* Malmgren (Thorson 1946), *H. floridus* (Hartman) (Zottoli 1974), *M. cristata* (Sars) (Nyholm 1950), and *Schistocomus sovjeticus* Annekova (Okuda 1947).

Environmentally predictable deep-sea communities are inhabited for the most part by k-selected species, characterized by low reproductive potentials, long life spans, and long maturation periods (Sanders and Hessler 1969; Sanders 1979). One might predict, therefore, that numbers and biomass of juveniles in the deep-sea would tend to be lower than those of adults over a given time span. This hypothesis is supported by data on deep-sea bivalves (Grassle and Sanders 1973), two isopod species (Hessler 1970), one species of tanaid (Gardiner 1975), and certain large bathypelagic euphausiids (Mauchline 1972). The deep-sea brittle-star *Ophiura ljungmani* (Lyman), however, is an exception to this rule (Tyler and Gage 1980).

Lonsdale (1977) observed large numbers of dead mussels in certain vent areas suggesting that this unique environment is unstable. Instability tends to favor opportunistic or r-selected species (Grassle and Grassle 1974) that are characterized by high reproductive rate, short maturation time, short life span, large population size, high mortality rate, wide physiological tolerances and broad cosmopolitan distributions (Sanders 1979). High reproductive rates allow opportunists to increase numbers under favorable conditions, thus enhancing their ability to colonize new areas, and ensure survival of the species. The deep-sea wood boring bivalve *Xylophaga* (Turner 1973), the ampharetid polychaete *Decemunciger*, associated with *Xylophaga* (Zottoli 1982), possibly the Galapagos Rift vesicomyid clams (Turekian and Cochran 1981) and undescribed mussels (Rhoads *et al.* 1981) have these characters more than many other deep-sea organisms.

The presence of numerous (300) small eggs (150 μm maximum diameter) in the body cavity of some female worms and the presence of numerous juveniles in most samples (Fig. 3) imply a high reproductive rate and suggest that *A. galapagensis* is relatively opportunistic. Long planktonic development associated with opportunism would improve the chances of worms reaching and colonizing new vent areas. Egg size is often suggestive of whether or not a species has planktonic development. Thorson (1951) suggested that polychaete species with egg diameters less than 150 μm generally have long pelagic planktotrophic development. This generalization does not apply to most ampharetids investigated to date. *H. floridus* (Hartman) (Zottoli 1974), *H. kowalewskii* (Grimm) (Marinescu 1964) and *Melinnexis arctica* Annekova (Annekova 1931), which have eggs roughly the same width as *A. galapagensis,* retain developing larvae in the maternal tube until they are able to crawl on the bottom. Eggs of *Alkamaria romijni* Horst, a protandric hermaphrodite, either develop in the body cavity or in the maternal tube (Wesenberg-Lund 1934). On the basis of its similarity to the above mentioned ampharetids, it is here hypothesized that *A. galapagensis* produces larvae that swim or crawl along the bottom in the area where they were released. This would allow continuous repopulation without relying on larvae from geographically separated areas. As regards emigration to new sites, larvae would probably be swept by bottom currents to new vent areas. Lonsdale (1977) recorded a current speed of 18 cm/sec along the bottom in a vent area on the East Pacific Rise. Cold water would reduce the metabolic rate as larvae are swept away from warm vent areas, thereby prolonging survival time and enhancing the chances of reaching a new vent site.

Acknowledgments

Thanks are due to Dr. J. Fred Grassle, for making specimens available and to Dr. J. Fred Grassle, Charlene D. Long, and Dr. Meredith Jones for reviewing the manuscript. The study is contribution No. 34 of the Galápagos Rift Biology Expedition, supported by the National Science Foundation.

Literature Cited

Annekova, N. 1928. Über die pontokaspischen Polychaeten. 2. Die Gattungen *Hypaniola, Parhypania, Fabricia* und *Manajunkia.*—Annuaire du Musée Zoologique de l'Academie des Sciences de l'URRS 30:13–20.

———. 1931. Zur Polychaetenfauna von Franz-Joseph-Land (*Melinnexis* gen. nov. *arctica* sp.n.).—Zoologischer Anzeiger, Leipzig 95:269–272.

Cavanaugh, C. M., S. L. Gardiner, M. L. Jones, H. W. Jannasch, and J. B. Waterbury. 1981. Prokaryotic cells in the hydrothermal vent tube worm *Riftia pachyptila* Jones: Possible chemoautotrophic symbionts.—Science 213:340–342.

Crane, K., and R. D. Ballard. 1980. The Galapagos Rift at 86°W: 4. Structure and morphology of hydrothermal fields and their relationship to the volcanic and tectonic processes of the Rift Valley.—Journal of Geophysical Research 85(B3):1443–1445.

Day, J. H. 1964. A review of the family Ampharetidae (Polychaeta).—Annals of the South African Museum 48(4):97–120.

Dragoli, A. L. 1961. Peculiar feeding habits in the Black Sea polychaete *Melinna palmata* Grube.—Doklady Akademii Nauk SSR 138(4):970–973. [In Russian.]

Fauchald, K., and P. A. Jumars. 1979. The diet of worms: A study of polychaete feeding guilds.—Oceanography Marine Biology Annual Review 17:193–284.

Fauvel, P. 1897. Recherches sur les Ampharétiens, Annélides polychètes sédentaires. Morphologie, Anatomie, Histologie, Physiologie.—Bulletin Scientifique de la France et de la Belgique 30: 277–488.

———. 1927. Polychètes Sédentaires.—Faune de France 16:1–494.

Felbeck, H. 1981. Chemautotrophic potential of the hydrothermal vent tube worm *Riftia pachyptila* Jones (Vestimentifera).—Science 213:336–338.

———, J. J. Childress, and G. N. Somero. 1981. Calvin-Benson cycle and sulphide oxidation enzymes in animals from sulphide-rich habitats.—Nature 293:291–293.

Galapagos Biology Expedition Participants. 1979. Galapagos '79: Initial findings of a deep-sea biological quest.—Oceanus 22(2):2–10.

Gardiner, L. F. 1975. The systematics, postmarsupial development, and ecology of the deep-sea family Neotanaidae (Crustacea: Tanaidacea).—Smithsonian Contributions to Zoology 170:1–265.

Grassle, J. F., and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes.—Journal of Marine Research 32:253–284.

———, and H. L. Sanders. 1973. Life histories and the role of disturbance.—Deep-Sea Research 20:642–659.

Hessle, C. 1917. Zur kenntnis der terbellomorphen Polychaeten.—Zoologische Bidrag från Uppsala 5:39–258.

Hessler, R. R. 1970. The Desmosomatidae (Isopoda, Asellota) of the Gay Head-Bermuda transect.—Bulletin of the Scripps Institution of Oceanography 15:1–185.

Jones, M. 1981. *Riftia pachyptila* Jones: Observations of the vestimentiferan worm from the Galápagos Rift.—Science 213:333–336.

Lonsdale, P. 1977. Clustering of suspension feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers.—Deep-Sea Research 24:857–863.

Malmgren, A. J. 1865–1866. Nordiska Hafs-Annulater.—Öfversigt Svenska Vetenskaps Akademiens Förhandlingar 22:181–192, 355–410.

Manoleli, D. 1975. On the distribution, biology and origin of polychaeta from the Danube and Danube delta.—Travaux du Muséum d'Histoire Naturelle "Grigore Antipa" 16:25–34.

———. 1977. La structure, la texture et la composition minéralogique des tubes de *Hypania invalida* et *Hypaniola kowalewskii* (Polychaeta, Ampharetidae) du Danube. Travaux du Muséum d'Histoire Naturelle "Grigore Antipa" 28:9–15.

Marinescu, V. P. 1964. La reproduction et le développement des polychètes reliques Ponto-Caspiens du Danube: *Hypaniola kowalewskii* (Grimm) et *Manayunkia caspica*.—Revue Roumaine de Biologie, Série de Zoologie 9:87–100.

Mauchline, J. 1972. The biology of bathypelagic organisms, especially Crustacea.—Deep-Sea Research 19:753–780.

Nilsson, D. 1912. Beiträge zur kenntnis des nervensystems der polychaeten.—Zoologiska Bidrag från Uppsala 1:85–161.

Nyholm, K. 1950. Contributions to the life-history of the ampharetid, *Melinna cristata*.—Zoologiska Bidrag från Uppsala 29:79–91.

Okuda, S. 1947. On an ampharetid worm, *Schistocomus sovjeticus* Annekova, with some notes on its larval development.—Journal Faculty Science Hokkaido Imperial University (ser. 6) 9:321–329.

Pilgrim, M. 1977. The functional morphology and possible taxonomic significance of the parapodia of the maldanid polychaetes *Clymenella torquata* and *Euclymene oerstedi*.—Journal of Morphology 152:281–302.

Rhoads, D. C., R. A. Lutz, E. C. Revelas, and R. M. Cerrato. 1981. Growth of bivalves at deep-sea hydrothermal vents along the Galápagos Rift.—Science 214:911–913.

RISE Project Group. 1980. East Pacific Rise: Hot springs and geophysical experiments.—Science 207:1421–1444.

Sanders, H. L. 1979. Evolutionary ecology and life-history patterns in the deep-sea.—Sarsia 64: 1–7.

———, and R. R. Hessler. 1969. Ecology of the deep-sea benthos.—Science 163:1419–1424.

Southward, A. J., E. C. Southward, P. R. Dando, G. H. Rau, H. Felbeck, and H. Flügel. 1981. Bacterial symbionts and low $^{13}C/^{12}C$ ratios in tissues of Pogonophora indicate unusual nutrition and metabolism.—Nature 293:616–620.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund).—Meddeleser Fra Kommissionen for Danmarks Fiskeri-og Havundersogelser, serie: Plankton 4(1):1–523.

———. 1951. Zur jetzigen lage der marinen bodentierökologie.—Verhandlungen der Deutschen Zoologischen Gesellshaft 12(17):276–326.

Turekian, K. K., and J. K. Cochran. 1981. Growth rate of a vesicomyid clam from the Galápagos spreading center.—Science 214:909–911.

Turner, R. D. 1973. Wood-boring bivalves, opportunistic species in the deep-sea.—Science 180: 1377–1379.

Tyler, P. A., and J. D. Gage. 1980. Reproduction and growth of the deep-sea brittlestar *Ophiura ljungmani* (Lyman).—Oceanolica Acta 3(2):177–185.

Uschakov, P. V. 1957. Bristleworms of the far eastern seas of USSR (Polychaeta). Opredeliteli po faune SSSR (Keys to the fauna of the USSR) 56:1–445. [In Russian.]

Wesenberg-Lund, E. 1934. A viviparous brackish-water ampharetid, *Alkmaria romijni* Horst from Ringkøbing Fjord.—Videnskabelige Meddelelser Naturhistorisk Forening 98:215–222.

Wilson, D. P. 1928. The post-larval development of *Loimia medusa* Sav.—Journal of the Marine Biological Association of the United Kingdom 15(1):129–147.

Zottoli, R. A. 1974. Reproduction and larval development of the ampharetid polychaete *Amphicteis floridus*.—Transactions of the American Microscopical Society 93(1):78–89.

———. 1982. Two new genera of deep-sea worms of the family Ampharetidae and the role of one species in deep-sea ecosystems.—Proceedings of the Biological Society of Washington 95(1): 48–57.

Department of Biology, Fitchburg State College, Fitchburg, Massachusetts 01420.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 392–399

A NEW SCALE WORM (POLYCHAETA: POLYNOIDAE) FROM THE HYDROTHERMAL RIFT-AREA OFF WESTERN MEXICO AT 21°N

Marian H. Pettibone

Abstract.—A unique polynoid polychaete, *Lepidonotopodium fimbriatum* n. gen., n. sp., is described from the hydrothermal vent area at 21°N off western Mexico and referred to a new subfamily of Polynoidae, the Lepidonotopodinae.

During *Alvin* dives 1213 and 1223 in 1982 to the East Pacific Rise hydrothermal vent area at 21°N in the Pacific Ocean off western Mexico, three adults and one young specimen of a unique polynoid polychaete were collected at 2600 meters depth in the Clam Acres area. They were made available to me by Dr. Kenneth Smith of Scripps Institution of Oceanography, University of California, San Diego. This is OASIS Expedition Contribution number 10.

The types are deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Family Polynoidae
Lepidonotopodinae, new subfamily
Lepidonotopodium, new genus

Type-species.—*Lepidonotopodium fimbriatum*, new species.

Diagnosis.—Body short, flattened, subrectangular; 28 segments (first achaetous). Elytra and prominent elytrophores 11 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, with dorsal cirri on posterior 7 segments. Prostomium deeply bilobed; median antenna with ceratophore inserted in anterior notch, with short style; without lateral antenna but with small frontal filaments on subtriangular lobes of prostomium; paired palps cylindrical, smooth, with filamentous tips; without eyes. First or tentacular segment fused to prostomium, not visible dorsally; tentaculophores lateral to prostomium, each with pair of tentacular cirri, single aciculum, without setae; without facial tubercle. Second segment with first pair of elytra, biramous parapodia, and ventral or buccal cirri attached to basal parts of parapodia lateral to mouth; styles longer than following ventral cirri. Parapodia biramous, with notopodia shorter than neuropodia. Notopodia subconical, with projecting acicular processes and well-developed bracts encircling notopodia anteriorly and dorsally. Neuropodia diagonally truncate, deeply notched dorsally, without projecting acicular processes. Distal tips of notopodia, notopodial bracts, and neuropodia fimbriated with slender papillae. Notosetae numerous, subequal in width to neurosetae, with single rows of widely spaced spines and blunt tips. Neurosetae numerous, with 2 rows of numerous spines along one side and slightly hooked blunt tips. Dorsal cirri on segments lacking elytra, with cylindrical cirrophores attached on posterodorsal sides of notopodia, with tapered styles; ventral cirri short, tapered, attached near middle of neuropodia. Dorsal tubercles on cirrigerous segments large, inflated. Elytrophores, dorsal tubercles

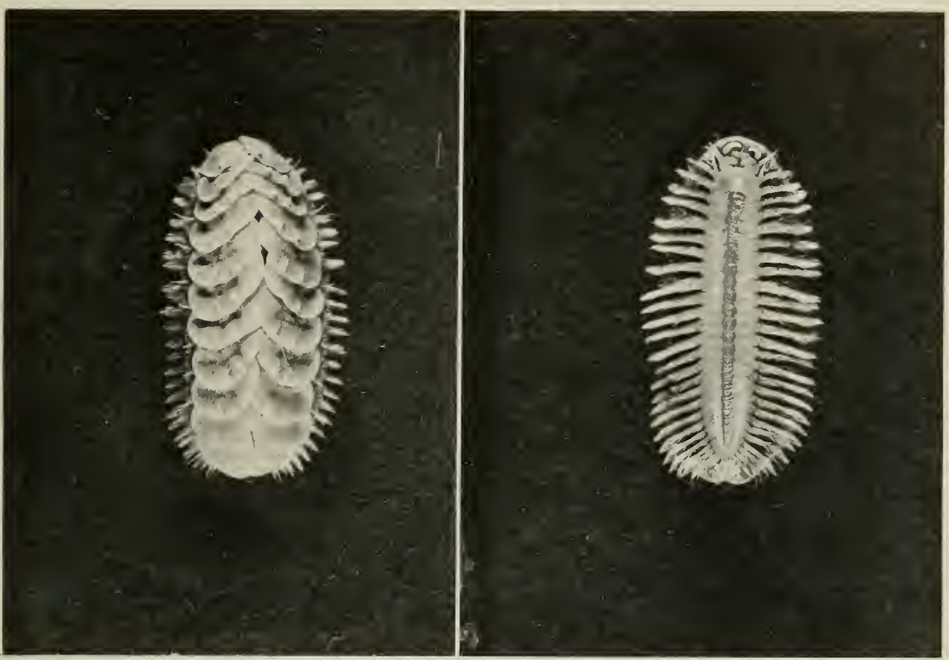


Fig. 1. *Lepidonotopodium fimbriatum,* holotype, USNM 80113: Dorsal view, left; ventral view, right. 2×.

and their bases with numerous ciliated ridges separated by thin-walled integument. Ventral segmental papillae lacking or with 2 pairs of large papillae on segments 11 and 12, extending dorsally between neuropodia. Pygidium dorsal, large, bulbous, wedged between parapodia of posterior 3 segments, with pair of ventral anal cirri. Pharynx with 7 pairs of papillae—7 dorsal with median one larger and 7 ventral with median one short; 2 pairs of jaws with few (5–7) basal teeth.

Etymology.—The generic name is derived from Greek, *lepidos,* scale or bract; *notos,* back; *podos,* foot, referring to the bracts on the notopodia. Gender: masculine. The specific name is derived from Latin, *fimbria,* fringe, referring to the fimbriated parapodia.

Lepidonotopodium fimbriatum, new species
Figs. 1–5

Material examined.—Pacific Ocean off western Mexico, 20°50′N, 109°06′W, 2600 m, *Alvin* dive 1213, sample B21, 19 April 1982, Clam Acres—holotype, USNM 80113, and 2 paratypes, USNM 80114, 80115. Same area, *Alvin* dive 1223, sample 10A, 7 May 1982—paratype, young, USNM 80116.

Description.—The 3 adult types are similar in size: 23–24 mm in length, 12–13 mm in width, including setae, with 28 segments, the last segment very small. All specimens are uniformly dark greyish in color, stout, short-bodied, rectangular in outline, flattened ventrally, strongly arched dorsally, and slightly tapered and rounded anteriorly and posteriorly (Fig. 1). The elytra are thick, leathery, imbri-

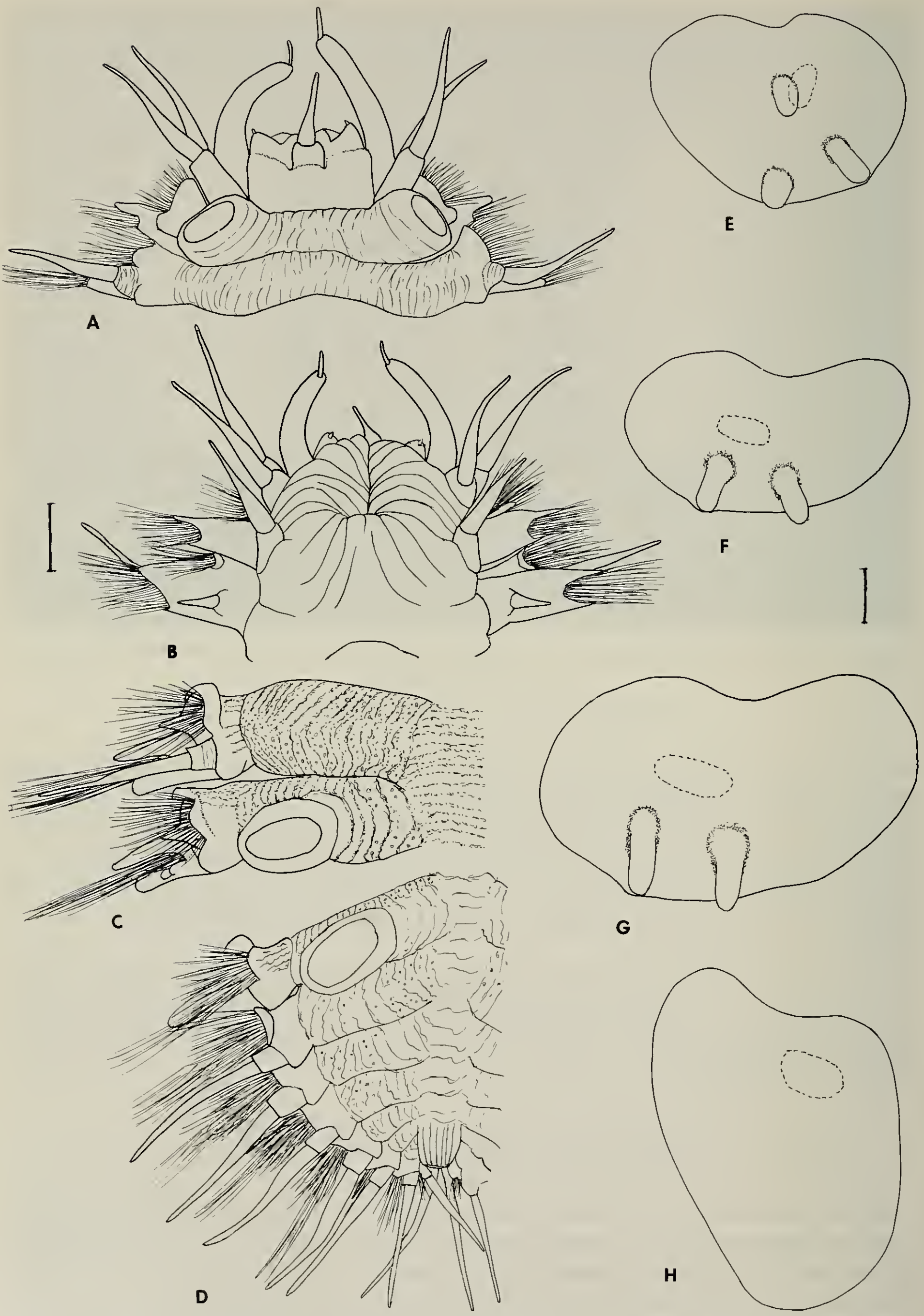


Fig. 2. *Lepidonotopodium fimbriatum*, paratype, USNM 80115: A, Anterior end, dorsal view; B, Anterior end, ventral view; C, Left side of segments 12 (cirrigerous) and 13 (elytrigerous), dorsal view; D, left side of posterior end (segments 21–27 and pygidium), dorsal view; E, Left first elytron, place of attachment dotted; F, Left second elytron; G, Left middle elytron; H, Right eleventh elytron. Scales = 1.0 mm for A–D; 1.0 mm for E–H.

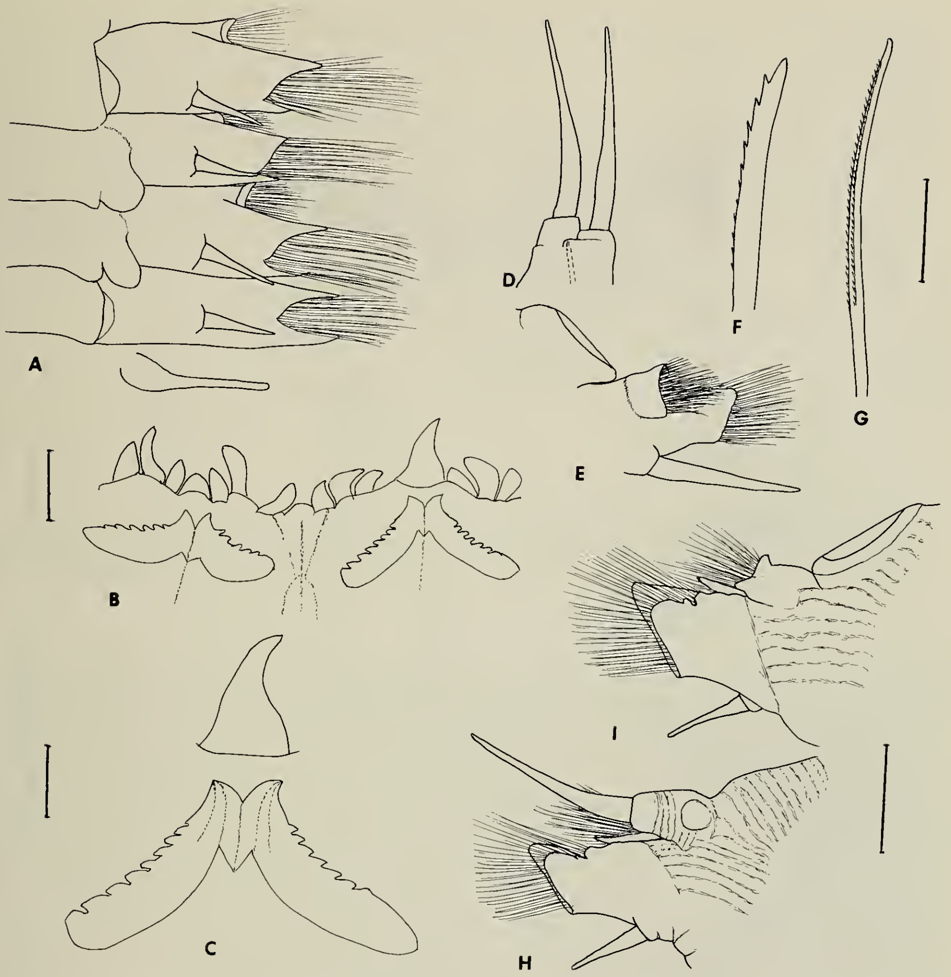


Fig. 3. *Lepidonotopodium fimbriatum,* paratypes, A, USNM 80114; B-I, USNM 80115: A, Left side of segments 10–13, ventral view; distal tip of segmental papilla extending dorsally between parapodia shown separately; B, Distal part of pharynx cut open and spread apart, ventral half on left, dorsal half on right; C, Dorsal jaws and median dorsal papilla; D, Tentacular parapodium, inner view, aciculum dotted; E, Elytrigerous parapodium from segment 2, anterior view; F, Notoseta from same; G, Neuroseta from same; H, Cirrigerous parapodium from segment 3, posterior view; I, Elytrigerous parapodium from segment 4, posterior view. Scales = 1.0 mm for A, B; 0.5 mm for C; 1.0 mm for D, E, H, I; 0.1 mm for F, G.

cated, covering the dorsum (Fig. 1). There are 11 pairs of elytra attached on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19 and 21, with dorsal cirri on the posterior 7 segments (Fig. 2D). Except for the first and last pairs, each elytron has 2 raised smooth macrotubercles on the posterior one-third, not sharply set off from the surface (Figs. 1, 2F, G). The first pair of elytra (on segment 2) have an additional tubercle on the medial side of the place of attachment (Fig. 2E). The last pair of elytra (on segment 21) lack macrotubercles; they are more elongated and cover the posterior cirrigerous segments and pygidium (Fig. 2H). The elytra are reni-

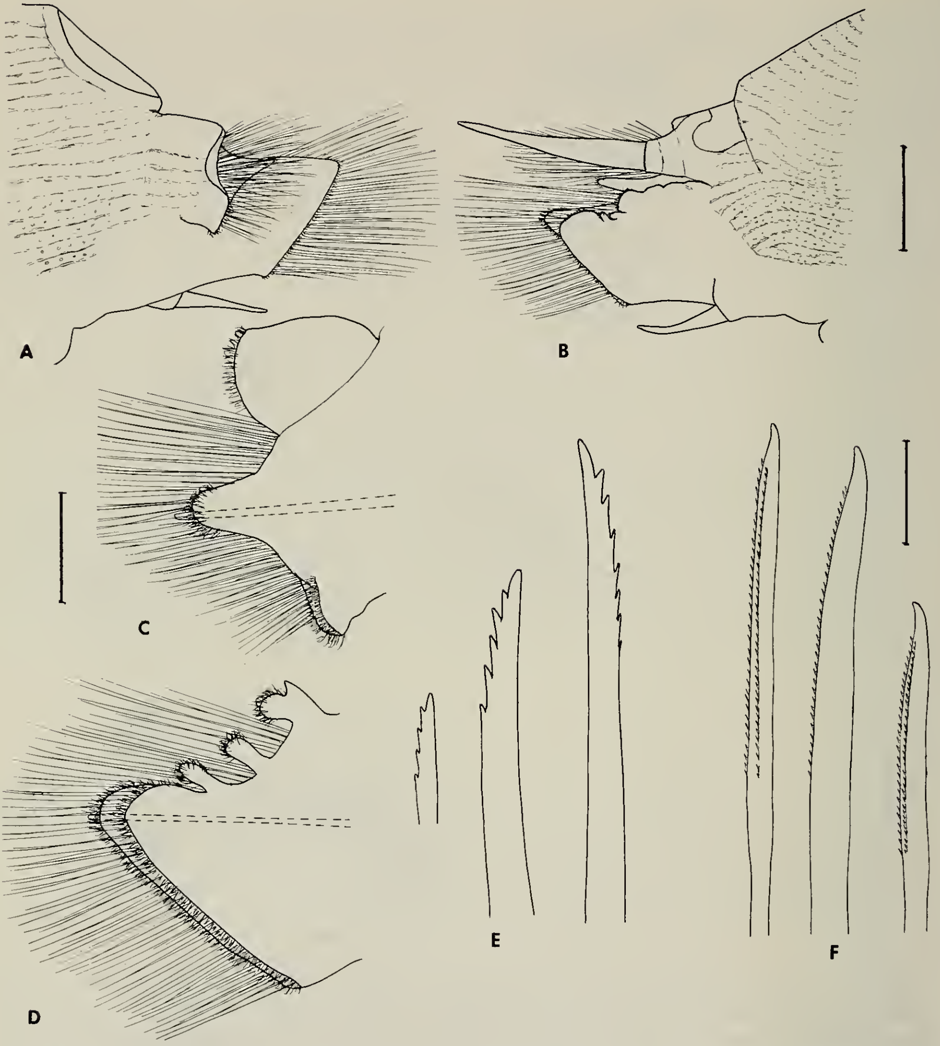


Fig. 4. *Lepidonotopodium fimbriatum*, paratype, USNM 80115: A, Left middle elytrigerous parapodium, anterior view; B, Left middle cirrigerous parapodium, posterior view; C, Enlarged notopodium and bract, posterior view, notoaciculum dotted; D, Enlarged distal part of neuropodium, posterior view, neuroaciculum dotted; E, Notosetae from middle parapodium; F, Upper, middle and lower neurosetae from middle parapodium. Scales = 1.0 mm for A, B; 0.5 mm for C, D; 0.1 mm for E, F.

form, attached eccentrically to large prominent elytrophores (Figs. 2A, C, D, 3I, 4A). The elytral surface appears smooth but is covered with numerous round microtubercles giving a dotted appearance, along with some scattered globular micropapillae. The dorsal cirri on the segments lacking elytra have cylindrical cirrophores attached dorsoposteriorly on the notopodia; they are wider basally with a bulbous lobe on the posterior side; the styles are tapering and extend to about the tips of the neurosetae (Figs. 2A, C, 3H, 4B). The dorsal tubercles on

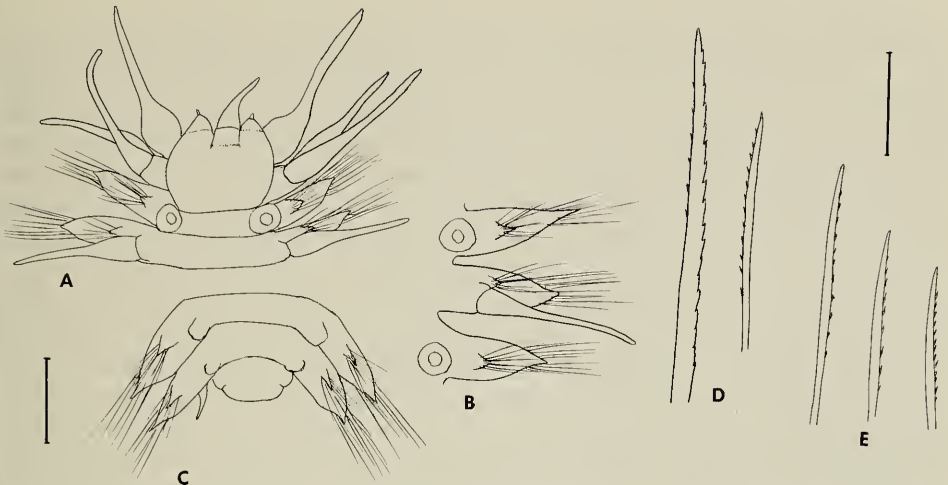


Fig. 5. *Lepidonotopodium fibriatum*, young paratype, USNM 80116: A, Anterior end, dorsal view; B, Right parapodia of segments 5–7, dorsal view; C, Posterior end, dorsal view; D, Notosetae; E, Neurosetae. Scales = 0.2 mm for A–C; 0.1 mm for D, E.

the cirrigerous segments, corresponding in position to the elytrophores, are large and inflated. The surfaces of both the elytrophores and dorsal tubercles, including their bases, have numerous ciliated ridges interspersed with thin integument, sometimes appearing as pits (Figs. 2C, D, 3H, I, 4A, B). The ridges continue on the upper halves of the anterior and posterior sides of the parapodia altogether forming well-developed ciliated lacunar areas. The surface of the middorsum is wrinkled, that of the ventral surface essentially smooth.

The prostomium is bilobed, the anterior lobes subtriangular, each with a small frontal filament; lateral antennae are absent (Fig. 2A, B). The median antenna is inserted in the anterior notch, having a short clyindrical ceratophore and short subulate style. The palps are cylindrical, smooth, with filamentous tips, about twice the length of the prostomium. Eyes are lacking. The first or tentacular segment is not visible dorsally; the tentaculophores are lateral to the prostomium, each with a single aciculum but without a distinct acicular lobe and without setae (Figs. 2A, B, 3D). The styles of the 2 pairs of dorsal and ventral tentacular cirri are similar in length, smooth, tapered, slightly shorter than the palps. A facial tubercle is lacking.

The second or buccal segment bears the first pair of large elytrophores, biramous parapodia and ventral or buccal cirri attached basally on prominent cirrophores lateral to the mouth; their styles are similar to the tentacular cirri and longer than the following ventral cirri (Figs. 2A, B, 3E). The ventral mouth is enclosed in upper, lateral, and posterior lips between segments 1 to 3 (Fig. 2B). The pharynx was not extended but was dissected out and slit open (Fig. 3B, C). The opening of the large muscular pharynx is encircled by 7 pairs of large bulbous papillae: 7 dorsal with the median one larger and 7 ventral with the median one smaller. The 2 pairs of dorsal and ventral jaws are fused medially and the basal parts are serrated with 5–7 teeth.

The biramous parapodia have shorter notopodia located on the anterodorsal sides of the longer neuropodia (Figs. 3H, I, 4A, B). The notopodia are conical, with projecting acicular lobes and enclosed anterodorsally by well-developed large flaring bracts (Figs. 2C, D, 4A–C). The neuropodia are diagonally truncated and deeply cleft on the upper part. The presetal acicular lobe projects dorsally beyond the rounded postsetal lobe; the upper margin of the latter has 3 rounded papillated extensions (Fig. 4B, D). The distal margins of the notopodial acicular lobes, notopodial bracts, and neuropodial lobes are fimbriated with slender papillae. The notosetae are numerous, forming radiating bundles; they vary in length, are similar in width to the neurosetae and have relatively few (4–7; 7–11 on segment 2) widely-spaced spines along one side and blunt rounded tips (Figs. 3F, 4E). The neurosetae are numerous, forming fan-shaped bundles. They are all similar, the upper ones being slightly more slender and the lower ones shorter (more slender on segment 2); they have 2 rows of numerous spines along one side, with slightly hooked bare tips (Figs. 3G, 4F). The ventral cirri are short, tapered, smooth and attached on the middle of the neuropodia (Fig. 3A).

Segmental or nephridial papillae are not obvious. On one of the 3 adult types (USNM 80114), there are 2 pairs of large bulbous papillae on the ventral side of segments 11 and 12, narrowing and projecting dorsally between the parapodia (Fig. 3A). The pygidium is visible dorsally as a bulbous lobe wedged between the parapodia of the 3 posterior smaller segments (26–29), the last one being quite small; there is a pair of long ventral anal cirri, similar to the posterior dorsal cirri (Fig. 2D).

The small paratype (USNM 80116), collected from the same site but on a later dive, is 1 mm long, 1 mm wide including setae, with 11 segments plus a growing zone and pygidium (Fig. 5C). No elytra remain. The prostomium resembles that found in the adults except that the palps are bulbous basally and slender more distally (Fig. 5A). The tentacular and dorsal cirri are also wider basally (Fig. 5A, B). The notosetae have more numerous spines (Fig. 5D); the neurosetae are more slender and have fewer and larger spines (Fig. 5E).

Remarks.—Based on the structure of the prostomium and tentacular segment, *Lepidonotopodium* could be placed in the subfamily Macellicephalinae, as revised by Pettibone (1976), in having the prostomium bilobed with short frontal filaments on the anterior lobes, a median antenna with a distinct ceratophore in the anterior notch, without lateral antennae, with paired palps and two pairs of tentacular cirri lateral to the prostomium. Of the genera in the Macellicephalinae, *Lepidonotopodium* is closest to *Bathykurila* Pettibone, based on the type of notosetae and neurosetae. The shapes of the parapodia differ, however.

Jaws with serrated basal plates, characteristic of the aphroditacean family Acoetidae (=Polyodontidae), are not the usual type in the Polynoidae but they are known for some bathyal species, such as *Bathyvitiazia pallida* (Levenstein) and *Bruunilla natalensis* Hartman in the Macellicephalinae and for *Bathyedithia berkeleyi* (Levenstein) and *B. tuberculata* Levenstein in the Bathyedithinae (Pettibone 1976, 1979; Levenstein 1981).

Lepidonotopodium is unique in the Polynoidae in having well-developed bracts encircling the notopodia. This is known in some other families of the scaled polychaetes or Aphroditacea, such as the Sigalionidae, but not in the Polynoidae.

The numerous ciliated ridges separated by thin integument on the elytrophores, dorsal tubercles and anterior and posterior sides of the parapodia appear to be unique in the Polynoidae. Beneath the surface there appear to be sponge-like areas with ciliated lacunar passages, perhaps serving for respiratory exchange, a feature worthy of future investigation.

The presence of fimbriated parapodia, formed of filiform papillae on the distal margins of the notopodia, notopodial bracts, and neuropodia, are also at least unusual in the Polynoidae. Filiform papillae are found on the distal margins of the neuropodia in some members of the Lepidonotinae, such as *Hermenia* Grube, *Halosydnopsis* Uschakov and Wu, *Parahalosydnopsis* Pettibone, and *Lepidonopsis* Pettibone, as indicated by Pettibone (1975, 1977).

The type of elytra with nodular macrotubercles not sharply set off from the surface, as found in *Lepidonotopodium fimbriatum*, is also unusual in the Polynoidae. Similar structures are found on the elytra of *Bathynoe nodulosa* Ditlevsen (1917:42, pl. 3: fig. 12), collected in the North Atlantic south of Iceland in a depth of 1992 meters, and in *Bathynoe nodulosa pacifica* Uschakov, 1950, from the Okhotsk Sea in a depth of 1366 meters (see Uschakov 1955:134, fig. 24C; 1965: 115, fig. 24C, as *Weberia*). *Lepidonotopodium* and *Bathynoe* (=*Weberia*, preoccupied) differ in a number of other features.

Acknowledgments

My thanks go to the OASIS group of Scripps Institution of Oceanography for the privilege of working up this interesting material. The manuscript benefited from the reviews by my colleagues Dr. Meredith L. Jones and Dr. Kristian Fauchald. Mr. Michael Carpenter kindly photographed the holotype.

Literature Cited

Ditlevsen, Hj. 1917. Annelides I.—The Danish Ingolf-Expedition, Copenhagen 4(4):1–71, 6 pls.

Levenstein, R. J. 1981. [Some peculiarities in the distribution of the polychaetes (Family Polynoidae) in the Canada basin of the Arctic Ocean.]—Transactions of the P. P. Shirshov Institute of Oceanology 115:26–36, figs. 1–4. [In Russian, English summary.]

Pettibone, M. H. 1975. Review of the genus *Hermenia*, with a description of a new species (Polychaeta: Polynoidae: Lepidonotinae).—Proceedings of the Biological Society of Washington 88(22):233–248, figs. 1–5.

———. 1976. Revision of the genus *Macellicephala* McIntosh and the subfamily Macellicephalinae Hartmann-Schröder (Polychaeta: Polynoidae).—Smithsonian Contributions to Zoology 229:1–71, figs. 1–36.

———. 1977. Review of *Halosydnopsis* and related genera (Polychaeta: Polynoidae: Lepidonotinae). *In* Essays on polychaetous annelids in memory of Dr. Olga Hartman, D. J. Reish and K. Fauchald, editors.—Allan Hancock Foundation, University of Southern California, pp. 39–62, figs. 1–6.

———. 1979. Redescription of *Brunnilla natalensis* Hartman (Polychaeta: Polynoidae), originally referred to Fauveliopsidae.—Proceedings of the Biological Society of Washington 92(2):384–388, figs. 1–2.

Uschakov, P. V. 1950. [Polychaete Worms (Polychaeta) from the Okhotsk Sea.]—Issledovaniia Dalnevost Morei SSSR 2:140–234, 39 figs., 2 pls. [In Russian.]

———. 1955. [Polychaeta of the Far Eastern Seas of the U.S.S.R.] *In* Keys to the fauna of the U.S.S.R.—Zoological Institute of the Academy of Sciences of the U.S.S.R. No. 56:1–445, 164 figs. [In Russian; 1965. English translation by Israel Program for Scientific Translations, 419 pp.]

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

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 400–406

MINUSCULISQUAMA HUGHESI, A NEW GENUS AND SPECIES OF SCALE WORM (POLYCHAETA: POLYNOIDAE) FROM EASTERN CANADA

Marian H. Pettibone

Abstract.—A new polynoid polychaete, *Minusculisquama hughesi* n. gen., n. sp., from Northumberland Strait and Nova Scotia is described. The species is remarkable for its elongate and flattened body with only 15 pairs of minute elytra confined to the anterior region. It shows features characteristic of some polynoids found living commensally in the tubes of other polychaetes.

Some polynoids from Eastern Canada were sent to me for identification from two sources. A single specimen from Northumberland Strait, off Prince Edward Island, collected by J. F. Caddy *et al.* in 1975, was sent to me by Mrs. Leslie E. Linkletter of the Biological Station in St. Andrews, New Brunswick. It was collected at station 95 listed by Caddy *et al.* (1977:9). Nine specimens were collected in St. Margaret's Bay, Nova Scotia, by T. G. Hughes in 1976 and sent to me by Mrs. Patricia Pocklington of the Nova Scotia Museum. They were collected at station 1 reported by Hughes (1979:530). The specimens proved to belong to a new genus and species.

The types are deposited in the Biological Station at St. Andrews, New Brunswick (BSNB), the National Museum of Canada, Ottawa (NMC), the Nova Scotia Museum, Halifax (NSM) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Family Polynoidae

Minusculisquama, new genus

Type-species.—*Minusculisquama hughesi*, new species.

Diagnosis.—Body elongate, with numerous segments (about 100). Elytra 15 pairs, minute, on slightly developed elytrophores on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, and 32. Dorsal cirri on non-elytra-bearing segments. Dorsal tubercles indistinct. Prostomium bilobed, with small cephalic peaks, 3 antennae, paired palps and 2 pairs of eyes. Median antenna with distinct ceratophore in anterior notch, lateral antennae with ceratophores inserted ventrally and converging midventrally. Tentaculophores of first or tentacular segment lateral to prostomium, achaetous, with 2 pairs of tentacular cirri; without facial tubercle. Second or buccal segment with first pair of elytra, setigerous parapodia and ventral buccal cirri; without nuchal fold. Parapodia subbiramous, notopodia small, with notoaciculum only, without notosetae (rarely single one present). Neuropodia with rounded anterior acicular and posterior lobes, deeply cut dorsally and ventrally, without projecting acicular lobes. Neurosetae stout, relatively few, with few spines, tapering to slender tips; upper ones stouter, smooth, with blunt tips.

Pygidium with pair of anal cirri. Nephridial papillae small, beginning on segment 6. Pharynx with 9 pairs of papillae and 2 pairs of jaws.

Etymology.—The generic name is derived from the Latin, *minusculus,* small, *squama,* scale, referring to the small scales or elytra. Gender: feminine. The species is named for Dr. Trevor G. Hughes, one of the collectors.

Minusculisquama hughesi, new species
Figs. 1–3

Material examined.—EASTERN CANADA: Northumberland Strait off Prince Edward Island, 46°19′20″N, 62°10′10″W, 34 m, red mud over clay, sta. 95, 23 July 1975, J. F. Caddy *et al.,* collectors—paratype, BSNB 2290. St. Margaret's Bay, Nova Scotia, 44°32′N, 63°59′W, 70 m, silty mud and sand, sta. 1, 28 August 1976, T. G. Hughes, collector—holotype, USNM 72887, 3 paratypes, USNM 72888, 2 paratypes, NSM 976Z351.49 and 3 paratypes, NMC 1982-0885-7.

Measurements.—The holotype from St. Margaret's Bay (USNM 72887) is 98 mm long, 7.5 mm wide, including setae, with 108 segments. The length of 3 paratypes from the same collection (USNM 72888) are 66–89 mm, widths 7–8 mm, with 76–113 segments. The single paratype from Northumberland Strait (BSNB 2290) has a length of 46 mm, a width of 5 mm, including setae, with 58 segments plus a small regenerating posterior end of about 10 segments.

Description.—The body is elongate, flattened, of about equal width along the body, tapering slightly anteriorly and posteriorly, with a rather deep midventral longitudinal groove. The body is dusky dorsally, especially on the posterior half and ventrally along the rather deep midventral longitudinal groove and extending laterally as transverse bands.

There are 15 pairs of minute nipple-like elytra on segments 2, 4, 5, 7, alternate segments to 23, 26, 29 and 32. They are not the usual polynoid type and are easily overlooked (Figs. 1A, C, D, 2B). They are somewhat flattened, disc-like, attached to rather indistinct, slightly bulbous elytrophores. They lack tubercles; some micropapillae are present on the surface (Fig. 2B). Dorsal cirri are present on the rest of the segments (Figs. 1A, C, F, 2A, D, E, 3A, B, D). Dorsal tubercles on the cirrigerous segments are indistinct.

The prostomium is bilobed with small cephalic peaks (Fig. 1A–C). The median antenna has a large ceratophore in the anterior notch, with a style of about the same length as the prostomium, with a tapered tip. The lateral antennae have small ceratophores inserted ventrally and converge midventrally (Fig. 1B); the styles are subulate and about a third as long as the median antenna. The palps are stout, tapered, slightly longer than the median antenna. The 2 pairs of eyes are rather small, the anterior pair in the region of greatest prostomial width is slightly larger than the posterior pair. The tentaculophores of the achaetous first or tentacular segment are lateral to the prostomium, with 2 pairs of tentacular cirri similar to the median antenna; the dorsal tentacular cirri are about equal in length to the median antenna, the ventral ones slightly shorter. There is no facial tubercle. Segment 2 bears the first pair of small elytra, subbiramous parapodia and ventral buccal cirri that are slightly longer than the following ventral cirri (Fig. 1A–D). Notosetae are lacking. The neurosetae are similar to the following

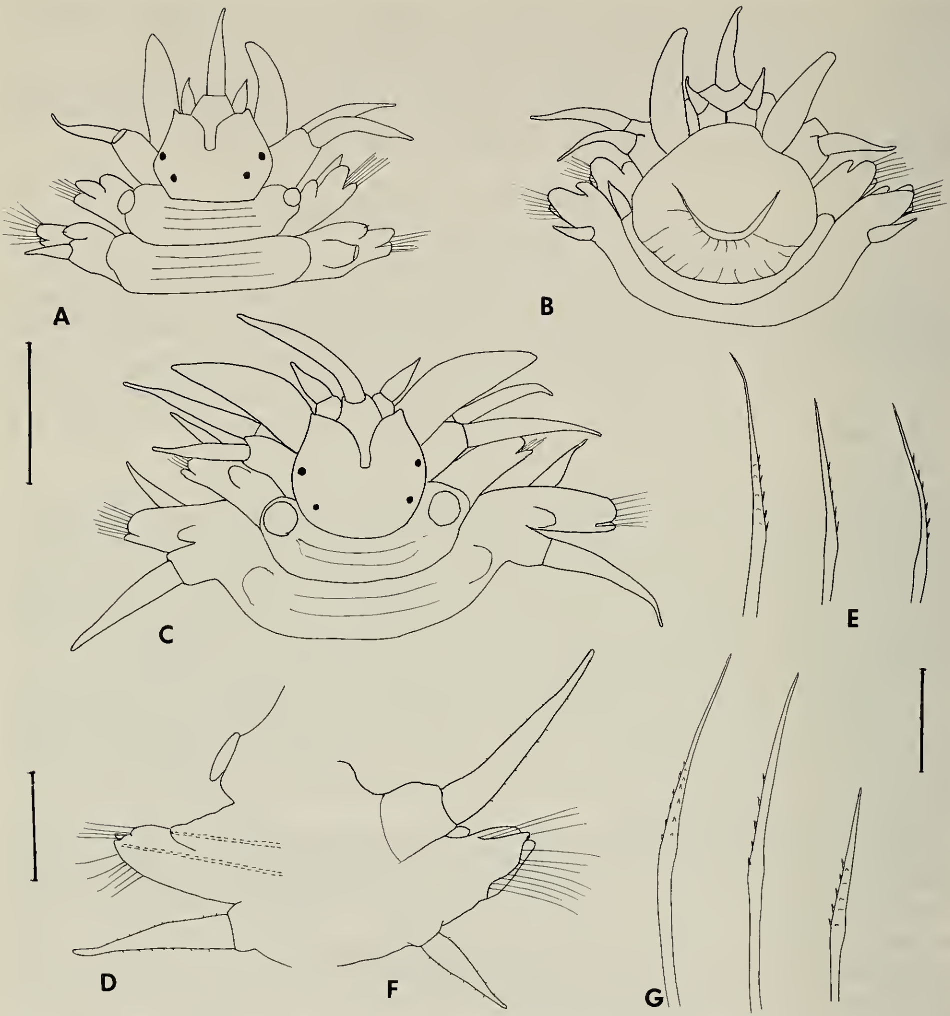


Fig. 1. *Minusculisquama hughesi,* A, B, paratype, BSNB 2290; C–G, holotype, USNM 72887: A, Anterior end, dorsal view, styles of left dorsal tentacular cirrus and right dorsal cirrus from segment 3 missing; B, Anterior end, ventral view, pharynx partially extended; C, Anterior end, dorsal view, left dorsal tentacular cirrus shorter, regenerating; D, Right elytrigerous parapodium from segment 2, anterior view, acicula dotted; E, Upper, middle and lower neurosetae from same; F, Right cirrigerous parapodium from segment 3, posterior view; G, Upper, middle and lower neurosetae from same. Scales: = 1.0 mm for A–C; 0.5 mm for D, F; 0.1 mm for E, G.

ones except that they are more slender (Fig. 1E). The ventral mouth is enclosed in the anterior 3 segments (Fig. 1B).

The parapodia are subbiramous and similar along the length of the long body (Figs. 1A–D, F, 2A, B, D, E, 3A, B, D). The notopodia are small, subconical, located on the anterodorsal bases of the neuropodia, each with a notoaciculum only. Notosetae are lacking. However, a single notoseta was found on segment

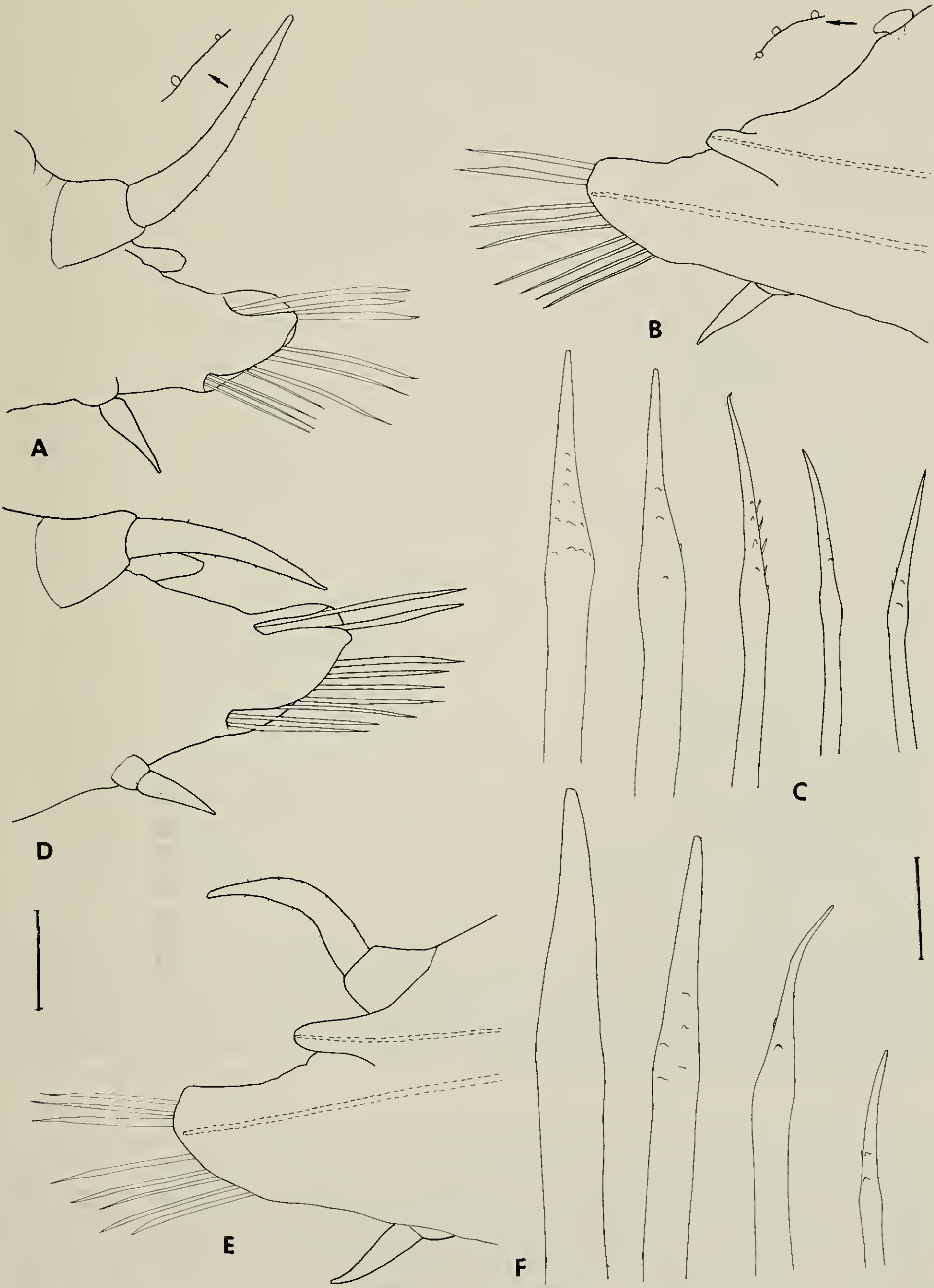


Fig. 2. *Minusculisquama hughesi*, holotype, USNM 72887: A, Right cirrigerous parapodium from segment 12, posterior view, micropapillae shown separately; B, Right elytrigerous parapodium from segment 13, anterior view, elytral micropapillae shown separately, acicula dotted; C, Upper, middle and lower neurosetae from same; D, Right middle parapodium (about segment 64), posterior view; E, Same, anterior view; F, Upper, middle and lower neurosetae from same. Scales: = 0.5 mm for A, B, D, E; 0.1 mm for C, F.

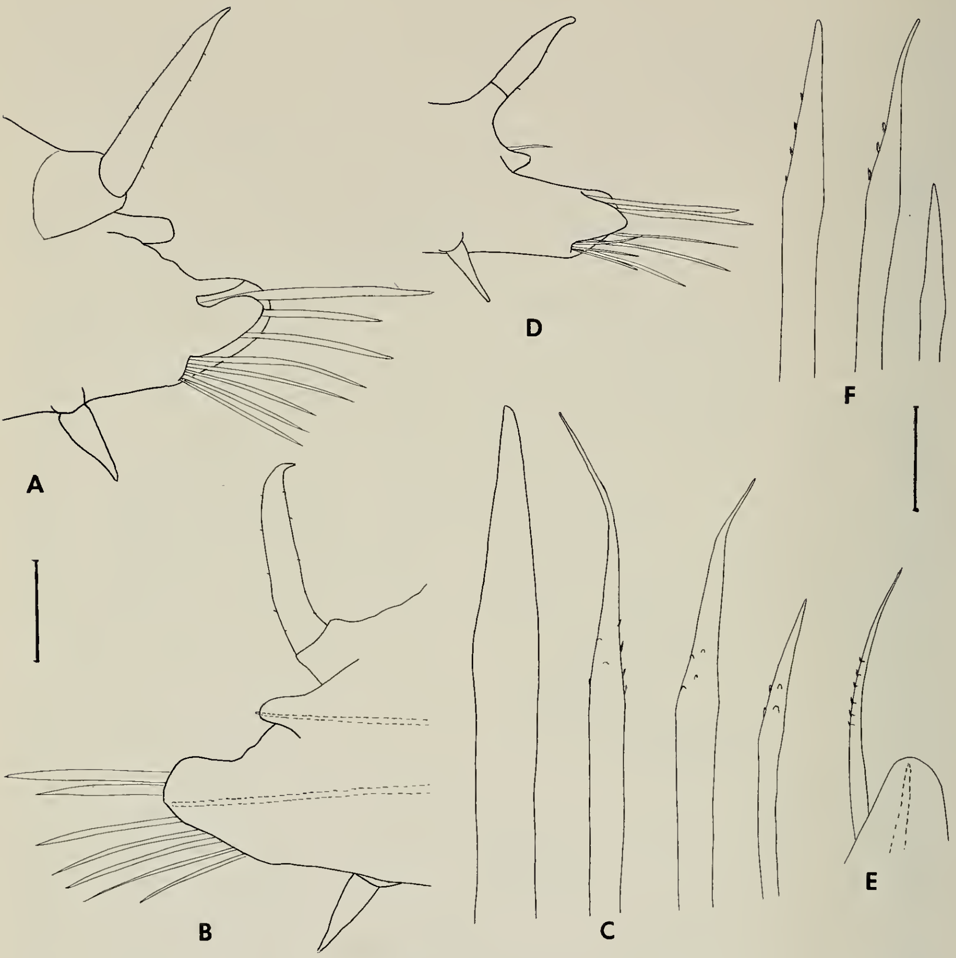


Fig. 3. *Minusculisquama hughesi,* A–C, holotype, USNM 72887; D–F, paratype, USNM 72888; A, Right parapodium from posterior region (about segment 84), posterior view; B, Same, anterior view; C, Upper, middle and lower neurosetae from same; D, Right parapodium from segment 85, posterior view; E, Notoseta and distal tip of notopodium from same; F, Upper, middle and lower neurosetae from same. Scales: = 0.5 mm for A, B, D; 0.1 mm for C, E, F.

85 on one of the paratypes (USNM 72888). It is slender, with 6 spinous rows, and tapers to a slender tip (Fig. 3D, E). The neuropodia are elongate, deeply cut dorsally and ventrally. The presetal acicular lobes are larger, diagonally truncate on the lower half, truncate on the upper half; the postsetal lobes are smaller, subconical and rounded, the upper part straight forming a deep notch with the anterior lobe. The neurosetae are rather stout and relatively few in number (6–13). They are wider subdistally and taper to pointed tips, not hooked (Figs. 1E, G, 2C, F, 3C, F). They are variable in size, the upper ones (1–3) are stouter, darker and smooth, with blunt tips (perhaps worn). The middle and lower neurosetae have a few spines on the wider part (2–4 pairs). The spines may be broken off with only their bases evident. The lower posterior group of neurosetae (4–5)

are shorter and more slender. The dorsal cirri have cylindrical cirrophores attached posterodorsally on the notopodia; the styles are short, tapering and extend to about the tips of the neuropodia or beyond. The styles have scattered micropapillae (Fig. 2A). The ventral cirri, attached on the middle of the neuropodia, are short, thick and subulate, smooth or with scattered micropapillae.

The muscular pharynx has the usual 9 pairs of papillae and 2 pairs of jaws. The nephridial papillae begin on segment 6; they are short, cylindrical, extending posterolaterally. The pygidium is small, rounded, with a pair of anal cirri, longer than the dorsal cirri.

Biology.—*Minusculisquama hughesi* was collected in silty mud and sand in 70 meters in St. Margaret's Bay and in red clay over mud in 34 meters in Northumberland Strait. Although there is no data with the specimens to confirm it, their structure suggests that they were probably living commensally in the tubes of other polychaetes, such as maldanids. In his report on the collections from St. Margaret's Bay, Hughes (1979:531) indicated that "the top 20 cm of sediment were permeated by numerous tubes made by various species of maldanid polychaetes. Some of the tubes protruded above the surface of the sediment." I suggest that the host of *M. hughesi* may very well have been a maldanid. Commensalism is suggested by the following features of *M. hughesi*: the elongate flattened body of about equal width, the small prostomial eyes, the minute elytra confined to the anterior region, the reduced notopodia and missing notosetae, the enlarged upper neurosetae, such as are found in *Lepidametria commensalis*.

Minusculisquama agrees with *Arctonoe* Chamberlin, 1920, and *Adyte* Saint-Joseph, 1899, in that all three have elongated bodies with numerous segments, similar type of prostomia with the lateral antennae having distinct ceratophores inserted terminoventrally, and subbiramous parapodia with the neuropodia deeply cut dorsally and ventrally forming rounded presetal acicular and postsetal lobes. In *Arctonoe*, the elytra are large, more numerous, continuing to the posterior end of the long body, and with a different arrangement; also the neurosetae are strongly hooked, rather than tapered (see Pettibone 1953:56–66). *Minusculisquama* agrees further with *Adyte* in having 15 pairs of elytra confined to the anterior region of the long body and in similar arrangement. In *Adyte*, notosetae are present rather than absent, the elytra are large and attached to prominent elytrophores rather than minute with indistinct elytrophores, and the neurosetae have basal semilunar pockets and the upper neurosetae are not larger, as they are in *Minusculisquama* (see Pettibone 1969:5–8).

Minusculisquama hughesi resembles *Lepidasthenia accolus* Estcourt, 1967, commensal in the burrow of an arenicolid polychaete, in having very small elytra, an elongated body, similar prostomia and neuropodia and in lacking notosetae. In *L. accolus*, the elytra are more numerous and arranged on segments 2, 4, 5, 7, continuing on alternate segments to the end of the long body; the presetal acicular lobes of the neuropodia are notched distally and the dorsum is finely papillated (see Estcourt 1967:68–69).

Acknowledgments

My thanks go to Leslie E. Linkletter of the Biological Station in St. Andrews and Patricia Pocklington of the Nova Scotia Museum for sending me the polynoid specimens, as well as furnishing data regarding their collection. My colleagues, Meredith L. Jones and Kristian Fauchald, kindly reviewed the manuscript.

Literature Cited

Caddy, J. F., T. Amaratunga, M. J. Dadswell, T. Edelstein, L. E. Linkletter, B. R. McMullin, A. B. Stasko, and H. W. van de Poll. 1977. 1975 Northumberland Strait Project, Part I: Benthic fauna, flora, demersal fish and sedimentary data.—Fisheries and Marine Service Manuscript Report 1431, The Biological Station, St. Andrews, New Brunswick, pp. 1–46.

Estcourt, I. N. 1967. Burrowing polychaete worms from a New Zealand estuary.—Transactions of the Royal Society of New Zealand 9:65–78, 10 figs.

Hughes, T. G. 1979. Studies on the sediment of St. Margaret's Bay, Nova Scotia.—Journal of the Fisheries Research Board of Canada 36:529–536.

Pettibone, M. H. 1953. Some scale-bearing polychaetes of Puget Sound and adjacent waters.—University of Washington Press, Seattle, 89 pp., 40 pls.

———. 1969. Review of some species referred to *Scalisetosus* McIntosh (Polychaeta, Polynoidae).—Proceedings of the Biological Society of Washington 82:1–30, 12 figs.

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

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 407–410

ARCTODRILUS WULIKENSIS, NEW GENUS, NEW SPECIES (OLIGOCHAETA: TUBIFICIDAE) FROM ALASKA

Ralph O. Brinkhurst and R. Deedee Kathman

Abstract.—*Arctodrilus* is a new tubificine tubificid genus with hair and pectinate setae but no genital setae, male ducts with vasa deferentia about as long as the atria and penes plus ejaculatory ducts, and atria spindle-shaped with median prostates. The type (and only) species *A. wulikensis* from the Wulik River system in Alaska has all the postclitellar setae with long upper teeth. In the bifid anterior ventrals and in the pectinate dorsals the teeth are more nearly equal; the hair and pectinate setae occur from II to XIV. *Psammoryctides hadzii* Karaman has male ducts like those of *Arctodrilus* (which are very general in form) but it does have spermathecal setae. While it is not (as described) a typical member of *Psammoryctides, P. hadzii* is left *incertae sedis* in that genus pending a revision of the species based on examination of the type-material.

During an environmental investigation into natural mineral seepages into the Wulik River system headwaters, a new tubificine tubificid was discovered that cannot be attributed to any known genus. The species was only found at locations not affected by the seepages.

Arctodrilus, new genus

Definition.—Tubificine tubificid with male ducts having vas deferens little longer than atrium and ejaculatory duct combined, entering atrium apically, atrium spindle-shaped with median prostate, ejaculatory duct 1.5 times the length of the atrium, of one width and histological composition throughout. Penis present, with thin cuticular sheath no thicker than cuticularized penis sac wall. No modified genital setae. Hair and pectinate setae present in at least some species.

Type-species.—*Arctodrilus wulikensis*, new species, by monotypy.

Etymology.—Found in Alaska north of the Arctic circle.

Discussion.—The male ducts of the single new species are simple unspecialized structures. The most similar male ducts are those of *Limnodrilus* Claparède and *Spirosperma* Eisen species (*sensu* Brinkhurst 1981) but there are no other similarities, and the body wall, setae, prostomium, spermathecae and penes differ from those of both genera. The genus *Tubifex* Lamarck lacks ejaculatory ducts, and while some species currently included within the genus have the vas deferens entering the atrium apically and unassociated with the prostate stalk (see *T. superiorensis* (Brinkhurst and Cook) *sensu* Brinkhurst 1981), the type and other characteristic *Tubifex sensu strictu* species have the vas deferens and prostate stalk close together under the curved head of a broad, comma-shaped atrium. All species in the genus *Isochaetides* Hrabě emm. Brinkhurst 1981, have very long vasa deferentia, and lack hair and pectinate setae, but most have modified genital setae.

While it seems surprising at first glance that an animal with such a simple male duct cannot be attributed to an existing genus, this new species cannot even be attributed to the genus *Tubifex sensu latu*, and to do so would simply defer the decision that is taken here.

Distribution.—Alaska, Wulik River watershed, DeLong Mountains above Kivalina (see species description).

Arctodrilus wulikensis, new species
Fig. 1

Description.—Up to 43 segments, length 8.0 mm, width 0.2 mm. Dorsal setae anteriorly 2–4 or even 5 long serrate hairs, with serrations probably on one side; thin and as long as body width; 2–4 or 5 pectinate setae which, under lower power magnification, appear to have long, thin outer teeth and thin intermediate teeth arranged in a broad, semi-palmate form but which appear more typically pectinate under oil immersion lens (Fig. 1). Hair setae and pectinate setae absent beyond XIV, where they are replaced by 2–3 bifid setae resembling the ventral setae. Ventral anterior setae 3–5 per bundle, bifid with upper teeth thinner than but only a little longer than the lower, behind XIV with upper tooth thinner but twice as long as the lower; no modified genital setae. Reproductive system as for the Tubificinae, with all organs paired. Spermatheca with short stout duct, voluminous and thin-walled ampulla and lateral pore. Spermatozeugmata present, broad. Male duct with thin vas deferens which widens distally but narrows immediately prior to insertion at apex of atrium; atrium tubular, widest just above the midpoint where a substantial stalked prostate enters. A substantial ejaculatory duct connects the atrium with the penis sac; the penis sac is ovoid-oblong with cuticular walls, the contained penis is of similar shape and has a thin cuticular sheath no thicker than the cuticle on the penis sac wall. The penis sac may be eversible, but there is a true penis within the sac (Fig. 1).

Type-locality.—Red Dog Creek and Ikalukrok Creek, part of Wulik River system, DeLong Mountains, Brooks Range, Alaska (68°05′N, 162°45′W), in areas not affected by seepages containing large amounts of zinc, cadmium, iron, or manganese. July–August 1982.

Etymology.—From the Wulik River drainage.

Holotype.—USNM 80444, a dissected whole mount in Canada Balsam.

Paratypes.—USNM 80445–80453, 7 whole mounts and 70 specimens in fluid. Brinkhurst collection 5 whole mounts, Kathman collection 2 whole mounts.

Discussion.—As with the generic diagnosis, there is little of a specialized nature to comment upon in the species description. The setation is somewhat unusual in that the upper teeth of the dorsal and ventral postclitellar setae are longer than the lower teeth, whereas the opposite trend is more usual. A similar tendency to elongation of the upper tooth posteriad is seen in the naidid genus *Amphichaeta* Tauber, but in the new taxon considered here the change from one form to the other is abrupt and coincides with the loss of hair and pectinate setae dorsally. The tendency to loss of hair and pectinate setae posteriad is common in tubificids but is usually progressive, with replacement of pectinates by bifids of essentially similar shape occurring before shortening and reduction in number or total loss of hair setae.

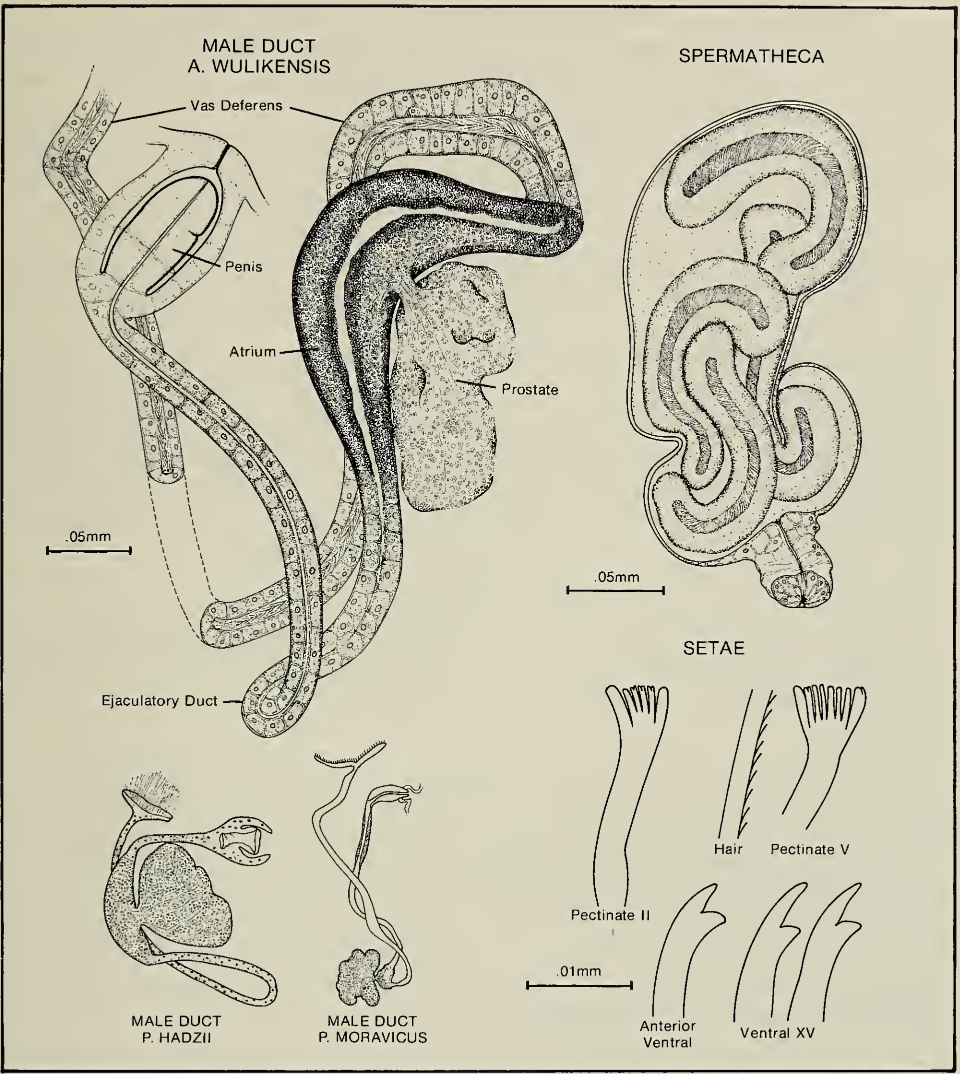


Fig. 1. *A. wulikensis,* reproductive structures and setae, from holotype and paratype respectively; *Psammoryctides hadzii* and *P. moravicus,* male ducts, redrawn from literature in comparable position.

We are aware of only one other species with male ducts that are supposed to resemble those of *A. wulikensis* to some extent, and that is *Psammoryctides hadzii,* described by Karaman (1974). According to the illustration (Fig. 1), that species cannot be attributed to *Psammoryctides* as there is no enlargement of the ejaculatory duct and the atrium is not the usual small globular body, both essential characteristics of that genus. *Psammoryctides hadzii* is discussed by its author in relation to *P. ochridanus* (Hrabě), although that species has male ducts and spermathecal setae of the form typical of the genus and *P. hadzii* has only the latter. Similar spermathecal setae are found in other genera, however, so this character by itself is not diagnostic. There remains the very unlikely possibility that the male ducts of *Psammoryctides* species resemble those of *Arctodrilus* prior to full maturation or during the early stages of post copulatory resorption. Specimens of *A. wulikensis* had sperm in the spermathecae, and while the male ducts are of a delicate construction, they do appear to be fully formed. No mention of spermatozeugmata appears in the description of *P. hadzii* and so the degree of maturation of these worms from an underground river in Jugoslavia is unknown. We conclude that no useful purpose would be served by placing *P. hadzii* in *Arctodrilus* until the latter is better known, especially as the former does possess genital setae, and the zoogeographic evidence supports that decision. *Psammoryctides hadzii* should remain a species *incertae sedis* of *Psammoryctides.*

Five specimens of *A. wulikensis* were collected in early July, 12 were found in late July, and 68 were obtained in late August, in both Red Dog and Ikalukrok creeks. The lumbriculid *Rhynchelmis brooksi* Holmquist and unidentified Enchytraeidae were also collected with our specimens. All were found in cold, fast riffle areas characterized by cobble/pebble/gravel substrate. Other dominant macrofauna included Ephemeroptera, Plecoptera, Simuliidae, and Chironomidae.

Acknowledgments

The authors are indebted to E.V.S. Consultants Limited and to the Alaska Department of Environmental Conservation for access to this material and permission to publish a description of it. The illustration was prepared by Ian McSorley.

Literature Cited

Brinkhurst, R. O. 1981. A contribution to the taxonomy of the Tubificinae.—Proceedings of the Biological Society of Washington 94:1048–1067.

Karaman, S. 1974. Beitrag zur Kenntnis der Süsswasseroligochaeten Sloweniens.—Bioloski vestnik Ljubljana 22:223–228.

Institute of Ocean Sciences, P. O. Box 6000, 9860 West Saanich Road, Sidney, British Columbia V8L 4B2, Canada.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 411–419

A CONTRIBUTION TO THE TAXONOMY OF THE ENCHYTRAEIDAE (OLIGOCHAETA). REVIEW OF *STEPHENSONIELLA,* WITH NEW SPECIES RECORDS

Kathryn A. Coates

Abstract.—The marine enchytraeid genus *Stephensoniella* Cernosvitov, 1934, (Oligochaeta: Annelida) is revised. Type-materials of four nominate species, *S. marina* (Moore, 1902), *S. barkudensis* (Stephenson, 1915), *Lumbricillus sterreri* Lasserre and Erséus, 1976, and *Marionina trevori* Coates, 1980, were examined. *Stephensoniella barkudensis* possesses a spermatheca with the same diverticulate ampullar structure as, and is a junior synonym of, *S. marina,* the type-species of the genus. *Lumbricillus sterreri* and *Marionina trevori* are transferred to *Stephensoniella* because they possess large, paired, unlobed seminal vesicles; nephridia with only the funnels in front of the septa; diverticulate spermathecal ampullae; thickened septa anteriorly; and only two or three setae in each setal bundle. *Stephensoniella* is structurally close to *Marionina* and *Lumbricillus*; however, a conservative evaluation of nephridial, spermathecal, and seminal vesicular characteristics distinguishes the species of each.

Stephensoniella was erected by Cernosvitov (1934) based on a redescription of the type-species, *Enchytraeus marinus* Moore, 1902. New material was collected from the type-locality, Gilson Hil Tip, Coney Sol, Bermuda, at the time of the redescription because the original material had been lost. Cernosvitov (1934) also transferred *Enchytraeus barkudensis* Stephenson, 1915 to *Stephensoniella* and these have remained the only recognized species. The major generic characters used by Cernosvitov (1934) to separate *Stephensoniella* from the closely related *Lumbricillus* and *Marionina* were the unlobed form of the seminal vesicles, the shape and distribution of the setae, and the diverticulate form of the spermathecal ampulla; and from *Enchytraeus,* the absence of peptonephridia and compact form of the penial bulb.

Nielsen and Christensen (1959) indicated that both species of *Stephensoniella* could be referred to *Marionina* but their unfamiliarity with the species caused them to refrain. They did point out, however, that *Marionina* is very heterogeneous, including several groups of species with only remote relations among them. Lasserre and Erséus (1976) echoed the view of Cernosvitov regarding the affinities of *Stephensoniella* and, although they could not clarify the genus definition, preferred to conserve it intact.

The examination of specimens of *S. marina* collected and identified by C. Erséus and the comparison of these with specimens of *Marionina trevori* Coates, 1980, revealed numerous structural similarities. Structural characteristics of *Lumbricillus sterreri* Lasserre and Erséus, 1976, brought to my attention by C. Erséus, led to the reexamination of that species and to the subsequent transferral of both these species to *Stephensoniella.*

I have attempted in the following systematic section to establish a homogeneous species grouping and to clarify those characteristics that distinguish *Stephensoniella.* All the described species that could be determined undoubtedly to belong in *Stephensoniella* have been included.

Materials

Type and additional material of the four species *Stephensoniella marina, S. barkudensis, Marionina trevori,* and *Lumbricillus sterreri* were borrowed from the British Museum (Natural History) (BMNH); the National Museum of Natural Sciences, Canada (NMCIC); the Muséum National d'Histoire Naturelle, Paris, France (AH); Smithsonian Institution, National Museum of Natural History (USNM); the personal collection of C. Erséus, Sweden (CE); and from EVS Consultants Ltd., Sidney, British Columbia (EVS). New, unmounted material was stained in alcoholic borax carmine, dehydrated through an ethanol to xylene series and mounted whole in Canada balsam.

Stephensoniella Cernosvitov, 1934 (emended)

Type-species.—*Enchytraeus marinus* Moore, 1902.

Definition.—Brackish and littoral marine enchytraeids. Setae in 4 bundles from II; 2 or 3 setae per bundle in preclitellar segments, 2 (infrequently 3) in intra- and postclitellar segments; single-pointed, straight or slightly sigmoid, bent proximally. Head pore just anterior to 0/1, other dorsal, coelomic pores absent. Oesophageal-intestinal transition gradual, intra- or postclitellar. Peptonephridia, oesophageal and intestinal diverticula lacking, but with solid, paired, dorsal, postpharyngeal bulbs. Pharyngeal glands well-developed, broadly united at 3/4, 4/5, and 5/6. Dorsal blood vessel origin intra- or postclitellar; dorsal vessel bifurcating anterior to brain, in prostomium. Lymphocytes nucleate. Chloragocytes present from preclitellar segments. Preseptal part of nephridia includes funnel only; interstitial tissue around postseptal nephridial canal well-developed; ectal duct terminal, ventral. Muscle layers of some of septa 6/7 to 9/10 thickened. Ovaries, testes and associated ducts and pores all paired, in typical familial positions. Seminal vesicles paired, unlobed. Sperm funnels (glandular vasa deferentia) well-developed; non-glandular vasa deferentia contained in XII, surrounded medially at ectal pores by compact penial bulbs, accessory prostatic glands absent. No ventral copulatory glands. Spermathecae paired in V, always attached to, if not actually communicating with, oesophagus via short ental ducts. Each ampulla with a rounded or ovoid diverticulum. Spermathecal ectal duct with or without glands.

Habitat and distribution.—Coastal marine, usually tropical or subtropical. Caribbean Sea; Atlantic Ocean—Bermuda, Florida, and Brazil; Indian Ocean—Barkuda Island, India; Persian Gulf—Saudi Arabia; northeast Pacific Ocean—British Columbia.

Remarks.—The primary distinguishing characteristics of the genus are the distribution of almost straight setae in bundles of only two or three; the thickened, muscular, preclitellar septa and well developed pharyngeal glands; the paired, unlobed seminal vesicles; and the single, rounded diverticulum found on each spermathecal ampulla. Rudimentary peptonephridia (see Stephenson 1915a), also referred to in the literature as solid postpharyngeal bulbs and dorsolateral pharyngeal appendages, have been reported in species of *Marionina* (Kossmagk-Stephan 1983) and *Fridericia, Mesenchytraeus, Lumbricillus, Bryodrilus, Buchholzia,* and *Henlea* (Stephenson 1930) and are therefore not a good distinguishing characteristic.

Cernosvitov (1934) discussed the significance to the generic definition of *Stephensoniella* of the two-layered longitudinal epidermal musculature that he observed in *S. marina.* Stephenson (1930) had previously remarked that a two-layered longitudinal musculature occurred frequently in *Enchytraeus* and *Fridericia.* Later, Cernosvitov (1937) pointed out that two types of longitudinal muscle fibres (round and ribbon-like) were found in some species of *Achaeta, Guaranidrilus, Hemienchytraeus,* and *Fridericia.* These genera were not considered to be phylogenetically close and were placed (Cernosvitov 1937) in three different subfamilies. With only a limited amount of information about this musculature character and knowledge that the same arrangement occurs in phylogenetically dissimilar groups it is not possible to ascertain the taxonomic significance of the characteristic.

The species of *Stephensoniella* can be distinguished from each other by their different absolute sizes and by the distribution of gland cells around the spermathecal ectal ducts.

Stephensoniella marina (Moore, 1902) (emended)

Figs. 1–3

Enchytraeus marinus Moore, 1902:80–82.

Stephensoniella marina (Moore).—Cernosvitov, 1934:233–237, 242–243; Cernosvitov, 1935:8.

Stephensionella marina (Moore).—Lasserre and Erséus, 1976:455.

Enchytraeus barkudensis Stephenson, 1915b:142.—Stephenson 1915a:45–47; 1923: 113–114.

Stephensoniella barkudensis (Stephenson)—Cernosvitov, 1934:242–243.

Stephensoniella barcudensis (Stephenson)—Cernosvitov, 1937:291.

Material examined.—BMNH 1949.3.1.1010, whole mount (originally labelled by Cernosvitov as *Enchytraeus neotropicus* n. sp. [a name which was never subsequently published], Mus. Paris #3764), BMNH 1949.3.1.1011, 3 slides of a transversely sectioned specimen, one slide of a longitudinally sectioned specimen, French Guyana (see Cernosvitov 1935); BMNH 1949.3.1.1012–1014, 4 whole mounts, 3 slides, immature, BMNH 1949.3.1.1015, 3 slides of a longitudinally sectioned specimen, collected by J. A. G. Wheeler, Gilson Hil Tip, Coney Sol, Bermudas, 8 Feb 1933 (see Cernosvitov 1934); CE 22H, 2 whole mounts, partially mature, collected by P. Lasserre, Coney Island, Bermuda, 1973 (see Lasserre and Erséus 1976); CE M77-1, one slide of a longitudinally sectioned specimen, CE M77-2, one whole mount and 2 mounted, partly dissected specimens, 2 slides, collected by C. Erséus, Virginia Key, Florida, 15 Nov 1977; and EVS, 17 whole mounted specimens, collected by Saudi Arabian Tetra Tech Inc., Persian Gulf, Saudi Arabia, 1981–1982.

As *S. barkudensis:* BMNH 1933.5.25.348, one slide of a longitudinally sectioned specimen, and BMNH 1933.5.25.351, one slide of a lontidudinally sec-

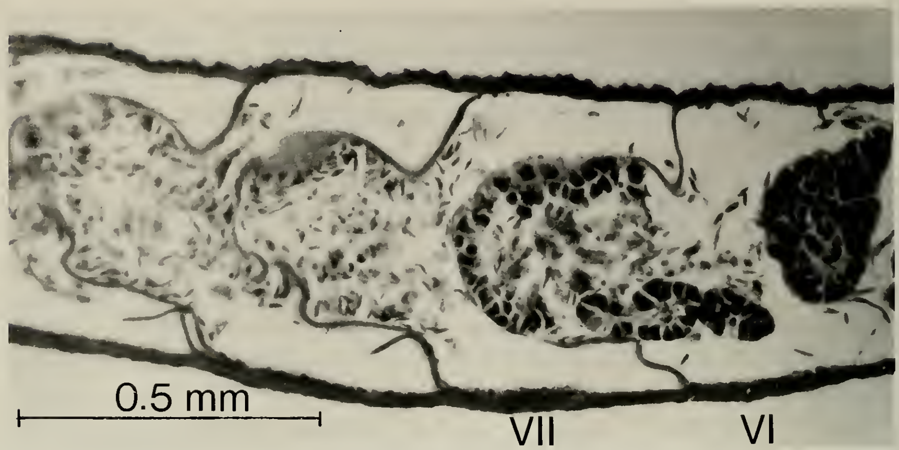


Fig. 1. *Stephensoniella marina*, section through anterior segments showing posteriorly distended, thickened septa 6/7, 7/8 and 8/9 (from *Enchytraeus barkudensis*, BMNH 1933.5.25.348).

tioned specimen, syntypes, Chilka Lake, Barkuda Island, India, collected 1914 (see Stephenson 1915b); BMNH 1933.5.25.355–357, 3 slides, 2 longitudinally sectioned specimens, Ennur, Madras, India (see Stephenson 1915a).

Description.—Length 6 to 10 mm, 46 to 73 segments; diameter to 0.5 mm. Cutaneous glands in 3 or 4 transverse rows per segment. Clitellum over XII and XIII, glands in numerous, regular transverse rows. Setae straight, 33, 50 to 120, usually 80 to 90 μm long; setae of II markedly short, 50 to 60 μm; lateral setae shorter than ventrals of same segment. Two or 3 setae in anterolateral bundles, 3 setae in ventral bundles to X or XI, 2 (occasionally 3) setae in postclitellar segments. Septa (rarely 6/7) 7/8 to 9/10 thickened (Fig. 1). Lymphocytes abundant anteriorly, 20 to 30 μm long. Dorsal blood vessel origin postclitellar, to XXIII. Postclitellar segments with intra-segmental muscular bands extending from the circular epidermal muscles to muscles of gut. Seminal vesicles extending to 9/10; eggs confined to clitellar segments. Sperm funnels 2 to 3 times as long as wide, length just less than body width; glands differentially developed around ciliated duct; collar 2 or more times as wide as glandular part. Vas deferens 14 to 24 μm wide, non-muscular. Penial bulbs (Fig. 2A) 53 to 68 μm high, medial to vasa deferentia. Male pore simple. Spermathecal pores at 4/5, just ventral to level of lateral setae. Ectal ducts of spermathecae 14 to 26 μm wide, 3 to 4 times as long as wide; aglandular; communicating basally with ampulla at constriction between ampulla and thinner walled, dorsally directed diverticulum. Ampulla approximately 50 μm wide × 80 μm long, diverticulum approximately 30 μm wide × 80 μm long, more or less ovoid (Fig. 2B–D). Ampullae connecting laterally to oesophagus in posterior of V. Sperm densely bundled in diverticula, in random masses in ampullae.

Habitat.—Estuarine salt lakes and littoral and supralittoral marine, usually in medium coarse sands. With *Pontodrilus bermudensis,* in India (Stephenson 1915b).

Distribution.—Barkuda Island, India; French Guyana; Florida, U.S.A.; Bermuda; Persian Gulf, Saudi Arabia.

Remarks.—Examination of syntypes of *S. barkudensis,* BMNH 1933.5.25.348 and .351, and other specimens from Ennur, Madras, and Cernosvitov's material of *S. marina* revealed a few misinterpretations in, and omissions from, the literature. It was found that the spermathecal ampullae of *S. barkudensis* (Fig. 2D) each bore a basal, ovoid diverticulum as in *S. marina* (Fig. 2B, C). It is recorded at the British Museum (personal communication, E. G. Easton) that their material of *S. barkudensis* originated from the Indian Museum; it was simply labelled "types" when received and it is doubtful that a designated holotype remains in the Indian Museum.

Other than a broad geographical separation, partially bridged by the new records from the Persian Gulf, reasons supporting a classificatory distinction of *S. barkudensis* from *S. marina* are not found (Fig. 3). By seniority, *S. marina* (Moore, 1902) has precedence for the specific name; by original designation (Cernosvitov 1934), it is the type-species of the genus.

Stephensoniella sterreri (Lasserre and Erséus, 1976), new combination
Fig. 3

Lumbricillus sterreri Lasserre and Erséus, 1976:453–454 (partim).

Material examined.—Holotype: AH 193, a whole mount, Ireland Island, Bermuda, collected by P. Lasserre, 1973. Paratypes: AH 195, 196, 2 whole mounts, Coot Pond, Bermuda, collected by P. Lasserre, 1973.

Description.—Holotype with 47 segments, paratypes with 41 and 39 segments. Setae 3 per bundle in at least some preclitellar ventral bundles, 2 in other bundles, slightly sigmoid, 50 to 60 μm long. Clitellum incomplete ventromedially, between male pores. Some of septa 7/8 to 9/10 thickened. Vasa deferentia approximately 13 μm wide, opening ectally via simple pore, lateral to small penial bulb. Seminal vesicles and testes unlobed. Spermathecal ectal duct relatively short, 33 to 43 μm long, bulbous near middle, 17 to 26 μm wide. Glandular cells originating along length of duct, rosette of larger glands originating around ectal pore (Fig. 3). Spermathecal ampulla ovoid, approximately 51 to 61 μm wide and 86 to 91 μm long, approximately 1.5 times as long as wide. Subapical diverticulum nearly globular, 51 to 54 μm in diameter.

Remarks.—Characteristics not given in the description are as originally described (Lasserre and Erséus 1976) or as for the genus. The primary characteristics distinguishing *S. sterreri* from the type species (Fig. 3) are its small size and its spermathecal structure including the position of the origin of the diverticulum, relative shapes and sizes of the ampulla and diverticulum, and the presence of glandular cells on the ectal duct. Three setae may be present in very few anteroventral setal bundles, as in paratype AH 196 with three setae only in X and XI.

The Muséum National d'Histoire Naturelle in Paris had no deposition records for paratype AH 197 (J. Renaud-Mornant, personal communication) (see Lasserre and Erséus 1976). Paratype AH 194 has been referred to *S. trevori* (see page 416).

Habitat.—Mid-littoral in medium or coarse sands rich with organic debris.

Distribution.—Bermuda.

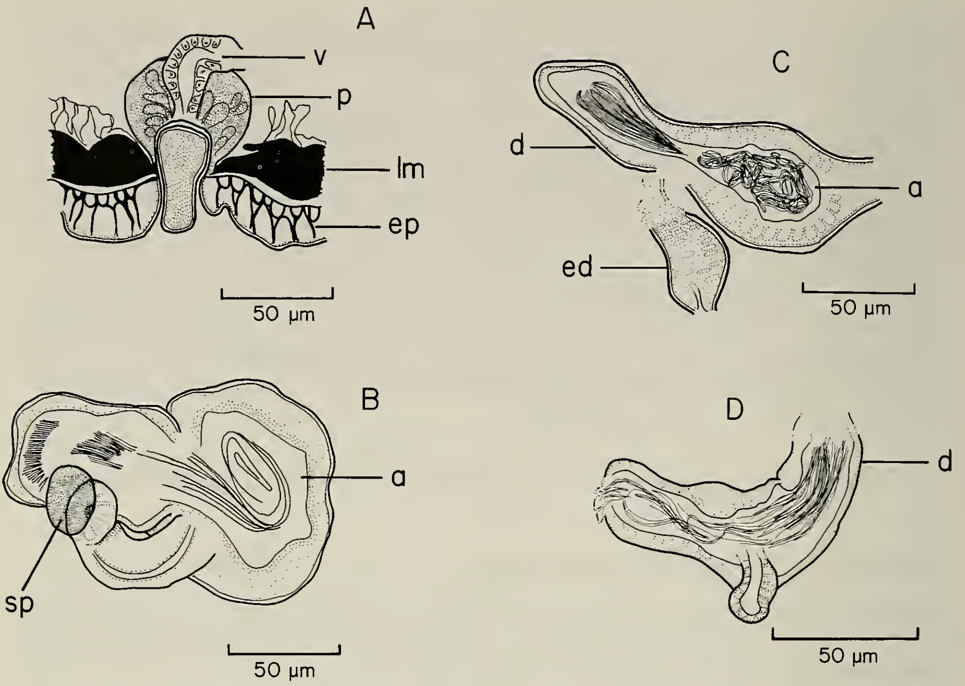


Fig. 2. *Stephensoniella marina*. A, Longitudinal section of glandular penial bulb (p) in XII, vas deferens (v) opens into a narrow epidermal invagination (from CE M77-1, Virginia Key, Florida); B, Lateral view of spermatheca in V, foreshortened, whole mounted specimen (from CE M77-2, Virginia Key, Florida); C, Sectioned spermatheca in V (from CE M77-1); D, Sectioned spermatheca showing distinct ampulla and diverticulum, with ectal duct communicating with the ampulla at the origin of the diverticulum (from *Enchytraeus barkudensis*, BMNH 1933.5.25.356, Madras, India). Other abbreviations: a, spermathecal ampulla; d, ampullar diverticulum, extending dorsad; ed, ectal duct; ep, circular muscle (black) and epithelial cell layer covered by cuticle; lm, longitudinal muscle; sp, ectal spermathecal pore.

Stephensoniella trevori (Coates, 1980), new combination
Fig. 3

Marionina trevori Coates, 1980:1311–1313.—Coates and Ellis, 1981:2137.
Lumbricillus sterreri Lasserre and Erséus, 1976:453–454 (partim).

Material examined.—Holotype: NMCIC 1979-1599, whole mount, Qualicum Beach, British Columbia, Canada, collected by K.A. Coates, 10 June 1976. Paratypes: NMCIC 1979-1600; and USNM 58913, whole mounts, Qualicum Beach, British Columbia, Canada, collected by K. A. Coates, 10 June 1976. Other material: AH 194, a paratype of *Lumbricillus sterreri,* whole mount, Shelly Bay, Bermuda, collected by P. Lasserre, 1973; CE, 10 whole mounted specimens, just north of Cabo Frio, coast of Brazil, collected by J. Renaud-Mornant, 15 Oct. 1976; and EVS, 56 whole mounted specimens, Persian Gulf, Saudi Arabia, collected by Saudi Arabian Tetra Tech Inc., 1981–1982.

Description.—Setae slightly sigmoid, to 74 μm long; infrequently with 3 setae in postclitellar bundles. Clitellum incomplete medioventrally between male pores. Septa 8/9 and 9/10 thickened. Seminal vesicle extending as far anteriad as pos-

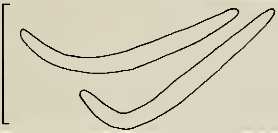
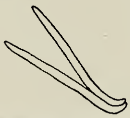
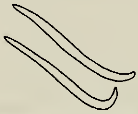
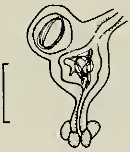
	marina **(Moore)**		***sterreri***	***trevori***
	as marina	as barkudensis	**(Lasserre & Erseus)**	**(Coates)**
no. of segments	55-73	46-48, 64-67	39-47	35-50
dorsal vessel origin	XIV-XXIII	XII-XXII	XII-XIII	XII-XIII
sperm funnel L:D	2-3:1	2-3:1	2-4:1	2:1
sperm funnel collar	wide		equal funnel	equal funnel
thickened septa	(6/7) 7/8-9/10	7/8-9/10	7/8-9/10	8/9-9/10
setae				
spermathecae				

Fig. 3. Distinguishing characteristics of three species of *Stephensoniella*. Scale bar equals 50 μm. Figure of spermatheca of *S. sterreri* modified after Lasserre and Erséus (1976: fig. 3C).

terior thickened septum. Vas deferens 10 to 14 μm wide, regular throughout length, 2 to 3 times as long as sperm funnel; exiting via simple pore lateral to small penial bulb. Spermathecal ampulla and subapical diverticulum approximately globular, both 41 to 65 μm in diameter; spermathecal ectal duct long and uniformly narrow, 11 to 17 μm wide by 36 to 56 μm long; with glands originating only around ectal pore.

Remarks.—Other characteristics are as described for the genus or as previously described (Coates 1980; Coates and Ellis 1981). *Stephensoniella trevori* is distinguished from *S. marina* (Fig. 3) by size and spermathecal characteristics, as discussed for *S. sterreri*. It is distinguished from the latter species by the distribution of gland cells only around the pore of the ectal duct of the spermatheca and by the relative dimensions of the duct, ampulla and diverticulum of the spermatheca (Fig. 3).

Spermathecal characteristics have been relied upon quite heavily to distinguish the two smaller species of *Stephensoniella*; however, the uniformity of spermathecal structure observed between and within widely separated populations of both *S. marina* and *S. trevori* provides a good basis for this reliance.

The whole mounted specimen of *S. trevori* from Bermuda (paratype AH 194 of *Lumbricillus sterreri*) illustrated by Lasserre and Erséus (1976: Plate 1B) is 0.2 mm wide, not 0.5 mm as would be determined from the illustration. The extension posteriad of the seminal vesicles previously noted (Coates 1980) may be an artefact of fixation or simply related to the volume of the seminal vesicles which do not extend anterior to the most posterior thickened septum.

Habitat.—Upper or mid-intertidal in sand with organic debris and finer sediments.

Distribution.—Qualicum Beach, British Columbia, Canada; Shelly Bay, Bermuda; Persian Gulf, Saudi Arabia; and Brazil.

Discussion

When *Stephensoniella* was first diagnosed (Cernosvitov 1934) it was recognized as phylogenetically close to *Lumbricillus* and *Marionina*. More recently (Nielsen and Christensen 1959) the structural diversity in *Marionina* has been allowed broader limits and the species of *Stephensoniella* could be included in that genus. *Stephensoniella,* however, combines at least two character states that are uncommon in *Marionina,* a nephridium with only the funnel anterior to the septum and paired, voluminous seminal vesicles. Distinct, large spermathecal diverticula, seen in all of *S. marina, S. trevori,* and *S. sterreri,* are unknown in both *Marionina* and *Lumbricillus*. Thickened, muscular, preclitellar septa are also distinctive for the three *Stephensoniella* species. It would not be surprising if other species presently classified, with reservations, as *Marionina* or *Lumbricillus* were found to belong in *Stephensoniella*.

Acknowledgments

I am indebted to Mr. E. G. Easton, Mr. R. Sims, Dr. J. Renaud-Mornant, Ms. J. A. Fournier, Ms. R. Carson, and Dr. C. Erséus for loans of material and for providing other useful information. Ms. D. Kathman of EVS Consultants, Sidney, B.C., made the Arabian material collected for Saudi Arabian Tetra Tech Inc. available to me. Dr. R. O. Brinkhurst and H. R. Baker discussed this work with me and provided useful criticisms of the manuscript. Material support was made available by Dr. R. O. Brinkhurst, and the University of Victoria provided financial support through a Graduate Fellowship.

Literature Cited

Cernosvitov, L. 1934. Zur Kenntnis der Enchytraeiden. I.—Zoologischer Anzeiger 105: 233–247.

———. 1935. Oligochäten aus dem Tropischen Süd-Amerika.—Capita Zoologica 6:1–36.

———. 1937. System der Enchytraeiden.—Bulletin Association Russe des Recherches Scientifique, Prague 5:263–295.

Coates, K. A. 1980. New marine species of *Marionina* and *Enchytraeus* (Oligochaeta, Enchytraeidae) from British Columbia.—Canadian Journal of Zoology 58:1306–1317.

———, and D. V. Ellis. 1981. Taxonomy and distribution of marine Enchytraeidae (Oligochaeta) in British Columbia.—Canadian Journal of Zoology 59:2129–2150.

Kossmagk-Stephan, K. 1983. Marine Oligochaeta from a sandy beach of the Island of Sylt (North Sea) with descriptions of four new enchytraeid species.—Mikrofauna Meeresboden (In press).

Lasserre, P., and C. Erséus. 1976. Oligochètes marins des Bermudes. Nouvelles espèces et remarques sur la distribution géographique de quelques Tubificidae et Enchytraeidae.—Cahiers de Biologie Marine 17:447–462.

Moore, J. P. 1902. Some Bermuda Oligochaeta, with a description of a new species.—Proceedings of the Academy of Natural Sciences of Philadelphia 54:80–84.

Nielsen, C. O., and B. Christensen. 1959. Studies on Enchytraeidae. Critical revision and taxonomy of European species.—Natura Jutlandica 8–9:1–160.

Stephenson, J. 1915a. On some Indian Oligochaeta from Southern India and Ceylon.—Memoirs of the Indian Museum 6:38–108.

———. 1915b. Oligochaeta, in fauna of Chilka Lake.—Memoirs of the Indian Museum 5:139–146.

———. 1923. Oligochaeta. Enchytraeidae. *In* The fauna of British India including Ceylon and Burma. Edited by Sir A. E. Shipley.—Taylor and Francis, London. Pp. 110–116.

———. 1930. The Oligochaeta.—Clarendon Press, Oxford, England.

Department of Biology, University of Victoria, P. O. Box 1700, Victoria, British Columbia V8W 2Y2, Canada; and Aquatic Zoology Division, British Columbia Provincial Museum, Victoria, British Columbia V8V 1X4, Canada.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 420–428

DISTOCAMBARUS (DECAPODA: CAMBARIDAE) ELEVATED TO GENERIC RANK, WITH AN ACCOUNT OF *D. CROCKERI,* NEW SPECIES, FROM SOUTH CAROLINA

Horton H. Hobbs, Jr., and Paul H. Carlson

Abstract.—The previously monotypic subgenus *Distocambarus* proposed by Hobbs, 1981, is elevated to generic status, and a new species, *Distocambarus crockeri,* is described from the Savannah River basin of the Piedmont Province of South Carolina. The genus now embraces two species: *Distocambarus devexus* (Hobbs, 1981) of the Savannah piedmont of Georgia and *D. crockeri* which frequents the piedmont section of the same river basin in South Carolina. Both members of the genus are primary burrowers.

In describing *Procambarus* (*Distocambarus*) *devexus* ''from the Piedmont Province in the Broad River basin (Savannah River watershed) of Oglethorpe and Wilkes counties, Georgia,'' Hobbs (1981:306) chose the subgeneric name to denote his conviction of the remoteness of this crayfish from all known members of the genus. He pointed out its similarities to members of the subgenera *Girardiella, Capillicambarus, Leconticambarus,* and *Villalobosus* and to ''certain members of the genus *Fallicambarus,*'' but he emphasized its distinctive features. With the discovery of a close ally of this disjunct species occupying the Savannah basin in the Piedmont Province of South Carolina, we believe that these two crayfishes, exhibiting such a combination of unique and distinctive characters (see the discussion of ''Relationships'' below), should be recognized at the generic level. Therefore we propose that the subgenus *Distocambarus* be elevated to generic rank, and that it encompass *Distocambarus devexus* (Hobbs) and the new species described herein.

Genus *Distocambarus*

Subgenus *Distocambarus* Hobbs, 1981:301 [Type-species, *Procambarus* (*Distocambarus*) *devexus* Hobbs, 1981:302].

Diagnosis.—Antennal flagellum never with conspicuous fringe on mesial border. Third maxilliped with teeth on mesial margin of ischium. Mesial margin of palm of chela with row of as many as 8 tubercles; lateral margin of fixed finger never bearing spiniform tubercles; opposable margin of dactyl with shallow excision proximally. Areola 8 to almost 40 times as long as broad. Ischium of third pereiopod only with hook. Coxa of fourth pereiopod lacking caudomesial boss. First pleopods of first form male symmetrical, widely separated at base, bearing prominent caudoproximal lobe, flexed caudally slightly distal to midlength, and partly concealed by sternal setae extending from ventrolateral part of sternum and coxae of third, fourth, and fifth pereiopods; terminal elements consisting of subtriangular to subconical mesial process, directed caudally to caudodistally, and similarly disposed platelike to bladelike central projection; cephalic process, if present, represented by small rounded to subacute knob on cephalodistal end of appendage; sternite corresponding to fourth pereiopod conspicuously produced ventromesially. Female with annulus ventralis hinged anterodorsally and moving through arc of 30 to 90 degrees; sternal plate immediately anterior to annulus with narrow median fissure; first pleopod represented by inconspicuous tuberculiform swelling. Branchial count 17 + epipodite.

Distocambarus crockeri, new species

Diagnosis.—Body and eyes pigmented, latter small but well developed. Rostrum without marginal spines, tubercles, and median carina. Carapace with one to several small cervical tubercles. Areola 7.3 to 13.9 (average 10.2) times as long as broad, and constituting 37.6 to 40.9 (average 39.0) percent of entire length of carapace (42.7 to 48.4, average 45.3, percent of postorbital carapace length). Ventral surface of ischium of third maxilliped only partly obscured by plumose setae. First 3 pairs of pereiopods without conspicuous brush of setae extending from basis to merus. First pair of pereiopods with ventral surface of merus densely tuberculate and corresponding surface of proximal part of both fingers tuberculate. Second pair of pereiopods with conspicuous brush of setae on carpus and propodus. First form male with simple hook on ischium of third pereiopod only; coxa of fourth pereiopod lacking caudomesial boss. First pleopods widely spaced at base, symmetrical, reaching coxae of third pereiopods, with proximomedian lobe but without proximomesial spur; cephalic surface with weak shoulder near bases of terminal elements; subapical setae absent; shaft of appendage bent caudodistally near midlength at angle of approximately 40 degrees; terminal elements restricted to slender, tapering, distally directed mesial process, and short, subquadrate, platelike, corneous central projection directed caudodistally and rather strongly mesially; cephalic process absent. Mesial ramus of uropod with small distomedian spine premarginal. Female with annulus ventralis capable of arclike motion in longitudinal axis of body; large postannular sclerite abutting but not covering part of annulus; first pleopods consisting of rudiment in form of small tuberculiform protrusion from sternum.

Holotypic male, form I: Cephalothorax (Fig. 1a, i) subovate, compressed laterally; maximum width of carapace slightly greater than height at caudodorsal margin of cervical groove (15.2 and 14.5 mm). Abdomen narrower than thorax (12.3 and 15.2 mm). Areola 10.0 times as long as wide with 2 rows of punctations across narrowest part. Cephalic section of carapace about 1.6 times as long as areola, latter comprising 38.3 percent of total length of carapace (45.8 percent of postorbital carapace length). Surface of carapace distinctly punctate dorsally becoming weakly granulate laterally, tubercles slightly larger in hepatic region than on most of branchiostegite but largest in anteroventral branchiostegal area. Rostrum broad, gently rounded apically with short triangular acumen reaching midlength of distal podomere of antennular peduncle; margins not thickened; upper surface shallowly excavate with usual submarginal punctations and scattered moderately large ones. Subrostral ridge clearly defined. Suborbital angle subacute and rather prominent. Postorbital ridge moderately strong, ending somewhat abruptly anteriorly, neither spine nor tubercle present. Branchiostegal spine small

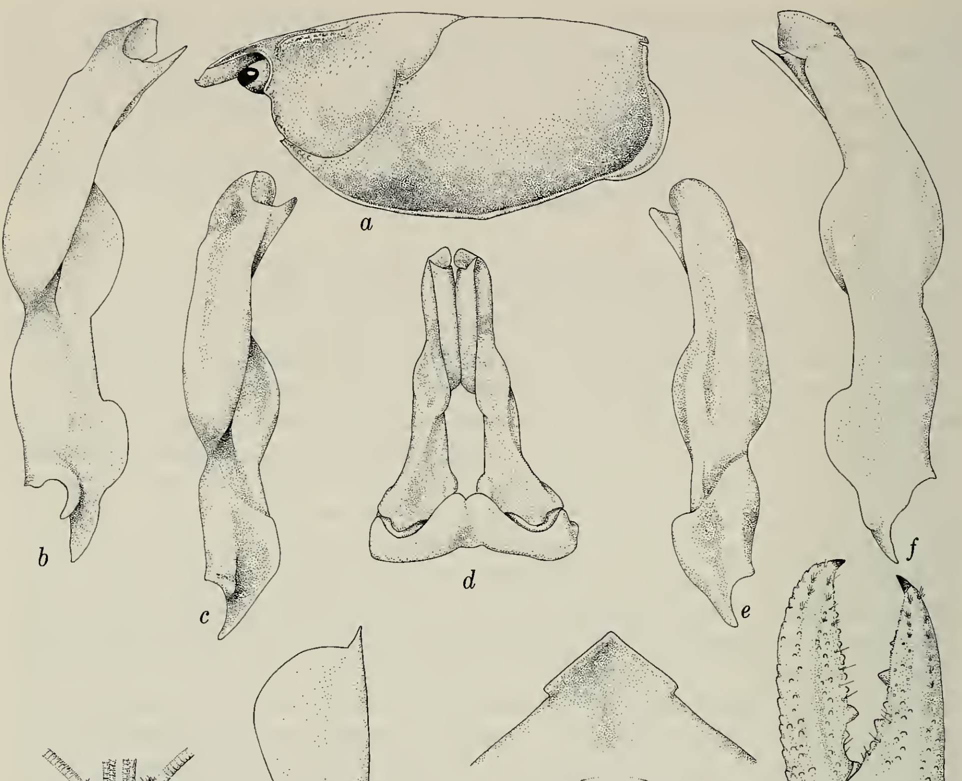


Fig. 1. *Distocambarus crockeri* (all illustrations from holotype except c, e from morphotype, and k from allotype): a, Lateral view of carapace; b, c, Mesial view of first pleopod; d, Caudal view of first pleopods; e, f, Lateral view of first pleopod; g, Antennal scale; h, Epistome; i, Dorsal view of carapace; j, Proximal podomeres of third, fourth, and fifth pereiopods; k, Annulus ventralis; l, Dorsal view of distal podomeres of cheliped.

but acute; cervical spine absent but row of small tubercles along posterior side of region of junction of anterior and posterior arms of cervical groove.

Abdomen shorter than carapace (26.6 and 31.3 mm). Pleura of second through fifth abdominal segments broadly rounded to subtruncate ventrally, lacking caudoventral angles. Cephalic section of telson with 2 spines (more mesial one movable) in each caudolateral corner. Cephalic lobe of epistome (Fig. 1h) triangular, anterolateral margins elevated ventrally; main body of epistome with anteromedian depression but lacking fovea; epistomal zygoma broadly arched. Ventral surface of proximal podomere of antennular peduncle with very small spine distinctly distal to midlength. Antennal peduncle without tubercles and spines on basis and ischium; flagellum with distal articles lacking but reaching second abdominal tergum. Antennal scale (Fig. 1g) about 2.1 times as long as broad, widest distal to midlength; greatest width of lamellar area almost twice that of thickened lateral part.

Third maxilliped extending anteriorly beyond antennal peduncle by length of dactyl and half that of propodus; mesial sector of ventral surface of ischium densely clothed in long plumose setae; lateral sector with closely spaced shorter ones proximally and yet shorter, more widely placed ones distally; distolateral margin of article produced in short spine; merus with setae similarly disposed.

Right chela (left probably regenerated) (Fig. 1l) subelliptical in section, somewhat depressed; mesial margin of palm 1.1 times as long as greatest width, former about two-fifths that of length of palm; almost entire surface of palm with squamous to subsquamous tubercles. Mesial margin of palm with row of 8 (right) or 6 (left) tubercles flanked dorsally by row of 8 (right) or 6 (left) and irregular ventral row of 8, few additional tubercles present between rows; ventral surface with 2 prominent tubercles opposite base of dactyl. Both fingers with moderately well defined dorsomedian ridges; that on fixed finger flanked along proximal half by tubercles and distally by row of punctations, that on dactyl by tubercles along proximal three-fourths and by punctations distally. Opposable margin of fixed finger with row of 9 (right) or 7 (left) tubercles, second from base largest, scattered along almost entire length of fingers, and single row of minute denticles extending between, and some under, tubercles; 2 tubercles also present slightly below row: larger one at about midlength and smaller at about base of apical third of finger; lateral surface with row of tubercles on proximal third replaced along distal part of finger by row of setiferous punctations. Opposable margin of dactyl with row of 10 (right) or 11 (left) tubercles, second from base largest, dispersed along almost entire length of finger, interrupting row of minute denticles; basal fourth of margin shallowly excavate; mesial surface of dactyl tuberculate with row extending from base almost to corneous tip of finger, becoming subacute on distal part of podomere; ventral surface of fingers with tubercles flanking median ridge proximally and punctations distally.

Carpus of cheliped distinctly longer than mesial margin of palm (10.5 and 8.1 mm), its dorsal surface with broad, slightly sinuous, shallow furrow extending from almost 0.2 length of podomere from proximal end to about same distance from distal end, and with scattered punctations and few tubercles proximomesially; mesial surface with irregular dorsal row of 7 or 8 small tubercles below which 14 or 15 additional tubercles, only one of which decidedly larger than others, also present, and premarginal setal band distomesially; distoventral margin of carpus with 2 tubercles, larger, more lateral one bearing articular socket receiving ventrolateral condyle of propodus.

Merus with usual tubercles dorsally, none acute, and more distal ones not conspicuously larger than several proximal to it; mesial and lateral surfaces mostly smooth, but distomesial area bearing number of very small tubercles; ventral surface studded with crowded tubercles, irregular mesial and lateral rows consisting of 15 or 16 tubercles, spiniform. Ischium with row of 4 small tubercles mesially.

Hook on ischium of third pereiopod (Fig. 1j) simple, comparatively heavy, and overreaching basioischial articulation, latter not opposed by tubercle on basis. Coxa of neither fourth nor fifth pereiopods with boss; ventral membrane of coxa of fifth conspicuously setose.

Sternum between third pereiopods rather shallow; that between both fourth and fifth comparatively deep; lateral part of that between fourth produced ventrally in moderately strong, posteroventrally projecting lobe. Plumose pubescence associated with sternum and coxae of all pereiopods very prominent.

First pleopods (Fig. 1b, d, f) as described in "Diagnosis." Uropods with both lobes of proximal podomere bearing acute corneous spines; mesial ramus with distomedian spine small and situated premarginally.

Allotypic female: Differing from holotype, other than in secondary sexual features, in following respects: areola 9.6 times as long as broad; postcervical groove, which not evident in holotype, clearly defined and situated 0.2 areola length posterior to cervical groove; tubercles on carapace much weaker; rostrum almost reaching distal margin of ultimate podomere of antennular peduncle. Suborbital angle weak and obtuse; branchiostegal spine smaller but distinct; only 1 or 2 cervical tubercles present; third maxilliped only slightly overreaching antennal peduncle. Length of mesial margin of palm of chela equal to width and about 0.4 as long as chela; only 1 tubercle (injured) on ventral surface at base of dactyl; opposable margin of fixed finger with only 1 tubercle below principal row; 7 tubercles on corresponding margin of dactyl, and more mesial of 2 tubercles on distoventral margin of carpus less conspicuous than in holotype. (See measurements in Table 1.)

Annulus ventralis (Fig. 1k) 1.7 times as wide as long, hinged cephalically, moving through arc of 90 degrees, D-shaped with anterior margin almost straight and slightly elevated; ventral surface sloping posteriorly and mesially from anterolateral angles; sinus almost straight, beginning at about midlength of annulus, slightly dextral to median line, and extending caudosinistrally, ending on caudosinistral wall of annulus; sinistral wall of sinus increasing in height posteriorly, forming conspicuous prominence on caudal wall. Postannular sclerite subtrapezoidal in shape, its maximum width 1.5 times its length; sclerite 0.9 as wide and 0.9 as long as annulus, its anteroventral margin with symmetrical pair of broad excavations rendering margin with 3 short rounded projections.

Sternum anterior to annulus with narrow, median, longitudinal cleft. First pleopod represented by tuberculiform rudiment.

Morphotypic male, form II: Differing from holotype, other than in development of secondary sexual characters, in only few minor respects: epistome, while subtriangular, with more irregular anterolateral margins; mesial margin of palm of

Table 1.—Measurements (mm) of *Distocambarus crockeri.*

	Holotype	Allotype	Morphotype
Carapace			
Entire length	31.3	34.6	23.8
Postorbital length	26.2	29.5	20.4
Width	15.2	16.2	11.1
Height	14.5	15.0	10.5
Areola			
Width	1.2	1.4	1.1
Length	12.0	13.5	8.9
Rostrum			
Width	5.0	5.7	4.0
Length	6.8	7.0	5.1
Right chela			
Length, palm mesial margin	8.1	9.2	4.9
Palm width	7.6	9.2	5.2
Length, lateral margin	20.8	21.4	12.5
Dactyl length	6.9	12.7	7.2
Abdomen			
Width	12.3	13.8	9.0
Length	26.6	31.8	23.3
Carpus of cheliped			
Width	5.7	6.2	3.7
Length	10.5	10.8	6.4

chela with row of 8 or 9 tubercles; opposable margin of fixed finger with row of 3 or 4 tubercles along proximal half, and corresponding margin of dactyl with 2 tubercles representing proximal 2 in holotype. (See measurements in Table 1.)

Hook on ischium of third pereiopod much less conspicuous and not projecting over basioischial articulation. First pleopod (Fig. 1c, e) not distinctly reflexed; mesial process longer and distal part more slender than in holotype; central projection rounded and non-corneous but disposed as in holotype; juvenile suture evident.

Color notes.—(Based upon specimens from burrows at junction of U.S. Highway 378 and County Road 423, northwest of Edgefield, Edgefield County, South Carolina.) Ground color shades of brown. Dorsum of cephalic region and areola dark brown, rostral margins and V-shaped marking in posterior gastric region almost black; areola flanked by grayish brown longitudinal stripes which flanked laterally by dark chocolate stripes extending from cervical groove to posterior margin of carapace; lateral surface of branchiostegites with irregular tan splotches on brown fading ventrally from just-mentioned chocolate stripe to pale brown along ventral margin. Abdomen with orange tan dorsomedian stripe flanked by broad dark chocolate stripes (continuous with those on carapace) extending from first to anterior part of sixth segment; terga ventrolateral to chocolate stripe tan with reticulate darker brown mottlings; pleura, except for anteroventral tan sections, bearing reticulate pattern of dark brown; tergum of sixth segment, telson, and uropods with brown mottlings on tan. Cheliped basically dark tan with brown tubercles; very dark brown markings on distal margin of merus, dorsolateral surface of carpus, dorsomesial part of palm, and dorsal part of fingers; tips of latter reddish orange; remaining pereiopods with broad irregular bands, darker at distal ends of podomeres; merus and carpus each with proximal and distal bands.

Type-locality.—Roadside ditch 0.7 miles south of Parksville, McCormick County, South Carolina, on U.S. Highway 221. The ditch from which the specimens were dug was partly shaded by trees of the genera *Pinus, Juniperus,* and *Acer* and had been scraped in making road repairs. Water stood in the lower section, and many burrows that were not inundated were surrounded by pellets composed of sandy clay that recently had been brought to the surface. The burrows were comparatively simple: none that were excavated had more than three openings, and although branching, possessed only one deep passage. Some of the burrows contained several individuals, but whether or not the multiple occupancy resulted from the young-of-the-year not having left the parent burrow could not be determined. Burrows elsewhere containing more than one individual housed only a first form male and a female, or a female with few to several juveniles. No other crayfish species was found in the colony at this locality.

Disposition of types.—The holotypic male, form I, the allotype, and the morphotypic male, form II, are deposited in the National Museum of Natural History (Smithsonian Institution), nos. 178582, 178583, and 178584, respectively, as are the paratypes consisting of 7 males, form I, 2 males, form II, 15 females, 7 juvenile males and 7 juvenile females.

Size.—The largest specimen available is a first form male having a carapace length of 34.7 mm (postorbital carapace length 30.0 mm); corresponding lengths of the smallest first form male are 27.8 (24.1) mm, and those of the largest female, the allotype, 34.6 (29.5) mm. Ovigerous females have not been found.

Range and specimens examined.—This crayfish appears to be restricted to the eastern watershed of the Savannah River in the Piedmont Province of South Carolina. Specimens have been examined from the following localities: McCORMICK COUNTY—(1) type-locality, 1 ♂I, 1 ♂II, 4 ♀, 4 j♂, 5 j♀, 19 Apr 1981, G. B. Hobbs, J. E. Pugh, HHH; (2) roadside seepage area 0.9 mi S of Abbeville Co line on Co Rd 81, 1 ♂I, 1 ♀, 1 j♂, 18 Apr 1981, GBH, JEP, HHH; (3) roadside ditch 0.5 mi E of Stephens Cr on St Rte 283, 2 ♀, 1 j♂, 24 Apr 1982, GBH, HHH. ABBEVILLE COUNTY—(4) seepage and wet area around farm pond 2.6 mi NE of Calhoun Falls on St Rte 72, 2 ♂I, 17 Apr 1981, JEP, HHH; (5) roadside ditch 100 yds S of Gill Creek on Co Rd 32, 1 ♂I, 1 ♀, 25 Apr 1982, GBH, HHH. EDGEFIELD COUNTY—(6) roadside ditch at westernmost tributary to Rocky Creek at U.S. Hwy 378, 2 mi W of Co Rd 51, 1 ♂I, 1 ♂II, 4 ♀, 1 j♂, 2 j♀, 9 Apr 1982, P. H. Carlson and E. M. Younginer; (7) roadside ditch at jct of U.S. Hwy 378 and Co Rd 423, NW of Edgefield, 2 ♂I, 1 ♂II, 4 ♀, 24 Apr 1982, GBH, HHH. (Burrows of *Cambarus* (*D.*) *latimanus* (LeConte) were excavated within a meter of that of one of these specimens.)

Variations.—Although there are many minor variations among the specimens that have been examined, none involves the differences between this and closely or distantly related species. The rostral margins are often more strongly convergent than that illustrated, and the carpus of the cheliped may not be so narrow as that reported for the holotype, but never are there massive tubercles on the mesial surface of the latter; always the carpus appears abnormally long, and though tuberculate, the mesial surface lacks the conspicuously dominant major spine that is typical of most crayfishes in the eastern part of the United States. The only difference noted in the first pleopods of the first form male in specimens from the few localities from which they are available is in the degree of sclerotization of the central projection, but none of the variations seems to be correlated with specimens from a restricted part of the range of the species.

Relationships.—*Distocambarus crockeri* is more closely allied to *D. devexus* than to any other crayfish. Except for references to the secondary sexual features, most of the description of the latter (Hobbs 1981:302) applies quite well to *D. crockeri*. The only striking differences between the two exist in features of the first pleopod of the male and those of the annulus ventralis. Ecologically, one appears to vicariate for the other on opposite sides of the Savannah River. Whereas their broad areolae and ungainly legs suggest a better adaptation to life in surface lentic or lotic habitats, both are primary burrowers. Their relationships to other members of the Cambarinae are not understood, but perhaps the kinships suggested by Hobbs (1981:43, and fig. 11) are not totally erroneous.

These two crayfishes may be distinguished from all others by the following combination of characters: rostrum without marginal spines; ventral surface of merus of cheliped densely tuberculate; ischia of only third pereiopods with hooks; coxae of fourth pereiopods without caudomesial boss; first pleopods of first form male symmetrical, widely separated basally, with prominent caudoproximal lobe, deflected caudodistally near midlength, and lacking caudal process; carpus of cheliped twice as long as wide; annulus ventralis moving through arc of approximately 90 degrees; postannular sclerite large and platelike; and sternum of female anterior to annulus narrowly cleft.

Distocambarus crockeri may be separated from *D. devexus* by the first pleopod of the male, which lacks a cephalic process and possesses a more acute mesial process and a much larger quadrangular central projection, and by the annulus ventralis which when depressed is not partly overlapped by the postannular sclerite.

Ecological notes.—The burrows of *Distocambarus crockeri* do not differ in any obvious way from those of *D. devexus,* which Hobbs (1981:307) described as "moderately complex." Most of those excavated had two or three passageways leading to the surface, at least one topped by a crude turret; these tunnels converged to form one subvertical gallery that penetrated the water table and occasionally branched into two or three passages directed downward; all ended blindly, in some instances more than a meter below the surface. Burrows were found in seepage areas, bogs, and in both waterlogged and comparatively dry roadside ditches. In all except one of the localities, clumps of a sedge, 0.3 to 0.6 m in height, were among the most conspicuous plants present. In fact, the presence of the sedge led one of us (H.H.H.) to choose collecting sites where this crayfish was found as he was driving along the county roads and highways. (See "Type-locality.")

Etymology.—This crayfish is named in honor of Denton W. Crocker, a fellow student of crayfishes and a friend, whose contributions to our knowledge of the American crayfish fauna are invaluable.

Acknowledgments

We extend our thanks to Georgia B. Hobbs and Jean E. Pugh, Christopher Newport College, both long time collecting companions, and to Edward M. Younginer, South Carolina Department of Health and Environmental Control, for their help in obtaining the specimens on which this description is based, and to Raymond W. Bouchard, Wildwood Crest, New Jersey, and Raymond B. Manning of the Smithsonian Institution, for their criticisms of the manuscript.

Literature Cited

Hobbs, Horton H., Jr. 1981. The crayfishes of Georgia.—Smithsonian Contributions to Zoology, 318: vi + 549 pages, 262 figures.

(HHH) Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560; (PHC) Department of Health and Environmental Control, 2600 Bull Street, Columbia, South Carolina 29201.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 429–439

DISTOCAMBARUS (*FITZCAMBARUS*) *CARLSONI*, A NEW SUBGENUS AND SPECIES OF CRAYFISH (DECAPODA: CAMBARIDAE) FROM SOUTH CAROLINA

Horton H. Hobbs, Jr.

Abstract.—A new subgenus, *Fitzcambarus*, is proposed to receive *Distocambarus* (*Fitzcambarus*) *carlsoni*, the third species assigned to the genus. This crayfish, differing from its relatives in possessing a comparatively narrow areola, has been found in a single locality in the Saluda River basin of Anderson County, South Carolina. Like its congeners, it is a primary burrower and shares a swamp-seepage area with the crayfish *Cambarus* (*Jugicambarus*) *carolinus* (Erichson), the only primary burrower previously reported from the basin.

The crayfish described here was discovered in burrows constructed in a swampy area bordering a tributary to the Saluda River in Anderson County, South Carolina. Late in the afternoon of 27 April 1982, after having collected crayfishes in a small sand and silt bottomed stream, I discovered burrows in the adjoining swamp. The only burrowing crayfish that I had encountered previously in the upper Saluda Basin was *Cambarus* (*Jugicambarus*) *carolinus* (Erichson, 1846), and I anticipated that this was the crayfish responsible for the piles of earth scattered over the swamp floor. Because of the densely matted roots just beneath the surface of the ground, attempts to excavate two of the burrows resulted in failure to obtain an adult individual, but a very small juvenile was retrieved from one of them. The specimen was brought into the laboratory where it was found to belong to an unknown species. My friend Paul H. Carlson was advised of the find, and he visited the locality in May when he obtained several representatives of *C.* (*J.*) *carolinus*. Another attempt by him to obtain additional specimens of the new crayfish was made in June when he succeeded in securing several specimens; however, not until early in November, when both of us spent the better part of seven hours digging in the swamp, was an adequate series, including two first form males obtained by Dr. Carlson, acquired for preparing this description.

This crayfish is named in honor of Dr. Carlson, of the South Carolina Department of Health and Environmental Control, in token of his indefatigable efforts in sampling so many burrowing crayfish populations occurring in South Carolina.

Reasons for proposing the recognition of subgenera in the genus *Distocambarus* are pointed out in the discussion of "Relationships" below. Diagnoses and the compositions of the subgenera are as follows:

Genus *Distocambarus* Hobbs, 1981

Subgenus *Distocambarus*

Diagnosis.—Areola no more than 14 times as long as wide; mesial margin of palm of chela of male longer than maximum width of podomere and at least as long as carpus; terminal elements of first pleopod of first form male directed caudodistally, central projection platelike and comparatively short; annulus ventralis movable through arc of 90 degrees, and postannular sclerite large, subtrapezoidal, and almost as long as annulus.

Species.—*Distocambarus* (*Distocambarus*) *devexus* (Hobbs, 1981:302) and *Distocambarus* (*Distocambarus*) *crockeri* Hobbs and Carlson, 1983:421.

Fitzcambarus, new subgenus

Diagnosis.—Areola at least 15 times as long as wide; mesial margin of palm of chela of male shorter than wide and shorter than carpus; terminal elements of first pleopod of first form male directed caudally, central projection bladelike and comparatively long; annulus ventralis movable through arc of less than 50 degrees, and postannular sclerite small, subovate in outline, wedge-shaped, and distinctly shorter than annulus.

Gender.—Masculine.

Type-species.—*Distocambarus* (*Fitzcambarus*) *carlsoni* new species.

Etymology.—This name is derived from the surname Fitzpatrick and the crayfish genus *Cambarus.* I am pleased to propose this taxon honoring Joseph F. Fitzpatrick, Jr., a friend and an able student of crayfishes who has added much to our knowledge of the Cambaridae.

Distocambarus (*Fitzcambarus*) *carlsoni,* new species

Fig. 1

Diagnosis.—In addition to characters cited for genus, rostrum broadly acuminate, margins little thickened and devoid of spines or tubercles. Cephalic extremity of postrobital ridge merging almost imperceptibly with carapace. Suborbital angle obtuse and inconspicuous. Cervical spine lacking. Areola 15.2 to 38 times as long as wide, comprising 38.1 to 41.1 percent of entire length of carapace (43.7 to 47.3 percent of postorbital carapace length) and never with more than 1, often none, punctation in narrowest part. Chela with well defined row of 5 to 7 tubercles on mesial surface of palm, additional row flanking it dorsolaterally and 2 or 3 tubercles distoventrally. No tubercle on basis of third pereiopod opposing hook on ischium.

Holotypic male, form I: Cephalothorax (Fig. 1*a, m*) subcylindrical; maximum width of carapace slightly greater than height at caudodorsal margin of cervical groove (13.2 and 12.3 mm). Abdomen distinctly narrower than thorax (9.6 and 13.2 mm). Areola 38.3 times as long as wide, with room for no more than 1 punctation across narrowest part. Cephalic section of carapace about 1.4 times as long as areola, latter comprising 41.1 percent of total length of carapace (47.3 percent of postorbital carapace length). Surface of carapace mostly punctate, few tubercles present in hepatic region and in anteroventral branchiostegal region. Rostrum broad and short, gently rounded apically with small, poorly delimited acumen reaching base of distal podomere of antennular peduncle; margins not conspicuously thickened; upper surface shallowly concave with usual submarginal punctations and moderately large ones posteriorly. Subrostral ridge weak but clearly defined. Suborbital angle broadly obtuse, very weak. Postorbital ridge moderately well developed but merging insensibly with carapace cephalically. Branchiostegal and cervical spines absent.

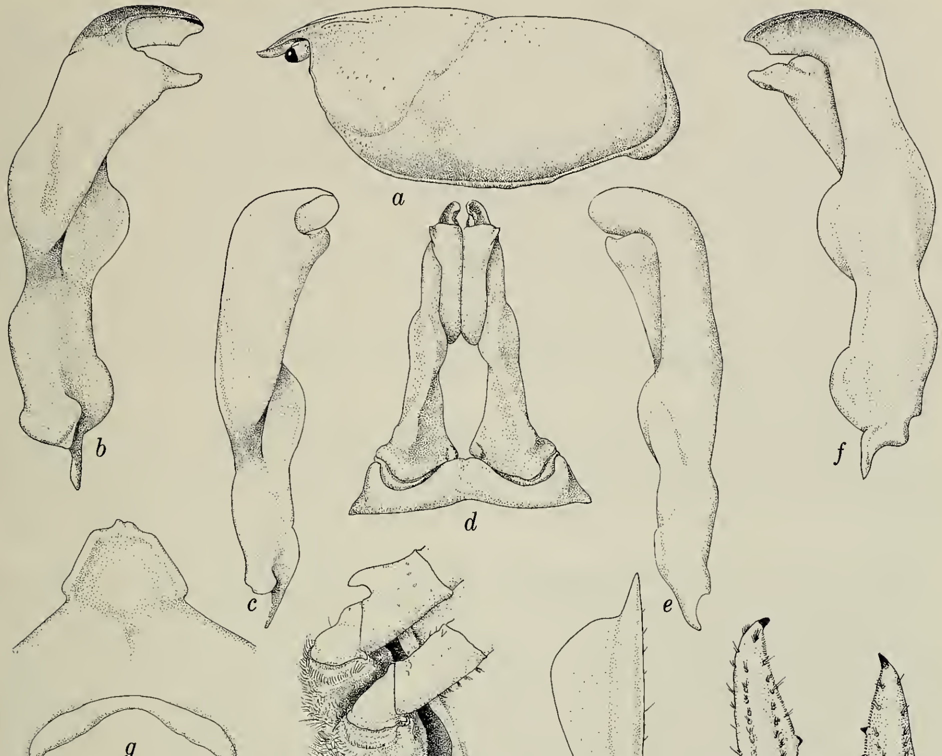


Fig. 1. *Distocambarus* (*F.*) *carlsoni* (all from holotype except *c*, *e* from morphotype, *i–l* from paratypic female, and *n* from allotype): *a*, Lateral view of carapace; *b*, *c*, Mesial view of first pleopod; *d*, Caudal view of first pleopods; *e*, *f*, Lateral view of first pleopod; *g*, Epistome; *h*, Proximal podomeres of third, fourth, and fifth pereiopods; *i*, Antennal scale; *j*, Incisor lobe of mandible; *k*, *l*, Molar lobe of mandible; *m*, Dorsal view of carapace; *n*, Annulus ventralis and adjacent sternites; *o*, Denuded ventrolateral parts of sternum and ventral articular regions of left third and fourth pereiopods showing distinctly produced posteroventral lobe on latter; *p*, Dorsal view of distal podomeres of cheliped.

Abdomen shorter than carapace (22.8 and 28.0 mm). Pleura of second through fifth abdominal segments rounded ventrally, lacking caudoventral angle. Cephalic section of scabrous telson with 2 spines (more mesial one movable) in each caudolateral corner. Cephalic lobe of epistome (Fig. 1*g*) subtrapezoidal, cephalic part truncate with small asymmetrical median projection, margins weakly elevated ventrally; main body of epistome with triangular median depression but lacking distinct fovea; epistomal zygoma broadly arched. Ventral surface of proximal podomere of antennular peduncle with heavy short spine distal to midlength. Antennal peduncle without tubercles and spines on basis and ischium; flagellum with distalmost articles lacking, but almost reaching midcaudal margin of carapace. Antennal scale (Fig. 1*i*) about 2.5 times as long as broad, widest slightly distal to midlength; greatest width of lamellar area about 1.5 times that of thickened lateral part.

Third maxilliped extending as far anteriorly as antennal peduncle; mesial sector of ventral surface of ischium with clusters of stiff, long setae some of which flanked laterally by shorter, plumose ones; latter also present in lateral sector where conspicuous in submarginal lateral row; merus with setae similarly disposed.

Right chela (Fig. 1*p*) subelliptical in section, rather strongly depressed; palm 1.4 times as broad as length of mesial margin; length of latter one-third that of entire length of chela; almost entire surface of palm with squamous to subsquamous tubercles. Mesial margin of palm with row of 7 tubercles flanked dorsolaterally by row of 4 (right) or 5 (left) and few additional ones. Both fingers with well defined dorsomedian ridges flanked by setiferous punctations. Opposable margin of fixed finger with row of 3 (left with 4) tubercles, second from base largest, along proximal two-fifths of finger and single row of minute denticles extending between and distal to tubercles from base of finger to corneous tip; acute tubercle also present slightly below row at about midlength of finger; lateral margin of finger weakly costate with row of punctations. Opposable margin of dactyl with 2 tubercles, more distal larger, on proximal half of finger interrupting single row of minute denticles extending from proximal base of proximalmost tubercle to corneous tip of finger, basal half of margin shallowly excavate; mesial margin of dactyl with row of 3 tubercles proximally followed by series of setiferous punctations, tubercles decreasing in size and becoming more squamous distally.

Carpus of cheliped distinctly longer than mesial margin of palm of chela (8.6 and 5.8 mm), with shallow sinuous furrow extending almost entire length of podomere, dorsal surface of which sparsely punctate; mesial surface with dorsal row of 5 or 6 small tubercles, below them 6 or 7 additional ones, distalmost of which conspicuous; prominent tuft of plumose setae situated distomesially; distoventral margin of carpus with 2 tubercles, larger, more lateral one bearing articular socket receiving ventrolateral condyle on propodus.

Merus with usual tubercles dorsally, 3 distal tubercles somewhat larger than others; mesial and lateral surfaces rather smooth; ventral surface with crowded tubercles, mesial row consisting of 11 tubercles, and less regular lateral row of 10 or 11. All tubercles on merus comparatively small, and none spiniform. Ischium with 1 well defined tubercle proximomesially and 2 or 3 vestigial ones distal to it.

Hook on ischium of third pereiopod (Fig. 1*h*) simple and acute, overreaching basioischial articulation, not opposed by strong tubercle on basis. Coxa of neither fourth nor fifth pereiopod with boss; ventral membrane of coxa of fifth conspicuously setose.

Sternum between third pereiopods rather shallow; that between both fourth and fifth comparatively deep, ventrolateral elements corresponding to third and fourth produced ventrally much beyond articulation with respective coxae; that associated with fourth very strong, subtriangular, and curved ventromesially (Fig. 1*o*). Plumose pubescence associated with sternum and coxae of all pereiopods very prominent.

First pleopods (Fig. 1*b, d, f*) symmetrical, not contiguous at base, reaching coxae of third pereiopods, bearing strong caudoproximal lobe and broadly rounded proximomedian lobe, flexed caudally slightly distal to midlength, and lacking subapical setae. Terminal elements limited to mesial process and central projection, directed caudolaterally and caudomesially, respectively, at about 90 degrees to axis of proximal half of appendage; mesial process non-corneous, tapering, and reaching almost as far caudally as corneous, bladelike central projection which provided with subapical notch.

Uropods with both lobes of proximal podomere bearing acute spines; mesial ramus with distomedian spine small and situated distinctly premarginally.

Allotypic female: Differing from holotype, other than in secondary sexual features, in following respects: areola 23.4 times as long as wide; cephalic section of carapace 1.5 times as long as areola, latter comprising 39.9 percent of total length of carapace (45.7 percent of postorbital carapace length); chela proportionately smaller than that in male, mesial margin of palm with row of 6 (right) or 8 (left) tubercles flanked dorsolaterally by row of 6; opposable margin of fixed finger with row of 3 tubercles, that of dactyl also with 3, second from base largest; mesial margin of dactyl with longitudinal row of 3 (left) or 4 (right) tubercles basally, row flanked by 2 tubercles proximoventrally; distal tubercle in ventromesial row on merus of cheliped subspiniform; 3 tubercles on ventromesial margin of ischium of cheliped better developed than those in holotype. (See Table 1.)

Sternum between fourth pereiopods with very narrow median fissure (expanding anteriorly and posteriorly) extending entire length.

Annulus ventralis (Fig. 1*n*) hinged cephalically (moving through arc of some 30 degrees), approximately 1.4 times as broad as long; elevated lateral areas separated by sinistrally disposed depression, latter broad anteriorly, gradually narrowing posteriorly, and terminating in fossa situated sinistral to median line slightly posterior to midlength of annulus; sinus, originating in fossa, coursing dextrally across median line before forming broad arc caudosinistrally and ending on caudal wall of annulus slightly dextral to median line.

Postannular sclerite ovate, 0.7 as wide and 0.5 as long as annulus; central area elevated (ventrally) with anterior face of elevation plane and posterior surface rounded.

Morphotypic male, form II: Except in secondary sexual characters, differing in no conspicuous way from holotype; few differences noted, probably reflecting juvenile condition of specimen: anterior section of telson with only 1 spine in each caudolateral corner; cheliped with fewer well developed tubercles on merus and carpus, and lateral lobe of proximal podomere of uropod without well defined

Table 1.—Measurements (mm) of *Distocambarus* (*F.*) *carlsoni*.

	Holotype	Allotype	Morphotype
Carapace			
Entire length	28.0	29.3	21.9
Postorbital length	24.3	25.6	18.8
Width	13.2	14.2	9.6
Height	12.3	12.5	9.0
Areola			
Width	0.3	0.5	0.4
Length	11.5	11.7	8.3
Rostrum			
Width	4.6	4.6	3.6
Length	4.5	4.6	3.7
Chela			
Length, palm mesial margin	5.8	5.4	3.6
Palm width	8.2	7.5	4.8
Length, lateral margin	17.6	15.7	11.2
Dactyl length	10.5	9.6	7.1
Abdomen			
Width	9.6	10.5	6.9
Length	22.8	24.5	16.0
Carpus of cheliped			
Width	5.7	5.4	3.6
Length	8.6	8.5	5.6

spine. Ischium of third pereiopod with only rudiment of prominent hook in holotype, but produced posteroventral lobe of ventrolateral element of sternum corresponding to fourth pereiopod clearly evident. First pleopod (Fig. 1*c*, *e*) lacking strong caudal flexure near midlength; central projection non-corneous, and both terminal elements bent caudally at about 90 degrees to shaft, but shorter, less sharply delimited, and distal parts more inflated than in holotype.

Color notes.—Dorsum of carapace brown with reddish or greenish suffusion. Lateral rostral carinae, postorbital ridges, and small lateral spot on posterior margin of cervical groove very dark, almost black. Dark dorsum of thoracic region abruptly replaced dorsolaterally by lavender cream extending ventrally over branchiostegites to very pale marginal carina; anteroventral branchiostegal region cream to white. Lateral surface of cephalic section of carapace with large irregular brownish area in hepatic region extending anteriorly as narrow stripe across upper orbital region, remainder pinkish lavender. Abdomen with first abdominal tergum very dark reddish purple, second through fourth segment with rectangular, dark, reddish brown markings along median line, decreasing in size posteriorly to sixth where sublinear, but expanding and forming triangular marking on anterior section of telson; longitudinal stripe extending along dorsal parts of pleura onto anterolateral surface of telson. Anteroventral parts of pleura pale pinkish cream, remainder pinkish tan. Ground color of telson and uropods pale tan with pinkish suffusion, although margins, sutures, and ridges pale brown. Antennular and antennal peduncles reddish brown, flagella tan. Chelipeds basically pinkish lavender with very dark brown dorsal stripe beginning at base of merus and broadening over distal part of podomere; carpus with dark stripes flanking dorsomedian depression and splotches around bases of mesial tubercles; propodus with dark dorsomesial area studded with very dark tubercles; band across distal part of palm extending distolaterally on fixed finger. Dactyl with triangular dark wedge on dorsomesial surface, its fading apex approaching distal end of finger. Second pereiopod with merus as in cheliped, and carpus with stripe on dorsal margin and another laterally, chela pale grayish tan. Remaining pereiopods with dorsal parts of podomeres from merus distally dark, intensifying at articular margins. Ventral surfaces of all pereiopods pale pinkish lavender, especially chela, to cream.

Type-locality.—A swampy area bordering an unnamed tributary of the Saluda River about 1 mile north of State Route 81 on Route 106. There, in an area shaded by *Liriodendron tulipifera, Liquidambar styraciflua, Alnus rugosa, Pinus* sp., and *Quercus* sp., the water table fluctuates from the surface to about 0.8 m below it. The soil is a sandy clay, in some areas rich in humus, and a layer of decaying leaves litters the ground. Chimneys constructed by *Distocambarus* (*F.*) *carlsoni* and *Cambarus* (*J.*) *carolinus* (Erichson, 1846) and a few fallen branches from the overhanging trees are the only conspicuous irregularities in the gently sloping swamp floor. Matted roots of the many trees and shrubs lie at and within a few centimeters below the surface. The colony from which the type-series was obtained occupies an area of some 200 square meters. (See "Ecological Notes" below.)

Disposition of types.—The holotype, allotype, and morphotype are deposited in the National Museum of Natural History (Smithsonian Institution), nos. 178599, 178600, and 178601, respectively, as are the paratypes consisting of 1 male, form I, 13 females, 2 juvenile males, 4 juvenile females, and 1 ovigerous female.

Size.—The largest specimen available is a female having a carapace length of 31.0 mm (postorbital carapace length 27.0 mm); corresponding lengths of the smaller of the two first form males are 25.8 (22.7) mm, and those of the ovigerous female, 27.1 (23.8) mm.

Range and specimens examined.—This crayfish is known from only the type-locality, in the Saluda River basin of South Carolina: Anderson County—(1) type-locality, 1 j♀, 27 Apr 1982, G. B. Hobbs and HHH; 1 ♂II, 1 ♀, 1 ovig. ♀ (carapace length 27.1 mm, carrying 25 eggs with diameters of 2.0 to 2.1 mm), 1 j♂, 2 j♀, 19 Jun 1982, P. H. Carlson; 3 ♀, 22 Oct 1982, PHC; 1 ♀, 1 j♀, 1 Nov 1982, GBH, HHH; 2 ♂I, 9 ♀, 1 j♂ and some 20 very small juveniles which are being maintained alive, 2 Nov 1982, PHC, GBH, HHH.

Relationships.—*Distocambarus* (*Fitzcambarus*) *carlsoni* is a unique crayfish which, while bearing strong resemblances to members of the genus *Cambarus*, does not share several characteristics that typify all of the now recognized species assigned to that genus. The features that are unlike those in any member of *Cambarus* are:

(1) The bent shaft of the first pleopod of the first form male (Figs. 1*b*, *f*). In all members of *Cambarus* it is straight, or at most slightly curved, and the terminal elements, with few exceptions, project from it at no less than 90 degrees. In *D.* (*F.*) *carlsoni*, the shaft is rather strongly reflexed slightly distal to midlength, and the terminal elements are disposed caudally at much less than 90 degrees to the *distal segment* of the shaft.

(2) A strong caudoproximal lobe on the first pleopod of the first form male (Fig.

1*b, f*). In most members of *Cambarus* there is hardly a trace of such a lobe, and in none is it nearly so prominent as it is in *D.* (*F.*) *carlsoni.*

(3) No boss on the coxa of the fourth pereiopods of the first form male (Fig. 1*h*). In all members of *Cambarus*, a well defined boss is present on the caudomesial angle of the coxa of this appendage; no such swelling is evident in the species described here.

(4) Produced lateral lobe of the sternum associated with the fourth pereiopods of the first form male (Fig. 1*o*). In *Cambarus*, a ventral production of the sternum is inhibited by the presence of a caudomesial boss on the coxa of this appendage; in *D.* (*F.*) *carlsoni*, however, the lateral lobes of the sternum are produced ventromesially much beyond the articulation between the coxa and the sternum.

(5) The relative length and width of the carpus of the cheliped (Fig. 1*p*). In no member of the genus *Cambarus* is the length of the carpus so much greater than its width.

(6) The cleft sternum anterior to the annulus ventralis (Fig. 1*n*). The narrow suture that lies between the sternal plates associated with the fourth pereiopods in *D.* (*F.*) *carlsoni* is not evident in any member of the genus *Cambarus*.

(7) The articulation of the annulus ventralis. The hinge-like motion of the annulus ventralis is accomplished between the annulus and the sternum anterior to it rather than, as in *Cambarus*, in a transverse, weakly sclerotized area across the annulus proper.

These differences seem sufficiently significant to conclude that this crayfish is not closely allied to members of any of the subgenera of *Cambarus*. Closer relatives seem to exist in the two members of the genus *Distocambarus*, for both *Distocambarus* (*D.*) *devexus* (Hobbs, 1981) and *D.* (*D.*) *crockeri* Hobbs and Carlson (1983) exhibit all of the features of *carlsoni* mentioned above. To be sure, there are marked differences in the form of the terminal elements of the first pleopod of the male, and in neither of the previously described species of *Distocambarus* is the central projection so elongate or disposed so distinctly caudally as it is in *D.* (*F.*) *carlsoni*. The similarities between the first pleopods of the latter (Fig. 1*b*, herein) and *D.* (*D.*) *crockeri* (see Hobbs and Carlson 1983: fig. 1*b*) are indeed striking, and a shortening of the shaft of the latter with a concomitant elongation of the central projection and reflection of the central projection would produce an appendage that would be little different from that of *D.* (*F.*) *carlsoni*.

The assumption might be made that *Distocambarus* (*F.*) *carlsoni* links the genera *Distocambarus* and *Cambarus*. Assuming that the latter contains the more advanced species, if *D.* (*F.*) *carlsoni* links the two genera, and if one maintains the current concept of the origin of at least some *Cambarus* from an orconectoid ancestor (see Hobbs 1969), the conclusion might well be reached that the genus *Cambarus* as currently constituted has had a diphyletic origin. In my opinion, the *Cambarus*-like characteristics of *D.* (*F.*) *carlsoni* have been acquired independently. If such a conclusion is accepted then the genus *Cambarus* may be assumed to represent a group of species with a more recent common ancestry than any member has had with crayfishes assigned to other groups. But what recognition should be accorded the species described here?

The fact that *D.* (*F.*) *carlsoni* shares the list of features just cited with the two species placed in *Distocambarus* by Hobbs and Carlson (loc. cit.) suggests that assigning it to that genus is appropriate; however, there are several characteristics that set it apart from them: (1) The blade-like central projection on the first pleopod of the first form male. This feature, so strikingly resembling that typical of most members of the genus *Cambarus,* represents an apomorphic (lengthening of the terminal element) departure from the rather shorter and more distally oriented projection in the other two members of *Distocambarus.*

(2) The restricted hinge motion of the annulus ventralis. Whereas in the two members of the subgenus *Distocambarus* the annulus is broadly hinged and swings through an arc of some 90 degrees, that of *Fitzcambarus* has an indistinct, narrow hinge anteriorly, and its arc of motion is no greater than 30 to 40 degrees.

(3) The comparatively small postannular plate. This small wedge-like sclerite bears little resemblance to its conspicuous homologue in the subgenus *Distocambarus.* In the two species belonging to the latter, this plate-like structure may extend anteriorly, covering the posterior part of the depressed annulus ventralis (in *D.* (*D.*) *devexus*), or project more ventrally when the annulus is depressed (in *D.* (*D.*) *crockeri*); in *D.* (*F.*) *carlsoni* it is not plate-like and does not extend so far ventrally as the annulus even when the latter is depressed.

(4) The shorter, proportionately broader chela. The comparatively shorter, broad chela of *D.* (*F.*) *carlsoni* is cambaroid, resembling that of members of the subgenus *Depressicambarus,* whereas that of the two members of the nominate subgenus is distinctly procambaroid, possessing an elongate palm and resembling the chelae of certain members of the subgenera *Austrocambarus, Girardiella,* and *Ortmannicus.*

(5) The more extreme adaptations to a fossorial habitat. The rostrum of *D.* (*F.*) *carlsoni* is decidedly shorter than that in the two species included here in the nominate subgenus; the areola is conspicuously narrower; the abdomen is proportionately smaller, and the pereiopods are decidedly more stocky.

As pointed out above, in my opinion, the affinities of this crayfish are clearly with the disjunct species pair that has been assigned to the genus *Distocambarus.* Because of the unique combination of characters demonstrated by his *Procambarus* (*Distocambarus*) *devexus,* and believing it to be more closely allied to members of *Procambarus* than to those of other genera, Hobbs (1981) assigned it to that genus and erected for its reception the monotypic subgenus *Distocambarus* signifying its remoteness from other species groups within the genus. With the discovery of a closely allied species, *Distocambarus* (*D.*) *crockeri,* Hobbs and Carlson (1983) believed that a better representation of the kinship of these with other crayfishes would be had if *Distocambarus* were elevated to generic rank. Taking cognizance of the unique features that these two crayfishes share, and suggesting the similarities and differences between them and *D.* (*F.*) *carlsoni,* I am proposing that the latter be assigned to the monotypic subgenus *Fitzcambarus* within the genus *Distocambarus.*

Ecological notes.—Distocambarus (*F.*) *carlsoni* is a primary burrower, and I suspect that it is rare that members of the species are found far from one of the mouths of its complex tunnel system. In the type-locality, it shares the low-lying swamp and seepage area with another primary burrower, *Cambarus* (*Jugicambarus*) *carolinus* (Erichson, 1846:87), but the two seem to have partitioned the area on the basis of comparatively static and flowing groundwater. The occurrence of the latter species in the swampy area may well be limited to sections where there is an active movement of the ground water, at least some of which emerges to the surface and flows toward the nearby creek; indeed, on 2 November 1982, water was issuing from the mouths of the tunnels of two of the specimens obtained, and the other two individuals were taken from burrows out of which water trickled when they were opened. There on the eastern periphery of the swamp, the land rises more abruptly than on the more gentle slope where the burrows of *Distocambarus* (*F.*) *carlsoni* were found. One to three openings which are often surrounded by irregular piles of earthen pellets mark the domiciles of the latter crayfish. There seems to be no pattern to the configuration of the complex system of galleries, and no doubt any model that might have been instituted would have been modified through necessity by the mats of roots of trees among which the resulting tunnels are entwined. In most burrows, horizontal passageways radiate irregularly from one or two vertical tunnels that are sufficiently deep to penetrate the water table. Side passages that end blindly may extend in almost any direction from the principal galleries. As in burrows of most crayfishes that spend the greater part of their lives in the soil, those inhabited by females are more highly branched than those occupied by males.

Both of the burrowing crayfishes found at this locality are infested with entocytherid ostracods. *Cambarus* (*J.*) *carolinus* harbors only one species, *Harpagocythere georgiae* Hobbs III (1965:163), whereas *Distocambarus* (*F.*) *carlsoni* is infested with two more wide ranging ones, *Ankylocythere ancyla* Crawford (1965:148) and *Entocythere dorsorotunda* Hoff (1944:332). The latter two ostracods have been found on a number of different crayfishes, but *H. georgiae*, which has been reported from a single locality, was obtained from a collection containing *C.* (*J.*) *carolinus* and *C.* (*Depressicambarus*) *latimanus* (LeConte, 1856). In the latter instance, whether or not both crayfishes bore this commensal is not known. Perhaps its host is limited to *C.* (*J.*) *carolinus*, the habitat of which is much more restricted than that of *C.* (*D.*) *latimanus*, a crayfish that tolerates a wide range of ecological conditions existing from the panhandle of Florida northward to northern North Carolina.

Acknowledgments

I am grateful to Paul H. Carlson and to Georgia B. Hobbs for their assistance in collecting the specimens on which this paper is based and to Denton W. Crocker, Skidmore College, H. H. Hobbs III, Wittenberg University, and C. W. Hart, Jr., a Smithsonian colleague, for their criticisms of the manuscript.

Literature Cited

Crawford, E. A., Jr. 1965. Three new species of epizoic ostracods (Ostracoda, Entocytheridae) from North and South Carolina.—American Midland Naturalist 74(1):148–154, 16 figures.

Erichson, W. F. 1846. Uebersicht der Arten der Gattung *Astacus*.—Archiv für Naturgeschichte, Berlin 12(1):86–103.

Hobbs, Horton H., Jr. 1969. On the distribution and phylogeny of the crayfish genus *Cambarus*. *In* Perry C. Holt, Richard L. Hoffman, and C. Willard Hart, Jr., The distributional history of the biota of the southern Appalachians, Part I: Invertebrates.—Virginia Polytechnic Institute, Research Division Monograph 1:93–178, 20 figures.

———. 1981. The crayfishes of Georgia.—Smithsonian Contributions to Zoology 318:viii + 549 pages, 262 figures.

———, and Paul H. Carlson. 1983. *Distocambarus* (Decapoda: Cambaridae) elevated to generic rank, with an account of *D. crockeri,* new species, from South Carolina.—Proceedings of the Biological Society of Washington 96(3):420–428, 1 figure.

Hobbs III, H. H. 1965. Two new genera and species of the ostracod family Entocytheridae, with a key to the genera.—Proceedings of the Biological Society of Washington 78(19):159–164, 6 figures.

Hoff, C. Clayton. 1944. New American species of the ostracod genus *Entocythere.*—American Midland Naturalist 32(2):327–357, 33 figures.

LeConte, John. 1856. Descriptions of new species of *Astacus* from Georgia.—Proceedings of the Academy of Natural Sciences of Philadelphia 7:400–402.

Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 440–451

DISPOSITION OF THREE SPECIES OF ONISCOIDEA FROM WESTERN ATLANTIC SEASHORES (CRUSTACEA: ISOPODA: HALOPHILOSCIIDAE AND PHILOSCIIDAE)

George A. Schultz

Abstract.—Three species of terrestrial isopods from the seashore, *Alloniscus compar* Budde-Lund, *Philoscia culebrae* Moore, and *Philoscia vittata* Say, are discussed. The first two are placed in *Vandeloscia* Roman (family Halophilosciidae), and *P. vittata* is placed in the new genus *Sayoscia* (family Philosciidae). Other related species are discussed briefly. Distribution and some general biology of the species are considered.

Three species of terrestrial isopod crustaceans, *Alloniscus compar* Budde-Lund (1893), *Philoscia culebrae* Moore (1901) and *Philoscia vittata* Say (1818), were among those included by Van Name (1936) in his comprehensive work on isopods from the New World. The true identity of the three has never been adequately resolved (Lemos de Castro 1965; Schultz 1974; Ferrara 1974) so with additional morphological evidence they are discussed and reclassified here. *Alloniscus compar* is considered to be too indefinitely known to be classified further, but records of specimens which have been called by Budde-Lund's name are reconsidered and placed in *Vandeloscia* Roman (1977). *Philoscia culebrae* is also placed in *Vandeloscia*. The species *Philoscia vittata* is placed in a new genus.

The two species of *Vandeloscia* are placed in the family Halophilosciidae (=Halophilosciinae Kesselyák, 1930, family Oniscidae as defined by Vandel 1962: 474) because they have similar genital apophyses, among other characters, which are used to define members of the group. The subfamily has been considered to be a full family by Vandel (1973:27) followed by Ferrara (1974:207) and Ferrara and Taiti (1979:110). No formal or actual raising of it to the full family level appears in the literature. The nominate genus *Halophiloscia* was described in the tribe Halophilosciini of the family Oniscidae by Verhoeff (1908:521). *Philoscia vittata*, although in many ways similar to species of *Vandeloscia*, is retained in Philosciidae principally because it lacks a bilobed genital apophysis.

Vandeloscia Roman, 1977

Vandeloscia Roman, 1977:146.—Ferrara and Taiti, 1979:110.

The genus was described on a species determined by Chelazzi and Ferrara (1978) and by Ferrara and Taiti (1979) to be a synonym of "*Littorophiloscia*" *compar* (Budde-Lund). The species "*compar*" has been placed in *Philoscia*, *Alloniscus*, *Littorophiloscia*, and "*Littorophiloscia*" so that Roman's description is the first time that "*compar*" as a species has been placed in a distinct genus. The inadequately defined, erroneously used name *Alloniscus compar* Budde-Lund (1893) which has been used several times in the past remains an uncertain species. The species name of Strouhal (1966) has priority over that of Roman as will be shown below. *Alloniscus compar* of Vandel (1952) was adequately described and is identical to *Halophiloscia* (*Stenophiloscia*) *riedli* Strouhal (1966) and to *Vandeloscia orientalis* Roman (1977). The taxonomic status of the species is discussed under *V. riedli* here.

The genus was not defined in a separate section by Roman, who distinguished it from *Halophiloscia* Verhoeff by the setation of the palp of the maxilliped. Pleopod 1 of the male is used here to distinguish the genus and species rather than the much less definitive arrangement of setae on the palp of the maxilliped. A brief diagnosis of the genus is given here based on the two species now in the genus. The diagnosis of *Vandeloscia* Roman is written with the criteria for defining genera of Philosciidae, compiled by Vandel and listed by Taiti and Ferrara (1980:56), in mind.

Diagnosis.—Pleon narrower than peraeon; edges on pleonal segments show slightly (dorsal view). Pigmentation, especially on edges of peraeonal segments and on peraeopods, conspicuously arranged in chromatophores. No glands, but tiny lateral nodes present on peraeonal segments. Cephalon with no frontal line; supra-antennal line well defined. Tip of genital apophysis strongly bilobed. Endopod of male pleopod 1 with short, narrow apex strongly folded laterally. Peraeopod I sexually dimorphic. Dactylar organs present on peraeopods.

Type-species.—*Halophiloscia* (*Stenophiloscia*) *riedli* Strouhal (1966), by monotypy.

Derivation and gender of name.—The genus is named for the late French carcinologist, Dr. Albert Vandel. The gender is feminine.

Other species.—*Vandeloscia culebrae* (Moore, 1901) (see below).

Affinities.—The lobes on the tip of the genital apophysis are not as long in species of *Vandeloscia* as they are in species of *Halophiloscia*.

Vandeloscia riedli (Strouhal, 1966)
Fig. 1J–R

Alloniscus compar Budde-Lund.—Vandel, 1952:112, figs. 30–33.—Arcangeli, 1958: 242.—Cloudsley-Thompson, 1971:10.—Schultz, 1974:149 (as *P. compar* Budde-Lund, 1885).—Vandel, 1977:393.—Roman, 1977:135.

Littorophiloscia compar (Budde-Lund).—Lemos de Castro, 1965:94, figs. 31–33.—Chelazzi and Ferrara, 1978:192.—Ferrara and Taiti, 1979:110.

"*Littorophiloscia*" *compar* (Budde-Lund).—Ferrara, 1974:207, figs. 63–79.

Halophiloscia (*Stenophiloscia*) *riedli* Strouhal, 1966:325, figs. 1–23.

Philoscia (*Setaphora*) sp.—Roman, 1970:168.

Vandeloscia orientalis Roman, 1977:146, figs. 20–23.

Stenophiloscia riedli Strouhal.—Ferrara, 1974:212, fig. 82.

nec Alloniscus compar Budde-Lund, 1893:124.—Dollfus, 1893:345.—Van Name, 1936:218.—Arcangeli, 1960:47 (=*incertae sedis*).

The species is the same as that described by Vandel (1952) and Lemos de Castro (1965) from the New World, and Ferrara (1974), Roman (1977) and Strouhal (1966) from the Old World as comparison of their illustrations and those here will show. According to Arcangeli (1958:242) Vandel's *A. compar* is certainly not conspecific with Budde-Lund's *A. compar*. In fact there is no reason to believe

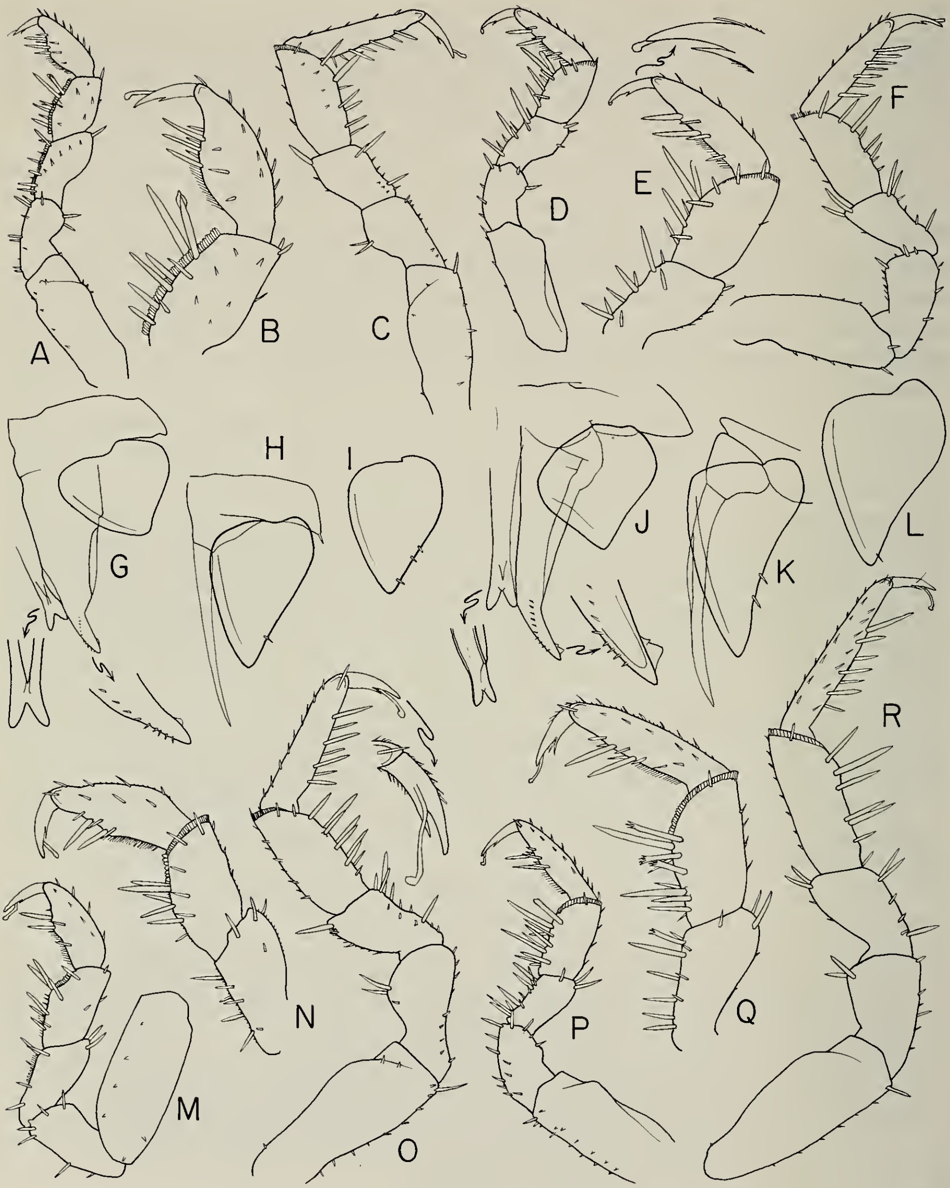


Fig. 1. A–I, *Vandeloscia culebrae*: A, Male peraeopod I; B, Detail male peraeopod I; C, Male peraeopod VII; D, Female peraeopod I; E, Detail female peraeopod I; F, Female peraeopod VII; G–I, Male pleopods 1–3. J–R, *Vandeloscia riedli*: J–L, Male pleopods 1–3; M, Male peraeopod I; N, Detail male peraeopod I; O, Male peraeopod VII; P, Female peraeopod I; Q, Detail female peraeopod I; R, Female peraeopod VII.

that it is the briefly described *Alloniscus compar* Budde-Lund (1893) which was not illustrated and which has as its type-locality "La Moka and vicinity of Caracas," Venezuela. The type-locality apparently is not a beach, nor near a beach, which is where all specimens like those described by Vandel (1952) and others were collected. Until more specimens from the type-locality (the exact location of "La Moka" has yet to be determined) are available, *A. compar* Budde-Lund must be considered to be *incertae sedis.*

From Budde-Lund's brief Latin description without illustrations of *A. compar,* it can only be concluded that the species has eyes and three flagellar articles on antenna 2. The other characters of Budde-Lund's species are so generally described that they might be present on any oniscoid. Vandel (1952), when he used Budde-Lund's name for his specimens, made no mention of Budde-Lund's brief description. Since the locations of the collections of other species included by Budde-Lund (1893) were not at the seashore, *A. compar* probably was not collected there or it would have been mentioned. The location where the specimens of Vandel were collected was "Orchilla, Iles-sous-le-Vent, à l'est de l'Archipel de los Roques." The location is a tiny islet and, although not directly stated by Vandel, the specimens most probably were taken on the seashore as were some other species included by Vandel. The only thing which the collection locations of the two species have in common (assuming that "vicinity of Caracas" is inland like the city) is that they are in Venezuela.

Based on Vandel's description, Arcangeli (1958:243) removed *Alloniscus compar* of Vandel from *Alloniscus* Dana. Arcangeli stated that Vandel's *A. compar* probably belonged to a different genus of philoscomorph, which he did not name; he continued, however, to keep *A. compar* in *Alloniscus.* Roman (1977:135) also included *A. compar* in her list of species of *Alloniscus,* never relating it to *A. compar* of Vandel. Ferrara and Taiti (1979:110) finally showed the similarities of Vandel's and Roman's specimens, but did not discuss any of the taxonomic implications. *Vandeloscia riedli* is not completely redescribed here because Vandel (1952), Ferrara (1974), Roman (1977), and Strouhal (1966) adequately illustrated and described it. Details of male and female peraeopods I and VII and of male pleopods 1 and 2 are included here so the species can be easily distinguished from *V. culebrae* (Moore) with which it has been confused in the past.

Diagnosis.—Tiny, but obscure, lateral nodes present on all peraeonal segments. Endopod of pleopod 1 of male with large scalelike subapical process on laterally folded tip. Propodus of male peraeopod I with 2 large setae on inner margin. Exopod of pleopod 2 of male with 2 setae on posterolateral border.

Description.—See Vandel (1952:112, figs. 30–33), Ferrara (1974:207, figs. 53–79), Roman (1977:146, figs. 20–23) and Strouhal (1966:325, figs. 1–23) for descriptions. Strouhal illustrated the small lateral nodes on peraeonal segment I of his specimens, and they were present but very obscure on the specimens examined here. More than one specimen had to be examined before they were discovered. Apparently lateral nodes were missed by Roman (1977).

Measurements.—Males up to 5.9 mm long; females up to 6.0 mm long.

Type-locality.—Isle of Abu Mengar, south of Ghardaga, in the Red Sea of Egypt.

Distribution.—Gulf of Aquaba and Red Sea coast of Egypt; Suakin, Sudan; Sar Uanle and Gesira, Mogadishu, Somalia; Tulear, Madagascar; St. Helena Island, South Atlantic; Bay of Bengal, India; Yucatan, Mexico; San Pedro, Belize; Orchilla, Venezuela; Cabo Frio, Brazil.

Type-specimens.—Strouhal (1966) makes no mention of the disposition of the type-specimens, but they are probably in the Natural History Museum in Vienna.

Material examined.—Yucatan, Mexico, and Belize, Central America. Specimens from both locations have been deposited in the National Museum of Natural History.

Affinities.—See Affinities section under *Vandeloscia culebrae.*

Vandeloscia culebrae (Moore, 1901)
Fig. 1A–I

Philoscia culebrae Moore, 1901:176, pl. 11, figs. 13–17.—Richardson, 1905:604, fig. 660.—Boone, 1918:602.—Van Name, 1924:194, 195;—1936:168, fig. 86.—Vandel, 1968:114.—Schultz, 1974:149.

Halophiloscia culebrae (Moore).—Vandel, 1945:242;—1949:8.—Arcangeli, 1948: 482.—1958:242.

Littorophiloscia compar culebrae (Moore).—Lemos de Castro, 1965:96, figs. 36–39.

Philoscia miamiensis Schultz, 1966:457, figs. 1–33.

Alloniscus culebrae Moore, 1901.—Roman, 1977:137.

nec Philoscia culebrae.—Pearse, 1915:534, fig. B.

Moore (1901) gave a very general description of the two females which he collected on a beach on Culebra Island off Puerto Rico. The species generally is darker in color than *V. riedli,* but the chromatophores are still very conspicuous on the edges of the peraeonal segments and the peraeopods. The species is much like *V. riedli,* but differs from that species in the characters which are included in the diagnosis.

Diagnosis.—Tiny lateral nodes present on peraeonal segments. Endopod of pleopod 1 of male with small scalelike subapical process on laterally folded tip. Propodus of male peraeopod I with 3 large setae on inner margin. Exopod of pleopod 2 of male with 1 seta on posterolateral border.

Description.—See Schultz (1966) for overall view and Lemos de Castro (1965) for detail of male pleopods. Some differences or additions to the description include the fact that there are 9, not 21, ocelli, and tiny lateral nodes are present on the peraeopods. Even though the lateral nodes are tiny, they are more distinct than those of *V. riedli.*

Measurements.—Males up to 5.0 mm long; females up to 6.1 mm long.

Type-specimens.—Moore (1901) deposited his specimens (2 females) in the National Museum of Natural History. Very little is to be learned from them without dissection other than that they are similar when compared to fresh female specimens of the species from Cedar Key, Florida, and St. John, Virgin Islands.

Type-locality.—Culebra Island (east of Puerto Rico).

Distribution.—Culebra Island, Puerto Rico; Puerto Rico; St. John, Virgin Islands; east and west coasts of Florida. Abundant in maritime drift and other organic detritus on beaches.

Material examined.—Cedar Key, west coast of Florida, and St. John, Virgin Islands. Specimens from each location have been deposited in the National Museum of Natural History.

Affinities.—It is difficult to tell females of the two species apart so no attempt is made here to distinguish them. Although the range of color of individuals in a freshly preserved group of specimens of both species is great, the average density of color of fresh specimens of *V. culebrae* is greater. The two species can best be distinguished by comparing the size of the scalelike process on the tip of the endopod of male pleopod 1. It is smaller and not always too distinct in *V. culebrae*; whereas it is larger and divided into one large and one small process as shown here (Fig. 1J) for *V. riedli*. The propodus of male peraeopod I bears three large setae in *V. culebrae* and only two in *V. riedli*. Other consistent differences are present on other appendages and can be seen by comparing the illustrations given here and those of other workers.

The differences present here which are used to distinguish the two species, in general, are valid if one also compares the two species as described from other locations or from the descriptions of other workers from the literature. Specimens of *V. culebrae* described by Schultz (1966, as *Philoscia miamiensis*) and Lemos de Castro (1965, as *Littorophiloscia compar culebrae*) have the same type of small scalelike process on the tip of the endopod of male pleopod 1. They also have the same corresponding configuration of setae on the inner margins of the propodus and carpus on male peraeopod I.

Specimens of *V. riedli* as presented in the illustrations of Vandel (1952, as *Alloniscus compar*), Lemos de Castro (1965, as *Littorophiloscia compar compar*), Strouhal (1966, as *Halophiloscia* (*Stenophiloscia*) *riedli*), Ferrara (1974, as "*Littorophiloscia*" *compar*) and Roman (1977, as *Vandeloscia orientalis*) have the same large scalelike process on the tip of the endopod of male pleopod 1. Correspondance between the configurations of other structures illustrated for the two species are also quite striking so that the two species can be said to be distinct both by using fresh specimens and by comparisons of illustrations and descriptions of the specimens in the literature. The differences are much more consistent than is to be expected at the subspecies level as was considered to be so by Lemos de Castro (1965). *Vandeloscia culebrae* is tropical in distribution, but it also ranges into subtropical Florida. *Vandeloscia riedli* is much more widespread on tropical beaches in the West Indies, Central America, and northern South America and is common in parts of the Old World as well.

Sayoscia, new genus

The single species of the genus lives along the eastern shore of North America from Canada to Texas. The genus is placed in the broadly defined Philosciidae, not Halophilosciidae, because the type-species does not have the bilobed genital apophysis characteristic of the Halophilosciidae. When more species of the philoscomorph complex of species of oniscoids are adequately defined, better criteria for separating the Halophilosciidae from the Philosciidae will be distinguished. The species is darkly pigmented with distinct chromatophores on the peraeonal segments and on the peraeopods. The genital apophysis is without a bilobed tip, but has well developed grooves on the edges into which the very broad endopods of pleopod 1 fit.

Diagnosis.—Peraeonal segments without glands, but with tiny lateral nodes (with seta about twice size of other body setae) on segments I–IV. Short apical extensions markedly bent laterally on tips of very broad endopod of male pleopod 1. Peraeopods I, II, and VII similar in males and females. Dactylar organs present

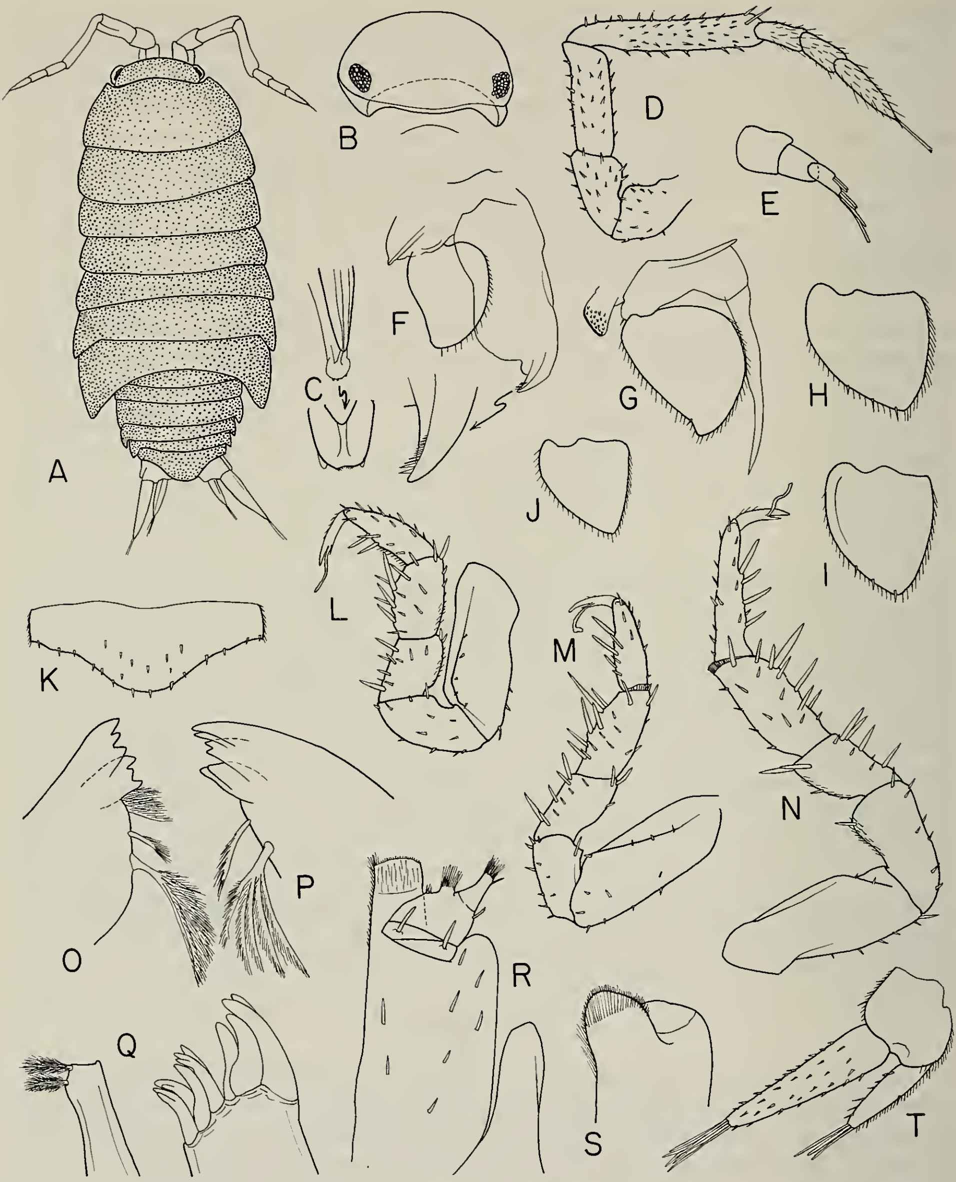


Fig. 2. *Sayoscia vittata*: A, Dorsal view male 4.3 mm long; B, Frontal view cephalon; C, Tip of genital apophysis; D, Antenna 2; E, Antenna 1; F–J, Male pleopods 1–5; K, Pleotelson; L–N, Male peraeopods I, II and VII; O, Left mandible; P, Right mandible; Q, Maxilla 2 (endopod and exopod); R, Maxilliped; S, Maxilla 1; T, Uropod.

on peraeopods. Mandibles with molar setae narrow at base with compound apex. Lacinia mobilis on each mandible.

Type-species.—Philoscia vittata Say (1818).

Derivation and gender of name.—The genus is named for Thomas Say, American entomologist and naturalist, who described the type-species. The gender is feminine.

Affinities.—The single species of the new genus is similar to species of *Vandeloscia* Roman, but lacks the bilobed tip of the genital apophysis found in species of that genus.

Sayoscia vittata (Say, 1818)
Fig. 2A–F

Philoscia vittata Say, 1818:429.—DeKay, 1844:50.—White, 1847:99.—Verrill and Smith, 1873:569.—Harger, 1879:157;—1880:306 (not pl. 1, fig. 1).—Budde-Lund, 1885:209.—Underwood, 1886:361.—Richardson, 1900:305;—1901:565;—1905: 605, figs. 662–663 (not fig. 661).—Paulmier, 1905:181 (not fig. 53).—Rathbun, 1905:45, 4.—Fowler, 1912:233 (not pl. 66).—Sumner, Osborn, and Cole, 1913: 661.—Pratt, 1951:442 (not fig. 611).—Kunkel, 1918:240 (not fig. 77).—Van Name, 1936:115 (not fig. 52).—Schultz, 1974, fig. 3b, c, f;—1975:186;—1977:154.

Philoscia robusta Schultz, 1963:27, figs. 1–22;—1965:108;—1966:461.

Philoscia (*Philoscia*) *muscorum* (Scopoli), var. *sylvestris* (Fabricius).—Blake, 1931:351.—Procter, 1933:248.

Philoscia muscorum (Scopoli).—Pratt, 1951:442.

Littorophiloscia vittata (Say).—Alexenburg, 1962:23.—Bousfield, 1962:51.—Lemos de Castro, 1965:90, figs. 21–30.

partim Philoscia muscorum (Scopoli).—Harger, 1880:306 (pl. 1, fig. 1).—Schultz, 1965:107.—1974:147.

The species was redescribed by Schultz (1963) as *Philoscia robusta*. It was further discussed as *P. vittata* Say by Schultz (1974) who showed how it and *P. muscorum* (Scopoli), which shares part of its range, were confused by early workers. Indeed, the illustration of Harger (1880, pl. 1, fig. 1) of *P. muscorum* has been repeated by most other workers who encountered *P. vittata* on the east coast of the United States. The two species easily can be distinguished by comparing male pleopods 1. The illustrations of the species here are of specimens collected in south New Jersey not far from the type-locality as recorded by Van Name (1936).

Diagnosis.—See generic diagnosis.

Description.—Schultz (1966) completely described the species as *Philoscia robusta* and into that description the information in the generic diagnosis section can be incorporated.

Measurements.—Males to 5.8 mm long; females to 6.0 mm long.

Type-locality.—Great Egg Harbor, New Jersey (Van Name 1936), or according to Say (1818), "United States, common." Say worked at the Academy of Natural Sciences, Philadelphia, and field trips frequently were taken to the New Jersey seashore. Say also toured much of the shore of the then United States and perhaps collected the species as far south as Georgia.

Type-specimens.—Dry specimens were deposited in the Academy of Natural Science in Philadelphia, but they are no longer present (Lemos de Castro 1965: 92). One dry specimen is present in the British Museum (Natural History) (White 1847) apparently presented by Thomas Say himself. Types and other specimens

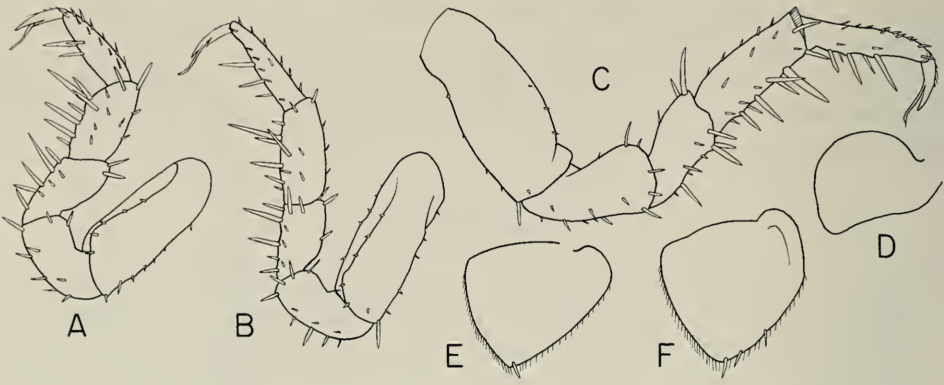


Fig. 3. *Sayoscia vittata*: A–C, Female peraeopods I, II and VII; D–F, Female pleopods 1–3.

of *Philoscia robusta* Schultz, a junior synonym, from near Beaufort, North Carolina, are in the National Museum of Natural History and more specimens from New Jersey have been deposited there in connection with this redescription.

Material examined.—The specimens examined here are from south Cape May County, New Jersey, on the edge of Grassy Sound.

Distribution.—The species is present on the Atlantic coast of North America from the Bay of Fundy, Canada, to the mouth of the St. Marys River, Georgia. Specimens are present on the Gulf shore at least to the southern Texas coast. They are abundant in decayed organic vegetation, under the maritime drift in marine swamps, and in places regularly moistened by marine or estuarine waters.

Disposition of some species of philoscomorphs from the New World which have been considered related to the three species considered above are those of the ''Halophiloscia'' group of Van Name (1936:167, 515). The species are *Philoscia bermudensis, P. brasilensis, P. culebrae, P. culebroides, P. nomae,* and *P. richardsonae.* Vandel (1945:242, 1949:8) gives maps of the distribution of the species of *Halophiloscia* Verhoeff including members of Van Name's ''Halophiloscia'' group. Vandel (1962:475) considered *Littorophiloscia* Hatch (1947) to be a junior synonym of *Halophiloscia* Verhoeff, but later (1968:113) he considered it to be valid with one species *L. richardsonae* (Holmes and Gay), the type-species. Lemos de Castro (1958a, 1965) included *Alloniscus compar* Budde-Lund and *Philoscia vittata* Say and some of the above species of the ''Halophiloscia'' group as definitely or tentatively in *Littorophiloscia* Hatch. He based his conclusions on similarities of certain characters, especially general similarities of the shapes of the endopods of male pleopod 1, to those of *L. richardsonae.*

The disposition of all species considered in the ''Halophiloscia'' group of Van Name (1936) and *Littorophiloscia* as expanded by Lemos de Castro (1965) is given below. Formal synonymies for species in the list and not included in synonymies above are to be found in the works mentioned after the valid name of the species.

Philoscia bermudensis Dahl = *Halophiloscia couchi* (Kinahan); see Vandel (1962: 477), and Schultz (1972:86).

Philoscia bonariensis Giambiagi de Calabrese = *Halophiloscia couchi* (Kinahan); see Reca (1972:407).

Halophiloscia brasilenses Moreira = *Benthana olfersi* (Brandt); see Lemos de Castro (1958b:98), and Vandel (1962:475).

Alloniscus compar Budde-Lund = *incertae sedis*; see text.

Alloniscus compar Budde-Lund of Vandel (1952:112) = *Vandeloscia riedli* (Strouhal); see text.

Philoscia culebrae Moore = *Vandeloscia culebrae* (Moore); see text.

Philoscia culebroides Van Name = *Nesophiloscia culebroides* (Van Name); see Vandel (1968:113).

Philoscia nomae Van Name = *Nesophiloscia culebroides* (Van Name); see Vandel (1968:113).

Philoscia richardsonae Holmes and Gay = *Littorophiloscia richardsonae* (Holmes and Gay); see Lemos de Castro (1965:88), and Vandel (1968:113).

Philoscia vittata Say = *Sayoscia vittata* (Say); see text.

Acknowledgments

I would like to thank Dr. Thomas E. Bowman of the National Museum of Natural History for reviewing the manuscript. I would also like to acknowledge the use of Separately Budgeted Research Funds from Jersey City State College for the project.

Literature Cited

Arcangeli, A. 1948. Il genere *Halophiloscia* Verhoeff nella regione mediterranea.—Archivo Zoologico Italiano 33:473–485.

———. 1958. Le specie di Isopodi terrestri che furono erroneamente assegnate al genere *Alloniscus* Dana.—Memorias del Museo Civico di Storia Naturale di Verona 6:239–252.

———. 1960. Revisione del genere *Alloniscus* Dana. Il sistema respiratorio speciale agli exopoditi dei pleopodi delle specie appartenenti allo stesso genere (Crostacei isopodi terrestri).—Bolletino Istituto e Museo di Zoologia dell'Universita di Torino 6:17–79.

Alexenburg, M. L. 1962. A key to the sowbugs of Long Island, New York.—Turtox News 40(1): 22–23.

Blake, C. H. 1931. Distribution of New England wood lice (on Isopoda Oniscoida, third paper).—Occasional Papers of the Boston Society of Natural History 5:349–355.

Boone, P. L. 1918. Description of ten new isopods.—Proceedings of the United States National Museum 54(2253):591–604.

Bousfield, E. L. 1962. Studies on the littoral marine arthropods from the Bay of Fundy region.—Bulletin of the National Museum of Canada 183:42–62.

Budde-Lund, G. 1885. Crustacea Isopoda terrestria per familias et genera et species descripta.—Hauniae, pp. 1–319.

———. 1893. Landisopoder fra Venezuela, indsamlede af Dr. Fr. Meinert.—Entomologiske Meddelelser, pp. 111–129.

Chelazzi, G., and F. Ferrara. 1978. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 19. Zonation and activity of terrestrial isopods (Oniscoidea).—Monitore Zoologico Italiano N.S. Supplemento XI, 8:189–219.

Cloudsley-Thompson, J. L. 1971. The littoral terrestrial fauna of Suakin, Sudan.—Entomologist's Monthly Magazine 107:10.

DeKay, J. E. 1844. Zoology of New York, or the New York fauna. Part IV. Crustacea (Isopoda, pp. 42–54) Carroll and Cook: Albany.

Dollfus, A. 1893. Voyage de M. E. Simon au Venezuela (Décembre 1887–Avril 1888).—Annales de la Société Entomologique de France 62:339–346.

Ferrara, F. 1974. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 3. Terrestrial isopods.—Monitore Zoologico Italiano N.S. Supplemento V, 15:191–220.

———, and S. Taiti. 1979. A check-list of terrestrial isopods from Africa (south of the Sahara).—Monitore Zoologico Italiano N.S. Supplemento VII, 1:1–114.

Fowler, H. W. 1912. The Crustacea of New Jersey.—Annual Report of the New Jersey State Museum 1911:29–651.

Harger, O. 1879. Notes on New England Isopoda.—Proceedings of the United States National Museum 2(79):157–165.

———. 1880. Report on the marine Isopoda of New England and adjacent waters.—Report of the United States Commissioner of Fish and Fisheries, for 1878. Part 6:297–462.

Hatch, M. H. 1947. The Chelifera and Isopoda of Washington and adjacent regions.—University of Washington Publications in Biology 10:155–274.

Kesselyák, A. 1930. Halophiloscinae n. subfam. für die Gattungen *Halophiloscia* und *Stenophiloscia*.—Zoologischer Anzeiger 98:282–285.

Kunkel, B. W. 1918. The Arthrostraca of Connecticut. Part II. Isopoda.—Connecticut State Geological and Natural History Survey Bulletin 26:185–261.

Lemos de Castro, A. 1958a. On the systematic position of some American species of *Philoscia* Latreille (Isopoda, Oniscoidea).—American Museum Novitates 1908:1–10.

———. 1958b. Revisão do gênero *Benthana* Budde-Lund, 1908 (Isopoda, Oniscidae).—Arquivos do Museu Nacional Rio de Janeiro 46:85–118.

———. 1965. On the systematics of the genus *Littorophiloscia* Hatch (Isopoda, Oniscidae).—Arquivos do Museu Nacional Rio de Janeiro 53:85–98.

Moore, H. F. 1901. Report on Porto Rican Isopoda.—Bulletin Number 20, United States Fisheries Commission 2:163–176.

Paulmier, F. C. 1905. Higher Crustacea of New York City.—Bulletin New York State Museum 91: 117–189.

Pearse, A. S. 1915. An account of the Crustacea collected by the Walker Expedition to Santa Marta, Colombia.—Proceedings of the United States National Museum 49(2123):531–556.

Pratt, H. S. 1951. A manual of the common invertebrate animals (exclusive of insects).—The Blakiston Co., Philadelphia, xviii + 854 pp.

Procter, W. 1937. Biological survey of the Mount Desert region. Part V. Marine fauna.—Wister Institute of Anatomy and Biology, Philadelphia, 402 pp.

Rathbun, M. J. 1905. Fauna of New England. 5. List of the Crustacea.—Occasional Papers of the Boston Society of Natural History 7:1–117.

Reca, A. R. 1972. Oniscoideos Argentinos. II. Tres especies de isopodos terrestres de la costa maritima Bonaerense (Crustacea, Isopoda).—Physis 31:405–410.

Richardson, H. 1900. Synopses of North-American invertebrates. VIII. The Isopoda.—American Naturalist 34:207–230.

———. 1901. Key to the isopods of the Atlantic coast of North America with descriptions of new and little known species.—Proceedings of the United States National Museum 23(1222):493–579.

———. 1905. A monograph on the isopods of North America.—Bulletin of the United States National Museum 54:I–LIII + 1–727.

Roman, M.-L. 1970. Écologie et répartition de certains groupes d'Isopodes dans les divers biotopes de la région de Tuléar (Sud-ouest de Madagascar).—Recueil des Travaux de la Station Marine d'Endoume, Marseille, Fascicule Hors Séries, Supplément 10:163–208.

———. 1977. Les oniscoides halophiles de Madagascar (Isopoda, Oniscoidea).—Beaufortia 26:107–152.

Say, T. 1818. An account of the Crustacea of the United States. By Thomas Say. Read September 22, 1918 (Concluded).—Journal of the Academy of Natural Sciences of Philadelphia 1:423–444.

Schultz, G. A. 1963. *Philoscia robusta*, a new species of terrestrial isopod crustacean from southeastern United States.—Journal of the Elisha Mitchell Scientific Society 79:26–29.

———. 1965. The reduction of *Philoscia vittata* Say, 1818, to a synonym of *Philoscia muscorum* (Scopoli, 1763).—Crustaceana 8:107–108.

———. 1966. *Philoscia miamiensis* n. sp., an isopod crustacean from Florida with ecological notes on the new species.—Transactions of the American Microscopical Society 85:457–462.

———. 1972. Ecology and systematics of terrestrial isopod crustaceans from Bermuda.—Crustaceana, Supplement 3:79–99.

———. 1974. The status of the terrestrial isopod crustaceans *Philoscia muscorum, P. vittata, P. robusta* and *P. miamiensis* in the New World (Oniscoidea, Philosciidae).—Crustaceana 27: 147–153.

———. 1975. Terrestrial isopod crustaceans (Oniscoidea) from coastal sites in Georgia.—Bulletin of the Georgia Academy of Science 34:185–194.

———. 1977. Terrestrial isopod crustaceans (Oniscoidea) from St. Catherines Island, Georgia.—Georgia Journal of Science 35:151–158.

Strouhal, H. 1966. Eine neue halophile *Stenophiloscia* aus dem Rotmeergebiete (Isop. terr.).—Annalen des Naturhistorischen Museum in Wien 69:323–333.

Sumner, F. B., R. C. Osborn, and L. J. Cole. 1913. A biological survey of the waters of Woods Hole and vicinity. Part II, Section III. A catalogue of the marine fauna.—Bulletin of the United States Bureau of Fisheries 31:547–794.

Underwood, L. 1866. List of the described species of fresh water Crustacea from America, north of Mexico.—Bulletin of the Illinois State Laboratory of Natural History 2:323–326.

Vandel, A. 1945. La répartition géographique des Oniscoidea (Crustacea Isopoda terrestres).—Bulletin Biologique de la France et de la Belgique 79:221–272.

———. 1949. La fauna Nord-Atlantique.—Revue Française d'Entomologie 16:1–11.

———. 1952. Étude des Isopodes terrestres récoltes au Venezuela par le Dr. G. Marcuzzi.—Memorie dell Museo Civico di Storia Naturale di Verona 3:59–203.

———. 1962. Isopodes terrestres (Deuxième Partie).—Faune de France 66:417–931.

———. 1968. I. Isopodes terrestres. *In* Mission zoologique Belge aux îles Galapagos et en Ecuador (N. et J. Leleup, 1964–1965).—Musée Royal de l'Afrique Centrale: Tervuren 1:37–168.

———. 1977. La faune terrestre de l'île de Sainte-Helene. Part 4. 1. Isopodes terrestres.—Annales Musée Royal de l'Afrique Centrale, Série 8, Sciences Zoologiques 220:385–426.

Van Name, W. G. 1924. Isopods from the Williams Galapagos Expedition.—Zoologica 5:181–210.

———. 1936. The American land and fresh-water isopod Crustacea.—Bulletin of The American Museum of Natural History 71:i–vii + 1–535.

Verhoeff, K. W. 1908. Ueber Isopoden. 15. Isopoden-Aufsatz.—Archiv für Biontology 2:335–387.

Verrill, A. E., and S. I. Smith. 1873. Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region.—Report of the United States Commissioner of Fish and Fisheries for 1871–1872, part 8:295–778, pls. 1–38.

White, A. 1847. List of the specimens of Crustacea in the collection of the British Museum.—Trustees of the British Museum: London, 143 pp.

15 Smith St., Hampton, New Jersey 08827.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 452–467

AN UNUSUAL SPECIES COMPLEX IN THE GENUS *EURYCOPE* (CRUSTACEA: ISOPODA: ASELLOTA) FROM THE DEEP NORTH ATLANTIC OCEAN

George D. F. Wilson

Abstract.—A finely differentiated species flock or species complex in the asellote isopod genus *Eurycope* is described. The complex consists of four new species, plus three individuals that may belong to a fifth new species. The characters of these closely related species agree with the present definition of *Eurycope,* but several features of this complex make them distinct from their congenors. The most unusual of these traits is the very elongate stylet on the male pleopod II. The occurrence of this character in the Asellota and its phylogenetic significance are discussed. The elongate stylet is considered to be a derived trait that has evolved independently on numerous occasions in the Asellota Janiroidea.

Introduction

The genus *Eurycope,* recently revised by Wilson and Hessler (1981), contains numerous discrete species groups. Two such groups are the *E. complanata* complex and the *E. inermis* cluster (Wilson 1983). Here, another species complex is described within the genus which, while classifiable as *Eurycope* under the present system, is unique compared to its congenors.

This group is designated the *longiflagrata* complex, after its most completely known species *E. longiflagrata* n. sp. The species of the complex all fit the present diagnosis of *Eurycope,* but are distinct in several traits from the other species in the genus. All males have a very distinctive external sexual apparatus: extremely long and whiplike stylets of the second pleopods that lie external to the pleopodal cavity, sometimes in grooves on the pleotelson dorsal surface. The body is generally longer and narrower than in typical species of *Eurycope.* The medial length of pereonite 4 is less than that of pereonites 1–3, in contrast to the typical situation of 4 anterior pereonites of similar length. The body depth is also unusual: deepest at pereonite 1 instead of at pereonite 5 or 6 as generally found within *Eurycope.*

The complex of species described here illustrates problems common in the study of deep-sea asellotes.

1. Even though the genus *Eurycope* has been revised, with a number of species removed to other genera, many species in the genus are poorly known, creating uncertainty about additional divisions of the genus. The characters of the *longiflagrata* complex fall within the definition of the genus, but its possession of unusual characters opens the possibility of the creation of a new genus, or the division of *Eurycope* into subgenera. Lack of knowledge prevents making a clear decision, so this complex is retained in *Eurycope* for the present.

2. Separation of the species of the *longiflagrata* complex is often difficult, because they are rare in deep-sea samples. Consequently, there are few individuals for a study of character variation, making range overlaps, where they occur, difficult to interpret. In addition, females are difficult to classify because the

species are very similar and the most definitive characters are found in the males. Therefore, one species is described here on a provisional basis, with the hope that additional material will appear which will clarify some of the problems remaining. Three specimens are described without any specific designation, although they may belong to a fifth new species.

Materials and Methods

The specimens on which this paper is based came from two sources. A longstanding deep-sea benthic ecology program at the Woods Hole Oceanographic Institution (WHOI samples), directed by H. L. Sanders, J. F. Grassle, and previously R. R. Hessler, has provided isopods collected on sampling transects on most of the major basins of the Atlantic Ocean. The Centre National de Tri d'Océanographie Biologique, directed by M. Segonzac is the second important source of specimens. This French national sorting center has kindly sent isopods that were collected on three major oceanographic expeditions: Intercalibration (INCAL samples), led by M. Sibuet; Abyplaine (ABYPL samples), led by C. Monniot; and Demeraby (DEMERABY samples), led by M. Sibuet and C. Monniot.

Types have been deposited at the United States National Museum of Natural History (cited as USNM). Remaining paratype and non-type specimens are retained in the research collection of Robert R. Hessler, Scripps Institution of Oceanography (RRH).

The methods and terminology used in this paper are those developed by Wilson and Hessler (1980) and Wilson (1983). Measurement characters are generally stated as ratios to factor out allometric variation; these values are given to a precision of two significant figures. Because the sample sizes are very small, no statistical accuracy is implied for these values, although ranges are given where measurements for more than one individual were available. Descriptions are based on adult type-specimens.

In the figures, mouthparts (except the mandible), pleopods, and uropods are shown in ventral view. Arrows indicate either enlarged sections of a limb, or structures of special interest which are labelled by a letter. In some cases, all setae are not shown but are indicated by u-shaped or circular marks at their insertions.

Systematics

Eurycope Sars, 1864

The *Eurycope longiflagrata* complex

Type species.—Eurycope longiflagrata n. sp.

Diagnosis.—Eurycope with elongate body, body length approximately 3 times body width, body deepest at pereonite 1. Rostrum of cephalon short, narrow, anteriorly rounded, often overhanging frons, lacking cephalic keels but with small stout setae. Cephalic frons sloping anteriorly in front of rostrum; frons-clypeal ridge distinct, rounded, not shaped like an inverted V, often projecting anteriorly above clypeal insertion. Posterolateral corner of mandible inserting on cephalon into distinct notch (Fig. 1C, D–N). Pereonite 4 dorsomedial length reduced compared to other pereonites. Male sexual morphology modified: pleopod I distally u- or v-shaped with lateral lobes extending posteriorly and medial lobes reduced or absent; pleopod II stylet extremely elongate, about 3–4 times protopod length in adult; pleotelson dorsal surface often with groove or incision beginning on posterolateral margin behind uropod insertions and extending anteriorly (Fig. 1F–G). Uropodal protopod not broadened medially; rami longer than protopod width.

Description.—Cephalon posterior to antennulae shorter than and almost as deep as pereonite 1. Lateral spine blunt and broad. Rostrum separated from cephalic dorsal surface by transverse depression; male rostrum often longer and narrower than that of female.

Pereonite 7 and pleon lateral margins flattened, with cuticular ridges. Pereonite 1 with greatest medial length of ambulosomites, lengths decrease to pereonite 4. Dorsal surfaces with scattered fine setae. Pereonite 7 longest natasomite, pereonite 6 shortest. Pereonite 7 ventrolateral area anterior to coxae of pereopod VII lacking bulla, with single large seta anterior to coxa; posterior margin of pereon with dense row of plumose setae.

Pleotelson lateral margin rounded, with anterior corners curving medially.

Antennulae approximately one-third body length; more robust, longer, and with more flagellar articles in male than in female. Article 1 medial lobe short, not protruding, shorter than article 2; lateral plate rounded, not angular or protruding, with unusually large broom seta on lateral margin.

Mandible typical, with palp shorter than mandibular body length and condyle shorter than molar process.

Maxilliped with broad palp, palp article 4 medial lobe much shorter than article 5. Epipod longer than wide, slightly shorter than basis, distally pointed; lateral projection small, angular.

Pereopod I–II bases broader than in pereopods III–IV. Coxal plate of pereopod IV short, rounded, not projecting anteriorly as in more anterior pereonites.

Pereopod V–VII bases slightly different in length: basis VI longest, basis V shortest. Carpus V–VII widest at less than quarter distance from distal edge.

Pleopod II of female deep, with broad keel; posterior margin rounded or flattened. Apex variably expressed. Lateral margins with plumose (not hemiplumose) setae.

Pleopod II of male with subterminal exopod having brush of long thin setae on posterolateral rounded edge.

Uropodal protopod with long unequally bifid setae on ventral and distal margin. Endopod and exopod with distal rosette of robust unequally bifid setae.

Remarks.—Members of the *longiflagrata* complex are most easily identified by their specialized male pleopod morphology, the somewhat narrowed body, the reduced dorsomedial length of pereonite 4 and by the sloping and protruding frons of the cephalon. The condition of the uropod is very similar to that seen in *E. cornuta.*

The elongate stylet on the endopod of the male second pleopod is the most unusual feature of the *longiflagrata* complex. This type of stylet is not found in other Eurycopidae, but it makes scattered appearances in various forms on the species level in other Janiroidean genera. The advanced deep-sea genera in which this character is found are *Munnopsis, Ischnomesus, Haploniscus, Acanthomunna,* and *Dendromunna.* Illustrations of this condition may be found in Sars (1899), Wolff (1962), and Menzies (1962). An elongate stylet also occurs frequently in the more primitive janiroideans: *Acanthaspidia, Ianthopsis, Ectias, Neojaera,* and *Caecianiropsis* (see Hansen 1895; Kensley 1977; Nordenstam 1933; Schultz 1976; Sivertsen and Holthuis 1980; Menzies and Pettit 1956). One could speculate that this type of stylet is a primitive character in the Janiroidea because of its widespread occurrence, and because of its appearance in the primitive groups. On the other hand, the stylet is quite variable in the genera in which it is elongated. For example, in *Munnopsis* one sees a range from an elongate stylet (*M. typica*) to a highly reduced stylet (*M. abyssalis*). In the very primitive genus *Notasellus,* which might be considered to be an outgroup to the more advanced Janiroidea by virtue of its non-opercular second pleopods, the stylet is not elongate. Therefore, the elongate stylet must be an apomorphy that appears convergently in many diverse janiroidean groups, comparable to the loss of the seventh pereopod in adults (Wilson 1976). The *longiflagrata* complex is unusual in that this character has become established in all of its species.

Eurycope longiflagrata, new species

Figs. 1, 2

Material examined.—Holotype preparatory female, 3.8 mm, USNM 195071. Paratypes: copulatory male, 3.2 mm, USNM 195072; 8 individuals, RRH. Type-locality WHOI 131, 36°28.9′N, 67°58.2′W, 2178 m. Other material: Juvenile female, WHOI GH4, 39°29′N, 70°34′W, 2469 m, RRH.

Distribution.—Continental slope off New England, USA, 2178–2469 m.

Etymology.—*Longiflagrata* is a Latin compound adjective meaning "with long whip."

Diagnosis.—Adult body length approximately 3–4 mm. Rostrum not overhanging frons; medial part of frons ridge low, sloping smoothly into clypeal articulation. Pleotelson of male with dorsal groove extending no further than anterior articulation of uropod. Male pleopod I with tapering lateral lobes, medial region smoothly v-shaped, medial lobes not expressed; distance from dorsal orifice to distal tip 0.27 pleopod I length. Female pleopod II with definite apex approximately quarter pleopod length from distal tip. Uropodal endopod length 1.5 or greater protopod width.

Description.—Body characters (Fig. 1A–B, E–F): Length 2.7–2.9 width. In holotype, pereonite 1 depth 0.3 length. In female, pleotelson round posteriorly. In male, pleotelson distal tip folds down abruptly, somewhat flattened in dorsal view.

Cephalic rostrum (Fig. 1C–D, G): Anterior tip with 2 small but stout setae, rostrum length-cephalic width ratio 0.15 in female, 0.19 in males (2 measured).

Antennula (Figs. 1G, 2A): Length 0.3–0.4 body length, longest and most robust in males. Flagellum (distal to article 4) with 7–11 annuli and 2 distal aesthetascs in females, and 14–25 annuli, each supplied with single aesthetasc, in males. Article 2 length 0.5 medial length of article 1 in females, 0.7 in males. Article 3 length 1.3–1.6 article 2 length.

Mandible (Fig. 2B–D): Left incisor process with 3 subequal teeth, right incisor process with 4 irregularly spaced teeth. Lacinia mobilis with 6 short teeth. Spine row with 4–6 members. Molar process distal surface oval, with only low bumps

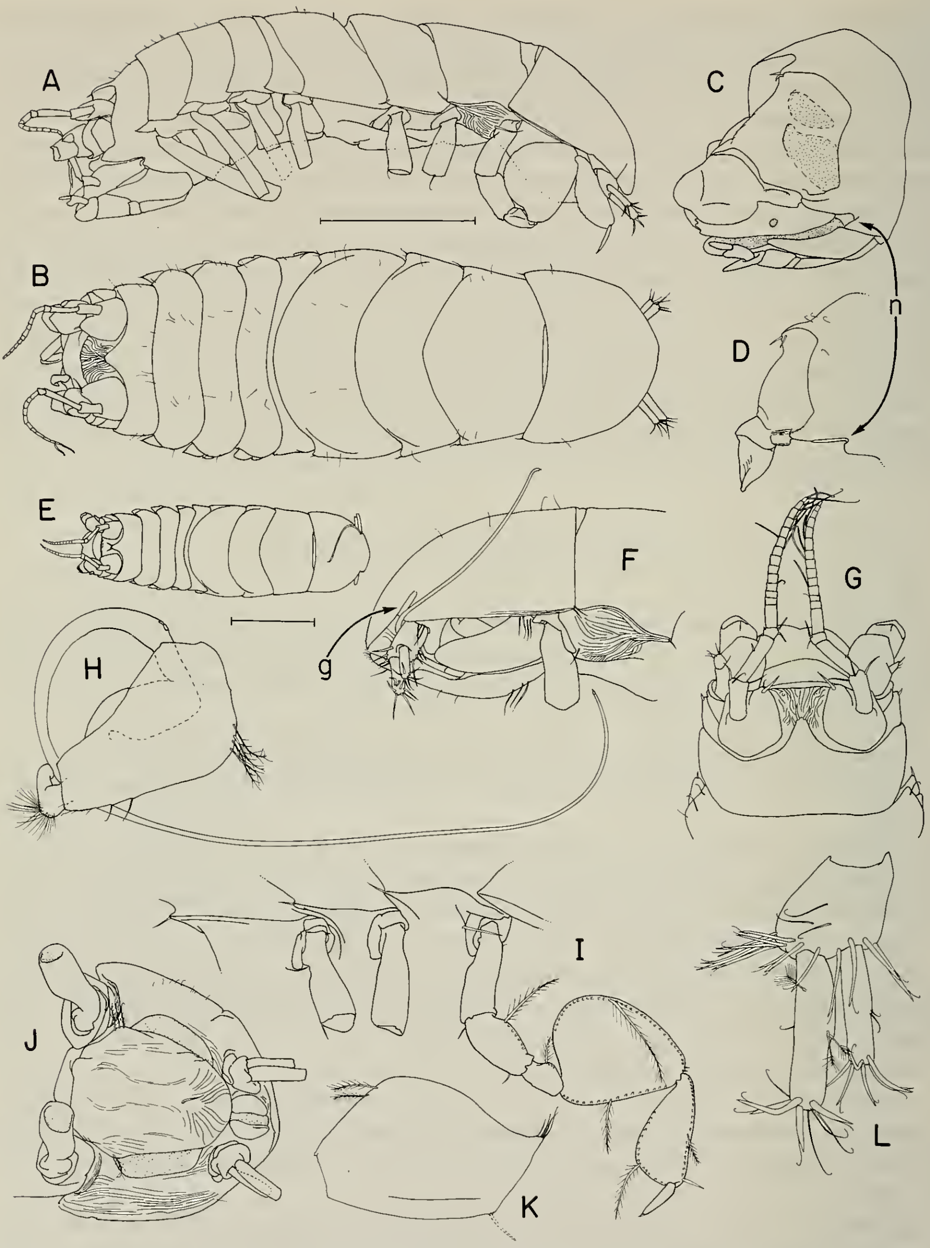


Fig. 1. *Eurycope longiflagrata*, types: A–B, I–J, 3.8 mm holotype preparatory female; C, H, 3.6 mm copulatory male; D, brooding female fragment; E–F, 3.2 mm copulatory male; K–L, 3.0 mm preparatory female. A–B, Holotype, lateral and dorsal views, scale bar 1.0 mm; C–D, Cephalon, oblique and lateral views, antenna and antennula removed, n = notch at posterior part of mandibular insertion; E, Copulatory male, dorsal view, scale bar 1.0 mm; F, Pleotelson and pereonite 7, lateral view, g = groove in dorsal surface; G, Male cephalon, dorsal view; H, Male pleopod II, ventral view; I, Lateral margin of natasomites, pereopod VII intact, in plan view; J, Female pleotelson, ventral view; K, Female pleopod II, lateral view; L, Uropod, ventral view.

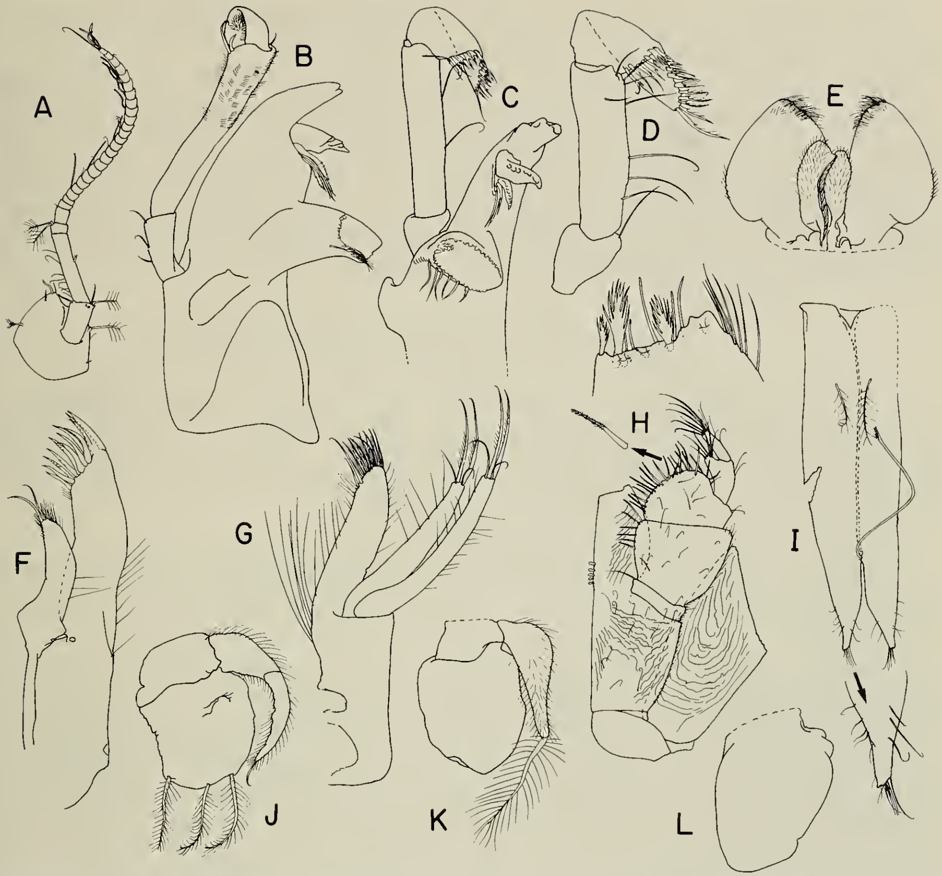


Fig. 2. *Eurycope longiflagrata*, paratypes: A, D, H–I, 3.6 mm copulatory male; B–C, E–G, J–L, 3.0 mm preparatory female. A, Antennula; B–D, Mandible; B, Dorsal view; C, Medial view; D, Male palp; E, Paragnaths; F, Maxillula; G, Maxilla; H, Maxilliped, with enlargements of endite distal tip and seta on medial margin of palp article 3; I, Male pleopod I, spermatophore protruding from dorsal orifice, with enlargement of lateral lobe; J–L, Pleopods III–V.

and 4–6 setae on posterior edge. Condyle length 0.19 mandibular body length. Palp second article length 0.51 mandibular body length.

Maxilliped (Fig. 2H): Endite with 5 small and 1 large fan setae distally, and 5 coupling hooks medially; lateral part of distal margin with one bicuspid projection. Palp articles 2 and 3 medial to lateral length ratios 0.67, 3.4 respectively. Epipod length 0.91 basis length, length 2.2 width.

Pleopod I of male (Fig. 2I): Length 4.5 width at dorsal orifice. Ventral surface with 2 plumose setae, and 2 rows of fine setae near each distal tip. Lateral lobe tip somewhat truncate, sloping anteromedially, with fine setae; dorsal part of lateral lobe not curling into ventral view.

Pleopod II of male (Fig. 1H): Protopod length 1.8 width; lateral margin with 4 plumose setae. Endopod length including stylet 5.1 protopod length.

Pleopod II of female (Fig. 1J, K): Depth 0.31 length. Lateral margin with 2 plumose setae.

Uropod (Fig. 1L): Endopod width 0.25 length. Exopod length 0.75 endopod length. Protopod ventral surface with circa 3 setae.

Remarks.—Males of *Eurycope longiflagrata* are most easily recognised by their short dorsal grooves on the pleotelson and smoothly tapering lateral lobes on pleopod I. As typical in all *longiflagrata* complex species, the females of *E. longiflagrata* are difficult to separate from the other species. The frons-rostral characters, and the female pleopod II shape are most useful to identify female specimens that are in good condition. At present this species is known only from the continental slope off New England at 2178–2469 meters.

Eurycope friesae, new species

Fig. 3

Material examined.—Holotype copulatory male, 4.2 mm, USNM 195073. Paratype brooding female, 4.7 mm, RRH. Type-locality WHOI 156, 0°46.0–46.5′S, 29°28.0–24.0′W, 3459 meters. Other material: Preparatory female, DEMERABY 29, 8°09.2–10.2′N, 49°04.4–04.8′W, 4430 m, RRH.

Distribution.—Equatorial Atlantic, 3459–4430 m.

Etymology.—In honor of my wife, M. Katherine Fries-Wilson, whose constant encouragement has made important contributions to this work and to my research in general.

Diagnosis.—Adult body length approximately 4–5 mm. Rostrum not overhanging frons; medial part of frons ridge low, sloping smoothly into clypeal articulation. Pleotelson of adult male with elongate dorsal groove, extending well anterior to insertion of uropod; groove length greater than two thirds pleotelson length. Male pleopod I with narrow elongate lateral lobes, medial region u-shaped, medial lobes expressed by presence of 3–4 simple setae; distance from dorsal orifice to distal tip 0.34 total pleopod length. Female pleopod II with rounded keel and no distinct apex. Uropodal endopod length 1.5 protopod width.

Description (in ranges, holotype male value stated first, female second).—Body characters (Fig. 3A–C): Length 3.0–3.1 width. In holotype, pereonite 1 depth 0.23 body length. Pleotelson posterior to uropods obtusely angular in dorsal view.

Rostrum (Fig. 3E): Anterior margin with 4 stout and 2 fine setae. Length 0.19–0.16 cephalon width.

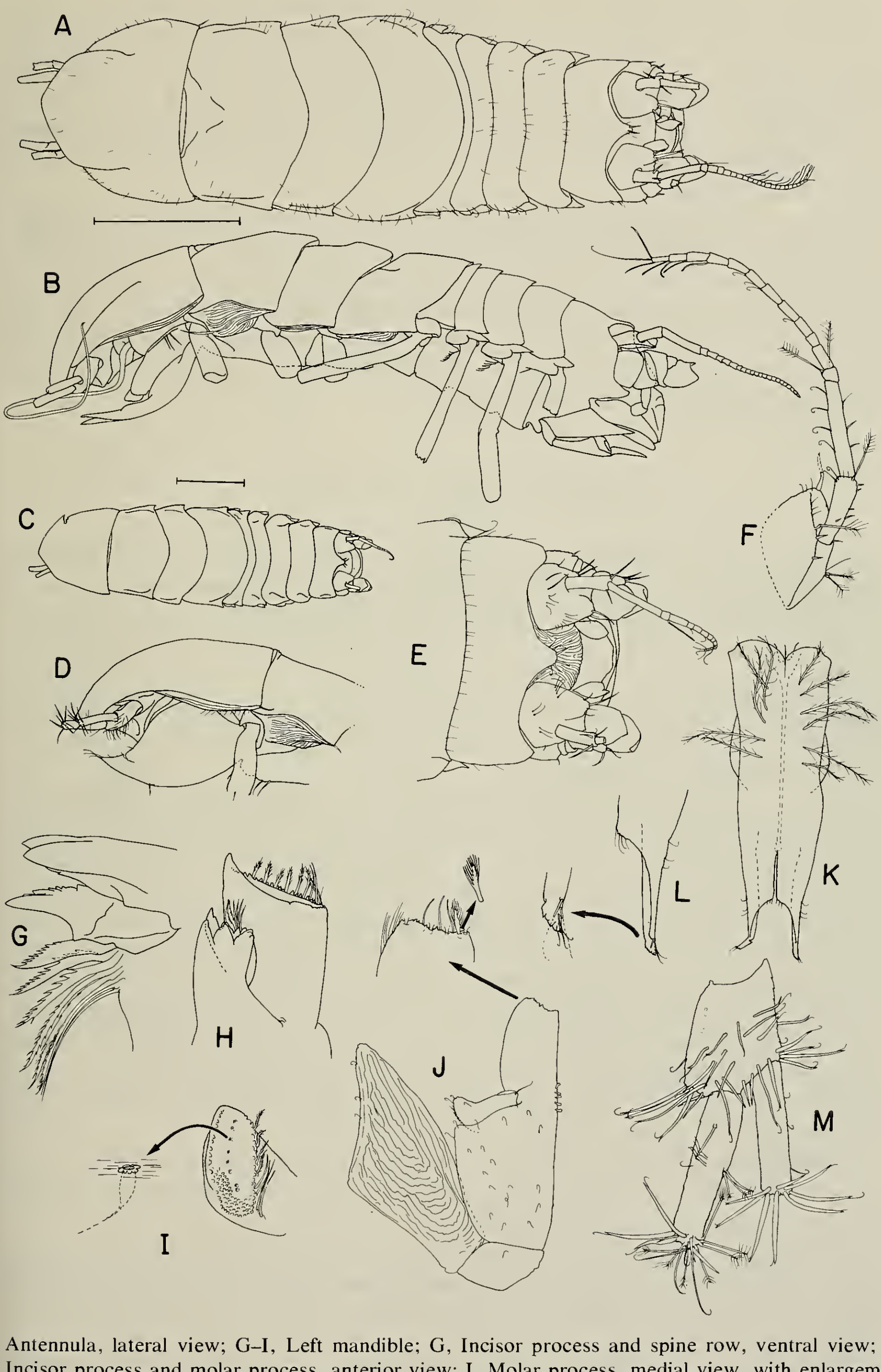
Antennula (Fig. 3E–F): Length–body length ratio 0.34–0.29. Flagellum with 20–11 annuli. Article 2 length 0.70–0.62 medial length of article 1. Article 3 length 1.8–1.4 article 2 length.

Left mandible (Fig. 3G–I): Spine row with 8 members. Molar process triturating surface with 11 setae and numerous distinct teeth on posterior margin. Condyle length 0.17 mandibular body length. Palp second article length 0.51 mandibular body length.

Maxilliped (Fig. 3J): Endite distal tip with tiny pointed denticles laterally. Epipod length 0.95 basis length; length 2.2 width.

→

Fig. 3. *Eurycope friesae*, types: A–B, K–M, 4.2 mm holotype copulatory male; C–J; 4.7 mm paratype brooding female; A–B, Holotype, dorsal and lateral views, scale bar 1.0 mm; C, Female paratype, dorsal view, scale bar 1.0 mm; D, Pleotelson, lateral view; E, Cephalon, dorsal view; F,



Antennula, lateral view; G–I, Left mandible; G, Incisor process and spine row, ventral view; H, Incisor process and molar process, anterior view; I, Molar process, medial view, with enlargement of sensory pore; J, Maxilliped with enlargement of endite distal tip; K–L, Male pleopod I and enlargement of lateral lobe, respectively; M, Uropod.

Pleopod I of male (Fig. 3K–L): Length 4.2 width at dorsal orifice. Ventral surface with 2 rows of 5–6 plumose setae each. Distal tip of lateral lobes sloping anteromedially with fine setae in row on lateral margin and tiny denticles on medial margin; dorsal part of lateral lobe curling into ventral view.

Uropod (Fig. 3M): Endopod width 0.24 length. Exopod length 0.80 endopod length. Protopod ventral surface with circa 9 setae; dorsal surface of male with medial row of 8 setae.

Remarks.—The male of *Eurycope friesae* is the most strikingly modified of the *longiflagrata* complex: the stylet groove in the pleotelson is very long and distinct. The females, which are similar to those of *E. longiflagrata,* can be recognised by the rounded keel of the second pleopod. The shape of the frons and rostrum separates *E. friesae* from the other known species of the complex. This species has been collected from the southern part of the Demerara Abyssal Plain and from the equatorial Atlantic deep sea.

Eurycope hessleri, new species
Fig. 4

Material examined.—Holotype copulatory male, USNM 195074. Paratypes: Brooding female, 3.5 mm, USNM 195075; 8 damaged or fragmentary individuals, RRH. Type-locality WHOI 334, 40°42.6–44.0′N, 46°13.8–14.6′W, 4400 meters.

Distribution.—Eastern Sohm Abyssal Plain in the North Atlantic Ocean, 4400 m.

Etymology.—In honor of Dr. Robert R. Hessler, who has made numerous important contributions to deep-sea systematics, and who has been a valued mentor, colleague, and friend to me.

Diagnosis.—Adult body length approximately 3–4 mm. Rostrum overhanging frons; medial part of frons ridge rounded in lateral view, protruding over clypeal insertion. Pleotelson of male without dorsal stylet groove. Male pleopod I with short dorsally curling lateral lobes, medial region sinusoidally v-shaped in ventral view with numerous fine setae anteriorly; distance from dorsal orifice to distal tip 0.23 pleopod I length. Female pleopod II with rounded keel, definite apex, and flattened posterior surface; distance from apex to distal tip 0.3 total pleopod length. Rami of uropod comparatively short, endopod length 1.2 protopod width.

Description.—Body characters (Fig. 4A–B, D): Length 3.0 width. Pleotelson distal tip rounded in dorsal view; anterior corners not curving medially.

Rostrum (Fig. 4E): Anterior tip with 2 small stout setae and several simple setae. Length 0.15 cephalic width.

Antennula (Fig. 4F–G): Proximal article lengths not sexually dimorphic (ratios apply to both male and female types). Article 2 length 0.6 medial length of article 1. Article 3 length 1.25 article 2 length.

Left mandible (Fig. 4H–K): Spine row with 6 members. Distal surface of molar process with numerous elongate teeth and 7 setae on posterior margin. Condyle length 0.17 mandibular body length. Palp article 2 length 0.53 mandibular body length.

Maxilliped (Fig. 4M): Endite with 4 coupling hooks; lateral part of distal margin with 2 triangular projections. Palp article 2 medial margin with 3 setae, medial length 0.61 lateral length. Epipod length 0.96 endite length.

Fig. 4. *Eurycope hessleri,* types: A–C, F, 3.2 mm holotype copulatory male; D–E, G, Q, 3.5 mm brooding female; N–P, Copulatory male pleotelson fragments; H–M, R, 2.9 mm copulatory male. A, Male, dorsal view, scale bar 1.0 mm; B, Male pleotelson, lateral view; C, Cephalon, lateral view; D, Dorsal view of female; E, Cephalon, lateral view, antennula and antenna removed; F–G, Male and female antennulae, respectively; H–K, Left mandible; H, Dorsal view; I, Incisor process and lacinia mobilis, posterior view; J, Spine row, dorsal view; K, Molar process, anterior view; L, Right mandible, incisor process, posterior view; M, Maxilliped with enlargement of endite distal tip; N–O, Male pleopod I; N, Ventral and lateral views; O, Distal tip with enlargement of lateral lobe; P, Male pleopod II; Q, Female pleopod II, lateral view; R, Uropod.

Pleopod I of male (Fig. 4N): Length 4.1 width at dorsal orifice. Ventral surface with 2 rows of plumose setae, 4–5 setae per row in adults, 0–2 in juveniles; 2 rows of simple setae on posterior third of ventral surface. Distal groups of simple setae on lateral base of lateral lobes, on tip of lateral lobes, and on medial region. Lateral lobes distally rounded with dorsal surface strongly curving into ventral view.

Pleopod II of male (Fig. 4P): Protopod length 1.8–2.0 width; lateral margin with 3 plumose setae. Endopod (including stylet) length 3.8 protopod length.

Pleopod II of female (Fig. 4Q): Depth 0.27 length. Lateral margin with 2–4 plumose setae.

Uropod (Fig. 4R): Endopod width 0.37 length. Exopod length 0.89 endopod length. Protopod ventral surface with circa 7 setae; medial edge of dorsal surface with row of 4 setae in male only.

Remarks.—*Eurycope hessleri* has a small but distinct rostral overhang, and rather short and stocky rami of the uropods; these characters are sufficient to distinguish *E. hessleri* from *E. longiflagrata* and *E. friesae*. The males are distinct in lacking a dorsal groove in the pleotelson, and in having short, dorsally curled lateral lobes on the pleopod I distal tips. *E. hessleri* is known only from the type-locality in the eastern part of Sohm Abyssal Plain.

Eurycope errabunda, new species

Fig. 5

Material examined.—Holotype preparatory female, 6.2 mm, USNM 195076. Paratypes: head fragment, pleotelson fragment, WHOI 330, RRH. Type locality: WHOI 330, 50°43.5–43.4′N, 17°51.7–52.9′W, depth 4632 meters. Other Material: possibly male head fragment and juvenile male with choniostomatid copepod parasite, 4.7 mm, WHOI 287, 13°16.0–15.8′N, 54°52.2–53.1′W, 4980–4934 m. Three individuals: manca 3, instar 4, and fragmentary female, WHOI 334 (see *E. hessleri* for data). Cephalon and anterior pereon fragment, ABYPLAINE CP19, 43°00′N, 14°02.9–04.3′W, 5280 m.

Distribution.—Widely scattered localities in the abyssal regions of the North Atlantic Ocean, 4632–5280 m.

Etymology.—*Errabunda* is a Latin adjective meaning "wandering."

Diagnosis (adult male characters not known).—Adults large, body length exceeding 6 mm. Cephalic rostrum overhanging frons; frons ridge medially overhanging clypeal articulation. Female pleopod II with distinct apex approximately quarter pleopod length from distal tip. Uropodal endopod length 1.8 protopod width (1.6–1.7 in specimens from non-type localities).

Description of type-material.—Body characters (Fig. 5A–B): Body narrow, length 3.2 width, depth at first pereonite 0.22 body length. Pleotelson rounded posteriorly.

Rostrum (Fig. 5C–D): Length 0.16 cephalic width. Anterior tip with 2 stout setae and several fine setae.

Antennula (Fig. 5F): Article 2 length 0.7 medial length of article 1. Article 3 length 1.7 article 2 length.

Left mandible: Spine row with 12 members. Molar process with 14 distal setae. Condyle length 0.18 mandibular body length. Palp article 2 length 0.49 mandibular body length.

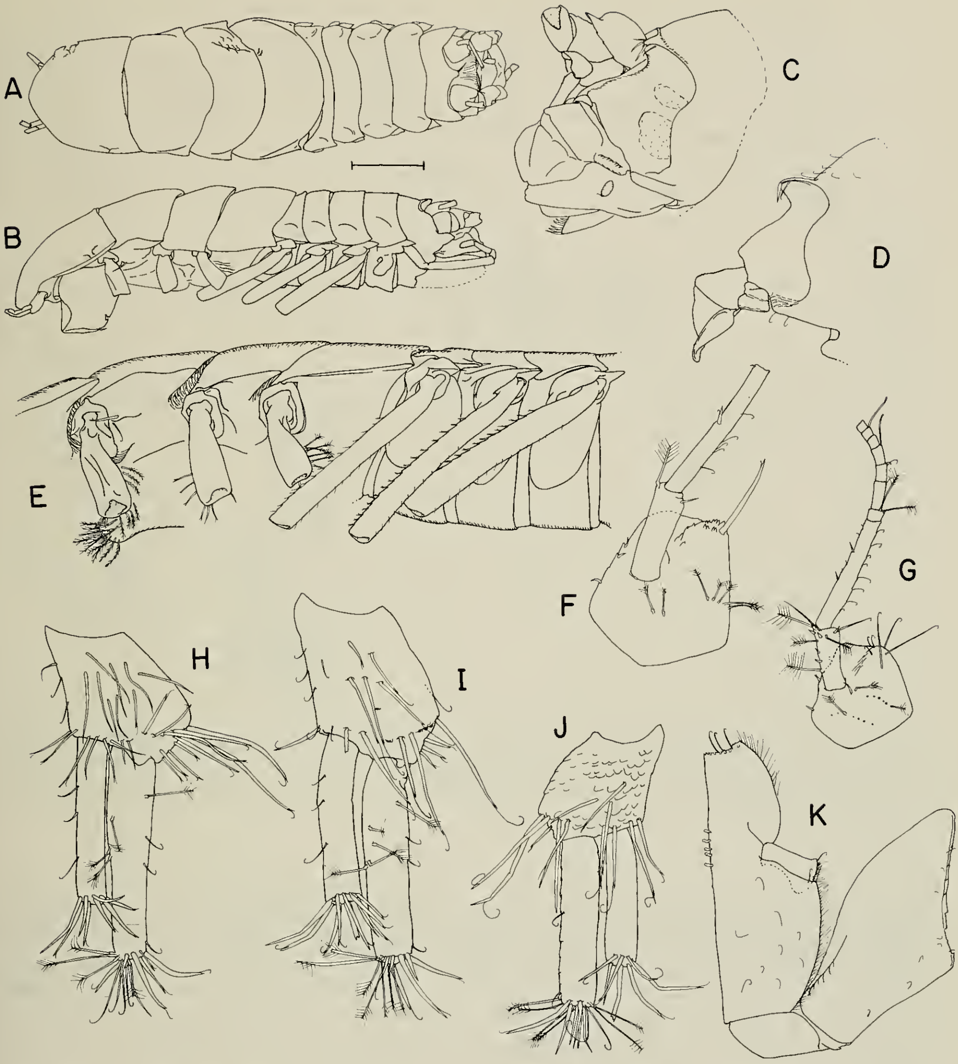


Fig. 5. *Eurycope errabunda*: A–B, E–F, H, 6.2 mm holotype preparatory female; C–D, Paratype female cephalon fragment; G, K, Adult male head fragment, WHOI 287; I, 4.7 mm juvenile male, WHOI 287; J, Instar 4 female, WHOI 334. A–B, Holotype, dorsal and lateral views; C–D, Cephalon, oblique and lateral views, antennula and antenna removed; E, Pereonites 2–7, oblique ventral view, pereopod bases in plan view; F–G, Female and male antennulae, respectively; H–J, Uropods, comparison of individuals from WHOI 330, WHOI 287, and WHOI 334, respectively; K, Maxilliped.

Uropod (Fig. 5H): Endopod width 0.21 length. Exopod length 0.77 endopod length. Protopod ventral surface with circa 9 setae.

Description and variation in specimens from other localities.—WHOI 334, instar 4 juvenile female (Fig. 5J): Uropodal endopod 1.6 protopod width. Endopod width 0.23 length. Exopod length 0.83 endopod length. Protopod ventral surface with 3 setae.

WHOI 287, parasitized juvenile male (Fig. 5I): Uropodal endopod 1.7 protopod

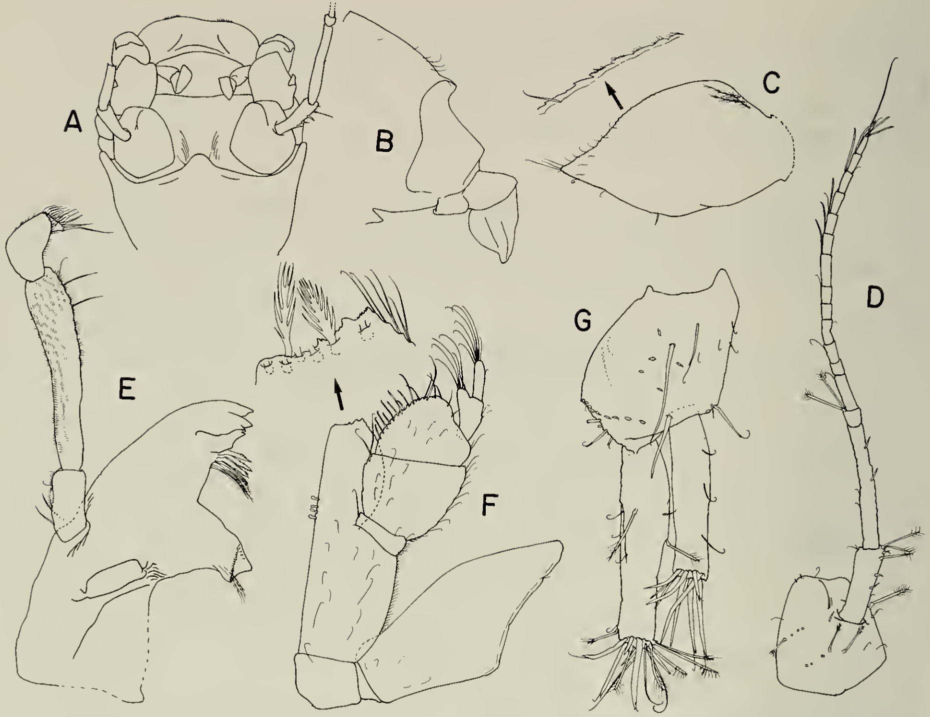


Fig. 6. *Eurycope* sp., *longiflagrata* complex, 4.7 mm preparatory female, ABYPL DS11: A, cephalon, dorsal view; B, cephalon, lateral view, antennula and antenna removed; C, Pleopod II, lateral view, with enlargement of dorsal margin; D, Antennula; E, Left mandible; F, Maxilliped with enlargement of endite distal tip; G, Uropod.

width. Endopod width 0.22 length. Exopod length 0.80 endopod length. Protopod ventral surface with 6 setae; dorsomedial surface with 1 seta.

WHOI 287, head fragment, possibly male (Fig. 5G): Antennular article 2 length 0.81 medial length of article 1; article 3 length 1.92 article 2 length; aesthetascs on proximal annuli of flagellum (evidence for male classification). Maxillipedal endite with 7 small and one large fan setae distally, and 5 coupling hooks medially; lateral part of distal margin with quadrate projection. Maxillipedal epipod length 0.93 basis length; length 2.0 width.

Remarks.—The individuals classified as *Eurycope errabunda* are recognizably different from the other species in the *longiflagrata* complex: all are large, and have a distinctive configuration of the frons and rostrum. Because the adult male pleopods are unknown it is uncertain whether *E. errabunda* represents one or several species. The variation observed in the uropods and in the antennulae of specimens from the different localities could be explained by ontogenetic changes or sexual dimorphism (Wilson 1981), but differences characteristic of geographically-separated populations cannot be ruled out. Therefore, *E. errabunda* is provisionally considered to be a single species pending the collection of additional material and characterization of the male pleopods.

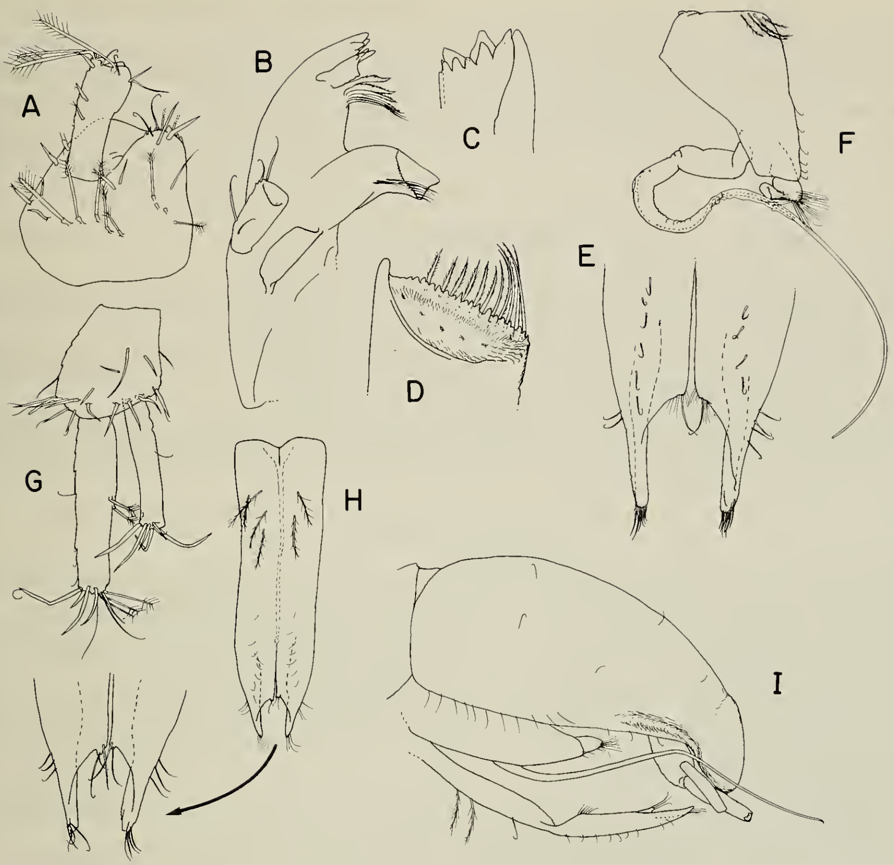


Fig. 7. *Eurycope* sp., *longiflagrata* complex. 3.5 mm copulatory male, INCAL 45: A, Antennula; B–D, Left mandible; B, Dorsal view; C, Incisor process and lacinia mobilis, posterior view; D, Molar process anterior view; E, Pleopod I, distal tip; F, Pleopod II; G, Uropod. Copulatory male fragment, estimated body length 3.7 mm, WHOI 330: H, Pleopod I with enlargement of distal tip; I, Pleotelson, lateral view.

Eurycope sp. (spp.?)
Figs. 6–7

Three individuals in the available material of the *longiflagrata* complex were not assignable to any of the species described above. The specimens occur at three different localities and are damaged or fragmented. At least one new species is represented in this material, but because of the condition and ambiguities in character states, a new species is not proposed here. The individuals are described and figured separately with the hope that future collections of the *longiflagrata* complex will aid in their classification.

Specimen no. 1.—Preparatory female, body length 4.7 mm, RRH. ABYPL DS11, 42°59.7–59.2′N, 14°05.4–03.4′W, 5260 m.

Description.—Frons and Rostrum (Fig. 6A–B): Anterior tip slightly overhanging frons. Rostrum length 0.13 cephalon width. Medial part of frons ridge slightly overhanging clypeal insertion.

Antennula (Fig. 6D): Length 0.33 body length, with 13 flagellar articles. Distal 5 annuli with single aesthetascs and 2 on tip. Article 2 length 0.68 medial length of article 1. Article 3 length 1.6 article 2 length. Medial lobe of article 1 lacking large setae or teeth.

Left mandible (Fig. 6E): Spine row with 8 members. Molar process with 15 setae on posterior margin of distal edge. Condyle length 0.16 mandibular body length. Palp article 2 length 0.54 mandibular body length.

Maxilliped (Fig. 6F): Endite with 6 small and 1 large fan setae distally, and 4 coupling hooks medially. Epipod length 0.97 basis length.

Pleopod II (Fig. 6C): Length 0.28 depth. Apex distance to distal tip 0.36 total pleopod length. Keel somewhat rounded in lateral view.

Uropod: Endopod length 1.5 protopod width; width 0.24 length. Exopod length 0.82 endopod length. Protopod ventral surface with 7 large setae; dorsal surface with 2 setae near medial margin.

Specimen no. 2.—Male, body length approximately 3.5 mm, RRH. INCAL 45, 48°18.9–18.3′N, 15°14.4–13.3′W, 4829 m.

Description.—Rostrum and frons similar to preparatory female (ABYPL DS11). Pleotelson lacking dorsal groove, with only slight indentation above uropod.

Antennula (Fig. 7A): Article 2 length 0.8 medial length of article 1. Medial lobe of article 1 distal tip with 2 thick setae and 6 tiny denticles.

Left mandible (Fig. 7B–D): Spine row with 6 members. Setal row on molar process with 11 members; triturating surface with 5 sensory pits. Condyle length 0.18 mandibular body length.

Maxilliped: Endite distal tip with 5 small and 1 large fan setae; medial margin with 3 coupling hooks. Epipod length 0.91 width.

Pleopod I (Fig. 7E): Length 4.4 width at dorsal orifice. Distance from dorsal orifice to distal tip 0.30 total length. Ventral surface with pair of plumose setae proximally and 2 rows of fine setae distally. Lateral lobes similar to those in *E. hessleri* but longer; distally rounded with curved row of fine setae. Medial area of distal tip u-shaped with paired tufts of setae on inner edge.

Pleopod II (Fig. 7F): Protopod length 1.9 width; lateral margin with 4 plumose setae. Endopod (including stylet) length 3.0 protopod length.

Uropod (Fig. 7G): Endopod length 1.7 protopod width; width 0.23 length. Exopod length 0.76 width. Ventral surface of protopod with 4 large setae; medial edge of dorsal surface with 1 seta.

Specimen no. 3.—Male fragment, cephalon missing, estimated body length 3.7 mm, RRH. WHOI 330, see *E. errabunda* for station data.

Description.—Pleopod I (Fig. 7H): Length 3.8 width; distance from distal tip to dorsal orifice 0.33 total length. Ventral surface and distal tip similar to male from INCAL 45 except: 2 plumose setae on left side and 4 plumose setae on right; medial area of distal tip with setae on small projections.

Pleopod II: Protopod length 1.8 width; lateral margin with 2 plumose setae. Endopod length 3.1 protopod length.

Remarks.—These individuals are most similar to *Eurycope hessleri* although the uropod of *Eurycope* sp. has much longer rami, and the antennular article 3 is longer in the female. Differences in the pleopods from the two males (WHOI

330, INCAL 45) made identifying them as the same species uncertain. All three individuals occur in the same general area, the deep-sea adjacent to the Bay of Biscay, so they may possibly be the same species. The male from WHOI 330 was not classified as *E. errabunda* because it was estimated to be only 3.7 mm long and was fully adult; *E. errabunda* specimens are adult at much larger sizes, approximately 6 mm body length.

Acknowledgments

Sincere thanks are due the individuals and institutions mentioned in the Materials and Methods section above for providing the specimens discussed in this paper. Helpful reviews of this paper by Robert R. Hessler, Scripps Institution of Oceanography and by Thomas E. Bowman and Brian Kensley, Smithsonian Institution, improved its content and form. This research was funded by grants from the National Science Foundation, DEB 77-24614 and DEB 80-07150, R. R. Hessler, principal investigator.

Literature Cited

Hansen, H. 1895. Isopoden, Cumaceen und Stomatopoden der Plankton-Expedition.—Ergebnisse der Plankton-Expedition der Humboldt-Siftung 2:1–105.

Kensley, B. 1977. New records of the marine Crustacea Isopoda from South Africa.—Annals of the South African Museum 72:239–265.

Menzies, R. 1962. The isopods of abyssal depths in the Atlantic Ocean.—Abyssal Crustacea, Vema Research Series, Columbia University, New York 1:79–206.

———, and J. Pettit. 1956. A new genus and species of marine asellote isopod, *Caecianiropsis psammophila*, from California.—Proceedings of the United States National Museum 106:441–446.

Nordenstam, A. 1933. Marine Isopoda of the families Seroloidae, Idotheidae, Pseudidotheidae, Arcturidae, Parasellidae and Stenetriidae mainly from the South Atlantic.—Further Zoological Results of the Swedish Antarctic Expedition 1901–1903, 3:1–284.

Sars, G. 1864. Om en anomal Gruppe af Isopoder.—Forhandlinger i Videnskaps-Selskapet in Kristiana 1863:205–221.

———. 1899. Isopoda.—Crustacea of Norway 2:1–270, Bergen.

Schultz, G. 1976. Species of asellotes (Isopoda: Paraselloidea) from Anvers Island, Antarctica.—Antarctic Research Series 26:1–35.

Sivertsen, E., and L. Holthuis. 1980. The marine isopod crustacea of the Tristan da Cunha Archipelago.—Gunneria 35:1–128.

Wilson, G. 1976. The systematics and evolution of *Haplomunna* and its relatives (Isopoda, Haplomunnidae N. Fam.).—Journal of Natural History 10:569–580.

———. 1981. Taxonomy and postmarsupial development of a dominant deep-sea eurycopid isopod (Crustacea).—Proceedings of the Biological Society of Washington 94:276–294.

———. 1983. Systematics of a species complex in the deep-sea genus *Eurycope*, with a revision of six previously described species (Crustacea, Isopoda, Eurycopidae).—Bulletin of the Scripps Institution of Oceanography 25:1–64.

———, and R. Hessler. 1980. Taxonomic characters in the morphology of the genus *Eurycope* (Crustacea, Isopoda) with a redescription of *E. cornuta* Sars, 1864.—Cahiers de Biologie Marine 21:241–263.

———, and ———. 1981. A revision of the genus *Eurycope* (Isopoda, Asellota) with descriptions of three new genera.—Journal of Crustacean Biology 1:401–423.

Wolff, T. 1962. The systematics and biology of bathyal and abyssal Isopoda Asellota.—Galathea Report 6:1–320.

A-002, Scripps Institution of Oceanography, La Jolla, California 92093, USA.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 468–477

SPONGE-INHABITING BARNACLES (CIRRIPEDIA: ARCHAEOBALANIDAE) OF THE CAROLINIAN PROVINCE, SOUTHEASTERN UNITED STATES, WITH THE DESCRIPTION OF A NEW SPECIES OF *MEMBRANOBALANUS* PILSBRY

Victor A. Zullo and Jon D. Standing

Abstract.—*Acasta cyathus* Darwin, 1854, previously known from the tropical western Atlantic north to Sapelo Island, Georgia, is reported from a variety of demosponges on the middle and outer continental shelf between Cape Fear and Cape Lookout, North Carolina. *Membranobalanus declivis* (Darwin, 1854), known previously from the tropical western Atlantic south of Cape Canaveral, Florida, occurs in *Spheciospongia vesparium* (Lamarck) from the mid-shelf region off Cape Fear, North Carolina. *Membranobalanus costatus,* new species, is found in *Anthosigmella varians* (Duchassaing and Michelotti) off Cape Fear. The new species is most readily distinguished from *M. declivis* by its prominently ribbed shell and rostrum of normal length. The number and distribution of specimens encountered in this study suggest that sponge-inhabiting barnacles are a common, but overlooked element of the Carolinian Province.

Species of the archaeobalanid barnacle genera *Acasta* Leach and *Membranobalanus* Pilsbry are obligate symbionts of sponges, occurring in tropical, subtropical, and warm temperate regions of the world. Most of the species ascribed to these genera are found in Indo-West Pacific waters, and only two species, one of each genus, have been reported from the western Atlantic. *Acasta cyathus* Darwin, 1854, is known from southern Georgia, southern Florida, the eastern Gulf of Mexico, and the Caribbean (Wells 1966; Newman and Ross 1976; Zullo and Lang 1978; Spivey 1981), but is also found in the eastern Atlantic, Red Sea, and Indo-west Pacific (Newman and Ross 1976). *Membranobalanus declivis* (Darwin, 1854) has been reported from Bermuda, southern and western Florida, and the West Indies (Wells 1966; Newman and Ross 1976; Spivey 1981).

The U.S. Bureau of Land Management (BLM) Live Bottom Study, conducted by the Duke University Marine Laboratory on the North Carolina continental shelf, has yielded an array of sponges, some of which contain sponge barnacles. *Acasta cyathus* is the most ubiquitous species, occurring in several different sponges at depths between 17 and 116 m. *Membranobalanus declivis* was discovered in two specimens of the loggerhead sponge, *Spheciospongia vesparium* (Lamarck), between 22 and 30 m depth southwest of Cape Lookout. Specimens of another sponge, *Anthosigmella varians* (Duchassaing and Michelotti), collected off Cape Fear at depths between 28 and 32 m, contain a new and rather unusual species of *Membranobalanus* characterized by a prominently ribbed shell and a rostrum of normal length. The presence of *Acasta* and *Membranobalanus* on the North Carolina continental shelf extends the western Atlantic range of these

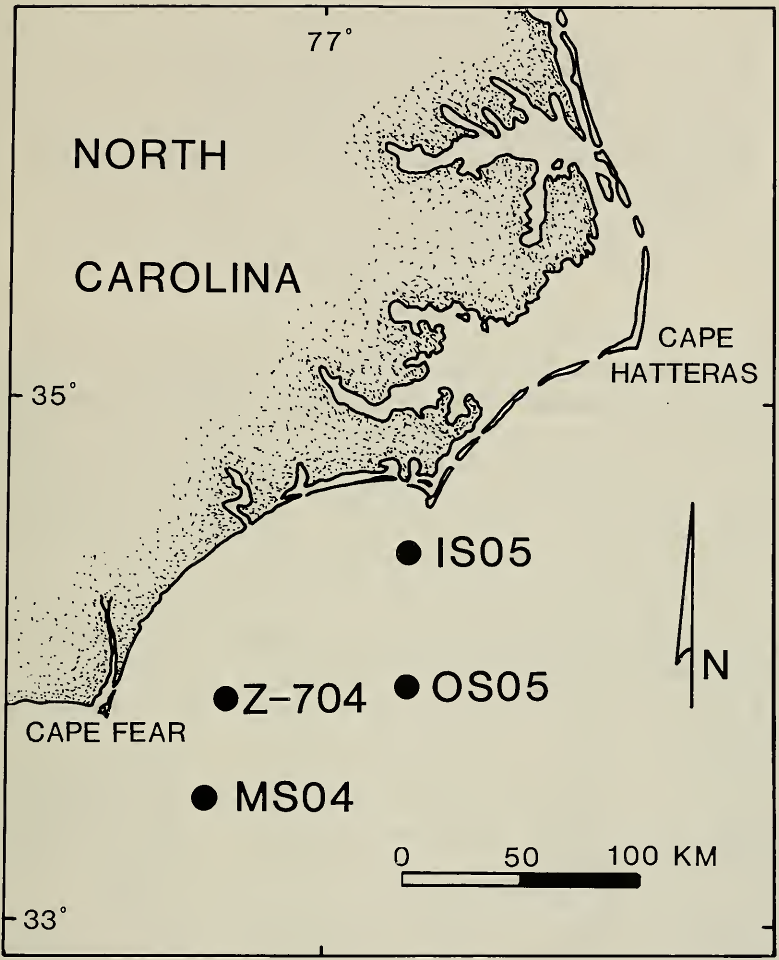


Fig. 1. General location of stations for sponge-inhabiting barnacles off the North Carolina coast.

genera nearly to the northern limit of the Carolinian Province. North Carolina localities are shown in Fig. 1.

Station Descriptions

IS05.—South-southwest of Cape Lookout, North Carolina, 34°23.0′N, 76°34.0′W, 19–27 m, BLM Live Bottom Study station, 1981.

MS04.—Southeast of Cape Fear, North Carolina, 33°31.0′N, 77°25.0′W, 27–55 m, BLM Live Bottom Study station, 1981.

OS05.—East of Cape Fear, North Carolina, 33°49.0′N, 76°33.5′W, 55–100 m, BLM Live Bottom Study station, 1981.

Z-704.—WR-4 buoy, east-northeast of Cape Fear, North Carolina, 33°51.9′N, 77°29.4′W, on superstructure of wreck, 17 m, Department of Earth Sciences collection, University of North Carolina at Wilmington, T. Prestia and P. Wheaton, collectors, 10 July 1982.

Systematic Account

Subclass Cirripedia Burmeister, 1834
Order Thoracica Darwin, 1854
Suborder Balanomorpha Pilsbry, 1916
Superfamily Balanoidea (Leach), Newman and Ross, 1976
Family Archaeobalanidae Newman and Ross, 1976
Subfamily Archaeobalaninae Newman and Ross, 1976
Genus *Acasta* Leach, 1817

Acasta cyathus Darwin, 1854

Fig. 2a–e

Acasta cyathus Darwin, 1854:312, pl. 9, figs. 3a–c (Madeira; West Indies).—Pilsbry, 1916:244, text-figs. 79–80, pl. 57, figs. 1–3 (Dry Tortugas, Florida; Colon, Panama; St. Croix, U.S. Virgin Islands).—Wells, 1966:85 (Gulf coast of Florida).—Newman and Ross, 1976:53 (Florida; Caribbean; Madeira; Morocco; East Africa; Red Sea; Gulf of Manaar; Singapore; Kei Islands; Sulu Archipelago; Philippines; western Australia; 15–180 m; see for complete synonymy).—Zullo and Lang, 1978:159 (off Sapelo Island, Georgia).—Spivey, 1981:172.

Material examined.—Specimens of *Acasta cyathus* were obtained from the following localities and sponges off North Carolina:

USNM hypotype lot	Station	Depth	Date	Host sponge
USNM 195285	MS04	34 m	7 Feb 1981	*Verongula ardis* (de Laubenfels)?
USNM 195286	OS05	66 m	3 Mar 1981	Family Coppatiidae sp. A
USNM 195287	OS05	77 m	3 Mar 1981	Family Coppatiidae sp. A
USNM 195288	OS05	62 m	3 Mar 1981	*Cinachyra keukenthali* Uliczka
USNM 195289	OS05	69 m	4 Mar 1981	Family Coppatiidae sp. A
USNM 195290	OS05	64 m	4 Mar 1981	*Erylus ministrongulus* Hechtel
USNM 195291	OS05	116 m	14 May 1981	Family Coppatiidae sp. A
USNM 195292	OS05	104 m	14 May 1981	Family Coppatiidae sp. A
USNM 195293	OS05	99 m	14 May 1981	Family Coppatiidae sp. A
USNM 195294	MS04	32 m	18 May 1981	Family Mycalidae sp. A
USNM 195295	MS04	30 m	10 May 1981	*Ircinia campana* (Lamarck)
	Z-704	17 m	10 Jul 1982	undetermined

Remarks.—The 40 *Acasta cyathus* specimens from station Z-704 (from a single 25 cm diameter, bowl-shaped sponge) represent a northern range extension of 2°22′ in latitude and indicate that the species is common in North Carolina waters. The absence of prior records from this region is most likely the result of lack of collection, rather than a recent immigration from southern regions.

The North Carolina *Acasta* were found in at least six different species of Demospongea, occurring most frequently in an unidentified coppatiid sponge. Other host records for *A. cyathus* from the western Atlantic include sponges of the genus *Aplysina* (=*Verongia*), *Ircinia campana* (Lamarck), *Ircinia felix* (Duchassaing and Michelotti) (=*I. fasiculata*), *Spinosella* (=*Callyspongia*) *vaginalis* (Lamarck), and *Spongia tubulifera* Lamarck, (=*S. officinalis*) (Darwin 1854; Wells 1966).

Comparison of North Carolina and Georgia specimens of *Acasta cyathus* revealed no important morphological differences between the two populations. *Acasta cyathus* is readily distinguished from other western Atlantic sponge barnacles by its pink-hued, globose shell, spinose parietes, small and nearly flat calcareous basis, obviously striate scutum lacking a depressor muscle pit, and narrow, rather long tergal spur.

Membranobalanus Pilsbry, 1916
Membranobalanus declivis (Darwin, 1854)
Fig. 2f–o

Balanus declivis Darwin, 1854:275, pl. 7, figs. 4a–d (West Indies; Jamaica).—Pilsbry, 1916:230, text-figs. 73–74, pl. 55, figs. 1–1d (off Cape Sable, Florida; Bermuda).—Pearse, 1932:119 (Dry Tortugas).—Wells, 1966:83 (Gulf coast of Florida).

Balanus declivis var. *cuspidatus* Verrill, 1901:22 (Bermuda).

Membranobalanus declivis (Darwin).—Newman and Ross, 1976:53 (see for synonymy).—Spivey, 1981:172.

Material examined.—One individual in a specimen of *Spheciospongia vesparium* (Lamarck), off Cape Lookout, North Carolina, Hypotype USNM 195282, Station IS05, 34°23.6′N, 76°34.9′W, 22 m, 9 Feb 1981; 5 individuals in a specimen of *S. vesparium*, off Cape Fear, North Carolina, Hypotype USNM 195283, Hypotype lot USNM 195284, Station MS04, 33°31.4′N, 77°24.0′W, 30 m, 19 May 1981.

Remarks.—The *Membranobalanus declivis* specimen from Station IS05 extends the northern range of this species by 9°15′ of latitude.

Both Pearse (1932) and Wells (1966), who are the only authors to our knowledge that identified the host sponge for *M. declivis*, list the loggerhead sponge, *Spheciospongia vesparium*. Their records, together with the new North Carolina records, suggest that *S. vesparium* is the sole host for *Membranobalanus declivis*. The North Carolina *M. declivis* agree with the descriptions and illustrations presented by Darwin (1854) and Pilsbry (1916). *Membranobalanus declivis* is distinguished from *Acasta cyathus* by its membranous basis and non-spinose parietes, and from other Western Hemisphere species of *Membranobalanus* by its noncostate shell bearing narrow to broad radii and an elongate rostrum.

Membranobalanus costatus, new species
Figs. 2p–x, 3a–x

Holotype.—Complete shell, opercular plates, and body, USNM.

Dimensions of holotype.—Height, 8.8 mm; carinorostral diameter 10 mm; lateral diameter, 7.8 mm.

Type locality.—Station MS04, 33°31.0′N, 77°25.0′W, off Cape Fear, North Carolina, 28 m depth, 12 Aug 1981.

Material examined.—8 individuals from a specimen of *Anthosigmella varians* at the type-locality, Holotype USNM 195270, paratypes USNM 195271 through 195277; 4 individuals from a specimen of *A. varians*, Station MS04, 33°32.8′N, 77°24.3′W, 32 m, 18 May 1981, paratypes USNM 195278 through 195281.

Diagnosis.—Shell thin, white, with radii lacking or incipient; orifice deeply

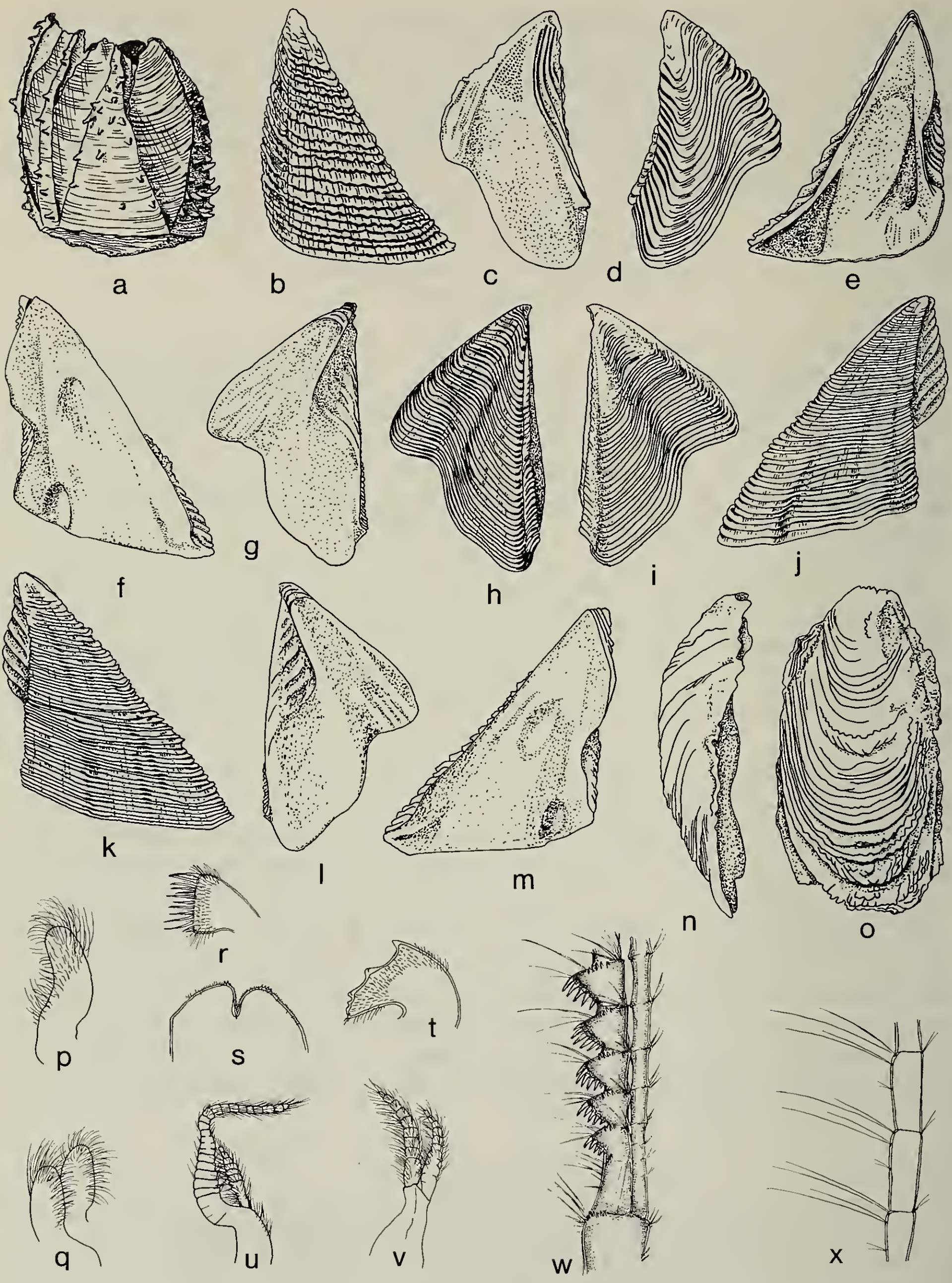


Fig. 2. *Acasta cyathus* Darwin, station Z-704: a, Shell, hypotype USNM 195285; b–e, Outer and inner views of opercular plates, hypotype USNM 195285. *Membranobalanus declivis* (Darwin), station MS04: f–m, Outer and inner views of opercular plates, hypotype USNM 195282; n–o, Side and exterior view of rostrum, hypotype USNM 195282. Mouth parts and cirri of *M. costatus* n. sp., paratype USNM 195278, station MS04: p, Palp; q, Second maxillae; r, First maxilla; s, Labrum; t, Mandible; u, Cirrus I; v, Cirrus II; w, Cirrus VI; x, Medial articles of Cirrus VI. Scale: Fig. a, ×3; figs. b–m, ×6; figs. n–o, ×4; figs. p–q, ×20; figs. u–v, ×10; figs. w–x, ×20.

toothed; rostrum same length as other compartmental plates; exterior of parietes with narrow, prominent, irregularly-spaced costae; opercular plates without intercalated chitinous lamellae; scutal adductor ridge incipient or lacking; tergal spur short, broad, usually occupying two-thirds of basal margin; outer ramus of Cirrus IV with up to 6 recurved teeth per article; medial articles of Cirrus VI with 3 pairs of spines per article, proximal pair minute.

Description.—Shell (Fig. 3a–j) high-conic, white, with deeply-toothed orifice; compartmental plates solid, thin, easily disarticulated; parietes ornamented externally with fine, closely-spaced, irregular growth lines crossed by fine, longitudinal striae on upper (younger) third and by prominent, narrow, irregularly-spaced costae on lower two-thirds; costae extend slightly below basal margin of parietes giving base of shell wall a denticulate appearance; rostrum larger than other compartmental plates, but not of greater length, narrow in upper third and increasing in width towards broadly V-shaped basal margin; carina narrow with nearly parallel parietal borders; apices of rostra and carinae with deeply incised notches, probably caused by cirral rasping; radii absent or at best represented by extremely narrow and irregular ledges; alae narrow and steeply oblique in upper third of compartmental plate, broadening markedly in central third, and narrowing abruptly in lower third; alar sutural edges smooth; sheath of rostrum one-half length of plate; sheath of other compartmental plates one-half to two-thirds length of plate; lower margin of sheath continuous with shell wall; interior of parietes often ribbed below sheath; internal ribs obverse of sulcations between external costae; basis membranous.

Scutum (Fig. 3k–n, u–x) thick, markedly convex, white, with adherent exterior yellow-brown epidermis bearing fine hairs; basal margin shorter than tergal margin; tergal margin reflexed about 45°; exterior ornamented by narrow, closely-spaced, semi-erect growth ridges crossed by very fine radial striae, especially evident in medial part of plate, every other external growth ridge forming raised "tooth" on occludent margin; articular ridge prominent, triangular, between three-fifths and three-fourths length of tergal margin, and reflexed over narrow, shallow articular furrow; reflexed articular ridge extends well beyond tergal margin of scutum; adductor ridge represented by low, rounded, raised border of small, deep, oval adductor muscle pit just above and tergad of center of plate; depressor muscle pit large, deep, triangular, extending up under inner lamina of scutum and located at basal margin in angle formed by reflexed tergal margin; narrow, triangular "radius," broadest at apical end, extending length of occludent margin.

Tergum (Fig. 3o–t) thin, about same width as scutum, white; basal margin slightly shorter or equal to length of scutal margin; exterior ornamented by fine, closely-spaced growth ridges, and covered in lower half by yellow-brown epidermis bearing fine hairs; spur furrow broad, very slightly depressed, bounded on either side by impressed lines; narrow strip along carinal border of tergum depressed below exterior surface of plate and with upturned growth lines; tergal spur short, broad (base of spur occupying about two-thirds of basal margin), basally truncate at angle to basal margin, and placed close to basiscutal angle; length of spur about one-half basal width of spur; depressor muscle crests absent, or represented by few inconspicuous, irregular ridges; articular ridge straight, erect, short, restricted to apical half of plate; articular furrow very broad, shallow.

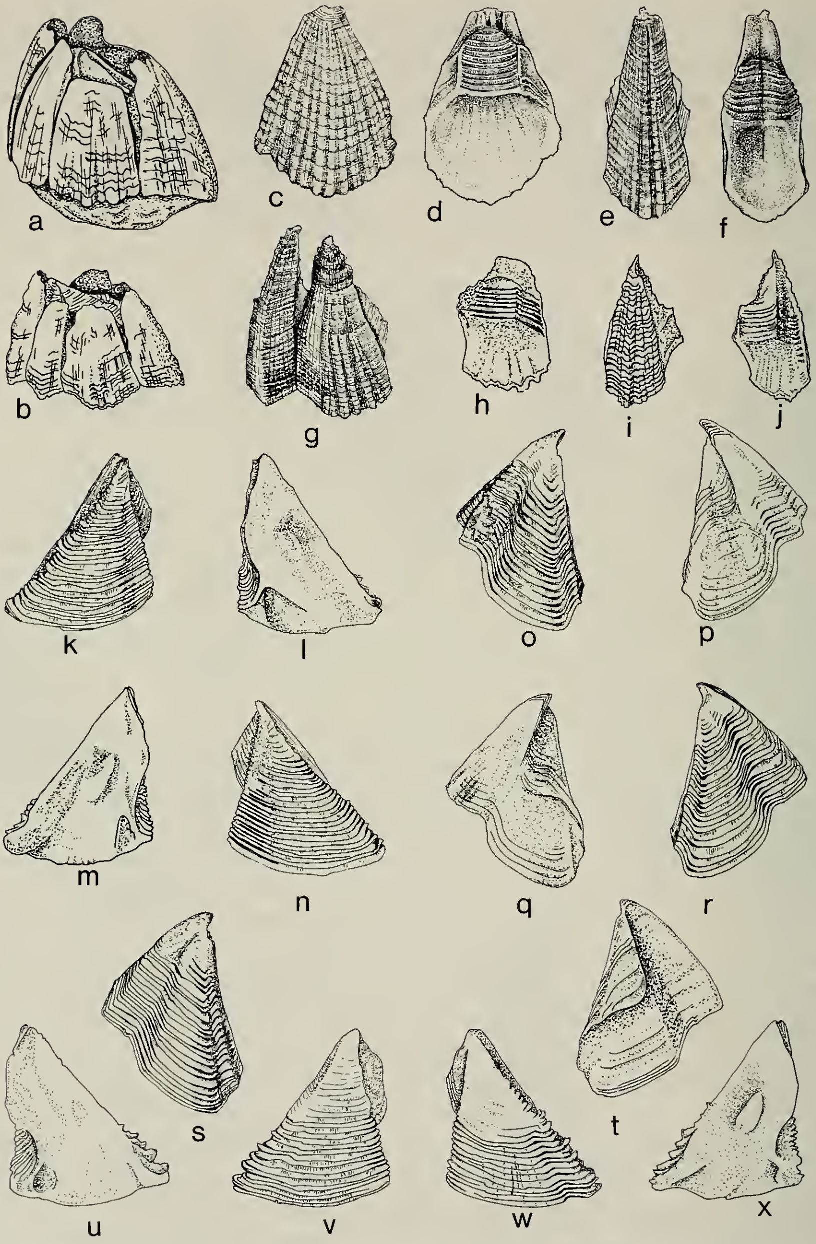


Fig. 3. *Membranobalanus costatus* n. sp., station MS04: a, Shell, holotype USNM 195270; b, Shell, paratype USNM 195271; c–d, Outer and inner view of rostrum, paratype USNM 195273; e–f, Outer and inner views of lateral, same specimen; g–h, Outer and inner views of carinolateral, same specimen; i–j, Outer and inner views of carina, same specimen; k–n, Outer and inner views of scuta, paratype USNM 194274; o–r, Outer and inner views of terga, same specimen; s–t, Outer and inner views of tergum, paratype USNM 195275; u–x, Outer and inner views of scuta, same specimen. Scale: Figs. a–b, ×4; figs. c–j, ×7; figs. k–x, ×8.

Labrum (Fig. 2s) triangular, with deep notch at apex of crest; two to six teeth present on one or both sides of notch.

Palp (Fig. 2p) kidney-shaped, superior margin concave, densely setose, setae short, pectinate; inner margin densely setose, setae longer, pectinate; inferior margin nearly devoid of setae.

Mandible (Fig. 2t) with fine teeth on cutting edge; upper tooth largest; second tooth not bifid, slightly smaller than first tooth, and located at center of cutting edge; third tooth slightly smaller than second, located at center of lower half of cutting edge; fourth and fifth teeth considerably smaller, fourth larger than fifth, fifth barely visible in some specimens; inferior angle without obvious denticles or spines (may be result of wear); inferior and superior margins setose.

Maxilla I (Fig. 2r) with straight edge; uppermost 2 large spines of equal size; notch lacking or incipient below uppermost 2 spines, its position indicated by 1 or 2 minute spinules; middle section bears 4 or 5 shorter, more slender, and non-alternating spines; lower third of edge bears 4 or 5 spines of same size as uppermost pair; inferior angle with tuft of small spinules; inferior and superior margins setose, with those of inferior margin longer, more numerous.

Maxilla II (Fig. 2q) bilobed; outer lobe ovate, superior and posterior margins densely setose, setae of posterior margin primarily non-pectinate, those of superior margin pectinate; inner lobe small, circular, densely clothed with coarsely pectinate setae.

Cirrus I (Fig. 2u) with grossly unequal rami; anterior ramus about 3 times length of posterior ramus, anterior ramus reversed, antenniform; posterior ramus more setose than anterior, with slightly protuberant articles; Cirrus II (Fig. 2v) short, with outer ramus one-third again as long as inner ramus; articles of both rami slightly protuberant, covered with pectinate setae somewhat longer than those of Cirrus I, outer distal margins of articles bear comb-like patches of minute spinules at bases of setae; Cirrus III longer and more slender that Cirrus II; outer ramus longer than inner; articles of rami not protuberant; setation and distribution of spinule comb rows similar to those of Cirrus II; Cirri IV–VI longer and more slender than Cirri I–III, gradually increasing in length posteriorly; Cirrus IV (Fig. 2v) with inner ramus slightly longer than outer; pedicel about one-half length of outer ramus; outer ramus less slender than inner, bearing large, recurved teeth, up to 6 in number, on medial articles; distal margins of outer surface of pedicel and articles each bearing row of upright denticles; inner ramus with few upright denticles at distal-anterior corner, and comb-like rows of minute spinules along outer distal borders of articles; Cirrus V longer and more slender than Cirrus IV, with denticles and comb-like rows of spinules on both rami arranged as on inner ramus of Cirrus IV Cirrus VI (Fig. 2x) longer than Cirrus V, with 3 pairs of spines on medial articles, distal pair long, median pair short, proximal hair minute; distal margins of outer surface of articles with few comb-like patches of spinules.

Etymology.—The specific name *costatus* is Latin for ribbed or costate, and refers to the externally costate shell of the new species.

Discussion.—*Membranobalanus costatus* is readily distinguished from previously described species of *Membranobalanus* by its costate parietes. The new species is related to Western Hemisphere *Membranobalanus*, all of which bear large, recurved teeth on the outer ramus of Cirrus IV. Of these species, *M.*

costatus is most similar in appearance to *M. nebrias* (Zullo and Beach, 1973) from the Galapagos Archipelago. In both species the shells lack radii, the rostra are short, and the opercular plates, trophi, and cirri are similar in overall conformation. *Membranobalanus costatus* differs consistently from *M. nebrias* in several features: (1) the rostrum is of ''normal'' length; (2) the opercular plates lack intercalated chitinous lamellae; (3) the scutum lacks a rostral depressor muscle pit in the basioccludent angle; (4) the scutal articular ridge is longer; (5) a ''radius'' is developed along the occludent margin of the scutum; (6) the tergal spur is broader; (7) the tergal articular ridge is longer; (8) the outer lobe of Maxilla II is much shorter; (9) the outer ramus of Cirrus IV bears up to six, rather than four, recurved teeth per article; and (10) the medial articles of Cirrus VI have up to three, rather than five, pairs of spines.

Membranobalanus costatus also resembles *M. declivis,* especially in features of the trophi and cirri and in the possession of a ''radius'' along the occludent margin of the scutum. *Membranobalanus costatus* is distinguished by its much shorter rostrum, absence of radii, shorter and thicker scutum that is markedly bowed from side to side, rather than nearly flat, its shorter and more equally triangular tergum, shorter and broader tergal spur, and vertical rather than oblique articular ridge.

Membranobalanus costatus differs from *M. orcutti* in having a short rostrum, a broader scutum with a much shorter adductor ridge and a ''radius'' along the occludent margin, a narrower tergum with a longer tergal spur, a simpler armature on the outer ramus of Cirrus IV, and three, rather than four, pairs of spines on the medial articles of Cirrus VI. The new species is most readily distinguished from the Indo-West Pacific species *M. brachialis* (Rosell), *M. cuneiformis* (Hiro), and *M. longirostrum* (Hoek) by the presence of large, recurved teeth on Cirrus IV.

If *M. costatus* is specific to *Anthosigmella varians,* as *M. declivis* appears to be with its host sponge, then this new barnacle species might be expected to occur in Florida, the Gulf of Mexico, the West Indies, and the Caribbean side of Central America (cf. Wiedenmayer 1977:245). We hope that queries such as this will stimulate further research on this interesting group of symbiotic barnacles.

Key to Western Hemisphere Species of *Acasta* and *Membranobalanus*

1. Basis membranous; shell high-conic, without calcerous spines on exterior of parietes 2
– Basis calcareous, slightly cup-shaped; shell globular, with calcareous spines on exterior of parietes .... *Acasta cyathus*
2. Rostrum considerably longer than other compartmental plates, usually at least twice length of carina 3
– Rostrum slightly longer or not noticeably longer than other compartmental plates 4
3. Radii present, narrow to broad; basal margin of scutum about same length as tergal margin; scutal adductor ridge, if present, confined to adductor muscle pit border; occludent margin of scutum bordered by sunken ledge (''radius'') .... *Membranobalanus declivis*
– Radii lacking; basal margin of scutum considerable shorter than tergal

margin; scutal adductor ridge prominent, extending to basal margin; occludent margin of scutum lacks accessory ledge ... *Membranobalanus orcutti*

4. Exterior of parietes smooth, except for growth bands; chitinous lamellae intercalated with calcareous lamellae of opercular plate apices; occludent margin of scutum lacks accessory ledge .... *Membranobalanus nebrias*

– Exterior of parietes prominently costate; apices of opercular plates lack chitinous lamellae; occludent margin of scutum bordered by sunken ledge ("radius") .... *Membranobalanus costatus*

Acknowledgments

We thank Kirstin Sandoy for first calling our attention to the sponge barnacles in the BLM material; William Kirby-Smith for allowing us access to the specimens; F. L. Nicholson and Kirstin Sandoy for identifying the sponges; and Thomas Prestia and Patricia Wheaton for donation of *Acasta cyathus* specimens from locality Z-704. This study was funded by the Marine Sciences Program, University of North Carolina at Wilmington, the National Science Foundation (Grant no. DEB-8020379), and the Crustacean Research Fund.

Literature Cited

Darwin, C. 1854. A monograph on the subclass Cirripedia with figures of all the species. The Balanidae, the Verrucidae, etc.—Ray Society, London, 684 pp.

Newman, W. A., and A. Ross. 1976. Revision of the balanomorph barnacles; including a catalog of the species.—San Diego Society of Natural History, Memoir 9, 108 pp.

Pearse, A. S. 1932. VII. Inhabitants of certain sponges at Dry Tortugas. Papers from Tortugas Laboratory.—Carnegie Institution of Washington (Publ. 435) 28:117–124.

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.—Bulletin of the United National Museum 93:1–366.

Spivey, H. R. 1981. Origins, distribution, and zoogeographic affinities of the Cirripedia (Crustacea) of the Gulf of Mexico.—Journal of Biogeography 8:153–176.

Verrill, A. E. 1901. II. Additions to the fauna of the Bermudas from the Yale Expedition of 1901, with notes on other species.—Transactions of the Connecticut Academy of Arts and Sciences 11:15–62.

Wells, H. W. 1966. Barnacles of the northeastern Gulf of Mexico.—Quarterly Journal of the Florida Academy of Sciences 29:81–95.

Wiedenmayer, F. 1977. Shallow-water sponges of the western Bahamas.—Birkhäuser, Basel and Stuttgart, 287 pp.

Zullo, V. A., and D. B. Beach. 1973. New species of *Membranobalanus* Hoek and *Hexacreusia* Zullo (Cirripedia, Balanidae) from the Galapagos Archipelago.—Los Angeles County Natural History Museum Contributions in Science 249:1–16.

Zullo, V. A., and W. H. Lang. 1978. Subclass Cirripedia. Pp. 158–160 *in* R. G. Zingmark, ed., An annotated checklist of the biota of the coastal zone of South Carolina.—University of South Carolina Press, Columbia, 364 pp.

(VAZ) Department of Earth Sciences, University of North Carolina at Wilmington, Wilmington, North Carolina 28403; (JDS) Duke University Marine Laboratory, Beaufort, North Carolina 28516; present address: Bodega Marine Laboratory, Bodega Bay, California 94923.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 478–480

ZEUGOPHILOMEDES, A NEW GENUS OF MYODOCOPINE OSTRACODE (PHILOMEDINAE)

Louis S. Kornicker

Abstract.—Zeugophilomedes, a new genus of myodocopine ostracode in the subfamily Philomedinae is proposed for 5 species in the Red Sea and Indian, Atlantic and Pacific Oceans. A key to the species is given and pertinent morphological characters illustrated.

A new genus is proposed for 5 species previously referred to either *Philomedes* Liljeborg, 1853 or *Euphilomedes* Poulsen, 1962: *Zeugophilomedes oblongus* (Juday, 1907:145), *Z. polae* (Graf, 1931:5), *Z. multichelatus* (Kornicker, 1958:230), *Z. fonsecensis* (Hartmann, 1959:197), and *Z. arostratus* (Kornicker, 1967a:2). *Euphilomedes grafi* (Hartmann, 1964:37) may, when more completely known, be referred to *Zeugophilomedes*.

Zeugophilomedes, new genus
Figs. 1–3

Type-species.—Philomedes multichelata Kornicker, 1958.

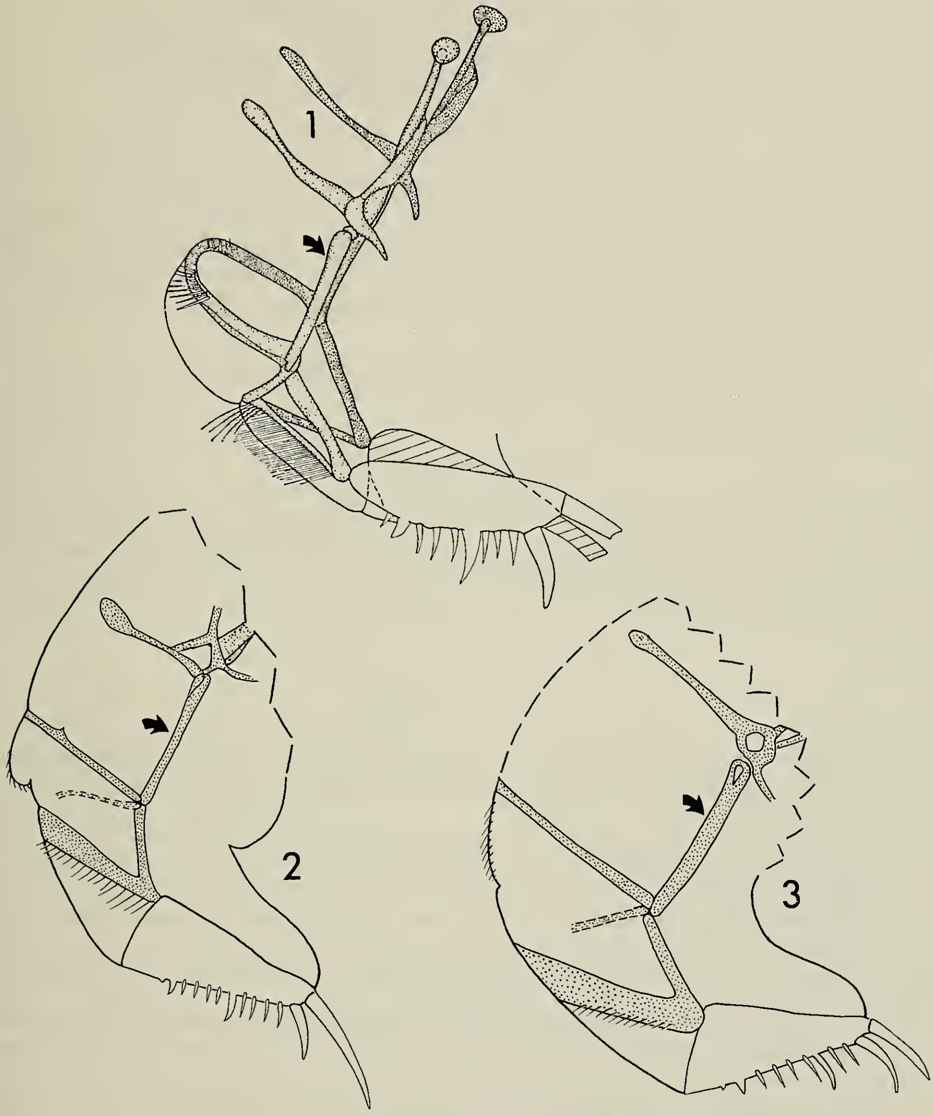
Etymology.—The name derived by combining the Greek *zeugos* (=pair, team) and *Philomedes*. Gender: masculine.

Diagnosis.—Sixth limb: End joint with relatively slight posterior projection.

Furca (Figs. 1–3): Each limb with 4 or 5 primary claws: 2 anterior claws separated from lamella by suture; remaining claws fused to lamella. One or more secondary claws between primary claws 2 and 3, and 3 and 4. Primary claw 4 followed by minute primary claw or additional secondary claws.

Internal sclerites in posterior part of body (Figs. 1–3): Y-sclerite unbranching, fairly stout. Complex of sclerites connected to proximal end of Y-sclerite. (Sclerites are visible through body in transmitted light.)

Comparisons.—Other genera in the Philomedinae have 6th limbs with end joints having considerable posterior projection. The slight posterior projection of the end joint of 6th limbs of *Zeugophilomedes* resembles that of members of the Pseudophilomedinae. I consider this to be the result of parallelism or convergence. (Because the 6th limb of *Z. oblongus* and *Z. fonsecensis* had not been described, I examined a female of the former [USNM 139159] from Monterey Bay, California, and an A-1 female of the latter from El Salvador and found the 6th limbs to have only slight posterior projection.) The furcae of members of *Zeugophilomedes* are unique for the Philomedidae in having some primary claws fused to the lamella (Figs. 1–3). The Y-sclerites (see Kornicker 1975:684 for discussion) of species in other genera of Philomedinae branch proximally (Y-shaped), and the combined stem and dorsal branch is concave dorsally; it is not linear and unbranched as in *Zeugophilomedes* (Figs. 1–3). The complex of sclerites of the type connected to the proximal end of the Y-sclerite of *Zeugophilomedes* (Figs. 1–3) has not been described in other genera.



Figs. 1–3. Posterior of body of 3 species of *Zeugophilomedes* showing furca and internal sclerites (arrow indicates Y-sclerite): 1, *Z. arostratus* ♂, USNM 112659; 2, *Z. multichelatus* ♂, USNM 152449; 3, *Z. oblongus* ♀, USNM 139159.

Known distribution.—*Z. oblongus,* San Diego Bay and off San Pedro, California (Juday 1907:147), Monterey Bay, California (herein). *Z. polae,* Gulf of Suez, Red Sea (Graf 1931:38; Kornicker 1967c:4). *Z. multichelatus,* Bimini, Bahamas (Kornicker 1958:232, 1967b:2), Aransas Pass, Gulf of Mexico (herein). Z. *arostratus,* Maldive Islands, Indian Ocean (Kornicker 1967a:14). *Z. fonsecensis,* El Salvador (Hartmann 1959:198).

Key to the Species of *Zeugophilomedes*

1. Furca with minute primary claw following the 4th primary claw 2
– Furca with 1 or more secondary claws following 4th primary claw 3
2. Furca with 1 secondary claw following 2nd primary claw .... *Z. fonsecensis*
– Furca with 2 or 3 secondary claws following 2nd primary claw .... *Z. oblongus*
– Furca with 4 or 5 secondary claws following 2nd primary claw .... *Z. multichelatus*
3. Incisur of female carapace very shallow; 2nd endopodial joint of male 2nd antenna with 2 subterminal bristles .... *Z. polae*
– Incisur of female carapace fairly deep; 2nd endopodial joint of male 2nd antenna with 2 midbristles; .... *Z. arostratus*

Acknowledgments

I thank the following people for their help: Gerd Hartmann for loan of a specimen of *Z. fonsecensis* from El Salvador; Peter M. Slattery for gift of a specimen of *Z. oblongus* from Monterey Bay, California; Carolyn Gast for inking illustrations; and Anne C. Cohen and Thomas E. Bowman for comments on the manuscript.

Literature Cited

Graf, H. 1931. Expedition S.M.S. "*Pola*" in das Rote Meer: Die Cypridinae des Roten Meeres.—Denkschriften der Akademie der Wissenschaften in Wien, Mathematsch, Naturwissenschaftliche Klasse 102:32–46.

Hartmann, Gerd. 1959. Zur Kenntnis der lotischen Lebensbereiche der pazifischen Küste von El Salvador unter besonderer Berücksichtigung seiner Ostracodenfauna.—Kieler Meeresforschungen 15(2):187–241.

———. 1964. Zur Kenntnis der Ostracoden des Roten Meeres.—Kieler Meeresforschungen, Sonderheft 20:35–127.

Juday, Chauncy. 1907. Ostracoda of the San Diego Region, II. Littoral forms.—University of California Publications in Zoology 3(9):135–156.

Kornicker, Louis S. 1958. Ecology and taxonomy of Recent marine ostracodes in the Bimini area, Great Bahama Bank.—Publications of the Institute of Marine Science (The University of Texas) 5:194–300.

———. 1967a. *Euphilomedes arostrata*, A new myodocopid ostracod from Maldive Islands, Indian Ocean.—Proceedings of the United States National Museum 120(3563):1–21.

———. 1967b. Supplementary description of the myodocopid ostracod *Euphilomedes multichelata* from the Great Bahama Bank.—Proceedings of the United States National Museum 120(3566): 1–16.

———. 1967c. Supplementary descriptions of two myodocopid ostracods from the Red Sea.—Proceedings of the United States National Museum 121(3571):1–18.

———. 1975. Antarctic Ostracoda (Myodocopina).—Smithsonian Contributions to Zoology 163:1–720 p.

Liljeborg, Wilh. 1853. Ostracoda. Pp. 92–130 *in* De Crustaceis ex ordinibus tribus: Cladocera, Ostracoda et Copepoda in Scania Occurrenibus.

Poulsen, E. M. 1962. Ostracoda-Myodocopa, 1: Cypridiformes-Cypridinidae.—Dana-Report 57:1–414. Copenhagen: Carlsberg Foundation.

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

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 481–488

A NEW SPECIES OF *MUNIDOPSIS* FROM SUBMARINE THERMAL VENTS OF THE EAST PACIFIC RISE AT 21°N (ANOMURA: GALATHEIDAE)[1]

Austin B. Williams and Cindy Lee Van Dover

Abstract.—A new galatheid, *Munidopsis lentigo,* is described from depths of 2600 m on a thermally active area of the East Pacific Rise. The species has distinctive organs on the chelae and strikingly flattened eyes. Similarities to other species in the genus are discussed.

Exploration of thermally heated vent areas on rift zones of the East Pacific Rise has yielded yet another previously unknown decapod crustacean species which is here described. One of us (CLVD) participated in the OASIS Expedition to vent sites at 21°N aboard the R/V *Melville,* 12 April to 8 May 1982, during which collections of *Munidopsis* and other decapods were made by various investigators with the aid of the deep submersible *ALVIN* on Dives 1211 and 1221.

Munidopsis lentigo, new species
Figs. 1–3

Diagnosis.—Differs from all other species of *Munidopsis* in possession of lenticular-shaped, flattened, smooth, light brown spot on ventral surface of each chela, and flattened eyes with depressed cornea shielded by projecting flat dorsal spine and ventral plate.

Description.—Carapace, exclusive of rostrum, distinctly longer than broad, moderately arched transversely; cervical and transverse grooves faintly indicated, slight depression in cardiac region, scattered obsolescent rugosities on each anterior branchial region, more distinct and transversely arranged rugosities on each posterior branchial region; posterior margin deeply, sometimes angularly emarginate medially. Frontal margin armed with strong triangular spine lateral to eye; anterior ⅔ of lateral margin armed typically with 7 spines. Rostrum slender, dorsally flattened, slightly deflexed and with serrate borders anteriorly, tip acute (bent to left in holotype). Lateral plate lightly rugose, projecting anteriorly below antennal peduncle and tipped anteriorly with obscure serration.

Abdomen unarmed, second and third segments bearing low dorsal transverse ridge paralleled by shorter ridge bordering posterior margin; obsolescent anterior transverse ridge on fourth segment; fifth and sixth segments smooth.

Eyes large, dorsoventrally flattened. Cornea cupped within overgrowths of ocular peduncle consisting of flat, broadly triangular, projecting dorsal spine with obscurely serrate margins having distal ⅓ slightly upturned and bent mesad to reach about ⅔ length of rostrum, continuous at each side with spatulate ventral lip serrated on margin.

---

[1] OASIS Expedition Contribution No. 5.

Basal article of antennular peduncle with single outer terminal spine; preceded by slender spine on dorsal margin, a very short terminal spine on mesial margin. Antennal peduncle with 2 fixed spines on basal article, lateral one spatulate and acutely tipped, ventral one slender; short second and fourth articles each bearing short buttressed lateral spine, much larger third article with serrated lateral flange.

Third maxilliped with ischium ⅓ longer than merus and bearing mesial ridge armed with finely uniform, evenly spaced teeth; merus with distolaterally directed strong spine at midlength of ventrolateral border; carpus densely setose mesially, propodus and dactyl so on ventromesial borders. Projecting third thoracic somite with anterior margin nearly straight, lacking spines or median notch.

Epipods absent from pereopods.

Chelipeds of mature male asymmetrical, rugose proximally but becoming smoother distally, spined and sparsely but inconspicuously setose; cutting edges of fingers placed toward dorsal side. Major (right) cheliped of holotype robust; ischium unarmed; merus with very strong subdistal spine preceded by smaller spine on mesial margin, distolateral spine small and acute, rounded mesioventral ridge bearing acute spine near midlength and terminating in blunt distal spine; carpus with 2 strong spines on mesial margin; chela broad, obscurely rugose, palm as long as fingers, convex irregular lateral margin bearing 4 remote dorsal spines, similar mesial margin bearing 5 obsolescent spines, swollen ventral surface marked with 3 longitudinal lines of remote setal tufts on obsolescent ridges, middle ridge becoming pronounced rib on fixed finger and curving mesad to terminate in hooked tooth; shallow concavity near base of fixed finger bearing slightly raised, flattened, smooth, light brown, bean-shaped spot (1.28 × 2.11 mm); fingers stout, more or less flattened above; cutting edges crenate, closing closely; fixed finger with single basal tooth fitting into notch distal to single basal tooth on dactyl, terminating in small dorsal tooth and slightly hooked ventral tooth; dactyl ending in hooked tooth confluent ventrally with truncate accessory cusp on rib running length of finger. Minor (left) cheliped of holotype acutely spined and sparsely but conspicuously setose; ischium unarmed; merus somewhat prismatic, dorsal crest bearing row of small spines, 2 strong spines on mesial margin distally plus a smaller distoventral and still smaller distolateral spine; carpus with 4 mesial spines grading from small proximally to very strong distally; chela somewhat broadened, more or less flattened above but palm with fixed finger and dactyl independently somewhat trigonal below; slight convexity on lateral margin at base of fixed finger adjacent to ventral, slightly raised, flattened, smooth, light brown oval spot (1.34 × 1.98 mm); palm slightly longer than fingers, 5 or 6 spines on lateral margin, 4 less outstanding spines on mesial margin; fingers nearly straight, cutting edges closing closely, straight and indistinctly crenate, hooked tip of dactyl closing between hooked acute upper and broader based lower terminal teeth of fixed finger.

Female with chelipeds analogous to minor cheliped of male; those of paratype 191161 slightly asymmetrical and rather slender, ventral smooth spot on palm at base of fixed finger conspicuous (on right chela 0.54 × 0.99 mm, left 0.64 × 1.22 mm); those of paratype 191162 also slightly asymmetrical but with chelae broader (fingers broken left side), ventral spot on palm at base of fixed finger (on right chela 1.02 × 1.34, left 0.96 × 1.34 [est.] mm).

First walking legs reaching to or beyond base of dactyl on cheliped, second and third legs reaching about to base of dactyl on preceding legs. Merus of each walking leg slender; row of small spines dorsally, strongest and most numerous on third, less developed on second and first; first and second with strong distolateral spine. Carpi armed with distodorsal spine and smaller distoventral spine. Propodi compressed, slightly shorter than meri, each bearing 2 or 3 slender movable spines ventrally and unequal pair of slender movable spines distoventrally near articulation of dactyl. Dactyls about ⅓ length of propodi, compressed, curved, corneous tip preceded by comb of anteriorly directed spinules on ventral margin.

Measurements in mm.—

	M	M	F	F	F
	Holotype	Paratype	Paratype	Paratype	Paratype
	191160	191163	191163	191162	191161
Carapace					
Base ocular peduncles to notch in posterior margin	12.8	10.6	8.2	11.5	11.9
Rostrum	3.8	3.1	2.6	3.2	3.5
Total length	16.6	13.7	10.8	14.7	15.4
Width	10.9	8.7	8.8	9.5	10.4
Chelae					
Major					
Length propodus	16.6(R)	missing		12.8(R)	12.1(L)
Width propodus	6.8			5.0	3.1
Length dactyl	7.7			5.5	6.1
Minor					
Length propodus	16.6(L)	missing		*11.1(L)	10.5(R)
Width propodus	4.4			4.1	2.7
Length dactyl	7.7			*4.5	5.3
Eggs				2.00 × 2.20	2.24 × 2.24

* Broken (estimated).

Variation.—The posterior border of the carapace varies from evenly concave (usual) to notched medially (paratype F 191161). The latter specimen also has a more prominent and distinctly outlined cardiac region than do other members of the type-series, and the ventral margin of lateral plates on its cephalothorax is more rounded. Variability in chelae is noted in the description.

Type-locality.—Pacific Ocean, East Pacific Rise, 20°49.6′N, 109°6′W, 2600 m.

Material studied.—Confined to the type-series listed under *measurements* and deposited in the crustacean collection of the United States National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.

Etymology.—The name is a noun in apposition from the Latin "lentigo," meaning a lentil-shaped spot, referring to the oval spot on the ventral side of each chela.

Remarks.—*Munidopsis lentigo* has features that set it well apart from other species in the richly diverse genus *Munidopsis,* but a more comprehensive study than we have made should precede any attempts to separate it from that genus

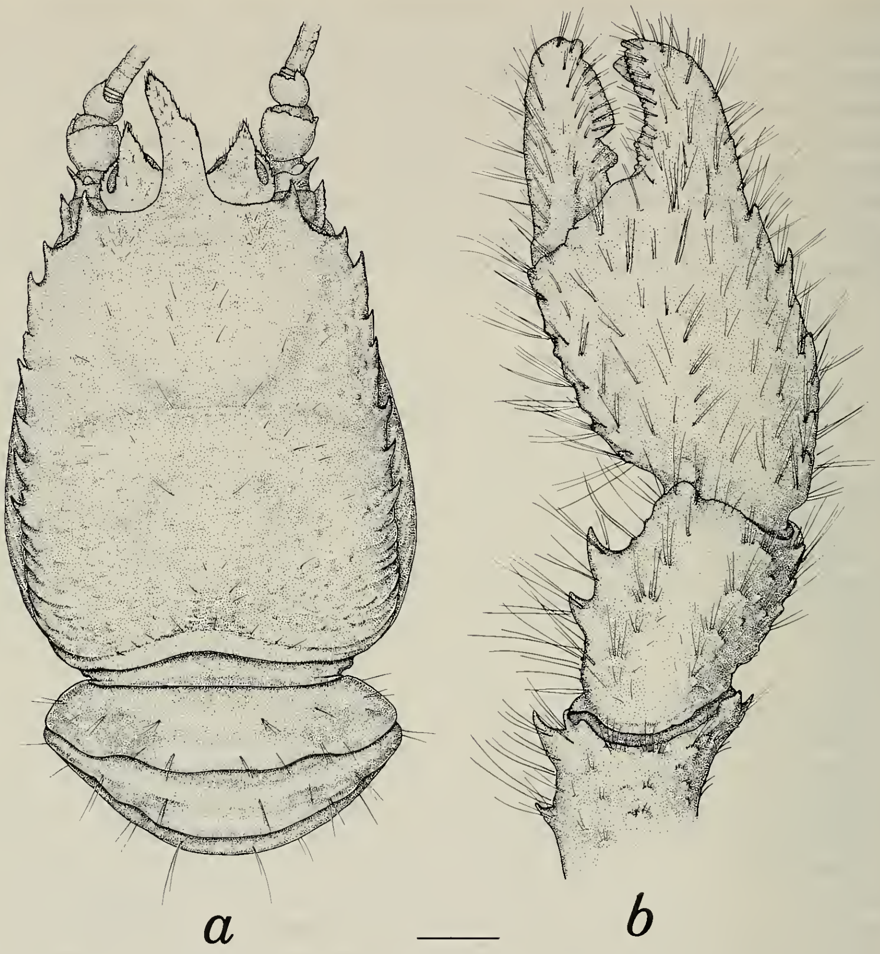


Fig. 1. *Munidopsis lentigo.* Male holotype USNM 191160: a, Dorsal view (tip of rostrum bent to left), appendages not shown; b, Right chela, carpus, and distal part of merus. Scale = 2 mm.

(see Chace 1942; Ambler 1980). No other known members of *Munidopsis* possess the peculiar oval organs on the chelipeds nor do any have flattened eyes with depressed cornea covered by a projecting flat dorsal spine as well as shielded by a ventral plate. Several species, however, have eyes armed with spines. Among those that can be compared with *M. lentigo* in this respect, *M. beringana* Benedict, 1902, *M. ciliata* Wood-Mason, 1891, *M. crassa* Smith, 1885, *M. pilosa* Henderson, 1885 (illustrated 1888), and *M. verrilli* Benedict, 1902 each have a slender compressed, somewhat upturned rostrum which leaves the eyestalks exposed to dorsal view. In all of these species except *M. pilosa,* the eyestalk is drawn into a prominent mesial spine exceeding the subglobular lateral cornea, and in *M. ciliata* and *M. verrilli* there is a small posterolateral spine as well. The eyestalk of *M. pilosa* terminates in a long slender spine that covers only the middorsal part of the subglobular cornea and reaches about half the length of the rostrum beyond it; there is also a short acute ventral spine but no ventral plate.

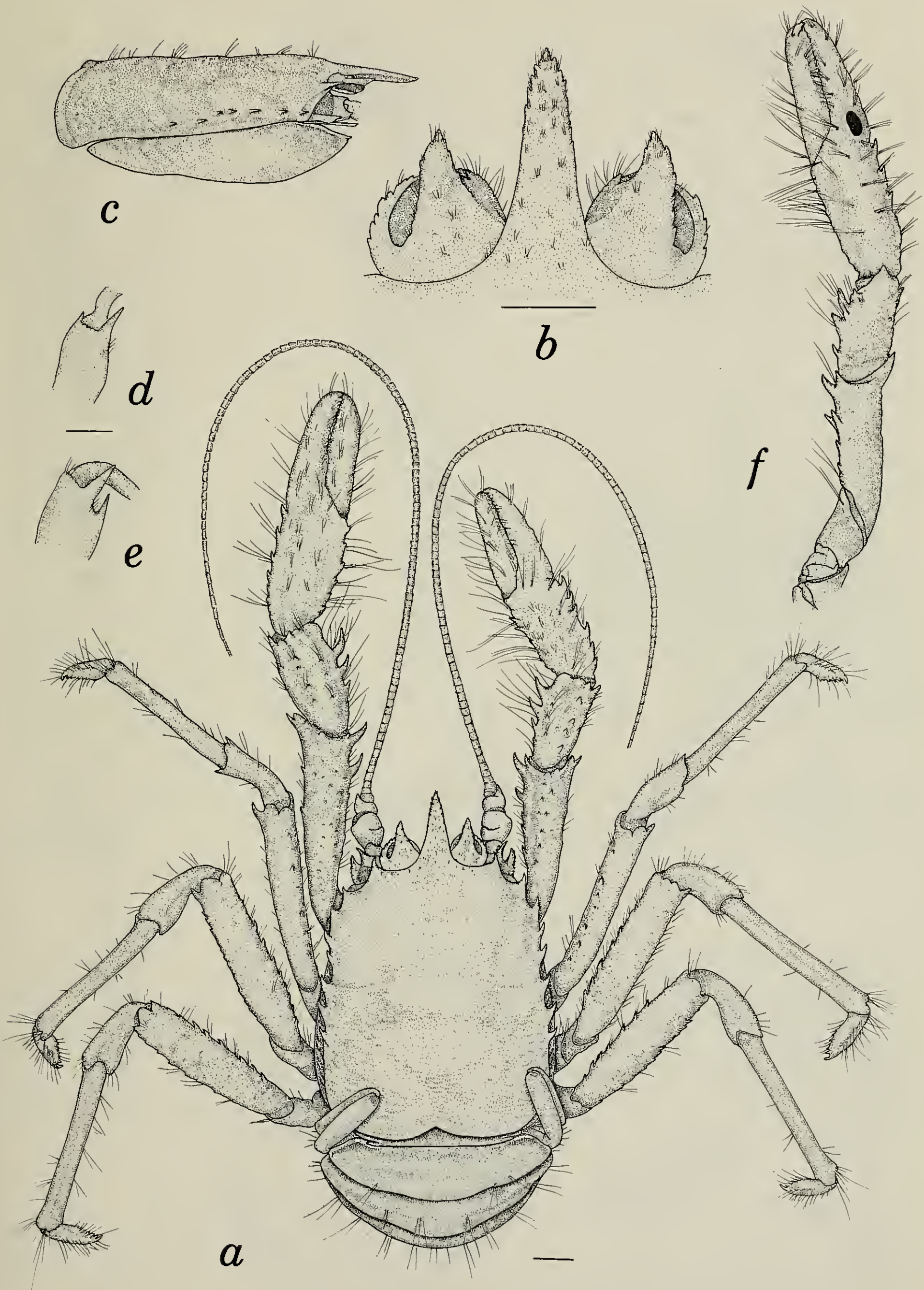


Fig. 2. *Munidopsis lentigo.* Female paratype USNM 191161: a, Dorsal view; b, Rostrum and eyes; c, Carapace, eye and base of antenna, lateral view; Basal article of antennal peduncle, distal part; d, Ventral view; e, Same, lateral view; f, Left cheliped, ventral view. Scales = 1 mm.

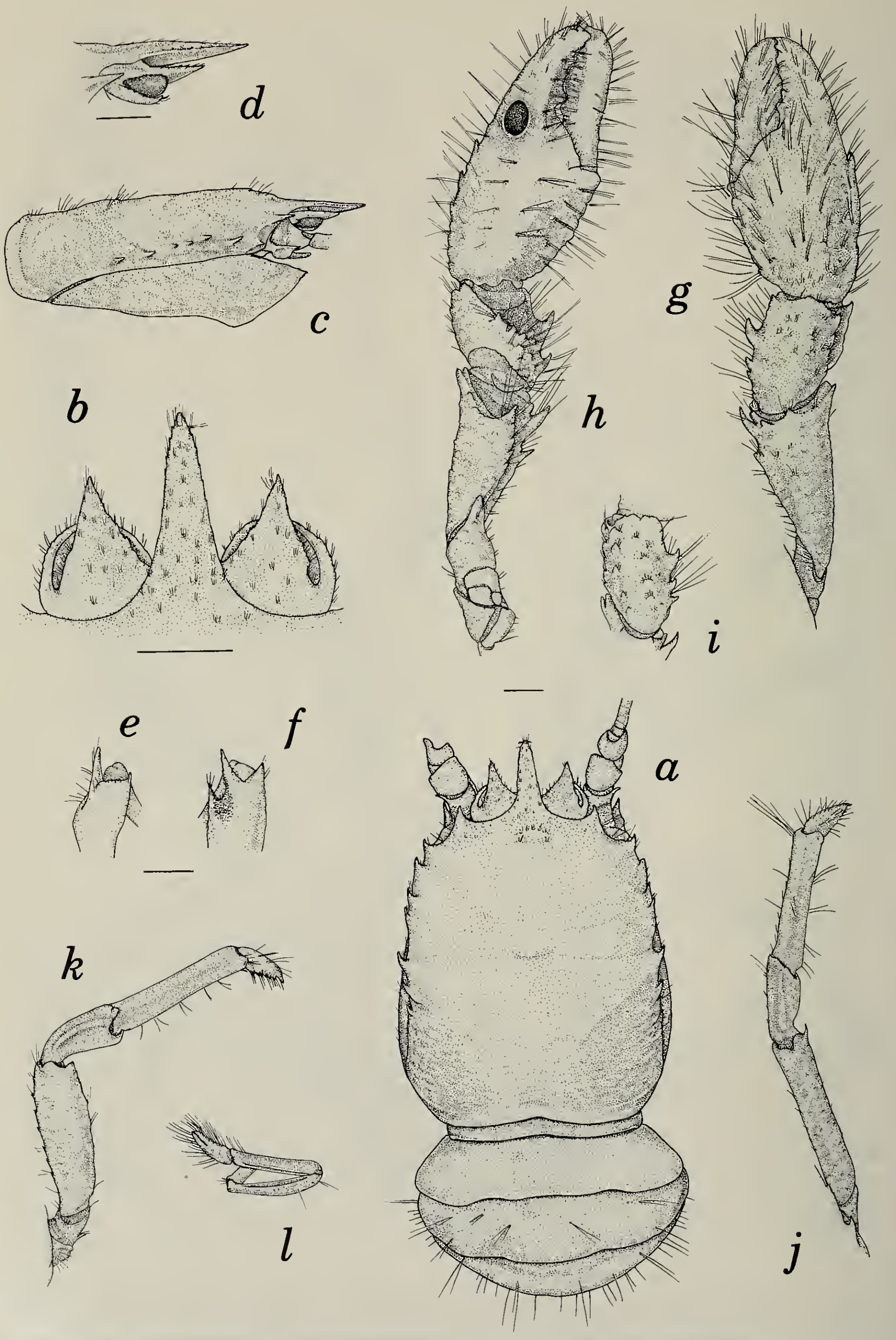


Fig. 3. *Munidopsis lentigo.* Female paratype 191162: a, Dorsal view, appendages not shown; b, Rostrum and eyes; c, Carapace, eye and base of antenna, lateral view; d, Rostrum and eyes, lateral view; e, Basal article of antennal peduncle, distal part, dorsal view; f, Same, lateral view; g, Right cheliped, dorsal view; h, Same ventral view; i, Carpus, left cheliped; j, Right second pereopod; k, Right third pereopod; l, Left fifth pereopod. Scales = 1 mm.

Other species such as *M. bermudezi* Chace, 1942, have eyestalks resembling those of species mentioned above, but the rostrum is broader at its base, while species such as *M. nitida* (A. Milne Edwards, 1880, illustrated by Milne Edwards and Bouvier, 1897) and *M. scabra* Faxon, 1895, have eyestalks with short, extremely slender mesiodorsal spines which hardly conceal the prominent globular cornea at all. The broad rostrum of *M. latirostris* Faxon, 1895, is emarginate basally, exposing fixed eyestalks with subglobular cornea partly covered by a broad, mesiodorsal outgrowth of the peduncle.

The oval spots on the chelipeds recall similar organs in homolid crabs of the genus *Hypsophrys* both in shape and placement at the base of the fixed finger (Williams 1974, 1976). Species of *Hypsophrys* displays a spot on both inner and outer surface of the chelae whereas *M. lentigo* has them only on the ventral surface, analogous to the inner surfaces in *Hypsophrys*. Fingers on the right chela of female 191162 were broken by an accidentally dropped camera lens during study, the break on the fixed finger passing through the spot on that hand. Inspection of the broken spot under a binocular dissecting microscope indicates an internal structure resembling that in the organs on *H. noar* Williams, 1974, and *H. superciliosa* Wood-Mason, 1891, whose function is unknown (Williams 1976). Histological structure of the spots in *M. lentigo* remains to be studied.

In none of the comparable species of *Munidopsis* does armature of the integument closely resemble that of *M. lentigo*. The narrow, compressed and upturned rostrum of the first five species is unlike the rather slender, dorsally flattened and somewhat distally downturned rostrum of *M. lentigo*; moreover, all of these species except *M. pilosa* have both lateral and gastric spines on the carapace. The species with a broad rostrum have hairy or scabrous surfaces quite unlike that of *M. lentigo*.

Finally, *M. lentigo, nitida, pilosa, scabra,* and *verrilli* lack epipods on the pereopods whereas the remaining species mentioned above have them on the chelipeds.

Acknowledgments

We are indebted to K. Smith, Scripps Institution of Oceanography, who as chief scientist made cabin space available aboard the R/V *Melville*, and to expedition personnel who helped to collect the material studied. We thank F. A. Chace, Jr., and B. B. Collette for critical reading of the manuscript, Keiko Hiratsuka Moore for making the illustrations, and Virginia R. Thomas for entering the text on a word processor.

Literature Cited

Ambler, J. W. 1980. Species of *Munidopsis* (Crustacea, Galatheidae) occurring off Oregon and in adjacent waters.—Fishery Bulletin 78(1):13–34.

Benedict, J. E. 1902. Description of a new genus and forty-six species of crustaceans of the family Galatheidae, with a list of the known marine species.—Proceedings of the United States National Museum 26(1311):243–334.

Chace, F. A., Jr. 1942. Reports on the scientific results of the Atlantis expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. The anomuran Crustacea. I. Galatheidae.—Torreia, Havana 11:1–106.

Faxon, W. 1895. 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. XV. The stalk-eyed Crustacea.—Memoirs of the Museum of Comparative Zoology 18:292 pp., 67 pls. (10 pls. colored).

Henderson, J. R. 1885. Diagnoses of the new species of *Galatheidea* collected during the "Challenger" Expedition. Annals and Magazine of Natural History (5) 16(96):407–421.

———. 1888. Report of the Anomura collected by H.M.S. Challenger during the years 1873–76. Challenger Expedition, 1872–76.—Report on the Scientific Results of the Voyage of H.M.S. *Challenger* during the years 1873–76. Zoology 27(69):i–xi, 1–221, 21 pls.

Milne-Edwards, A. 1880. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, '78, '79, by the United States Coast Survey Steamer "Blake," Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. VIII.—Études préliminaires sur les Crustacés.—Bulletin of the Museum of Comparative Zoology, at Harvard College 8(1):1–68, 2 pls.

———, and E. L. Bouvier. 1897. Reports on the results of dredging under the supervision of Alexander Agassiz in the Gulf of Mexico (1877–78) in the Caribbean Sea (1878–79) and along the Atlantic coast of the United States (1880) by the U.S. Coast Steamer "Blake" . . . . Description des Crustacés de la famille des Galathéidés recueillis pendant l'expédition.—Memoirs of the Museum of Comparative Zoology 19(2):1–141, 12 pls.

Smith, S. I. 1885. On some new or little known decapod Crustacea, from recent Fish Commission dredging off the east coast of the United States.—Proceedings of the United States National Museum 7(32):493–511.

Williams, A. B. 1974. A new species of *Hypsophrys* (Decapoda: Homolidae) from the Straits of Florida, with notes on related crabs.—Proceedings of the Biological Society of Washington 87(42):485–492.

———. 1976. Integumental organs of unknown function on chelipeds of deep-sea crabs, genus *Hypsophrys*.—Journal of Morphology 150(4):889–899.

Wood-Mason, J., and A. Alcock. 1891. Natural history notes from H. M. Indian Marine Survey Steamer "Investigator," Commander R. F. Hoskyn, R.N., commanding.–No. 21. Note on the results of the last season's deep-sea dredging.—Annals and Magazine of Natural History, (6) 7(27):258–272.

(ABW) National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Washington, D.C. 20560; (CLVD) Department of Biology, University of California at Los Angeles, Los Angeles, California 90024.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 489–523

THE NEARCTIC SPECIES OF THE *BEZZIA BIVITTATA* GROUP (DIPTERA: CERATOPOGONIDAE)

Willis W. Wirth and William L. Grogan, Jr.

Abstract.—The *bivittata* Group of the genus *Bezzia* Kieffer, subgenus *Bezzia*, is comprised in North America of at least 15 species, of which the following 12 are described as new: *aklavakensis* from Canadian Northern Territory, *andersonorum* from Maryland, *capitata* from Honduras and Arizona, *chelistyla* from Arizona, *gibberella* from Maryland, *luteiventris* from Virginia, *mohave* from California, *nigripes* from Utah, *sandersoni* from Arizona, *setosinotum* and *spathula* from Maryland, and *texensis* from Texas. Diagnoses are given of all taxa, a key is presented, and all species are illustrated.

This review is one of a series in which additions and corrections are made to the "Revision of the Nearctic Species of the Genus *Bezzia*" by Dow and Turner (1976). In the present series six groups have already been studied in depth since 1976: Grogan and Wirth (1981) on the genus *Amerohelea* Grogan and Wirth; Wirth and Grogan (1982) on the genus *Phaenobezzia* Haeselbarth; Wirth (in press) on the *bicolor* Group, Wirth (in press) on the *cockerelli* and *dorsasetula* Groups, and Wirth *et al.* (in press) on the *annulipes* Group of *Bezzia*, subgenus *Homobezzia*; and Wirth (in press) on the *nobilis* Group of the subgenus *Bezzia* s.s. The present paper deals with a second group of *Bezzia* s.s., here named the *bivittata* Group.

In addition to the revision by Dow and Turner, we urge that users of our *Bezzia* papers also refer closely to the excellent revisions of the Soviet species by Remm (1974a, 1974b). We believe that Remm reached a sound basic understanding of the characters useful in recognition of natural groups within the genus *Bezzia*, although we would disagree in one or two instances whether certain groups should be given generic or subgeneric status. Starting with the characters used by Remm, we will offer short diagnoses that should explain the basis of our group classification. We wish to stress that our present treatment is to be considered provisional and for this reason we will try to be as conservative as possible.

In addition to Remm's important papers, we have drawn on several other recent works on *Bezzia* for an evaluation of group characters. Clastrier (1962) presented excellent descriptions and figures of a large number of Palaearctic species but made very little attempt to place them in systematic groups or to take into account the species poorly described by earlier authors. Haeselbarth (1965a, 1965b, 1975) treated three groups of African species in similar detail, but added excellent diagnoses and taxonomic discussions of the *africana* and *nicator* groups, and the group which he separated off as the genus *Phaenobezzia* Haeselbarth. Tokunaga (1966) made no attempt at group classification when he offered excellent descriptions and figures of the New Guinea species.

Taxonomic characters employed for identification of adult ceratopogonids were described by Wirth (1952), Dow and Turner (1976), and Wirth *et al.* (1977). Wing length is measured from the basal arculus to the wing tip and costal length from the basal arculus to the costal apex. Costal ratio is the costal length divided by the wing length. Antennal ratio of the female is the sum of the lengths of the elongated five distal flagellar segments divided by the sum of the lengths of the preceding eight; male antennal ratio is obtained similarly since the five distal antennal segments are also elongated in this group. Palpal ratio is the length of the third palpal segment divided by its greatest breadth.

The holotypes and allotypes of our new species are deposited in the U.S. National Museum in Washington, D.C. Paratypes as available will be deposited in the British Museum (Natural History), London; Muséum National d'Histoire Naturelle, Paris; Canadian National Collection, Agriculture Canada, Ottawa; and the California Academy of Sciences, San Francisco.

Genus *Bezzia* Kieffer

Bezzia Kieffer, 1899:69. Type-species, *Ceratopogon ornatus* Meigen, by original designation.

Diagnosis.—Large, nearly bare, predaceous midges. Body not unusually slender or dorsoventrally flattened. Antenna short to moderately long. Palpus 5-segmented, 3rd segment longest, not thickened, with scattered sensilla. Female mandible with 10–20 coarse teeth and with finer proximal teeth in series. Thorax robust, mesonotum usually with anterior spine or tubercle, with several strong supra-alar and postalar setae. Wing with 1 radial cell, vein R2+3 absent; costal ratio 0.6–1.0; vein M2 originating near r-m crossvein but may be slightly more distad or proximad; macrotrichia absent. Legs slender, sometimes with numerous spine-like setae; fore femur with 0–12 ventral spines; 4th tarsomere short and more or less cordiform; 5th tarsomere without ventral batonnets or strong, sharp-tipped setae; female claws simple and equal, usually with small basal tooth on inner face; male claws cleft apically. Female abdomen with 1–5 pairs of sclerotized gland rods arising from anterior margins of terga; 2 spermathecae present, occasionally a 3rd, rarely only 1 spermatheca. Male genitalia inverted, 9th tergum short with prominent setose cerci, without sclerotized apicolateral processes; aedeagus shaped variously, usually triangular in outline; parameres fused to form an unpaired distal process, usually rod-like but sometimes variously shaped; dististyle well developed and articulated.

Bezzia is closely related to the large, widespread genus *Palpomyia* Meigen. Most of the *Palpomyia* species groups can be distinguished from *Bezzia* by habitus or genitalic structure; in all cases the presence of vein R2+3 and 2 radial cells will distinguish species of *Palpomyia* and its relatives from *Bezzia*. Remm's doubts about the independence of *Bezzia* and *Palpomyia* arose from his inclusion in *Bezzia* of *Phaenobezzia* as a subgenus. We support Haeselbarth (1965b) in according generic status to *Phaenobezzia* in view of the remarkable structure of the male genitalia with non-articulated dististyle, presence of sharp, spine-like setae ventrally on the 5th tarsomere of the female, long costa (costal ratio 0.92–0.87), and slender legs without distinct bands or ventral spines on the fore femur. Likewise the species *Bezzia frontispina* Dow and Turner is anomalous in *Bezzia* and we (Grogan and Wirth 1981) placed it in the new genus *Amerohelea* with a Neotropical group of species with 1 spermatheca, 1 pair of gland rods placed extremely laterad on the anterior margin of the 8th tergum, and in most of the species with 2 radial cells in the wing.

Synoptic Key to Subgenera and Groups of Nearctic *Bezzia*

1. Male antennal segment 12 no longer than 13, antennal plume weakly developed; (mesonotum dull, occasionally weakly shiny, brownish or grayish with or without vittae; tibiae pale or with a dark medial or basal ring; spines of fore femur stout when present; female with 0–5 pairs of gland rods; males considerably smaller than females; male aedeagus triangular with minute spinules or hairs) (Subgenus *Homobezzia* Macfie) 2
– Male antennal segment 12 longest; antennal plume well developed, extending at least to apex of 13th segment; (mesonotum black, shiny or dull or with silvery hairs, if grayish brown with dark vittae, the hind tibia is yellow in midportion, apex broadly black, and all femora bear spines; tibiae often black; fore femur with spines slender when present; female abdomen with 1–2 pairs of gland rods; males about same size as female; male aedeagus variable but not as above) (Subgenus *Bezzia* Meigen, s.s.) 5

Subgenus *Homobezzia* Macfie

2. Larger species, female wing 1.3–3.4 mm long; mesonotum without bristly setae on disc; (fore femur without spines or with 1–4 stout to slender spines of similar lengths, with or without strong basal tubercles; pupal respiratory horn with numerous (25–60) spiracular openings, apex more or less flared, abdominal tubercles well developed) 3
– Small species, female wing 1.2–1.3 mm long; mesonotum with 2 rows of strong bristly setae on disc; (fore femur with 5–7 stout ventral spines of alternating uneven lengths arising from distinct elevations; pupal respiratory horn with only 7–12 spiracular openings, abdominal tubercles small) .... *dorsasetula* Group
3. Fore femur unarmed ventrally .... *bicolor* Group
– Fore femur armed ventrally with one or more short black spines 4
4. Fore and mid femora entirely dark brown or with dark bands apical ... . *cockerelli* Group
– Fore and mid femora with subapical dark bands .... *annulipes* Group

Subgenus *Bezzia*, s.s.

5. Fore femur usually unarmed ventrally; legs brown to black; femora and tibiae usually with narrow pale rings, rarely femora pale at base or tibiae pale .... *bivittata* Group
– Fore femur armed ventrally with one or more slender black spines; legs brown to black, or if banded the pale bands broad 6
6. Legs broadly yellow or with broad yellow median bands on fore femora and tibiae .... *nobilis* Group
– Legs primarily dark brown to black, at most one pair of legs with broad yellowish bands .... *expolita* Group

Dow and Turner (1976) separated the subgenus *Pseudobezzia* Malloch from *Bezzia* s.s. by the presence of 1 or more very large stout setae on the vertex, but this seta varies so much in size among species that it is only useful but not reliable. Most of Dow and Turner's *Bezzia* s.s. would fall in *Homobezzia* Macfie according to Remm's (1974a) characterization. From the structure of the male genitalia and female spermathecae Remm's subgenus *Sivabezzia* appears to be very similar to the *expolita* Group of *Bezzia* s.s. Dow and Turner's subgenus *Aspinabezzia* is a combination of *Homobezzia* and *Bezzia* s.s. in which the fore femora lack ventral spines.

Subgenus *Bezzia,* s.s.

Diagnosis.—Thorax usually dark brown or black; mesonotum shining or dull with silvery hairs or pollinose markings. (In the *nobilis* Group the mesonotum is pollinose grayish brown with dark vittae but the hind tibia is yellow in midportion and the apex broadly black, and all the femora bear scattered spines.) Anteromarginal spine of mesonotum absent. Males and females more or less of same size. Male antennal plume well developed, extending at least to apex of 13th segment; 12th segment longest. Fore femur with 0–6 spines; tibiae often black. Female abdomen usually with a single pair of gland rods.

Bezzia (*Bezzia*) *bivittata* Group

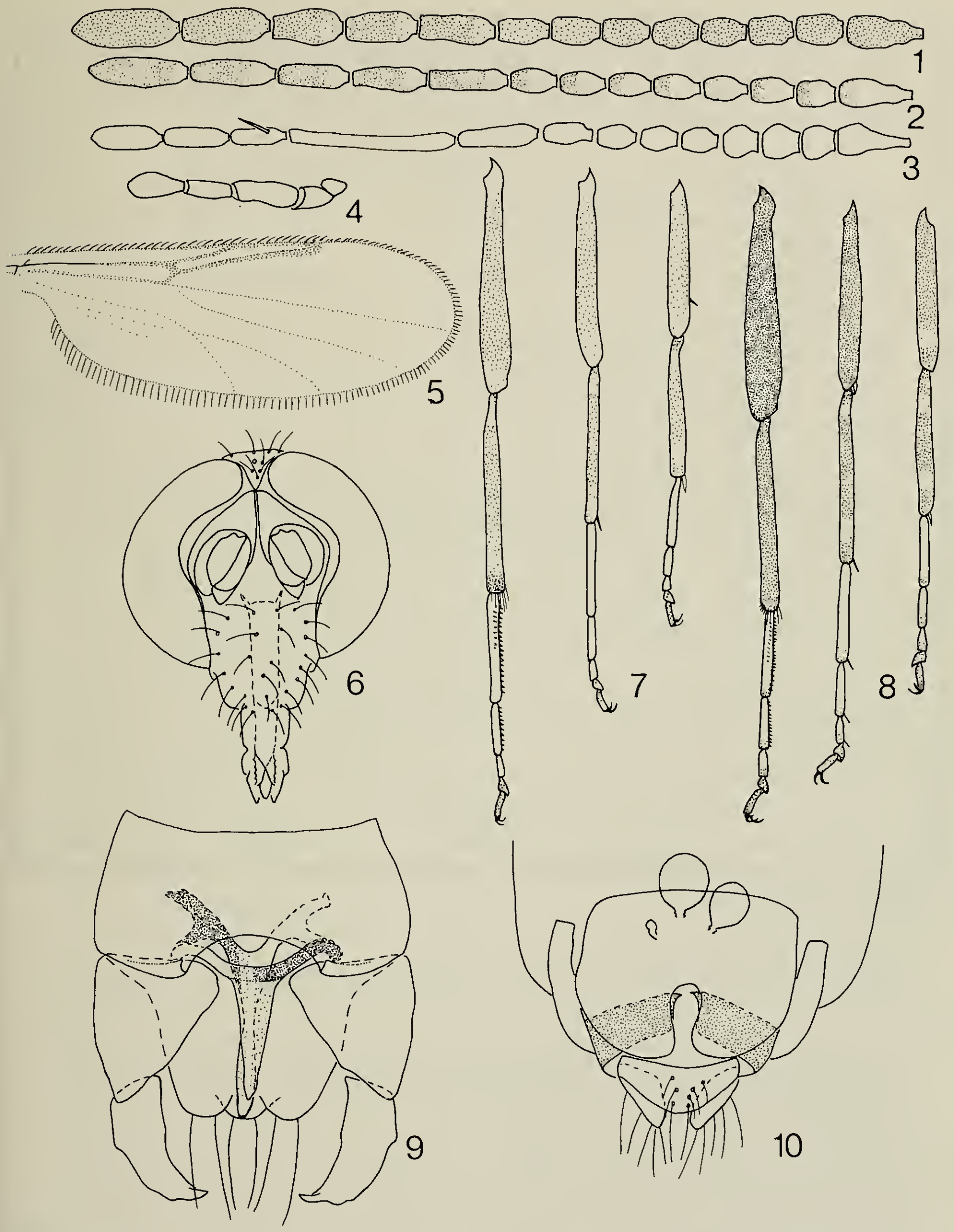
Figs. 1–10

Diagnosis.—Small, more or less black species, wing length 1.0–1.4 mm. Vertex (Fig. 6) with median seta not very strong. Segment 13 of male antenna with long black basal seta (Fig. 3). Legs (Fig. 8) usually black, narrow pale rings usually present subapically on some femora and tibiae and subbasally on some tibiae; hind femur and tibia usually without pale rings. Fore femur usually without ventral spines (one rarely present as in Fig. 7). Male aedeagus (Fig. 9) lacking ventral setulae and usually with a more or less hyaline, smooth, rounded tip. Distal process of parameres and basal arch of aedeagus variously shaped, affording good specific characters.

Species of this group may be separated for the most part from those of the *expolita* Group by the absence of femoral spines, presence of short, distinct necks on the spermathecae (Fig. 10), and the short setae on the vertex (Fig. 6).

Key to the Species of the *Bezzia bivittata* Group

1. Halter pale, at least on the knob; female abdomen usually contrasting bright yellow, eighth sternum brownish 2
– Halter dark brown; female abdomen brown 6
2. Femora and tibiae uniformly yellowish ....
.... *flavitibia* Dow and Turner (female)
– At least hind femur brown 3
3. Femora solid brown, tibiae uniformly pale; male basistyle bulbous 4
– Legs brown, at most with narrow pale rings; male basistyle various ... 5
4. Larger species, female wing length 1.23–1.24 mm; female antennal ratio 1.06–1.10; male aedeagus (Fig. 55) with distal process narrow proximally, tip broad and spatula-shaped, basal arms broader .. *spathula* n. sp.



Figs. 1–10. 1–10, *Bezzia bivittata*; 1–8, 10, female; 9, male: 1–3, antenna; 4, palpus; 5, wing; 6, head, anterior view; 7, hind, mid, and fore legs (left to right); 9, 10, genitalia.

– Smaller species, female wing length 1.05–1.11 mm; female antennal ratio 0.89; male aedeagus (Fig. 36) slender and rod-like to tip, basal arms narrower .... *luteiventris* n. sp.

5. Hind tibia uniformly dark to tip; male basistyle short and stout but without prominent basal lobe; lobes of aedeagus very long and proximally

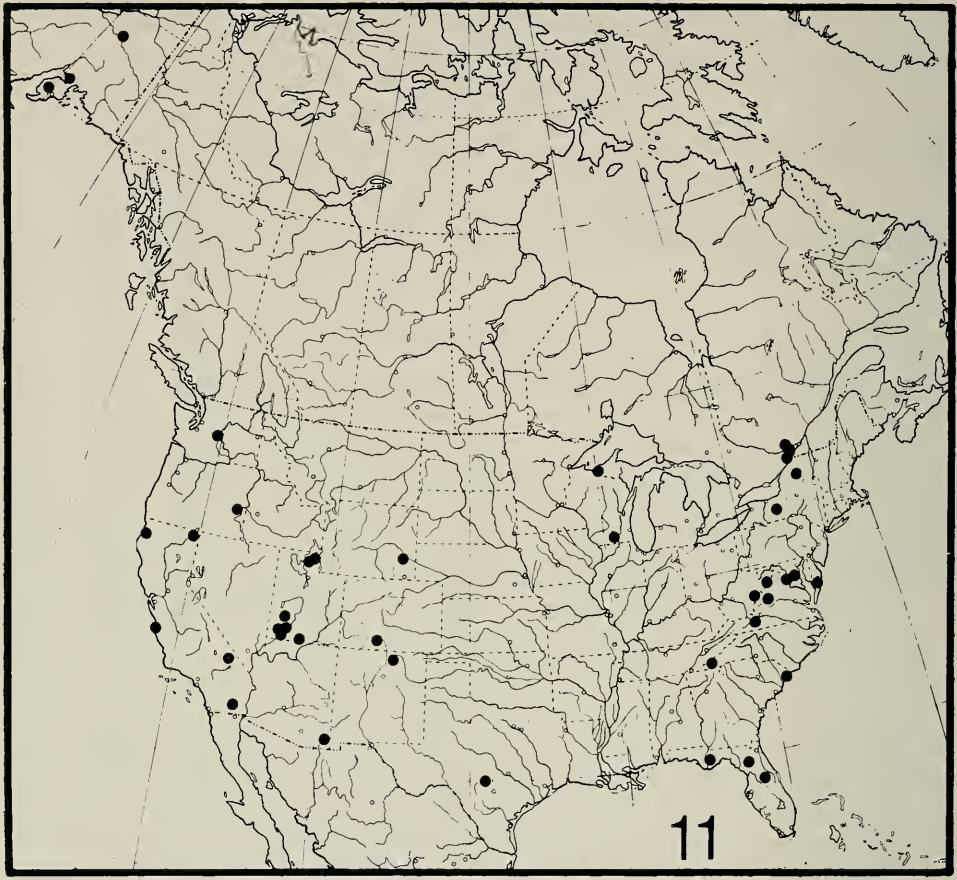


Fig. 11. Distribution of *Bezzia bivittata.*

slender, hastate distally; parameres with broad capitate distal expansion . . . . *setosinotum* n. sp.

– Hind tibia with subapical pale ring; male basistyle with broad basal swelling with ventral cluster of long setae and shallow distomesal fold; lobes of aedeagus short and stout, blunt-tipped; parameres with apex slender but with distinct subbasal swelling . . . . *andersonorum* n. sp.

6. All femora uniformly dark brown; fore tibia pale brown, mid and hind tibiae yellowish; legs with spiny setose vestiture; mesonotum with dense fine pubescence and sparse setae . . . . *flavitibia* Dow and Turner (male)

– Legs and mesonotum otherwise 7

7. Tarsi uniformly white, at most fourth and fifth tarsomeres somewhat brownish; antenna more or less pale at base; spermathecae elongate oval; mesonotum unusually gibbous anteriorly, polished black without pollen . . . . *gibbera* (Coquillett)

– Tarsomeres 1–3 dark at apices, 4–5 uniformly brown; antenna brown at base; spermathecae and mesonotum various 8

8. Femora and tibiae saturate black, without pale bands . . . . . *nigripes* n. sp.

– Femora with subapical and tibiae with subbasal and subapical pale bands, at least on fore leg 9

9\. Color saturate black, subapical pale band on fore femur and subbasal and subapical bands on fore femur and mid tibia white, definite and strongly contrasting; female antennal segments very short 10

– Color not so black and contrasting; leg bands less distinct or absent; female antennal segments short to long 12

10\. Male parameres with distal swelling or expansion 11

– Male parameres slender to tip; (female spermathecae short oval with distinct necks) .... *texensis* n. sp.

11\. Male paramere with short, broad, spatulate distal expansion; female and mesonotal pattern unknown .... *capitata* n. sp.

– Male parameres with bulbous distal swelling; mesonotum with numerous pollinose white spots easily seen in anterior view of dry or fresh specimens; female spermathecae elongate oval, with short necks .... *sandersoni* n. sp.

12\. Femora and tibiae uniformly dark brown, without pale bands; tarsi uniformly brownish; antennal segments (Fig. 12) short oval, distal five segments in female scarcely elongated, antennal ratio 0.79 (spermathecae with long tapering necks (Fig. 15); male dististyle short and stout, curved to sharp distal point (Fig. 16)) .... *aklavikensis* n. sp.

– Legs with pale rings; antenna with distal segments elongated, female antennal ratio 0.97–1.10 13

13\. Hind tibia with distinct subbasal and subapical pale rings; femora extensively pale at bases; female with one spermatheca; male aedeagus with truncate tip .... *mohave* n. sp.

– Hind tibia rarely with subbasal and/or subapical pale rings; female with two large spermathecae; male aedeagus with tip slender and rounded 14

14\. Spermathecae subspherical with short necks; male basistyle broad at base, tapering distally; dististyle short, stout nearly to tip; aedeagus with distal process long and tapering with straight sides .. *bivittata* (Coquillett)

– Spermathecae not as above; male basistyle globular with patch of long, mesally directed hairs or stout setae; dististyle hook-like, tapering to slender tip; distal process of aedeagus with slender point and concave sides 15

15\. Mid femur with subapical pale ring; mid tibia with subbasal and subapical pale rings; female antenna shorter and stouter; spermathecae with long tapering necks; male basistyle with mesal patch of stout setae; dististyle short and stout, curved to sharp distal point (eastern U.S.) .... *gibberella* n. sp.

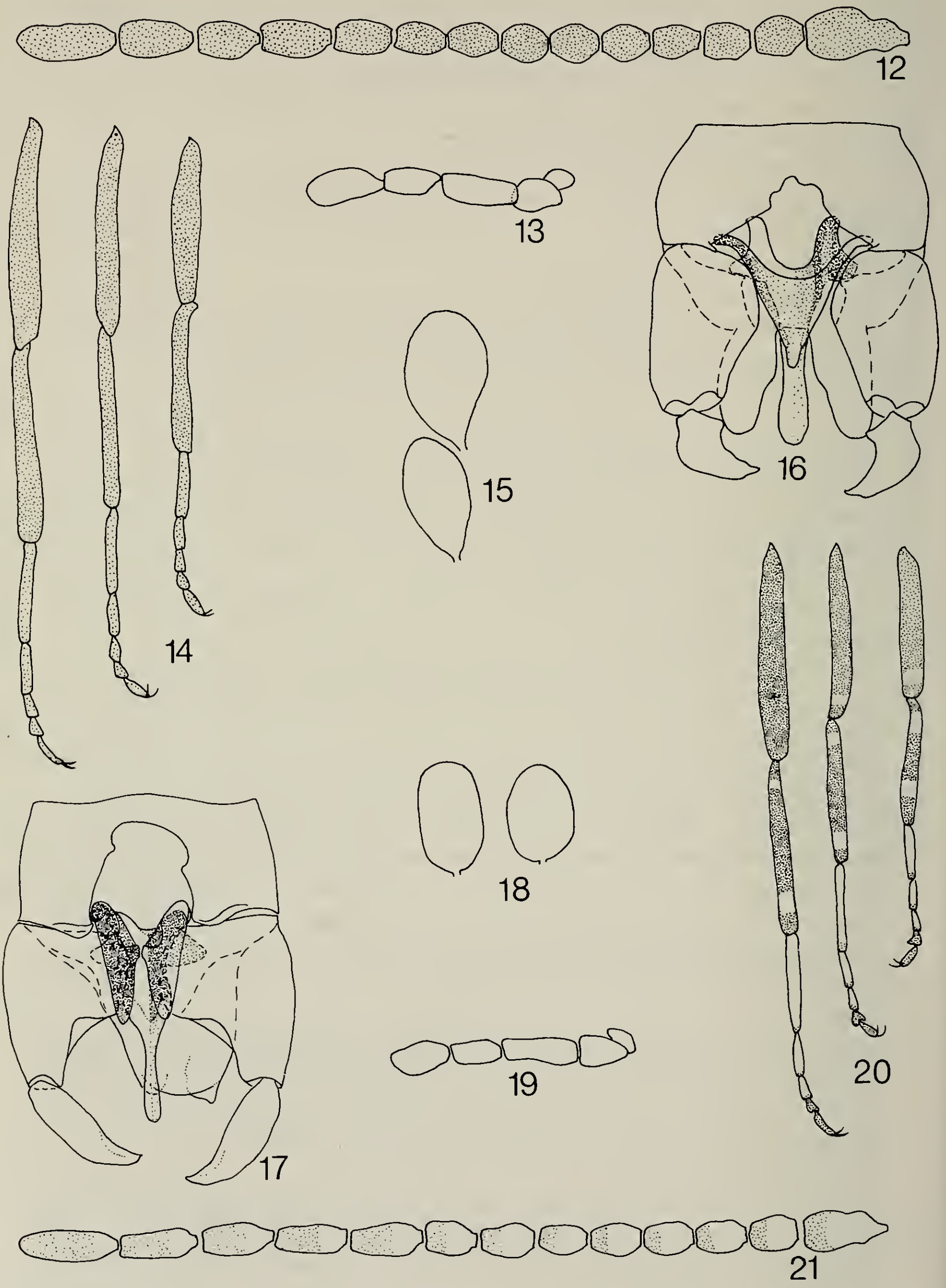
– Pale rings absent subapically on mid femur and base of mid tibia; female antenna elongate; spermathecae elongate oval with short necks; male basistyle with mesal patch of long fine hairs; dististyle elongate, slender and hook-like (Arizona) .... *chelistyla* n. sp.

Bezzia aklavikensis, new species

Figs. 12–16

Diagnosis.—A large species distinguished from all other species in the *bivittata* group by its unbanded, uniformly dark brown legs, short stout antenna (antennal ratio of female 0.79, of male 0.87), and large elongate ovoid spermathecae.

Allotype Female.—Wing length 1.68 mm; breadth 0.61 mm. Head: Dark brown.



Figs. 12–21. 12–16, *Bezzia aklavikensis*; 17–21, *andersonorum*; 12–15, 18–21, female; 16–17, male: 12, 21, antenna; 13, 19, palpus; 14, 20, hind, mid, and fore legs (left to right); 15, 18, spermathecae; 16, 17, genitalia.

Eyes broadly separated, a space of four ommatidial facets, a distance of 0.06 mm. Antennal flagellum (Fig. 12) brown; flagellar segments with lengths in proportion of 23-11-11-10-10-10-11-11-12-14-15-17-19; antennal ratio 0.79. Palpus (Fig. 13) brown; lengths of segments in proportion 6-10-16-12-16; palpal ratio 2.67. Mandible with 11–12 large coarse teeth.

Thorax: Dark brown. Mesonotum, scutellum and postscutellum with dense short setae and finer pubescence. Legs (Fig. 14) including tarsi uniformly dark brown. Wing hyaline, anterior veins brown, posterior veins lighter in color; costal ratio 0.68. Halter dark brown.

Abdomen: Dark brown. Spermathecae (Fig. 15) large, elongate ovoid with short necks, measuring 0.104 by 0.063 mm and 0.093 by 0.052 mm.

Holotype male.—Wing length 1.61 mm; breadth 0.46 mm. Similar to allotype female with the following differences: Antennal plume dense, dark brown; flagellar segments with lengths in proportion of 35-12-12-12-11-12-12-14-20-35-17-16-16; antennal ratio 0.87. Palpus with more slender third segment; palpal ratio 3.29. Costal ratio of wing 0.62. Genitalia as in Fig. 16. Ninth sternum slightly more than twice as broad as long, bulbous in appearance, caudomedian excavation deep, broadly V-shaped; ninth tergum tapers abruptly distally to a broad truncate margin where it joins the large divergent cerci that extend beyond the basistyles. Basistyle 1.6 times longer than broad, broadest basally, tapering slightly distally on mesal portion; dististyle about half the length of the basistyle, very short truncated in appearance, broadest basally, greatly curved and tapering abruptly distally to a broadly pointed tip. Aedeagus triangular, 1.2 times broader than long, basal arch 0.3 of total length; basal arm very heavily sclerotized, slightly recurved; distal portion more lightly sclerotized, tapering abruptly distally to a narrowly rounded, hyaline tip. Parameres heavily sclerotized on proximal portion, more lightly sclerotized on distal portion; basal arm broad and slightly recurved with a small lateral winglike lobe; distal portion broad proximally, tapering distally to broad rodlike form with bulbous rounded tip.

Distribution.—Canada; known only from the type-locality in the Northwest Territory.

Types.—Holotype male, allotype female, CANADA, NORTHWEST TERRITORY, Aklavik, 21 June 1953, C. D. Bird (deposited in CNC).

Discussion.—The specific epithet refers to the type-locality in northwest Canada where this species was taken.

The only other species with unbanded dark legs is *B. nigripes* n. sp. from Utah and California. That species differs readily from *B. aklavikensis* in having darker femora and tibiae and paler tarsi, more rounded spermathecae with long, slender necks, a more slender palpus (female palpal ratio 5.14), and smaller size (female wing length 1.27 mm).

Bezzia andersonorum, new species

Figs. 17–21

Diagnosis.—A medium-sized species most closely resembling *B. setosinotum* in having banded legs and white halter but differing from that species and all other species in the group by its short, broad, H-shaped, bipartite aedeagus, parameres with slender distal portion, and female abdomen pale yellow with ovoid spermathecae with very short necks.

Holotype Male.—Wing length 1.15 mm; breadth 0.36 mm.

Head: Dark brown. Eyes well separated, the width of five ommatidial facets, a distance of 0.056 mm. Antennal flagellum uniformly brown; flagellar segments with lengths in proportion of 21-10-10-10-10-10-11-13-21-34-13-14-16; antennal ratio 1.04; plume dense, dark brown. Palpus with lengths of segments in proportion of 5-7-13-9-9; palpal ratio 3.25.

Thorax: Dark brown; mesonotum with moderately dense short setae and finer setae giving a pubescent appearance. Legs (Fig. 20) dark brown with banded pattern very similar to that of *B. setosinotum* (Fig. 61) except hind tibia with broad subapical pale band. Wing hyaline, veins pale but easily discernible; costal ratio 0.60. Halter white.

Abdomen: Brown. Genitalia as in Fig. 17. Ninth sternum nearly twice as broad as long, caudomedian excavation very deep, U-shaped; ninth tergum tapering rather abruptly on basal half, then more gradually on distal half, cerci very short, extending to tip of basistyle. Basistyle slightly longer than broad with a broad basal swelling with ventral cluster of long setae and a shallow distomesal fold; dististyle 0.8 the length of basistyle, broadest in mid-portion, curving and tapering on extreme distal portion to broadly pointed tip. Aedeagus very heavily sclerotized, short, broad, H-shaped, and bipartite, slightly longer than broad; basal arch to 0.45 of total length, basal arm with tip broadly rounded and recurved ventrally; distal portion joined by a slender median bridge that appears to be broken due to mounting, each portion tapering slightly distally to narrow rounded tip. Parameres very heavily sclerotized; basal arm short, slightly recurved with broad, triangular, lateral portion; distal portion constricted at base then broad on basal third and tapering abruptly on distal two-thirds to slender rounded tip.

Allotype female.—Wing length 1.10 mm; breadth 0.43. Similar to holotype male with the following differences: Antennal flagellum (Fig. 21) pale on proximal portions of flagellomeres, distal portions light brown; flagellar segments with lengths in proportion of 14-8-8-8-8-8-8-8-11-11-11-12-15; antennal ratio 0.86. Palpus (Fig. 19) with lengths of segments in proportion of 5-8-12-7-10; palpal ratio 2.40. Mandible with 10–12 large coarse teeth. Legs dark brown with banded pattern as figured, fore femur palest. Costal ratio 0.70. Abdomen pale yellow; two ovoid spermathecae (Fig. 18) with very short necks measuring 0.074 by 0.052 and 0.067 by 0.044 mm.

Distribution.—Maryland, North Carolina, Quebec.

Types.—Holotype male, 1 male paratype, MARYLAND, Worcester Co., Snow Hill, 19 June 1968, W. H. Anderson, light trap, from along margin of Nassawango Creek one mile upstream from its confluence with the Pocomoke River (Type no. 76584, USNM). Allotype female, QUEBEC, Rowanton Depot, 28 June 1954, J. A. Downes (CNC). Paratype, 1 female, NORTH CAROLINA, Carteret Co., 19 June 1977, M. A. Tidwell, light trap.

Discussion—The species is named in honor of William and Jean Anderson of Snow Hill, Maryland, in appreciation of their continued interest in collecting Ceratopogonidae for us. The distinctive short, bipartite aedeagus in combination with the white halter, yellow female abdomen, and banded legs is sufficient to distinguish this species from all others in the *bivittata* Group.

Bezzia bivittata (Coquillett)
Figs. 1–11

Ceratopogon bivittatus Coquillett, 1905:60 (female; California).
Bezzia bivittata (Coquillett):—Kieffer, 1906:58 (combination):—Wirth, 1965:141 (listed); 1952:238 (male; female redescribed; figs.; California).
Probezzia bivittata (Coquillett):—Johannsen, 1908:267 (combination):—Malloch, 1914b:138 (in key); 1915:357 (listed):—Johannsen, 1943:785 (listed).
Bezzia (*Aspinabezzia*) *bivittata* (Coquillett):—Dow and Turner, 1976:126 (redescribed; status; figs.; distribution).

Diagnosis.—A medium-sized to large species with dark legs banded as follows: pale bands on subapex of fore femur, subbase and subapex of fore and mid tibiae (rarely hind tibia banded); spermathecae small, spheroid with short necks, mesonotum with two short silvery longitudinal lines; male genitalia with slender aedeagus, short globose basistyles, ninth sternum with shallow caudomedian excavation, parameres with slender distal portion and well-developed bifurcate basal arms.

Female.—Wing length 1.40 (1.17–2.11, n = 28) mm; breadth 0.55 (0.78–0.77, n = 27 mm.

Head (Fig. 6): Dark brown including antenna and palpus, vertex silvery pollinose. Antenna (Fig. 1) dark in majority of specimens, occasionally with narrow bases of flagellar segments yellowish (Fig. 2); lengths of flagellar segments in proportion of 16-9-9-9-9-9-9-9-12-12-12-14-18; antennal ratio 1.00 (0.77–1.23, n = 28). Palpus (Fig. 4) with lengths of segments in proportion of 4-6-15-8-12; palpal ratio 3.24 (2.40–4.00, n = 28). Mandible with 8–10 large coarse teeth.

Thorax: Subshining black; anterior fourth of mesonotum with a pair of submedian silvery pollinose spots continued as lines to lateral margins, a pair of short, fine, silvery, longitudinal lines continued back from inner edge of spots after a short break to half the length of mesonotum; mesonotum and scutellum with dense long black pubescence; three black bristles above wing base; scutellum with four black marginal bristles. Legs (Fig. 8) dark brown; fore femur with subapical, and fore and mid tibiae with subbasal and subapical, narrow yellow rings; hind tibia often with faint subbasal and subapical pale rings (Fig. 7); first three tarsomeres yellow with apices narrowly dark, last two tarsomeres dark; fore femur occasionally with one strong ventral spine (Fig. 7); on hind leg, basitarsus with two rows of palisade setae, second tarsomere with one row; claws (Figs. 7–8) small with basal inner teeth. Wing (Fig. 5) grayish hyaline, anterior veins yellowish; costal ratio 0.72 (0.68–0.76, n = 28). Halter dark brown.

Abdomen: Subshining dark brown; one pair of gland rods as long as four segments. Genitalia as in Fig. 10. Spermathecae two (rarely one or three), subspherical with very short necks, slightly unequal, measuring 0.046 by 0.037 mm and 0.037 by 0.034 mm.

Male.—Wing length 0.84–0.124 mm. Similar to female with the following differences: Antennal flagellum (Fig. 3) brown; flagellar segments in proportion of 28-12-12-12-12-12-14-18-25-55-20-21-24; antennal ratio 1.21; plume dark brown. Costal ratio 0.62–0.67. Genitalia as in Fig. 9. Ninth sternum about twice as broad as long, hind margin slightly convex with shallow caudomedian excavation. Basistyle stout, about as long as basal breadth, base often expanded into a prominent ventromesal lobe; dististyle as long as basistyle, stout, setose, tapering to a distal point. Aedeagus about as long as broad with low basal arch; basal arm heavily sclerotized, recurved about 60°; distomedian process tapering to moderately slender tip, sides concave in outline. Parameres heavily sclerotized; basal arm bilobed; distal portion slender, sides subparallel, tip rounded, hyaline.

Distribution (Fig. 11).—North America from Alaska to California, east to Ontario and Florida.

Types.—Described from four pinned syntypes, CALIFORNIA, Eureka, "5–6," H. S. Barber (Type no. 8353, USNM). One pinned syntype has been selected and labelled as lectotype. Two syntypes from which the diagnosis was partially made have been mounted on slides.

Specimens examined.—ALASKA: Highway Anchorage to Girdwood, 22 June 1964, K. M. Sommerman, jeep trap, 1 male. Fairbanks, June 1967, Sommerman, jeep trap, 2 females.

ARIZONA: Cochise Co., Portal, Southwest Res. Sta., 2–9 June 1972, W. W. Wirth, light trap, 4 females.

CALIFORNIA: Fresno Co., Orosi, 8 July 1947, W. W. Wirth, 1 female (CIS). Humboldt Co., Eureka, 5–6, H. S. Barber, 4 female syntypes. Imperial Co., Hot Mineral, 30 Apr 1952, J. N. Belkin, 4 males; Westmoreland, 6 Apr 1949, Wirth, 1 female (CIS). Inyo Co., Saratoga Springs, Death Valley, 30 May 1953, Belkin, 1 male, 39 females. Mono Co., Fales Hot Springs, 7 June 1948, Wirth, 1 female (CIS); Leavitt Meadow, 7200 ft, 14 Aug 1963, H. B. Leech, flight trap, 1 female (CAS); Topaz Lake, July 1948, R. Coleman, light trap, 1 female; Virginia Creek, 21 June 1916, H. G. Dyar, 3 females. Monterey Co., Arroyo Seco Ranger Sta., 1 July 1948, Wirth, light trap, 1 male, 1 female; Pebble Beach, 26 Aug 1964, R. Schoeppner, 1 male with pupal exuviae. Siskiyou Co., Hornbrook, Aug 1948, R. Coleman, light trap, 1 female (CIS); 4 mi W Weed, 14 May 1948, Wirth, 1 male (CIS). Ventura Co., Piru Canyon, 22 Apr 1948, Wirth, 1 male.

COLORADO: Rio Grande Co., Beaver Creek, 10,000 ft, 21 June 1972, Wirth, Malaise trap, 2 males, 2 females; South Fork, 8000 ft, 20 June 1972, Wirth, Malaise trap, 4 males.

FLORIDA: Alachua Co., Gainesville, Chantilly Acres, 19 Apr, 7 May 1967, F. S. Blanton, light trap, 2 females. Liberty Co., Torreya State Park, 27 Apr 1958, Blanton, light trap, 2 males; 20 May 1966, H. V. Weems, light trap, 4 males, 1 female; 22 Apr 1967, Wirth, 2 males, 20 females.

MARYLAND: Prince George's Co., Patuxent Wildlife Res. Center, May 1976, W. L. Grogan, Jr., Malaise trap, 5 males, 6 females; 17 Apr 1977, S. Navai, reared from moss on wood over stream, 1 female; 19 May 1978, Wirth, Malaise trap, 1 female. Worcester Co., Snow Hill, 1 June 1966, W. H. Anderson, light trap, 1 male, 2 females.

MICHIGAN: Cheboygan Co., Douglas Lake, 24 June 1954, R. W. Williams, 1 male. Gogebic Co., 15 June 1960, R. and K. Dreisbach, 1 female.

MONTANA: Laurel, 16 July 1917, Dyar, 1 female.

NEW BRUNSWICK: Kouchibouguac, 2–13 July 1977, J. R. Vockeroth, 4 males, 3 females; 11 July 1977, M. Iranochko, 1 male, 2 females; 9–12 July 1978, J. A. Downes, 5 females; 10 July 1978, L. Forster, 5 males, 2 females (CNC).

NEW MEXICO: Taos Co., Taos, 27 July 1968, Wirth, light trap, 14 males, 7 females.

NEW YORK: St. Lawrence Co., Cranberry Lake, swamp, 25 June 1963, Wirth, 5 males, 3 females. Tompkins Co., Ellis Hollow, 15 June 1963, C. O. Berg, light trap, 1 female.

NORTH CAROLINA: Jackson Co., Balsam, 7 July 1968, R. E. Woodruff, light trap, 1 male.

ONTARIO: Almonte, 1 July 1954, J. A. Downes, 1 female (CNC). Ottawa, Mer Bleue, 27 May 1960, Wirth, 2 females.

OREGON: Malheur Co., Little Valley sw Vale, 19 June 1963, K. Goeden, light trap, 1 male, 4 females.

QUEBEC: Chelsea, 26 May 1960, Wirth, 1 male. Rowanton Depot, 30 May, 1 June, 7 Aug 1954, J. A. Downes, 2 male, 1 female (CNC).

TEXAS: Kerr Co., Kerrville, 21 May 1954, L. J. Bottimer, light trap, 1 male.

UTAH: Beaver Co., Beaver, 14 July 1949, G. L. Knowlton, at light, 1 male. Cache Co., Logan, 1 July 1957, Knowlton, light trap, 1 female. Iron Co., Parowan, 20 June 1960, Knowlton, 1 male. Kane Co., Kanab, 21 June 1950, Knowlton, 1 female.

VIRGINIA: Alexandria, Dyke Marsh, 13 May 1958, Wirth, 1 female. Fairfax Co., Falls Church, 4 July 1950, Wirth, stream margin, 1 female. Montgomery Co., Blacksburg, Apr–June 1960, D. H. Messersmith, 1 male, 2 females.

WASHINGTON: Kittataus Co., DeRoux Forest Cpgd., 11 Aug 1971, K. Goeden and A. Gurney, light trap, 2 females.

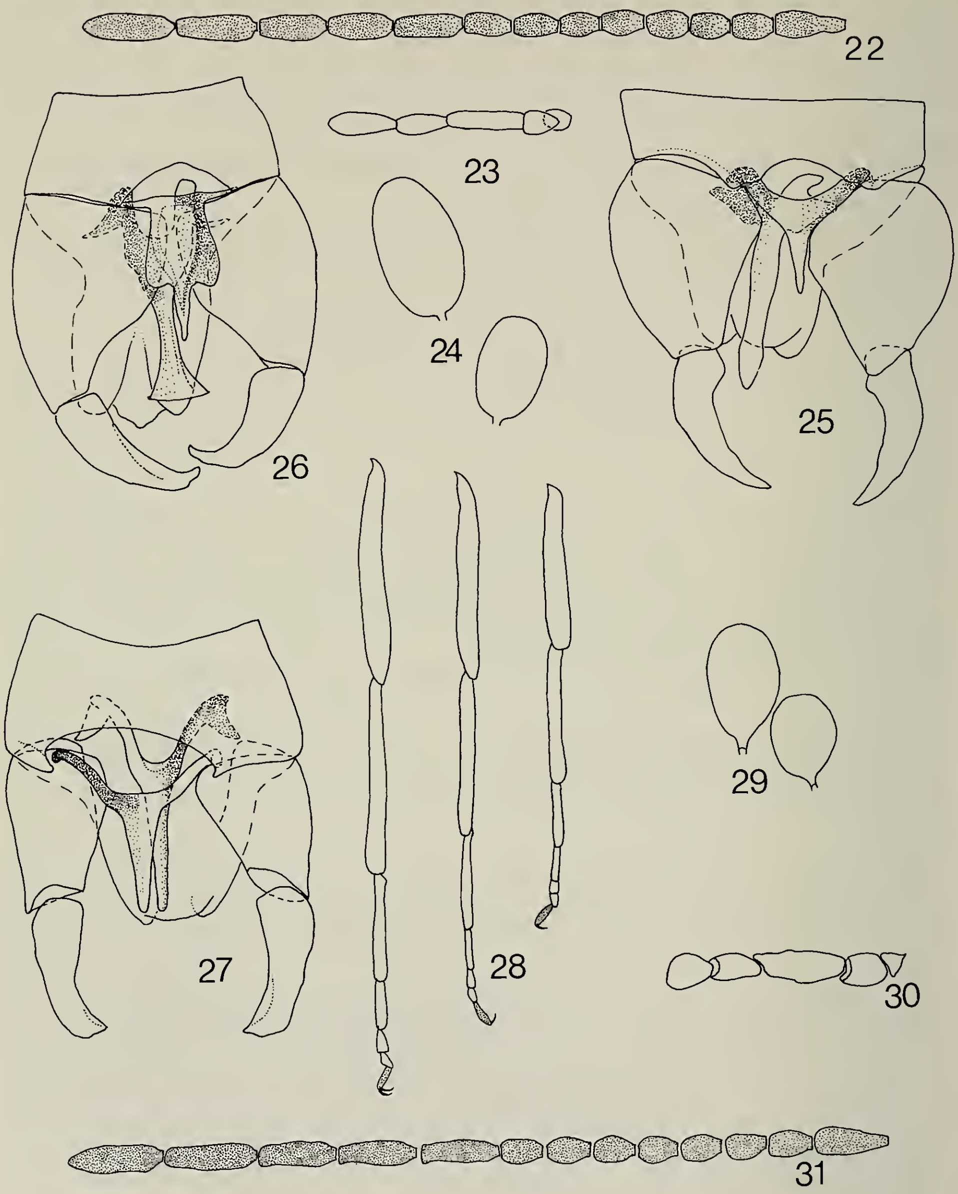
WEST VIRGINIA: Pocahontas Co., Cranberry Glades, 16 July 1955, Wirth, 1 female.

WISCONSIN: Dane Co., 30 May–7 June 1954, R. J. Dicke, light trap, 5 males, 8 females; Oregon, 25 May 1962, Wirth, light trap, 1 female.

WYOMING: Platte Co., Brown Ranch, 1 Aug 1967, M. Griffith, light trap 1 female.

Discussion.—As often seen in species with wide distribution, there is considerable variation in some characters, especially color. The syntypes, and a significant number of other specimens from the Pacific Coast states, are considerably darker, with the hind tarsus completely brown. A small number of specimens were seen with pale bands, usually indistinct, basally and subapically on the hind tibia. Occasionally one strong ventral spine occurs on the fore femur; this feature at first led to serious consideration as a specific character, but where it occurred in about a third of the specimens collected at Torreya State Park in Florida, in all instances except one it was found on one leg of a specimen and not on the other. Similar presence and absence was seen on occasional individuals from other localities.

A series of males from Kouchibouguac, New Brunswick, however, was relatively uniform in the correlation of presence of one spine on both fore femora, more distinct pale leg bands, more unequal spermathecae, shallower caudal emargination on the female eighth sternum, and more slender base of the median process of the male parameres in one set of specimens; and in another set collected at the same time and place with a contrasting set of correlated characters in the absence of femoral spine, less distinct leg markings, less unequal spermathecae, deeper caudal emargination on the female eighth sternum, and rather stout base of the median process of the male parameres. Further collections and study will be necessary to determine if *B. bivittata* is indeed a variable polytypic



Figs. 22–31. 22–25, *Bezzia chelistyla*; 26, *capitata*; 27–31, *flavitibia*; 22–24, 28–31, female; 25–27, male: 22, 31, antenna; 23, 30, palpus; 25–27, genitalia; 24, 29, spermathecae; 28, hind, mid, and fore legs (left to right).

species similar to *Culicoides variipennis* (Coquillett) or if we are dealing with a complex of very similar species that we have not learned to distinguish.

Bezzia capitata, new species
Fig. 26

Diagnosis.—A small species with banded legs and dark halter; most closely resembling *B. setosinotum* n. sp. by its parameres with broad capitate tip but differing from that species by its aedeagus with broad base and slender pointed tip.

Holotype male.—Wing length 0.86 mm; breadth 0.30 mm.

Head: Dark brown. Eyes narrowly separated, the wide of three ommatidial facets, a distance of 0.03 mm. Antennal flagellum lighter brown on basal half of segments 3–7, all of 8 and 9, proximal two-thirds of 10, and extreme bases of 11–13; flagellar segments with lengths in proportion of 16-8-8-8-8-8-9-10-12-15-11-11-11; antennal ratio 0.90. Palpus lighter brown than rest of head; lengths of segments in proportion of 4-6-8-7-7; palpal ratio 1.60.

Thorax: Dark brown; mesonotum and scutellum with dense short setae and fine pubescence. Legs dark brown with banding of femora and tibiae typical of *B. bivittata* (Fig. 8); tarsi paler than those of typical *bivittata* and more similar to those of atypical *bivittata* (Fig. 7), with only fourth and fifth tarsomeres slightly darkened. Wing hyaline, anterior veins light brown, posterior veins paler; costal ratio 0.66. Halter brown.

Abdomen: Brown. Genitalia as in Fig. 26. Ninth sternum twice as broad as long, base slightly convex, caudomedian excavation very shallow; ninth tergum tapering very abruptly distally to a constriction, then nearly parallel-sided, cerci very long and quite broad, extending beyond basistyles. Basistyle slightly curved, about 1.3 times longer than broad, very broad basally then tapering and curved distally; dististyle nearly as long as basistyle, greatly curved and tapering distally to slender pointed tip. Aedeagus heavily sclerotized only on well-defined mid-portion; basal arch absent, basal arms nearly straight, directed laterad and tapering to slender pointed tip; main body triangular in shape with flap-like lateral expansions and long slender apical process with narrow pointed tip. Parameres heavily sclerotized; basal arm recurved, broad basally, tapering to slender, doubly recurved tip; distal portion broad basally, tapering to slender rod which then expands to broad, truncate, capitate tip.

Female.—Unknown.

Distribution.—Extreme southern Arizona south to Costa Rica.

Types.—Holotype male, HONDURAS, Comayagua, Rancho Chiquito, 7 June 1964, F. S. Blanton (Type no. 76585, USNM). Two male paratypes as follows: ARIZONA: Santa Cruz Co., Pena Blanca, 10 mi w Nogales, Werner, Nutting and Johnson, light trap. COSTA RICA: Puntarenas, Palmar Sur, 5 Aug 1964, F. S. Blanton.

Discussion.—The specific name *capitata* is in reference to the capitate tip of the parameres which is similar to that of *B. setosinotum* n. sp. The distinctively shaped aedeagus of *B. capitata* is, however, sufficient to distinguish it from *setosinotum* as well as all other species in the *bivittata* Group.

Bezzia chelistyla, new species
Figs. 22–25

Diagnosis.—A medium-sized species with leg markings as in *B. bivittata* but distinguished from that species as follows: Male genitalia wing pincer-like dististyles; aedeagus short, broad with a slender pointed tip; female spermathecae large, elongate ovoid with short necks; mesonotum covered with fine pubescence only.

Allotype Female.—Wing length 1.39 mm; breadth 0.48 mm.

Head: Brown. Eyes narrowly separated, a space of two ommatidial facets, a distance of 0.026 mm. Antennal flagellum (Fig. 22) brown, lighter brown on bases of all segments; lengths of flagellar segments in proportion of 18-10-10-9-9-10-10-10-15-14-15-17-22; antennal ratio 0.97. Palpus (Fig. 23) brown; lengths of segments in proportion of 6-8-17-10-11; palpal ratio 4.25. Mandible with 10–12 large coarse teeth and 2–3 smaller basal teeth.

Thorax: Brown; mesonotum covered with fine pubescence only. Legs patterned as in *B. bivittata* (Fig. 8). Wing hyaline, anterior veins brown, posterior veins pale; costal ratio 0.69. Halter stem brown; knob dark brown.

Abdomen: Brown. Spermathecae (Fig. 24) large, unequal, elongate ovoid with short necks, measuring 0.070 by 0.052 mm and 0.063 by 0.044 mm.

Holotype Male.—Wing length 1.57 mm; breadth 0.44 mm. Similar to female allotype with the following differences: Antennal flagellum with proximal 7 segments indistinctly separated; lengths of flagellar segments in proportion of 27-12-12-12-12-13-13-18-30-38-16-19-25; antennal ratio 1.08; plume dark brown. Palpus with lengths of segments in proportion of 5-9-19-11-13; palpal ratio 4.75. Wing more slender with shorter radial cell; costal ratio 0.64. Genitalia as in Fig. 25. Ninth sternum over twice as broad as long, with a shallow caudomedian excavation; ninth tergum tapering abruptly distally to broad rounded tip where it joins the long cerci which extend just below the length of the basistyles. Basistyle 1.3 times longer than broad, globular, with long ventral and mesal setae; dististyle 0.83 the length of basistyle, greatly curved, and tapering distally to slender pointed tip. Aedeagus broadly triangular, slightly broader than long, basal arch low, about 0.2 of total length, basal arms heavily sclerotized, tips broadly rounded and recurved more than 90°; distal portion more lightly sclerotized, tapering distally to the long, slender, pointed tip. Parameres heavily sclerotized proximally, more lightly sclerotized distally; basal arms with broad lateral lobe and a curved posterior portion; distal portion slender, rodlike, with slender rounded tip extending just beyond basistyles.

Distribution.—Arizona.

Types.—Holotype male, allotype female, ARIZONA, Coconino Co., Fort Valley Exp. Sta., 10 mi NW Flagstaff, 9–12 July 1959, L. A. Carruth, light trap (Type no. 76586, USNM). Paratypes, 5 females, ARIZONA: Cochise Co., Portal, Southwest Res. Sta., 4 June 1967, C. W. Sabrosky, light trap, 2 females; 5–9 June 1972, W. W. Wirth, light trap, 2 females; 4 Oct 1967, V. Roth, light trap, 1 female.

Discussion.—The specific name *chelistyla* is in reference to the pincer-like or claw-like male dististyles.

Bezzia flavitibia Dow and Turner
Figs. 27–31

Bezzia flavitibia Dow and Turner, 1976:140 (male; New York; figs.).

Diagnosis.—A medium-sized species distinguished from all other species in the group by the following combination of characters: female with pale yellowish halter, legs, and abdomen, the head including antenna and thorax contrasting dark brown; male with dark brown halter, femora and abdomen, paler tibiae, and genitalia essentially the same as those of *B. bivittata.*

Female.—Wing length 1.42 (1.35–1.45, n = 7) mm; breadth 0.51 (0.50–0.52, n = 7) mm.

Head: Dark brown. Eyes narrowly separated, a space of three ommatidial facets, a distance of 0.04 mm. Antennal flagellum (Fig. 31) brown; flagellar segments with lengths in proportion of 19-10-10-9-10-10-10-10-16-15-16-19-23; antennal ratio 0.99 (0.96–1.08, n = 7). Palpus (Fig. 30) brown; lengths of segments in proportion of 6-10-17-9-10; palpal ratio 3.31 (2.89–4.25, n = 7). Mandible with 8 large coarse teeth and 2–3 small basal teeth.

Thorax: Dark brown; mesonotum and scutellum with sparse long setae and dense fine pubescence. Legs (Fig. 28) yellowish, femora occasionally light brownish; tarsi pale on proximal 3–4 tarsomeres, brown on distal 1–2; legs with spiny setose vestiture. Wing hyaline, veins pale; costal ratio 0.73 (0.71–0.76, n = 7). Halter pale.

Abdomen: Pale yellowish. Spermathecae (Fig. 29) small, unequal, ovoid to spheroid with short necks, measuring 0.059 by 0.044 mm and 0.048 by 0.035 mm.

Male.—Wing length 1.01–1.57 mm; breadth 0.38–0.45 mm. Similar to female with following differences: Antennal flagellum with dark brown plume; lengths of flagellar segments in proportion of 23-12-13-13-13-14-15-19-24-47-18-24-24; antennal ratio 1.12. Legs with dark brown femora and occasionally tibiae light brown. Wing more slender; costal ratio 0.63–0.69. Halter dark brown. Abdomen brown. Genitalia as in Fig. 27, similar to those of *B. bivittata* (Fig. 9). Dow and Turner (1976) in their original drawing illustrate a small basal lateral tooth on the basal arms of the parameres that is not present in the holotype or any other males examined.

Distribution.—New Brunswick, New York, Ontario.

Type.—Holotype male, NEW YORK, St. Lawrence Co., Cranberry Lake, 25 June 1963, W. W. Wirth (Type no. 76587, USNM).

Specimens examined.—NEW BRUNSWICK: Kouchibouguac, 2–11 July 1978, L. Forster, 11 males, 5 females (CNC).

NEW YORK: Cattaraugus Co., Allegany St. Park, 3 June 1963, W. Wirth, 3 males (paratypes). Hamilton Co., Newcomb, Hamilton-Essex, 11 May 1959, H. A. Jamnback, Berlese trap, 1 male with pupal exuviae (paratype). St. Lawrence Co., same data as holotype, 12 males (6 are paratypes), 7 females.

ONTARIO: Ottawa, Brittania Bay, 26 May 1960, Wirth, 1 male; Ottawa, Mer Bleue, 27 May 1960, Wirth, 2 males.

Discussion.—This species is distinguished by the uniformly pale tibiae; in the male by the uniformly dark brown femora, especially on the mid and hind legs;

on some males the fore tibia is somewhat brownish. The association of the female was overlooked by Dow and Turner (1976), and is based on the following: In the large collection made by Wirth in the swamp at Cranberry Lake, N.Y., seven females were found with leg markings similar to those of male *B. flavitibia*, but with pale halter, yellowish abdomen, and uniformly yellowish legs. There were 5 males and 2 females of *B. bivittata* in this collection, but these have distinctly dark legs with pale bands on femora and tibiae. The dark brown pigmentation of the *B. flavitibia* thorax is the same for males as for females from Cranberry Lake, and the palpi and antennae, allowing for sexual dimorphism, are similar in color and shape. Such distinct color dimorphism between sexes is rare but not unheard of in Ceratopogonidae. An example is seen in *Probezzia pallida* Malloch (Tribe Sphaeromiini), in which the female is uniformly pale yellowish and the male has contrasting black thorax and femora, but is otherwise pale (Wirth and Grogan 1979). There is also less striking but nevertheless distinct dimorphism between the pale female abdomen and the brownish male abdomen of *Bezzia nobilis* (Winnertz) and *B. magnisetula* Dow and Turner in the *Bezzia nobilis* Group.

Bezzia gibbera (Coquillett)
Figs. 32–35, 37

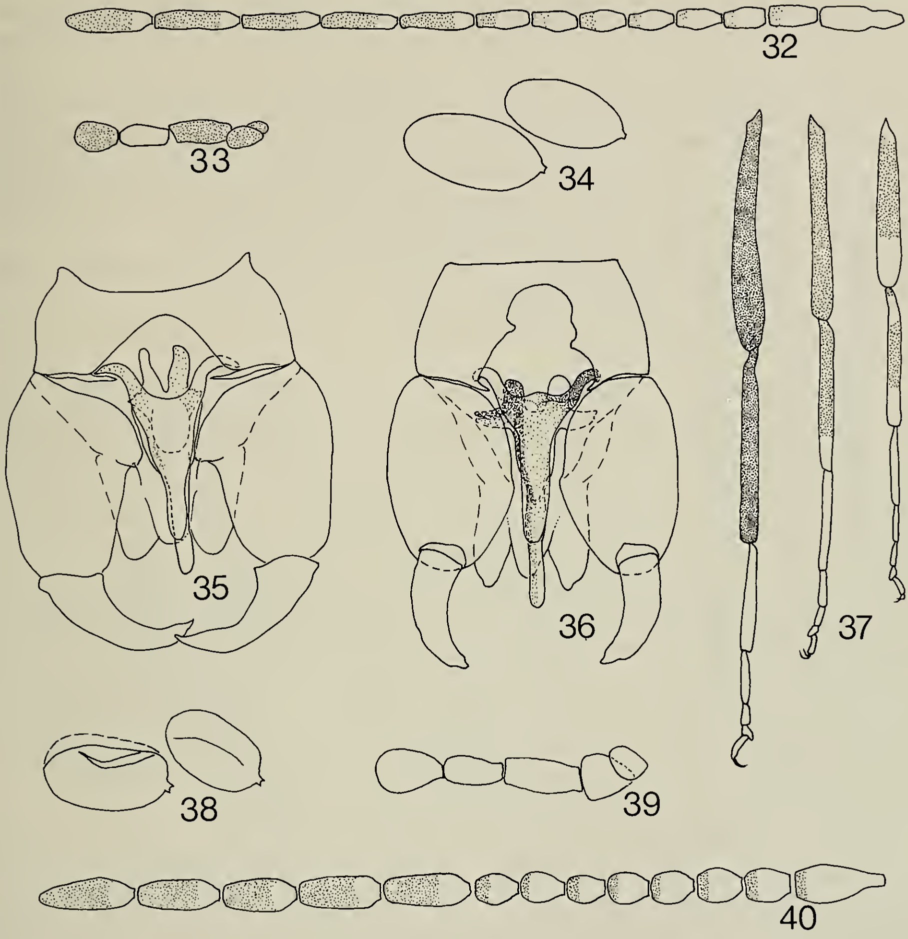
Ceratopogon gibber Coquillett, 1905:60 (female; Cuba).
Probezzia gibber (Coquillett):—Johannsen, 1908:267 (combination):—Malloch, 1914b:138 (in table); 1915:357 (noted):—Johannsen, 1943:785 (in list).
Bezzia gibber (Coquillett):—Kieffer, 1917:330 (combination).
Bezzia gibbera (Coquillett):—Wirth, 1965:141 (list; distribution); 1974:53 (catalog reference).—Dow and Turner, 1976:142 (misidentification in part; female redescribed; figs.; distribution).

Diagnosis.—A small species distinguished by its bright yellow antennal scape; fourth palpal segment pale, other segments brown; halter stem whitish, knob dark brown; setae on scutum arising from raised tubercles; spermathecae large, elongated, ovoid, subequal; male genitalia with setose lobe on ventromesal base of basistyle.

Female.—Wing length 1.26 (1.11–1.38, n = 9) mm; breadth 0.44 (0.40–0.47, n = 9) mm.

Head: Brown. Eyes narrowly separated, a space of 2.5 ommitidial facets, a distance of 0.03 mm. Antennal scape bright yellow, pedicel brown; flagellum (Fig. 32) yellow on first flagellar segment and proximal ½–⅔ of segments 4–10 and basal ¼ of distal five segments, distal portions of segments light brown; lengths of flagellar segments in proportion of 19-11-11-11-11-11-12-14-17-18-18-19-23; antennal ratio 0.85 (0.75–0.98, n = 9). Palpus (Fig. 33) brown, fourth segment pale; lengths of segments in proportion of 4-7-11-9-8; palpal ratio 2.36 (2.00–2.75, n = 9). Mandible with 10–12 large coarse teeth and 3–4 smaller basal teeth.

Thorax: dark brown; mesonotum with setae arising from raised tubercles. Legs (Fig. 37) dark brown on hind femur and tibia, lighter brown on mid femur and tibia except apex, and proximal ⅔ of fore femur and broad midportion of fore tibia, yellow on apex of mid tibia, distal fourth of fore femur and base and apex of fore tibia; tarsi pale on all tarsomeres; fifth tarsomeres light brown on some



Figs. 32–40. 32–35, 37, *Bezzia gibbera*; 36, 38–40, *luteiventris*; 32–34, 37–40, female; 35–36, male: 32, 40, antenna; 33, 39, palpus; 34, 38, spermathecae; 35–36, genitalia; 37, hind, mid, and fore legs (left to right).

specimens. Wing grayish hyaline, veins brownish; costal ratio 0.72 (0.69–0.76, n = 9). Halter stem whitish, knob dark brown.

Abdomen: Brown. Spermathecae (Fig. 34) large, elongated ovoid with short necks; measuring 0.081 by 0.041 mm and 0.074 by 0.037 mm.

Male.—Wing length 1.15 mm; breadth 0.36 mm. Similar to female with the following differences: Antennal flagellum with lengths of flagellar segments in proportion of 22-11-11-11-11-11-11-14-20-29-14-15-20, proximal 10 flagellar segments indistinctly separated; antennal ratio 0.96; plume golden brown. Fourth palpal segment brown. Genitalia as in Fig. 35. Ninth sternum 1.8 times broader than long, caudomedian excavation deep, broadly U-shaped; ninth tergum tapering abruptly distally and becoming rounded where it joins the long, broad cerci that extend almost the length of the basistyles. Basistyle curved, base with setose ventromesal lobe; dististyle 0.65 length of basistyle, greatly curved and tapering distally to sharply pointed tip. Aedeagus 1.2 times longer than broad; basal arch 0.20 of total length, basal arms nearly sclerotized, recurved nearly 90°; distal portion more lightly sclerotized except along margins, tapering distally to narrow rounded tip, margins with lateral flaps that extend almost entire length. Parameres heavily sclerotized proximally, more lightly sclerotized distally; basal arms with short lateral point and a longer, nearly straight posterior portion; distal portion tapering to a slender, rod-like structure with narrow rounded tip.

Distribution.—Southern Arizona, Texas and Florida south to Panama and throughout the islands of the Caribbean.

Type.—Holotype female, CUBA, Cayamas, 16 Jan, E. A. Schwartz (Type no. 8355, USNM).

Specimens examined.—ARIZONA: Maricopa Co., Wickenburg, Hassayampa River, 29 June 1953, W. W. Wirth, 1 male. Pima Co., Quitobaquito, 26 Apr 1959, M. S. Adachi, 1 female. Yavapai Co., Oak Creek at Cornville, 10 June 1977, M. W. Sanderson, light trap, 1 female. EL SALVADOR: San Vicente, Santo Domingo, Oct 1966, F. S. Blanton, light trap, 1 female. FLORIDA: Monroe Co., Big Pine Key, 7 June 1950, St. Bd. Health, light trap, 1 male. JAMAICA: Clarendon Parish, Milk River Bath, 19 Nov 1968, R. E. Woodruff, light trap, 1 female. Runaway Bay, 1–8 Mar 1970, W. W. Wirth, malaise trap, 1 female. Westmoreland Parish, Negril Beach, 10 Dec 1969, E. G. Farnworth, light trap, 1 female. MEXICO: Oaxaca, Palomares, 5–21 Sept 1961, R. and K. Dreisbach, 1 female. TEXAS: Kerr Co., Kerrville, May–Sept 1953, 1954 L. J. Bottimer, light trap, 13 males, 6 females. Llano Co., Enchanted Rock, 1–5 June 1953, W. W. Wirth, 1 female. TOBAGO: St. John Prov., Charlotteville, Hermitage River Bridge, 12–21 Mar 1979, D. Hardy and W. Rowe, Malaise trap, 1 female.

Comment.—This species is easily recognized by the bright yellow antennal scape, the pale fourth palpal segment, the gibbous mesonotum without pruinose white spots, but with setae arising from raised tubercles, and the tarsi whitish to the tips. Dow and Turner (1976) confused several species under this name. Our description is based primarily on the female from Runaway Bay, Jamaica, which agreed in external characters with the pinned holotype from Cuba. The description and figures of the hitherto unknown male are made from the series from Kerrville, Texas.

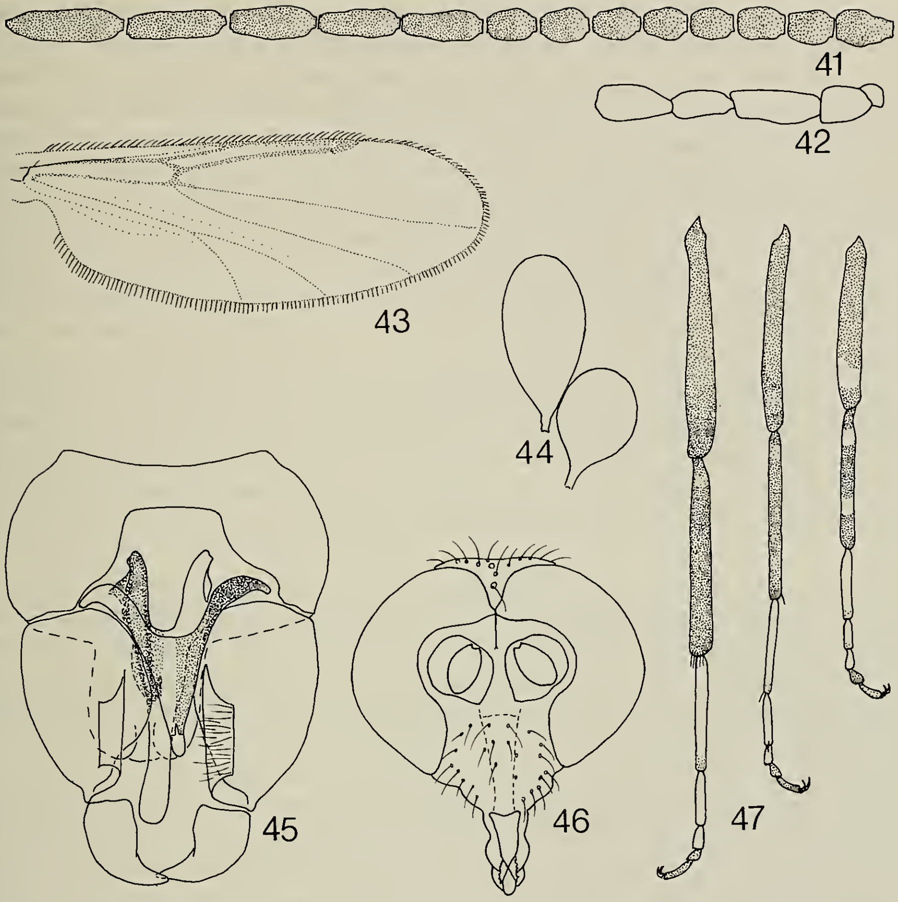
Bezzia gibberella, new species

Figs. 41–47

Diagnosis.—A medium-sized species with dark legs banded on fore leg and mid tibia as in *B. bivittata* but differing from that and all other species in the group by having the mid femur with a pale subapical, and hind tibia with a subbasal pale band; spermathecae large and ovoid, unequal with long tapering necks; male genitalia with triangular aedeagus with hyaline tip, and basistyle with dense setae on ventromesal portion.

Allotype female.—Wing length 1.18 mm; breadth 0.43 mm.

Head: Dark brown. Eyes narrowly separated, a space of two ommatidial facets, a distance of 0.027 mm. Antennal flagellum (Fig. 41) brown, lighter brown on basal half of proximal eight flagellar segments and bases of distal five segments; flagellar segments with lengths in proportion of 13-9-8-8-8-8-8-9-13-14-15-17-19;



Figs. 41–47. 41–47, *Bezzia gibberella*; 41–44, 46–47, female; 45, male: 41, antenna; 42, palpus; 43, wing; 44, spermathecae; 45, genitalia; 46, head, anterior view; 47, hind, mid, and fore legs (left to right).

antennal ratio 1.10. Palpus (Fig. 42) brown, slender; lengths of segments in proportion of 4-7-13-8-9; palpal ratio 3.25. Mandible with 7–8 large coarse teeth and 2–3 smaller basal ones.

Thorax: Dark brown. Mesonotum and scutellum with short dense setae and shorter pubescence; postscutellum with dense pubescence, the setae more or less in linear groups of 3 or 4. Legs (Fig. 47) dark brown with pale banding on fore leg and mid tibia typical of *B. bivittata* (Fig. 8), mid femur with pale subapical and hind tibia with pale subbasal band; tarsi pale on most of proximal three tarsomeres, distal two tarsomeres brown. Wing (Fig. 43) hyaline, veins brown; costal ratio 0.73. Halter dark brown.

Abdomen: Dark brown, terga darkest. Spermathecae (Fig. 44) large, ovoid; unequal, the larger elongated; with tapering long necks; measuring 0.110 by 0.054 mm and 0.074 by 0.044 mm.

Holotype male.—Wing length 1.14 mm; breadth not measurable due to folding. Similar to female with following differences: Antennal flagellum more uniformly brown on proximal 8 flagellar segments, segment 9 pale; flagellar segments with lengths in proportion of 21-10-10-10-10-10-10-13-19-35-15-18-22; antennal ratio 1.16. Palpus with third segment more slender; palpal ratio 4.29. Costal ratio of wing 0.64. Genitalia as in Fig. 45. Ninth sternum nearly twice as broad as long, caudomedian excavation very deep, quadrately U-shaped; ninth tergum very short due to abrupt tapering distally to where it joins the long broad cerci which extend much less caudad than the basistyles. Basistyle slightly longer than broad, greatly swollen on mesal side basally, then tapering abruptly on mesal side; ventromesal area with long setae directed mesad, distomesal area folded with shorter finer setae; dististyle 0.67 the length of basistyle, broadest and straightest basally, then tapering and greatly curved distally to point tip. Aedeagus triangular, as broad as long, basal arch to 0.27 of total length; basal arms very heavily sclerotized, recurved more than 90°, tapering to narrow pointed tip; distal portion more lightly sclerotized, tapering gradually distally a narrowly rounded, hyaline tip. Parameres heavily sclerotized on proximal half, distal half more lightly sclerotized; basal arm straight with slightly curved, truncate tip and a small lateral lobe; distal portion broad proximally, then tapering distally to a more or less bulbous, rounded tip.

Variation.—Female wing length 1.30 (1.18–1.41, n = 4) mm; breadth 0.47 (0.43–0.53, n = 4) mm. Antennal ratio 1.03 (0.95–1.10, n = 4). Palpal ratio 3.01 (2.89–3.25, n = 3). Costal ratio 0.72 (0.71–0.73, n = 6). There is considerable variation in the shape of the spermathecae in the type series. Specimens varied from the typical spermathecae figured for the allotype to more quadrate spermathecae with short, more abrupt necks.

Distribution.—Maryland to Michigan and Quebec, south to Florida.

Types.—Holotype male, MARYLAND, Prince George's Co., Patuxent Wildlife Res. Center, 29 July 1978, W. W. Wirth, Malaise trap (Type no. 76588, USNM). Allotype female, same data as holotype except taken 30 May 1978; 1 female paratopotype taken 8 June 1979; 3 female paratopotypes taken June 1976 by W. L. Grogan, Jr. Five male and 3 female paratypes as follows: FLORIDA: Alachua Co., Gainesville, Chantilly Acres, 10 May–1 Nov 1967, F. S. Blanton, 2 males, 1 female. MICHIGAN: Cheboygan Co., Douglas Lake, 24, 29 June 1954, R. W. Williams, 1 male, 1 female. QUEBEC: Rowanton Depot, 6–7 July 1954, J. A. Downes, 2 males (CNC). VIRGINIA: Alexandria, 25 May 1952, Wirth, Osmunda bog, 1 female.

Discussion—The species takes its name from its superficial resemblance to *Bezzia gibbera* (Coquillett). It differs from all other species in the *bivittata* Group in having narrow pale bands on each side of the mid knees, and spermathecae with long tapering necks. The male genitalia are distinguished by the conspicuous patch of long stout setae on the mesal face of the basistyle, and the unusually broad and deep, quadrate excavation on the ninth sternum.

Bezzia luteiventris, new species
Figs. 36, 38–40

Diagnosis.—A small species most closely resembling *B. flavitibia* Dow and Turner in its dark brown femora with contrasting yellow tibiae and pale abdomen and halter, but differing from that species as follows: Size smaller, female wing 1.05–1.11 mm (1.35–1.45 mm for *B. flavitibia*); tip of female abdomen brown;

spermathecae larger, more quadrately ovoid; antennal flagellum distinctly banded; male genitalia with deep caudomedian excavation on ninth sternum.

Holotype female.—Wing length 1.08 mm; breadth 0.39 mm.

Head: Dark brown. Eyes narrowly separated, a space of three ommatidial facets, a distance of 0.037 mm. Antennal flagellum (Fig. 40) pale on proximal ¾ of each of proximal eight segments and proximal ¼ of distal five segments; light brown on distal portions of all segments giving flagellum a distinctly banded appearance; lengths of flagellar segments in proportion of 16-9-9-8-8-8-8-8-12-13-13-14-14; antennal ratio 0.89. Palpus (Fig. 39) light brown; lengths of segments in proportion of 4-7-10-7-9; palpal ratio 2.22. Mandible with 7–8 large coarse teeth and 2–3 smaller basal teeth.

Thorax: Dark brown; mesonotum and scutellum covered with scattered setae and fine pubescence. Legs dark brown on femora; tibiae and proximal four tarsomeres pale yellow, 5th tarsomeres brown. Wing hyaline, veins pale; costal ratio 0.70. Halter knob pale yellow.

Abdomen: Bright yellow; brown on distal three segments, particularly so on eighth sternum. Spermathecae (Fig. 38) large; quadrately ovoid, measuring 0.078 by 0.041 mm and 0.067 by 0.041 mm.

Allotype male.—Wing length 1.04 mm; breadth 0.30 mm. Similar to female with the following differences: Antennal plume brown (distal three segments damaged so that flagellar proportions and antennal ratio could not be determined; proportions in a paratype are 27-10-11-11-11-11-12-15-20-35-16-19-23; antennal ratio 1.05). Wing more slender with shorter radial cell; costal ratio 0.61. Abdomen brown. Genitalia as in Fig. 36. Ninth sternum 1.7 times broader than long, caudomedian excavation very deep, in shape of a broad U; ninth tergum tapering abruptly distally on extreme base, then more gradually and becoming rounded where it joins the long, slender, divergent cerci, which extend just beyond basistyles. Basistyle 1.6 times longer than broad, mesal surface covered with sparse long setae; dististyle 0.65 as long as basistyle, curved and gradually tapering distally to broadly pointed tip. Aedeagus 1.3 times longer than broad, basal arch shallow, 0.17 of total length; basal arms very heavily sclerotized, distal portion more lightly sclerotized, slender, rod-like with rounded tip. Parameres very heavily sclerotized; basal arms with wing-like lateral process and posterior extension; distal portion slightly broader proximally, then more slender and rod-like distally to the rounded tip that extends beyond basistyles.

Distribution.—Virginia.

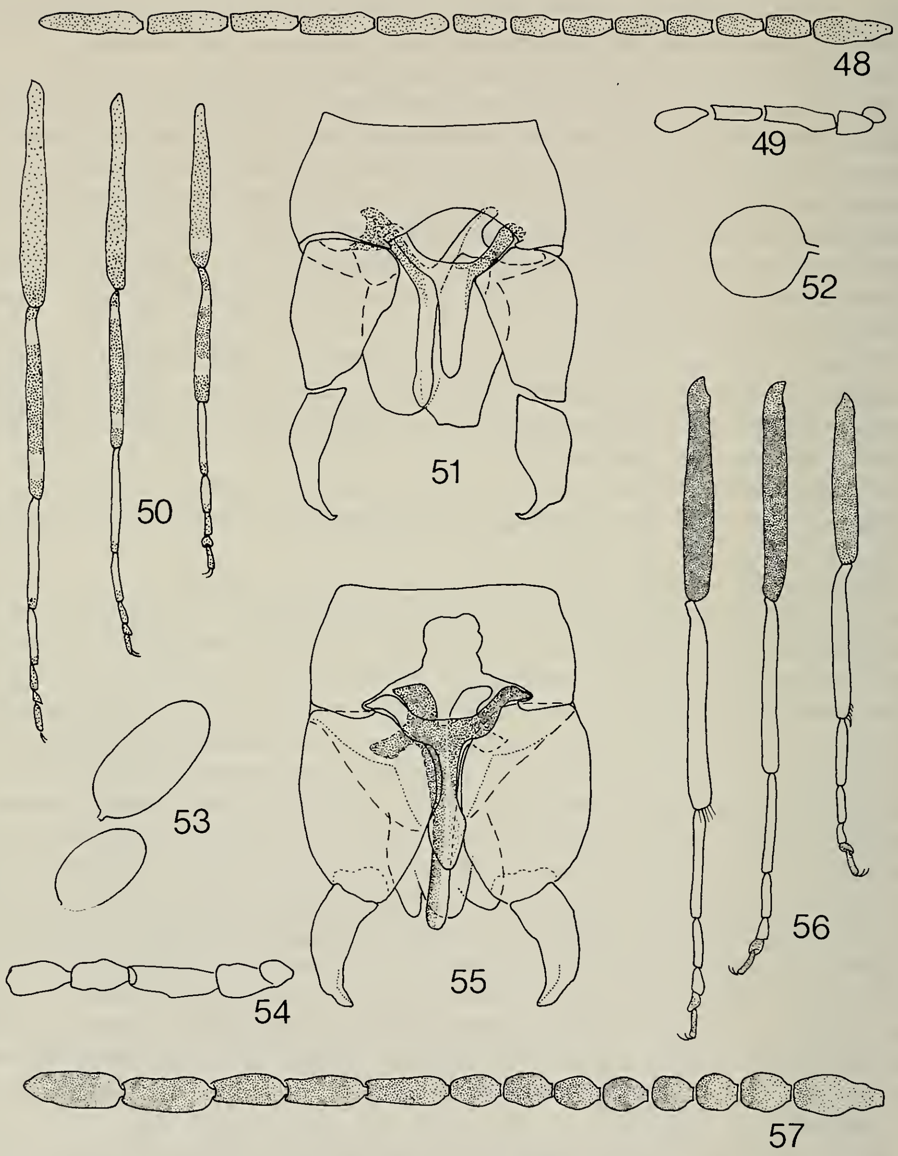
Types.—Holotype female, allotype male, 2 male, 2 female paratypes, VIRGINIA, Alexandria, reared from pupae from *Osmunda* bog, 6–30 June 1951, W. W. Wirth (Type no. 76589, USNM).

Discussion.—The specific epithet is a reference to the yellow abdomen and tibiae which serve to distinguish this distinctly marked species from all other species in the *bivittata* Group except *B. flavitibia*. That species can be distinguished by the characters outlined in the diagnosis.

Bezzia mohave, new species

Figs. 48–52

Diagnosis.—A large species with all tibiae with distinct subbasal and subapical bands but differing from all other species in the *bivittata* Group in that the female



Figs. 48–57. 48–52, *Bezzia mohave*; 53–57, *spathula*; 48–50, 52–54, 56–57, female; 51, 55, male: 48, 57, antenna; 49, 54, palpus; 51, 55, genitalia; 52-53, spermathecae; 56, hind, mid, and fore legs (left to right).

possesses only a single spermatheca and the femora are paler than tibiae distally becoming palest proximally; the male resembles the female with genitalia nearly identical to those of *B. bivittata*.

Holotype female.—Wing length 1.64 mm; breadth 0.57.

Head: Brown. Eyes narrowly separated, the space of one ommatidial facet, a distance of 0.015 mm. Antennal flagellum (Fig. 48) very light brown on proximal portions of flagellomeres, slightly darker on distal portions; flagellomeres with lengths in proportion of 21-12-11-11-12-12-12-12-16-16-14-17-21; antennal ratio 0.82. Palpus (Fig. 49) brown, slender; lengths of segments in proportion 13-10-18-9-5; palpal ratio 3.60. Mandible with 8 large coarse teeth and 4–5 smaller basal teeth.

Thorax: Dark brown. Mesonotum and scutellum with short dense setae and finer pubescence; postscutellum with shorter setae. Legs (Fig. 50) with light brown femora proximally becoming slightly darker distally; fore femur with a pale subapical band; tibiae darker brown with distinct subbasal and subapical light bands; tarsomeres 4 and 5 of tarsi pale except darker on extreme apical portions, distal 3 tarsomeres brown. Wing hyaline, anterior veins light brown, posterior veins pale; costal ratio 0.71. Halter brown.

Abdomen: Brown. A single spheroid spermatheca with short neck measuring 0.059 by 0.048 mm (Fig. 52).

Allotype male.—Wing length 1.54 mm; breadth 0.43. Similar to holotype female with the following differences: Antennal flagellum with dense, light brown plume; flagellomeres with lengths in proportion of 28-13-13-13-13-13-15-19-29-46-18-18-24; antennal ratio 1.06. Palpus with more slender third segment; palpal ratio 4.75. Genitalia as in Fig. 51. Ninth sternum twice as broad as long, with a shallow caudomedian excavation; ninth tergum very short due to abrupt tapering distally to a broadly rounded tip where it joins the long, broad cerci which extend slightly beyond basistyles. Basistyle 1.4 times longer than broad, broadest basally tapering distally; dististyle 0.7 the length of basistyle, broadest subbasally, tapering and curved on distal half to a slender pointed tip. Aedeagus slightly longer than broad, basal arch 0.3 of total length; basal arm heavily sclerotized, recurved slightly more than 90°; distal portion lightly sclerotized, tapering slightly distally to a rounded tip. Parameres heavily sclerotized on proximal portion, distal portion lightly sclerotized; basal arm bilobed as in *B. bivittata* (Fig. 9); distal portion broad basally then becoming slender with a round tip.

Distribution.—California; known only from the Mojave Desert in Riverside County.

Types.—Holotype female, CALIFORNIA, Riverside Co., Whitewater Canyon, 6 Apr 1949, W. W. Wirth, at light (Type no. 76598, USNM). Allotype male, CALIFORNIA, Riverside Co., Thousand Palms, Willis Palms Oasis, 5 Apr 1955, W. R. Richards (CNC). Paratype, 1 female, CALIFORNIA, Riverside Co., Thousand Plams, 20 Feb 1955, W. R. Richards (CNC).

Discussion.—The specific epithet is in reference to the Mojave Desert, the only known habitat of this species.

The presence of a single spermatheca easily distinguishes this species from all other species in the *bivittata* Group with banded legs.

Bezzia nigripes, new species
Figs. 64–67

Diagnosis.—A medium-sized species distinguished by its slender legs with dark, unbanded femora and tibiae; spermathecae large, ovoid, subequal, with long slender necks; palpus slender, third segment very slender (female palpal ratio 5.14).

Holotype female.—Wing length 1.27 mm; breadth 0.46 mm.

Head: Dark brown. Eyes broadly separated, a space of about five ommatidial facets, a distance of 0.074 mm. Antennal flagellum slightly lighter in shade on extreme bases of distal five segments flagellar segments with lengths in proportion of 19-9-9-9-9-9-8-9-11-12-13-13-18; antennal ratio 0.83. Palpus (Fig. 66) slender; segments with lengths in proportion of 6-10-18-10-13; palpal ratio 5.14. Mandible with eight large teeth and three shorter basal ones.

Thorax: Dark brown. Mesonotum with scattered short setae, but not pubescent. Legs (Fig. 67) slender with unbanded, dark brown femora and tibiae; tarsi dark on apices of tarsomeres 1 and 2, most of 3 and all of 4 and 5. Wing hyaline, anterior veins light brown, posterior veins pale; costal ratio 0.70. Halter dark brown.

Abdomen: Brown, pleura darkest. Genitalia very similar to those of *B. vittata* (Fig. 10). Spermathecae (Fig. 64) large, ovoid with long slender parallel-sided necks; subequal, measuring 0.096 by 0.056 mm and 0.078 by 0.052 mm.

Allotype male.—Wing length 1.35 mm; breadth 0.37 mm. Similar to holotype female with the following differences: Antennal flagellum uniformly brown in color, plume dense, dark brown; flagellar segments with lengths in proportion of 28-11-11-11-10-11-12-15-26-47-15-15-18; antennal ratio 1.09. Palpus with third segment shorter, palpal ratio 3.56. Mesonotum without long setae but with two lengths of relatively dense pubescence. Legs with very faint subbasal band on fore tibia; hind tarsus entirely brown and mid tarsus more suffused with brown. Genitalia as in Fig. 65, very similar to those of *B. bivittata* (Fig. 9) but differing essentially as follows: Aedeagus without well-defined, heavily sclerotized, basal portion; parameres broader across basal arms.

Distribution.—Utah and California.

Types.—Holotype female, UTAH, Washington Co., Leeds, Red Cliffs Recreation Area, 22 May 1974, W. L. Grogan, Jr., swept from margin of small stream. Allotype male, 2 male paratypes, CALIFORNIA, Imperial Co., Hot Mineral, 30 Apr 1952, J. N. Belkin (Type no. 76590, USNM).

Discussion—The specific epithet *nigripes,* is a reference to the unbanded, dark brown femora and tibiae which are sufficient to distinguish this species from all other species in the *bivittata* Group.

Bezzia sandersoni, new species

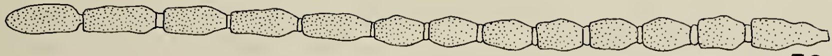
Figs. 68–71, 73

Diagnosis.—A small species distinguished by its vivid, contrasting pale bands on the fore and mid femora and tibiae; female antennal flagellum very short, distal segments moniliform to short ovoid (antennal ratio 0.71–0.87); spermathecae large, elongate ovoid; male genitalia with deeply emarginate 9th sternum and bulbous tip of parameres.

Allotype female.—Wing length 1.05 mm; breadth 0.47 mm.

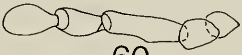
Head: Dark brown. Eyes barely contiguous, joined at midline for the space of one antennal facet. Antennal flagellum (Fig. 68) brown, lighter in color on basal portions of flagellar segments, darker on apical portions; distal five segments very short, ovoid; lengths of flagellar segments in proportion of 15-8-8-8-7-7-7-8-9-9-9-10-13; antennal ratio 0.74. Palpus (Fig. 69) light brown, lengths of segments in proportion of 4-8-11-8-8; palpal ratio 2.75. Mandible with eight large coarse teeth and 5–6 smaller basal teeth.

Thorax: Dark brown; mesonotum and scutellum covered with short setae and

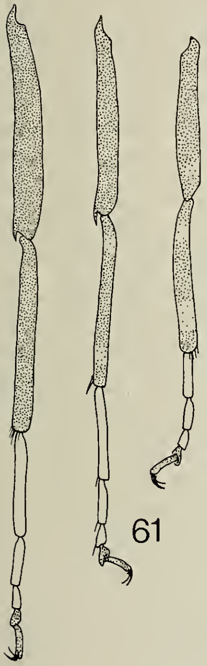


58

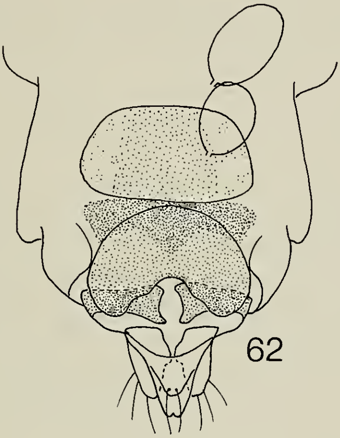
59



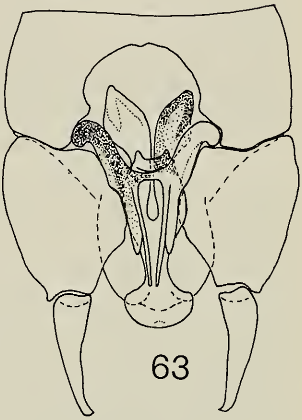
60



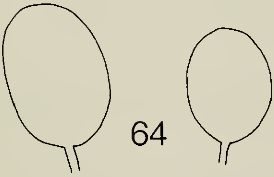
61



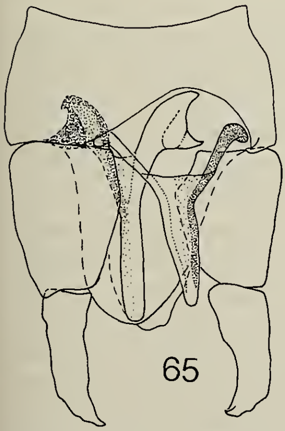
62



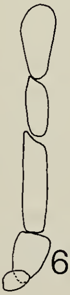
63



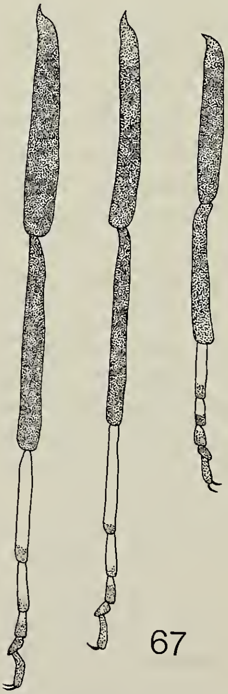
64



65



66



67

Figs. 58–67. 58–63, *Bezzia setosinotum*; 64–67, *nigripes*; 58–62, 64, 66–67, female; 71–72, male: 58, antenna; 59, wing; 60, 66, palpus; 61–67, hind, mid, and fore legs (left to right), 62, 63, 65, genitalia; 64, spermathecae.

fine pubescence. Legs (Fig. 73) dark brown on femora and tibiae, pale bands on subapices of fore and mid femora, subbases of all tibiae, and subapices of fore and mid tibiae; tarsi brown on tarsomeres 4 and 5 and apices of 1–3, pale on remainder of 1–3. Wing grayish hyaline, veins light brown; costal ratio 0.69. Halter stem light brown, know dark brown.

Abdomen: Dark brown, pleura purplish. Spermathecae (Fig. 70) large, elongate ovoid with short necks; unequal, measuring 0.081 by 0.037 mm and 0.063 by 0.033 mm.

Holotype male.—Wing length 0.98 mm; breadth 0.36 mm. Similar to female with the following differences: Antennal flagellum pale on basal halves of segments 3-10, plume golden brown; lengths of segments in proportion of 19-10-9-10-10-11-11-11-16-19-11-12-15; antennal ratio 0.81. Wing more slender with shorter radial cell; costal ratio 0.64. Genitalia as in Fig. 71. Ninth sternum twice as broad as long, caudomedian excavation deep, broadly U-shaped; ninth tergum tapering abruptly and becoming broadly rounded where it joins the long slender cerci which extend to the apices of the basistyles. Basistyle bulbous, slightly longer than broad, ventral and mesal surface with a few long setae; dististyle as long as basistyle, curved and tapering slightly distally to truncate tip. Aedeagus triangular, 1.1 times longer than broad, basal arch 0.25 of total length; basal arms heavily sclerotized, tapering to recurved, pointed tip; distal portion more lightly sclerotized except for margins, tapering at extreme distal end to slender pointed tip, apex of which is hyaline. Parameres heavily sclerotized; basal arm with broad wing-like lateral extension and rounded posterior portion; distal portion slender, rod-like, tip bulbous.

Variation.—Wing length 1.04 (0.95–1.24, n = 10) mm; breadth 0.46 (0.41–0.56, n = 10) mm. Antennal ratio 0.77 (0.71–0.87, n = 10). Palpal ratio 2.36 (2.00–3.25, n = 10). Costal ratio 0.69 (0.65–0.71, n = 10).

Distribution.—Southwestern Utah through Arizona and New Mexico and east to Kansas.

Types.—Holotype male, allotype female, ARIZONA, Coconino Co., Manzanita Forest Camp, 6 July 1977, M. W. Sanderson, light trap (Type no. 76591, USNM). Paratypes, 27 males, 28 females, as follows:

ARIZONA: Cochise Co., Portal, Southwest Res. Sta., May–June 1967, C. W. Sabrosky, light trap, 4 males; 5–9 June 1973, W. W. Wirth, light trap, 1 male. Coconino Co., Mormon Lake Village, 26 June 1978, M. W. Sanderson, 3 males, 3 females; Oak Creek Canyon, 25 June 1959, W. L. Nutting, light trap, 1 male, 6 females; 22 July 1959, C. W. O'Brien, light trap, 1 female; Oak Creek, Bootlegger Campground, 13 July 1978, Sanderson, 2 males; Oak Creek at Chavez Crossing, 20 July 1977, 14 June 1978, Sanderson, 1 male, 2 females; Oak Creek, Encinoso Picnic Ground, 3 Aug 1977, Sanderson; Oak Creek at Grasshopper Point, 12 June 1977, 27 Aug 1978, Sanderson, 6 males, 3 females; Oak Creek at East Fork, 19 July 1979, Sanderson, 1 male; Manzanita Forest Camp, 6 Aug 1977, 7 July 1978, Sanderson, 2 males, 3 females. Santa Cruz Co., Ruby, Sycamore Canyon, 22 May 1954, G. D. Butler, light trap, 1 female. Yavapai Co., Oak Creek at the following points: Baldwin Crossing, Deer Pass Crossing, Josephine Tunnel, Oak Creek Village, Page Springs, Red Rock Crossing Verde River, May–Sept 1977–82, Sanderson, at light, 4 males, 6 females.

KANSAS: Riley Co., May 1964, N. Marston, Malaise trap, 1 female.

NEW MEXICO: Catron Co., 5 mi E Glenwood, 24 June 1953, W. W. Wirth, at light, 1 male, 1 female.

UTAH: Washington Co., Leeds, Red Cliffs Rec. Area, 22 May 1974, W. L. Grogan, Jr., near stream, 1 female.

Discussion.—This species is named for Milton W. Sanderson in appreciation of his interest and cooperation in collecting and sending us extensive biting midge collections from Oak Creek Canyon, Arizona.

Bezzia sandersoni resembles *B. gibbera* in its large elongate oval spermathecae, but differs in its dull mesonotum with numerous pollinose white spots and setae not arising from tubercles, its black legs with strongly contrasting pale rings, apically dark tarsi, entirely black halter, the extremely short antenna, bulbous basistyles without setose basal lobe, and parameres with bulbous tip.

Bezzia setosinotum, new species
Figs. 58–63

Diagnosis.—A medium-sized species with legs banded typically as in *B. bivittata,* but differing from that and all other species in the group by the following combination of characters: halter white; female antenna short (mean antennal ratio 0.86); female abdomen light brown to yellowish with large, elongate-ovoid spermathecae with short slender necks; male genitalia with broadly rounded tip of parameres and bifurcate aedeagus.

Allotype female.—Wing length 1.23 mm; breadth 0.47 mm.

Head: Dark brown. Eyes well separated, a space of about four ommatidial facets, a distance of 0.044 mm. Antennal flagellum (Fig. 58) lighter brown than head, flagellar segments paler proximally on basal portion, getting progressively darker overall distally the distal-most segment darkest; flagellar segments with lengths in proportion of 15-10-9-9-9-9-10-9-12-14-13-14-16; antennal ratio 0.86. Palpus (Fig. 60) light brown, moderately slender; lengths of segments in proportion of 5-9-15-8-9; palpal ratio 3.75. Mandible with eight large teeth and 3–4 smaller basal teeth.

Thorax: Dark brown; mesonotum and scutellum with numerous short scattered setae; mesonotum not pubescent, but scutellum and postscutellum with fine pubescence. Legs (Fig. 61) with dark brown femora, and tibiae with banding typical of *B. bivittata,* tarsi pale on proximal three tarsomeres, distal two tarsomeres brown. Wing (Fig. 59) hyaline, veins light brown; costal ratio 0.67. Halter white.

Abdomen: Light brown. Genitalia as in Fig. 62, Seventh sternum lightly sclerotized with long setae on distal half. Eighth sternum heavily sclerotized on proximal third with a shallow caudal notch, covered with long setae. Ninth sternum heavily sclerotized, each arm broadly bifurcate. Tenth sternum with five pairs of long setae. Spermathecae large, ovoid, elongate, subequal, quadrate with short, slender necks, measuring 0.089 by 0.052 mm and 0.070 by 0.048 mm.

Holotype male.—Wing length 1.24 mm, breadth 0.37 mm. Similar to female with the following differences: Antennal flagellum more uniformly dark brown; plume dense, dark brown; flagellar segments with lengths in proportion of 29-15-11-11-10-11-12-14-21-30-17-18-22; antennal ratio 1.10. Palpal ratio 3.56. Wing more slender with shorter radial cell; costal ratio 0.60. Abdomen slightly darker brown. Genitalia as in Fig. 63. Ninth sternum 1.7 times broader than long, caudomedian excavation very deep, U-shaped; ninth tergum tapering very abruptly distally into conical shape to where it joins the short broad cerci which extend to tip of basistyles. Basistyle 1.4 times longer than broad, nearly globose, swollen basally on mesal side then tapering rather abruptly on that side, ventral surface covered with numerous long setae directed mesally; dististyle 0.7 length of basistyle nearly straight, tapering gradually distally to curved, broadly pointed tip. Aedeagus H-shaped; basal arms very heavily sclerotized, broadly rounded; distal portion bifurcate and joined by a slender bridge, heavily sclerotized basally, becoming more lightly sclerotized distally, a slender apical process arising at bridge and tapering distally to narrow tip that extends to ends of basistyles. Parameres heavily sclerotized proximally, more lightly sclerotized distally; basal arms broad, hastate in shape, becoming constricted at base distal portion broad and bulbous basally, then tapering distally before rapidly expanding to the broadly rounded, capitate tip.

Variation.—Female wing length 1.22 (0.95–1.33, n = 10) mm; breadth 0.44 (0.36–0.48, n = 10) mm. Antennal ratio 0.86 (0.82–0.98, n = 9). Palpal ratio 2.87 (2.60–3.75, n = 9). Costal ratio 0.69 (0.67–0.72, n = 10). There is considerable variation in the type-series in the color of the female abdomen, varying from light brown to pale yellowish, but in all specimens, even the palest ones, the genitalia are well sclerotized.

Distribution.—New Jersey south to Florida.

Types.—Holotype male, allotype female, 9 male and 17 female paratopotypes, MARYLAND: Prince George's Co., Patuxent Wildlife Res. Center, June 1976, W. L. Grogan, Jr., Malaise trap (Type no. 76592, USNM). Eight male and three female paratypes as follows:

FLORIDA: Alachua Co., Gainesville, Chantilly Acres, 8 May 1967, F. S. Blanton, 1 male.

MARYLAND: Wicomico Co., Salisbury, 20–30 June 1981, Grogan and E. Y. Nichols, Malaise trap, 6 males, 1 female.

NEW JERSEY: Middlesex Co., 11 July 1958, W. W. Wirth, light trap, 1 male.

WEST VIRGINIA: Pocahontas Co., Cranberry Glades 15 July 1955, C. W. Sabrosky, 1 female.

Discussion.—The specific name *setosinotum* is in reference to the short, abundant, stiff, spine-like setae present on the mesonotum and scutellum. It and *B. andersonorum* n. sp. are unique among members of the *bivittata* group in having typically banded legs but white halteres. Males of *B. andersonorum* have a short H-shaped but bipartite aedeagus, and the apex of the distal process of the parameres is slender.

Bezzia spathula, new species

Figs. 53–57

Diagnosis.—A small species most closely resembling *B. luteiventris* in its dark brown femora with contrasting pale yellow tibiae and abdomen, and white halter, but differing from that species as follows: male aedeagus with tip broad and spatula-shaped and basal arms broader; size larger, female wing length 1.23–1.24 mm (1.05–1.11 mm for *B. luteiventris*); female antennal ratio 1.06–1.10 (0.89 for *B. luteiventris*); female antennal flagellum indistinctly banded.

Allotype female.—Wing length 1.23 mm; breadth 0.44 mm.

Head: Dark brown. Eyes narrowly separated, a space of one ommatidial facet, a distance of 0.019 mm. Antenna with flagellum (Fig. 57) brown, paler on proximal 0.75 of proximal segments decreasing to proximal 0.25 on distal segments, thus giving flagellum an indistinctly banded appearance; lengths of flagellar segments in proportion of 19-10-8-8-9-9-9-9-21-16-14-17-18; antennal ratio 1.06. Palpus (Fig. 54) light brown, base of third segment darker, lengths of segments in proportion of 5-9-14-8-10; palpal ratio 2.80. Mandible with 7–9 large coarse teeth and 2–3 smaller basal teeth.

Thorax: Dark brown; mesonotum and scutellum covered with numerous scattered setae and fine pubescence. Legs (Fig. 56) dark brown on femora; tibiae, and proximal three tarsomeres pale yellow, distal two tarsomeres light brown. Wing hyaline, veins pale; costal ratio 0.71. Halter stem pale, knob white.

Abdomen: Pale yellow; brown on distal four segments. Spermathecae (Fig. 53) large, elongate oval; unequal, measuring 0.085 by 0.052 mm and 0.067 by 0.048 mm.

Holotype male.—Wing length 1.15 mm; breadth 0.34 mm. Similar to female with the following differences: Antenna more brownish on proximal segments; plume dark brown; flagellar segments with lengths in proportion of 25-10-11-11-11-11-13-15-20-29-17-20-20; antennal ratio 0.99. Abdomen brown. Wing more slender with shorter radial cell; costal ratio 0.62. Genitalia as in Fig. 55. Ninth sternum nearly twice as broad as long, caudomedian excavation very deep, in the shape of a truncate U; 9th tergum tapering abruptly distally and becoming rounded where it joins the long slender cerci which extend just beyond basistyles. Basistyle 1.5 times longer than broad, covered with scattered long setae; dististyle 0.6 the length of basistyle, curved and gradually tapering distally to bluntly pointed tip. Aedeagus 1.2 times longer than broad, basal arch 0.2 of total length; basal arms very heavily sclerotized, very broad on proximal portions, then tapering and recurving about 60°; distal portion more lightly sclerotized, particularly so on the broad, spatula-shaped tip. Parameres very heavily sclerotized; basal arms with lateral wing-like expansion and a posterior more truncate extension; distal portion bulbous proximally, becoming more slender distally with the rounded tip continuing to just beyond basistyles.

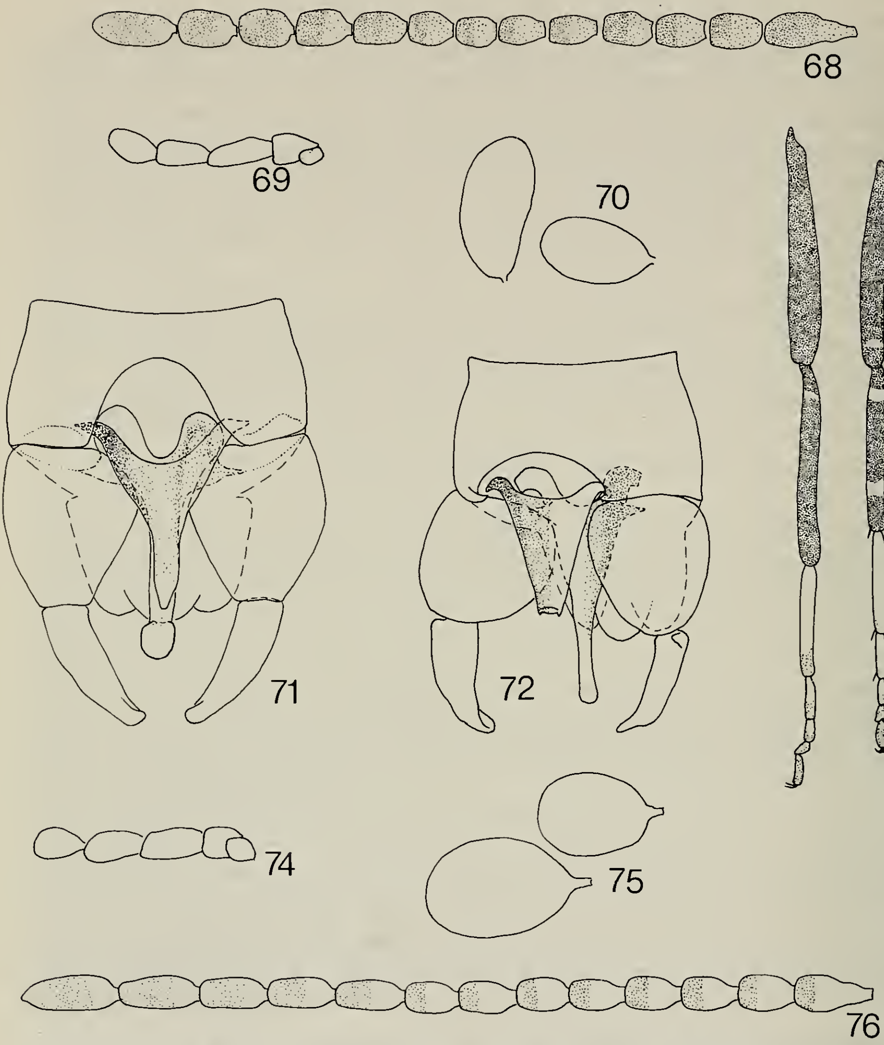
Distribution.—Maryland.

Types.—Holotype male, allotype female, 1 female paratype, Maryland, Wicomico Co., Salisbury, 25 May–7 June 1982, W. L. Grogan, Jr., Malaise trap (Type no. 76597, USNM). One male paratype, MARYLAND, Worcester Co., Snow Hill, 19 June 1968, W. W. Wirth, swept from margin of Nassawango Creek 1 mile upstream from its confluence with the Pocomoke River.

Discussion.—The specific epithet is in reference to the spatula-shaped tip of the male aedeagus which serves to distinguish this species from its closest relatives, *B. luteiventris* n. sp., and *B. flavitibia* Dow and Turner.

Bezzia texensis, new species
Figs. 72, 74–76

Diagnosis.—A small species with dark legs banded as in typical *B. bivittata*, but differing from that and all other species in the group by the following com-



Figs. 68–76. 67–71, 73, *Bezzia sandersoni*; 72, 74–76, *texensis*; 68–70, 73–76, female; 71–72, male: 68, 76, antenna; 69, 74, palpus; 70, 75, spermathecae; 71–72, genitalia; 73, hind, mid, and fore legs (left to right).

bination of characters: Small size (female wing length 0.95–1.02 mm); short, stout, banded antennal flagellum (antennal ratio 0.80); large, unequal, ovoid spermathecae with long tapering necks; male genitalia with globose basistyles, triangular aedeagus with truncate tip, and parameres broad at base with a subbasal, lateral, pointed projection.

Holotype female.—Wing length 0.95 mm; breadth 0.41 mm.

Head: Brown. Eyes very narrowly separated, a space of about two ommatidial facets, a distance of 0.022 mm. Antennal flagellum (Fig. 76) pale on basal halves of segments, light brown on distal halves; flagellar segments with lengths in proportion of 13-8-8-8-8-8-8-8-10-10-10-12-13; antennal ratio 0.80. Palpus (Fig. 74) light brown; lengths of segments in proportion of 4-6-9-8-7; palpal ratio 2.25. Mandible with 9–10 large coarse teeth and 3–4 smaller basal teeth.

Thorax: Dark brown; mesonotum and scutellum with dense short stout setae on dorsal portions, entire surfaces covered with finer pubescence. Legs dark brown, wth banding typically like that of *B. bivittata* (Fig. 8); tarsi pale on proximal four tarsomeres, 5th tarsomeres light brown. Wing hyaline, veins pale; costal ratio 0.72. Halter brown.

Abdomen: Brown. Spermathecae (Fig. 75) large, unequal, ovoid with long tapering necks, measuring 0.081 by 0.048 mm and 0.055 by 0.041 mm.

Allotype male.—Wing length 0.92 mm; breadth 0.32 mm. Similar to female with the following differences: Antennal flagellum with golden brown plume; lengths of segments in proportion of 22-10-9-10-10-10-10-13-18-25-13-15-17; antennal ratio 0.94. Palpal ratio 2.44. Wing more slender with shorter radial cell; costal ratio 0.63. Genitalia as in Fig. 72. Ninth sternum 1.7 times broader than long, caudomedian excavation shallow; ninth tergum tapering abruptly on basal portion until it joins the long cerci that extend to tip of basistyles. Basistyle slightly longer than broad, globose, ventral and msesal surface with long setae; dististyle about the length of basistyle, curved and tapering slightly distally to broad pointed tip. Aedeagus triangular, slightly longer than broad; basal arms heavily sclerotized, short; distal portion more lightly sclerotized except on margins, tapering distally to truncate tip. Parameres heavily sclerotized proximally, more lightly sclerotized distally; basal arms broad, recurved about 90° with pointed subbasal lateral projection; distal portion broad basally, tapering apically to a slender rod with slightly expanded, rounded tip.

Distribution.—Texas; known only from the type-locality.

Types.—Holotype female, TEXAS, Gillespie Co., Fredericksburg, 28 July 1967, Blanton and Borchers, light trap (Type no. 76593, USNM). Allotype male, 1 female paratype, same data except taken 2 July 1967.

Discussion.—The small size, pale-banded antennal flagellum, and distinctive spermathecae and male genitalia should be sufficient to distinguish this species from all others in the *bivittata* Group with banded legs and dark halteres.

Acknowledgments

We are very grateful to J. Antony Downes of the Biosystematics Research Institute, Agriculture Canada, Ottawa, and Walter I. Knausenberger of the College of the Virgin Islands Extension Service, St. Croix, for critical reviews of our manuscript and their many helpful comments and suggestions. Dr. Downes also furnished us with many new Canadian records from the Canadian National Collection.

We also extend thanks to the following institutions and persons for the loan of specimens: California Academy of Sciences, San Francisco (CAS) by courtesy of Paul H. Arnaud, Jr.; California Insect Survey, University of California, Berkeley (CIS) through David Wagner; Cornell University (COR), Ithaca, New York, through Q. D. Wheeler; Illinois Natural History Survey, Urbana (INHS) through D. W. Webb; Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ) through Karen Jepson; University of California, Riverside (UCR) through Saul Frommer; and Washington State University, Pullman (WASH) through W. J. Turner.

Literature Cited

Clastrier, J. 1962. Notes sur les Cératopogonidés XVI.—Espèces du genre *Bezzia* Kieffer ou apparentées de la Région Paléarctique. Archives de l'Institut Pasteur d'Algérie. 40:53–124.

Coquillett, D. W. 1905. New nematocerous Diptera from North America.—Journal of the New York Entomological Society 13:56–69.

Dow, M. I., and E. C. Turner, Jr. 1976. A revision of the Nearctic species of the genus *Bezzia* (Diptera: Ceratopogonidae).—Virginia Polytechnic Institute Research Division Bulletin 103:1–162.

Grogan, W. L., Jr., and W. W. Wirth. 1981. A new American genus of predaceous midges related to *Palpomyia* and *Bezzia* (Diptera: Ceratopogonidae).—Proceedings of the Biological Society of Washington 94:1279–1305.

Haeselbarth, E. 1965a. Notes on *Bezzia nicator* de Meillon, 1959 (Diptera: Ceratopogonidae). Descriptions of two related new species from Southern Africa.—Novos Taxa Entomológicos 40: 1–16.

———. 1965b. *Phaenobezzia* a new genus of biting midges (Diptera: Ceratopogonidae), with a review of the African species.—Zeitschrift für Angewandte Entomologie 52:297–324.

———. 1975. Zur Kenntnis von *Bezzia africana* und verwandten Gnitzen-Arten aus der Äthiopischen Region (Diptera: Ceratopogonidae).—Entomologica Germanica 1:352–370.

Johannsen, O. A. 1908. New North American Chironomidae.—Bulletin of the New York State Museum 124:264–285.

———. 1943. A generic synopsis of the Ceratopogonidae (Heleidae) of the Americas, a bibliography, and a list of the North American species.—Annals of the Entomological Society of America 36:763–791.

Kieffer, J. J. 1899. Description d'un nouveau genre et tableau des genres européens de la famille des Chironomides (Dipt.).—Bulletin de la Société Entomologique de France 1899:66–70.

———. 1906. Diptera, Fam. Chironomidae. *in* P. Wytsman (ed.), Genera Insectorum. Fasc. 42:1–78, 4 plates.

———. 1917. Chironomidés d'Amérique conservés au Musée National Hongrois de Budapest.—Annales Historico-Naturales Musei Nationalis Hungarici 14:81–121.

Malloch, J. R. 1914. Synopsis of the genus *Probezzia*, with description of a new species (Diptera).—Proceedings of the Biological Society of Washington 27:137–139.

———. 1915. The Chironomidae, or midges, of Illinois, with particular reference to the species occurring in the Illinois River.—Bulletin of the Illinois State Laboratory of Natural History 10:275–543, 23 plates.

Remm, H. 1974a. A review of the species of the genus *Bezzia* Kieffer (Diptera, Ceratopogonidae) from the fauna of the USSR. I. (In Russian, English summary).—Entomologicheskoe Obozrenie 53:429–442 (English translation in Entomological Review 53(1):136–145).

———. 1974b. A review of the species of the genus *Bezzia* Kieffer (Diptera, Ceratopogonidae) from the USSR. II. Subgenus *Bezzia* s. str. (In Russian, English summary).—Entomologicheskoe Obozrenie 53:888–902 (English translation in Entomological Review (53(4):113–124).

Tokunaga, M. 1966. Biting midges of the Palpomyiinae from New Guinea (Diptera: Ceratopogonidae).—Pacific Insects 8:101–152.

Wirth, W. W. 1952. The Heleidae of California.—University of California Publications in Entomology 9:95–266.

———. 1965. Family Ceratopogonidae. Pp. 121–142 *in* A. Stone *et al.*, (eds.), A Catalog of the Diptera of America North of Mexico.—United States Department of Agriculture, Agriculture Handbook 276:1696 pp.

———. 1974. A catalogue of the Diptera of the Americas south of the United States. 14. Ceratopogonidae.—Museu du Zoologia, Universidade de São Paulo. 89 pp.

———. In Press. A review of the American predaceous midges of the *Bezzia nobilis* Group (Diptera: Ceratopogonidae).—Proceedings of the Entomological Society of Washington.

———. In Press. The North American predaceous midges of the *Bezzia bicolor* Group (Diptera: Ceratopogonidae).—The Florida Entomologist.

———. In Press. The North American species of the *cockerelli* and *dorsasetula* Groups of the preedaceous midge genus *Bezzia*, subgenus *Homobezzia* (Diptera: Ceratopogonidae).—Proceedings of the Entomological Society of Washington.

———, and W. L. Grogan, Jr. 1979. Natural History of Plummers Island, Maryland. XXIV. Biting midges (Diptera: Ceratopogonidae). 2. The species of the tribes Heteromyiini and Sphaeromiini.—Proceedings of the Biological Society of Washington 91:847–903.

———, and ———. 1982. The predaceous midges of the genus *Phaenobezzia* in North America (Diptera: Ceratopogonidae).—Memoirs of the Entomological Society of Washington 10:179–192.

———, S. M. Palchick, and L. Forster. In Press. The North American predaceous midges of the *Bezzia annulipes* Group (Diptera: Ceratopogonidae).—Proceedings of the Entomological Society of Washington.

———, N. C. Ratanaworabhan, and D. H. Messersmith. 1977. Natural History of Plummers Island, Maryland. XXII. Biting midges (Diptera: Ceratopogonidae). 1. Introduction and key to genera.—Proceedings of the Biological Society of Washington 90:615–647.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 524–547

A COMPARATIVE STUDY OF SELECTED SKELETAL STRUCTURES IN THE SEASTARS *ASTERIAS FORBESI* (DESOR), *A. VULGARIS* VERRILL, AND *A. RUBENS* L., WITH A DISCUSSION OF POSSIBLE RELATIONSHIPS

E. K. Worley and David R. Franz

Abstract.—Morphological structures from the congeneric North Atlantic seastars, *Asterias forbesi* (Desor), *A. vulgaris* Verrill, and *A. rubens* L., were measured and compared. Significant differences in size and/or shape were found between *A. forbesi* and *A. vulgaris* in the following structures: ventral pedicellariae, adambulacral spines, oral spines, the madreporite, skeletal ossicles, and the shape of the arms. Slight but insignificant differences in size, but not shape of these structures was shown between *A. vulgaris* and the few samples of *A. rubens* examined.

The firmer, more rounded, less tapering shape of the arms in *A. forbesi* was attributed to the shape of the ossicles and their long processes which form junctions directly, or by one plate, with adjacent processes throughout the length of the arm. In the more flaccid, tapering arms of *A. vulgaris* (and *A. rubens*) short, blunt ossicle processes connect with adjacent processes by several plates in the proximal dorsolateral region forming a more open meshwork and more flaccid skeleton. The uniformly small size of these plates throughout the length of the arms in young *A. vulgaris* may account for the less tapered conditions sometimes found in small specimens causing them to resemble the shape of the *A. forbesi* arms. Furthermore, variation in size and number of these plates is suggested to be associated with the production of morphs in *A. vulgaris* and *A. rubens*. The *forbesi*-like animals from the Maine population were therefore diagnosed as local morphological variations of the variable species *A. vulgaris*, and not hybrids.

Earlier ideas and hypotheses concerning the relationships and origins of the three *Asterias* species are summarized and evaluated; and an hypothesis is formulated to account for the origin of all *Asterias* species from a common North Pacific ancestor.

The two seastars, *Asterias forbesi* and *Asterias vulgaris* of the Northwestern Atlantic coast show many similarities in ecology and morphology. Both species, however, exhibit phenotypic variability within and among populations which has resulted in problems of identification, especially in those coastal regions where the two species are sympatric. While there are no comparative studies to ascertain the differences between the species from the extremes of their ranges or from the region of overlap on the continental shelf of the Middle Atlantic Bight (MAB), the taxonomic traits tabulated by Aldrich (1956) are generally accepted as diagnostic (Schopf and Murphy 1973; Walker 1974) for all areas.

While isolated and local populations of *A. forbesi* or *A. forbesi*-like animals may occur in various shallow embayments along the Maine coast (C. Towle, pers. comm.), *A. forbesi* is distributed more or less continuously from Casco Bay, Maine to North Carolina, and may occur south to Florida, although rare south of 20°N (Franz *et al.* 1981). It has been collected over the entire breadth of the continental shelf between Cape Hatteras (North Carolina) and Cape Cod (Massachusetts), except north of 40°N, where it is confined to the inner shelf, on the Nantucket Shoals and Cape Cod Bay. In the SW Gulf of Maine (Isle of Shoals) *A. forbesi* is restricted to depths of 10 m or less (Hulburt 1980), and is generally absent from the subtidal zone of the Gulf of Maine. On the shelf south of Cape Cod, *A. forbesi* occurs most frequently at depths <30 m. *Asterias vulgaris* is uncommon or *absent* from the inshore waters (<20 m) of the Middle Atlantic Bight (MAB) but occurs in the deeper, colder waters as far south as Cape Hatteras. Between Cape Cod and Cape Hatteras, both species co-occur in a broad zone of overlap on the continental shelf. North of Cape Cod, *A. forbesi* is rapidly replaced by *A. vulgaris* which occurs commonly on Georges Bank and the continental shelf of the Gulf of Maine, northward to the Gulf of St. Lawrence.

Asterias rubens which is widely distributed along the northeast Atlantic coast, resembles *A. vulgaris* morphologically, hence, they have been considered to be closely related species (Coe 1912; Fisher 1930; Nesis 1961) and even identical (Clark 1923; Tortonese 1963). In this paper, we examine inter- and intraspecific variability in selected skeletal features of all three species in order to evaluate the potential usefulness of measurable skeletal characters in taxonomic evaluation, and to gain insight into the possible relationships and origins of the Atlantic species of *Asterias*.

Materials and Methods

Asterias forbesi and *A. vulgaris* used in this study were collected along the northwestern Atlantic Continental Shelf and from the coastal shores of Maine and Long Island, New York. Specimens (105) were hand picked from the low intertidal shores of Muscongus Bay, Chamberlain, Maine, in August 1978 and 1979. Other inshore animals (46) were obtained by SCUBA at Shoreham, Long Island Sound, in December 1978, and from East Rockaway Inlet (50 animals), Far Rockaway, New York (southwestern Long Island) in September 1978 and December 1979. Specimens from the northwestern Atlantic Continental Shelf were collected, using an otter trawl, by the National Marine Fisheries Service during the Ground Fish Survey (Del. II Cruise 78-1, Jan–Feb 1978; Del. II Cruise 79-01 and Alb. IV Cruise 79-04, Jan–Mar 1979). The Gulf of Maine region (42°02′–44°37′) included 25 stations ranging in depth from 35–348 m, and yielded 97 specimens. Between Cape Cod and Cape Hatteras (42°00′–35°58′), the Middle Atlantic Bight (MAB), 1450 specimens of *Asterias* spp. were obtained from 177 stations ranging in depth from 9–220 m. Many of the stations in both the Gulf of Maine and the Middle Atlantic Bight yielded only one or two specimens of a species and the size range from many stations was very narrow. In order to make valid comparisons between the species, measurements of the traits selected for study were based on animals within the same size range (R = 4–9 cm). Since the magnitude of size variability of these characters in a species was found to be no greater between stations of a region than between members of the same population, data from all populations of a species from a given geographic area were pooled.

For comparison, studies were made on formalin-preserved specimens (25) of *Asterias rubens* collected from St. Andrews, Scotland, and a small number of museum specimens (alcohol preserved) from Northwest Iceland (10) and southwest Greenland (18).

Observations on living starfish were made only on those collected from Muscongus Bay and Rockaway Beach. Material supplied by the Ground Fish Survey in 1979 was frozen immediately on collection and brought to the laboratory in this condition. All other specimens were preserved in formalin when collected and later studied in the laboratory.

Four morphological features which are usually considered of diagnostic value for *Asterias* spp. (Coe 1912; Mortensen 1927; Aldrich 1956; Gray *et al.* 1968) were selected for measurement and comparison: the shape of the rays; the size and shape of the madreporite; the size and shape of the straight (major) pedicellariae; and the structure of the skeleton, including the ossicles and the size and shape of the adambulacral and oral spines.

Gross measurements were made with Vernier calipers on the middle arm of the trivium. Body radius (R) measured from the center of the disc to the tip of the arm, was used for size comparisons between individuals of the same and different populations and species. Tapering of the rays was calculated from the ratio (a/b) between the diameter of the arm at the base (a) and the diameter measured 1 cm from the tip (b). Thus, more tapered rays exhibit higher a/b ratios than blunt, parallel-sided rays.

Spines, straight pedicellariae, and the madreporite were removed from at least 10 animals from each region and measured with a calibrated Wild Dissecting Scope. Spines and pedicellariae were selected at random from the proximal third of the arms, and each recorded value, based on the measurement of the calcareous skeleton, represents the average of a minimum of 10 samples per animal.

After removal of podia and internal organs, animals were skeletonized by placing one or more arms or the entire specimen, depending on size, in undiluted commercial Clorox (sodium hypochlorite) for 10–25 minutes, or until the soft outer covering was dissolved. Skeletons were washed in several changes of water and dried at room temperature.

Color variations were noted and compared in live and frozen specimens only, but no detailed studies were made. Preserved material showed color loss and could not be considered reliable for comparisons.

Observations

Shape of arms.—The a/b ratios, measured on animals over a size range of R = 2–8 cm, from MAB populations of *A. forbesi* and *A. vulgaris* were weakly correlated with body size (R), but the degree of tapering was greater in all sizes of *A. vulgaris* (Table 1). The a/b ratios from Shoreham and Rockaway Beach populations of *A. forbesi* were not significantly correlated with body size and had similar mean a/b ratios (Shoreham $\bar{x}$ = 2.23; Rockaway Beach $\bar{x}$ = 2.16). *Asterias vulgaris* from Muscongus Bay likewise showed no statistically significant correlation between a/b and R, and had essentially the same a/b mean value ($\bar{x}$ = 2.13) as that of the two shallow, coastal water populations of *A. forbesi*. In shape, therefore, small *A. vulgaris* from Muscongus Bay resembled *A. forbesi* of comparable size.

Table 1.—Correlation between body size (R) and shape of the ray (ratio a/b).

	Asterias forbesi			*Asterias vulgaris*			*Asterias rubens*	
Population	Rockaway	MAB	Shoreham	Gulf of Maine	MAB	Muscongus Bay	St. Andrews	NW Iceland
a/b ratio range	1.7 to 2.5	1.2 to 3.3	1.0 to 3.4		2.0 to 5.0	1.1 to 3.3	1.7 to 6.2	1.7 to 3.1
$\bar{x} \pm s$	2.16 ± 0.28	2.32 ± 0.47	2.23 ± 0.47		3.52 ± 0.39	2.13 ± 0.39	3.195 ± 1.008	2.39 ± 0.46
r	−0.082	0.506	0.219		0.502	−0.175	0.613	0.741
P	NS	0.01	NS		0.01	NS	0.01	0.01
N	21	55	45		47	50	23	18
Slope	—	0.190	—		0.187	—	0.365	0.375
Intercept	—	1.254	—		2.273	—	1.189	0.678

Asterias rubens, in the range of R = 2–9 cm, from the St. Andrews and West Greenland populations exhibited statistically significant positive correlation between R and a/b ratios. The slopes for these populations were distinctly steeper than for MAB *A. vulgaris* of comparable size (Table 1).

Madreporite.—Madreporites from a wide range of animal sizes were measured, but only data from specimens of R = 5–9 cm were used for comparison of the diameter (size) and height (convexity) between the species. Few *A. forbesi* from the Shoreham and Rockaway Beach populations were under 4 cm and none of the *A. vulgaris* from Muscongus Bay or available specimens of *A. rubens* were over 9 cm. Within this size range, there was little intrapopulation variability in either size or convexity of the madreporites in any species.

The average diameter of the madreporites from animals of comparable size from the three populations of *A. forbesi* studied was $\bar{x}$ = 4.13 mm, which was greater than diameters from populations of *A. vulgaris* ($\bar{x}$ = 3.30 mm) or *A. rubens* ($\bar{x}$ = 2.82 mm), a variation hardly perceptible to the naked eye (Table 2).

The height (convexity) of the madreporites showed no significant correlation with body size (R) within any populations. *Asterias forbesi* from all regions had slightly higher (more convex) madreporites ($\bar{x}$ = 1.18 mm) than *A. vulgaris* ($\bar{x}$ = 0.76 mm) and *A. rubens* ($\bar{x}$ = 0.80 mm) from all populations (Table 2).

Pedicellariae.—Dorsal: Numerous dorsal, straight (major) pedicellariae of the short, rounded type (Coe 1912) were distributed over the abactinal surface between the dorsal spines in *A. forbesi* from all populations. These pedicellariae ranged in size from 0.33–0.49 mm (Table 2), with little size difference between the population.

Narrow, pointed major pedicellariae (Coe 1912) were the usual dorsal type in both *A. vulgaris* and *A. rubens*, but both broad and pointed forms were sometimes found together. In both species, major pedicellariae were always less numerous and more widely distributed than in *A. forbesi*. Dorsal pedicellariae from animals of comparable size from populations of *A. vulgaris* from the Gulf of Maine (0.47–0.63 mm) and the MAB (0.58–0.72 mm), and from the samples of *A. rubens* from Northwest Iceland (0.44–0.88 mm) were longer than those of *A. forbesi* (Table 2). On the other hand, the range of length of the dorsal pedicellariae (0.29–0.41 mm) in the Muscongus Bay population of *A. vulgaris* was shorter than in *A. forbesi*, but comparable to the range found in the St. Andrews specimens (0.31–0.47 mm) of *A. rubens* (Table 2). There was no correlation between length of the dorsal pedicellariae and body size (R) in any population (Table 3).

Ventral: All ventral, straight pedicellariae were longer than the dorsal pedicellariae. However, in all three species, we selected for study only the major pedicellariae from both the inner and outer adambulacral spines of the proximal region of the arm. Each spine usually carried from one to eight major pedicellariae on the outer surface of the distal half. The number and size of the pedicellariae gradually decreased distally in the arm.

In *A. forbesi*, the major pedicellariae were broad and blunt. Comparing the pedicellariae from animals of comparable size, the differences in mean length were statistically insignificant between those from subtidal populations (Rockaway Beach $\bar{x}$ = 0.54 mm; Shoreham $\bar{x}$ = 0.50 mm) and those from deeper (15–60 m) MAB stations ($\bar{x}$ = 49 mm) (Table 2). In no population was there a significant correlation between body radius (R) and length of the pedicellariae (Table 3).

Table 2.—Size of skeletal structure, based on animals in size range R = 5–9 cm, except NW Iceland population which ranged from R = 4–9.5 cm.

	Asterias forbesi			*Asterias vulgaris*			*Asterias rubens*	
Population	Rockaway	MAB	Shoreham	Gulf of Maine	MAB	Muscogus Bay	St. Andrews	NW Iceland
				Madreporite (diameter)				
Range (mm)	3.32–4.98	3.32–4.56	3.82–4.98	2.90–4.15	3.32–4.15	4.29–4.15	2.49–4.15	1.41–2.90
$\bar{x} \pm s$	4.15 ± 0.5	4.03 ± 0.3	4.29 ± 0.3	3.17 ± 0.4	3.56 ± 0.3	3.18 ± 0.4	3.42 ± 0.5	2.26 ± 0.4
n	5	14	9	8	5	15	9	6
				Madreporite (height)				
Range (mm)	0.83–1.24	0.83–1.24	0.83–1.66	0.66–0.83	0.66–1.00	0.41–1.24	0.41–1.66	0.41–0.83
$\bar{x} \pm s$	1.15 ± 0.1	1.15 ± 0.2	1.24 ± 0.3	0.78 ± 0.07	0.79 ± 0.1	0.73 ± 0.2	0.93 ± 0.3	0.67 ± 0.14
n	5	14	9	8	5	15	9	6
				Dorsal Pedicellaria				
Range (mm)	0.39–0.46	0.33–0.49	0.37–0.46	0.47–0.63	0.58–0.73	0.29–0.41	0.31–0.47	0.44–0.88
$\bar{x} \pm s$	0.41 ± 0.037	0.40 ± 0.46	0.412 ± 0.27	0.54 ± 0.041	0.54 ± 0.034	0.37 ± 0.046	0.41 ± 0.047	0.55 ± 0.06
n	6	6	6	17	5	6	10	6
				Ventral Pedicellaria				
Range (mm)	0.41–0.62	0.37–0.88	0.42–0.60	0.55–0.88	0.58–0.73	0.47–0.65	0.48–0.70	0.66–0.89
$\bar{x} \pm s$	0.54 ± 0.07	0.49 ± 0.18	0.50 ± 0.06	0.68 ± 0.08	0.67 ± 0.06	0.59 ± 0.06	0.60 ± 0.06	0.77 ± 0.07
n	6	6	6	17	5	6	10	6
				Outer Adambulacrals				
Range (mm)	2.67–3.73	1.93–2.89	1.58–2.89	1.33–2.93	1.87–2.78	1.97–2.54	1.60–2.51	1.83–2.82
$\bar{x} \pm s$	2.94 ± 0.04	2.49 ± 0.03	2.43 ± 0.05	2.31 ± 0.5	2.38 ± 0.3	2.20 ± 0.2	2.16 ± 0.3	2.34 ± 0.3
n	6	6	6	17	6	6	10	6
				Inner Adambulacrals				
Range (mm)	2.47–3.28	1.88–2.94	1.97–3.33	1.47–2.89	2.09–2.58	1.99–2.77	1.88–2.44	1.58–2.49
$\bar{x} \pm s$	2.82 ± 0.3	2.42 ± 0.4	2.76 ± 0.5	2.29 ± 0.5	2.34 ± 0.2	2.33 ± 0.3	2.27 ± 0.2	2.08 ± 0.3
n	6	6	6	17	6	6	10	6
				Outer Orals				
Range (mm)	3.48–3.79	2.24–4.23	2.56–3.79	2.49–4.56	2.90–3.79	2.49–2.98	2.49–3.73	1.58–4.98
$\bar{x} \pm s$	3.70 ± 0.1	3.16 ± 0.7	3.24 ± 0.5	3.21 ± 0.6	3.39 ± 0.4	2.82 ± 0.3	2.99 ± 0.3	3.25 ± 1.1
n	6	6	6	15	5	6	10	6
				Inner Orals				
Range (mm)	2.20–3.13	1.16–3.11	1.76–3.30	0.83–2.82	1.16–2.36	1.00–2.55	0.96–1.93	1.16–2.32
$\bar{x} \pm s$	2.68 ± 0.3	2.36 ± 0.7	2.38 ± 0.5	1.73 ± 0.6	1.55 ± 0.5	1.62 ± 0.5	1.35 ± 0.3	1.85 ± 0.6
n	6	6	6	15	5	5	10	6

Table 3.—Correlation between body size (R) and structure.

	Asterias forbesi			*Asterias vulgaris*			*Asterias rubens*		
	Rockaway	MAB	Shoreham	Gulf of Maine	MAB	Muscongus Bay	St. Andrews	W. Greenland	NW Iceland
Range (R) (cm)	6.5–10.0	2.8–8.9	3.8–10.0	2.3–12.5	3.7–13.5	4.2–10.4	2.2–8.9	3.1–6.0	2.0–9.5
Dorsal Pedicellaria									
Structure range (mm)	0.35–0.48	0.32–0.49	3.5–0.46	0.41–0.67	0.47–0.77	0.29–0.49	0.23–0.47	0.33–0.50	1.7–4.8
N	10	10	10	32	10	14	17	10	8
r	0.243	0.465	0.320	0.561	0.816	0.258	0.439	0.758	0.796
P	NS	NS	NS	0.01	0.01	NS 0.05	NS 0.05	0.05	0.05
Slope	—	—	—	0.010	0.022	0.006	—	0.056	0.299
Intercept	—	—	—	0.482	0.412	0.349	—	0.668	1.00
Ventral Pedicellaria									
Structure range (mm)	0.41–0.64	0.36–0.48	0.42–0.60	0.50–0.88	0.55–0.74	0.41–0.68	0.39–0.70	0.55–0.75	0.40–0.63
N	10	10	10	32	10	14	18	18	8
r	0.097	0.554	0.298	0.545	0.650	0.536	0.702	0.296	0.468
P	NS	NS	NS	0.01	0.05	0.05	0.01	NS	NS
Slope	—	—	—	0.017	0.017	0.185	0.034	—	—
Intercept	—	—	—	0.570	0.528	0.452	0.367	—	—
Outer Adambulacral Spine									
Structure range (mm)	2.71–3.75	1.69–2.89	1.58–2.89	1.14–3.90	1.50–4.01	1.73–3.48	0.93–2.51	1.41–1.99	1.49–2.66
N	10	10	10	32	10	14	18	18	8
r	0.708	0.958	0.901	0.830	0.907	0.942	0.792	−0.231	0.856
P	0.05	0.01	0.01	0.01	0.01	0.01	0.01	NS	0.01
Slope	0.193	0.702	0.195	0.179	0.207	0.881	0.204	—	0.151
Intercept	1.408	1.047	0.823	1.11	0.967	0.753	0.741	—	1.26

Table 3.—Continued.

	Asterias forbesi			*Asterias vulgaris*			*Asterias rubens*		
	Rockaway	MAB	Shoreham	Gulf of Maine	MAB	Muscongus Bay	St. Andrews	W. Greenland	NW Iceland
				Inner Adambulacral Spine					
Structure range (mm)	2.47–3.48	1.70–2.94	1.66–3.33	1.17–4.32	1.56–4.02	1.56–3.76	1.22–2.51	1.21–1.99	1.41–2.49
N	10	10	10	32	10	14	18	18	8
r	0.569	0.913	0.974	0.828	0.949	0.942	0.841	0.231	0.948
P	NS	0.01	0.01	0.01	0.01	0.01	0.01	NS	0.01
Slope	—	0.191	0.762	0.197	0.218	0.881	0.207	—	0.135
Intercept	—	1.067	0.617	1.01	0.897	0.653	0.787	—	1.16
				Outer Oral Spine					
Structure range (mm)	3.48–4.92	2.24–4.23	2.34–3.94	1.08–5.67	1.99–4.15	2.49–4.40	1.24–3.73	1.41–2.90	1.49–4.98
N	10	10	10	28	10	14	18	10	8
r	0.772	0.256	0.913	0.563	0.750	0.712	0.789	0.881	0.964
P	0.01	NS	0.01	0.01	0.05	0.01	0.01	0.01	0.01
Slope	0.251	—	0.215	0.180	0.170	0.240	0.277	0.451	0.430
Intercept	1.812	—	1.627	1.749	2.07	1.51	1.008	0.100	0.355
				Inner Oral Spine					
Structure range (mm)	2.20–3.88	1.16–3.11	1.77–3.30	0.75–3.30	1.16–3.24	1.00–2.82	0.75–1.93	0.83–1.41	0.50–2.90
N	10	10	10	29	10	12	18	9	8
r	0.459	0.501	0.818	0.708	0.863	0.696	0.699	0.733	0.936
P	NS	NS	0.01	0.01	0.01	0.05	0.01	0.05	0.01
Slope	—	—	0.172	0.176	0.199	0.196	0.128	0.150	0.261
Intercept	—	—	1.158	0.462	0.266	0.706	0.447	0.428	0.068

The major ventral pedicellariae in *A. vulgaris* and *A. rubens* were longer and more pointed than those of *A. forbesi* (Table 2). Variation in the mean length of the pedicellariae did not differ significantly between populations of *A. vulgaris* (Gulf of Maine $\bar{x}$ = 0.68 mm; MAB $\bar{x}$ = 0.67 mm; Muscongus Bay $\bar{x}$ = 0.59 mm) and *A. rubens* (St. Andrews $\bar{x}$ = 0.60 mm; N.W. Iceland $\bar{x}$ = 0.77 mm) (Table 2). A weak but significant correlation with body radius (R) was noted in all populations of *A. vulgaris,* but only in the St. Andrews population of *A. rubens* (Table 3).

Skeleton and spines.—The main divisions of the *Asterias* skeleton (ambulacral, actinal, marginal, dorsolateral, carinal) are based on the principal longitudinal rows of inbricated ossicles, rigidly held together throughout life, except in the dorsolateral region where there is a loose, irregular connection between ossicles which forms an open meshwork. Details of ossicle morphology have not been adequately described in *Asterias* and a standard terminology has not been established. Consequently, many of the terms used in this study to describe skeletal structures follow those presented by Turner and Dearborn (1972) for the mudstar *Ctenodiscus crispatus,* in addition to those employed for *A. amurensis* (Fisher, 1930) and for *A. forbesi* and *A. vulgaris* by Hyman (1955).

Ossicle designates the large, calcarious structures which make up the basic rigid framework of the skeleton (Fig. 1A). Ossicles are typically quadrilateral, except in the dorsolateral region where 2–6 sided forms are found. They regularly have one or more *pustules,* mound-like elevations or *bosses,* with a central depression, the *spine pit,* for the attachment of the spine (Fig. 1A). A projection, or *process* from each side of the ossicle forms a suture or junction with a process from an adjacent ossicle either directly, by overlapping or underlapping, or indirectly by one or more narrow, bar-like, overlapping *plates.* These are flattened, calcareous structures, smaller than ossicles and usually without processes, pustules, or spines (Fig. 1B). Connections between the ossicles are called *arches* (Hyman 1955). Longitudinal rows of parallel arches were designated *channels* by Fisher (1930). In the spaces between the arches, the *fenestrae* (Hyman 1955), a membrane stretched between the walls of the arches, is perforated by a regularly arranged ring of a fairly specific number of openings for the papulae (Fig. 1B).

Actinolateral ossicles.—In all three species of *Asterias,* the actinolaterals usually do not overlap but form a row along the outer edge of the adambulacral ossicles (Figs. 2–4). Each actinolateral forms sutures internally with two or three underlying adambulacral ossicles. The actinolaterals are small, dorsoventrally thickened and have short, blunt anterior and posterior processes. In *A. forbesi* the dorsal (abactinal) process of each ossicle is elongated and forms a suture directly with the elongated ventral (actinal) process of the adjacent inferomarginal ossicle to form a small, round arch, within which the fenestra membrane bears a single ring of 4–6 openings (Fig. 1B). This row of arches forms the actinal channel of Fisher (1930).

In *A. vulgaris,* and *A. rubens,* the dorsal processes of the actinolateral ossicles are short and connect with the short, blunt ventral processes of adjacent inferomarginal ossicles by single plates, each of which may bear a spine in the proximal part of the arm (Figs. 3, 4). The arches thus formed are dorsoventrally oblong, larger than those in *A. forbesi,* and the membrane within the fenestra has a ring of 5–8 openings.

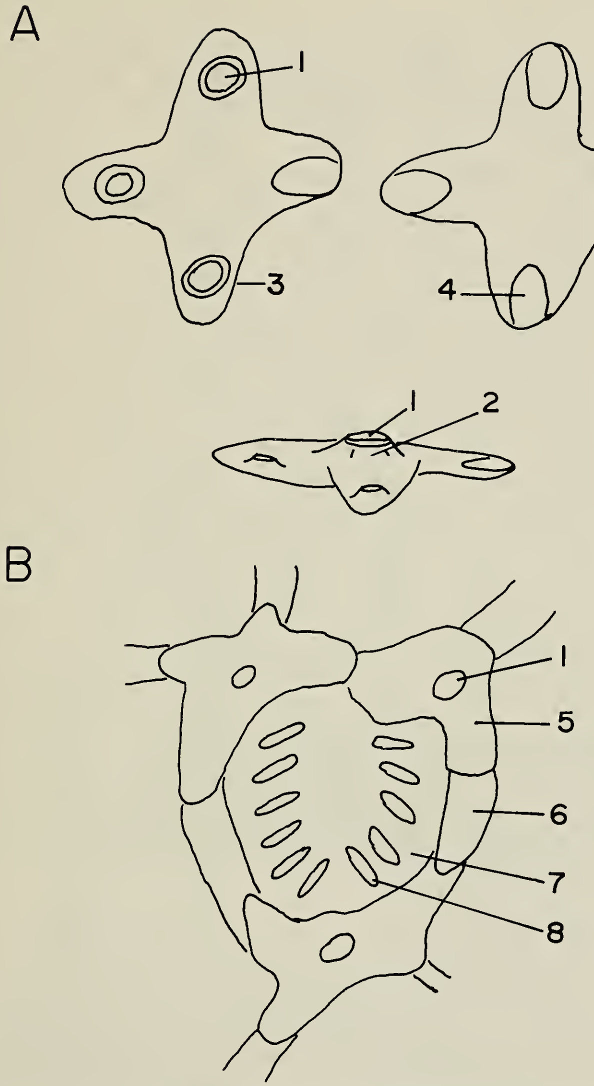


Fig. 1. *Asterias forbesi*. A, Diagrammatic views of a typical dorsolateral ossicle: outerside (above left), inner side (above right), side view (center). B, Diagram of a typical arch: 1, spine pit; 2, pustula; 3, process; 4, articulation depression; 5, ossicle; 6, plate; 7, membrane in fenestra; 8, opening for papula.

Inferomarginal ossicles.—The inferomarginal ossicles in all three species of *Asterias* form a prominent longitudinal row of large, closely imbricated, quadrilateral ossicles dorsal to the actinolaterals on the ventral (actinal) side of the animal. Each ossicle bears 3–4 pustules with slit-shaped, obliquely arranged spine pits, the most posterior of which lies nearest the ambulacral groove (Figs. 2–4). In *A. forbesi*, the dorsal (abactinal) processes of the interomarginal ossicles are elongated and pointed. Each articulates either directly, or by a single plate, with the ventral (actinal) process of the adjacent superomarginal ossicle (Fig. 2), thus forming a row of rounded arches, designated the intermarginal channel by Fisher

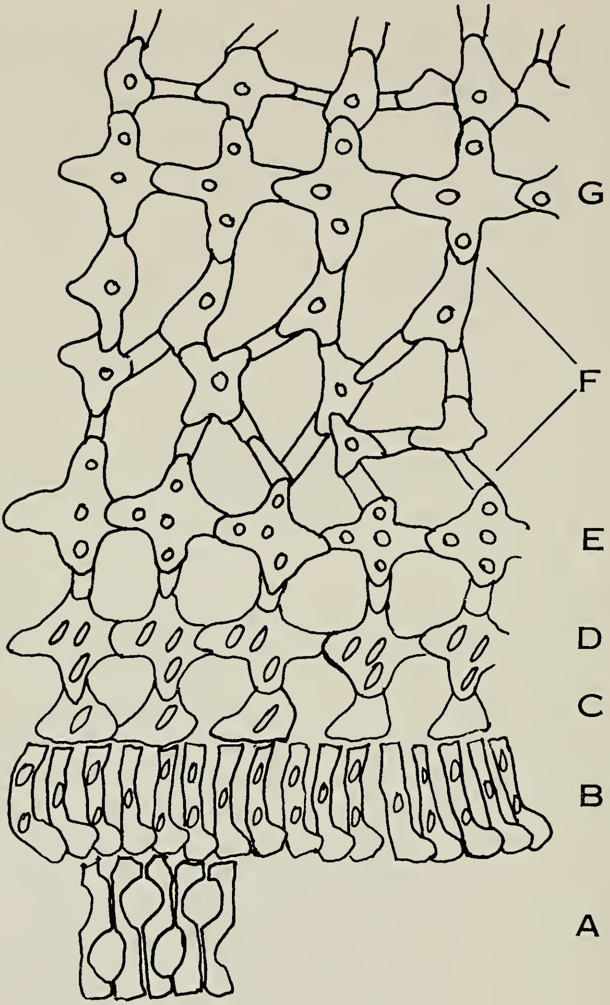


Fig. 2. *Asterias forbesi*. Semidiagrammatic drawing of a section of skeleton from proximal region of left side of animal (MAB). a, ambulacral ossicles; b, adambulacral ossicles; c, actinolateral ossicles; d, inferomarginal ossicles; e, superomarginal ossicles; f, dorsolateral ossicles and plates; g, carinal ridge. ×3.

(1930). The membrane within each fenestra contains an elongated ring of 8–10 openings.

In *A. vulgaris* and *A. rubens*, the dorsal processes of the inferomarginal ossicles are short and blunt and connect with the ventral processes of the superomarginals by at least one plate, thus forming oval arches which are larger than those of *A. forbesi*, especially in large animals (Figs. 3, 4). The membrane within each fenestra may have as many as 16–18 openings arranged in an elongated ring.

Superomarginal ossicles.—The superomarginal ossicles in all three species of *Asterias* form a strong, prominent longitudinal overlapping row along each margin (ambitus) of the ray dorsal to the inferomarginals (Figs. 2–4). Each ossicle has a

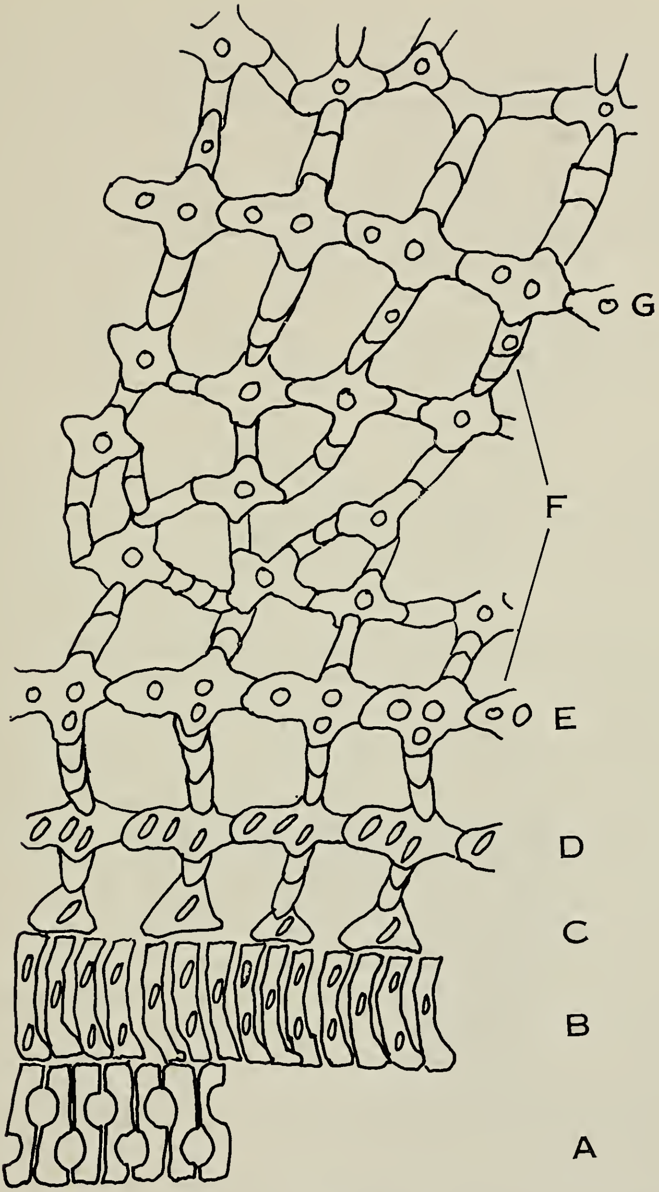


Fig. 3. *Asterias vulgaris*. Semidiagrammatic drawing of a section of skeleton from proximal region of left side of animal (MAB). a–g. See Fig. 2. ×3.

short anterior process which overlaps a longer posterior process of the preceding ossicle, a ventral (actinal) process which forms a suture with a dorsal (abactinal) process forming a junction, either directly or indirectly by one or more plates with an actinal process of the adjacent dorsolateral ossicle.

In *A. forbesi*, the superomarginal ossicles are smaller and flatter than the inferomarginals. Each ossicle has 3–5 round spine pits, one on the anterior process,

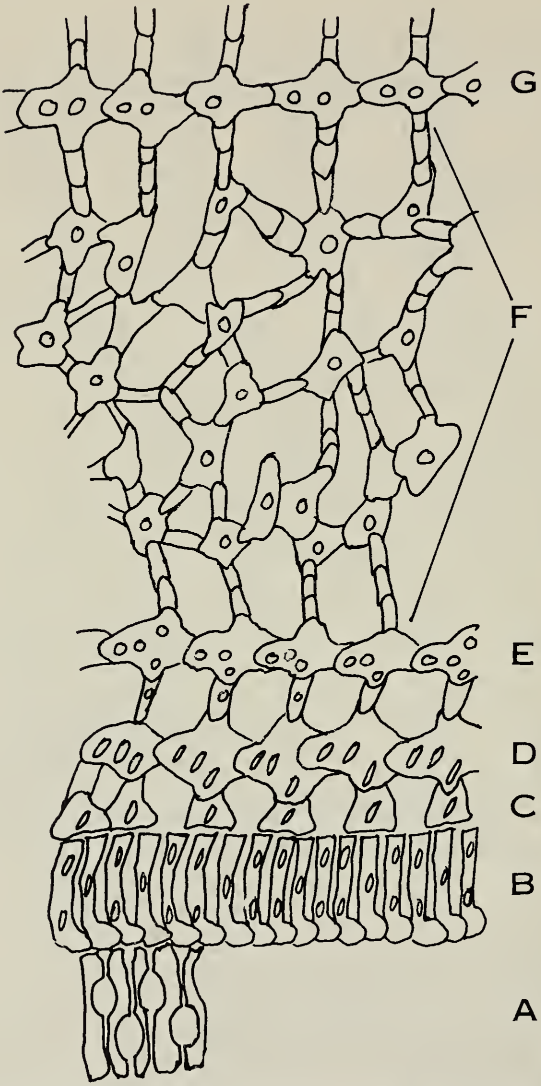


Fig. 4. *Asterias rubens*. Semidiagrammatic drawing of a section of skeleton from proximal region of left side of animal (St. Andrews). a–g. See Fig. 2. ×3.

one or two on the central boss, and one on each lateral process. Both of the lateral processes are elongated and articulate directly, or by a single short plate, with adjacent processes, thus forming two rows of arches. Each fenestra membrane contains 16–20 openings which are scattered throughout the entire area.

The anterior and posterior processes of the superomarginals in *A. vulgaris* and *A. rubens* are elongated, but the lateral processes are short and blunt (Figs. 3, 4). Each ossicle has three round spine pits, two on the central boss and one on the actinal process. Articulation with the adjacent dosolateral ossicles is by 1–3 elongated plates forming a row of large arches. The 16–20 openings in each fenestra membrane are arranged in a ring along the periphery of the arch.

Dorsolateral ossicles.—The dosolaterals in all three species of *Asterias* are typically irregular, rectangular (also 2–6 sided), non-overlapping ossicles whose processes articulate with processes from adjacent ossicles, either directly or by one or more plates, forming an irregular meshwork which is not symmetrical on the two sides of the arm. In smaller (2–3 cm) animals, ossicles show more regular anterior-posterior orientation to form 2–3 longitudinal rows on either side of the mid-dorsal carinals. In larger specimens, however, this arrangement is usually obscured by unequal lengthening of processes and/or plates. Each ossicle has at least one central pustule with a round spine pit, and frequently, one or two small spine pits are on the processes (Figs. 1A, 2–4).

In *A. forbesi,* the processes of the ossicles are elongated, tapered, and articulate directly, or by not more than one plate, with processes of adjacent ossicles to form small, firm, round arches. The membrane in each fenestra has 8–10 openings.

The processes of the dorsolaterals in *A. vulgaris* and *A. rubens* are shorter, more rounded and usually articulate with processes of adjacent ossicles by 1–3 plates, thus forming larger, more oblong and irregular arches which are quite long in large specimens. The 16–20 openings in the fenestra membrane are arranged in a ring around the periphery. In large specimens, additional openings may be present within the center of the ring.

Rarely, a skeleton was obtained from widely separated populations (Shoreham, *A. forbesi*; St. Andrews, *A. rubens*) which showed no discernible pattern in the arrangement of the ossicles of the abactinal side. They were small, nearly square with short, rounded processes, and no intervening plates between the processes. The arches were small and irregular, and the ossicles often were superimposed on other ossicles. These individuals had a very rigid and compact skeleton.

Carinal ossicles.—A median row of anterior-posteriorly aligned, overlapping carinal ossicles extends between the dorsolaterals from the edge of the disc to the tip of each ray, forming a central, dorsal ridge or keel (carinal ridge) in all three species of *Asterias* (Figs. 2–4). In *A. forbesi,* the lateral processes are elongated and pointed, forming sutures directly or by a single plate, with processes of adjacent dorsolaterals. A regular row of arches (channel) on either side of the carinal ossicles is usually evident in the skeleton. Each carinal ossicle has 3–4 pustules each with a round spine pit, arranged in a regular pattern; one on the anterior process, one or two directly posterior on the central body of the ossicle, and at least one small spine pit on each lateral process.

In *A. vulgaris* and *A. rubens,* the lateral processes of the carinal ossicles are short, blunt, and connect with adjacent dorsolateral processes by 2–3 overlapping plates forming a distinct row of arches on either side of the carinal ossicles. Each ossicle has one or two pustules, one in front of the other along the median ridge of the ossicle. This arrangement results in a more or less straight, single row of spines along the median dorsal ridge of the arm (the carinal ridge).

Adambulacral spines.—The adambulacral spines in the proximal region of the arms in all three species of *Asterias* were more or less regularly arranged in the typical *Asterias* alternating 1-2-1-2 etc. pattern (Mortensen 1929) forming three rows, an inner series along the edge of the ambulacral groove, a middle, and an outer row. Only spines from the inner and outer rows were measured and compared (Fig. 5A, B).

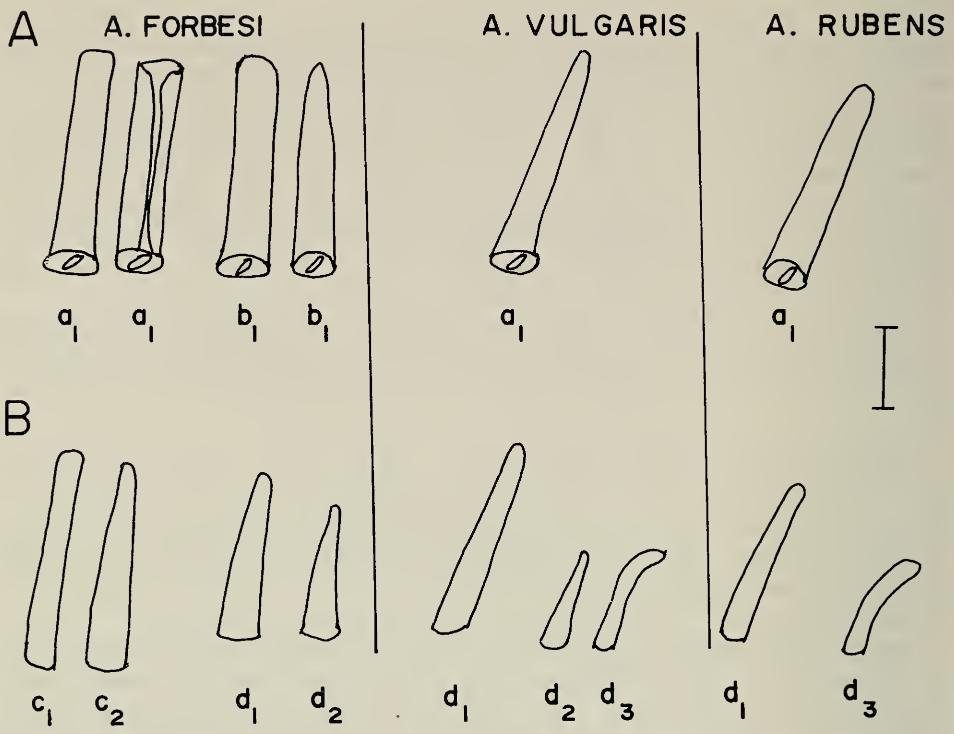


Fig. 5. Diagrammatic outer views of typical adambulacral and oral spines from *Asterias forbesi, A. vulgaris* and *A. rubens*. A, Adambulacral spines: a_1, typical form of outer spines; a_2, grooved form; b_1, typical form of inner adambulacral spines; b_2, pointed form. B, Oral spines: c_1, typical outer oral spine; c_2, pointed form; d_1, typical inner oral spine; d_2, pointed form; d_3, curved form. Scale line equals 1 mm.

The length of the inner and outer adambulacral spines in *A. forbesi* was comparable in the three populations studied (Table 2), ranging between a low of 1.58 mm to a high of 3.33 mm. In all populations, both inner and outer ambulacral spines were truncate, wide, ($\bar{x}$ = 0.66 mm) and flattened. The outer spines were frequently grooved on the outer side (Fig. 5). Thinner, more pointed spines were sometimes found among the more truncate forms.

In *A. vulgaris* and *A. rubens*, both inner and outer adambulacral spines were typically round, pointed (Fig. 5), and approximately within the same length range (1.33–2.93 mm) as those in *A. forbesi* in animals within the same size range (Table 2). The slightly narrower average width ($\bar{x}$ = 0.5 mm) of the *A. vulgaris* spines tended to give the rows a more delicate and crowded appearance, but in animals in the same size range, there was no significant difference among the species in the actual number of spines present per row. Double-pointed as well as flat, but ungrooved, truncate spines sometimes occurred along with the pointed spines.

The adambulacral spines in all species exhibited a strong correlation with body radius (R) (Table 3). While the slope for both types of spines was steep in all populations (Table 3), the Muscongus Bay population (*A. vulgaris*) showed the steepest slope for both inner and outer adambulacral spines (Table 3).

Oral spines.—The inner and outer oral spines in *A. forbesi* were about the same length or slightly longer than the adambulacral spines (Table 2), and resembled them in shape, but were not grooved. Occasionally an animal was found with larger and more pointed oral spines. Significant correlation between length of the outer oral spines and body radius (R) was evident in the Rockaway Beach ($r = 0.772$) and Shoreham ($r = 0.913$) populations (Table 3) but not in those from the MAB ($r = 0.256$). Inner oral spines showed significant size correlation only in the Shoreham population ($r = 0.818$) (Table 3). There was no significant difference in the three populations in the mean ratio between length of inner/outer oral spines (Rockaway Beach $\bar{x} = 0.72$ mm; Shoreham $\bar{x} = 0.76$ mm; MAB $\bar{x} = 0.74$ mm).

In both *A. vulgaris* and *A. rubens*, however, there was a difference in size and shape between the inner and outer oral spines (Table 2). The inner oral spines were shorter, slightly curved, narrow, and sharply pointed while the outer oral spines were longer, straight, narrow, round, and pointed (Fig. 5C, D). Neither truncate nor grooved oral spines were found in any population. The correlation of body radius (R) and oral spine length was significant in all populations (Table 3). The mean inner/outer spine ratios in *A. vulgaris* (Gulf of Maine $\bar{x} = 0.58$; Muscongus Bay $\bar{x} = 0.54$; MAB $\bar{x} = 0.516$) were lower than those in *A. forbesi*, but not significantly different from *A. rubens* (St. Andrews $\bar{x} = 0.46$, West Greenland $\bar{x} = 0.53$; Northwest Iceland $\bar{x} = 0.54$). There was greater difference in length between the inner and outer oral spines in both *A. vulgaris* and *A. rubens* than was found in *A. forbesi*.

Color.—Color patterns and intensities in both *A. forbesi* and *A. vulgaris* showed wide variation between different stations but in each species, a distinct intrapopulation color pattern tended to predominate in a given locality (Coe 1912). In *A. vulgaris* from the MAB, the basic color of the abactinal surface was yellowish to reddish brown with varying amounts of bluish purple ranging from a narrow band along the carinal ridge to being suffused over the aboral surface from the dark purple disc to the tips of the arms, hence the name of ''purple starfish.'' Specimens of *A. vulgaris* from deep locations (200 m) from the Gulf of Maine were cream colored to light tan. Animals from Muscongus Bay ranged from light brown to deep reddish brown and purplish blue. Spines on animals from all locations were light yellow and not conspicuous against the pale color of the dermis.

Asterias forbesi from the MAB were reddish and abactinal markings were darker blue than those of the lighter, yellowish colored, sympatric *A. vulgaris*. Live Rockaway Beach animals were usually a uniform, deep red, but occasionally lighter forms were found. Light (white or yellowish) colored spines outlined the arms and frequently formed a definite carinal ridge. Irregular longitudinal rows of dorsolateral spines often made a distinct pattern against the dark color of the aboral surface.

Discussion

Characters that showed significant size-relationship to body radius (R) included inner and outer adambulacral spines and inner and outer oral spines in all three species; and the tapering of the arm (a/b ratio) in *A. vulgaris* (except from Muscongus Bay), and *A. rubens*.

Characters that did not show significant size relationships in any species included dorsal pedicellariae; ventral pedicellariae; madreporites.

Characters that were significantly different in size and/or shape among the species included ventral pedicellariae; inner oral spines; inner and outer adambulacral spines (shape); ossicles (shape); madreporite (shape).

Some of the structures which show correlation between size and body radius (R) are associated with functions which increase with growth of the animal. The adambulacral spines, for example, extend over the ambulacral canal and protect the underlying podia (Hyman 1955). As the canal widens with growth of the animal, the spines lengthen to continue coverage of the canal. The oral spines, which cover the oral region, also lengthen with increase in body size to maintain their protective function. Tapering of the arms (greater a/b ratio), on the other hand, in *A. vulgaris* and *A. rubens* increases as the animal grows due to the lengthening of the greater number of connections (plates) between the ossicles in the proximal region of the arms than in the distal portion. In *A. forbesi* where growth of the arm is more uniform throughout its length, there is less tapering (a lower a/b ratio).

Ventral and dorsal pedicellariae and the madreporite, which are not significantly size-related, serve essential functions which do not change as the animal grows. These structures attain their optimal size at an early age of the animal and do not change significantly.

Structures (ventral pedicellariae, madreporite) which show significant differences among the three species in size and/or shape have long been considered diagnostic. Coe (1912) suggested that the difference in size and shape of the major ventral pedicellariae in *A. forbesi* and *A. vulgaris* was the most reliable criterion for species identification. Comparison of measurements of these structures from widely separated populations justifies this conclusion. While the shape of the ventral pedicellariae is similar in *A. vulgaris* and *A. rubens*, there are differences in size. Ventral pedicellariae from *A. vulgaris* of Muscongus Bay have a slightly lower size range than (other) *A. vulgaris* from the Gulf of Maine or MAB. However, this range falls within that of ventral pedicellariae from the St. Andrews population of *A. rubens*, but is shorter than those of *A. rubens* from N.W. Iceland. Variations in size would therefore appear to be population related and not species specific.

The difference in the color of the madreporites in *A. forbesi* and *A. vulgaris* has usually been considered more significant for species identification than shape and size (Coe 1912; Aldrich 1956; Gray *et al.* 1968). However, the greater convexity of the structure in *A. forbesi* was described in detail by Verrill (1866). This difference in shape is slight but significant and may not be readily detected except by comparison of measurements.

Some structures which are significantly different in *A. forbesi* and *A. vulgaris* are variable and have not been listed as diagnostic. In this group are included the outer and inner adambulacral and outer and inner oral spines. Verrill (1866) and later Clark (1904) noted the predominance of blunt, grooved adambulacral spines in *A. forbesi* compared to the slender, often pointed spines of *A. vulgaris*. In the specimens available for the present study, the shape of most of the adambulacral spines of a specimen corresponded to this distinction, although both types of spines were often found together in the same animal. This situation is not an indication of hybridization, but rather the expression of a polymorphic structure (Schopf and Murphy 1975).

Clark (1904) noted that the oral spines in *A. forbesi* and *A. vulgaris* were "not peculiar." However, in the animals of the present study, the inner oral spines showed variability both in size and shape. In *A. vulgaris* and *A. rubens,* the inner oral spines were on the average shorter than the outer oral spines and usually curved, while in *A. forbesi,* the inner orals were straight and approximately equal in length to the outer orals. The difference between the lengths of the inner orals measured in *A. vulgaris* and in the few representatives of *A. rubens* available suggest that it would be interesting to evaluate the mean size of these structures between and within larger samples of both *A. vulgaris* and *A. rubens* populations. When inner oral spines of *A. vulgaris* from all areas were compared with those of the St. Andrews population only, the difference between the mean size was slightly greater in *A. vulgaris* ($\bar{x}$ = 1.85 mm) than in the *A. rubens* population ($\bar{x}$ = 1.33 mm) and statistically significant at the P = 1.0 level but not at the P = 0.5 level.

If the observations of Fisher (1930) on *A. amurensis,* the North Pacific species, are compared with the present results, the resemblance, especially in the adambulacral spines and the inner oral spines, to the North Atlantic species is evident. Fisher described the adambulacral spines of *A. amurensis* as long, compressed, tapered, bluntly pointed and grooved, a description resembling that for the adambulacral spines usually found in *A. forbesi.* The inner oral spines were described as curved, tapering and blunt, the shape which is comparable to that regularly found in *A. vulgaris* and *A. rubens* and infrequently in *A. forbesi.* These, and other close resemblances suggest a common ancestor for the species.

Descriptions in the literature of the skeletal structures of *Asterias* spp. are generalized and incomplete. Mortensen (1927) called the dorsal skeleton of *A. rubens* faintly developed. Verrill (1866) distinguished the skeleton of *A. forbesi* from that of *A. vulgaris* by the larger number of plates in the dorsal area which gave it a "stout" condition. In *A. vulgaris,* the lateral plates were described as separated by large spaces and were connected by plates broken into distinct pieces. Hyman (1955) recognized a basic, reticulate pattern but the diagram she presented was reproduced from Fisher (1928) and was based on Pacific forms of *Asterias.* Gray *et al.* (1968) called the skeleton of *A. forbesi* a mosaic of interlocking plates of ossicles, and that of *A. vulgaris* a network of narrow, bar-like plates forming a weak skeleton.

Basically, the skeletons of the three species of *Asterias* are equally strong and well developed, and the arrangement of the main ossicles all follow the same general pattern (Figs. 2–4). The essential differences in the skeletal structure among the species are the shape of the lateral processes (long, pointed in *A. forbesi*; short, blunt in *A. vulgaris* and *A. rubens*), and the greater number of plates between the processes in *A. vulgaris* and *A. rubens.* These differences are associated with the rigidity, shape, and tapering (a/b ratio) of the arms. In *A. vulgaris* and *A. rubens,* where the plates elongate during the growth of the animal, lateral distance between the ossicles, especially in the dorsolateral region, increases and forms the open meshwork with elongate fenestrae resulting in a more flaccid skeleton. This less rigid arrangement also gives the arms a flatter and wider appearance, especially in the proximal portion. However, in the distal part of the arms, the plates between the processes remain small or absent forming a tight, rigid meshwork and producing the tapering of the arms and an increased a/b ratio. In *A. forbesi,* on the other hand, where the skeletal meshwork is formed by sutures between elongated processes with only one or no connecting plates, a more rounded and rigid framework results throughout the length of the arm giving a lower a/b ratio. Elongation of the several plates between processes in *A. vulgaris* and *A. rubens* may be one explanation for these species attaining a greater size than is possible in *A. forbesi* where growth of the skeleton is limited principally to elongation of the processes directly connecting the ossicles.

Local populations of *A. rubens* with rigid, straight and rounded arms have been described from several locations (N.W. Iceland, Heding 1892 museum label; Scandinavia, Masden, pers. comm.; Great Britain, Vevers 1947). These morphs may result from variations in the size and/or number of the connecting plates. Similarily, the *forbesi*-like animals from the Muscongus Bay population may be juveniles of *A. vulgaris* in which the plates in the proximal dorsolateral region have not elongated. No specimens of otherwise typical *A. forbesi* have been described as having flaccid skeletons. Hence, the invariably rigid skeleton would appear to have become a genetically fixed characteristic in *A. forbesi.*

The more frequent occurrence of a prominent carinal ridge in *A. vulgaris* and *A. rubens* than in *A. forbesi* may also be related to the greater dependence of the more flexible skeletons on a stronger, more rigid central keep for support.

Our observations, as well as those of all other workers, clearly demonstrate distinctive differences between *Asterias forbesi* and *A. vulgaris,* differences both at the morphological and structural as well as the physiological and ecological levels. These differences are clearcut in spite of marked genetic similarity (Schopf and Murphy 1975). The co-occurrence of such closely-related congeners in the shallow shelf of the N.W. Atlantic is rather remarkable, particularly in view of the overlapping ecological and spatial niches of the species, and the probable high degree of competition in areas of sympatry, and the generally low overall diversity of asteroids in the Middle-Atlantic continental shelf of the NW Atlantic. We attempt to provide a historical hypothesis to account for the co-occurrence of these species in the following section.

The specific identity of *A. vulgaris* vis-a-vis *A. rubens* is not resolved in this study; moreover, descriptive analyses of morphological characteristics probably can not produce a definitive answer. Our results indicate that populations of *A. vulgaris* from the Gulf of Maine and MAB differ from the St. Andrews population of *A. rubens* in skeletal structures such as the dorsal and ventral pedicellaria (Table 2), but that these small differences disappear in significance when the Muscongus Bay population of *A. vulgaris* and the N.W. Iceland population of *A. rubens* are included in the comparison. Thus, from a strict descriptive taxonomic viewpoint, we can provide no basis for maintaining *A. vulgaris* as distinct from *A. rubens,* even though populations of *A. vulgaris* are geographically isolated from *A. rubens.* Even assuming the questionable existence of a permanent population of *A. rubens* in S.W. Greenland, the directional flow of surface currents along the W. Greenland coast in the Davis Strait, and the absence of *Asterias* populations in Labrador, imply essentially complete geographical isolation of populations of *A. vulgaris* in the Gulf of St. Lawrence from the nearest major concentrations of *A. rubens* in Iceland.

Since the major difference between the geographical zone of *A. rubens* in the N.E. Atlantic and *A. vulgaris* in the N.W. Atlantic is the thermal environment rather than the structure of biotic communities, we would predict that genetic differentiation would involve primarily physiological rather than morphological traits—and these have not been investigated. Until this is done, we believe that the most parsimonious approach to the question of taxonomy would be to conserve the status quo, i.e., while recognizing the very close genetic and taxonomic relationships between *A. vulgaris* and *A. rubens*, to continue to consider them as separate species until more relevant aspects of their biology can be evaluated.

Hybridization Between *Asterias forbesi* and *Asterias vulgaris*

Hybridization between *A. forbesi* and *A. vulgaris* is often assumed to occur, and to account for the existence of individuals with external characters intermediate between typical *A. forbesi* and *A. vulgaris*. Given the genetic similarity demonstrated by Schopf and Murphy (1975), such hybridization might be expected. However, evidence for hybridization is very weak; and, to the best of our knowledge, is limited to the occurrence of morphological "intermediates." Even the work of Ernst (1967), cited as containing experimental evidence for hybridization, contains no conclusive evidence proving that hybridization occurs under natural conditions.

After examining thousands of individuals of both species from the Middle Atlantic continental shelf, including many from the geographical zone of sympatry, we have never observed an individual which could not be assigned with confidence to one or the other species. While it is possible that hybrids may occur in shallow waters near Cape Cod, this was discounted by Clark (1923:235), who stated unequivocally that ". . . if such hybrids occur they must be very rare, for there are no authentic specimens on record or extant, as far as I know." Moreover, sympatric populations of *A. forbesi* and *A. vulgaris* which occur in the SW Gulf of Maine (Isle of Shoals area) are distinguishable morphologically and ecologically (Hulbert 1980, pers. comm.).

The possibility that *A. forbesi*-like animals occurring in embayments along the Maine Coast may represent hybrids seems unlikely to us. Inshore populations of typical *A. forbesi* occur in the SW Gulf of Maine and south of Cape Cod, but not on Georges Bank or the inner shelf of the Gulf of Maine, where summer bottom temperatures remain below 15°C (Franz *et al.* 1981). More likely, these unique coastal populations of *A. forbesi*-like seastars are either morphological variants of *A. vulgaris* (as is the case in the Muscongus Bay intertidal population reported in this paper) or relict populations of *A. forbesi* which are retained within and restricted to shallow coastal embayments. Relict populations of oysters (*Crassostrea virginica*) occur in the Sheepscot Estuary, and McAlice (1981) has presented evidence for the existence of relict populations of other estuarine transhatteran invertebrates in Maine coastal estuaries. If relict populations of *A. forbesi* date from the Hypsithermal Period (7000–9000 years BP), it would not be surprising if they had undergone a degree of morphological and genetic differentiation from the main body of *A. forbesi* populations further south.

The Origin of *Asterias forbesi* and *Asterias vulgaris*

Several workers have speculated on the origins of *Asterias forbesi* and *A. vulgaris*. A. H. Clark (1923) observed that no species of *Asterias* ranged farther south than *A. forbesi,* indicating to him the likelihood that *A. forbesi* evolved from *A. vulgaris* as a general consequence of adapting to warmer waters. No mechanism of speciation was suggested.

More recently, Schopf and Murphy (1973) postulated that *A. vulgaris* evolved from *A. forbesi* during the Pleistocene as a result of geographic isolation brought about by the emergence of Georges Bank during the last glacial episode. This land barrier effectively isolated northern populations from the remaining southern populations. Presumably, natural selection favoring individuals living in the cold and increasingly harsh environment brought about the evolution of *Asterias vulgaris.* With the submergence of this land barrier during the Holocene, the recently differentiated "semispecies" again converged to produce the partially overlapping species which presently exist.

While this hypothesis does provide for allopatric speciation and accounts for the major thermal adaptations of the species, as well as their close genetic relationship, there are several problems. The time period allocated for speciation may be too short—roughly 7000 years (the period between the minimum sea level, *ca* 15,000 years BP, to about 7000 years BP when rising sea levels would have again united the separated areas). Another, more serious, objection is presented by the severity of environmental conditions believed to have existed on the coastal shelf north of 42°N during glacial periods. While many questions remain, recent studies (McIntyre 1976) indicate that essentially arctic conditions prevailed during glacial maxima. *Asterias vulgaris* presently does not live in arctic waters. It reaches its northern limit in the Gulf of St. Lawrence, and is not found in the Strait of Belle Isle (Grainger 1966). This suggests that *A. vulgaris* could not have persisted north of 42°N, i.e., north of the land barrier, during glacial maxima. Schopf and Murphy's hypothesis also fails to account for, or explain the relationships between the NW Atlantic species and the North Pacific and NE Atlantic congeners *A. amurensis* and *A. rubens.*

Tortonese (1963) suggested that *Asterias rubens* (including, in his opinion, *A. vulgaris*), *A. forbesi* and *A. amurensis* comprise a superspecies, i.e., a set of allopatric species sharing a common ancestor which, in his opinion, was probably *A. rubens.* He further suggested that the center of dispersion was the North Atlantic, and that *A. forbesi* and *A. amurensis* differentiated from *A. rubens* (or a closely-related ancestor) following westward dispersion into the NW Atlantic (*A. forbesi*) and, either eastward dispersion across Siberia or westward through the Canadian Arctic into the North Pacific (*A. amurensis*). He provided no explanation as to how or when such dispersions may have occurred or under what conditions *A. forbesi* differentiated from sympatric *A. vulgaris.*

While agreeing with Tortonese that the species of *Asterias* comprise a superspecies (*sensu* Mayr 1963) we do not agree with his suggestion of an Atlantic origin. While an Atlantic origin of some boreal North Pacific invertebrate species is probable (Durham and MacNeil 1967), there is an emerging consensus that the amphiboreal fauna of the North Atlantic is largely derived via transarctic dispersals in the Pliocene (or, in some cases, earlier) (Durham and MacNeil 1967; Franz *et al.* 1980; Franz *et al.* 1981).

We suggest that the common ancestor of all North Pacific and North Atlantic *Asterias* probably lived in the North Pacific during the Miocene. After the opening of the Bering Straits at the end of the Pliocene, the climate warmed and this species, or one of its descendants, migrated from the North Pacific into the North Atlantic via the Arctic, entering the North Atlantic via the straits and sounds of the Canadian Archipelago and/or Norwegian Sea (Nesis 1961).

As populations spread southward along both coasts of the North Atlantic, geographic and genetic connections were broken, possibly facilitated in the late Pliocene, by the closure of the Isthmus of Panama and the development of the Labrador Current system. These events brought about a strengthening and modification of the axis of the Gulf Stream (Berggren and Hollister 1977) and provide an explanation for environmental changes in the Atlantic which, as argued by Franz and Merrill (1980), may account for the evolution of a separate boreal fauna in the North Atlantic, as well as the ecological separation of NW Atlantic and NE Atlantic *Asterias* populations to produce *A. forbesi* and *A. rubens*.

During one or more of the extensive interglacial periods, or possibly as late as the Holocene, *A. rubens* may have extended its range westward along the island arc of the North Atlantic (Faroes, Iceland, Greenland) and via the Davis Strait to Labrador and New England, becoming partly sympatric with *A. forbesi*. During glacial maxima, *A. forbesi* would have been displaced southward (as would have *A. rubens* on the European coast). Possibly, relict populations of *A. rubens* remaining in the NW Atlantic may have been able to survive these periods in the NW Atlantic by extending their ranges southward into the Middle Atlantic Bight. Alternately, the westward range extensions of *A. rubens* into the NW Atlantic may have occurred in the Holocene. In either case, these relict populations of *A. rubens* in the NW Atlantic are now known as *A. vulgaris*.

Evidence to support this hypothesis is circumstantial. The diversity of asteroids in the North Pacific is very great, leading to the conclusion that this area marks the center of origin of the Asteridae. Since species of *Asterias* do not occur in subtropical or tropical waters, it follows that North Atlantic populations were derived from North Pacific ancestors via transarctic migration. Caenozoic migrations are thought to have occurred at least twice: the well-documented late Pliocene/early Pleistocene Beringian Transgression, 1 million years BP (Allison 1978); and a less well documented late Miocene transgression which is substantiated primarily on zoogeographic evidence (MacNeil 1965; Durham and MacNeil 1967).

Evidence for the westward range extensions of boreal invertebrates during the Pleistocene is summarized in Franz and Merrill (1980). In spite of the North Atlantic Drift, some European species have extended their ranges westward via Iceland to Greenland (Kraeuter 1974). Populations of *A. rubens* presently occur abundantly in Iceland and, at least periodically, in West Greenland (Einarsson 1948). Since *A. rubens* could not have survived in these areas during the Wisconsin glacial maximum, it follows that *A. rubens* extended its range westward during the Holocene. It seems reasonable to assume that if *A. rubens* can extend its range westward as far as West Greenland during present conditions, it may have been able to extend its range into the Davis Strait and to Labrador, and hence southward to New England, during the unusually warm conditions which prevailed during the Hypsithermal. Alternately, if the westward range extension occurred earlier, e.g., during a late interglacial, *A. rubens* may have been able to survive glacial conditions in the Middle Atlantic zone of the NW Atlantic, based on the analysis of environmental conditions in this zone during the Wisconsin glacial maximum (McIntyre 1976). We have no basis for distinguishing between these alternatives.

Unfortunately, we are unable, at this point, to propose a definitive procedure to falsify the hypotheses discussed above. Ultimately, when taxonomic relationships within the *A. amurensis* complex are more clearly established, it may be possible to investigate evolutionary relationships among geographical groups of *Asterias* using both biochemical (isoenzyme) and morphological (cladistic) approaches.

Acknowledgments

We thank Dr. Arthur E. Merrill of the National Marine Fisheries Service (ret.) for supplying the starfish from the Groundfish Surveys (1978 and 1979), and P. J. Fallon, Jr., for samples of *A. forbesi* from Shoreham, New York. We also appreciate the kindness of Dr. Chris Todd, University of St. Andrews, Scotland, and Dr. F. Jensensium Madsen of the Zoologisk Museum, University of Denmark, Copenhagen, for providing specimens of *A. rubens.* This research was supported in part by a grant from the City University of New York (PSC-CUNY Grant Nos. 13315, 14059).

Literature Cited

Aldrich, F. R. 1956. A comparative study of the identification characteristics of *A. forbesi* and *A. vulgaris.*—Notulae, Natural Academy of Natural Sciences of Philadelphia 285:1–3.

Allison, R. C. 1978. Late Oligocene through Pleistocene molluscan fauna in the Gulf of Alaska region.—The Veliger 21(9):171–188.

Berggren, W. A., and C. O. Hollister. 1977. Plate tectonics and paleocirculation—a condition in the ocean.—Tectonophysics 38:11–48.

Clark, H. L. 1904. Echinoderms of the Woods Hole region.—Bulletin of the United States Fish and Wildlife Service 1902 22:545–576.

———. 1923. The distribution and derivation of some New England echinoderms.—American Naturalist 57:229–237.

Coe, W. R. 1912. Echinoderms of Connecticut.—Connecticut State Geological and Natural History Survey, Bulletin 19, 152 pp.

Durham, J. W., and F. S. MacNeil. 1967. Coenozoic migrations of marine invertebrates through the Bering Strait Region, *in* The Bering Land Bridge (ed. David M. Hopkins), Stanford University Press, pp. 327–349.

Einarsson, E. 1948. Echinoderms.—Zoology of Iceland 4(70):1–67.

Ernst, E. J. 1948. The distribution, ecology, environmental behavior and possible hybridization of the sea stars *Asterias forbesi* (Desor) and *Asterias vulgaris* Verrill in the subtidal zone of Long Island.—Ph.D. Dissertation, New York University (Univ. Microfilms 468-6060, 84 pp.).

Fisher, W. K. 1928. Asteroidea of the North Pacific and adjacent waters. Pt. 2. Forcipulata.—Bulletin of the United States National Museum 76, 245 pp.

———. 1930. Asteroidea of the North Pacific and adjacent waters. Pt. 3. Forcipulata.—Bulletin of the United States National Museum 76, 356 pp.

Franz, D. R., and A. S. Merrill. 1980. The origins and determinants of molluscan faunal groups on the shallow continental shelf of the Northwest Atlantic.—Malacologia 19(2):227–248.

———, E. K. Worley, and A. A. Merrill. 1981. Distribution patterns of common seastars of the Middle Atlantic Continental Shelf of the Northwest Atlantic (Gulf of Maine to Cape Hatteras).—Biological Bulletin 160:394–418.

Grainger, E. H. 1966. Seastars (Echinodermata: Asteroidea) of Arctic North America.—Fisheries Research Board of Canada, Bulletin 152, 70 pp.

Gray, I. E., M. Downey, and M. J. Cerame-Vivas. 1968. Sea stars of North Carolina.—United States Fish and Wildlife Service Fisheries, Bulletin 87(1):127–163.

Hulbert, A. W. 1980. The functional role of *Asterias vulgaris* Verrill (1866) in three subtidal communities.—Ph.D. Thesis, University of New Hampshire, 174 pp.

Hyman, L. H. 1955. The invertebrates. Vol. IV. Echinodermata. McGraw-Hill Book Co., Inc., New York, 763 pp.

Kraeuter, J. N. 1974. Offshore currents, larval transport, and establishment in southern populations of *Littorina littorea* along the U.S. Atlantic coast.—Thalassia Jugoslavica 10(1/2):150–170.

MacNeil, F. S. 1965. Evolution and distribution of the genus *Mya* and Tertiary migrations of Mollusca.—United States Geological Survey Professional Paper 483-G, 51 pp.

Mayr, E. 1963. Animal species and evolution.—The Belknap Press of Harvard Univ. Press, 797 pp.

McAlice, B. J. 1981. On the post-glacial history of *Acartia tonsa* (Copepoda: Calanoida) in the Gulf of Maine and the Gulf of St. Lawrence.—Marine Biology 64(3):267–272.

McIntyre, A., *et al.* [35 others Authors] 1976. Glacial North America 18,000 years ago: A CLIMAP reconstruction.—Geological Society of America 145:43–75.

Mortensen, T. H. 1927. Handbook of the echinoderms of the British Isles.—Oxford University Press, London, 471 pp.

Nesis, K. N. 1961. The routes and periods and formation of the interrupted area of distribution of amphiboreal species of marine bottom animals.—Okeanologiya 1(5):894–903.

Schopf, T. J. M., and L. S. Murphy. 1973. Protein polymorphism of the hybridizing seastars *Asterias forbesi* and *Asterias vulgaris* and implications for their evolution.—Biological Bulletin 145:587–597.

Tortonese, E. 1963. Differenziazione geografica e superspecie nel genere *Asterias* (Echinodermata).—Monitore Zoologica Italiano 80–81:212–221.

Turner, R., and J. H. Dearborn. 1972. Skeletal morphology of the mud star, *Ctenodiscus crispatus* (Echinodermata: Asteroidea).—Journal of Morphology 138(2):239–262.

Verrill, A. E. 1866. On the polyps and echinoderms of New England with descriptions of new species.—Proceedings of the Boston Society of Natural History 10:345–349.

Vevers, H. G. 1949. The biology of *Asterias rubens* L. 1. Growth and reproduction.—Journal of the Marine Biological Association of the United Kingdom 28:165–187.

Walker, C. W. 1974. Studies on the reproductive systems of the seastars. I. The morphology and histology of the gonads of *Asterias vulgaris*.—Biological Bulletin 147:661–677.

Biology Department, Brooklyn College/CUNY, Brooklyn, New York 11210.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 548–559

NOTES ON THE FROG GENUS *CYCLORAMPHUS* (AMPHIBIA: LEPTODACTYLIDAE), WITH DESCRIPTIONS OF TWO NEW SPECIES

W. Ronald Heyer

Abstract.—Examination of the types of *Telmatobius duseni* Andersson indicates that a new name is required for the taxon previously referred to as *Cycloramphus duseni*. The name *Cycloramphus izecksohni* is proposed for this taxon. A second new species, *Cycloramphus cedrensis,* is described for material recently collected near Rio dos Cedros, Santa Catarina, Brazil. New distributional data are reported for *Cycloramphus valae* and the advertising call and larva of *C. valae* are described for the first time.

Information has recently become available that extends our knowledge of the systematics and natural history for members of the frog genus *Cycloramphus*. The purpose of this paper is to report these data, which augment those presented in a recent revision (Heyer 1983).

Materials and Methods

Morphological data were taken and are reported on in a standard manner (e.g., Heyer 1983). Advertisement calls were recorded on a Sony TCM-280 cassette recorder using a Sennheiser K30 microphone. Calls were analyzed on a Kay Sonagraph 6061B, narrow filter, AGC in the off position. Call parameters are based on analysis of 5 calls of *C. cedrensis* and 3 calls each of *C. valae* from the two localities reported.

The Identity of *Telmatobius duseni* Andersson

I had the opportunity to examine two syntypes of *Telmatobius duseni* after my previous study (Heyer 1983) was completed. In that study, the name *duseni* was applied to specimens mostly from the State of Santa Catarina, with one outlier locality in the State of São Paulo (Heyer 1983: fig. 42). Examination of the types of *T. duseni* indicates they do not represent the species I referred to as *duseni*.

The types show that *duseni* is a member of the *C. fuliginosus* group; that is, the species has toe webbing and dorsal warts and tubercles (Fig. 1). They further resemble the species previously referred to as *C. duseni* and differ from all other members of the *C. fuliginosus* group in small size (types of *T. duseni* males 31.3, 33.5 mm SVL), in having a dorsum with shagreen and tubercles with the large tubercles sometimes arranged in regular rows (as in Fig. 1), and the posterior surface of the thigh with distinct light spots (as in Fig. 1). The types of *T. duseni* differ significantly from the species previously referred to as *C. duseni* in the amount of toe webbing. The types of *T. duseni* have reduced webbing (webbing formula of right foot of lectotype: I trace II 1¾–3^+ III 2¼–3½ IV 3⅓–2^+ V), the species previously referred to as *C. duseni* has moderate toe webbing. The web-

Fig. 1. Lectotype of *Telmatobius duseni* Andersson, dorsal and ventral views.

bing formula for the outer side of toe IV in the types of *T. duseni* ranges from 3½ to 4^-, whereas webbing in the species previously referred to as *C. duseni* ranges from 2½ to 3^+, as an example. Such a difference is indicative of species level differentiation in the genus *Cycloramphus* (Heyer 1983).

At present, the species *Cycloramphus duseni* (Andersson) is known only from the type series. The type locality, "Brazil, Parana, Sierra do mar; Ypiranga, in crevices and cracks in the vertical cliffs along the railway, 3/9 1911," (Andersson 1914:2) was incorrectly plotted in the review paper (Heyer 1983) as discussed in Heyer and Maxson (1983). In order to clarify the precise locality where Dusén collected the specimens named by Andersson, Dr. P. E. Vanzolini kindly made arrangements for me to interview officials of the Rede Ferroviária Federal S/A in Curitiba, Paraná. At the railroad office I learned that there is no railway station named Ipiranga on the railway line from Curitiba to Paranaguá. Rather, Dusén collected at Casa Ipiranga, a house on the railway line where the railroad construction engineers lived during the railroad line construction. The Casa Ipiranga today is a state historical preservation site (patrimonio), that can be reached only by railroad. Although Casa Ipiranga is not a regular railroad stop, the officials of the railway arranged an overnight visit for me on 7 January 1982. Vertical cliffs where water was seeping and dripping were found along the railway line. No *Cycloramphus* were found at night along the vertical cliffs or along the stream near the house. The habitat looked suitable for *Cycloramphus*; a longer trip earlier in the wet season would likely yield positive results.

For nomenclatural stability, I hereby designate the 31.3 mm SVL specimen, Naturhistoriska Rijksmuseet, Stockholm No. 1606 (Fig. 1), as the lectotype of *Telmatobius duseni* Andersson. The Stockholm Museum has two of the original series of five specimens. One specimen was exchanged with the British Museum and two specimens are apparently lost (Bengt-Olov Stolt, pers. comm.). Additional characteristics of the lectotype, not apparent in the photograph (Fig. 1) or mentioned above are: thumb lacking asperities; snout sloping in profile (Heyer 1983: fig. 6C); distinct inguinal disk; head length 12.4 mm; head width 13.9 mm; eye–nostril distance 2.6 mm; eye–eye distance 5.9 mm; femur length 15.6 mm; tibia length 15.8 mm; foot length 16.0 mm.

Subsequent to my visit to the type locality of *duseni* at Casa Ipiranga, Werner C. A. Bokermann informed me that he had collected at Banhado, the nearest regular train station to Casa Ipiranga on the line from Paranaguá to Curitiba. I had not seen these *Cycloramphus* previously, so Bokermann loaned them to me for purposes of this paper. The specimens (which include two males 37.4 and 41.4 mm SVL) are *C. rhyakonastes,* the only known species of *Cycloramphus* to have red bellies in life. Andersson (1914:2) gives the belly color of *T. duseni* as ''yellowish dirty white,'' but it is not apparent from the description whether these are life colors or those in preservative when Andersson described them. The types of *T. duseni* are similar to *Cycloramphus rhyakonastes* in dorsal texture, posterior thigh surface pattern and foot webbing (the reduced webbing of *T. duseni* is matched by some individuals of *C. rhyakonastes*). The types of *T. duseni* differ from *C. rhyakonastes* males in being smaller (males of *T. duseni* 31–37 mm SVL; males of *C. rhyakonastes* 37–50 mm). The size difference, probable differences in life belly color, and habitat (*C. rhyakonastes* have only been collected along streams, not on rock wall seeps) suggest that *duseni* and *rhyakonastes* represent two distinct species. Thus I prefer to recognize *duseni* and *rhyakonastes* as valid species of *Cycloramphus,* pending the availability of fresh topotypic material of *duseni.*

Cycloramphus duseni (Andersson) will key out to couplet 16 in the key to species published previously (Heyer 1983). The smaller size of *C. duseni* distinguishes it from both *C. rhyakonastes* and *semipalmatus,* the species contrasted in that couplet.

A New Name for the Form Previously Referred to as *Cycloramphus duseni*

The species previously referred to as *C. duseni* (Heyer 1983; Heyer and Maxson 1983) is not the same form represented by the types of *Telmatobius duseni* Andersson. There is no available name for the species, so it is described as:

Cycloramphus izecksohni, new species

Fig. 3

Holotype.—Museu de Zoologia, Universidade de São Paulo (MZUSP) 57775, an adult male from Brazil; Santa Catarina, 13 km W Pirabeiraba, 26°12′S, 49°07′W. Collected by Annelise Gehrau and W. Ronald Heyer on 17 December 1978.

Paratopotypes.—MZUSP 57772–74, 57776–98; USNM 217869–96, 217931.

Referred specimens: All other specimens listed in the distribution section in the species account for *C. duseni* for the States of Santa Catarina and São Paulo in Heyer (1983).

Diagnosis.—The species with toe webbing and distinctly black and/or white dorsal tubercles that might be confused with the new form are *C. asper, bora-*

Fig. 2. Map of several *Cycloramphus* distributions in the States of São Paulo, Paraná, and Santa Catarina, Brazil. Base map is adapted from predicted areas of stream associated *Cycloramphus* distributions (Heyer and Maxson 1983). Dashed line is approximate east boundary of the Atlantic Forest Morphoclimatic Domain. Stippled areas are zones of sharp relief within the Atlantic Forest Morphoclimatic Domain where mountain brooks would be expected. Open circle is previously plotted (Heyer 1983) type locality of *Telmatobius duseni*. Solid circle is correct type locality of *T. duseni*. Triangles are known localities for *Cycloramphus izecksoni*, new species. Hexagon is only known locality for *Cycloramphus cedrensis*, new species. Squares are known localities for *Cycloramphus valae*.

ceiensis, cedrensis, duseni, lutzorum, mirandaribeiroi, ohausi, rhyakonastes, and *semipalmatus*. *Cycloramphus izecksohni* differs from *C. ohausi* in lacking thumb spines. The moderate web of *C. izecksohni* differentiates it from the forms with reduced webbing (*C. duseni, rhyakonastes* and *semipalmatus*) or considerable webbing (*asper, cedrensis* and *mirandaribeiroi*). *Cycloramphus izecksohni* is smaller (males 29–38 mm, females 31–44 mm SVL) than *asper, boraceiensis, lutzorum, mirandaribeiroi,* and *rhyakonastes* (smallest male 35.9 mm, smallest female 42.6 mm SVL).

Description of holotype.—Snout rounded from above and in profile; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum hidden;

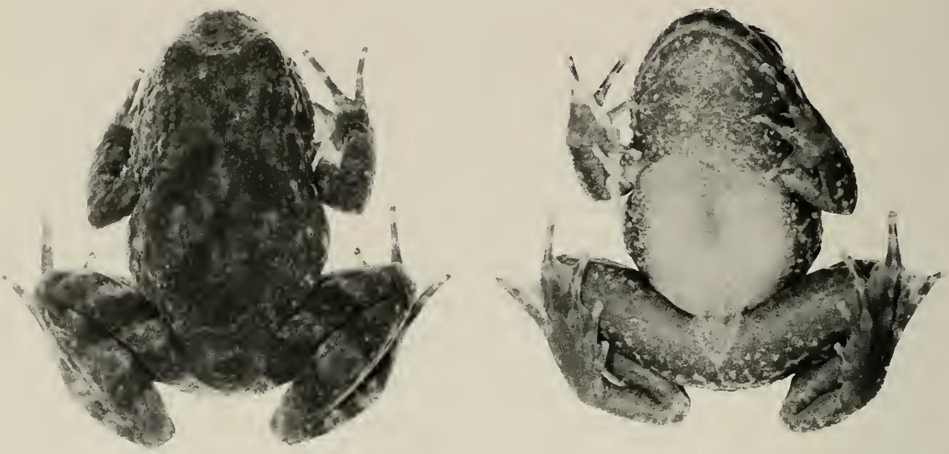


Fig. 3. Holotype of *Cycloramphus izecksohni*, dorsal and ventral views.

vomerine teeth in transverse series almost in medial contact, between and posterior to choanae; vocal fold present, but vocal slits absent; first finger just shorter than second; outer metacarpal tubercle a rounded square with an inner anterior projection, inner metacarpal tubercle ovoid, separated from subarticular tubercle of thumb by about diameter of subarticular tubercle; thumb lacking asperities; dorsal texture with shagreen and small to large warts each bearing a keratinized brown or black tubercle; large warts and tubercles arranged in short symmetrical rows behind the eyes; weak fold over ear region; inguinal gland large, disk-shaped, diameter between ¼ and ⅓ femur length; venter weakly granular; toe tips just wider than digits; toes moderately webbed, I 1–2^- II 1–2^+ III 1^+–2¼ IV 2½–1 V; toe subarticular tubercles moderately developed; outer metatarsal tubercle round, smaller than large ovoid inner metatarsal tubercle; no tarsal or metatarsal folds; outer tarsus covered with small tubercles, sole of foot smooth.

SVL 34.9, head length 12.8, head width 14.5, eye–nostril, distance 3.3, eye–eye distance 6.6, femur 17.4, tibia 17.3, foot 17.8 mm.

In preservation, dorsum brown with slightly darker brown amorphous blotches, broad lighter interorbital band; loreal and upper lip region with three ill-defined light vertical stripes; upper limbs barred; throat, chest, and under sides of limbs brown with irregular white spots and marks, belly mostly cream with some brown punctations; posterior surface of thigh mostly uniform brown with a few small distinct light spots.

Etymology.—Named for Professor Eugênio Izecksohn, who has contributed much to the understanding of the anuran fauna of Brazil and who has consistently helped my research efforts.

The data for adult specimens, advertising call, and larval description are presented elsewhere (Heyer 1983, as *C. duseni*).

The currently known distribution of *C. izecksohni* centers on the northern portion of the Atlantic Forests in the State of Santa Catarina (Fig. 2). There are three specimens of this species (Museu Nacional, Rio de Janeiro 98) with the locality data of Alto da Serra, Santos, São Paulo. This locality (Fig. 2, locality in State of São Paulo) does not make zoogeographic sense according to the scheme proposed by Heyer and Maxson (1983). However, there is no reason to doubt the veracity of the data and, there is unfortunately little likelihood of verification of this species at that locality. In the hundreds of preserved specimens examined from the area of Alto da Serra, only one small juvenile was found that might represent *C. izecksohni* (MZUSP 13909). Today, much of the area has been deforested by pollution from steel mills.

A New Species of *Cycloramphus* from Santa Catarina

One of the purposes of the field trip of 1982 was to test the accuracy of predictions as to areas of distribution for stream associated *Cycloramphus* (see Heyer and Maxson 1983), particularly in the southern portion of its range. As expected, much of the easily accessible area has been deforested, precluding *Cycloramphus*. We did find a stream with *Cycloramphus* near the town of Rio dos Cedros, Santa Catarina, however. To my knowledge this locality had not been sampled previously; examination of the specimens in the laboratory indicates that they represent a new species, which is named:

Cycloramphus cedrensis, new species

Fig. 4

Holotype.—MZUSP 59260, an adult male from Brazil; Santa Catarina, 12 km E of Rio dos Cedros on road to rio São Bernardo, approximately 26°44′S, 49°20′W. Collected by W. Ronald Heyer on 10 January 1982.

Paratopotypes.—MZUSP 59256–59, USNM 229781–86, same data as holotype, except collected on 9 and 10 January 1982.

Diagnosis.—The other species that share toe webbing and distinct black and/or white dorsal tubercles with the new form are *C. asper, boraceiensis, duseni, izecksohni, lutzorum, mirandaribeiroi, ohausi, rhyakonastes,* and *semipalmatus*. *Cycloramphus cedrensis* differs from *C. ohausi* in lacking thumb spines. The considerable web of *C. cedrensis* separates it from *C. duseni, rhyakonastes,* and *semipalmatus,* which have reduced webbing, and from *boraceiensis, izecksohni,* and *lutzorum,* which have moderate webbing. *Cycloramphus cedrensis* is smaller (males to 44, females to 50 mm SVL) than *mirandaribeiroi* (minimum male size 49, female 62 mm SVL). *Cycloramphus cedrensis* most closely resembles *C. asper* since both have considerable webbing. Most *C. asper* are more fully webbed than *C. cedrensis*: modal web formula for female *C. asper* (female *C. asper* have a little less web than male *asper*) I 0–2^- II 0–2^+ III 0–2¼ IV 2^-–0 V, modal web formula for *cedrensis* I 1–2^- II 1–2¼ III 1–2½ IV 2½–1 V. The differences in webbing, although difficult to verbalize, are apparent when series of specimens are compared directly.

Description of holotype.—Snout rounded from above and in profile, lip flared; canthus rostralis indistinct; loreal region slightly concave; tympanum hidden; vomerine teeth in almost contiguous transverse series, posterior to choanae; vocal slits present; first finger just shorter than second; outer metacarpal tubercle large, roughly heart-shaped, inner metacarpal tubercle ovoid, separated from thumb subarticular tubercle by distance equal to about ½ diameter of subarticular tubercle; thumbs lacking asperities; dorsal texture rough, with shagreen and larger

Fig. 4. Holotype of *Cycloramphus cedrensis*, dorsal and ventral views.

and smaller warts bearing black or white tipped tubercles, tubercles and warts not particularly regularly arranged; fold over ear region distinct; inguinal disk large, diameter about ¼ length of femur; ventral texture granular; toe tips just wider than digits; toes considerably webbed, I 0–2 II 0–2^+ III 0–2 IV 2½–0 V; rounded outer metatarsal tubercle smaller than ovoid inner metatarsal tubercle; no metatarsal fold, a tarsal ridge, but not developed into a fold; outer tarsus with many black tipped tubercles; lateral sole of foot with black tipped tubercles, inner sole smooth.

SVL 40.5, head length 16.1, head width 17.3, eye–nostril distance 4.0, eye–eye distance 8.3, femur 19.5, tibia 18.7, foot 18.7 mm.

In preservation, dorsum brown with indistinct tan mottling; upper lip and loreal region with three very faint light vertical stripes; upper limbs barred; throat brown with white flecks, belly with pattern of small scale brown and white mottle, under limbs more or less uniform brown except for light axillary region on arms; posterior surface of thigh with small regular and irregular light spots.

Variation.—The 5 adult males and 3 adult females range in size from 40.4–43.9 and 41.9–49.9 mm respectively. The paratypes resemble the holotype in most features, but differ in the following features. The posterior surface of the thigh is uniform in one specimen, mottled in three others. Light lip stripes are distinct in two specimens. The belly is uniform in five specimens. Three individuals have the large tuberculate dorsal warts arranged in irregular rows.

The colors in life of USNM 229784 were: chin and chest with small white dots on a maroon background; sides of body and posterior surface of thighs with distinctive small yellow dots; iris very dark brown.

Etymology.—Named for the type locality.

Advertising call.—Call of sporadic single notes; call short, duration 0.06–0.10 s; call not well tuned, maximum energy between 1100–1400 Hz, call pulsatile with sidebands or harmonics of about 200 Hz (Fig. 5).

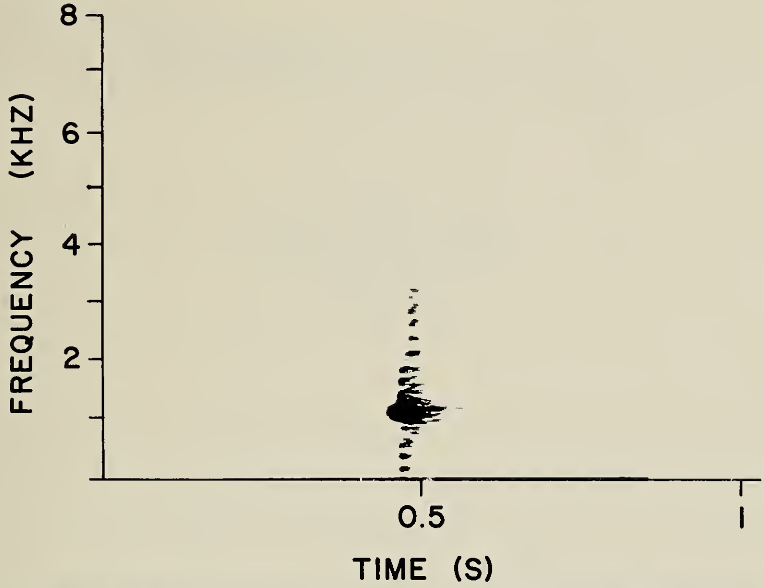


Fig. 5. The advertising call of *Cycloramphus cedrensis*. Recorded while calling from plastic bag. Male individuals in bag were MZUSP 59256–57, 59259–60. Air temperature approximately 27°C.

Larval definition.—Larvae unknown.

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

Cycloramphus cedrensis is very similar morphologically to *C. asper* and the two taxa differ only in the degree of webbing. An argument could be made that the population described here as *C. cedrensis* is a geographic variant of *C. asper*. Toe webbing is generally an indicator of species differentiation in the other species of *Cycloramphus* (Heyer 1983; Heyer and Maxson 1983); but the differences in webbing are often more pronounced than in this case. The differences between *C. asper* and *cedrensis* are within the considerably webbed category. The differences are consistent and I interpret them to reflect species differentiation. The two species also differ in life color. The bright yellow spots on the sides of the body and posterior surfaces of the thighs in *C. cedrensis* are very distinctive; *C. asper* has no flash colors. Most *C. asper* are found in the southern half of the Atlantic Forest region in the State of Santa Catarina (Heyer 1983, fig. 30). A single specimen of *C. asper* is known from Serra Alta, near São Bento do Sul in the northern half of the Atlantic Forest region in the State of Santa Catarina

Table 1.—Size ranges (in mm) of adult *Cycloramphus valae* from three localities. Numbers in parentheses are numbers of individuals.

Locality	Males	Females
Gruta	28.7–32.4 (5)	31.0–39.6 (27)
nr. Timbé do Sul	30.4–37.3 (10)	34.9–38.4 (3)
nr. Praia Grande	26.1–32.1 (7)	29.2–34.0 (7)

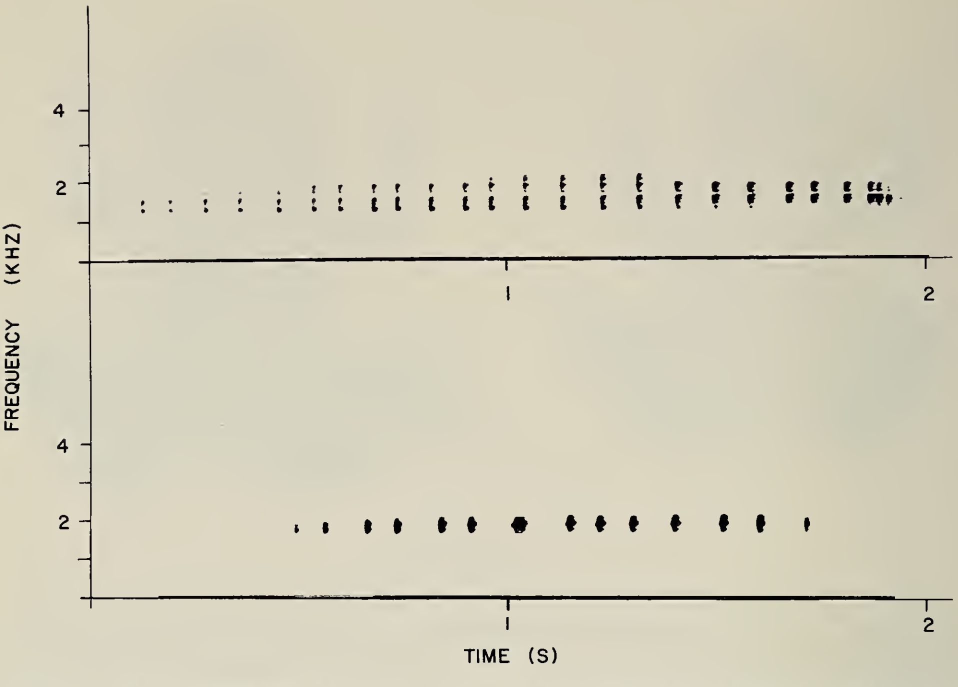


Fig. 6. The advertising call of *Cycloramphus valae*. Upper figure from USNM 229814, Brazil; Santa Catarina, 15 km from Timbé do Sul on road to Bom Jesus (Rio Grande do Sul), 20:45 h, estimated air temperature 18–20° C, 16 January 1982. Lower figure from Brazil; Santa Catarina, 10 km by road from Itaimbezinho to Praia Grande, 20:10 h, 17–18° C, 14 January 1982, specimen not captured.

(Adolfo Lutz previously unnumbered specimen 176, Museu Nacional, Rio de Janeiro). This specimen has not been reexamined for this study, but the webbing formula is consistent with *C. asper*.

No other *Cycloramphus* were found along the stream where *C. cedrensis* was taken. Another species, *C. izecksohni* has been taken from a nearby locality, Timbó do Sul (unnumbered series in E. Izecksohn collection, examined for this study) (Fig. 2, triangle next to hexagon).

New Data for *Cycloramphus valae*

Distribution.—The previously documented southernmost record of *Cycloramphus* was for *Cycloramphus valae* (Fig. 2, northernmost square; the locality reported by Braun and Braun, 1980, for Rio Grande do Sul is in error, see Heyer 1983). The Atlantic Forest Morphoclimatic Domain extends further south than this previous locality record; transects across the southernmost extent of the Atlantic Forest Domain produced two more records for *C. valae* (Fig. 2, two most southern squares). We did not collect the species in the State of Rio Grande do Sul, but further field work is necessary before its absence from the coastal mountain range in northern Rio Grande do Sul is accepted.

There are no noticeable morphological differences among the three available geographic samples of *C. valae*. The southernmost individuals are somewhat

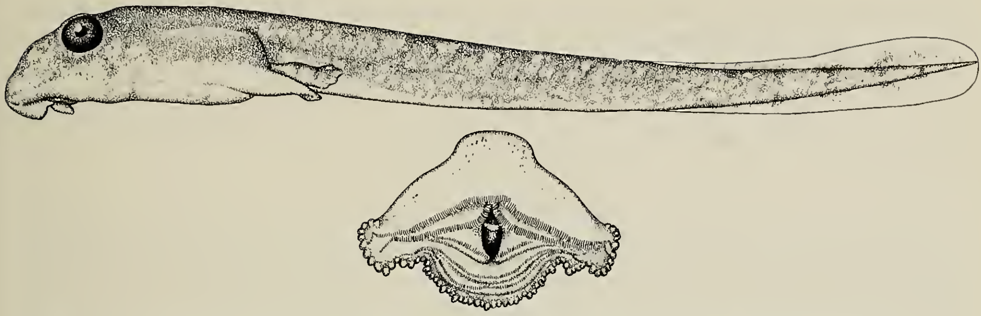


Fig. 7. The larva of *Cycloramphus valae,* USNM 229809, lateral view and mouthparts.

smaller in size than the others, although the difference may be due to sampling error (Table 1).

Advertising calls.—The call of *C. valae* is reported here for the first time. Three calls each were recorded from two individuals, one from near Timbé do Sul (middle square, Fig. 2) and one from near Praia Grande (bottom square, Fig. 2). As the calls differ between localities, they are described separately.

The call of *C. valae* from near Timbé do Sul consists of 23–26 notes lasting from 1.6 to 1.9 s; the dominant frequency ranges between 1250–2250 Hz; each note lasts about 0.02 s; the notes are pulsatile, with sidebands or harmonics of about 100 Hz; the call intensity is modulated, beginning quietly, ending loudly (Fig. 6, top).

The call of *C. valae* from near Praia Grande consists of 16–19 notes lasting from 1.3 to 1.5 s; the dominant frequency ranges between 1750–2200 Hz; each note lasts about 0.02–0.03 s; the notes are pulsatile, with sidebands or harmonics of about 80–100 Hz; the call intensity is modulated, beginning quietly, ending loudly (Fig. 6, bottom).

Additional recordings are not available to determine the degree of intraspecific variation. The calls of the two individuals available differ in degree of call length and number of notes per call. Otherwise, the calls are similar. The similarity of calls suggests that the samples are conspecific, although geographic variation may prove to be present.

Larval definition.—Larvae are elongate and depressed (Fig. 7). The tail fins are low, present only on the distal half of the tail. The belly is flattened and has a shallowly bilobed flap which extends posteriorly past the body. The spiracle, if present, is not visible. The anus is median. The eye is moderately large, 16–19% of the head–body length. The oral disk is broad, 39–41% of the head–body length. The oral disk is entire. The anterior papilla gap is broad, almost the width of the disk. The oral papillae are in a single row, continuous posteriorly. The tooth row formula is $\dfrac{\begin{matrix}1\\ 1\text{-}1\end{matrix}}{\begin{matrix}1\text{-}1\\ 2\end{matrix}}$, the split tooth row halves either abutting or overlapping medially. The beak has strong and deep central cusps. The head–body length is 24–29% the total length. The largest total length is 29.3 mm of a stage 36 (Gosner 1960) larva. The body is uniform dark brown above, mottled on the sides, and unpigmented below; the tail ranges from almost uniform brown above to a pattern with light dorsal ocelli, the tail venter is unpigmented.

Larvae were collected from water film covered vertical rock walls of a road cut. Of the many tadpoles collected from this habitat at this locality, only three were *C. valae*; the other larvae were all *Thoropa*.

Discussion

The distributional data reported herein do not particularly clarify any zoogeographical patterns aside from establishing the southern distributional limit of *C. valae*. In the latter case, *Cycloramphus* was predicted to occur in the places reported above (Heyer and Maxson 1983), and either *C. valae* or an unknown congener would have been expected to occur in the southernmost part of the generic range. Resolution of the location of the type locality of *C. duseni* removes one zoogeographic enigma caused by faulty map plotting (Heyer 1983). As presently understood, the distributions of *C. asper* and *C. izecksohni* are enigmatic in that each species has a central range with a geographic outlier population. These outlier populations are difficult to explain.

Cycloramphus valae is a member of the *C. granulosus* morphological group (based on adult morphology, Heyer 1983). The relationships of this group lie with the *C. fuliginosus* group: either the groups are closely related or the *granulosus* group is comprised of ectomorph species, each of which has as its closest relative a member of the *fuliginosus* group (Heyer and Maxson 1983). Neither advertising calls nor tadpoles were known for any member of the *C. granulosus* group previous to this report. The larvae share the same derived habitat and morphology as the known larvae of the *C. fuliginosus* group; there is nothing in the larval features to suggest that *C. valae* differs significantly from members of the *fuliginosus* group. The advertising call of *C. valae* differs in kind from the calls known for other members of the *fuliginosus* group. The calls of the *fuliginosus* group consist either of three note calls, the first note differing from the final two, or single note calls (which are similar to the final two notes of the three note call) (Heyer 1983). The call of *C. valae,* in contrast, consists of a multi-note call, similar in overall call pattern to that of *C. ohausi,* the sole representative of the *C. ohausi* group. The individual notes of the *C. valae* call are similar to notes of *fuliginosus* group members in having harmonics or sidebands. The individual notes of *C. ohausi* lack these features. The call of *C. valae* thus combines components found in calls of members of other species groups. Conclusions regarding relationships based on calls must await analysis of this feature in other members of the *granulosus* morphological group.

Acknowledgments

Bengt-Olov Stolt (Naturhistoriska Rijksmuseet, Stockholm) facilitated the loan of the types of *Telmatobius duseni*. Srs. Denisar Zanello Miranda and João Fernando Corsico, Rede Ferroviária Federal S/A, Curitiba, most graciously arranged the trip to Casa Ipiranga. Francisca Carolina do Val (Museu de Zoologia, Universidade de São Paulo, MZUSP) made the field work possible and enjoyable. P. E. Vanzolini (MZUSP) clarified points concerning localities and collectors and reviewed the manuscript. Frances Irish prepared Fig. 7. Ronald I. Crombie and

George R. Zug (National Museum of Natural History, USNM) also reviewed the manuscript. Field work was supported by the International Environmental Sciences Program, Smithsonian Institution, and the Museu de Zoologia da Universidade de São Paulo.

Literature Cited

Andersson, L. G. 1914. A new Telmatobius and new Teiidoid lizards from South America.—Arkiv för Zoologi 9:1–12.

Braun, P. C., and C. A. S. Braun. 1980. Lista prévia dos anfibios do Estado do Rio Grande do Sul, Brasil.—Iheringia 56:121–146.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification.—Herpetologica 16:183–190.

Heyer, W. R. 1983. Variation and systematics of frogs of the genus *Cycloramphus* (Amphibia, Leptodactylidae).—Arquivos de Zoologia 30:235–339.

Heyer, W. R., and L. R. Maxson. 1983. Relationships, zoogeography, and speciation mechanisms of frogs of the genus *Cycloramphus* (Amphibia, Leptodactylidae).—Arquivos de Zoologia 30: 341–368.

W. Ronald Heyer, Amphibians and Reptiles, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 560–566

LEPTODACTYLUS RIVEROI, A NEW FROG SPECIES FROM AMAZONIA, SOUTH AMERICA (ANURA: LEPTODACTYLIDAE)

W. Ronald Heyer and William F. Pyburn

Abstract.—A new species of the frog genus *Leptodactylus* is described based on specimens from scattered localities in Amazonia. The new species has characteristics which bridge the morphological gap between the previous definitions of the *melanonotus* and *ocellatus* species groups.

Rivero (1968) recognized that a collection of 27 individuals of *Leptodactylus* from Caño Iguapo, Venezuela represented a distinctive species of *Leptodactylus*, different from those he had treated previously in the "Salientia of Venezuela" (1961). In the 1961 publication, Rivero questionably included the species *L. rhodomystax* in the Venezuelan fauna, based on a single juvenile in the collections of the American Museum of Natural History. At the same time he pointed out that Boulenger's (1883) description of *L. rhodomystax* was based on a juvenile. Rivero later (1968) concluded that the series of specimens from Caño Iguapo represented *L. rhodomystax* Boulenger. Boulenger's *L. rhodomystax* is a different species, however (Heyer 1979), leaving the species Rivero recognized as distinct without a name. In recognition of Dr. Rivero's contributions, we describe the species as

Leptodactylus riveroi new species
Fig. 1

Holotype.—USNM 232400, an adult male from Colombia; Vaupes; Timbó, 01°06′S, 70°01′W, elevation 170 m. Collected by William F. Pyburn and J. K. Salser, Jr., 25 May 1973.

Paratypes.—UTACV 3888-3898 (Colombia; Vaupes; Timbó); UTACV 3721 (Colombia; Vaupes; Wacará); UTACV 3792, 4295, 4319, 6025, 7971–7974 (Colombia; Vaupes; Yapima).

Referred specimens.—All non-Colombian specimens listed in the distribution section.

Diagnosis.—*Leptodactylus riveroi* has extensive toe fringing and thumb spines in the males, characteristics shared with members of the *Leptodactylus melanonotus* and *ocellatus* groups. *Leptodactylus riveroi* has a pair of low dorsolateral folds, indicated in preservative by a black border, extending from behind the eye to a point near the posterior end of the body above the groin; *L. dantasi, melanonotus, podicipinus, pustulatus,* and most *wagneri* lack dorsolateral folds. Some *L. wagneri* have short indications of dorsolateral folds, but they are never as extensive as those of *L. riveroi*. The light stripe from under the eye to the shoulder, uniformly found in *L. riveroi*, is not present in *L. dantasi, melanonotus, ocellatus, podicipinus, pustulatus,* and most *wagneri*. Some *L. wagneri* have a light stripe under the eye to the angle of the jaw, but the outlines of the stripe

Fig. 1. Watercolor of *Leptodactylus riveroi* by William F. Pyburn.

are usually vague and the stripe is not as clearly defined as in *L. riveroi*. *Leptodactylus bolivianus* often have distinct light canthal stripes, but the stripes begin well forward of the eye, not under it as in *L. riveroi*. The uniform or faintly blotched dorsal pattern and single pair of dorsolateral folds of *L. riveroi* differ from the distinctly spotted dorsal patterns and at least 4 dorsolateral folds of *L. chaquensis, macrosternum, ocellatus,* and *viridis*. Male *L. riveroi* further differ from all other *Leptodactylus* (males of *L. dantasi* not known) in lacking vocal slits.

Specimens of *L. riveroi* are most likely to be confused with *L. bolivianus, rhodomystax,* and *wagneri*. The light lip stripes of *L. riveroi* and *L. rhodomystax* are similar, but *L. rhodomystax* has no toe fringing in adults and the back of the thigh has distinct, discrete light spots, rather than the mottling found in *L. riveroi*. In addition to the differentiating characteristics listed above for *bolivianus* and *wagneri, L. bolivianus* lacks the red-orange ventral glands found in *L. riveroi* and most adult *L. wagneri* are smaller than adult *L. riveroi*.

Description of holotype.—Snout subovoid from above, rounded in profile; canthus rostralis rounded; lores concave in cross section; tympanum large, distinct, almost same diameter as eye diameter; no vocal slits; vomerine teeth in two arched series, approaching each other medially, posterior and medial to choanae; first finger just longer than second, second about equal to fourth, third much longer than others; fingers with lateral fleshy ridges; thumb with 2 cornified nuptial spines; arm not especially hypertrophied; no ulnar ridge; dorsal texture smooth; a pair of low dorsolateral folds, demarcated by black pigment laterally, folds extending from back of eye to back of body above groin, moderate supratympanic fold present; ill-defined parotoid glands present, sides of body generally glandular, red-orange glands in large blocks on throat, most of belly, and ventral surfaces of limbs; venter smooth, ventral disk fold indistinct; no chest spines; toe tips not expanded; toe fringe extensively developed; subarticular tubercles moderately developed; extensive metatarsal flap of skin; tarsal fold distinct, extending about ⅞ length of tarsus, just not continuous with toe fringe of first toe; upper tibia with many white tipped tubercles; posterior surface of tarsus and sole of foot with many black tipped tubercles.

Snout–vent length (SVL) 62.8 mm, head length 25.0 mm, head width 23.2 mm, interorbital distance 5.5 mm, eye–nostril distance 7.1 mm, femur 26.7 mm, tibia 29.9 mm, foot 35.8 mm.

Dorsum essentially uniformly brown (in preservative) between dorsolateral folds and in upper snout area; faint darker interorbital mark, straight anteriorly, indistinct posteriorly; two indistinct dark central blotches; dark, broken canthal stripe from nostril to eye; upper lip indistinctly marked, lighter area under eye becoming distinct light strip under tympanum, extending to beyond angle of jaw, ending in shoulder region; sides of body brown with darker spots above, with a lighter indistinct band between side and belly; upper limbs indistinctly barred; ventral surfaces boldly mottled with dark and light, overlain by red-orange glandular areas, posterior surface of thigh boldly mottled with red-orange and black-brown.

Variation.—Rivero (1968) gave the range of sizes of his sample as 29.0–72.5 mm, but did not indicate ranges of males and females within that sample. In the specimens we have examined, males range 52.2–62.8 mm and females 67.8–81.0 mm SVL. The ranges of body proportions among adults are: head length/SVL

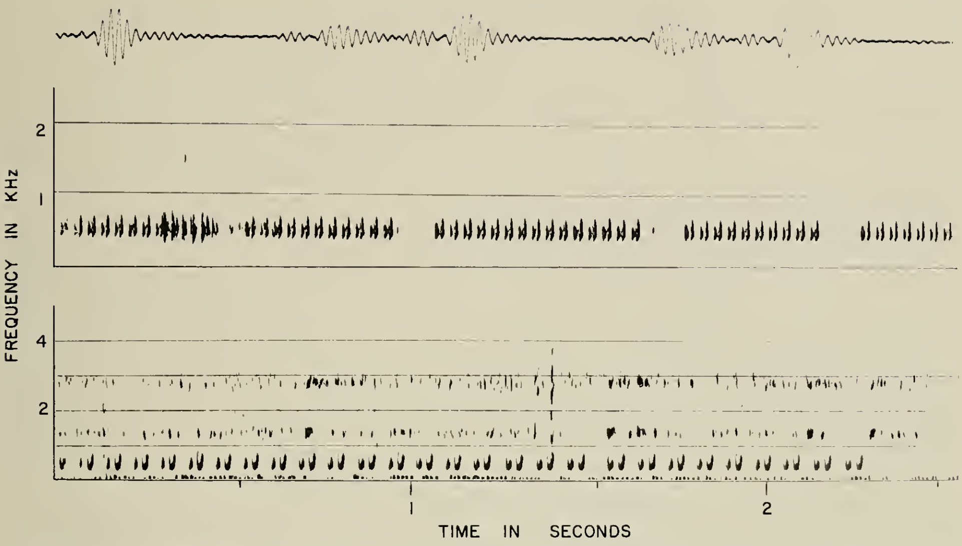


Fig. 2. Advertisement call of *Leptodactylus riveroi.* Wave form of filtered call as shown in top audiospectrogram, showing end of one note and two complete notes. Length of entire signal is 0.214 s. Upper audiospectrogram of bandpass filtered call, ⅓ octave at 500 Hz. Note that time axis is twice that of lower audiospectrogram. Lower audiospectrogram unfiltered call. All recordings from Colombia: Vaupes; Timbó, recorded on 28 May 1973 at about 21:30 h by W. F. Pyburn and J. K. Salser, Jr. Water temperature 24.0°C, air temperature 25.8°C. Specimen UTACV 3890 calling from burrow in a swamp.

38–48%, head width/SVL 35–37%, interorbital distance/SVL 8–10%, eye–nostril distance/SVL 10–11%, femur/SVL 40–46%, tibia/SVL 46–48%, and foot/SVL 53–57%.

There is little intraspecific variation in pattern or morphology among the individuals at hand. In some of the specimens, the tarsal fold is continuous with the outer toe fringe of toe one.

Rivero (1968) gave the following color notes from the Venezuelan individuals: dorsolateral folds at times maroon or cream red; the line that goes from the eye to the shoulder, and also at times the loreal area (although never as pronounced) ranges from a shade of rose to at times reddish. Charles W. Myers provided the following color data (also on Venezuelan individuals) through his notes and a color transparency: dorsal coloration basically brown, dorsolateral fold black outlined; the stripe under the eye cream anteriorly, orangish posteriorly in shoulder region; rear of thigh mottled black and yellowish brown; ventral surfaces mottled yellowish white and light brown; iris pale bronze, with reddish brown horizontal stripe, lower part of iris below stripe darkened by heavy black venation.

In life, specimens from southeastern Colombia are dark purplish brown on the dorsum and sides. Black bands cross the upper surface of the forearms and thighs, and irregular black spots occur on the upper surfaces of the shanks and on the sides of the body. Some specimens have a row of black spots above the groin that is partially concealed by the leg when the frog is at rest. Black reticulations or mottlings cover the posterior thigh surfaces and there is an interocular black

Fig. 3. Known distribution of *Leptodactylus riveroi*. Political boundaries indicated for Brazil, Colombia, and Venezuela.

bar. A bright cream lip stripe begins below the eye and extends posteriorly along the lower edge of the tympanum to the base of the upper arm. As the lip stripe approaches the arm base, it may gradually turn to orange. The lore is creamy gray, somewhat darker than the lip stripe. The edge of the upper lip is black crossed by one or two narrow cream bands. The dorsolateral fold is gray-bronze and its lower edge is marked by a broken or continuous black line. Large orange-yellow glandular areas cover most of the ventral surfaces, which are also marked with dark gray reticulations.

Advertisement call.—The call is quiet and consists of approximately 9–28 notes with a duration of from 0.7–2.3 s. Each note consists of two major pulses and the entire note has a duration of 0.04–0.05 s. The dominant frequencies range from 360–750 Hz to 360–830 Hz. There appears to be frequency modulation within each major pulse and the note is intensity modulated with the second pulse the loudest. There is no harmonic structure (Fig. 2).

Distribution.—The species is thus far known from the following localities (Fig. 3):

Brazil: Amazonas; Manaus (Reserva Ducke), MZUSP 50170, Reserva INPA-WWF (Rio Preto), MZUSP 57966.

Colombia: Vaupes; Timbó, USNM 232400, UTACV 3888–3898, Umuñá (uncatalogued voucher specimen), Wacará, UTACV 3721, Yapima, UTACV 3792, 4295, 4319, 6025, 7971–7974.

Venezuela: Amazonas; Upper Río Orinoco, Caño Iguapo (Rivero reported specimens, not examined by us), Upper Río Orinoco, Caño Cotúa (between Río Orinoco and Cerro Yapacana), 100 m, AMNH 100655, Upper Río Orinoco, SW base Cerro Yapacana, 110 m, AMNH 100654, E of Purunama on Río Guaname, USNM 229779–780.

Habitat.—AMNH 100654 was taken at night on the bank of a rocky stream in humid evergreen forest (not subject to flooding); AMNH 100655 was collected at night on the bank of Caño Cotúa in an area of seasonally inundated low scrubby forest (caatinga amazónica as used by Venezuelan botanists). At this latter habitat, *L. wagneri* was sympatric with *L. riveroi.*

In the forest of southeastern Colombia, *Leptodactylus riveroi* occurs at night along the edges of streams and on high ground in swamps that have been formed by flooding. When disturbed, it leaps directly into the water, but may turn and swim back to the bank where it emerges onto the land and sits quietly among dead leaves. In daylight, *L. riveroi* is occasionally found along forest trails away from water.

J. K. Salser, Jr. and the junior author found a calling male (USNM 232400) about 2100 h, 25 May 1973 by locating the source of the sound the animal produced. The frog called from the concealment of an underground cavity connected to the surface by a slanting tunnel near the edge of a swamp. The cavity was intersected by roots and contained a small pool. A regular sequence of quiet, closely spaced, low-pitched notes emanated from the cavity.

Another male (UTACV 3890) recorded (Fig. 2) 28 May 1973 at the same locality called from an underground chamber essentially like that of USNM 232400. The chamber was covered over by roots, dead leaves and humus. It contained a pool of water 25 cm deep and was located in a hillock surrounded by the water of the swamp. An adult female (UTACV 3891) sat on another hillock 2 m from the calling male.

Discussion

Leptodactylus riveroi demonstrates characters that straddle the previously defined *L. melanonotus* and *ocellatus* groups. The only characteristic that separated the two groups was the presence of well defined dorsolateral folds in the *ocellatus* group. Thus, on this basis, *L. riveroi* would be a member of the *ocellatus* group. However, the species has an overall habitus and color pattern strikingly similar to *L. wagneri*, a member of the *melanonotus* group. The unique condition in *L. riveroi* of having no vocal slits in males confuses the question of the precise relationships of *L. riveroi*. The call structure of *L. riveroi* stands out in its distinctiveness and is unlike any other *Leptodactylus* known. At the least, *L. riveroi* shows that there is no clear cut morphological distinction between the *L. melanonotus* and *ocellatus* groups. An albumin sample of *L. riveroi* is available and the micro-complement fixation analyses of *Leptodactylus* albumin including the sample of *L. riveroi* will be reported elsewhere (Maxson and Heyer, in prep.).

Acknowledgments and Museum Specimen Citation Symbols

We wish to thank Charles W. Myers, the American Museum of Natural History (AMNH) and P. E. Vanzolini, Museu de Zoologia da Universidade de São Paulo (MZUSP) for the loan of specimens in their charge. Dr. Myers also kindly made available his color and habitat notes of *L. riveroi*. We are indebted to J. K. Salser, Jr. and Nathan Waltz for their help in collecting and recording the specimens from Timbó and Yapima. Other specimens are deposited in the National Museum of Natural History (USNM) and the University of Texas at Arlington Collection of Vertebrates (UTACV). Field work by the junior author was made possible by a grant from the University of Texas at Arlington Organized Research Fund. Funds for publication of the color plate were provided by a Smithsonian Fluid Research Grant.

Literature Cited

Boulenger, G. A. 1883. On a collection of frogs from Yurimaguas, Huallaga River, northern Peru.—Proceedings of the Zoological Society of London 1883:635–638.

Heyer, W. R. 1979. Systematics of the *pentadactylus* species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae).—Smithsonian Contributions to Zoology 301:1–43.

Rivero, J. A. 1961. Salientia of Venezuela.—Bulletin of the Museum of Comparative Zoology 126: 1–207.

———. 1968. El problema de *Leptodactylus rhodomystax* Boulenger (Amphibia, Salientia).—Memoria de la Sociedad de Ciencias Naturales La Salle 28:145–150.

(WRH) Amphibians and Reptiles, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (WFP) Department of Biology, University of Texas at Arlington, Arlington, Texas 76019.

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 567–580

AN ANNOTATED CHECKLIST OF THE FOSSIL TORTOISES OF CHINA AND MONGOLIA

Charles R. Crumly

Abstract.—A review of published descriptions in some unavailable or obscure journals was done to collate and summarize useful morphological data on the fossil tortoises of Mongolia and China. Four genera of testudinids are recognized and tentatively diagnosed: *Testudo, Geochelone, Indotestudo,* and '*Manouria.*' *Sinohadrianus* and *Kansuchelys* are considered synonyms of '*Manouria,*' which is diagnosable, but not defined by shared derived characters.

Fossil land tortoises (Testudinidae) appear suddenly in Early Eocene sediments of North America and China. By the Late Eocene tortoises are also known from Europe (de Broin 1977; Mlynarski 1955; Schleich 1981) and North Africa (Andrews 1906), while persisting in North America and China. Fossil tortoises are among the most commonly encountered Tertiary remains and may be employed as useful stratigraphic markers (Hutchison 1980).

Although much is known of the structure, distribution, and evolutionary relationships of European and North American tortoises (Auffenberg 1963, 1966, 1971, 1974, 1976; Bramble 1971, in press; Van Devender *et al.* 1976), comparatively little is known of their Chinese counterparts. The acquisition of detailed information on the 24 named Chinese taxa has been hampered by two factors. Firstly, is the difficulty in examining the material. During the past forty or so years there has been very little interchange between oriental and occidental paleobiologists. Travel to the Institute of Vertebrate Paleontology and Paleoanthropology in China, where 17 of the 24 types reside, has not been possible until recently. Thus, western students of tortoise evolution, familiar with North American and European fossil remains have not had the opportunity to examine Chinese material. Secondly, the original descriptions of Chinese fossil land tortoises have often been published in journals not readily available to western researchers. The purpose of this checklist is to summarize the information published in those journals, to facilitate a useful synthesis.

The following list is arranged alphabetically by species name. Comments on materials, other than American Museum of Natural History specimens, are based on published figures and diagnoses. For this reason and because some of the figures are poor, remarks concerning morphology are often incomplete. The present status of the species and prevailing theories of relationship, if any, are noted. Generic names in quotes indicate that I have been unable to corroborate monophyly of the genus. The obvious limitations inherent in a checklist like this require that the reader regard generic assignments as tentative. Specimens in the American Museum of Natural History, New York (AMNH) were examined. Other unexamined material is housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing (IVPP), Zaklad Paleobiologii, Polska Akadamia Nauk, Warszawa (Z. Pal.), and the Geological Survey of China. The bone and scute terminology of Zangerl (1969) and the *Catalogue of American Amphibians and Reptiles* is followed.

Kansuchelys chiayukuanensis Yeh, 1963a:28

Type.—IVPP V.1006, right posterior carapace and plastron, damaged. Two paratypes are designated (IVPP 1006a, IVPP 1006b). Type locality: Shih-erh-ma-ch'eng, North of Hui-hui-p'u, Chia-yu-kuan, Kansu. Horizon: Unknown (? Oligocene or Late Eocene).

Remarks.—A very primitive tortoise, judging from the entirely hexagonal neurals, which are short-sided anteriorly, and the primitive suprapygal pattern (two suprapygal elements with the larger dorsal element embracing the ventral elliptical element. Extended discussion of this and other features will be the subject of another paper). Numerous other features show resemblances to '*Manouria*' (*sensu* Auffenberg 1971) species. These include the anal scute which is about the same median length as the femoral scute and the pleural scutes which are contacted by only the fifth and sixth marginals. The gular scutes but not the pectoral scutes overlap the entoplastron. The cervical scute is very large but slightly longer than broad.

Testudo chienfutungensis Yeh, 1963a:44

Type.—IVPP V.1030, carapace with connected plastron, damage to anterior carapace, posterior peripherals missing. Type locality: Taben-buluk, Tunhuang, Kansu. Horizon: Miocene (?).

Remarks.—Yeh (1963a) allocated this species to the genus *Testudo* on the basis of the position of the pleuro-marginal sulcus. Both Yeh (1963a) and Bohlin (1953) felt that the elongate shell, the presence of intergular scutes and the hexagonal neurals were abnormal conditions. Irrespective of the presence or absence of intergular scutes, the gular scutes overlap the entoplastron. Auffenberg (1974) thought this species may not be a testudinid. Bohlin (1953) noted two suprapygals arranged serially and of about equal size, whereas Yeh (1963a) characterized the suprapygal as entire. The four-sided fourth neural is odd for a tortoise, in which this neural is usually eight or six-sided. This species does possess some tortoise-like features, but most are shared primitive features. For example, the anal scute is much broader than the femoral scute and there is very little constriction at the anal and gular scutes posterolateral borders. Auffenberg's (1974) reservations concerning this species are understandable.

Testudo demissa Gilmore, 1931:239

Type.—AMNH 6670, right xiphiplastron (probably of large male). Type locality: Ardyn Obo, Chinese Postroad, Outer Mongolia. Horizon: Ardyn Obo formation, Lower Oligocene.

Remarks.—This species is distinguished on the basis of a thickened and downturned anal region of the plastron and very short anal scutes. Both these characters appear in many unrelated tortoises and are even more prominent in large males of these unrelated species. Mlynarski (1968) synonymized *T. demissa* with *Geochelone insolitus* (Matthew and Granger, 1923), and allocated both species to the genus *Geochelone*. Auffenberg (1974) tentatively allocated *G. insolitus* and *T. demissa* to the subgenus *Manouria*. The extreme narrowness of the anal scutes contradicts Auffenberg's allocation.

Testudo hipparionum Wiman, 1930:41

Type.—IVPP (Catalogue number not published), complete shell. Type locality: Shansi, Wu-Hsiang-Hsien, E 2 li (1 li equals about one-third of a mile) Huo-Shen-Miao-Kou. Horizon: Pliocene.

Remarks.—Very poorly described by Wiman (1930) but re-described and figured from non-type material by Yeh (1963a). Yeh (1963a) also refers four IVPP specimens to this species (IVPP V.1017, V.1018, V.1020, and V.1024). IVPP V.1024 includes a skull and parts of the appendicular skeleton. Yeh (1963a) noted that this may be the most common tortoise in northern Chinese red clay beds. Gilmore (1934) and Auffenberg (1974) contended that other tortoises named by Wiman may be variants of *T. hipparionum*. The shape and size of the cervical and questionably interpreted pleuro-marginal scute contacts support the allocation of this species to the genus *Testudo* (sensu stricto). Other characters include two suprapygal elements, the larger embracing the smaller elliptical element (primitive); the gular scutes, but not the pectoral scutes, overlap the entoplastron; some plastral constriction at the anal and epiplastral border; three marginals (numbers 5, 6, and 7) contact the second pleural scute (primitive); and neural formula 4-8-4-8-4-8-?4-?6.

Testudo honanensis Wiman, 1930:43

Type.—IVPP (Catalogue number not published), partial carapace and nearly complete plastron. Type locality: locality 12, Honan, Hsin-An-Hsien, Shan-Yin Kou. Horizon: Unknown (? Miocene).

Remarks.—Yeh (1963a) referred three IVPP specimens (IVPP V.1025, V.1026, V.1027) to this species but Auffenberg (1974) contended that Yeh's usage of this name is synonymous with *T. sphaerica*. Mlynarski (1955) believed that this form is assignable to the *antiqua-graeca* phyletic line. Cervical shape and size, and an anal scute having a greater median length than the femoral scute support the allocation of this species to the genus *Testudo*. The hexagonal third neural is unusual. The neural formula is 4-8-6-8-?4-6-6-6.

Testudo hypercostata Wiman, 1930:35

Type.—IVPP (Catalogue number not published), nearly complete shell. Type locality: locality 114 south, Shansi, Ho-Ch'u-Hsien, SE 60 li (1 li equals about one-third of a mile) of Nan-Skha-Wa, 1 li from Ma-Hua-T'an. Horizon: Pliocene.

Remarks.—Yeh (1963a) contended that this species is specialized because it possesses a supernumerary neural. Auffenberg (1974) disagreed and claimed that this form is conspecific with *T. shensiensis*. The neural formula is 4-8-4-8-4-6-6-6-4. The anal midline length is only slightly less than the femoral length. The entoplastron is not overlapped by either the gular or pectoral scutes. There is some constriction at the lateral borders of the epiplastral and anal regions. The second pleural scute is contacted by three marginal scutes.

Testudo insolita Matthew and Granger, 1923:5

Type.—AMNH 6275, parts of carapaces and plastra of several individuals. Type locality: Promontory Bluff, on the Sair-Usu-Kalgan trail, about 150 miles from Sair-Usu and 350 miles from Kalgan, Ardyn Obo basin, Mongolia. Horizon: Oligocene.

Remarks.—Gilmore (1931) felt the poor description of this species made the determination of its affinities impossible. Mlynarski (1968), nonetheless, synonymized *Geochelone demissa* (Gilmore, 1931) with *T. insolitus*. The entoplastron is not overlapped by the pectoral scutes, which narrow abruptly as they extend medially. The xiphi-hypoplastral sutures are located far posterior from the femoral-abdominal sulcus. The cervical scute is long and thin and recessed from the anterior margin of the carapace. Mlynarski's (1968) assertion that the neural bones are octagonal, hexagonal and tetragonal cannot be confirmed until fossil material of that region of the shell is found. This large tortoise with abbreviated anal scutes is referable to *Geochelone*, as Auffenberg (1974) and Mlynarski (1968) suggest.

Chkikvadze (1972) described *Ergilemys*, type-species *G. insolitus*, and considered that Early Oligocene genus ancestral to *Protestudo* Chkikvadze (1970), '*Manouria*,' *Geochelone*, and *Indotestudo*. The distinctive features of *Ergilemys* are primitive characteristics. Mlynarski (1976) demotes *Ergilemys* to a subgenus of *Geochelone*. In addition to the five species assigned to *Ergilemys* by Chkikvadze, de Broin (1977) has included another newly named species. Thus, although its affinities are often considered, *T. insolita* remains enigmatic.

Testudo kalganensis Gilmore, 1931:247

Type.—AMNH 6701, anterior part of carapace, most of anterior lobe of plastron minus entoplastron, and carapacial and plastral parts of right side of bridge. Type locality: Kalgan Area, North China. Horizon: Tertiary (?).

Remarks.—Gilmore (1931) did not remark upon the relationships of this species; such reticence is understandable given the greatly thickened and extraordinarily sculptured shell. Auffenberg (1974), citing two of his earlier works (1962 and 1963), assigned this species to the *turgida* phyletic line of the subgenus *Hesperotestudo*. The pectoral scute overlaps the entoplastron, a feature that characterizes *Indotestudo* and *Testudo horsfieldii*. The gular scutes also overlap the entoplastron. The cervical is long and thin and slightly recessed. Although questionable, it is possible that the femoral scutes do not contact the inguinal scutes, a feature common to *Testudo*. Assignment to *Hesperotestudo* seems premature.

Testudo kaiseni Gilmore, 1931:236

Type.—AMNH 6352, nearly complete carapace and plastron. Type locality: Ardyn Obo basin, Chinese Postroad, Outer Mongolia. Horizon: Ardyn Obo formation, Lower Oligocene.

Remarks.—Auffenberg (1974) questionably referred this species to *Indotestudo*, probably because the pectoral scute overlapped the entoplastron. Earlier, Glaessner (1935) contended that *T. kaiseni* was a member of the *Testudo antiqua* group, contrary to Mlynarski (1955). The femoro-abdominal sulcus, which is faintly visible on the type, was not figured by Gilmore (1931, fig. 17, p. 238). The anal scute is about the same median length as the femoral scute, perhaps slightly greater. Neither the gulars nor the pectorals overlap the entoplastron. The neural formula is 4-7-4-7-5-6-?6-?. In most tortoises, the neural series includes neurals with an even number of sides. Thus, the seven-sided neurals would probably be eight-sided and the five-sided neural would probably be four-sided in other specimens of *Testudo kaiseni.*

Testudo lunanensis Yeh, 1963a:50

Type.—IVPP V.1032, damaged plastron with left plastral bridge. Type locality: Wa-ya-chung, Ta-i-ma, Lunan, Yunnan. Horizon: Early Oligocene.

Remarks.—Yeh (1963a) distinguished this species, which is the largest tortoise known from China, primarily on the basis of size. He believed it to be closely related to *T. yunnanensis,* the other giant tortoise preserved in Chinese deposits. Auffenberg (1974) referred this species to the synonymy of *T. yunnanensis.* With reservation Auffenberg allocated this latter species to *Geochelone,* on the basis of its large size. Only the inside of the plastron, which possesses no particularly diagnostic features has been prepared; it is a very poorly known form in which size provides the only clue to its affinities. Nevertheless, Chkikvadze (1972) allocated this species to his new genus *Ergilemys.* This species is also represented by appendicular material.

Testudo nanus Gilmore, 1931:241

Type.—AMNH 6692, complete shell. Type locality: East Mesa, Shara Marun Region, Inner Mongolia. Horizon: ? Ulan Gochu, Lower Oligocene.

Remarks.—Gilmore (1931) anticipated the nomenclatorial change adopted by Loveridge and Williams (1957) in noting the mobile posterior plastral lobe in *Testudo graeca, T. nanus* and some other *Testudo.* In *T. nanus,* the supracaudal scute is divided, but whether it is divided on both the inside and outside of the pygal bone is not known. In *Geochelone emys* and *G. impressa* it is divided on both sides, but in *T. hermanni* and *Malacochersus tornieri* it is usually divided only on the outside of the shell. Other characteristics of *T. nanus* include an elongated prominent epiplastral projection, gular scutes that do not overlap the entoplastron which is in turn broadly overlapped by the pectoral scutes, two suprapygals with the smaller elliptical ventral element embraced by the larger superior element, and no constriction at the anal border. Gilmore (1931) was not able to locate the anal/femoral sulcus. However, detailed examination of the type material and examination of photos and Gilmore's plates suggests that the anal scute is broader than the femoral; the typical condition for *Testudo.* Only the posterior neural bones are known: ?-?-?-?-4-6-6-6.

Mlynarski (1968) was uncertain about the status of this species but was convinced that it is not referable to *Indotestudo.* Auffenberg (1974) allocated this species to *Geochelone,* subgenus questionably *Indotestudo.* I return this species to *Testudo* because of the mobile plastral lobe and the apparent large size of the anal scute.

Geochelone oskarkuhni Mlynarski, 1968:91

Type.—Z. Pal. MgCh/15, a plastron and a pygal region from the same individual. Type locality: Altan, Teli, Dzereg Valley, Western Mongolia. Horizon: Pliocene (*fide* Gradzinski *et al.* 1968:75).

Remarks.—The allocation of this species to *Geochelone* was accepted with reservation by Auffenberg (1974). Mlynarski (1968) noted similarities between *G. oskarkuhni,* and *Testudo sphaerica* Wiman and *T. kegenica* Khosatsky (1953). He also noted that material of *G. ulanensis* was in too poor a condition to allow meaningful comparisons. In order to express his ideas of phyletic relationships for Asian tortoises, Mlynarski coined the term "*hipparionum*" group and placed *G. oskarkuhni* within this group. He noted that this species group may be intermediate between *Geochelone* and *Testudo* and perhaps ancestral to the *antiqua-graeca* phyletic line.

The gulars, but not the pectoral scutes, overlap the entoplastron. The cervical scute is long and narrow and there are two suprapygal elements. The larger superior element embraces the more ventral, elliptical element. Mlynarski (1968) admitted that the bad condition of the material makes detailed descriptions largely a product of guesswork.

Kansuchelys ovalis Yeh, 1963a:33

Type.—IVPP V.1007, nearly complete shell. Type locality: Unknown (? Yushe, Shansi). Horizon: Unknown.

Remarks.—Yeh (1963a) distinguished this species from *K. chiayukuanensis* on the basis of plastral scute and bone patterns. He further hypothesized that *Kansuchelys* was more primitive than *Testudo,* but closely related. Auffenberg (1974) suggested that a specimen with such inexact data should not have been described.

The entoplastron is overlapped by the gular scutes but not by the pectoral scutes. The supracaudal scute is entire and the anals are longer medially than the femorals. There are two suprapygals, the larger superior element embracing the inferior elliptical element. The neural pattern is 4-6-6-6-6-6-6-6, and the hexagonal neurals are short-sided anteriorly.

Testudo shansiensis Wiman, 1930:38

Type.—IVPP (Catalogue number not published), complete carapace, and plastron missing the anterior lobe. Type locality: southern part of locality 114, Shansi, Ho-Ch'u-Hsien, SE 60 li (1 li equals about one-third of a mile) of Nan-Skha-Wa, 1 li from Ma-Hua-T'an. Horizon: Pliocene.

Remarks.—Yeh (1963) referred two IVPP specimens to this species (IVPP V.1015, V.1016) and noted its similarity to *T. hypercostata.* Auffenberg (1974) allocated this form to the synonymy of *T. hypercostata,* which has the same type locality.

The large dorsal suprapygal element is asymmetrical; only one 'arm' embraces the smaller elliptical ventral suprapygal. The anal and femoral scutes have similar median lengths. The gulars overlap the entoplastron. The pectoral scutes form a V-shaped sulcus which is posterior to the entoplastron on the midline but overlaps it laterally. This is similar to the condition in *Testudo horsfieldii.* The supracaudal is entire. The neural formula is 4-8-4-8-4-6-6-6. Three marginal scutes contact the second pleural scutes. Whether a valid species or not, this form is certainly referable to *Testudo*.

Testudo sharanensis Yeh, 1965:53

Type.—IVPP V.2868, complete plastron, partial carapace missing some elements of right side, and some fragments. A paratype was designated (IVPP V.2868.1) and consists of a complete plastron and a partial carapace. Type locality: Ula Usu, Inner Mongolian Autonomous Region. Horizon: Late Eocene.

Remarks.—Yeh (1965) considered this a very primitive species but discounted any close relationship to *Hadrianus* or *Stylemys* since all the neurals of these two are hexagonal whereas one neural (#2) of *T. sharanensis* is octagonal. He distinguished this species from *Sinohadrianus sichuanensis* on the basis of neural pattern differences. The position of the pleuro-marginal sulcus distinguished *T. sharanensis* from *T. ulanensis* Gilmore (1931), in which it extends along the lateral shell below the costo-peripheral suture.

The gular scutes, but not the pectoral scutes overlap the entoplastron. There is plastral constriction at the lateral borders of the anal and gular scutes. The medial length of the anal exceeds that of the femoral scutes. The supracaudal scute is divided. Although Yeh characterizes the cervical as "small," the cervical scute is large and broad in his fig. 3 (1965). There are notches in the anterior edge of the epiplastra. Yeh believes there are three suprapygal elements. I think it more likely that there is a supernumerary ninth neural yielding the following neural formula: 4-8-4-6-6-6-6-6-4. If this is the case, there are two suprapygal elements showing the primitive condition with the larger element embracing the more ventral elliptical element. These features suggest that this species is referable to '*Manouria*.'

Auffenberg (1974) did not refer to this species in his checklist. Chkikvadze (1973) contended that *T. sharanensis* possesses intergular scutes; I disagree. Mlynarski (1976) referred this species to the Testudinidae *incerta sedis* and noted posterior plastral similarities shared with *Ergilemys*.

Testudo shensiensis Wiman, 1930:28

Type.—IVPP (Catalogue number not published), complete shell. Type locality: locality 51, Shensi, Fu-Ku-Hsien, W 110 li Wu-Lan-Kou, SE 1 li Pei-Hou-Kou. Horizon: Pliocene.

Remarks.—Yeh (1963a) did not comment on the relationships of these species but refers four IVPP specimens to this taxon (IVPP V.1008, V.1009, V.1010, V.1019). Glaessner (1933) allied this form to the *antiqua-graeca* phyletic line. Auffenberg's (1974) cited Gilmore's (1931) [actually 1934] assignment of AMNH material to this species. Gilmore was critical of Wiman's (1930) work and predicted that further study would reveal that fewer species should be recognized.

The gular, but not pectoral scutes, overlap the entoplastron. The median length of the anal scutes is slightly less than that of the femoral scutes. There is no plastral constriction at the lateral border of either the gular or anal scutes. The cervical scute is relatively large according to Wiman's (1930) figure (Pl. V, Fig. 1). Three marginal scutes (numbers 5, 6 and 7) contact the second costal. The

Fig. 1. Localities in China and Mongolia where testudinid fossils have been unearthed (taken mostly from Yeh 1963a). The shaded area in the lower left is the present distribution of land tortoises in southeast Asia.

neural formula is 4-8-4-6-6-6-6-6. There are two suprapygal elements of about equal size divided by a transverse suture. This species is best allocated to *Testudo.*

Sinohadrianus sichuanensis Ping, 1929:232

Type.—Geological Survey of China (Catalogue number not published), nearly complete shell. Type locality: "It was collected from Fan Chuan of Si Chuan Hsien, Honan Province by Mr. C. Li, ... The locality, where the specimen was secured, is near the border of Chieh Chia Chi of Chun Hsien, Hupei Province, where Mr. Li's party happen to go across the boundary line between the two provinces while surveying" (Ping 1929:231). I have tried to locate this ambiguous type-locality without success. It is likely that this specimen was found north of the Han River on the northwestern border of Hupei Province and the southwestern border of Honan Province in the Mot'ien Ling Mountains. Horizon: Late Eocene.

Remarks.—Auffenberg (1974) suggested that *Sinohadrianus* is more primitive than North American *Hadrianus* and concurs with Yeh (1963a) that it is not closely related to *Hadrianus* (=junior synonym of *Manouria,* according to Auffenberg 1971).

The entoplastron is not overlapped by the pectoral scutes. Because the epiplastra and the anterior entoplastron are missing, it is not possible to determine if the gular scutes overlap the entoplastron. Other plastral sutures are faint, but it seems that the median length of the anal and femoral scutes are near the same. Both the anterior and posterior margins of the carapace are missing, so it is impossible to determine the morphology of the cervical, suprapygal(s), and supracaudal(s). The neural formula is 4-6-6-6-4-6-6-6, and there may be a ninth neural whose shape is uncertain.

Mlynarski (1976) included this species in the Testudinidae *incerta sedis.* If this species is a tortoise it might be referable to '*Manouria.*'

Testudo sphaerica Wiman, 1930:33

Type.—IVPP (Catalogue number not published), nearly complete carapace and plastron missing posterior lobe. Type locality: locality 110_2, Shansi, Pao-Te-Chou, 25 li NE of Chi-Chia-Kou, 5.5 li NE of Wang-Cia-Liang-Kou. Horizon: Pliocene.

Remarks.—Mlynarski (1955) removed this form from the *antiqua-graeca* line claiming its affinities lie with *T. horsfieldii.* He later (Mlynarski 1968) changed his mind and allocated this species to the *Geochelone.* Yeh (1963a) referred four IVPP specimens to this taxon (IVPP V.701, V.1011, V.1012, V.1013). Auffenberg (1974) followed Gilmore (1934) in considering *T. yushensis* a synonym. Yeh (1963a) also referred the type of *Terrapene sinica* (IVPP V.701) and material unearthed from the Pliocene sediments of Yushe, Shansi (IVPP V.1011–V.1013) to this species.

The gular, but not the pectoral scutes, overlap the entoplastron. Although the posterior lobe of the plastron is missing in the type, I expect that when discovered the anal scute will have about the same median length as the femoral scutes. There are two suprapygals of uncertain shape. The shape of the cervical scute is unknown. Only the anterior five neurals are known; the neural formula is 4-8-4-8-4?-?-?-?. Three marginal scutes contact the second pleural scute. Whether valid or not, this form is best allocated to *Testudo.*

Kansuchelys tsiyuanensis Yeh, 1979:310

Type.—IVPP (Catalogue number has not been published), complete shell. Type locality: Jiyuan, Henan Province. Horizon: Eocene.

Remarks.—This recently-named species is very primitive as Yeh (1979) noted. Neither the gular nor the pectoral scutes overlap the entoplastron. There is slight plastral constriction at the lateral anal border, but no constriction at the lateral gular border. The median length of the anal scutes is only slightly less than that of the femoral scutes. There are faint notches in the anterior lip of the epiplastral projection. The pectoral scutes narrow abruptly as they extend medially. The cervical is moderately broad dorsally, and may be even broader ventrally. There are two suprapygals; the larger superior element embraces the smaller ventral elliptical element. The supracaudal scute is divided. Most of the neurals are hexagonal with the short sides anterior; the neural formula is 4-6-6-6-6-6-6-6. The costal bones are alternatingly wide and narrow, medially and laterally. Marginals

6, 7 and 8 contact the second pleural scute. This species is best allocated to '*Manouria*.'

Testudo tungia Yeh, 1963b:224

Type.—IVPP V.2768, slightly broken carapace. Type locality: *Gigantopithecus* cave, Liucheng, Kwangsi. Horizon: Early Pleistocene.

Remarks.—Auffenberg (1974) believed this material is of a *Cuora* species. The neural formula, 4-6-4-4-4-4-?-?, supports this contention. Furthermore, the small size and characteristically emydid shell silhouette suggest that this species is not a testudinid. The plastron is not known.

Testudo tunhuanensis Yeh, 1963a:42

Type.—IVPP V.1029a, damaged anterior two-thirds of carapace. IVPP V.1029b, a complete plastron, is a paratype. Type locality: Taben-buluk, Tunhuang, Kansu. Horizon: Unknown (? Miocene).

Remarks.—This species was described but not named by Bohlin (1953). Yeh (1963a), followed by Auffenberg (1974), noted the similarity between this form and *T. sphaerica*.

The gular, but not the pectoral scutes, overlap the entoplastron. The median length of the anal scutes exceeds the median length of the femoral scutes. There is no plastral constriction at the lateral gular or anal borders. The cervical is moderate sized. The posterior half of the carapace is unknown. The neural formula is 4-8-4-7-5-6-6?-?. Probably the odd-sided neurals are in most specimens even-sided, as is usual in tortoises. Marginals 5, 6 and 7 contact the second pleural scute.

Testudo ulanensis Gilmore, 1931:245

Type.—AMNH 6691, a posterior plastral lobe attached to part of the left bridge, the median part of the plastron posterior of the entoplastron, a costal and peripherals 9, 10 and 11 of both the right and left sides of the carapace with some fragments of costal bones articulated. Type locality: North Mesa, Shara Marun Region, Inner Mongolia. Horizon: Ulan Shireh, Upper Eocene.

Remarks.—This difficult-to-allocate species was referred to *Geochelone* by Mlynarski (1968), and retained there with some reservation by Auffenberg (1974). Chkikvadze (1970), without stating his reasons, referred this species to *Hadrianus*.

The median length of the anal scutes is about equal to or exceeds the median length of the femoral scutes. The femoral scutes are separated from the inguinal scutes by the abdominal scutes. This condition is common in *Testudo* and accompanies the development of a hinge in the posterior plastral lobe. There is plastral constriction at the lateral border of the anal scutes, but not at the lateral border of the gular scutes.

Testudo yunnanensis Yeh, 1963a:47

Type.—IVPP V.1031, portions of anterior plastron. Type locality: Wa-yao-chung, Ta-i-ma, Lunan. Yunnan. Horizon: Early Oligocene.

Table 1.—The recommended nomenclatorial status of Chinese and Mongolian fossil tortoises.

Original trivial name	Original generic name	Recommended generic name
chiayukuanensis	*Kansuchelys*	*'Manouria'*
chienfutungensis	*Testudo*	*Testudo* (?)
demissa	*Testudo*	*Geochelone*
hipparionum	*Testudo*	*Testudo*
honanensis	*Testudo*	*Testudo*
hyercostata	*Testudo*	*Testudo*
insolitus	*Testudo*	*Geochelone*
kalganensis	*Testudo*	*Geochelone*
kaiseni	*Testudo*	*Indotestudo*
lunanensis	*Testudo*	*Geochelone* (?)
nanus	*Testudo*	*Indotestudo*
oskarkuhni	*Geochelone*	*Geochelone*
ovalis	*Kansuchelys*	*'Manouria'*
shansiensis	*Testudo*	*Testudo*
sharanensis	*Testudo*	*'Manouria'*
shensiensis	*Testudo*	*Testudo*
sphaerica	*Testudo*	*Testudo*
sichuanensis	*Sinohadrianus*	*'Manouria'*
tsiyuanensis	*Kansuchelys*	*'Manouria'*
tungia	*Testudo*	*Cuora*
tunhuanensis	*Testudo*	*Testudo*
ulanensis	*Testudo*	*Testudo* (?)
yunnanensis	*Testudo*	*Geochelone*
yushensis	*Testudo*	*'Manouria'* (?)

Remarks.—Auffenberg (1974) referred this species to *Geochelone* on the basis of size and believed *T. lunanensis* to be a junior synonym. Yeh (1963a) described the form because it is larger than most other Chinese tortoises. Chkikvadze (1972) allocated this species to his genus *Ergilemys.*

The pectorals do not overlap the entoplastron and narrow abruptly as they extend medially. They are slightly broader on the midline than parasagittally. This condition of the pectoral scutes is also present in *Geochelone sulcata* and some *Hesperotestudo* species. The gular scutes overlap the entoplastron. The median length of the femoral scutes greatly exceeds the median length of the anal scutes. There is prominent constriction at the lateral borders of the anal scutes and the postero-lateral tips of the xiphiplastra are elongate and thickened. Most of the carapace is unknown.

Testudo yushensis Yeh, 1963a:40

Type.—IVPP V.1028, almost complete shell. Type locality: Tsuan-tse-yao, Yushe, Shansi. Horizon: Pliocene.

Remarks.—Yeh (1963a) was careful to distinguish this species from *T. honanensis* but did so on the basis of highly variable characters. For this reason, Auffenberg (1974) considered this form a synonym of *T. sphaerica.*

The gular, but not the pectoral scutes, overlap the entoplastron. The median length of the anal scutes is less than the median length of the femoral scutes. Nevertheless, the anal scutes are large and not reduced as in *Geochelone.* There

Table 2.—The stratigraphic position of the testudinids of China and Mongolia is summarized below. Exact stratigraphic information is, at present, not available for most Chinese sediments. Correlation with North American and/or European sediments has not yet been attempted.

Epoch	Species
Pleistocene	*tungia**
Pliocene	*hipparionum, hypercostata, oskarkuhni, shansiensis, shensiensis, sphaerica, yushensis*
Miocene	*chienfutungensis* (?), *honanensis* (?), *insolita, tunhuanensis* (?)
Oligocene—Late	*lunanensis, yunnanensis*
—Early	*demissa, kaiseni, nanus* (?)
Eocene—Late	*chiayukuanensis* (?), *sharanensis, sichuanensis, ulanensis*
—Middle or Early	*tsiyuanensis*
Unknown horizon	*kalganensis, ovalis*

*—not a testudinid, probably *Cuora* (Auffenberg, 1974).
(?)—stratigraphic position uncertain.

is some plastral constriction at both the gular and anal lateral borders. The cervical scute is large and broadest posteriorly. There are two suprapygal elements; the larger superior element embraces the ventral elliptical element. The supracaudal is entire. The neural formula is 4-6-4-8-4-6-6-6. This species may best be allocated to '*Manouria*.'

Discussion

Although simple classifications have been advanced, there are no comprehensive phylogenetic hypotheses that incorporate Chinese and Mongolian fossil tortoises. Hypotheses have been formulated by allocating species to particular genera; subsequent re-allocation, although reasonable, often did not include discussion of the data upon which the re-allocations rely (Auffenberg 1974). The above checklist constitutes the first step in a re-assessment of the phylogenetic relationships of oriental fossil testudinids. However, this review relies extensively upon the literature and not upon a first hand examination of the material at present stored in the IVPP. For this reason, extensive changes in the classification of Chinese and Mongolian tortoises are deferred.

Four genera have been recognized from eastern Asia: *Testudo, Geochelone, Kansuchelys* and *Sinohadrianus*. None of these are well diagnosed; characterizations prevail instead of comparative diagnoses. I recommend that four genera continue to be recognized, but different genera than those presently accepted. Diagnoses are below.

Testudo: *Testudo* is the only testudinid (except *Pyxis* [Bour 1981] and *Gopherus berlandieri* [J. Howard Hutchison, pers. comm.] that develops an incipient hinge correlated with egg deposition in females) which normally possesses a posterior plastral hinge at the femoral-abdominal sulcus. Not all members of this genus have this hinge (e.g., *Testudo horsfieldii*) and it is sexually dimorphic in some species (Loveridge and Williams 1957). Tortoises of this genus differ further from *Geochelone* in possessing enlarged anal scutes whose median length is equal or exceeds that of the femoral scutes. *Testudo* differs from '*Manouria*' by possessing an entire supracaudal scute. *Testudo* is distinguished from both of the above genera in having undifferentiated marginals in which three marginals contact the second pleural scute (Roger Bour, pers. comm.). In *Testudo,* unlike *Indotestudo,* the pectoral scutes do not overlap the entoplastron; or if such overlap occurs it is parasagittal rather than medial.

Geochelone: *Geochelone* differs from all other Chinese tortoises except *Indotestudo,* by possessing small anal scutes whose median length is very much less than the median length of the femoral scutes. Unlike *Indotestudo,* the pectoral scutes do not overlap the entoplastron.

Indotestudo: This genus differs from all other tortoise genera by possessing a transversely extending humeral-pectoral sulcus which crosses the entoplastron. Bour's (1980) elevation of this subgenus of *Geochelone* to generic level is followed.

'*Manouria*': This primitive genus may or may not be monophyletic. It differs from all other tortoises in having a divided suprapygal which is always divided on both its dorsal and ventral surfaces. (In *Malacochersus* and *T. hermanni* the supracaudal is entire ventrally and divided dorsally.) Furthermore, unlike most tortoises, except *Stylemys,* the neurals are hexagonal and tetragonal, and usually not octagonal. Recent '*Manouria*' (i.e., *Geochelone emys* and *G. impressa*), sometimes have octagonal neurals anteriorly. Also unlike most other tortoises, except *Malacochersus,* the epiplastral projection is not greatly thickened, but is flattened and often concave upon its dorsal surface. *Hadrianus* is included within '*Manouria*' as suggested by Auffenberg (1971). *Kansuchelys* and *Sinohadrianus* are here referred to '*Manouria.*' '*Manouria,*' although easily recognizable, is presently diagnosed by shared primitive features.

Acknowledgments

I wish to thank Gene Gaffney, George Zug, Carl Ernst, Sam McDowell, Richard Vari, and Yeh Hsiang-k'uei for their help during the preparation of this checklist. The comments of an anonymous reviewer increased the clarity of this paper. This work was completed during my tenure as a predoctoral fellow at the National Museum of Natural History, Smithsonian Institution.

Literature Cited

Andrews, C. W. 1906. A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt.—British Museum (Natural History), 324 pp.

Auffenberg, W. 1962. A new species of *Geochelone* from the Pleistocene of Texas.—Copeia 1962(3): 627–636.

———. 1963. Fossil Testudinine turtles of Florida: Genera *Geochelone* and *Floridemys.*—Bulletin of the Florida State Museum 7(2):53–97.

———. 1966. The carpus of land tortoises (Testunidae).—Bulletin of the Florida State Museum 10(5):159–191.

———. 1971. A new fossil tortoise with remarks on the origin of South American tortoises.—Copeia 1971(1):106–117.

———. 1974. Checklist of fossil land tortoises (Testudinidae).—Bulletin of the Florida State Museum 18(3):121–251.

———. 1976. The genus *Gopherus* (Testudinidae). Pt. I. Osteology and relationships of extant species.—Bulletin of the Florida State Museum 20(2):47–120.

Bohlin, B. 1953. Fossil reptiles from Mongolia and Kansu.—Reports of Scientific Expedition, Northwestern Provinces of China. VI. Vertebrate Paleontology, no. 6. Statens Ethnografiska Museum (Stockholm), 109 pp.

Bramble, D. M. 1971. Functional morphology, evolution, and paleoecology of Gopher tortoises.—Unpub. Ph.D. Dissertation, University of California, Berkeley, 351 pp.

———. 1982. *Scaptochelys*: Generic revision and evolution of Gopher tortoises.—Copeia 1982(4): 852–867.

de Broin, F. 1977. Contribution à L'etude des Cheloniens. Cheloniens continentaux du Cretace et du Tertiaire de France.—Memoires du Muséum National d'Histoire Naturelle ser. C, 38:1–366, 115 figs., 38 pls.

Bour, R. 1981. Etude systematique du genere endemique Malagache *Pyxis* Bell, 1827 (Reptilia, Chelonii).—Bulletin de Société Linneene de Lyon 50(4):132–176.

———. 1980. Essai sur la taxonomie Testudinidae actuels (Reptilia, Chelonii).—Bulletin de Muséum National d'Histoire Naturelle, Paris 4, *2*, A(2):541–546.

Chkikvadze, V. 1970. Klassifikacija podklasa Testudinat.—16aja Naucnaja sesia Institute Paleobiologii AN Gruziya SSR., pp. 7–8, Tbilisi.

———. 1972. [On the systematic position of Tertiary gigantic land tortoises of the Palearctic].—Bulletin Academy of Sciences, Georgian SSR 65(3):745–748. [In Russian.]

———. 1973. Treticnyje cerepachi Zajsanskoj Kotliviny.—"Macnierba," 100 pp., Tbilisi.

Gilmore, C. W. 1931. Fossil turtles of Mongolia.—Bulletin of the American Museum of Natural History 59:213–257.

———. 1934. Fossil turtles of Mongolia: A second contribution.—American Museum Novitates 689:1–14.

Glaessner, M. F. 1933. Die Tertiarschildkroten Niedrosterichs.—Neues Jarhbuch für Minerologie, Geologie und Paleontologie, Abteilung B 69:353–387.

———. 1935. Bemerkungen zur tertiären Schildkrotenfauna.—Ungarisches Zentralblatt für Minerologie, Abteilung B, pp. 124–129.

Gradzinski, R., J. Kazmierczak, and J. Lefeld. 1968. Geographical and geological data from the Polish-Mongolian Palaeontological Expeditions. Results of the Polish-Mongolian Palaeontological Expeditions, I.—Palaeontologia Polonica 19:33–82.

Hutchison, J. H. 1980. Turtle stratigraphy of the Willwood formation, Wyoming: Preliminary results. *In* Early Cenozoic Paleontology and Stratigraphy of the Bighorn Basin, Wyoming.—University of Michigan, Papers in Paleontology 24:115–118.

Khozatsky, L. E. 1953. Voprosy Paleontologii 1:20–31.

Loveridge, A., and E. E. Williams. 1957. Revision of the African tortoises and turtles of the suborder Cryptodira.—Bulletin of the Museum of Comparative Zoology, Harvard 115:163–557.

Matthew, W. D., and W. Granger. 1923. The fauna of the Ardyn Obo formation.—American Museum Novitates 98:1–5.

Mlynarski, M. 1955. Zolwie zu Pliocenu Polski.—Acta Geologica Polonica 5(2):161–214.

———. 1968. Results of the Polish-Mongolian Paleontological Expedition. Pt. I. Notes of the tortoises of the Tertiary of Mongolia.—Palaeontologia Polonica (19):85–97.

———. 1976. Testudines.—Handbuch der Palaoherpetologie 7:1–130.

Ping, C. 1929. A new Eocene land turtle from Honan.—Bulletin of the Geological Society of China 8(3):231–238.

Schleich, H.-H. 1981. Jungtertiäre Schildkroten Suddeutschlands unter besonderer Berucksichtigung der Fundstelle Sandelhausen.—Courier Forschungsinstitut Senckenberg 48:1–372.

Van Devender, T., K. B. Moody, and A. H. Harris. 1979. The desert tortoise (*Gopherus agassizii*) in the Pleistocene of the northern Chihuahuan desert.—Herpetologica 32:298–304.

Wiman, C. 1930. Fossile Schildkroten aus China.—Paleontologica Sinica (Peking) ser. C 6(3):1–57.

Yeh, H.-k. 1963a. Fossil turtles of China.—Palaeontologica Sinica (150):1–122.

———. 1963b. A new Quaternary *Testudo* from the *Gigantopithecus* cave, Liucheng, Kwangsi.—Vertebrata PalAsiatica 7(3):224–229.

———. 1965. New materials of Fossil turtles of Inner Mongolia.—Vertebrata PalAsiatica 9(1): 48–69.

———. 1979. Fossil testudinids from Jiyuan, Henan.—Vertebrata PalAsiatica 17(4):310–317.

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

PROC. BIOL. SOC. WASH.
96(3), 1983, pp. 581–597

NEOTROPICAL MONOGENEA.* 5. FIVE NEW SPECIES FROM THE ARUANÃ, *OSTEOGLOSSUM BICIRROSUM* VANDELLI, A FRESHWATER TELEOST FROM BRAZIL, WITH THE PROPOSAL OF *GONOCLEITHRUM* N. GEN. (DACTYLOGYRIDAE: ANCYROCEPHALINAE)

Delane C. Kritsky and Vernon E. Thatcher

Abstract.—*Gonocleithrum* n. gen. (Dactylogyridae: Ancyrocephalinae) is proposed for five new species collected from the gills of the aruanã, *Osteoglossum bicirrosum* Vandelli, from Janauacá Lake, near the south bank of the Solimões River, Manaus, Amazonas, Brazil, as follows: *G. planacrus, G. aruanae, G. coenoideum, G. cursitans,* and *G. planacroideum* new species. *Gonocleithrum* is similar to *Urocleidoides* Mizelle and Price, 1964, but has a ventral gonadal bar lying near the anterior end of the ovary. A table is presented showing the known freshwater monogenean fauna of fishes from the Neotropical Region.

The Neotropical Region and particularly South America support an unique freshwater monogenean fauna which differs significantly from that of North America. Of the 26 known genera of Monogenea from this region (*Gonocleithrum* n. gen. included), 23 are at present restricted under natural conditions to the neotropics (Table 1). In addition, re-examination of the eight species included in *Cleidodiscus* and *Urocleidus* (both North American genera) will undoubtedly result in their transfer to other genera unique to the Neotropical Region.

Gussev (1978) suggests that the South American fauna of Monogenea has an ancient evolutionary relationship to that of Africa and in fact considers the African genus *Characidotrema* a junior synonym of *Jainus*. While we do not accept this synonymy, since it is based on information published in original articles and not on reexamination of the species involved, the apparent resemblance between species of these genera provides support for Gussev's hypothesis. Although studies on the Neotropical and the Ethiopian (African) Monogenea have just begun to determine the faunas present, a more thorough knowledge of both is necessary to substantiate the relationship.

Material and Methods

The host, *Osteoglossum bicirrosum* Vandelli, was collected on two occasions from Janauacá Lake, near the south bank of the Solimões River, Manaus, Amazonas, Brazil, on 21 March and 14 August 1978, respectively. These fish were

---

* The title of our series on Neotropical monogeneans is changed to conform with resolutions of the Round Table Discussion, *Monogenea: Problems of Systematics Biology and Ecology*, held on 23 August, 1978 during the IV International Congress of Parasitology in Warsaw, Poland (Euzet and Prost 1981, Review Advances Parasitology, Warszawa 1003-1004).

Table 1.—Monogenea from freshwater fishes of the Neotropical Region.

	Parasite	Host	Reference
Gyrodactylidae			
Gyrodactylinae			
"*Gyrodactylus*"	*G. neotropicalis*	*Astyanax fasciatus*	Kritsky and Fritts (1970)
	G. costaricensis	*Poecilia sphenops*	Kritsky and Fritts (1970)
	G. bullatarudis	*Poecilia sphenops*	Kritsky and Fritts (1970)
Phanerothecium	*P. caballeroi*	*Cephalosilurus zungaro*	Kritsky and Thatcher (1977)
Paragyrodactyloides	*P. superbus*	*Corydoras paleatus*	Szidat (1973)
Isancistrinae			
Anacanthocotyle	*A. anacanthocotyle*	*Astyanax fasciatus*	Kritsky and Fritts (1970)
Dactylogyridae			
Dactylogyrinae			
Trinidactylus	*T. cichlasomatis*	*Cichlasoma bimaculatum*	Hanek, Molnar, and Fernando (1974)
Trinigyrus	*T. hypostomatis*	*Hypostomus robinii*	Hanek, Molnar, and Fernando (1974)
Anacanthorinae			
Anacanthorus	*A. anacanthorus*	*Serrasalmus nattereri*	Mizelle and Price (1965)
	A. brazilensis	*Serrasalmus nattereri*	Mizelle and Price (1965)
	A. brevis	*Brycon melanopterus*	Mizelle and Kritsky (1969b)
	A. colombianus	*Salminus affinis*	Kritsky and Thatcher (1974)
	A. cuticulovaginus	*Salminus affinis*	Kritsky and Thatcher (1974)
	A. elegans	*Brycon melanopterus*	Kritsky, Thatcher, and Kayton (1979)
	A. kruidenieri	*Brycon melanopterus*	Kritsky, Thatcher, and Kayton (1979)
	A. neotropicalis	*Serrassalmus nattereri*	Mizelle and Price (1965)
	A. spathulatus	*Colossoma bidens*	Kritsky, Thatcher, and Kayton (1979)
		C. macropomum	Kritsky, Thatcher, and Kayton (1979)
	A. spiralocirrus	*Brycon melanopterus*	Kritsky, Thatcher, and Kayton (1979)
Anacanthoroides	*A. mizellei*	*Prochilodus reticulatus*	Kritsky and Thatcher (1976)
Ancyrocephalinae			
Amphocleithrium	*A. paraguayensis*	*Pseudoplatisma* sp.	Price and Romero (1969)
"*Cichlidogyrus*"	**C. sclerosus*	*Tilapia mossambica*	Kritsky and Thatcher (1974)
	**C. tilapiae*	*Tilapia mossambica*	Kritsky and Thatcher (1974)

Table 1.—Continued.

Parasite		Host	Reference
"*Cleidodiscus*"	*C. amazonensis*	*Serrasalmus nattereri*	Mizelle and Price (1965)
	C. microcirrus	*Hemiodus semitaeniatus*	Price and Schlueter (1967)
	C. piranhus	*Serrasalmus nattereri*	Mizelle and Price (1965)
	C. serrasalmus	*Serrasalmus nattereri*	Mizelle and Price (1965)
Dawestrema	*D. cycloancistrium*	*Arapaima gigas*	Price and Nowlin (1967)
Fridericianella	***F. ovicola*	*Arius commersonii*	Brandes (1894)
Gonocleithrum	*G. aruanae*	*Osteoglossum bicirrosum*	Kritsky and Thatcher (*nobis*)
	G. coenoideum	*Osteoglossum bicirrosum*	Kritsky and Thatcher (*nobis*)
	G. cursitans	*Osteoglossum bicirrosum*	Kritsky and Thatcher (*nobis*)
	G. planacroideum	*Osteoglossum bicirrosum*	Kritsky and Thatcher (*nobis*)
	G. planacrus	*Osteoglossum bicirrosum*	Kritsky and Thatcher (*nobis*)
Jainus	*J. amazonensis*	*Brycon melanopterus*	Kritsky, Thatcher, and Kayton (1980)
	J. hexops	*Astyanax fasciatus*	Kritsky and Leiby (1972)
	J. jainus	*Chalceus macrolepidotus*	Mizelle, Kritsky, and Crane (1968)
	J. robustus	*Creatochanes affinis*	Mizelle, Kritsky, and Crane (1968)
Longihaptor	*L. longihaptor*	*Cichla ocellaris*	Mizelle and Kritsky (1969a)
Monocleithrium	*M. lavergneae*	*Hemiodus semitaeniatus*	Price and McMahon (1966)
Tereancistrum	*T. kerri*	*Brycon melanopterus*	Kritsky, Thatcher, and Kayton (1980)
	T. ornatus	*Prochilodus reticulatus*	Kritsky, Thatcher, and Kayton (1980)
	T. parvus	*Leporinus fasciatus*	Kritsky, Thatcher, and Kayton (1980)
Trinibaculum	*T. brazilensis*	*Brycon melanopterus*	Kritsky, Thatcher, and Kayton (1980)
Unilatus	*U. unilatus*	*Hypostomus robinii*	Molnar, Hanek, and Fernando (1974)
		Plecostomus sp.	Mizelle and Kritsky (1967)
	U. anoculus	*Plecostomus bolivianus*	Price (1968)
	U. brittani	*Plecostomus* sp.	Mizelle, Kritsky, and Crane (1968)
Urocleidoides	*U. affinis*	*Creatochanes affinis*	Mizelle, Kritsky, and Crane (1968)
	U. alii	*Cichlasoma bimaculatum*	Molnar, Hanek, and Fernando (1974)
	U. amazonensis	*Phractocephalus hemiliopterus*	Mizelle and Kritsky (1969a)
	U. anops	*Characidium caucanum*	Kritsky and Thatcher (1974)
	U. carapus	*Gymnotus carapo*	Mizelle, Kritsky, and Crane (1968)
	U. catus	*Phractocephalus hemiliopterus*	Mizelle and Kritsky (1969a)
	U. chavarriai	*Rhamdia* sp.	Price (1938)

Table 1.—Continued.

	Parasite	Host	Reference
Urocleidoides.—Continued.		*R. quelen*	Molnar, Hanek, and Fernando (1974)
		R. sebae	Molnar, Hanek, and Fernando (1974)
	U. cichlasomatis	*Cichlasoma bimaculatum*	Molnar, Hanek, and Fernando (1974)
	U. corydori	*Corydoras aeneus*	Molnar, Hanek, and Fernando (1974)
	U. costaricensis	*Astynax fasciatus*	Price and Bussing (1967)
			Kritsky and Leiby (1972)
			Kritsky and Thatcher (1974)
		A. bimaculatus	Molnar, Hanek, and Fernando (1974)
		Curimata argentea	Molnar, Hanek, and Fernando (1974)
	U. curimatae	*Curimata argentea*	Molnar, Hanek, and Fernando (1974)
	U. dobosi	*Cichlasoma bimaculatum*	Molnar, Hanek, and Fernando (1974)
	U. gymnotus	*Gymnotus carapo*	Mizelle, Kritsky and Crane (1968)
	U. heteroancistrium	*Astyanax fasciatus*	Price and Bussing (1968)
			Kritsky and Leiby (1972)
			Kritsky and Thatcher (1974)
	U. kabatai	*Astyanax bimaculatus*	Molnar, Hanek, and Fernando (1974)
	U. lebedevi	*Pimelodus grosskopfi*	Kritsky and Thatcher (1976)
	U. mamaevi	*Cephalosilurus zungaro*	Kritsky and Thatcher (1976)
	U. margolisi	*Corydoras aeneus*	Molnar, Hanek, and Fernando (1974)
	U. megorchis	*Sorubim lima*	Mizelle and Kritsky (1969a)
	U. microstomus	*Hemigrammus microstomus*	Mizelle, Kritsky and Crane (1968)
	****U. minuta*	*Lebistes reticulata*	Kohn and Paperna (1964)
	U. reticulatus	*Lebistes reticulata*	Mizelle and Price (1964)
	U. robustus	*Rhamdia* sp.	Mizelle and Kritsky (1969a)
	****U. spiralocirra*	*Pterophyllum eimekei*	Kohn and Paperna (1964)
	U. stictus	*Hyphessobrycon stictus*	Mizelle, Kritsky, and Crane (1968)
	U. strombicirrus	*Astyanax fasciatus*	Price and Bussing (1967)
			Kritsky and Thatcher (1974)

Table 1.—Continued.

	Parasite	Host	Reference
Urocleidoides.—Continued.	*U. travassosi*	*Rhamdia* sp.	Price (1938)
		R. quelen	Molnar, Hanek, and Fernando (1974)
		R. sebae	Molnar, Hanek, and Fernando (1974)
	U. trinidadensis	*Astyanax bimaculatus*	Molnar, Hanek, and Fernando (1974)
	U. variabilis	*Symphysodon discus*	Mizelle and Kritsky (1969a)
	U. virescens	*Eigenmannia virescens*	Mizelle, Kritsky, and Crane (1968)
"*Urocleidus*"	*U. aequidens*	*Aequidens maroni*	Price and Schlueter (1967)
	U. cavanaughi	*Aequidens maroni*	Price (1966)
	U. crescentis	*Serrasalmus nattereri*	Mizelle and Price (1965)
	U. orthus	*Serrasalmus nattereri*	Mizelle and Price (1965)
Curvianchoratinae			
Curvianchoratus	*C. hexacleidus*	*Curimata argentea*	Hanek, Molnar, and Fernando (1974)
Linguadactyloidinae			
Linguadactyloides	*L. brinkmanni*	*Colossoma macropomum*	Thatcher and Kritsky (1983)
Monocotylidae			
Potamotrygonocotyle	*P. tsalickisi*	*Potamotrygon circularis*	Mayes, Brooks, and Thorson (1981)
Hexabothriidae			
Paraheteronchocotyle	*P. amazonensis*	*Potamotrygon circularis*	Mayes, Brooks, and Thorson (1981)

[1] Genera in quotes are not unique to the Neotropical Region.

* These species and their host are recent introductions to the Neotropical Region by man.

** This species is tentatively placed in Ancyrocephalinae until more is known about its internal anatomy and morphology of its haptoral armament.

*** These species, originally described in *Gussevia* Kohn and Paperna, 1964, are placed in *Urocleidoides* since we consider *Gussevia* a junior synonym of *Urocleidoides*.

After this paper went to press, we became aware of two papers by D. M. Suriano, in which three new species of Monogenea were described from freshwater fishes of Argentina: *Notodiplocerus singularis* Suriano, 1980 (Ancyrocephalinae) from *Pseudocurimata gilberti* (in Neotropica 26:131–143); and *Androspira triangula* Suriano, 1981, and *A. chascomusensis* Suriano, 1981 (Ancyrocephalinae) from *Pseudocurimata gilberti* (in Neotropica 27:67–78). Both *Notodiplocerus* and *Androspira* were proposed as new genera in Suriano's papers.

treated and parasites collected from the gills and stored according to the procedures of Kritsky and Thatcher (1974). Parasites were stained with Mayer's carmine or Gomori's trichrome and mounted in permount for observing internal organs. Other specimens were mounted unstained in Gray and Wess' medium for study of sclerotized structures. Measurements of parasites were made according to the guidelines of Mizelle and Klucka (1953) except that the cirrus measurement represents the diameter of the first ring (proximal) of the cirrus coil; all measurements are in micrometers. Figures were prepared with the aid of a microprojector or camera lucida. Type-specimens are deposited in the collections of the Instituto Nacional de Pesquisas da Amazônia (INPA), the helminthological collection of the National Museum of Natural History, Smithsonian Institution (USNM), and the University of Nebraska State Museum (UNSM) as indicated below.

Gonocleithrum, new genus

Diagnosis.—Dactylogyridae, Ancyrocephalinae. Body divisible into cephalic region, trunk, peduncle, and haptor. Tegument thin, smooth. Cephalic lobes, head organs, cephalic glands present. Four eyes. Mouth subterminal, midventral; pharynx muscular, glandular; esophagus present; intestinal crura 2, confluent posterior to testis, lacking diverticulae. Gonads intercecal, overlapping; testis dorsoposterior to ovary. Vas deferens looping left intestinal crus; seminal vesicle a simple dilation of vas deferens; copulatory complex comprising coiled or modified coiled cirrus, accessory piece. Vagina sinistral, seminal receptacle present. Ventral Y-shaped gonadal bar lying near anterior end of ovary. Vitellaria well developed. Haptor armed with dorsal and ventral pair of anchors, dorsal and ventral bar, 7 pairs of flexible hooks with ancyrocephaline distribution (Mizelle 1936). Parasites of Osteoglossidae.

Type-species and host.—*Gonocleithrum planacrus* n. sp. from *Osteoglossum bicirrosum* Vandelli, Janauacá Lake, near the south bank of the Solimões River, Manaus, Amazonas, Brazil.

Other species.—*Gonocleithrum aruanae* n. sp., *G. coenoideum* n. sp., *G. cursitans* n. sp., *G. planacroideum* n. sp., all from *Osteoglossum bicirrosum.*

Remarks.—*Gonocleithrum* is similar to the Neotropical genus *Urocleidoides* Mizelle and Price, 1964, in that the cirrus is comprised of a coil with few to many rings and by the general arrangement of the haptoral armament. The new genus differs from *Urocleidoides* by possessing a Y-shaped gonadal bar near the anterior end of the ovary.

Based on the fact that *Urocleidoides* species occur on fishes from several orders and families, Gussev (1978) suggests that this genus may be an assemblage of species representing several different genera. In fact, if it were not for the presence of the gonadal bar, the five following species could be placed in *Urocleidoides* as it is defined at present. All five species of *Gonocleithrum* are from *Osteoglossum bicirrosum* which is a member of the primitive order of bony-tongued fishes, Osteoglossiformes. No species of *Urocleidoides* has been reported from this host group.

Price and Nowlin (1967) reported *Dawestrema cycloancistrium* from the gills of *Arapaima gigas* (Osteoglossidae, Arapaiminae) in the Amazon River and its tributaries. Also, Paperna (1969) described *Heterotesia voltae* from *Heterotis* *niloticus* (Osteoglossidae, Heterotinae) in Africa. Species of *Gonocleithrum* are distinguished from these ancyrocephalines infesting fishes of the Osteoglossiformes by possessing a gonadal bar.

The function of the gonadal bar is not clear, but it could be involved in orientation during copulation. The protruding anterior arms of the bar form a pouch-like structure on the ventral surface of the worm that could assist in positioning of the copulating partner. We feel that the gonadal bar is not analogous to the vaginal sclerite of some *Urocleidoides* species (*U. reticulatus* Mizelle and Price, 1964, and *U. anops* Kritsky and Thatcher, 1974), which apparently functions as a supporting structure of the vagina.

Gonocleithrum planacrus, new species
Figs. 1–8

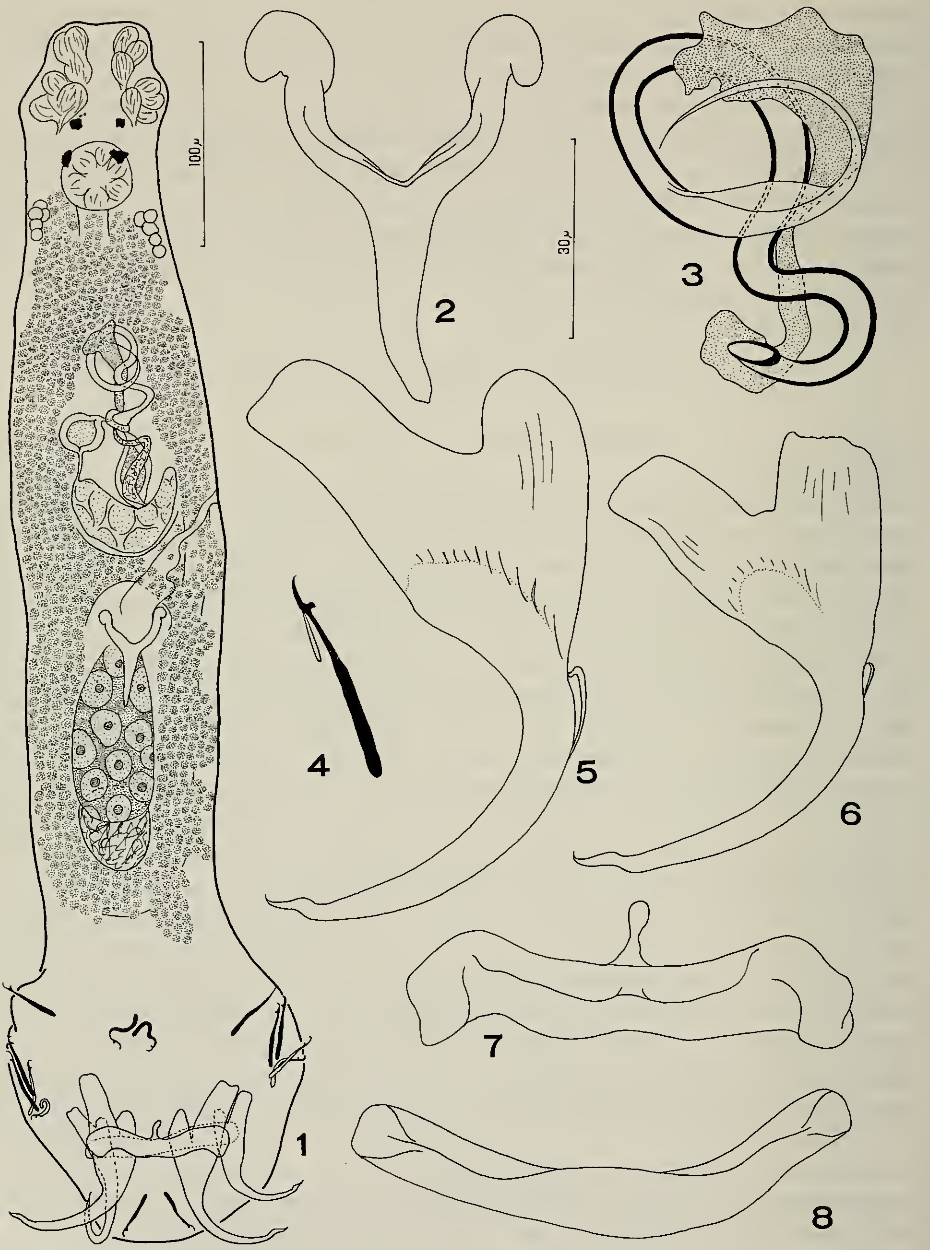
Type-specimens.—Holotype, INPA-234-1; paratype, USNM 77377; paratype, UNSM 21480.

Description (based on 3 specimens).—Body fusiform; length 616 (604–628), greatest trunk width 100 (98–102) near midlength. Cephalic lobes well developed, 2 terminal, 2 bilateral; head organs large, lying in cephalic lobes and adjacent cephalic area; cephalic glands unicellular, situated in 2 bilateral groups posterolateral to pharynx near ventral surface. Members of anterior pair of eyes smaller, usually closer together than members of posterior pair; eye granules small, irregular to subovate; accessory granules absent or very few in proximity of eyes. Pharynx spherical, 35 (33–37) in diameter. Peduncle broad; haptor subhexagonal, 147 (143–151) wide, 136 (128–144) long. Anchors similar in shape; each with large base, short shaft, point with subterminal bends; ventral anchor 83 (79–85) long, base 42 (35–50) wide; dorsal anchor 61 (60–64) long, base 38 (33–43) wide. Anchor filament variable, double. Ventral bar 71 (68–76) long, broad, rod-shaped, with anteriorly directed medial process; dorsal bar 80 (74–89) long, rod-shaped, with slight medial bend. Hooks similar; each with inflated proximal shank, depressed thumb, fine point; hook pairs 1, 2, 3, 4, 6, 7—31 (30–32) long, pair 5—20 to 21 long; FH loop ⅓ shank length. Cirrus a coiled, heavily sclerotized tube, with 2 rings, subterminal flange, finely tapered tip; diameter of complete ring 28 (27–29). Accessory piece a variable fleshy structure basally articulated to cirrus base. Testis subspherical, 38 to 39 in diameter; seminal vesicle inconspicuous; prostatic reservoirs 2, with thick walls; prostate a large crescent of cells located anterior to vitelline commissure. Ovary elongate ovate, 45 (42–49) wide, 105 (100–110) long; seminar receptacle, oviduct, ootype, uterus, genital pore not observed; vagina an irregular and lightly sclerotized tube; vitellaria dense, coextensive with gut. Gonadal bar 62 to 63 long; anterior arms expanded, recurved.

Remarks.—*Gonocleithrum planacrus* is the type-species for the genus. The specific name is from Greek (*plano* = wandering + *acrus* = tip) and refers to the shape of the anchor points.

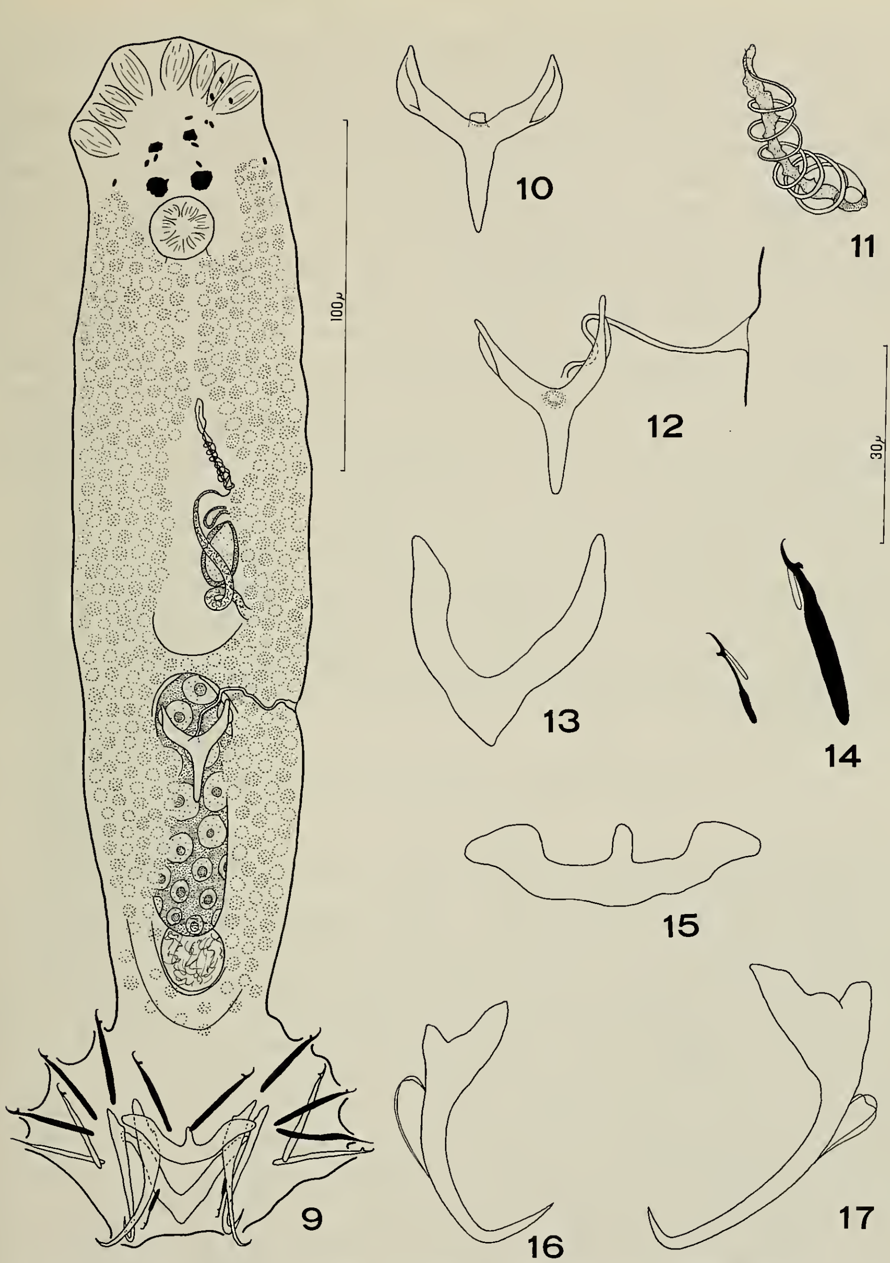
Gonocleithrum aruanae, new species
Figs. 9–17

Type-specimens.—Holotype, INPA-236-1; paratypes, INPA-236-2 to 5; paratypes, USNM 77379; paratype, USNM 21482.



Figs. 1–8. *Gonocleithrum planacrus*: 1, Ventral view of holotype; 2, Gonadal bar; 3, Copulatory complex; 4, Hook; 5, Ventral anchor; 6, Dorsal anchor; 7, Ventral bar; 8, Dorsal bar. All figures are drawn to the same scale (30 micrometers) except Fig. 1 (100 micrometers).

Description (based on 20 specimens).—Body foliform; length 334 (309–378), greatest trunk width 70 (52–91) in anterior half. Two terminal, 2 bilateral cephalic lobes inconspicuous; well-developed head organs usually in 4 distinct pairs; cephalic glands obscured by vitellaria. Eyes equidistant, members of anterior pair



Figs. 9–17. *Gonocleithrum aruanae*: 9, Composite drawing of whole mount (ventral); 10, Gonadal bar; 11, Copulatory complex; 12, Vagina and gonadal bar; 13, Dorsal bar; 14, Hooks; 15, Ventral bar; 16, Dorsal anchor; 17, Ventral anchor. All figures are drawn to the same scale (30 micrometers) except Fig. 9 (100 micrometers).

smaller than those of posterior pair; eye granules ovate, medium in size; accessory granules throughout cephalic area. Pharynx spherical, 18 (15–20) in diameter. Peduncle moderately broad; haptor subhexagonal, 92 (68–106) wide, 71 (60–76) long. Anchors dissimilar; ventral anchor 45 (38–50) long, with well-developed roots, elongate shaft, sharply recurved point, base 20 (18–22) wide; dorsal anchor 36 (34–38) long, with small base, curved shaft, straight point, base 14 (12–16) wide. Anchor filament variable, double. Ventral bar 36 (32–39) long, with enlarged terminations, anteriorly directed medial process; dorsal bar V-shaped, 35 (32–37) long. Hook pairs 1, 2, 3, 4, 6, 7—28 (24–32) long, similar; each with inflated shank, depressed thumb, fine point. Hook pair 5—15 (14–16) long, with basal inflation of shank, erect thumb, fine point. FH loop ¼ shank length except pair 5 (½ shank length). Cirrus a coil of about 7 rings, basal ring diameter 9 (8–10); accessory piece variable, lying within cirrus rings, articulated to cirrus base. Testis subspherical, 22 (15–27) in diameter; seminar vesicle poorly defined; prostatic reservoirs 2, each with thick wall; prostate not observed. Ovary elongate ovate 24 (20–31) wide, 53 (46–63) long; seminar receptacle, oviduct, ootype, uterus, genital pore not observed; vagina a simple sclerotized tube with distal flare; vitellaria dense, coextensive with gut. Gonadal bar 30 (28–33) long, with anterior arms slightly longer than base; small truncate process near base of anterior arms.

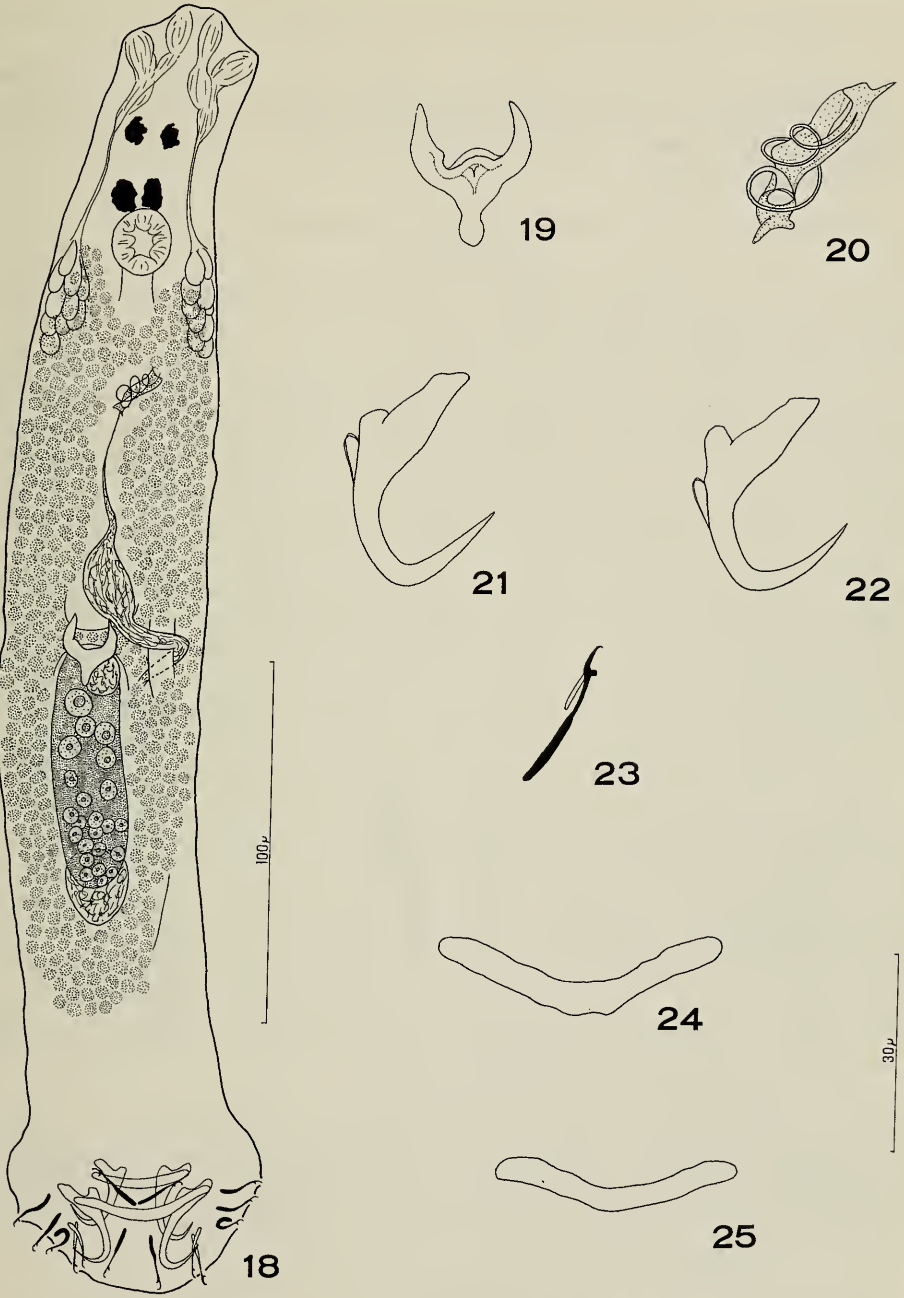
Remarks.—This species is easily confused with *Gonocleithrum cursitans* n. sp., with which it was found on *Osteoglossum bicirrosum* in about equal numbers. The anchors, bars, and hooks are nearly impossible to distinguish in these species. However, *G. aruanae* n. sp. is separated from *G. cursitans* by having 1) a stout, more robust gonadal bar, 2) cirrus rings with noticeably smaller diameter, and 3) a simple tubular vagina which lacks the proximal coils of *G. cursitans*. The species name is derived from the local name of the host.

Gonocleithrum coenoideum, new species

Figs. 18–25

Type specimens.—Holotype, INPA-238-1; paratypes, INPA-238-2 to 6; paratypes, USNM 77381; paratype, UNSM 21484.

Description (based on 34 specimens).—Body fusiform; length 389 (294–477), greatest trunk width 80 (45–117) near midlength. Cephalic lobes inconspicuous, 2 terminal, 2 bilateral; head organs well developed, one lying in each cephalic lobe and adjacent cephalic area; cephalic glands numerous, unicellular, lying posterolateral to pharynx. Eyes large; members of posterior pair larger, closer together than those of anterior pair; eye granules usually small, subovate; accessory granules usually absent. Pharynx spherical, 21 (18–23) in diameter. Peduncle broad; haptor subhexagonal, 67 (45–83) wide, 55 (38–76) long. Anchors similar, each with elongate superficial root, short shaft, long curved point; ventral anchor 32 (28–34) long, base 16 (13–19) wide; dorsal anchor 31 (28–35) long, base 16 (13–18) wide. Anchor filament variable, double. Bars similar, broadly V-shaped; ventral bar 37 (32–42) long; dorsal bar 29 (25–34) long. Hooks similar, each with inflated proximal shank, depressed thumb, fine point; hook pairs 1, 2, 3, 4, 6, 7—22 (20–24) long, pair 5—19 (18–20) long. FH loop ⅓ shank length. Cirrus a coil with 3–4 rings, basal ring diameter 11 (10–12); accessory piece variable, basally articulated to cirrus base. Testis subovate, 12 to 13 in diameter; seminal vesicle large; prostatic reservoirs not observed. Ovary bacilliform, 18 (13–22) wide, 59 (49–69) long; oviduct, ootype, uterus, genital pore not observed; vagina nonsclerotized; seminar receptacle subspherical, lying dorsal to gonadal bar; vitellaria



Figs. 18–25. *Gonocleithrum coenoideum*: 18, Composite drawing of whole mount (ventral); 19, Gonadal bar; 20, Copulatory complex; 21, Ventral anchor; 22, Dorsal anchor; 23, Hook; 24, Ventral bar; 25, Dorsal bar. All figures are reproduced to the same scale (30 micrometers) except Fig. 18 (100 micrometers).

dense, coextensive with gut. Gonadal bar 23 (20–26) long, with tapered arms and bulbous base.

Remarks.—*Gonocleithrum coenoideum* is not closely related to any of the species in the genus. However, the structure of the copulatory complex suggests affinity to *G. cursitans* and *G. aruanae*. The specific name is from Greek (*coeno* = common + *oides* = like).

Gonocleithrum cursitans, new species

Figs. 26–33

Type-specimens.—Holotype, INPA-237-1; paratypes, INPA-237-2 to 4; paratypes, USNM 77380; paratype, UNSM 21483.

Description (based on 18 specimens).—Body foliform; length 338 (279–378), greatest trunk width 69 (53–83) in anterior half. Two terminal, 2 bilateral cephalic lobes poorly developed; head organs well developed, 3 pairs; cephalic glands obscured by vitellaria. Eyes equidistant, members of posterior pair larger than those of anterior pair; eye granules elongate ovate, medium in size; accessory granules throughout cephalic region. Pharynx spherical, 15 (12–17) in diameter. Peduncle broad; haptor subhexagonal, 91 (75–121) wide, 66 (53–72) long. Anchors dissimilar; ventral anchor 43 (41–45) long, with well-developed roots, bent shaft, sharply recurved point, base 21 (20–23) wide; dorsal anchor 34 (32–36) long, with elongate superficial root, curved shaft, long point, base 14 (13–15) wide. Anchor filament variable, double. Ventral bar 40 (36–47) long, with enlarged ends, median anterior process; dorsal bar 40 (35–47) long, broadly V-shaped. Hook pairs 1, 2, 3, 4, 6, 7 similar, each with inflated shank, depressed thumb, fine point; hook pair 1—36, pair 2—26 (25–27), pairs 3, 4, 6, 7—30 (28–33) long; Hook pair 5—15 to 16 long, with inflated proximal shank, erect thumb, fine point. FH loop ⅓ shank length except hook 5 (½ shank length). Cirrus a coil with 5–6 rings, basal ring diameter 20 (18–23); accessory piece a spiral rod lying within cirrus rings, basally articulated to cirrus base. Testis subspherical, 19 (15–23) in diameter; seminal vesicle poorly defined; prostatic reservoirs 2, with conspicuous walls. Ovary bacilliform, 23 (22–24) wide, 60 (48–72) long; oviduct, seminal receptacle, ootype, uterus, genital pore not observed. Vagina a delicate sclerotized tube, coiled anterior to gonadal bar; vitellaria dense, coextensive with gut. Gonadal bar with inconspicuous flanges on anterior arms, small medial truncate process near base of anterior arms; bar 30 (27–33) long.

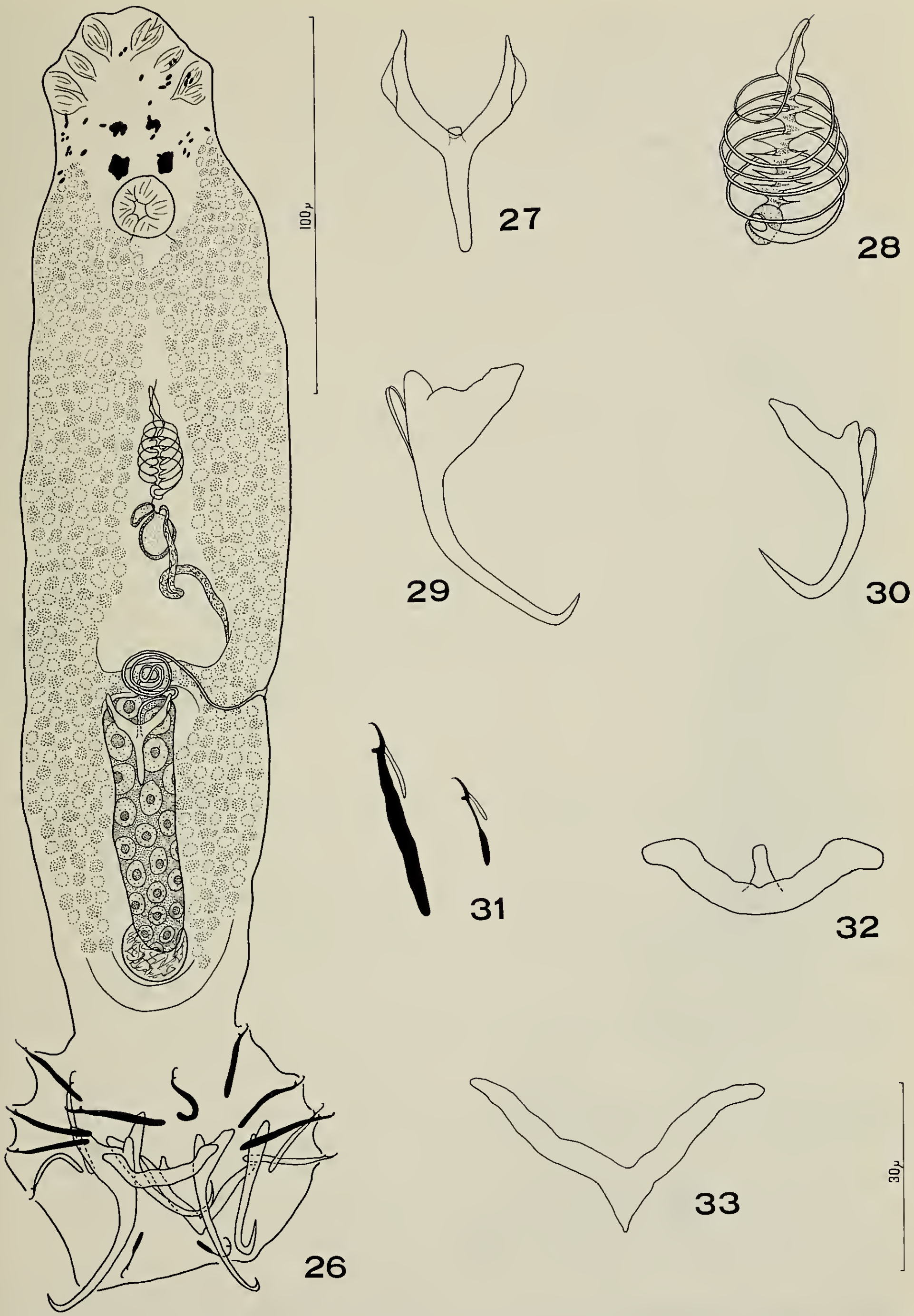
Remarks.—*Gonocleithrum cursitans* is obviously a close relative of *G. aruanae*. Distinguishing characteristics, which include the morphology of the gonadal bar, copulatory complex, and vagina, are explained in the remarks for *G. aruanae*. The specific name is from Latin (*cursitans* = running about).

Gonocleithrum planacroideum, new species

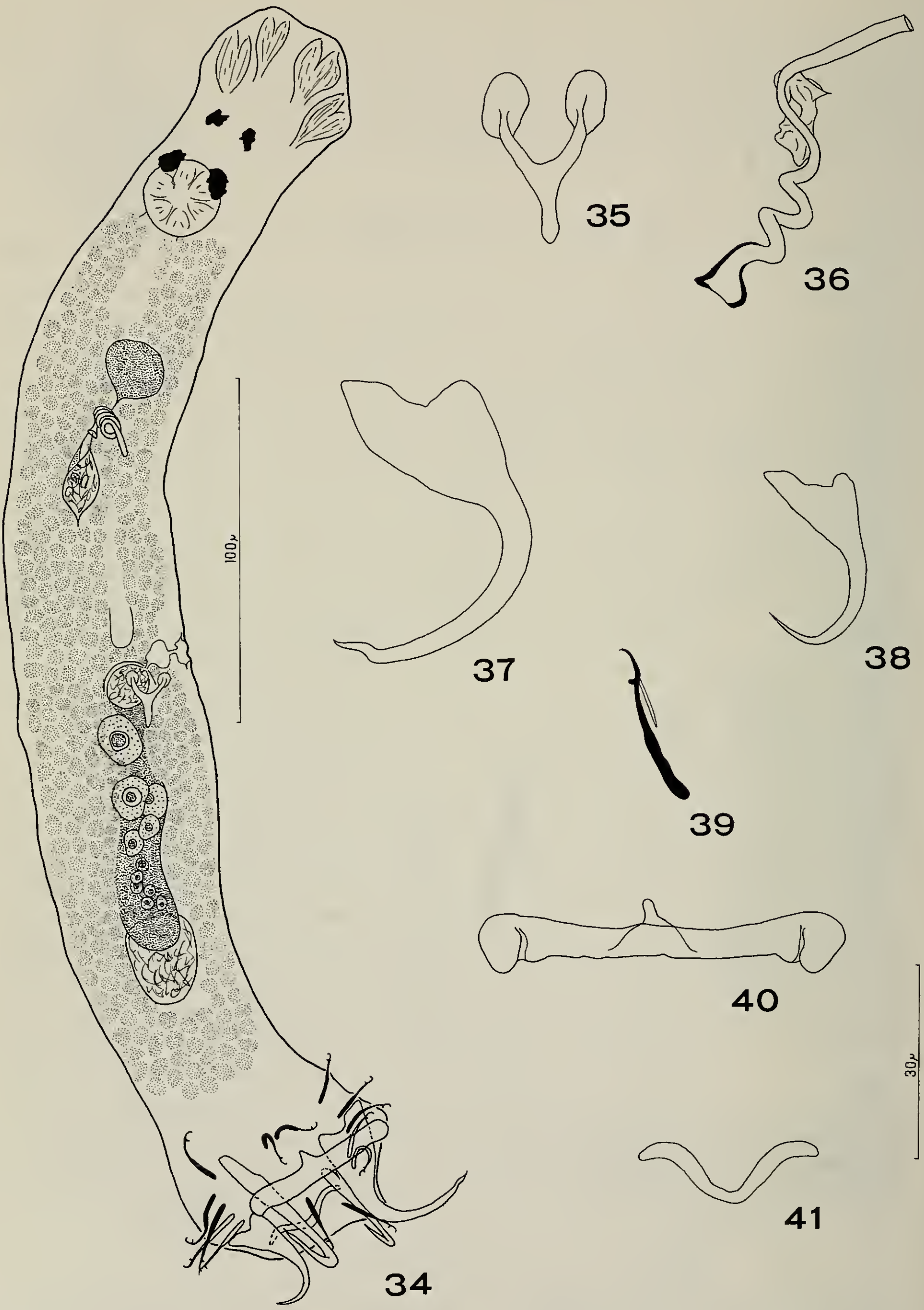
Figs. 34–41

Type-specimens.—Holotype, INPA-235-1; paratypes, USNM 77378; paratype, UNSM 21481; INPA-235-2.

Description (based on 6 specimens).—Body fusiform; length 372 (340–408), greatest trunk width 58 (53–72) at level of gonads. Two terminal, 2 bilateral cephalic lobes poorly developed; head organs well developed, usually 2 pairs; cephalic glands inconspicuous. Members of posterior pair of eyes larger, farther



Figs. 26–33. *Gonocleithrum cursitans*: 26, Composite drawing of whole mount (ventral); 27, Gonadal bar; 28, Copulatory complex; 29, Ventral anchor; 30, Dorsal anchor; 31, Hooks; 32, Ventral bar; 33, Dorsal bar. All figures are drawn to the same scale (30 micrometers) except Fig. 26 (100 micrometers).



Figs. 34–41. *Gonocleithrum planacroideum*: 34, Ventral view of holotype (specimen slightly rolled to left); 35, Gonadal bar; 36, Copulatory complex; 37, Ventral anchor; 38, Dorsal anchor; 39, Hook; 40, Ventral bar; 41, Dorsal bar. All figures are drawn to the same scale (30 micrometers) except Fig. 34 (100 micrometers).

apart than those of anterior pair; eye granules irregular; accessory granules absent. Pharynx spherical, 21 (19–22) in diameter; gut inconspicuous. Peduncle broad; haptor subhexagonal, 69 (64–76) wide, 64 (56–68) long. Anchors dissimilar; ventral anchor 41 (36–47) long, with large base, curved shaft, point with subterminal bends, base 20 (15–23) wide; dorsal anchor 28 (25–30) long, with well-developed roots, curved shaft and point, base 12 (11–13) wide. Anchor filament not observed. Ventral bar 51 (46–58) long, rod-shaped, with expanded ends, medial anterior process; dorsal bar broadly V-shaped, 30 (29–31) long. Hooks similar, each with inflated proximal shank, erect thumb, fine point; hook pairs 1, 2, 3, 4, 6, 7—23 (21–26) long, pair 5—17 to 18 long; FH loop 2/5 shank length. Cirrus a coiled tube with 3–4 rings, basal ring diameter 6 (5–7); accessory piece variable, not articulated to cirrus base. Testis subovate, 24 (16–32) in diameter; vas deferens not observed; seminal vesicle large; prostatic reservoirs with delicate wall (one observed). Ovary bacilliform, 28 wide, 66 (68–70) long; oviduct, uterus, ootype, genital pore not observed; vagina tubular with variable diameter; seminal receptacle subspherical, lying dorsal to gonadal bar; vitelleria dense, coextensive with gut. Gonadal bar 25 (23–28) long, with enlarged terminations of anterior arms.

Remarks.—This species most closely resembles *Gonocleithrum planacrus* as shown by the morphology of the ventral anchor. The two species are easily separated by the comparative morphology of the dorsal anchor, dorsal bar, gonadal bar, and copulatory complex. The specific name, from Greek, indicates the relationship of these two species.

Literature Cited

Brandes, G. 1894. *Fridericianella ovicola* n. g., n. sp. Ein neuer monogenetishcher Trematod.—Abhandlungen der Naturforschenden Gesellschaft zu Halle Bd. XX. Jubiläums–Festschrift: 303–310.

Gussev, A. V. 1978. Monogenoidea of freshwater fishes. Principles of systematics, analysis of world fauna and its evolution.—Parazitologicheskii Sbornik 28:96–198.

Hanek, G., K. Molnar, and C. H. Fernando. 1974. Three new genera of Dactylogyridae (Monogenea) from freshwater fishes of Trinidad.—Journal of Parasitology 60:911–913.

Kohn, A., and I. Paperna. 1964. Monogenetic trematodes from aquarium fishes.—Revista Brasileira de Biologia 24:145–149.

Kritsky, D. C., and T. H. Fritts. 1970. Monogenetic trematodes from Costa Rica, with the proposal of *Anacanthocotyle* gen. n. (Gyrodactylidae: Isancistrinae).—Proceedings of the Helminthological Society of Washington 37:63–68.

———, and P. D. Leiby. 1972. Dactylogyridae (Monogenea) from the freshwater fish, *Astyanax fasciatus* (Cuvier), in Costa Rica, with descriptions of *Jainus hexops* sp. n., *Urocleidoides costaricensis*, and *U. heteroancistrium* combs. n.—Proceedings of the Helminthological Society of Washington 39:227–230.

———, and V. E. Thatcher. 1974. Monogenetic trematodes (Monopisthocotylea: Dactylogyridae) from freshwater fishes of Colombia, South America.—Journal of Helminthology 48:59–66.

———, and ———. 1976. New monogenetic trematodes from freshwater fishes of western Colombia with the proposal of *Anacanthoroides* gen. n. (Dactylogyridae).—Proceedings of the Helminthological Society of Washington 43:129–134.

———, and ———. 1977. *Phanerothecium* gen. nov. and *Fundulotrema* gen. nov. two new genera of viviparous Monogenoidea (Gyrodactylidae), with a description of *P. caballeroi* sp. nov. and a key to the subfamilies and genera of the family.—Instituto de Biología, Publicaciones Especiales 4:53–60.

———, ———, and R. J. Kayton. 1979. Neotropical Monogenoidea. 2. The Anacanthorinae Price, 1967, with the proposal of four new species of *Anacanthorus* Mizelle & Price, 1965, from Amazonian fishes.—Acta Amazonica 9:355–361.

———, ———, and ———. 1980. Neotropical Monogenoidea. 3. Five new species from South America with the proposal of *Tereancistrum* gen. n. and *Trinibaculum* gen. n. (Dactylogyridae: Ancyrocephalinae).—Acta Amazonica 10:411–417.

Mayes, M. A., D. R. Brooks, and T. B. Thorson. 1981. *Potamotrygonocotyle tsalickisi*, new genus and species (Monogenea: Monocotylidae) and *Paraheteronchocotyle amazonensis*, new genus and species (Monogenea: Hexabothriidae) from *Potamotrygon circularis* Garman (Chondrichthyes: Potamotrygonidae) in Northwestern Brazil.—Proceedings of the Biological Society of Washington 94:1205–1210.

Mizelle, J. D. 1936. New species of trematodes from the gills of Illinois fishes.—American Midland Naturalist 17:785–806.

———, and A. R. Klucka. 1953. Studies on monogenetic trematodes. XIV. Dactylogyridae from Wisconsin fishes.—American Midland Naturalist 49:720–733.

———, and D. C. Kritsky. 1967. *Unilatus* gen. n., a unique Neotropical genus of Monogenea.—Journal of Parasitology 53:1113–1114.

———, and ———. 1969a. Studies on monogenetic trematodes. XXXIX. Exotic species of Monopisthocotylea with the proposal of *Archidiplectanum* gen. n. and *Longihaptor* gen. n.—American Midland Naturalist 81:370–386.

———, and ———. 1969b. Studies on monogenetic trematodes. XL. New species from marine and freshwater fishes.—American Midland Naturalist 82:417–428.

———, ———, and J. W. Crane. 1968. Studies on monogenetic trematodes. XXXVIII. Ancyrocephalinae from South America with the proposal of *Jainus* gen. n.—American Midland Naturalist 80:186–198.

———, and C. E. Price. 1964. Studies on monogenetic trematodes. XXVII. Dactylogyrid species with the proposal of *Urocleidoides* gen. n.—Journal of Parasitology 50:579–584.

———, and ———. 1965. Studies on monogenetic trematodes. XXVIII. Gill parasites of the piranha with proposal of *Anacanthorus* gen. n.—Journal of Parasitology 51:30–36.

Molnar, K., G. Hanek, and C. H. Fernando. 1974. Ancyrocephalids (Monogenea) from freshwater fishes of Trinidad.—Journal of Parasitology 60:914–920.

Paperna, I. 1969. Monogenetic trematodes of the fish of the Volta basin and South Ghana.—Bulletin de l'I.F.A.N. 31:840–880.

Price, C. E. 1966. *Urocleidus cavanaughi*, a new monogenetic trematode from the gills of the keyhole cichlid, *Aequidens maroni* (Steindachner).—Bulletin of the Georgia Academy of Science 24:117–120.

———. 1968. *Diaccessorius*, a new genus of Monogenea from the gills of an Amazon River teleost.—Acta Biológica Venezuelica 6:84–89.

———, and W. A. Bussing. 1967. Monogenean parasites of Costa Rican fishes. Part 1. Descriptions of two new species of *Cleidodiscus* Mueller, 1934.—Revista di Parassitologia 28:81–86.

———, and ———. 1968. Monogenean parasites of Costa Rican fishes. II. Proposal of *Palombitrema heteroancistrium* n. gen., n. sp.—Proceedings of the Helminthological Society of Washington 35:54–57.

———, and T. E. McMahon. 1966. *Monocleithrium*, a new genus of Monogenea from an Amazon River teleost.—Revista di Parassitologia 27:221–226.

———, and W. J. Nowlin. 1967. Proposal of *Dawestrema cycloancistrium* n. gen. n. sp. (Trematoda: Monogenea) from an Amazon River host.—Revista di Parassitologia 28:1–9.

———, and N. G. Romero. 1969. First account of a monogenetic trematode from Paraguay: *Amphocleithrium paraguayensis* n. gen. n. sp.—Zoologische Jahrbuecher 96:449–452.

———, and E. A. Schlueter. 1967. Two new monogenetic trematodes from South America.—Journal of the Tennessee Academy of Science 42:23–25.

Price, E. W. 1938. The monogenetic trematodes of Latin America.—Livro Jubilar Prof. Travassos, Rio de Janeiro, Brasil 3:407–413.

Szidat, L. 1973. Morphologie and Verhalten von *Paragyrodactylus superbus* n. g., n. sp., Erreger eines Fischsterben in Argentinien.—Angewandte Parasitologie 14:1–10.

Thatcher, V. E., and D. C. Kritsky. 1983. Neotropical Monogenoidea. 4. *Linguadactyloides brinkmanni* gen. et sp. n. (Dactylogyridae; Linguadactyloidinae subfam. n.) with observations on its pathology in a Brazilian freshwater fish, *Colossoma macropomum* (Cuvier).—Proceedings of the Helminthological Society of Washington 50:305–311.

(DCK) Department of Allied Health Professions and Idaho Museum of Natural History, Idaho State University, Box 8002, Pocatello, Idaho 83209; (VET) Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings* of the Biological Society of Washington contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers will be published in English (except for Latin diagnosis/description of plant taxa which should not be duplicated by an English translation), with a summary in an alternate language when appropriate.

Publication Charges.—Authors will be asked to assume publication costs of page-charges, tabular material, and figures, at the lowest possible rates.

Submission of manuscripts.—Manuscripts should be sent to the Editor, *Proceedings* of the Biological Society of Washington, National Museum of Natural History, 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 will be reviewed in order of receipt by a board of associate editors and appropriate referees.

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. Synonymy of abbreviated style (author, date, page) (except in botanical papers), with full citations of journals and books (no abbreviations) in the Literature Cited is required.

The establishment of new taxa must conform with the requirements of the appropriate international codes of nomenclature. Authors are expected to be familiar with these codes and to comply with them. New species-group accounts must designate a type-specimen deposited in an institutional collection.

The sequence of material should be: Title, Author(s), Abstract, Text, Acknowledgments, Literature Cited, Author's (s') Address(es), Appendix, List of Figures (entire figure legends), Figures (each numbered and identified), Tables (each table numbered with an Arabic numeral and heading provided).

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 a facsimile with the original, and retain an author's copy. Pages must be numbered on top. One manuscript page = approximately 0.5 printed page. Underline singly scientific names of genera and lower categories; leave other indications to the editor.

Figures and tables with their legends and headings should be self-explanatory, not requiring reference to the text. Indicate their approximate placement by a pencil mark in the margin of the manuscript.

Illustrations should be planned in proportions that will efficiently use space on the type bed of the *Proceedings* (12.5 × 20 cm) and should not exceed 24 × 15 inches. Figures requiring solid black backgrounds should be indicated as such, but not masked.

Art work will be returned only on request.

Proofs.—Galley proofs will be submitted to authors for correction and approval. Reprint orders will be taken with returned proof.

Costs.—Page charges @ $60.00, figures @ $10.00, tabular material $3.00 per printed inch.

All authors are expected to pay the charges for figures, tables, changes at proof stage, and reprints. Payment of full costs will probably facilitate speedy publication.

CONTENTS

(ISSN 0006-324X)

Proceedings
of the
BIOLOGICAL SOCIETY
of
WASHINGTON

Volume 96 29 December 1983 Number 4

THE BIOLOGICAL SOCIETY OF WASHINGTON

1983–1984
Officers

President: David L. Pawson
Vice President: Donald R. Davis
Secretary: Catherine J. Kerby
Treasurer: Leslie W. Knapp

Elected Council

Daryl P. Domning
Carl Ernst
C. W. Hart, Jr.
Robert P. Higgins
David A. Nickle

Custodian of Publications: Michael J. Sweeney

PROCEEDINGS

Editor: Brian Kensley

Associate Editors

Classical Languages: George C. Steyskal
Plants: David B. Lellinger
Invertebrates: Thomas E. Bowman
Vertebrates: Richard P. Vari
Insects: Robert D. Gordon

Membership in the Society is open to anyone who wishes to join. There are no prerequisites. Annual dues of $15.00 include subscription to the *Proceedings of the Biological Society of Washington. Library subscriptions to the Proceedings are: $18.00 within the U.S.A., $23.00 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 Instutution, 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.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 599–604

THREE NEW SPECIES OF *BRUEELIA* (MALLOPHAGA: PHILOPTERIDAE) FROM THE MIMIDAE (AVES: PASSERIFORMES)

N. Sandra Williams

Abstract.—Three new species of *Brueelia* from the Mimidae are described: one from *Oreoscoptes montanus,* one from *Toxostoma dorsale dorsale* and one from *Mimus polyglottos polyglottos.* A key is provided for their separation.

Of the 130 species of *Brueelia* recognized by Hopkins and Clay (1952, 1953, 1955), none have been described from the Mimidae. The present paper concerns the *Brueelia* from this host family and is a step toward a comprehensive review of the entire genus. Thus far, Ansari (1956, 1957) and Williams (1981, 1982) have revised the species found on the Corvidae and Meropidae, respectively. For a synonymy of the *Brueelia,* see Williams (1981).

This study deals with Mallophaga collected from 12 of the 35 recognized species of Mimidae. Gruson (1976) and A.O.U. (1957) were used for the nomenclature of the hosts.

In the following "Dimensions" sections, the numbers following each character represent its range, sample size, mean and standard deviation in mm. The "abdominal width" is the measurement of the widest abdominal segment which is the fourth, except for male *B. polyglotta,* where it is the fifth.

Abbreviations for the location of the collections are BM(NH) (British Museum (Natural History)), UU (R. E. Elbel Collection, University of Utah), NMNH (National Museum of Natural History), and EEM (K. C. Emerson Entomology Museum, Oklahoma State University).

The *Brueelia* from the Mimidae share the following characteristics with those from other hosts: ventral marginal carina interrupted medially, filiform antennae, prothorax small with lateral margins slightly concave, pterothorax broader than long with sides diverging and posterior margin evenly rounded, with tergal plates III and IV of the female separated medially.

Key to the *Brueelia* from the Mimidae

1. Setae on posterior edge of pterothorax (lateral to median) usually seven in number (four short, three long) in S-L-S-L-S-L-S pattern ...... *montana*
– Setae on posterior edge of pterothorax (lateral to median) usually seven in number (one short and six long) in a S-L-L-L-L-L-L pattern 2
2. Male genitalia narrow with two sensilla on each side of mesosome and distal edges of mesosome with ridges. Parameres elongate. Margin of vulval plate usually with eight setae of equal diameter on each side, three above and five below .... *dorsale*
– Male genitalia broad with two sensilla on each side of mesosome and distal edges of mesosome smooth. Parameres blunt. Margin of vulval plate usu-

ally with 13 setae on each side, nine of wide diameter above four slender ones .... *polyglotta*

Brueelia montana, new species
Figs. 4–6

Type host.—*Oreoscoptes montanus* (Townsend).

Brueelia montana is distinguished from other *Brueelia* species of the Mimidae in having four short and three long setae on the posterior margin of the pterothorax (lateral to median) in a S-L-S-L-S-L-S pattern. The male genitalia closely resemble that of *B. dorsalis* n. sp. but differs in being more narrow in the portion of the basal plate anterior to the parameres.

Diagnosis.—Thimble-shaped head; ventral marginal carina interrupted medially; dorsal marginal carina complete but indented medially; no dorsal anterior plate; antennae filiform and similar in both sexes; prothorax small with lateral margins slightly concave; pterothorax broader than long with sides diverging and posterior margin evenly rounded; abdomen elongate-oval, with tergal plates I–VII of male and female separated medially; male genitalia with slender basal plate; parameres narrow and short with proximal head simple; mesosome shield-like with two sensilla and ridges on distal edge; female vulval plate usually with seven setae of equal diameter on each side, three above and four below.

Dimensions.—Male: Total length, 1.39–1.71 (5:1.55 ± 0.1468); head length, 0.32–0.39 (5:0.36 ± 0.0324); head width, 0.25–0.34 (5:0.30 ± 0.0418); prothorax width, 0.16–0.20 (5:0.18 ± 0.0200); pterothorax width, 0.24–0.35 (5:0.30 ± 0.0482); abdominal width, 0.32–0.45 (5:0.39 ± 0.0638).

Female: Total length, 1.66–2.05 (18:1.87 ± 0.1070); head length, 0.34–0.52 (18:0.40 ± 0.0377); head width, 0.28–0.37 (18:0.33 ± 0.0320); prothorax width, 0.17–0.22 (18:0.20 ± 0.0196); pterothorax width, 0.27–0.34 (18:0.32 ± 0.0216); abdominal width, 0.36–0.51 (18:0.45 ± 0.0428).

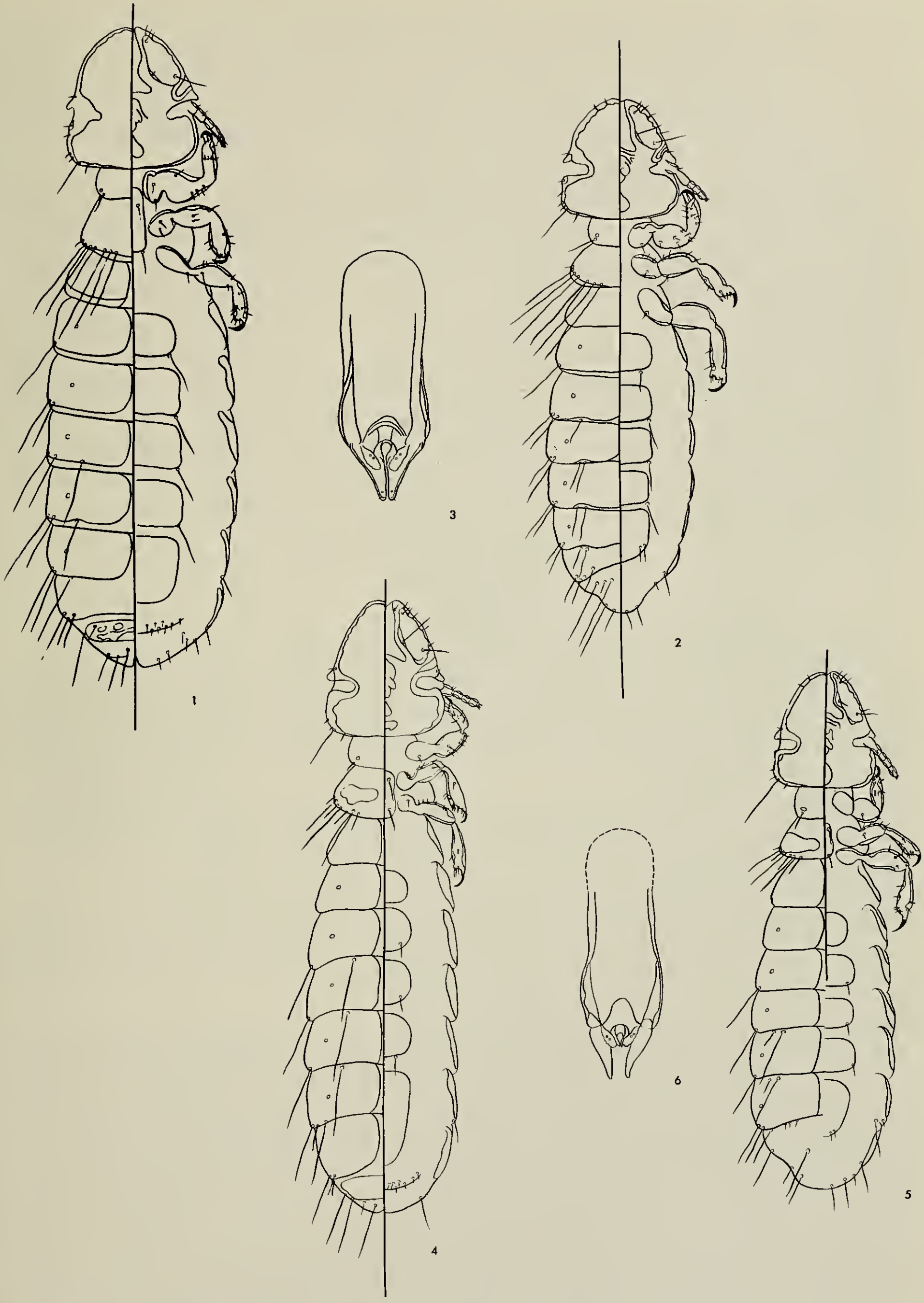
Material Examined.—Holotype ♂ and allotype ♀ from *Oreoscoptes montanus,* Ditto Dunes, Tooele Co., Utah, May 1969 (coll. E. and E. Branch, Dugway Proving Grounds), UU collection No. EE09054, deposited in NMNH; paratypes 2: ♂♂ 7 ♀♀, with same data; 2 ♀♀, with same data except No. EE09107; 1 ♂ 4 ♀♀, *O. montanus,* Vernon, Tooele Co., Utah, UU; 2 ♂♂ 5 ♀♀, *O. montanus,* N. Skull Valley, Tooele Co., Utah, UU.

Brueelia dorsale, new species
Figs. 1–3

Type host.—*Toxostoma dorsale dorsale* Henry.

This species is distinguished from *B. montana* to which it is otherwise similar by pterothorax setation, by features of the male genitalia and female vulval plate and the shape of the head. The posterior edge of the pterothorax with one short and six long setae on each side. The male genitalia of *B. dorsalis* are narrow and have mesosomes with ridges on the distal edge. The margin of the vulval plate of females usually has eight setae of equal diameter on each side. The heads of both sexes are broadly triangular with a flattened anterior edge.

Dimensions.—Male: Total length, 1.50–1.78 (38:1.64 ± 0.0619); head length, 0.36–0.42 (38:0.38 ± 0.0113); head width, 0.35–0.39 (38:0.37 ± 0.0094); pro-



Figs. 1–6. 1–3. *Brueelia dorsale*: dorsal and ventral views of (1) female and (2) male, and (3) male genitalia. 4–6. *Brueelia montana*: dorsal and ventral views of (1) female and (2) male, and (3) male genitalia.

thorax width, 0.19–0.22 (38:0.20 ± 0.0086); pterothorax width, 0.31–0.37 (38: 0.33 ± 0.0126); abdominal width, 0.48–0.55 (38:0.52 ± 0.0238).

Female: Total length, 1.47–2.10 (63:1.91 ± 0.1318); head length, 0.38–0.43 (63:0.41 ± 0.0094); head width, 0.37–0.45 (63:0.40 ± 0.0117); prothorax width, 0.20–0.26 (63:0.23 ± 0.0095); pterothorax width, 0.32–0.41 (63:0.37 ± 0.0142); abdominal width, 0.48–0.64 (63:0.58 ± 0.0291).

Material Examined.—Holotype ♂ (second specimen from the left as seen with compound microscope) and allotype ♀ (first specimen from the right with compound microscope) from *Toxostoma dorsale dorsale,* California, Mar 1939, (coll. Meinertzhagen), BM(NH) Collection, No. 13081 (slide #1 of 4), deposited in BM(NH); paratypes 27 ♂♂ 57 ♀♀, with same data; 1 ♂ 7 ♀♀, *T. dorsale,* Las Vacas, Coahuila, Mexico, UU; Other Material: from *T. rufum,* 1 ♀, Urbana, Illinois, NMNH; 1 ♀, John's Island, South Carolina, NMNH; 1 ♀, Gulfport, Mississippi, NMNH; from *T. curvirostre,* 1 ♀, Chihuahua, Mexico, NMNH; 1 ♀, Las Vacas, Coahuila, Mexico, UU; from *T. redivivum,* 9 ♂♂ 13 ♀♀, Pasadena, California, NMNH. In addition, K. C. Emerson has identified 1 ♂ 1 ♀ from *T. rufum,* Columbus, Ohio, and 1 ♀ from *T. rufum,* Orient, New York, EEM.

Brueelia polyglotta, new species
Figs. 7–9

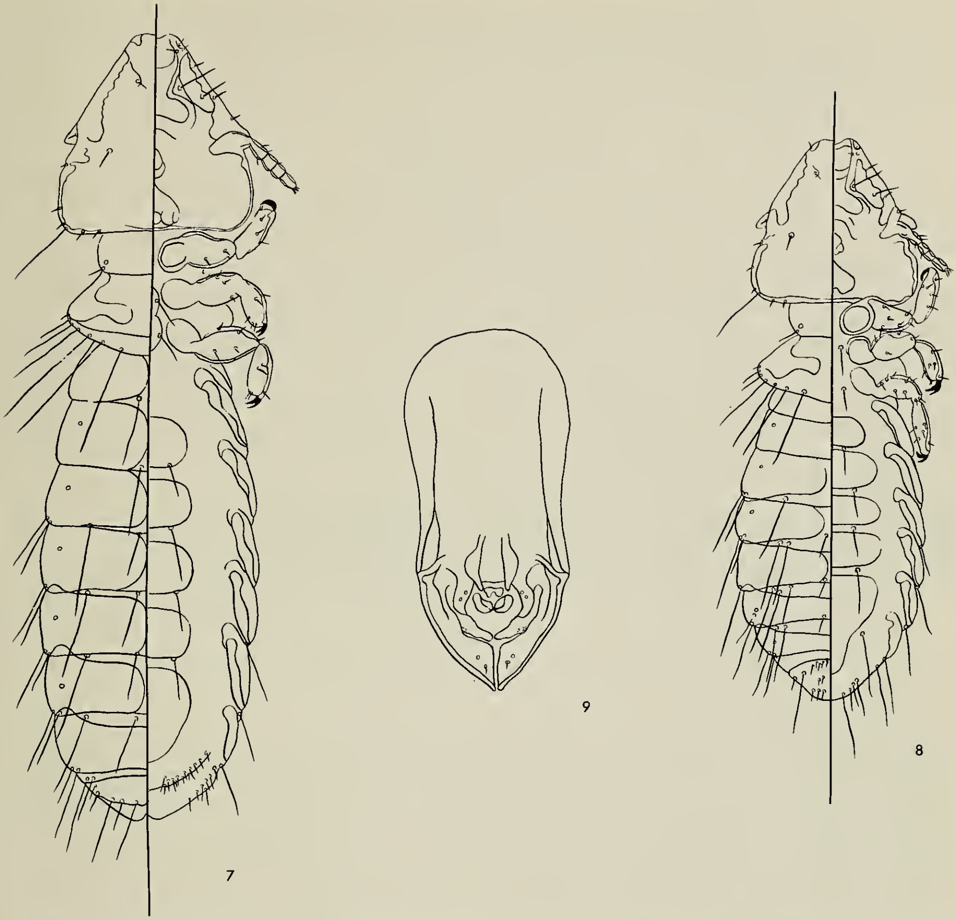
Type host.—*Mimus polyglottos polyglottos* (Linnaeus).

Brueelia polyglotta is distinguished from *B. dorsale* by a broad male genital plate, male genitalia with distal edges of the mesosome without ridges and blunt parameres, and the margin of the female vulval plate with 13 setae of varying diameters on each side.

Dimensions.—Male: Total length, 1.27–1.58 (70:1.39 ± 0.0070); head length, 0.39–0.45 (70:0.41 ± 0.0002); head width, 0.38–0.44 (70:0.40 ± 0.0002); prothorax width, 0.20–0.24 (70:0.23 ± 0.0001); pterothorax width, 0.32–0.39 (70: 0.35 ± 0.0002); abdominal width, 0.42–0.58 (70:0.50 ± 0.0007).

Female: Total length, 1.46–1.98 (160:1.64 ± 0.0102); head length, 0.41–0.48 (160:0.44 ± 0.0003); head width, 0.39–0.48 (160:0.43 ± 0.0003); prothorax width, 0.22–0.27 (160:0.24 ± 0.0001); pterothorax width, 0.33–0.42 (160:0.37 ± 0.0003); abdominal width, 0.45–0.62 (160:0.52 ± 0.0012).

Material Examined.—Holotype ♂, and allotype ♀ (first specimen on the right and middle specimen, respectively, as seen under the compound microscope) and paratype ♀ (first specimen from the left as seen under compound microscope) from *Mimus polyglottos polyglottos,* Fairhope, Alabama, Sep 1930, (coll. Ms. W. M. Edwards), No. 18364 (slide No. 1 of a set of 2), deposited in UMNH; paratypes: 13 ♂♂ 15 ♀♀ with same data except Nos. as follows: 18354, 18355 (2 slides), 18357 (2 slides), 18359, 18361, 18363, 18364 (2nd slide), 18366 (3 slides); from *M. polyglottos,* 2 ♂♂, Raleigh, North Carolina, UMNH; 6 ♀♀, Sonoro, Texas, UMNH; 9 ♂♂ 11 ♀♀, Alachua Co., Florida, UMNH; 5 ♂♂ 1 ♀, Savannah, Georgia, UMNH; 1 ♀, Nashville, Georgia, UMNH; 1 ♂ 3 ♀♀, James Is., South Carolina, UMNH; 2 ♂♂, Bloomington, Indiana, UMNH; 2 ♀♀, Dimmit Co., Texas, UMNH; 1 ♀, Jamaica, West Indies; 1 ♂ 1 ♀, Caja de Meurtos, Puerto Rico, UMNH; 2 ♂♂ 2 ♀♀, Vieques Island, W.I., UMNH; 6 ♂♂ 14 ♀♀, State College, Mississippi, EEM; 2 ♂♂ 2 ♀♀, Bloomington, Indiana, EEM; 1 ♂, Cromwell, Oklahoma, EEM; 1 ♀, New Jersey, EEM; Other Material: from *M. gilvus,* 3 ♂♂ 2 ♀♀, near Lethem, Rupununi,



Figs. 7–9. *Brueelia polyglotta*: dorsal and ventral views of (1) female and (2) male, and (3) male genitalia.

British Guiana, BM(NH); 1 ♀, Aguachica, Magdalena, Columbia, BM(NH); from *M. gundlachii,* 15 ♂♂ 46 ♀♀, Mariguana Is., Bahama Is., UMNH; 19 ♂♂ 57 ♀♀, Great Inagua Is., British W.I., UMNH; 1 ♂♂ 3 ♀♀, Ragged Is., B.W.I., UMNH; 1 ♀, Guantanamo, Cuba, UMNH; from *Dumetella carolinensis,* 2 ♀♀, Gamboa, Panama Canal Zone, Panama, UU; 3 ♂♂ 3 ♀♀, Ft. Collins, Colorado, EEM; 2 ♂♂ 2 ♀♀, Orient, New York, EEM; 1 ♂ 1 ♀, Mongohela Co., West Virginia, EEM; from *Melanotis hypoleucus,* 1 ♂ 1 ♀, Huehuetenango, Guatemala, UU; from *Ramphocinclus brachyurus,* 2 ♀♀, St. Lucia, W.I., BM(NH).

Also, from *Mimus longicaudatus,* 6 ♂♂ 5 ♀♀, from Ecuador were identified but not included in the measurements because they were collected from a captive bird for which insufficient collection data were available.

Acknowledgments

I wish to thank Mr. Christopher Lyal of the British Museum (Natural History), Dr. Don R. Davis of the National Museum of Natural History, Dr. Robert E.

Elbel, Salt Lake City, Utah, and Dr. K. C. Emerson, Sanibel, Florida, for loan of material. I am especially grateful to Dr. Emerson and Dr. Elbel for their assistance in the preparation of this manuscript.

Literature Cited

Ansari, M. A. E. 1956. A revision of the *Bruëlia* (Mallophaga) species infesting the Corvidae (Part I).—Bulletin of the British Museum (Natural History) Entomology 4:369–406.

———. 1957. A revision of the *Bruëlia* (Mallophaga) species infesting the Corvidae (Part II).—Bulletin of the British Museum (Natural History) Entomology 5:143–182.

American Ornithologists' Union. 1957. Check-List of North American birds. Baltimore. Port City Press. 691 pp.

Hopkins, G. H. E., and T. Clay. 1952. A check list of the genera and species of Mallophaga. British Museum (Natural History). London. 362 pp.

———, and ———. 1953. Additions and corrections to the check list of Mallophaga.—Annals and Magazine of Natural History (12):6:434–448.

———, and ———. 1955. Additions and corrections to the check list of Mallophaga (II).—Annals and Magazine of Natural History (12)8:177–190.

Gruson, E. S. 1976. Checklist of the world's birds. New York. Quadrangle. 212 pp.

Williams, N. S. 1981. The *Brueelia* (Mallophaga: Philopteridae) of the Meropidae (Aves:Coraciiformes).—Journal of the Kansas Entomological Society 54:510–518.

———. 1982. The status of *Brueelia superciliosa* (Mallophaga: Philopteridae).—Journal of the Kansas Entomological Society 55:334.

Biology Department, Simmons College, Boston, Massachusetts 02115.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 605–622

DESCRIPTION AND PHYLOGENY OF *ISAACSICALANUS PAUCISETUS*, N. GEN., N. SP., (COPEPODA: CALANOIDA: SPINOCALANIDAE) FROM AN EAST PACIFIC HYDROTHERMAL VENT SITE (21°N)

A. Fleminger

Abstract.—A new genus and species of Spinocalanidae is described under the name *Isaacsicalanus paucisetus.* It was collected from the submersible R/V *Alvin* adjacent to the seafloor of the East Pacific Rise off the mouth of the Gulf of California. The copepod was observed swimming in a small swarm, apparently unispecific and all adult females, among concentrations of macrobenthic invertebrates typical of known hydrothermal vent communities. The new copepod's most distinctive morphological features relative to other spinocalanids are the longer urosome, shorter antennule, and fewer setae on oral appendages. Phylogenetic analysis supports the hypotheses that the new genus occupies a highly derived position within the Spinocalanidae and that the family is the most primitive within the superfamily Clausocalanoidea.

Taxonomic reports on the recently discovered bathyal suspension-feeding macrobenthos assemblages immediately adjacent to hydrothermal vents along oceanic spreading centers (Lonsdale 1977) reveal that virtually all the constituent species and their respective genera are new to science. The taxonomically unique qualities of these assemblages suggest that these species have persisted within a hydrothermal vent-dominated habitat for appreciable periods of evolutionary time. Micro-invertebrates have also been represented; Humes and Dojiri (1980) described a new genus and species of thigmotactic siphonostome copepod found on the tentacular crown of tubicolous vestimentiferan worms from vent localities on the Galapagos rift. The present report considers a free-living planktobenthic calanoid copeod that appears to be a member of a hydrothermal vent community on the East Pacific Rise at the mouth of the Gulf of California.

The new form is morphologically most like *Teneriforma* Grice and Hulsemann, 1967; several unique character states in the new form require minor emendation of Damkaer's (1975) description of Spinocalanidae.

Materials and Methods

Thirty-two adult female individuals comprise the specimen series available for this study. They were collected adjacent to the seafloor at the East Pacific Rise several hundred kilometers west of Cabo Corrientes, Mexico; sampling details are presented below as part of the species' description. Initial preservation was by freezing in sea water at −20°C following transfer to the surface. The specimens were stored frozen at −70°C for about 10 weeks in the laboratory before transfer to formalin. They were immersed in glycerol for study. Internal organs are mostly indistinguishable, presumably a consequence of freezing at relatively high temperatures and precluding observations on the nature and contents of the midgut as well as limiting evaluation of ovarian development.

All measurements were made of specimens immersed in glycercol. Figures were drawn with the aid of a camera lucida. Habitus views were drawn from specimens in which soft tissues were removed by KOH digestion and the cuticle lightly stained with chlorozol black.

List of abbreviations used in text and figures.—A1, antennule; A2, antenna; B1, coxal segment of appendage; B2, basal segment of appendage; Li1, 2 . . . , medial lobe(s) on protopod of cephalic appendage; Md, mandible; Mx1, maxillule; Mx2, maxilla; Mxp, maxilliped; P1, 2, 3 . . . , paired swimming legs 1, 2, 3 . . . ; Re1, 2 . . . , exopod, segment 1, 2 . . . ; Ri1, 2 . . . , endopod, segment 1, 2 . . . ; Se1, 2 . . . , lateral spine on exopod of swimming leg; Si, seta; St, terminal spine on distalmost exopodal segment of swimming leg; ThI, II, III, IV, V pedigers (=thoracic segments, Bowman 1976:187) bearing swimming legs 1, 2, 3 . . . respectively.

Family Spinocalanidae Vervoort, 1951

Diagnosis (emended from Damkaer 1975).—Calanoids with P1 Re trimerous. P1 Re1 with 0 or 1 Se, Re2 with 0 or 1 Se, Re3 with 1 Se, 1 St and 4 Si; Ri with one segment and 3 to 5 Si. Re trimerous in P2–4, Re3 with 3 Se, 5 Si, and one finely serrate St; lateral margin of Re3 not serrate. P2 with bimerous Ri, Ri2 with 2 medial, 2 terminal and 0 or 1 lateral setae. P3–4 with trimerous Ri, Ri2 with 1 medial seta, Ri3 with 2 medial, 2 terminal and 0 to 2 lateral setae. In female, cephalosome and ThI separate, ThIV and V usually separate, ThV distal end sometimes prolonged, apex may be pointed; P5 absent; A1 with segments 8 and 9 fused, 24 and 25 articulating or fused; A2 Re usually equal to or longer than Ri; setation of mouthparts and other details given in Tables 1 and 2.

Isaacsicalanus, new genus

Diagnosis.—Robust spinocalanid; female with elongate urosome about half length of prosome. Short A1 about as long as prosome. Rostrum short, lobate without any semblance of bifurcation. Mx1 with B2 fused to proximal part of Ri and bearing 4 Si; Li 2 with 1 seta, Li3 lacking Si. Distal Si of Mx2 and Mxp unarmed except for very fine setules on proximal side. Mxp B1 with 2 Si. P1 Re1 and 2 lacking Se. P1 Ri with 5Si and prominent shoulder (lateral swelling produced anterodistad, knob-like) at segment's midlength and bearing spinules concentrated at apex. P2–P4 with Re3 Se3 about twice as long as Se1 and 2. A2 Re1 without Si, Re2 and 3 not fused, Re2 with 1 Si. Posterior surfaces of P2–P4 without spines.

Etymology.—The generic term *Isaacsicalanus* is masculine and a combination of the late John D. Isaacs' surname and *-calanus,* the suffix of many calanoid copepod genera. The name is proposed in memory of John D. Isaacs, a pioneering leader in oceanography, to acknowledge his many scientific contributions, the brilliant and the outrageous, and for his unwavering and most generous support of zooplankton research at Scripps Institution of Oceanography (SIO). It is also a personal expression of gratitude for the many kindnesses he showed me during 20 years of collegial association at SIO.

The type-species of the new genus is by original designation, *I. paucisetus,* described below.

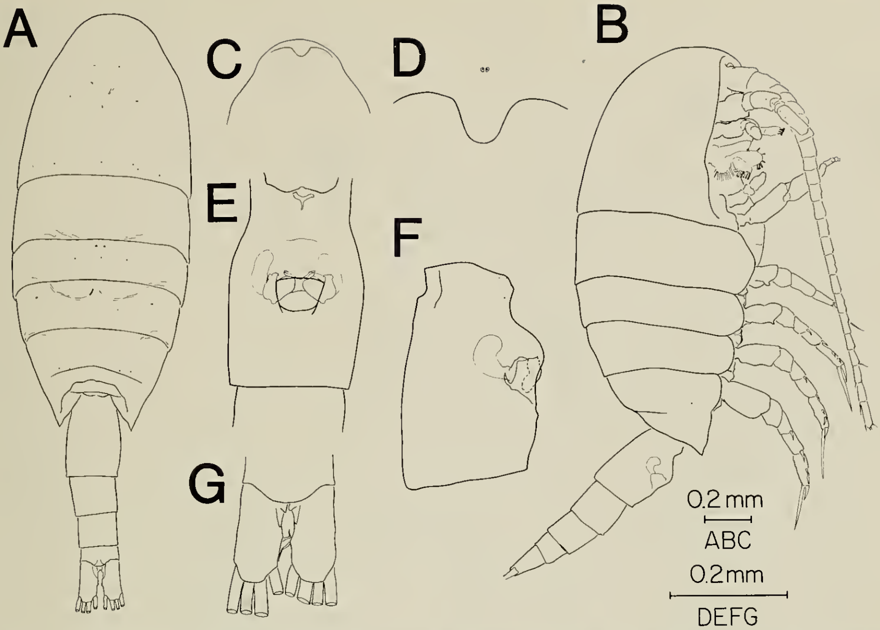


Fig. 1. *Isaacsicalanus paucisetus.* Adult female. A, Habitus, dorsal; B, Habitus, lateral; C, Forehead and rostrum, ventral; D, Rostrum, anterior; E, Genital segment, ventral; F, Genital segment, lateral; G, Furca, dorsal.

Key to Adult Females of Spinocalanid Genera

1.	P1 Re1 with Se; P2 to P4 with one or two rows of spines on posterior surface of Ri2	2
–	P1 Re1 without Se; P2 to P4 lacking row of spines on posterior surface of Ri2	3
2.	Rostrum produced into 2 strong spiniform processes	*Monacilla* Sars, 1905
–	Rostrum absent	*Spinocalanus* Giesbrecht, 1888
3.	Rostrum absent. Prosome at least 4 times length of urosome, caudal ramus length not more than 1.5 times width	*Mimocalanus* Farran, 1908
–	Rostrum present but not bifurcate. Prosome no more than 3 times length of urosome. Caudal ramus length about 2 times width	4
4.	A1, extended, reaching to anal segment, A2 with endopod longer than exopod, Mxp B1 with 5 Si	*Teneriforma* Grice and Hulsemann, 1967
–	A1, extended, reaching to ThV, A2 with exopod longer than endopod, Mxp B1 with 2 Si	*Isaacsicalanus,* gen. n.

Isaacsicalanus paucisetus, new species
Figs. 1, 2, 3

Measurements.—Adult female total length to distal end of caudal ramus, range 2.44 to 2.56 mm, $\bar{x}$ 2.501 ± 0.0259 mm (95% C.L., N = 10, s = 0.0368).

Prosome:urosome length ratio, measurements taken along mid-sagittal plane from apex of forehead to hinge between prosome and urosome and from hinge to distal end of right caudal ramus; range 2.03 to 2.19:1, median 2.15:1 (N = 10).

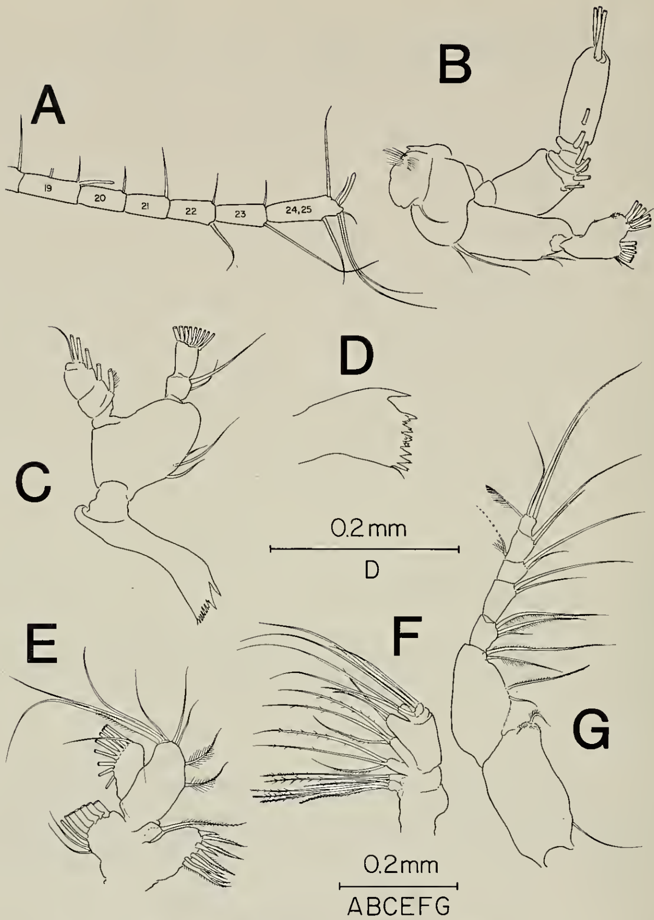


Fig. 2. *Isaacsicalanus paucisetus.* Adult female. A, Right A1 segments 19 to 25, dorsal; B, Right A2, posterior; C, Right Mnd, posterior; D, Right Mnd gnathobase, posterior; E, Right Mxl, posterior; F, Right Mx2, anterior; G, Left Mxp, anterior.

Description and diagnosis of adult female.—Habitus (Figs. 1A, B), forehead broadly rounded, prosome short, about 2.15 × length of urosome; in *Teneriforma naso* (Farran, 1936) prosome is at least 2.5 × length of urosome (measured as above using illustrations in Farran 1936, Grice and Hulsemann 1965 and Wheeler 1970); ThV distal end produced and terminating in a sharp point; A1 short, extended posteriorly not reaching beyond ThV. Caudal ramus about twice as long as wide (Fig. 1G) bearing 4 terminal setae and 1 short medial seta at about midlength of ramus. Cephalosome and ThI separated, ThIV and V incompletely separated, remnant of line of articulation appearing on dorsal side. Rostrum in lateral view short knob-like; in frontal and ventral views (Figs. 1C, D) a short simple lobate process. Genital segment with relatively large seminal receptacles curving anteriorly and swollen distally (Figs. 1E, F).

A1 with 23 articulating segments, segments 8 and 9 and 24 and 25 fused (Fig. 2A). A2 (Fig. 2B) with Re about 1.3 times longer than Ri. Re with total of 9 Si;

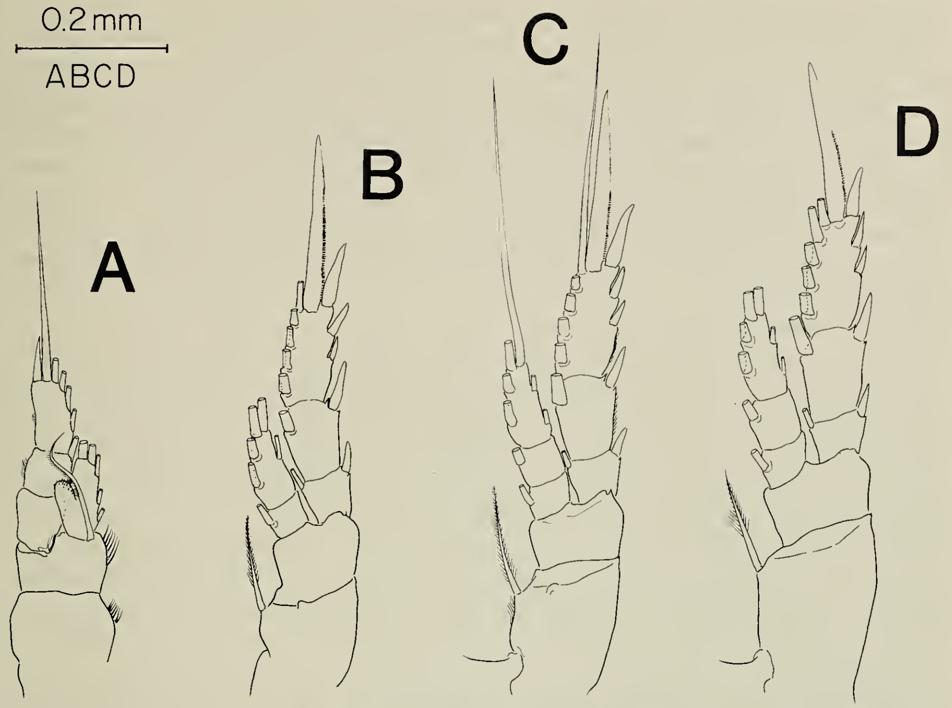


Fig. 3. *Isaacsicalanus paucisetus.* Adult female. A. Right P1, anterior; B, Right P2, posterior; C, Right P3, posterior; D, Right P4, posterior.

Re1 lacking Si, Re2 with 1 Si, remnant of apical segment (Re8) with 3 Si, distinctly separate from preceding segment, Re7, by visible remnant of intersegmental suture; Re7 with 1 Si. Re in *Teneriforma* with total of 11 Si.

Md palp (Fig. 2C) with setation similar to that in *Teneriforma* and *Mimocalanus.* Left and right gnathobase similar, with 8 major teeth of roughly equal size, a small intercalary tooth between the second and third and the third and fourth major teeth and a slender, short Si (Fig. 2D). Ventralmost tooth slender, spiniform, set off from others by deeply cut angular notch; remaining teeth distally bifid; 3 proximalmost teeth bordered by minute denticles.

Mx1 (Fig. 2E) with proximal portion of Ri totally fused to B2 and bearing 4 Si; these parts also fused in *Teneriforma* but combination bearing 10 setae; Ri and B2 not fused elsewhere in family. Li2 with 1 seta, Li3 much smaller than Li2 and lacking Si; elsewhere in family Li1 and 2 bear a total of 6 or more Si.

Mxp (Fig. 2G) with B1 bearing 2 Si, elsewhere in family this segment with 5 or more Si. Si on distalmost segments with minute setules. Ri segments 2 and 3 with 2 Si, Ri4 with 3 Si.

P1 (Fig. 3A) with B2 Si strongly curved as in *Monacilla*; this Si straight in *Teneriforma.* Lateral shoulder of Ri located at about midlength of segment, strongly produced anterodistad in knob-like process with apex bearing numerous spinules; Ri bearing 5 Si as in *Monacilla.* Both Re1 and Re2 lacking Se as in *Teneriforma* described by Farran (1936); Grice and Hulsemann (1965) show P1 Re2 in *Teneriforma* with 1 Se.

P2 to 4 (Figs. 3 B, C, D). Re3 of P2 to P4 with Se3 about twice as long as Se1 and Se2. Re2 of P2 to P4 with Se about 1.5× longer than Re1 Se. P2 Ri2 with 1 lateral Si; P3 and P4 Ri3 with 2 lateral Si as in *Teneriforma.* P2 to P4 Ri2 disto-lateral corner rounded as appears to be the condition in the Australian *Teneriforma naso* described by Farran (1936) but not in *T. naso* described by Grice and Hulsemann (1965) where this corner is produced in a short pointed denticle as it is elsewhere in the family.

Etymology.—The specific name, *paucisetus,* literally 'few setae,' signifies the reduced number of setae on oral appendages of the new species relative to other species of the family.

Types.—Female holotype, TL 2.63 mm, USNM No. 195066; 15 paratypes, USNM No. 195067, all taken together at the type-locality.

Sampling data and type locality.—All specimens obtained in one collection made at 20°49.05′N, 109°06.40′W on 23 April 1982 at R/V *Alvin* Dive no. 1217, Sample no. 1217-3B, during Oasis Expedition to the East Pacific Rise. The collection was made by Roberta Baldwin, SIO, with aid of a 4-chambered slurp gun respirometer (Smith and Baldwin, in press) within 1 m of the sea floor at a depth of 2600 m. The copepods were swimming in a tightly clustered swarm of several thousand individuals just above a small depression known as "Holger's Hole" about 1 m in diameter and 1 m deep formed in collapsed pillow lava. With regard to the macrobenthos at the site, I quote from R. Baldwin's field notes: "One side of the depression is bounded by a dense population of *Calyptogena magnifica* Bossand Turner (Vesicomyidae) and a small patch of *Riftia pachytila* Jones (Vestimentifera); the bottom, littered with broken lava pieces, is inhabited by the clams and *Munidopsis* sp. (Galatheidae). Water temperatures in the depression range from 5° to 15°C. The collapsed pillow lava site is located in an area known as "clam acres" (2613 m depth) where dense populations live in the mineral-rich waters of the hydrothermal vents off Baja California. The area is located 240 km south of the Baja peninsula and 21° north of the equator on the East Pacific Rise, an area of seafloor spreading where bottom-water temperatures range from 2.2°C over the clam fields to an excess of 350°C in the stalagmite chimneys known as "black smokers." The collection was incubated *in situ* in the respirometer for about 48 hours before being brought to the surface and frozen. Randomly selected subsamples from the copepod swarm, totalling 32 individuals are all adult females of the new species.

Phylogenetic Relationships among Spinocalanid Genera

The family Spinocalanidae was established to accommodate three genera, *Spinocalanus, Monacilla* and *Mimocalanus,* that Vervoort (1951) appropriately removed from the family Pseudocalanidae (=Clausocalanidae Giesbrecht in Bowman and Abele 1982). Knowledge of spinocalanid diversity and distribution accumulated rapidly during the ensuing 20 years in response to widespread oceanic exploration and increased use of opening-closing nets sampling meso- and bathypelagic depths where spinocalanids tend to be most commonly encountered. Damkaer (1975) brought these advances into full focus by virtue of his thorough review of the Spinocalanidae. He recognizes 32 species and 4 genera: 19 species in *Spinocalanus,* 4 in *Monacilla,* 8 in *Mimocalanus* and 1 in *Teneriforma.* Damkaer apparently regarded gaps in morphological knowledge of many spinocalanids sufficient reason to preclude consideration of phylogenetic relationships, but he suggested that *Monacilla* and *Spinocalanus* comprise a group and that *Mimocalanus* and *Teneriforma* comprise another group within the family.

Knowledge of species recognized by Damkaer (1975) has not advanced, but the new genus *Isaacsicalanus* provides additional infrastructure to the family and, in apparently expanding the family's range of habitats to a planktobenthic niche within the uniquely warm bathyal waters of a hydrothermal vent community, enhances interest in seeking its phylogenetic relationships. Classification of *Isaacsicalanus,* based solely on adult female morphology, derives from analysis of more than 30 characters. These characters reveal a number of apparent synapomorphies among spinocalanid genera. Following procedures discussed at length by Eldredge and Cracraft (1980:19–85) and briefly outlined by Sanders (1981:96–98), the available data set has been used to hypothesize a first approximation of phylogenetic relationships among the spinocalanid genera. In this exploratory attempt to order the genera phylogenetically, character states representing other spinocalanid genera were collated from published accounts of the species. Two criteria were stressed in hypothesizing apomorphies and deciding upon the transformation sequence of character states (Table 1), namely, uniqueness and relative abundance of meristic features. For repetitive segments or their armature I have assumed that within a monophyletic lineage the highest numbers of setae and segments are plesiomorphic, regardless of frequency of occurrence, and that reductions are apomorphic. The most primitive state for each character, found in one or more members of a genus was selected to represent that genus.

For some characters, determining the sequence of character state transformations is readily obvious from the first principles of apomorphy by reduction. Many calanoid morphological features are generally conservative and the plesiomorphic condition widespread. Derived states are immediately recognizable when meristic features are reduced by developmental modifications, e.g., by fusion of adjacent segments, loss of the fifth pair of legs in the females, reduced number of setae on certain appendages, the absence of the rostrum or its failure to bifurcate. The direction of transformation in other characters may not be obvious. Solution requires outgroup comparison, i.e., comparative analysis using as references closely related antecedent and derived taxa in which the character states in question are ummistakably primitive or derived relative to the states under consideration.

Selection of an appropriate outgroup for the Spinocalanidae is not immediately obvious. As is typical of supraspecific calanoid taxa, the present concept of Spinocalanidae is a constellation of mostly plesiomorphic states that distinguishes it from the other 10 families comprising the superfamily Clausocalanoidea (Bowman and Abele 1982). Assuming that convergent reversals have not contributed to the formation of spinocalanids, their ancestry must derive from calanoids with character states as follows:

1. Bifurcate rostrum
2. P2–4 with Re3 bearing 3 Se and 5 Si
3. A1 with 25 articulating segments or with 8 and 9 fused
4. Left and right members of male P5 biramous
5. Trunk segmentation and genital segment morphology: i.e., cephalosome and

Table 1.—Catalogue of characters.

*Character state symbols: 0 = primitive condition, derived states coded by integers;
→ → → hypothesized sequentially derived autapomorphies;
← → hypothsized irregularly derived autapomorphies;
↓ hypothesized autapomorphies reversing sequence.

Character code	Character	States recognized and proposed sequence of transformation*	Derived character state no.
SA	P1 Ri	1-segmented with lateral shoulder, 3 to 5 Si	01
SB	P1 Re3	with 4 Si	02
SC	P2–4 Re3	with 3 Se and 5 Si	03
SD	P5	lacking in female, endopod may be present in male but lacking setae	04
SE	A1 segments 8 and 9	partly to totally fused	05
SF	cephalic appendages	show reductions in size and setation in male relative to female	06
A	rostrum	bifurcated—0; absent—07; uniramous—08 hypothesized transformation 07←0→08	07, 08
B	A1 segments 24 and 25	articulated—0; fused—09	09
C	A2 Ri1 setae no.	*2*—0; *1*—10	10
D	A2 Ri2 setae no.	*18*—0; *16*—11; *15*—12 0 ↓ ↓ 11 12	11, 12
E	A2 Re1 setae no.	*1*—0; *0*—13	13
F	A2 Re2 setae no.	*4*—0; *3*—14; *1*—15; *0*—16 0→14→15 ↓ 16	14, 15, 16
G	A2 Re7 setae no.	*1*—0; *0*—17	17
H	Mnd, no. teeth	*8*—0; *7*—18	18
I	Mnd, B2 setae no.	*4*—0; *3*—19	19
J	Mnd, Ri setae no.	*14*—0; *13*—20; *11*—21 0→20→21	20, 21
K	Mx1 Re setae no.	*12*—0; *11*—22; *10*—23; *9*—24 0→22→23 ↓ 24	22, 23, 24
L	Mx1 Ri + B2 setae no.	*30*—0; *21*—25; *20*—26; *13*—27; *8*—28 0→27→28 ↓ 25 ↓ 26	25, 26, 27, 28
M	Mx1 Ri and B2 segments	articulated—0; fused—29	29
N	Mx1 Li3 setae no.	*4*—0; *2*—30; *0*—31 0→30→31	30, 31
O	Mx1 Li2 setae no.	*6*—0; *5*—32; *4*—33; *1*—34 0→33→34 ↓ 32	32, 33, 34

Table 1.—Continued

Character code	Character	States recognized and proposed sequence of transformation*	Derived character state no.
P	Mx1 Li1 setae no.	*14*—0; *13*—35; *12*—36; *10*—37 0→35→37 ↓ 36	35, 36, 37
Q	Mx2 Li1 setae no.	*6*—0; *5*—38; *3*—39 0→38 ↓ 39	38, 39
R	Mx2 Li2 setae no.	*3*—0; *2*—40	40
S	Mx2 Li5 setae no.	*4*—0; *3*—43	43
T	Mx2 Ri setae no.	*7*—0; *5*—41; *4*—42 0→42 ↓ 41	41, 42
U	Mxp B1 setae no.	*10*—0; *9*—44; *5*—45; *2*—46 0→44→45→46	44, 45, 46
V	Mxp B2 setae no.	*5*—0; *4*—47	47
W	Mxp Ri1 setae no.	*5*—0; *4*—48; *3*—49; *2*—50 0→48→49 ↓ 50	48, 49, 50
X	Mxp Ri2 setae no.	*4*—0; *3*—51; *2*—52 0→51→52	51, 52
Y	Mxp Ri3 setae no.	*3*—0; *2*—53	53
Z	Mxp Ri4 setae no.	*4*—0; *3*—54	54
AA	P1 B2Si shape	curved—0; straight—55	55
BB	P1 Re1 spine no.	*1*—0; *0*—56	56
CC	P1 Re2 spine no.	*1*—0; *0*—57	57
DD	P1 Ri setae no.	*5*—0; *4*—58 0 ↓ 58	58
EE	P2–4 spines on post. face of rami	yes—0; no—59	59
FF	P3–4 Ri2 outer distal corner	pointed—0; rounded—60	60
GG	ThV posterior corner	rounded—0; pointed—61	61

ThI not fused, ThIV and ThV not fused; female abdomen with 4 segments and genital segment with large vertically oriented seminal receptacles

6. Appreciable sexual dimorphism modifying appearance of male's prosome, A1, and setation of cephalic appendages

Spinocalanidae is the only family of the Clausocalanoidea with species exhibiting states 2 and 4 above in combination (*Monacilla* spp. and *Spinocalanus* spp.). Additional plesiomorphic states within the family (e.g., numbers 3 and 5 above, oral appendages with highest number of typical setae within superfamily) mark it as containing the most primitive taxa within the superfamily.

Within the Clausocalanoidea aetideid genera *Aetideopsis* Sars, 1902, *Pseudotharybis* T. Scott, 1909, and, to a somewhat lesser extent, *Bradyidius* Giesbrecht, 1897, came close to agreeing with the five character states characteristic of Spinocalanidae listed above. They are, however, apomorphic to spinocalanids in characters 2 and 5; i.e., relative to spinocalanids they all show a loss of 1 Si on Re3 of P2–P4 and their thoracic segmentation includes partial to total fusion of cephalon and ThI as well as ThIV and ThV or pronounced foreshortening of ThV. Based on all characters analyzed in this study (Table 1) it is conceivable and even likely that these three aetideid genera derive from a *Monacilla*-like ancestor. The search for a closely related outgroup differing from spinocalanids only in a plesiomorphic direction was extended to other superfamilies. Looking beyond the Clausocalanoidea, the family Megacalanidae of the Megacalanoidea (also containing Calanidae, Calocalanidae, Paracalanidae, and Mecynoceridae; Bowman and Abele 1982) appears to be the most promising candidate in that the majority of characters I examined (Table 1) are symplesiomorphic or synapomorphic to spinocalanids and the remainder are plesiomorphic. Two possible anomalous characters, 1., a noncatalogued condition of asymmetry in adult males and, 2., character L, require special consideration, however, before designating the Megocalanidae as the outgroup of choice for determining the direction of transformation sequences (i.e., polarity of morphoclines) in spinocalanids.

Among the males of *Spinocalanus* the orientation of asymmetries found in the A1 and P5, and presumably the position of the genital pore, may appear on the left or the right side of the body depending upon the species (Damkaer 1975:14). To my knowledge asymmetries in megacalanid males do not vary between or within the species. Interspecific reversals in asymmetry, however, are known to occur in *Clausocalanus* (Frost and Fleminger, 1968), *Calocalanus* Giesbrecht, 1888 (Andronov 1973) and the genital opening, typically on the left side in Calanoida, occurs on the right side of the urosome in *Mecynocera* Thompson, 1888 (Andronov 1973). I have infrequently observed intraspecific reversals of asymmetry in the P5 of males of *Eucalanus pileatus* Giesbrecht 1888 inhabiting southeast Asian waters (unpublished). Variation in male asymmetries is a well known feature of the Metridiidae (superfamily Augaptiloidea, a likely source of the Megacalanoidea). Thus, reversal in the asymmetry of spinocalanid males clearly is of no special phylogenetic significance *vis à vis* the Megacalanidae. Reversed asymmetry in males may be an old synapomorphy of the Augaptiloidea, Megacalanoidea, Clausocalanoidea and Eucalanoidea, or in view of its sporadic occurrences merely a number of convergent autapomorphies.

The second exception to the evidence favoring Megacalanidae as the most suitable antecedent outgroup for Spinocalanidae is the number of setae on Mxl Ri plus B2 (Character L, Table 1). I have not found any species of calanoid to match the total of 30 setae on these segments occurring in *Mimocalanus crassus* (Park 1970:479, Fig. 5). Within Spinocalanidae setal count values range from 21 or, less frequently, 20 setae in *Spinocalanus* (Park 1970: Figs. 27, 47, 73; Damkaer 1975: Figs. 15, 48, 71, 122), 18 to 20 in *Monacilla* (Farran 1908: Pl. 1, Fig. 17; Scott 1909: Pl. II, Fig. 14; Sars 1925: Pl. XI, Fig. 9), 19 to 30 in *Mimocalanus* (Tanaka 1956: Fig. 13d; Vervoort 1957: Fig. 13c; Park 1970: Fig. 5), 13 in *Teneriforma* (Grice and Hulsemann 1965: Fig. 8F), and 8 in *Isaacsicalanus* (Fig. 2E). The Mxl has not been characterized for a number of described spinocalanids.

Table 2.—Apparent synapomorphies among spinocalanid genera.

Character code	Character	*Monacilla*	*Spinocalanus*	*Mimocalanus*	*Teneriforma*	*Isaacsicalanus*	Reversals
Females							
A	Rostrum	bifurcated	absent		uniramous		
B	A1 segments 24 and 25		articulated		fused		
C	A2 Ri1 setae no.	1	2	2	2	2	x
D	A2 Ri2 setae no.	15	16	16	15	18	x
E	A2 Re1 setae no.	1	1	0	1	0	x
F	A2 Re2 setae no.	4	3	0	3	1	x
G	A2 Re7 setae no.	1	1	1	0	1	x
H	Mnd no. teeth	8	8	8	7	8	x
I	Mnd B2 setae no.	4	4	3	3	3	
J	Mnd Ri setae no.	14	14	14	13	11	
K	Mx1 Re setae no.	12	11	11	9	10	x
L	Mx1 Ri + B2 setae no.	20	21	30	13	8	x
M	Mx1 Ri and B2 segments		articulated		fused		
N	Mx1 Li3 setae no.	4	4	4	2	0	
O	Mx1 Li2 setae no.	5	6	4	4	1	x
P	Mx1 Li1 setae no.	12	14	13	10	10	x
Q	Mx2 Li1 setae no.	6	6	6	3	5	x
R	Mx2 Li2 setae no.	3	3	3	3	2	
S	Mx2 Li5 setae no.	4	4	3	3	3	
T	Mx2 Ri setae no.	5	7	4	4	4	x
U	Mxp B1 setae no.	10	9	9	5	2	
V	Mxp B2 setae no.	5	5	5	4	4	
W	Mxp Ri1 setae no.	5	4	4	2	3	x
X	Mxp Ri2 setae no.	4	4	4	3	2	
Y	Mxp Ri3 setae no.	3	3	3	2	2	
Z	Mxp Ri4 setae no.	4	4	4	4	3	
AA	P1 B2 seta		curved		straight	curved	x
BB	P1 Re1 spine no.	1	1	0	0	0	
CC	P1 Re2 spine no.	1	1	1	1	0	
DD	P1 Ri setae no.	5	5	4	4	5	x
EE	P2–4, spines on post. surfaces of rami		yes		no		
FF	P3–4 Ri2 outer distal corner			pointed		rounded	
GG	Th5 posterior corner			rounded		pointed	
Males							
HH	P5		biramous	uniramous		?	?

Mxl Ri plus B2 may bear 21 setae in *Clausocalanus* (Frost and Fleminger 1968: Pl. 6, Fig. c) and in metridiids (Giesbrecht 1892: Pl. 32, Fig. 4). Calanids do not appear to exceed 19 setae, whereas megacalanids, also the outgroup of choice for calanids (in prep.), have 17 or fewer setae (Sars 1925: Pl. I, Fig. 11; Pl. III, Fig.

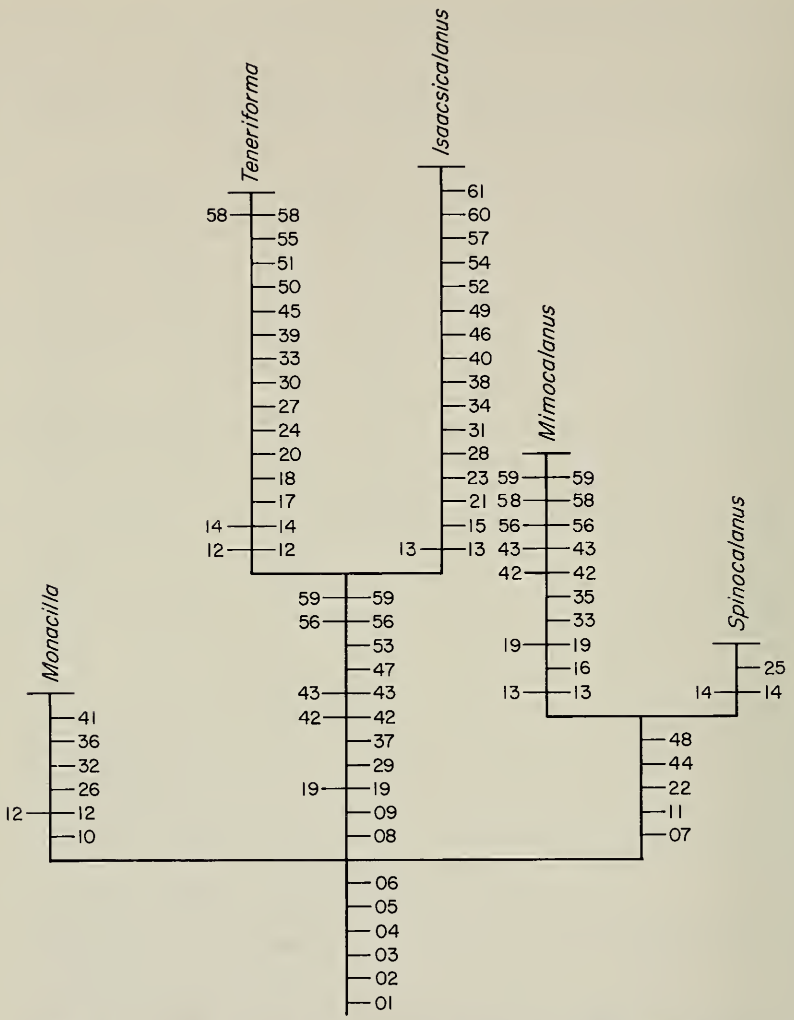


Fig. 4. Dendrogram to summarize distribution of derived character states among spinocalanid genera; derived states defined in Table 1 and discussed in text.

7; Pl. IV, Fig. 7; Bjornberg 1968: Figs. 7, 27, 48, 57, 66). The low number of setae on these segments of Mxl in megacalanids may be an autapomorphy in the known bathypelagic species that appear to be adapted for predation, carrion feeding or large particulate dentrital feeding. Considering the incomplete state of knowledge on Mxl setation in the families in question, the 30 setae found on the Mxl Ri plus B2 in *M. crassus* is tentatively regarded to be the plesiomorphic condition for Megacalanoidea and Clausocalanoidea.

In summary, I have hypothesized a megacalanid-like ancestry for the Spinocalanidae and present the direction of character state transformations, i.e., morphoclines, and proposed synapomorphies in Tables 1 and 2, respectively.

As noted above, morphocline direction may be determined from the first prin-

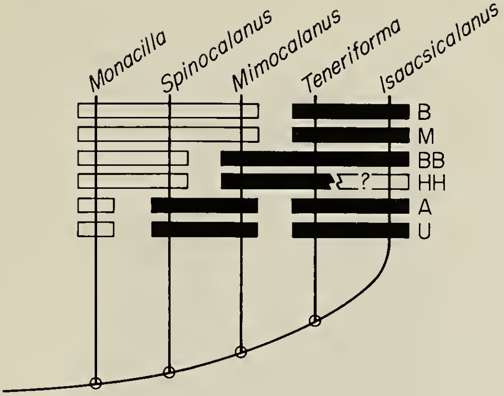


Fig. 5. Cladogram of hypothesized synapomorphies in transformation sequences whose direction is proposed on the basis of first principles of calanoid copepod morphology. Further discussion in text.

ciple of apomorphy by reduction in several instances. For example, the primitive condition of articulating segments of appendages or trunk are replaced autapomorphically by fused combinations of adjacent segments as in the case of Nos. A and M (Table 2). Another assumed plesiomorphy is the bifurcate rostrum produced in a pair of slender processes as found in *Monacilla.* Complete loss of the rostrum (Character No. A) is synautapomorphic in *Spinocalanus* and *Mimocalanus.* Extension of the base of the rostrum into a single nonbifurcate process constitutes a second synautapomorphy in *Teneriforma* and *Isaacsicalanus.*

Results of Phylogenetic Analysis

In the process of classifying *Isaacsicalanus* 33 intrafamilial and six interfamilial character states were determined by microscopic examination of available adult females. States in the other spinocalanid genera were collated from published accounts of the species (Damkaer 1975; Farran 1908, 1936; Giesbrecht 1892; 1971: Grice and Hulsemann 1965, 1967; Park 1970; Scott 1909; Sars 1903, 1925; Vervoort 1951, 1957; Farran and Vervoort 1951; Tanaka 1956; Wheeler 1970). Transformation sequences were proposed, generally on the basis of the first principle of calanoid copepod morphology and confirmed by outgroup comparison with Megacalanidae as described by Sars (1925), Sewell (1947), Bjornberg (1968), and my unpublished observations on *Megacalanus* and *Bathycalanus.* Character states and proposed transformation sequences are presented in Tables 1 and 2. States designated primitive indicate primitiveness of that state in that taxonomic category. This simplifying assumption is necessary due to the general lack of character surveys on calanoid families and genera as well as the logistic difficulties of obtaining specimens for study of seemingly critical species. In Table 1 all characters have been coded by letters, all derived, i.e., autapomorphic, states are coded by integers.

All derived states were used to construct a dendrogram (Fig. 4), following Johnson (1982) that depicts the distribution of derived states among genera of

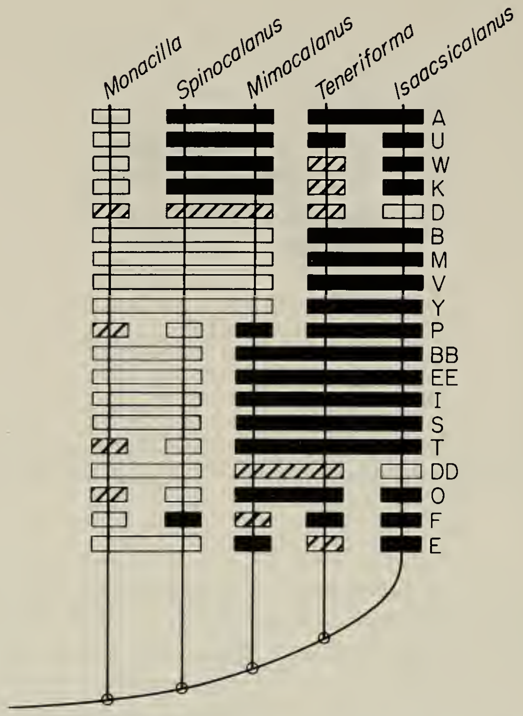


Fig. 6. Cladogram of hypothesized synapomorphies where criterion in meristic states is identical numbers. Transformation sequences determined by outgroup comparison; further discussion in text.

the Spinocalanidae. States 01 to 06 are familial and set Spinocalanidae apart from other families of the Clausocalanoidea. The remaining states provide compelling evidence of the distinctiveness of the five recognized genera and of the apparent synapomorphies that link *Spinocalanus* to *Mimocalanus* and *Teneriforma* to *Isaacsicalanus.* The handful of states appearing in more than one column, marked by the horizontal bar and integers appearing on both sides of the column, provide no indication of phylogenetic relationsips suggested by the analyses of proposed synapomorphies presented below.

Potential synapomorphies are presented in Table 2. Initially troubled by the seemingly considerable taxonomic distance between the outgroup Megacalanidae, a primitive member of the Megacalanoidea, and Spinocalanidae, a primitive member of the Clausocalanoidea, I utilized sets of synapomorphies chosen by three different criteria to construct three separate cladograms for comparison.

The first cladogram uses only those proposed synapomorphies (Table 2) whose transformation sequences appear reasonable and unequivocal solely on the basis of first principles of calanoid copepod morphology, i.e., the readily apparent transformation sequences B, M, BB, HH, A and U (Fig. 5). Reductions in the number of setae were arbitrarily omitted from consideration in this analysis, though a number of them (e.g., I, P, S, T, V, Y) satisfy the criteria as well as those characters that were selected. Knowledge of character HH, the presence or absence of endopods on the male's fifth pair of legs, remains incomplete pending discovery

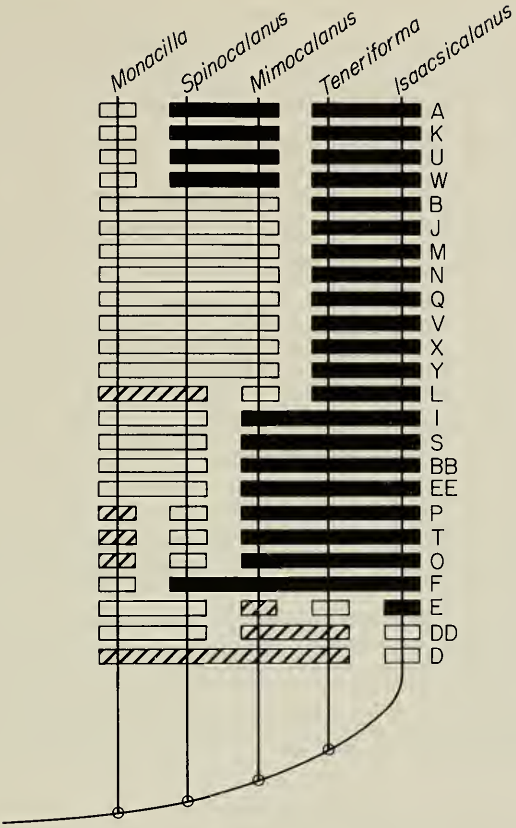


Fig. 7. Cladogram of hypothesized synapomorphies where criterion in meristic states is relaxed to group values with reductions trending similarly. Transformation sequences determined by outgroup comparison; further discussion in text.

of an adult *Isaacsicalanus* male. The six transformation sequences contain no reversals and support the hypothesized phylogenetic relationships shown by this cladogram.

The second cladogram uses transformation sequences in Table 2 that have two or more genera sharing identical derived states; e.g., synapomorphy is proposed when two or more genera share the same number of setae on a given structure other than the value designated primitive. Nineteen such synapomorphies were found, and the resulting hypothesized phylogenetic sequence (Fig. 6) agrees with that of Fig. 5. Nine of the characters show one or more reversals, 8 being readily accountable by assuming autapomorphic losses of one or more setae by the genus showing the reversal. Character D, however, requires autapomorphic losses in 4 genera. Altering the sequences of *Monacilla* and *Spinocalanus, Spinocalanus* and *Mimocalanus, Mimocalanus* and *Teneriforma,* or *Teneriforma* and *Isaacsicalanus* in each instance increases the number of reversals measurably. Obviously more extensive alterations in the sequence of genera would increase the number of reversals still further.

The third cladogram (Fig. 7) is based on the synapomorphies proposed for Fig. 6 and an additional category in which similar trends in loss of setae in a given character shown by 2 or more genera were also considered to be synapomorphic. This procedure increases the proposed synapomorphies to 24, produces the same hypothesized sequence of genera obtained by the two preceding cladograms, and decreases the number of reversals to seven.

The phylogenetic sequence of genera supported by all three analyses appears to be a reasonable expression of the data set. Corroboration by additional characters to be considered in the future should certainly include a., the sexually modified structures of adult males and females, and b., adult pore signatures.

The implications of these findings include a suggestion of past ages when the mixed-layer calanoids may have been taxonomically different from those dominating at present. Megacalanid-like forms with fully setose oral appendages adapted for smaller-particle feeding than extant megacalanids probably occupied at least some mixed-layer niches now held by more derived lineages of megacalanoids and clausocalanoids. Augaptiloid radiations in the mixed layer may have overlapped with or preceded those of the megacalanids, but the likelihood is a changing sequence of dominant microplankton feeders in the mixed layer over time. Megacalanid survivors, spinocalanids, and most of the augaptiloids are now confined to meso- and bathypelagic depths and appear to be predaceous or detrital feeders.

The prospects of developing a relative sequence of taxonomic changes in the mixed layer are favorable at this time. The difficulty yet to be faced in the continued absence of fossil history of calanoid copepods is the means by which these major changes may be related to established geological chronologies.

Acknowledgments

It is a pleasure to acknowledge the benefits of David Damkaer's (1975) excellent review of the Spinocalanidae, a work that greatly facilitated phylogenetic analysis of spinocalanid genera. For the opportunity to study this unique calanoid I thank Ken Smith of Scripps Institution of Oceanography (SIO), the chief Scientist on Expedition Oasis and co-worker Roberta Baldwin, SIO, the biological observer during ALVIN Dive no. 1217 who detected and sampled the swarm of copepods containing *I. paucisetus*; the paper is contribution no. 4 of Expedition Oasis. The final draft was improved by comments from readers of a previous version, namely, Thomas Bowman, Frank Ferrari, Mark Grygier, William Newman, and Richard Rosenblatt. This study was funded by the Marine Life Research Program of Scripps Institution of Oceanography.

Literature Cited

Andronov, V. N. 1973. Taxonomic status of *Mecynocera clausi* (Copepoda, Calanoida).—Zoologicheskii Zhurnal 52(11):1719–1721 [in Russian].

Björnberg, T. K. S. 1968. Four new species of Megacalanidae (Crustacea: Copepoda).—Antarctic Research Series 11:73–90.

Bowman, T. E. 1976. *Miostephos cubrobex,* a new genus and species of copepod from an anchialine pool in Cuba (Calanoida: Stephidae).—Proceedings of the Biological Society of Washington 89(11):185–190.

Bowman, T. E., and L. G. Abele. 1982. Classification of the recent Crustacea. Pp. 1–27 *in* Abele,

L. G., ed., The Biology of Crustacea. I. Systematics, the fossil record and biogeography. Academic Press, New York and London.

Damkaer, D. M. 1975. Calanoid copepods of the genera *Spinocalanus* and *Mimocalanus* from the central Arctic Ocean, with a review of the Spinocalanidae.—NOAA Technical Report NMFS CIRC-391:1–88.

Eldredge, N., and J. Cracraft. 1980. Phylogenetic patterns and the evolutionary process. Columbia University Press, New York, 349 pp.

Farran, G. P. 1908. Second report on the Copepoda of the Irish Atlantic slope.—Department of Agriculture and Technical Instruction for Ireland. Fisheries Branch. Scientific Investigations, 1906, 2:1–104.

———. 1936. Copepoda.—British Museum (Natural History), Great Barrier Reef Expedition 1928–29. Scientific Reports 5(3):73–142.

———, and W. Vervoort. 1951a. Copepoda. Suborder: Calanoida. Family: Spinocalanidae. Genus *Spinocalanus*.—Fiches Identification Zooplancton 39:1–4.

———, and ———. 1951b. Copepoda. Suborder: Calanoida. Family: Spinocalanidae. Genera *Mimocalanus, Monacilla*.—Fiches Identification Zooplancton 40:1–4.

Frost, B., and A. Fleminger. 1968. A revision of the genus *Clausocalanus* (Copepoda: Calanoida) with remarks on distributional patterns in diagnostic characters.—Bulletin of the Scripps Institution of Oceanography 12:1–99.

Giesbrecht, W. 1888. Elenco dei Copepodi pelagici raccolti dal tenete di vascella Gaetano Chierchia durante il viaggio della R. Corvetta "Vettor Pisani" negli anni 1882–1885 e del tenente de vascello Francesco Orsini nel Mar Rosso, nel 1884.—R. C. Accademia Nazionale del Lincei, Rome (4)4 sem. 2:284–287, 330–338.

———. 1892. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrenzenden Meeresabschnitte.—Fauna und Flora Neapel 19:1–831.

Grice, G. D. 1971. Deep water calanoid copepods from the Mediterranean Sea. Family Spinocalanidae.—Cahiers de Biologie Marine 12:273–281.

———, and K. Hulsemann. 1965. Abundance, vertical distribution and taxonomy of calanoid copepods at selected stations in the northeast Atlantic.—Journal of Zoology 146:213–262.

———, and ———. 1967. Bathypelagic calanoid copepods of the western Indian Ocean.—Proceedings of the United States National Museum 122(3583):1–67.

Humes, A. G., and M. Dojiri. 1980. A siphonostome copepod associated with a vestimentiferan from the Galapagos Rift and the East Pacific Rise.—Proceedings of the Biological Society of Washington 93(3):697–707.

Johnson, R. K. 1982. Fishes of the families Evermannellidae and Scopelarchidae: systematics, morphology, interrelationships, and zoogeography.—Fieldiana Zoology, new series, 12:1–252.

Lonsdale, P. 1977. Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers.—Deep-Sea Research 24:857–863.

Park, Tai Soo. 1970. Calanoid copepods from the Caribbean Sea and Gulf of Mexico. 2. New species and new records from plankton samples.—Bulletin of Marine Science 20(2):472–546.

Sanders, R. W. 1981. Cladistic analysis of *Agastache* (Limiaceae). Pp. 95–114 *in* Funk, V. A., and D. R. Brooks, eds., Advances in Cladistics.

Sars, G. O. 1903. An account of the Crustacea of Norway. IV. Copepoda, Calanoida.—Bergen, 171 pp.

———. 1925. Copépodes particulièrement bathypélagiques provenant des campagnes scientifiques du Prince Albert 1er de Monaco.—Resultats des Campagnes Scientifiques par Albert 1er, Prince souverain de Monaco 69:1–408.

Scott, A. 1909. The Copepoda of the Siboga Expedition. Part 1. Free-swimming, littoral and semiparasitic Copepoda.—Siboga-Expedition, monographie 29a:1–323.

Sewell, R. B. S. 1947. The free-swimming planktonic Copepoda. Systematic account.—The John Murray Expedition 1933–4 8(1):1–303.

Smith, K. L., Jr., and R. J. Baldwin. Deep-sea respirometry: *in situ* techniques.—*In* Forstner, H., and E. Gnaiger, eds., Handbook on Polarographic O_2 Sensors: Aquatic and Physiological Applications. Springer Verlag, Berlin. [in press].

Tanaka, O. 1956. The pelagic copepods of the Izu region, middle Japan. Systematic account II. Families Paracalanidae and Pseudocalanidae.—Publications of the Seto Marine Biological Laboratory 5(3):367–406.

Vervoort, W. 1951. Plankton copepods from the Atlantic sector of the Antarctic.—Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde. Tweede Sectie, Deel 47(4):1–156.

———. 1957. Copepods from Antarctic and Sub-Antarctic plankton samples.—B.A.N.Z. Antarctic Research Expedition, 1929–1931, Reports, Series B (Zoology and Botany) 3:1–160.

Wheeler, E. H. 1970. Atlantic deep-sea calanoid copeods.—Smithsonian Contributions to Zoology (55):1–31.

Scripps Institution of Oceanography, La Jolla, California 92093.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 623–631

EIGHT NEW SPECIES OF INDO-PACIFIC CRABS FROM THE COLLECTIONS OF THE SMITHSONIAN INSTITUTION

Tune Sakai

Abstract.—Four of the species described below were collected during the explorations of the U.S. Fish Commission vessel *Albatross* in 1908 and 1909. The remainder are from various sources and were found in the unidentified collections of the National Museum of Natural History. The new taxa include representatives of eight genera belonging to four families, including the Dorippidae, Leucosiidae, Cancridae, and Palicidae.

Most of the brachyuran crustaceans collected by the *Albatross* and deposited in the Smithsonian Institution were studied by Mary Jane Rathbun, and the remaining oxyrhynchous crabs have been studied by Dr. D. J. G. Griffin of the Australian Museum. I reexamined the *Albatross* collections and give herein descriptions of new species of crabs belonging to the families Dorippidae, Leucosiidae, Cancridae, and Palicidae. In addition, 4 new species of the family Leucosiidae are described; these were obtained from the Indo-Pacific by other collectors on various expeditions. All of these specimens have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Family Dorippidae MacLeay, 1838

Ethusa Roux, 1830

The genus *Ethusa* comprises about 14 species in the Indo-Pacific, the new species is therefore the fifteenth of this genus. In the Philippines, only one species of Dorippidae, *Ethusina gracilipes* Miers (1886), is known. Miers (1886) also reported *Ethusina sinuatifrons* from Japanese seas at a depth of 1875 fathoms, but this name is a *nomen nudum.*

Ethusa philippinensis, new species

Fig. 1a, b

Material.—1 ♂, holotype (USNM 195051), 4.5 miles NE of Legaspi Light, Lagonoy Gulf, Philippine Islands, 13°12′N, 123°49′18″E, 72 m, (146 fms), *Albatross* sta 5453, 7 Jun 1909.

Description.—The holotype is imperfect and soft-shelled. It is closely related to *E. hawaiiensis* Rathbun (1906; originally *E. mascarone hawaiiensis* Rathbun), the type of which is preserved in the Smithsonian Institution, and which was reexamined by the author in 1960. Front of new species produced anteriorly, composed of 4 teeth, median incision deepest. Outer orbital tooth triangular, situated apparently posterior to front, with its tip directed anteriorly, not laterally. Eyes very small. Anterolateral borders moderately swollen posteriorly; in *E. hawaiiensis,* they are subparallel and only slightly swollen.

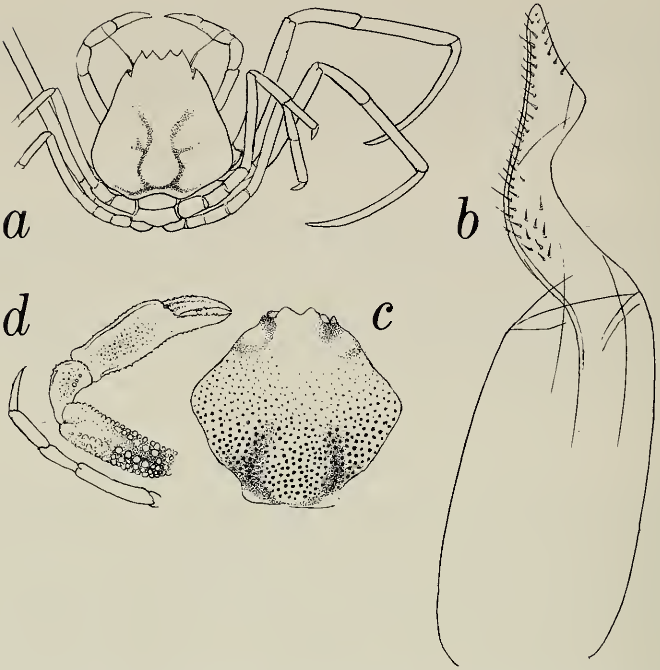


Fig. 1. *Ethusa philippinensis,* new species, male holotype, cl 11.3 mm: a, Dorsal view; b, Anterior male pleopod. *Ebalia punctulata,* new species, female holotype, cl 6.8 mm: c, Carapace; d, Cheliped and thoracic leg.

Dorsal surface of carapace smooth, "demon-faced" sculpture characteristic of Dorippidae faint, but groove around imaginary nose rather distinct.

Chelipeds slender and symmetrical. Dactyli of ambulatory legs very long, much longer than propodi. Anterior pleopod figured in Fig. 1b.

Measurements.—Length of carapace in the median line 11.3 mm, width 9.5 mm.

Leucosiidae Samouelle, 1819

Ebalia Leach, 1817

Ebalia punctulata, new species

Fig. 1c, d

Material.—1 ♀, holotype (USNM 195059), collected at Rongelap Lagoon, west of Rongelap Id., 10 m (20 fms), 21 Jun 1946, coll. Tayler.

Description.—Small species, carapace somewhat rhomboidal. Front moderately produced anteriorly, divided into 2 lobes by shallow median incision; anterior margins of these lobes straight. Lateral borders markedly convex. Posterolateral margins also slightly convex; posterior border transversely straight, lateral angles produced into plate-like crest.

Dorsal surface of carapace punctulate, but anterior third smooth. Surface inside hepatic region and on either side of intestinal region moderately depressed. Body lacking tubercles and spines.

Chelipeds equal, arm tuberculate along anterior and posterior borders, tubercles arranged in 2 or 3 longitudinal rows; wrist and palm punctulate. Movable and immovable fingers straight, prehensile margins finely denticulate.

Relationships.—This species is distinctive in having the dorsal surface of the carapace minutely punctulate, and in lacking granules and spines on the body.

Measurements.—Length of carapace 6.8 mm, width 7.1 mm.

Cryptocnemus Stimpson, 1858

Cryptocnemus marginatus, new species

Fig. 2a–c

Material.—1 ♂, holotype (USNM 195060), Benkoelen, Sumatra, coll. H. C. Kellers, U.S. Navy Eclipse Expedition to Sumatra, Nov 1925.

Description.—The genus *Cryptocnemus* is restricted to the Indo-Pacific, containing about 16 species until now; the new species is therefore the seventeenth. The holotype is soft and post-ecdysal. Most thoracic legs are missing and the right posterior corner of the carapace is broken and lost.

Carapace transversely ovoid, dorsal surface flat and smooth, margin elegantly bordered with tubercles, regularly and very closely arranged. Front only slightly produced beyond outline of carapace, median notch very shallow. Ventral preorbital edge also elegantly bordered with tubercles, its inner anterior notch deep, median portion distinctly notched. Outer maxilliped tightly closing the mouth, exognath longer and broader than endognath.

Chelipeds slender, arm, wrist, and palm very swollen, but anterior and posterior borders not carinate. Ambulatory legs very slender.

Male abdomen, and first and second pleopods lost; their characteristics not known.

Measurments.—Length of carapace 6.8 mm, width 7.2 mm.

Relationships.—This new species is closely related to *Cryptocnemus aberrans* Balss (1938) from Talagi, British Solomon Islands, but in the latter species the margin of the carapace is not bordered with tubercles and is strongly upturned.

Praebebalia Rathbun, 1911

Praebebalia septemspinosa, new species

Fig. 2d–h

Material.—2 ♂, holotype (USNM 195061) and paratype (USNM 195063), and 1 ♀ allotype (USNM 195063), NE of island lighthouse, Capitancillo Island, Visayan Islands, Philippine Islands, 11°10′N, 124°17′15″E, 90 m, (182 fms), *Albatross* sta 5403, 16 Mar 1909.

Description.—The genus *Praebebalia* also is restricted to the Indo-Pacific, containing 4 species until now; the new species is therefore the fifth. Carapace wide and subcircular, margin armed with 7 teeth, 1 pair on either side of lateral margin, 1 pair at midlength of each posterolateral margin, 1 pair on either side of posterior margin, and finally 1 on posterior slope of intestinal region. One or 2 small teeth on anterior margin of lateral tooth, and 1 small tooth on hepatic margin.

Dorsal surface of carapace covered with tubercles of various sizes, those on anterior and lateral surfaces large, those on posterolateral and posterior surfaces

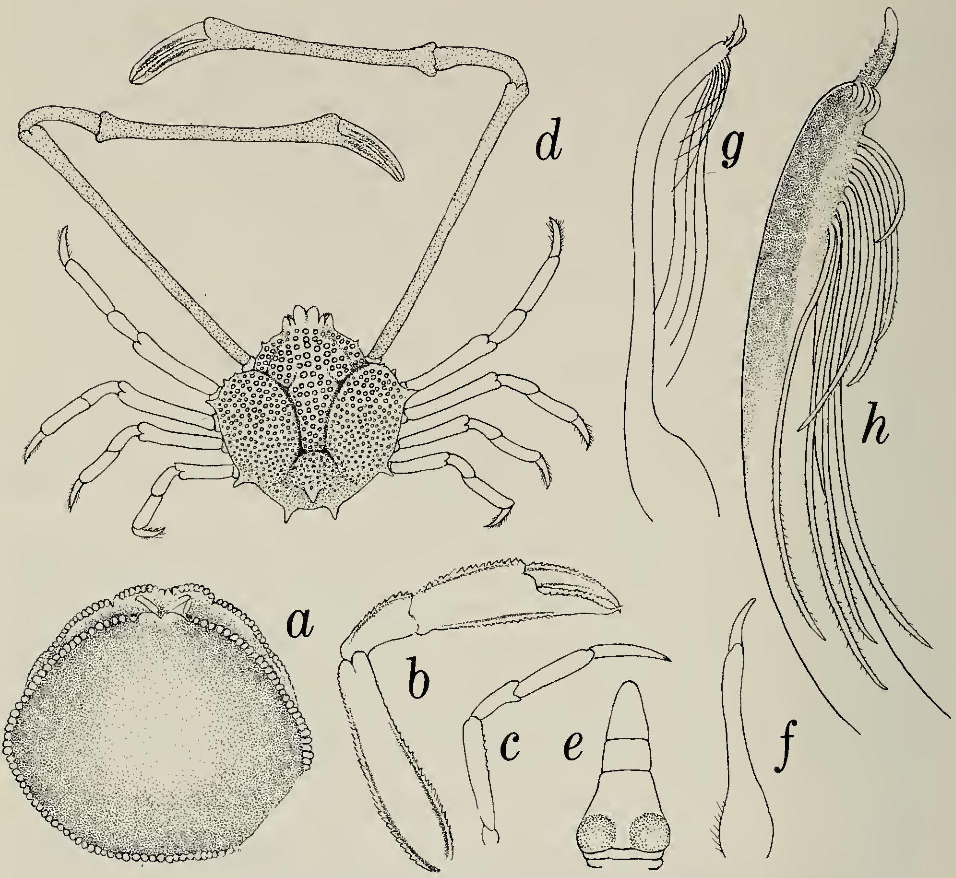


Fig. 2. *Cryptocnemus marginatus,* new species, male holotype, cl 6.8 mm: a, Carapace; b, Cheliped; c, First ambulatory leg. *Praebebalia septemspinosa,* new species, male holotype, cl 13.8 mm: d, Dorsal view; e, Abdomen; f, Second male pleopod; g, h, Anterior male pleopod.

small and indistinct to naked eye. Front produced, composed of 2 teeth, divided by median notch, intercalated spine small, external orbital spine larger.

Chelipeds very long, total length 4.5 times as long as carapace. Arm, wrist, and palm finely granulated; fingers inclined about 15 degrees to palm, their prehensile edges finely denticulate. Ambulatory legs slender, with no tubercles or granules.

Male abdomen composed of 5 segments, third to fifth fused, final segment very long. Anterior male pleopod slender, distal part furnished with 3 short, 4 median, and 4 very long hairs; apical process thin and projected laterally. Second pleopod simple (Fig. 2f).

Measurements.—Length of carapace 13.8 mm, width 14.5 mm, length of cheliped 62.0 mm.

Relationships.—The new species is related to *P. extensiva* Rathbun (1911), the type-species of this genus, but in the latter species, the carapace has only 5 marginal spines, and the dorsal surface is smooth, not granulated.

Pseudophilyra Miers, 1879
Pseudophilyra burmensis, new species
Fig. 3a, b

Material.—1 ♂, holotype (USNM 195049), Rangoon, Burma, coll. G. E. Gates, 1928.

Description.—The genus *Pseudophilyra* also occurs only in the Indo-Pacific, containing 12 species until now; the new species is therefore the thirteenth.

Carapace almost circular and moderately flattened. Dorsal surface granulate, but anterior part of gastric region, postorbital surface, interior of anterolateral and central part of intestinal region nongranular and smooth. Front bilobed, each lobe rounded and divided by median shallow notch, underlying which, small ventral frontal tooth. Intercalated spine small, outer orbital tooth strong and obtuse. Eyes very small. Prebuccal plate small and polished.

Chelipeds strong, arm covered with longitudinally arranged tubercles, distal part of arm smooth; wrist and palm smooth except upper and lower margins, both slightly granulated. Chelae as long as palm, prehensile edges finely denticulate. Ambulatory legs all slender.

Male abdomen composed of 5 narrow segments, third to fifth coalesced, seventh very long and distally narrowed. Anterior male pleopod cylindrical with tip cut off obliquely into oval surface, with one margin densely haired, and very long hair at base.

Measurements.—Length of carapace in median line 10 mm, width 10 mm.

Relationships.—In the arrangement of granules on the upper surface of the carapace, the new species is related to *Philyra adamsii* Bell (1855) but the latter species has the front narrower and no median ventral spinule in the median frontal sinus, in contrast to the new species. The anterior male pleopod of *P. burmensis* is distinctive (Fig. 3b).

Leucosia Weber, 1795
Leucosia bikiniensis, new species
Fig. 3c–e

Material.—1 ♂, holotype (USNM 195050), Sta 3605, 0.5 mi S of west end, Bikini Atoll, Marshall Islands, 5 m, (10 fms), 26 Aug 1947, coll. J. P. E. Morrison.

Description.—Carapace very broad, breadth exceeding length. Front produced slightly anteriorly, divided into 2 lobes by median shallow sinus. Hepatic border produced into low triangular lobe. Lateral border densely furnished with hairs; narrow crest present along posterolateral and posterior borders. Dorsal surface smooth, coloration faded; ocelli or stripes usually found in *Leucosia* not observed.

Chelipeds rather short and robust. Left cheliped, arm bearing 2 very large tubercles followed by 1 basal and 1 smaller distal tubercle on anterodorsal border; cluster of about 4 small tubercles at upper basal surface; about 6 medium-sized tubercles on posterior border; and finally, 5 smaller tubercles in cluster at posterior basal surface, covered with velvety tomentum.

Right cheliped, arm bearing 3 large tubercles on dorsoanterior border; otherwise arrangement of smaller tubercles about same as those of left cheliped.

Wrist, palm, and fingers carinate along inner and outer borders. Outer distal part of wrist bearing row of several small tubercles traversed by row of few tubercles; basal end of immovable finger armed with 2 oblique rows of small tubercles.

Male abdomen like that of related species, composed of 4 pieces, second, and third broad, third segment armed with spinule in middle. Anterior male pleopod thin, distal end thickened and divided into 2 hemispheres, covered with hairs. Inner hemispheres armed with low spine, outer hemisphere slightly higher, without spine.

Measurements.—Length of carapace 7.0 mm, width 7.3 mm.

Relationships.—This species is closely related to *Leucosia insularis* Takeda and Kurata (1976), from the Bonin Islands (=Ogasawara Islands), but in the latter species the thoracic sinus is marked with one large and several smaller tubercles instead of 2 ridges of small tubercles and a few larger tubercles between the 2 ridges in *L. bikiniensis.* In the Bonin species, the apex of the male pleopod is globular, while in the new species it is divided into two hemispheres.

Cancridae Latreille, 1803

Cancer Linnaeus, 1758

Cancer is the oldest and fundamental genus of the decapod crustaceans, established by Linnaeus in 1758. In the Indo-Pacific, this genus comprises 8 species until now:

Cancer gibbosulus (De Haan, 1835)
= *Trichocarcinus affinis* Miers, 1879
Cancer novaezelandae (Jacquinot, 1853)
Cancer japonicus Ortmann, 1893
Cancer amphioetus Rathbun, 1898
= *Trichocarcinus dentatus* Miers, 1879 (preoccupied)
    Not *Cancer dentatus* Herbst, 1785
    Not *Cancer dentatus* Bell, 1835
= *Cancer bullatus* Balss, 1922
Cancer tumifrons Yokoya, 1933
Cancer nadaensis Sakai, 1969
Cancer sakaii Takeda & Miyaki, 1972
= *Platepistoma anaglyptum* Balss, 1922 (preoccupied)
Cancer guezei Crosnier, 1976

Cancer luzonensis, new species

Fig. 3f

Material.—1 ♀, holotype (USNM 195064), off Matocot Point, Luzon Island, Philippine Islands, 13°41′50″N, 120°58′30″E, 86 m, (172 fms), *Albatross* sta 5289, 22 Jul 1907.

Description.—This species has 3 frontal teeth, median very small and in a lower ventral position. Orbital teeth strong. Anterolateral margin divided into 9 teeth, subequal in size and shape and arranged in arch, last tooth situated at outermost corner. Posterolateral border slightly concave, armed with about 8 teeth behind last anterolateral tooth. Posterior margin also slightly concave, smooth, without teeth.

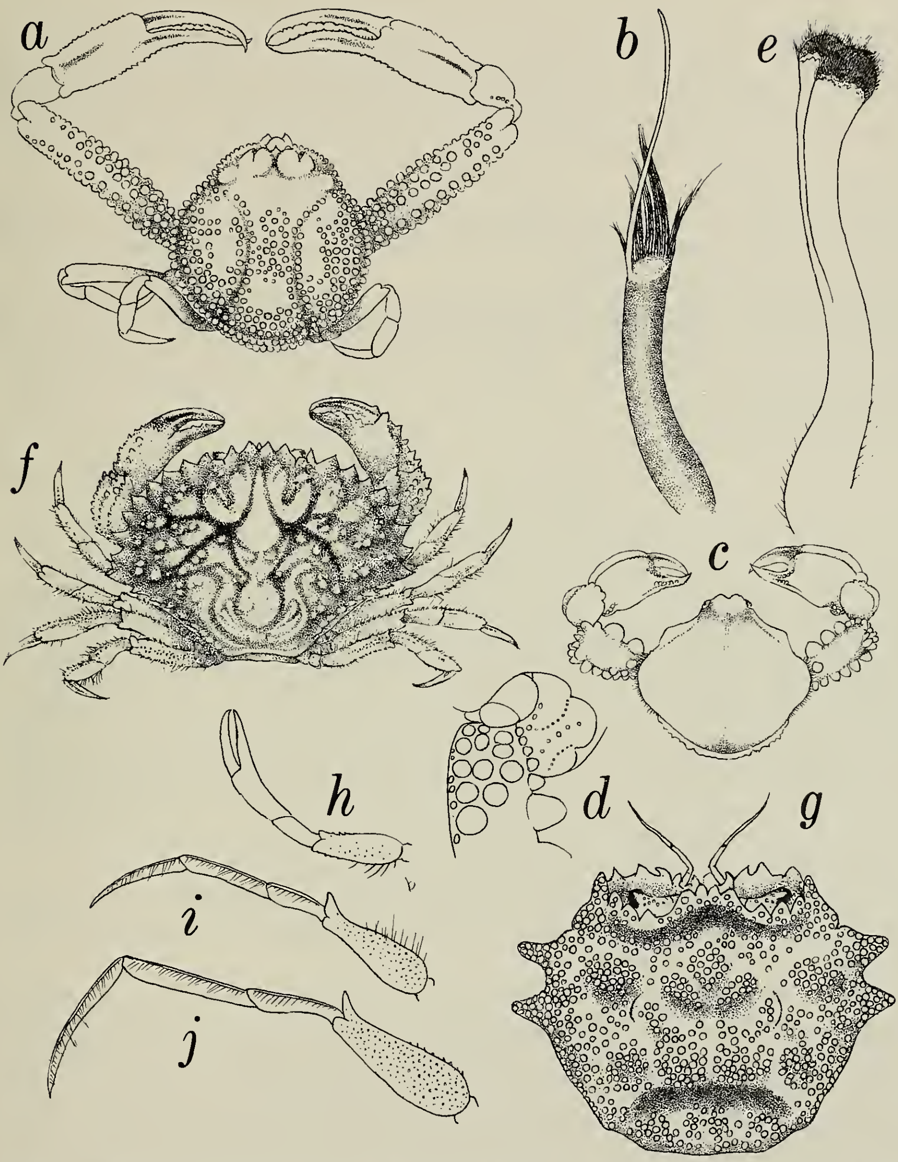


Fig. 3. *Pseudophilyra burmaensis,* new species, male holotype, cl 10 mm: a, Dorsal view; b, Anterior male pleopod. *Leucosia bikiniensis,* new species, male holotype, cl 7.0 mm: c, Carapace and chelipeds; d, Thoracic sinus; e, Anterior male pleopod. *Cancer luzonensis,* new species, female holotype, cl 34.0 mm: f, Dorsal view. *Palicus bidentatus,* new species, female holotype, cl 7.1 mm: g, Carapace; h, Cheliped; i, Second ambulatory leg; j, Third ambulatory leg.

Dorsal surface of carapace deeply areolate, grooves separating gastric, cardiac, and branchial regions deep and distinct. These regions divided into subregions; anterior surface of gastric region and lateral surfaces of hepatic and branchial regions sparingly tuberculate. Cardiac and intestinal regions also indistinctly tuberculate. Chelipeds subequal in size and shape; arm short and almost hidden beneath anterolateral margin, upper surface smooth. Upper surface of wrist smooth, anterior margin granulate and haired. Outer surface of palm marked with 5 longitudinal rows of granules, distal portions of these rows marked with large tubercles; outer surface marked with 4 longitudinal rows of granules. Fingers lightly pigmented with brown, prehensile margins armed with 4 or 5 teeth, proximal 1 or 2 large. Ambulatory legs rather slender, anterior edges of carpus and propodus spinulate and haired.

Measurements.—Length of carapace measured between the tips of the frontal teeth and the posterior margin 34 mm, width of same measured between the tips of the anterolateral teeth 47 mm.

Relationships.—This species is related to *Cancer nadaensis* Sakai (1969) in its general aspect, but the dorsal surface of the carapace is deeply areolated, differing from the smooth surface of *C. nadaensis,* and the last anterolateral tooth is less produced laterally.

Palicidae Rathbun, 1898

Palicus Philippi, 1838

Palicus bidentatus, new species

Fig. 3g–j

Material.—1 ♀, holotype (USNM 195065), SE of Hong Kong Island, 21°42′N, 114°50′E, 19 m, (38 fms), *Albatross* sta 5302, 9 Aug 1908.

Description.—This specimen is very old and fragmentary, the chelipeds and ambulatory legs have fallen off. Carapace broadly rectangular. Front not much produced anteriorly, composed of 4 teeth; upper orbital teeth also 4 in number, each separated by fissure. Upper surfaces of these teeth sparsely granulate, posterior to these teeth surface of anterior carapace transversely depressed. Around eyestalk, ventral ridge of orbit armed with 1 outer and 2 inner teeth; these teeth all strong and high compared with those of other species.

Hepatic border very short; branchial border armed with 2 obtuse densely granulate processes at lateral border. Posterolateral and posterior borders united, transverse, without teeth or spines.

Dorsal surface of carapace strongly uneven, sparingly covered with granules. Regions of carapace not clearly separated, but each with patches of thick granules. Gastric region with 3 rhomboidal patches of granules, cardiac region divided into 2 by median groove, intestinal region vaguely separated into 4. Between cardiac and intestinal regions, surface deeply and transversely depressed. Inner surfaces of the anterolateral and posterolateral borders each with patch of thick granules.

Chelipeds slender; arm, wrist, and palm not markedly granulate; prehensile edges entire, blade-like. Third ambulatory leg largest, second and first pairs little smaller, fourth pair very small and filiform. In first 3 ambulatory legs, merus thickened proximally, subdistal portion thin, distal outer part armed with strong tooth; carpus, propodus and dactylus with long hairs along anterior border.

Measurements.—Length of carapace 7.1 mm, width 10.5 mm.

Relationships.—Among the numerous species of *Palicus,* this species is peculiar in having the carapace transversely rectangular and its anterolateral border is armed with 2 obtuse processes, covered with granules. Around the orbit, this species has 3 dorsal, 1 lateral, 1 outer ventral, and 2 inner ventral teeth.

Acknowledgments

I wish to express my deep gratitude to Dr. Fenner A. Chace, Jr., who originally made the specimens available for study. Thomas E. Bowman and Raymond B. Manning edited the final drafts of the manuscript.

Literature Cited

Balss, H. 1938. Die Dekapoda Brachyura von Dr. Sixten Bocks Pazifik-Expedition 1917–1918.—Göteborgs Kungliga Vetenskaps-och Vitterhets-Samhälles Handlingar, Femte Följenden, series b 5(7):1–85.

Bell, T. 1855. A monograph of the Leucosiadae, with observations on the relations, structure, habits and distribution of the family; a revision of the generic characters; and descriptions of new genera and species. Hora Carcinologicae, or Notices of Crustacea, I.—Transactions of the Linnean Society 21:277–314.

Miers, E. J. 1886. Report on the Brachyura 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 1873–1876, Zoology, 17:xli + 362.

Rathbun, M. J. 1906. The Brachyura and Macrura of the Hawaiian Islands.—Bulletin of the U.S. Fish Commission for 1903, part 3:827–930.

———. 1911. Marine Brachyura. The Percy Sladen Trust Expedition to the Indian Ocean in 1905, 3(9).—Transaction of the Linnean Society, London, Zoology, (2)14(2):191–261, pls. 15–20.

Sakai, T. 1969. Two new genera and twenty-two new species of crabs from Japan.—Proceedings of the Biological Society of Washington 82:243–280.

Takeda, M., and Y. Kurata. 1976. Some species collected by coral fishing boats. Crabs of the Ogasawara Islands, III.—Bulletin of the National Science Museum, Tokyo, series A (Zoology) 2(1):19–32.

562 Jyomyoji-machi, Kamakura, Kanagawa-ken, Japan.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 632–637

A NEW SPECIES OF THE SERRANID FISH GENUS *PLECTRANTHIAS* (PISCES: PERCIFORMES) FROM THE SOUTHEASTERN PACIFIC OCEAN, WITH COMMENTS ON THE GENUS *ELLERKELDIA*

Phillip C. Heemstra and William D. Anderson, Jr.

Abstract.—*Plectranthias exsul,* new species, is described from six specimens collected off the Juan Fernandez Islands and from the Nazca Ridge off the coast of Chile. This new species is the first *Plectranthias* to be reported from the eastern Pacific Ocean. The distinction between *Plectranthias* and *Ellerkeldia* is discussed.

For several years we have been working on a revision of the American Anthiinae. Among the considerable material examined are six specimens of a new species of *Plectranthias* Bleeker, 1873, from the southeastern Pacific. Rather than delay description of this new species until the completion of our revision, we decided to publish the description separately.

Type-specimens are deposited in the Academy of Natural Sciences of Philadelphia (ANSP); Bernice P. Bishop Museum, Honolulu (BPBM); Museum of Comparative Zoology, Harvard University (MCZ); National Museum of Natural History, Smithsonian Institution (USNM); and Zoological Museum, Moscow State University (ZMMU). Measurements and counts were made following Anderson and Heemstra (1980).

Plectranthias exsul, new species
Figs. 1–2

Plectranthias sp., Parin *et al.,* 1981:14 (brief description of Nazca Ridge specimens).

Holotype.—ANSP 127843, 158 mm SL (standard length); Juan Fernandez islands (33°37′S, 78°49′W); Feb 1957; R. Manning, collector.

Paratypes.—MCZ 52520, 2 specimens 134 & 140 mm SL; Juan Fernandez islands; 140 to 165 m; 27 Jan 1966; R/V *Anton Brunn* Cruise 13, Stn. 35; 40′ otter trawl. USNM 176577, 158 mm SL; Juan Fernandez islands (33°38′S, 78°50′W); 31 Mar 1945. BPBM 27978, 133 mm SL; Nazca Ridge (25°45′S, 85°29′W); 200 to 225 m; 1 Nov 1979; R/V *Ikhtiandr* Trawl 59. ZMMU P-16022, 150 mm SL; data as for BPBM 27978.

Diagnosis.—Dorsal-fin rays X, 15 or X, 16. Anal-fin rays III, 7. Pectoral-fin rays 16 or 17 (usually 16); dorsalmost (and occasionally ventralmost) ray unbranched, the rest branched. Branched caudal-fin rays 8 + 7. Lateral-line scales 40 to 46; scales between middle of spinous dorsal fin and lateral line 1½ to 2½. Lateral part of snout and anterior part of lower jaw naked. Maxilla naked or with very few scales. Small splint-like supramaxilla usually present. Preopercle serrate, with or without antrorse spine on lower limb. Gillrakers 8 to 10 + 18 to 21, total 26 to 31. Second soft ray of dorsal fin and one of dorsalmost branched rays of

Fig. 1. *Plectranthias exsul*, holotype, ANSP 127843, 158 mm SL.

caudal fin elongate. Posterior margin of caudal fin truncate to slightly concave. Vertebrae 10 + 16. Arrangement of predorsal bones, anterior neural spines, and anterior pterygiophores of dorsal fin 0/0+0/2/1+1/1/ (using notation of Ahlstrom *et al.* 1976).

Description.—Morphometric data are given in Table 1. Dorsal fin continuous, not divided to base between spinous-and soft-rayed parts; fourth or fifth spine of dorsal fin longest, 1.6 to 2.0 times length of last spine of dorsal fin; second soft ray of dorsal fin elongate, longer than longest spine of dorsal fin. Anal fin margin subangular to slightly pointed; second spine of anal fin about twice length of first, much stouter than third; third shorter than second. Pectoral fin pointed; middle rays longest, usually reaching to vertical through base of third spine of anal fin. Pelvic fin reaching or falling well short of anus. Principal caudal-fin rays 9 + 8; procurrent caudal-fin rays 9 or 10 dorsally, 7 to 9 ventrally.

Body depth 2.5 to 3.0, head length 2.5 to 2.7 in SL. Orbit 3.8 to 4.5, interorbital width 5.8 to 6.7 in head length. Maxilla reaching or almost reaching vertical through posterior border of orbit; posteroventral corner of maxilla with rounded projection. Anterior naris oblique, at distal end of short tube (posterior border of tube highest); posterior naris elliptical to subcircular. Scales ctenoid. Scales on dorsum of snout extending anteriorly on each side of naked mid-dorsal area nearly to upper lip (in one specimen anterior part of mid-dorsal area covered with scales). Interorbital region, cheek, preopercle, opercle, subopercle, interopercle, and posterior ⅓ to ⅔ of ventral surface of lower jaw with scales. Scales on cheek extending

Table 1.—Morphometric data for *Plectranthias exsul.* The holotype is denoted by an asterisk. Standard length is in mm; other measurements, in percentage of standard length.

Measurement	BPBM 27978	MCZ 52520		ZMMU P-16022	ANSP 127843*	USNM 176577
Standard length	133	134	140	150	158	158
Head, length	37.7	38.4	39.1	38.2	37.6	37.8
Snout, length	10.6	9.3	10.0	10.3	9.4	9.8
Orbit, diameter	9.5	9.9	10.2	8.5	9.5	8.4
Postorbital length of head	17.2	20.0	18.8	18.5	18.6	19.4
Upper jaw, length	18.3	19.6	19.6	17.5	19.0	18.7
Maxilla, width	5.2	6.3	6.2	5.0	5.7	5.5
Interorbital width	6.0	6.3	5.9	6.1	6.5	6.3
Body, depth	33.7	37.3	39.6	36.1	35.2	36.5
Predorsal length	35.8	39.9	39.3	37.0	37.9	39.5
Preanal length	70.6	64.9	66.4	70.1	64.7	66.2
Caudal peduncle, length	21.2	20.9	20.4	22.1	22.7	22.3
Caudal peduncle, depth	10.3	12.4	13.1	10.7	11.2	10.7
Pectoral fin, length	ca. 31.7	33.3	30.7	33.3	33.2	32.5
Pelvic fin, length	22.9	26.1	25.2	ca. 22.3	23.4	24.1
Anal fin, length	28.0	29.9	28.9	26.5	ca. 30.8	26.8
Upper caudal-fin lobe, length	>30.4	28.2	28.6	ca. 24.5	ca. 29.9	—
Lower caudal-fin lobe, length	22.2	23.9	26.1	ca. 23.1	ca. 24.0	—
Third dorsal spine, length	15.7	15.9	16.3	>14.8	>16.8	>15.4
Fourth dorsal spine, length	18.2	18.7	18.4	>16.7	>18.8	>16.1
Longest dorsal spine, length	18.2	18.7	18.4	>16.7	19.9	18.1
	(4th)	(4th)	(4th, 5th)	(4th)	(5th)	(5th)
First anal spine, length	9.5	9.3	8.4	8.7	9.8	8.9
Second anal spine, length	19.0	17.3	—	16.1	18.7	16.6
Third anal spine, length	>15.3	14.9	15.9	14.7	15.7	14.7

anteriorly to vertical through middle of orbit. Branchiostegal rays and membranes, and gular area naked (few scales anteriorly along midline of gular area in some specimens). Opercle with 3 spines; dorsalmost blunt and inconspicuous, middle one largest. Few to numerous small to well-developed serrae and/or irregularities on distal margins of subopercle and interopercle at or near their junction. Branchiostegal rays 7; anterior 3 inserting along ventral edge of hyoid arch, posterior 4 inserting laterally on arch. Longest gillrakers slightly longer than longest gill filaments. Pseudobranch well developed, with 23 to 31 filaments.

Proximal half of soft dorsal and anal fins scaly; pectoral, pelvic and caudal fins scaly basally; no enlarged axillary scales at base of pelvic fin. Rows of cheek scales 8 to 12. Series of circum-peduncle scales 18 to 22. No smaller auxiliary scales at bases of body scales. Lateral line complete, extending to base of caudal fin; running a few scale rows below dorsal fin parallel to dorsal body contour, curving to midlateral axis of body somewhat posterior to vertical through posterior end of dorsal-fin base. Lateral-line tubes simple. Scales from dorsal-fin origin to lateral line 4 or 5; scales from lateral line to anal-fin origin 13 to 17.

Upper jaw with band of very small depressible teeth; band broadest in anterior portion of jaw where inner teeth are variously enlarged into posteriorly directed conical and caniniform teeth; 1 to 3 stout exserted canines on each side near symphysial diastema. Lower jaw with narrow band of small depressible conical

Fig. 2. *Plectranthias exsul,* paratype, MCZ 52520, 140 mm SL.

teeth; band broadened at anterior end of jaw; 1 to 3 stout exserted canines on each side of jaw near symphysial diastema; 1 to 3 stout recurved canines on each side of jaw about one-third distance from symphysis to posterior termination of dentition; inner teeth of band somewhat enlarged; inner teeth near symphysis recurved and distinctly enlarged. Vomer and palatines with cardiform teeth; vomerine teeth in chevron-shaped patch; palatine teeth in band, anterior portion of band somewhat broadened and usually slightly curved toward vomer. No teeth on tongue or pterygoids.

Eleventh and twelfth vertebrae with ventrolateral foramina. Epipleural ribs on anterior 12 or 13 vertebrae; pleural ribs on vertebrae 3 through 10. No hypural fusions. Trisegmental pterygiophores associated with anal fin 1 or 2, with dorsal fin none.

Color.—In alcohol, body and head uniformly straw colored; color in life unknown.

Comparisons.—*Plectranthias exsul* has more lateral-line scales than any other species in the genus except *P. taylori* Randall, 1980; however, it is separated easily from *P. taylori* in having more gillrakers (total on first gill arch 26 to 31 vs. 17 or 18), fewer dorsal soft rays (15 or 16 vs. 18), and more pectoral-fin rays (16 or 17 vs. 14).

Plectranthias exsul is also similar to *P. kelloggi* (Jordan & Evermann, 1903), with which it shares the following characters: second soft ray of dorsal fin and one of dorsalmost branched rays of caudal fin elongated, similar fin-ray counts, and similar dentition. In addition to having more lateral-line scales (40 to 46 vs. 32 to 38), *P. exsul* differs from *P. kelloggi* in having more gillrakers (total on first gill arch 26 to 31 vs. 20 to 24) and in possessing a naked or almost naked maxilla and a partially naked mandible (anterior one-third to two-thirds without scales) vs. a partially scaly maxilla and a scaly mandible.

Distribution.—*Plectranthias exsul* is known only from off the Juan Fernandez islands and from the Nazca Ridge off the coast of Chile. Depths of capture range from 140 to 225 meters.

Etymology.—The Latin noun *exsul* (meaning "exile") is used in allusion to the eastern Pacific distribution of this species; *P. exsul* is the first species of *Plectranthias* known from the eastern Pacific region.

Remarks.—In his revision of the genus *Plectranthias,* Randall (1980) recognized 30 species, 13 of which he described as new. Five other new species have recently been placed in *Plectranthias* by Fourmanoir and Rivaton (1980), Katayama and Masuda (1980), Fourmanoir (1982), and Raj and Seeto (1983). It should be pointed out that our assignment of *P. exsul* to *Plectranthias* is based on Randall's definition of the genus. In order to precisely place *P. exsul* or any other species currently assigned to the genus, more study, particularly of internal morphology, is needed. It seems likely that a reassessment of currently available data coupled with an analysis of new information will lead to a modification of the description of *Plectranthias* provided by Randall (1980) and to the recognition at the generic level of one or more of the eight genera subsumed by him into *Plectranthias.*

Although considerations of the limits and the diagnostic characteristics of the genus *Plectranthias* are beyond the scope of this study, we feel that a comment on the generic-level classification proposed by Randall is in order. Randall (1980: 102) considered the genus *Ellerkeldia* Whitley, 1927, to be "closely related to *Plectranthias.*" He distinguished the two genera by the "smaller scales (40 to 50 in the lateral-line series . . .)" and "the configuration of the head" being "more sharply linear" in *Ellerkeldia.* Nevertheless *Plectranthias taylori* Randall, 1980, has 40 to 41 lateral-line scales, our new species, *P. exsul,* has 40 to 46, and *E. jamesoni* (Ogilby, 1908) has 38 to 42. Judging by the available illustrations, there are several species of *Plectranthias* with head profiles as "sharply linear" as those of species of *Ellerkeldia.* Although neither of Randall's criteria will serve to distinguish these two genera, it appears that number of vertebrae is useful. Each of the six species of *Ellerkeldia* we examined has 27 vertebrae (10 + 17), whereas all species of *Plectranthias,* for which counts are available (Katayama and Masuda 1980; Randall 1980; and the present work), have 26. Provisionally then, we accept Randall's definition of the genus *Plectranthias* and consider it distinct from the genus *Ellerkeldia,* but are well aware that neither genus is satisfactorily defined or differentiated from related genera.

Acknowledgments

The curators of fishes at the Academy of Natural Sciences of Philadelphia, Museum of Comparative Zoology, and the National Museum of Natural History allowed us to examine specimens in their care. J. E. Randall forwarded material he received from the P. P. Shirshov Institute of Oceanology in Moscow; we are grateful to N. V. Parin of that Institute for permission to deposit a paratype in the Bernice P. Bishop Museum. J. L. Russo made the photograph for Fig. 1. Susan Jewett, J. F. McKinney, and G. C. Van Dyke provided radiographs. G. D. Johnson reviewed the manuscript. This paper is contribution number 58 of the Grice Marine Biological Laboratory. This research was supported in part by National Science Foundation Grant GB-40063 to P. C. Heemstra.

Literature Cited

Ahlstrom, E. H., J. L. Butler, and 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.

Anderson, W. D., Jr., and 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.

Bleeker, P. 1873. Sur les espèces indo-archipelagiques d'*Odontanthias* et de *Pseudopriacanthus.*—Nederlandsch Tijdschrift voor de Dierkinde 4:235–240.

Fourmanoir, P. 1982. Trois nouvelles espèces de Serranidae des Philippines et de la Mêr du Corail *Plectranthias maculatus, Plectranthias barroi, Chelidoperca lecromi.*—Cybium 6:57–64.

Fourmanoir, P., and J. Rivaton. 1980. *Plectranthias randalli* n. sp., un nouveau serranidé (anthiiné) du sud-ouest Pacifique.—Revue française d'Aquariologie 7:27–28.

Jordan, D. S., and B. W. Evermann. 1903. Descriptions of new genera and species of fishes from the Hawaiian Islands.—Bulletin of the United States Fish Commission 22:161–208.

Katayama, M., and H. Masuda. 1980. Two new anthiine fishes from Sagami Bay, Japan.—Japanese Journal of Ichthyology 27:185–190.

Ogilby, J. D. 1908. On new genera and species of fishes.—Proceedings of the Royal Society of Queensland 21:1–26.

Parin, N. V., G. A. Golovan, N. P. Pakhorukov, Yu. I. Sazonov, and Yu. N. Shcherbachev. 1981. Fishes from the Nazca and Sala-y-Gomez underwater ridges collected in cruise of R/V "Ikhtiandr." *In*: Fishes of the Open Ocean.—Institute of Oceanology, Academy of Sciences of the USSR, Moscow ("1980"). pp. 5–18.

Raj, U., and J. Seeto. 1983. A new species of the Anthiine fish genus *Plectranthias* (Serranidae) from the Fiji Islands.—Japanese Journal of Ichthyology 30:15–17.

Randall, J. E. 1980. Revision of the fish genus *Plectranthias* (Serranidae: Anthiinae) with descriptions of 13 new species.—Micronesica 16:101–187.

Whitley, G. P. 1927. Studies in ichthyology. No. 1.—Records of the Australian Museum 15:289–304.

(PCH) J. L. B. Smith Institute of Ichthyology, Private Bag 1015, Grahamstown 6140, Republic of South Africa; (WDA) Grice Marine Biological Laboratory, College of Charleston, Charleston, South Carolina 29412.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 638–644

REDESCRIPTION OF THE BRAZILIAN LABRISOMID FISH *STARKSIA BRASILIENSIS*

J. T. Williams and A. M. Smart

Abstract.—*Starksia brasiliensis* (Gilbert), known only from southern Brazil, is redescribed based on 16 specimens collected from near São Paulo, Brazil, and all *S. brasiliensis* specimens mentioned in earlier literature. *Starksia brasiliensis* is distinguished from other species in the *S. ocellata* complex by a combination of the following characters: narrow, pale Y-shaped mark on cheek; ring-shaped marks on cheek bright red in life; no bars on lips; typically 16 (range 15–17) scales in arched part of lateral line; and typically 7 (range 7–9) total gill rakers on the first arch.

The known geographic range of *Starksia brasiliensis* is extended from Maceió and Salvador, Brazil, some 1600 km south to São Paulo, Brazil.

Starksia brasiliensis, a poorly known labrisomid (sensu George and Springer 1980) previously represented by only five specimens, inhabits rocky, coralline areas in the shallow coastal waters of southern Brazil. Sixteen specimens of *S. brasiliensis,* collected by one of us (AMS) near São Paulo, allow an expanded analysis of character variation. The variation reported herein significantly increases the ranges for meristic characters given by Greenfield (1979), and has made it necessary to redescribe the species. These specimens also extend the geographic range of the species southward to São Paulo, Brazil.

The taxonomic validity of *Starksia brasiliensis* (Gilbert, 1900) has been in doubt since it was described. Longley and Hildebrand (1941) placed it in the synonymy of *S. ocellata* (Steindachner, 1876). They did not give reasons for taking this action, although they did examine one specimen of *S. brasiliensis* collected off the coast of Salvador, Brazil. Böhlke and Springer (1961) reviewed *Starksia* and commented on the low anal-fin ray and scale counts of a paratype of *S. brasiliensis.* Because there was so little material available, they chose to retain *S. brasiliensis* in the synonymy of *S. ocellata.* In his review of the *S. ocellata* complex, Greenfield (1979) examined four specimens (including both types) from southern Brazil and gave this population species status based on three major characters: a narrow, pale Y-shaped mark on the cheek, no bars on the lips, and a single row of infraorbital pores. We find the first two characters useful for species recognition but the infraorbital pores are frequently in a double row, thus limiting the usefulness of these pores as a distinguishing character.

Counts and measurements follow Greenfield (1979). In addition, tooth counts refer only to the teeth in the outermost row. The cephalic sensory pore series are delimited as shown in Fig. 1 (counts include all pores in each series). Predorsal, preanal, and prepelvic lengths refer to the distance from the snout tip to the anterior of the base of the respective fin. Procurrent caudal-fin rays are those caudal elements with less than two segments.

The following institutional abbreviations are used: BMNH—British Museum (Natural History); CAS-SU—Stanford University collection at the California Academy of Sciences; GCRL—Gulf Coast Research Laboratory in Ocean Springs,

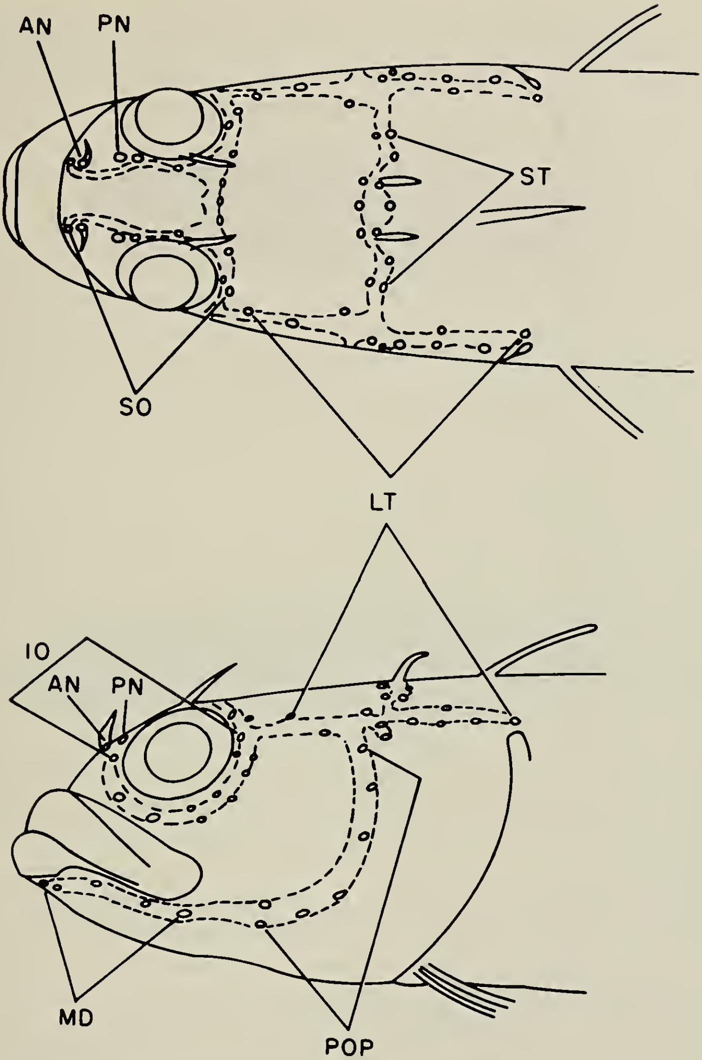


Fig. 1. Semidiagrammatic illustration of cephalic sensory pore series. Lines indicate first and last pores in each series. Abbreviations: AN, anterior nostril; IO, infraorbital series; LT, lateral temporal series; MD, mandibular series; PN, posterior nostril; POP, preopercular series; SO, supraorbital series; ST, supratemporal series.

Mississippi; MZUSP—Museu de Zoologia da Universidade de São Paulo; UF—Florida State Museum. Other abbreviations: IO, infraorbital pore series; LT, lateral temporal pore series; MD, mandibular pore series; POP, preopercular pore series; SO, supraorbital pore series; ST, supratemporal pore series.

Starksia brasiliensis (Gilbert, 1900)
Fig. 2

Brannerella brasiliensis Gilbert, 1900:180, pl. 9, fig. 1 (holotype CAS-SU 7750; type locality: coral reef near Maceió, Brazil).

Diagnosis.—Distinguished from other species in the *Starksia ocellata* complex by the following combination of characters: cheek with very narrow, pale Y-shaped mark; ring-shaped marks on cheek bright red in life; pigment on lips restricted to tips of jaws; typically 16 scales in arched part of lateral line (range 15–17); typically 7 total gill rakers on first arch (range 7–9).

Description.—Ranges for selected meristic characters are as follows: dorsal fin XX–XXI, 7–9 (mode XXI, 8); total dorsal elements 28–30 (mode 29); anal fin II, 16–18 (mode 17, spines not connected in males); pectoral fin 13–14 (mode 14); pelvic fin I, 2 apparent (a third rudimentary ray observable in some radiographs); caudal-fin rays 7 on dorsal hypurals, 6 on ventral hypural plate, none branched; procurrent dorsal caudal-fin rays 5–6 (mode 6); procurrent ventral caudal rays 4–6 (mode 5); precaudal vertebrae (those without distinct hemal spine) 10; caudal vertebrae (those with distinct hemal spine, plus the complex hypural bearing centrum) 23–25 (mode 24, CAS-SU 53510 paratype with 20 is anomalous); scales in arched part of lateral line 15–17 (mode 16), scales in straight part 19–22 (mode 20); gill rakers on first arch 2−3+1+4−6 (mode 2+1+4); last pleural rib on vertebra 10; last epipleural rib difficult to discern, but approximately on vertebra 17–19 (discernable in radiographs of only 3 specimens); pseudobranchial filaments 3–5 (mode 4); premaxillary teeth 46–57 (13 specimens); dentary teeth 51–73 (8 specimens); vomerine teeth 8–14 (mode 12); palatine teeth (left–right) 3-2 to 5-5 (mode 4-4). Cephalic sensory pores (Fig. 1, range followed by mode in parentheses): ST 12–13 (13), LT 8–11 (9), POP 7–11 (9), SO 6–10 (7), IO 8–13 (11–12), MD 5.

Upper and lower jaws each with outer rows of stout conical teeth enclosing band of small conical teeth near symphyses. Vomer and palatines with row of stout conical teeth, sometimes flanked posteriorly, or mesially, respectively, by small conical teeth. Small, conical upper pharyngeal teeth in rounded patch of about 3 irregular rows.

Pigmentation of preserved specimens as described by Greenfield (1979). Life colors taken from kodachrome slides of freshly collected specimens as follows: iris of eye yellow; bright red ring-like marks on cheeks, two on base of each pectoral fin, and one at upper end of gill opening. Red spots scattered over dorsal, anal, and caudal fins. Other markings the same as in preserved specimens.

Of the 21 known specimens of *Starksia brasiliensis,* there are 12 females and nine males. The largest female is 34.1 mm SL and the largest male is 30.9 mm SL.

The data for the São Paulo population (available on request) were analyzed for sexual differences using a t-test, but no statistically significant sexual differences were found for any of the characters examined. The northern and southern populations have mean numbers of segmented dorsal-fin rays (northern 7.4 vs. southern 8.1), segmented anal-fin rays (16.8 vs. 17.7), and total vertebrae (33.0 vs. 33.9) that are significantly different as indicated by t-tests (dorsal rays $P < 0.001$, $t = 6.182$; anal rays $P < 0.001$, $t = 7.877$; vertebrae $P < 0.001$, $t = 7.728$). These differences may represent clinal variation, but this cannot be confirmed until specimens from geographically intermediate areas become available.

Distribution.—*Starksia brasiliensis* is known from Maceió, south to São Paulo, Brazil, in depths to 13 m. One specimen collected from a cable was reported from 61 m (Longley and Hildebrand 1941; label with specimen gives 55–62 m), but

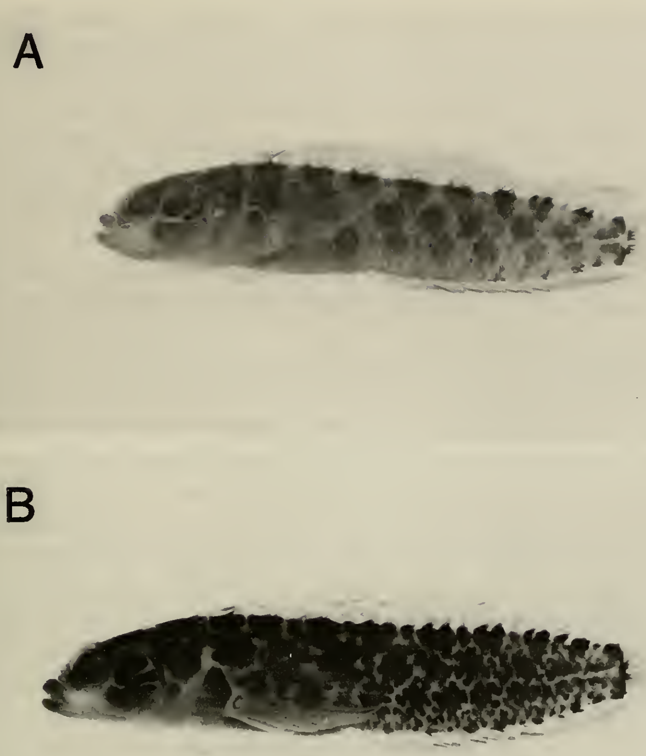


Fig. 2. *Starksia brasiliensis.* A. Male, 27.2 mm SL (MZUSP uncat.). B. Female, 31.8 mm SL (MZUSP uncat.).

we are hesitant to consider this depth within the normal range for the species (reasons discussed below).

The São Paulo specimens represent a southward range extension of approximately 1600 km to 23°44′S. We believe that the apparent disjunction in the species' distributional range reflects the limited collecting efforts in the intervening area and that the species will be commonly found in rocky and coral bottom habitats in that area.

The southern Brazil collecting sites were along the leeward shores of two steeply sloping, heavily forested islands. Large boulders (up to 5 × 5 × 2 m) covered the slopes above and below water, with those underwater covered with algae, bryozoans, sponges, small corals and other encrusting organisms. Small shrimp, lobsters, crabs, snails, and nudibranchs were observed on the encrusting growth.

Remarks.—The paratype (CAS-SU 53510) of *Starksia brasiliensis* has caused confusion regarding the range of certain counts. Böhlke and Springer (1961) commented on the low anal-fin ray and scale counts, and Greenfield (1979) gave an unusually low vertebral count for this specimen. Close examination of radiographs of this specimen reveals that two pairs of centra, 6–7 and 14–15, are almost completely fused, each pair appearing as only one centrum. Nonetheless, the complex nature of the centra is evident since each bears two neural spines and two hemal arches or two hemal spines. If each fused centrum is counted as two centra, a count of 10 + 23 = 33 vertebrae is obtained for the paratype. This count is in the range of the total number of vertebrae (33–35) for other specimens of this species. The low anal-fin ray count may be a result of the same factor that caused the fusions, which would make this count anomalous as well.

Comparisons.—Greenfield (1979) proposed that *Starksia ocellata* be recognized as a superspecies containing six allospecies, including *S. brasiliensis.* These allospecies are distinguished with certainty only by color pattern, all meristics and morphometrics overlapping to some extent among the species. Based on meristics and head color pattern, *S. brasiliensis* is most similar to a species group that includes *S. occidentalis* of the western Caribbean, *S. variabilis* of the southwestern Caribbean, and *S. guttata* of the southeastern Caribbean and the southern islands of the Lesser Antilles. Within this group, *S. brasiliensis* has a head color pattern that differs from that of *S. guttata* only in having a narrower Y-shaped marking on the cheek. *Starksia brasiliensis* also differs from *S. guttata* in having a mode of 16 scales in the arched portion of the lateral line (vs. 17), a mode of 20 scales in the straight portion of the lateral line (vs. 21), and a mode of 36 total lateral line scales (vs. 38, all counts for *S. guttata* based on Greenfield 1979). The two species overlap in each of these counts, but the least overlap occurs in the number of scales in the arched portion of the lateral line. Both *S. brasiliensis* and *S. guttata* have a dark area on the lips, restricted to the anterior tips of the jaws, and lack the dark bars on the lips found in *S. occidentalis* and *S. variabilis* (*S. culebrae* of the Lesser Antilles also has bars on the lips). *Starksia brasiliensis* differs from all of these in having a narrow Y-shaped mark on the cheek. Modes for all meristic characters are the same for *S. brasiliensis, S. occidentalis,* and *S. variabilis.* An additional character that distinguishes *S. brasiliensis* from, at least, *S. occidentalis* and *S. variabilis* is the color of the ring-like marks on the cheek. Greenfield (1979) stated that these marks were white in *S. occidentalis* and lemon yellow in *S. variabilis.* In our specimens of *S. brasiliensis,* these marks are bright red. The color of these marks has not been reported for *S. guttata* or *S. culebrae,* but it is orange in *S. ocellata* from the Tortugas (Longley and Hildebrand 1941) and from the eastern Gulf of Mexico (pers. observ. by JTW).

A cursory survey of the gill-raker counts for *Starksia* specimens in the Florida State Museum suggests that *S. brasiliensis* has fewer gill rakers on the first arch than other species in the *S. ocellata* superspecies. A specimen of *S. occidentalis* has a total gill-raker count of 10 (left)-9 (right), one *S. variabilis* has 9-9, and one *S. ocellata* has 11-11. This character also shows overlap as *S. brasiliensis* has 7 to 9 (one specimen with 9) gill rakers, but may prove useful in distinguishing some of the allospecies.

Additional support for the recognition of *Starksia brasiliensis* as a valid species in the *S. ocellata* superspecies comes from its geographic isolation from other allospecies. Collete and Rützler (1977) suggested that the fresh silt-laden waters of the Amazon and Orinoco rivers might serve as a barrier to dispersal of reef fishes confined to depths shallower than about 50 m. Although one specimen in the British Museum (Natural History) was collected from a cable in 55–62 m, there is some doubt as to the accuracy of this depth recording. This specimen was collected around 1890 when depths presumably were determined by taking soundings at regular intervals, thus the 55 and 62 m depths probably correspond to two soundings taken at separate points along the cable. Since the bottom topography between the two soundings is unknown, it is conceivable that a rocky or coralline outcropping on the bottom could significantly alter the 55–62 m depth range. Aside from this one specimen, no specimens belonging to the *S. ocellata* superspecies have been reported from depths greater than 25 m. One of us (JTW) has collected *S. ocellata* at a depth of about 36 m in the eastern Gulf of Mexico (specimens deposited in University of South Alabama Ichthyological Collection), but this is still much shallower than the Brazilian record. We feel that it would be premature to suggest that *S. brasiliensis* commonly occurs at depths of 50 m or more until additional collections are made at these depths. In view of the typically shallow (less than 13 m) depth distribution of *S. brasiliensis,* it seems likely that the Amazon-Orinoco barrier effectively isolates *S. brasiliensis* from its northern congeners, but additional collecting is needed to confirm its absence from this region.

In view of the distinctness of the Brazilian population from other populations of *Starksia* based on coloration, pigment pattern, and certain meristic characters, we agree with Greenfield (1979) and recognize *S. brasiliensis* as a valid species in the *S. ocellata* superspecies.

Material examined.—CAS-SU 7750 and 53510 (holotype and paratype, respectively, of *Brannerella brasiliensis*) both from near Maceió, Brazil, 1899. GCRL 9476 (2) Brazil, Bahia, Isla Itaparica, Barra do Gil, 13°00′00″S, 38°37′00″W, tidepools just inside outer edge of reef, rock-sand bottom, algae, bryozoa, 25 Aug 1972, 0–2 m. BMNH 1890.1.27.19(1), Brazil, 11°50′S, 38°47′W, from cable in 55–62 m. UF 32889(4), Brazil, Ilha das Couves, 23°25′05″S, 44°51′50″W, coral encrusted rocks on sand bottom, 18 Jul 1981, 10–13 m. MZUSP uncat. (3), same data as UF 32889. UF 32887 (1), Brazil, Ilha da Vitoria, 23°44′40″S, 45°01′40″W, bottom with large boulders encrusted with sponges, small corals, and sparse algal growth, 25 May 1981, 10–13 m. MZUSP uncat. (1), same data as UF 32887. UF 32888 (3), Brazil, Ilha da Vitoria, 23°44′S, 45°01′W, bottom with large boulders encrusted with corals and sponges, 14 Jun 1981, 10–13 m. MZUSP uncat. (4), same data as UF 32888.

Comparative material examined.—Starksia ocellata: UF 16018 (1), Delray Beach, Palm Beach County, Florida. *Starksia occidentalis:* UF 23348 (1 paratype), Frenchman's Cay, Belize. *Starksia variabilis:* UF 23349 (1 paratype), Santa Marta, Colombia.

Acknowledgments

We thank William N. Eschmeyer and Tomio Iwamoto for allowing us to borrow the type specimens from CAS, and Charles E. Dawson for the loan of GCRL specimens. Alwyne Wheeler kindly provided information about the method of determining depth for the specimen at the BMNH. James A. McGrath and Raymond Dee, assisted in taking radiographs. We particularly thank Rosemea De Souza Smart, who made the Brazilian collections possible. Victor G. Springer and Carter R. Glbert kindly reviewed an earlier draft of the manuscript and provided helpful comments. Examination of the specimen at the BMNH was made possible by NSF grant DEB 8207313 (predoctoral dissertation improvement grant) to J. T. W. The typescript was prepared by Grace Russell.

Literature Cited

Böhlke, J. E., and V. G. Springer. 1961. A review of the Atlantic species of the clinid fish genus *Starksia*.—Proceedings of the Academy of Natural Sciences of Philadelphia 113(3):29–60.

Collette, B. B., and K. Rützler. 1977. Reef fishes over sponge bottoms off the mouth of the Amazon River.—Proceedings, Third International Coral Reef Symposium, Rosenstiel School of Marine and Atmospheric Science, University of Miami, May 1977:305–310.

George, A., and V. G. Springer. 1980. Revision of the clinid fish tribe Ophiclinini, including five new species, and definition of the family Clinidae.—Smithsonian Contributions to Zoology 307:1–31.

Gilbert, C. H. 1900. Results of the Branner-Agassiz Expedition to Brazil. III. The fishes.—Proceedings of the Washington Academy of Sciences 2:161–184.

Greenfield, D. W. 1979. A review of the western Atlantic *Starksia ocellata*-complex (Pisces: Clinidae) with the description of two new species and proposal of superspecies status.—Fieldiana Zoology 73(2):9–48.

Longley, W. H., and S. F. Hildebrand. 1941. Systematic catalogue of the fishes of Tortugas, Florida with observations on color, habits, and local distribution.—Carnegie Institution of Washington Publication 535, Papers from Tortugas Laboratory 34:1–331.

Steindachner, F. 1876. Ichthyologische Beiträge (V).—Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien 74 (1–2, no. 1):49–240.

Florida State Museum and Department of Zoology, University of Florida, Gainesville, Florida 32611. (JTW: Present address, Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.)

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 645–657

DESCRIPTION OF A NEW SPECIES OF *ECHIODON* (TELEOSTEI: CARAPIDAE) FROM ANTARCTIC AND ADJACENT SEAS

Douglas F. Markle, Jeffrey T. Williams, and John E. Olney

Abstract.—*Echiodon cryomargarites,* a previously unrecognized species of carapid fish, is described from adult and larval specimens collected in relatively deep water from the Antarctic and adjacent seas. This species differs from *E. exsilium* and *E. dawsoni,* which have fewer precaudal vertebrae, and from *E. dentatus* and *E. drummondii* which have slightly higher D_{30} counts, fewer pectoral rays, and fewer vertebrae to the origin of the dorsal fin. The new species has a relatively deep, flaccid body and was collected over bottom depths ranging from 400–1200 m off Argentina, South Georgia Island, and New Zealand. Two other specimens that differ slightly in geographic and depth distribution, appearance, and have a shallow, firm body were caught at depths of 1500–1666 m off southern Chile.

The distal tips of the transverse processes of the first two vertebrae in *E. cryomargarites* are ligamentously attached to paired sclerified structures of the anterior swimbladder. This condition may represent a precursor to the rocker bone specialization of *Onuxodon.*

During independent investigations of the pearlfish genus *Echiodon* (Olney and Markle 1979; Williams and Shipp 1982), a previously undescribed species was encountered in samples from southern oceans. The species was apparently mentioned by Andriashev (1977) and a larva now assigned to this species was collected by Dr. Thor Mortensen from Campbell Island shepherds (Rendahl 1926).

In this report we examined 26 adults and five larvae of this deep-dwelling, southern ocean *Echiodon.* Our purpose is to document their distribution and describe the new species we recognize. *Echiodon,* as recognized herein, is defined by an eclectic group of characters taken from Arnold (1956), Cohen and Nielsen (1978), Robertson (1975), Maul (1976), Olney and Markle (1979) and Williams and Shipp (1982). For the purposes of this paper, the genus is diagnosed as those carapids[1] with 15–25 pectoral fin rays, 20–29 precaudal vertebrae, a free maxillary, enlarged canines at jaw symphyses, an anus posterior to a vertical through the pectoral fin base, no median rocker bone at anterior end of swimbladder, and larvae in which the first dorsal ray inserts immediately posterior to the vexillum and the vexillum origin is posterior to a vertical through the first anal ray. Hypotheses on phylogenetic relationships within *Echiodon* are beyond the scope of this paper, but such studies are in progress.

---

[1] We have been informed by G. S. Myers through G. C. Steyskal that the stem of the family name is *Carap*—rather than *Carapod*—(Steyskal 1980) since the derivation is from a native Brazilian word, çarapo, and not the Greek, pous. Thus, the family is Carapidae not Carapodidae.

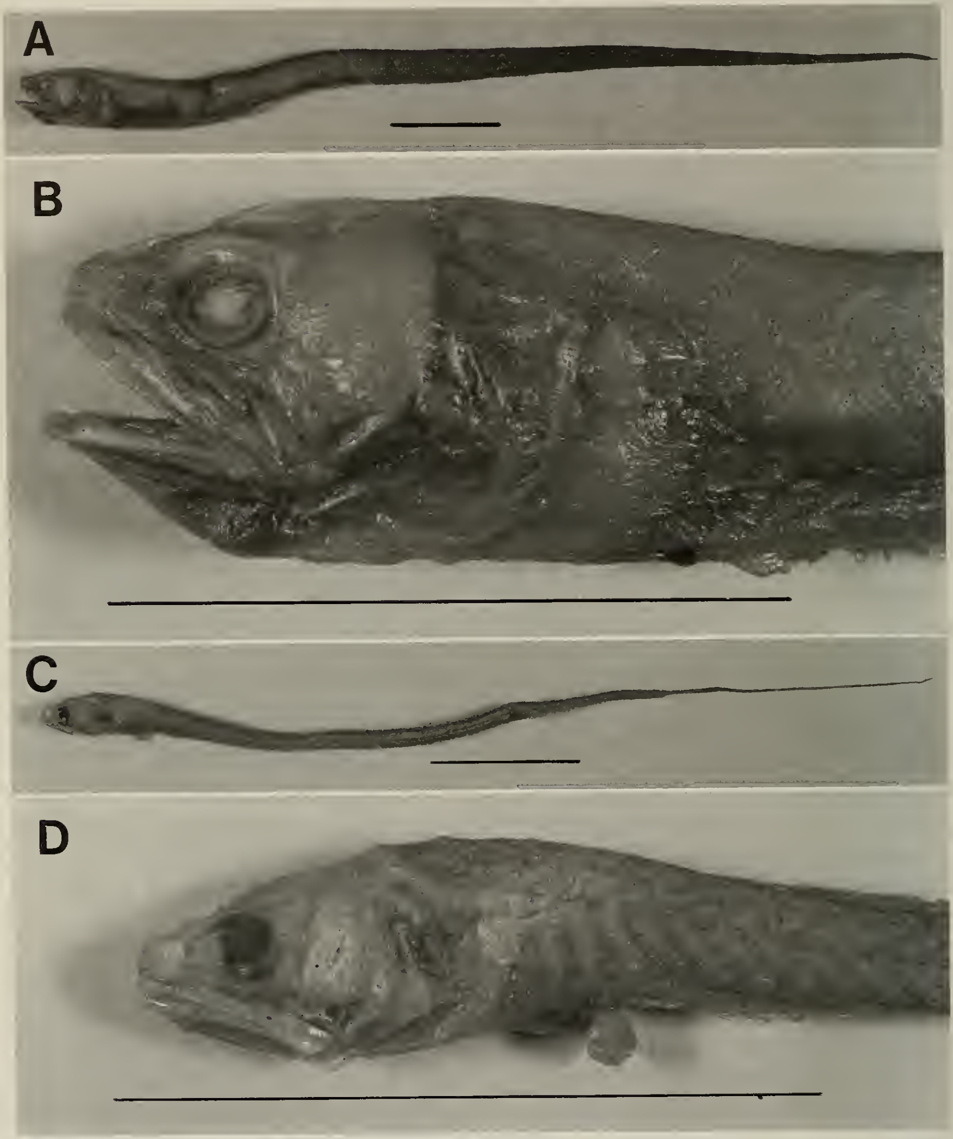


Fig. 1. *Echiodon cryomargarites,* holotype, LACM 10985-6. A, Left lateral view; B, View of head; *Echiodon* specimen, LACM 42593-2. C, Left lateral view; D, View of head.

Methods and Materials

Counts and measurements of adults follow Williams and Shipp (1982), and of larvae follow Olney and Markle (1979). Abbreviations D_{30} and A_{30} refer to the dorsal and anal rays whose bases lie anterior to vertebra 31.

Cephalic lateralis pore series terminology used in this paper follows Williams and Shipp (1982) except as follows. The lateral series (LT) is restricted to include those large pores of the lateral-temporal canal between that canal's junctions with

Table 1.—Summary of selected measurements for adult *E. cryomargarites* and *E.* specimens. Values for holotype listed in parentheses. All measurements given as percent of head length.

	E. cryomargarites	*E.* specimens
Snout length	19–27 (20)	18–21
Orbit diameter	23–29 (23)	24–25
Iris diameter	18–24 (20)	18–19
Upper jaw length	54–66 (56)	56–58
Lower jaw length	55–59 (55)	54–56
Predorsal length	160–200 (180)	180–190
Preanal length	120–150 (130)	120–130

the preopercular (POP) and the infraorbital (IO) canals. The supratemporal series (ST) includes those large pores on both sides of the head that are dorsad of the junctions of the supratemporal canal with the lateral temporal canals. Pores were located by directing a jet of air through the canals.

Gosline (1960) pointed out that there is confusion about the definition of ophidiiform "ribs," since some of the anterior transverse processes articulate basally with their respective vertebral centra ("sessile ribs" of Regan 1912), while posterior transverse processes fuse basally to their centra. Since pyramodontines have pleural ribs at the ventral ends of elongate transverse processes, we prefer to avoid the term "ribs." The term transverse process used herein follows Gosline (1960) and is equivalent to the "sessile ribs" and transverse processes of Regan (1912) and the "ribs" of Courtenay and McKittrick (1970).

Cranial vault length refers to the greatest anterior to posterior distance in a sagittal plane within the braincase as determined from radiographs and cleared and stained specimens.

Material examined is listed under individual species accounts. Museum acronyms used are LACM—Los Angeles County Museum, Los Angeles, California; ISH—Institut für Seefischerei, Zoological Museum, University of Hamburg, Hamburg, West Germany; ZMUC—Zoological Museum, University of Copenhagen, Copenhagen; and USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C. Other abbrevaitions used are TL—total length, SL—standard length, IKMT—Isaacs-Kidd Midwater Trawl, SO—supraorbital series, IO—infraorbital series, LT—lateral series, ST—supratemporal series, POP—preopercular series, and MD—mandibular series.

Echiodon cryomargarites, new species

Figs. 1A and B

Holotype.—LACM 10985-6, 410 mm TL, 37.3 mm HL, male; "*Eltanin*" sta 1422, 56°19′–21′S, 158°29′E, 12 Feb 1965, 3 m (10 ft) Blake trawl, 833–842 m bottom depth range.

Paratypes.—Off New Zealand: LACM 10985-8, 3 specimens, 230–310 mm TL, 21.8–27.3 mm HL, males; caught with holotype. LACM 10985-7, damaged; caught with holotype. LACM 10979-4, ca. 220 mm TL, ca. 16 mm HL, female; "*Eltanin*" sta 1414, 52°17′–22′S, 160°40′–34′E, 9 Feb 1965, 3 m Blake trawl, 659–798 m.

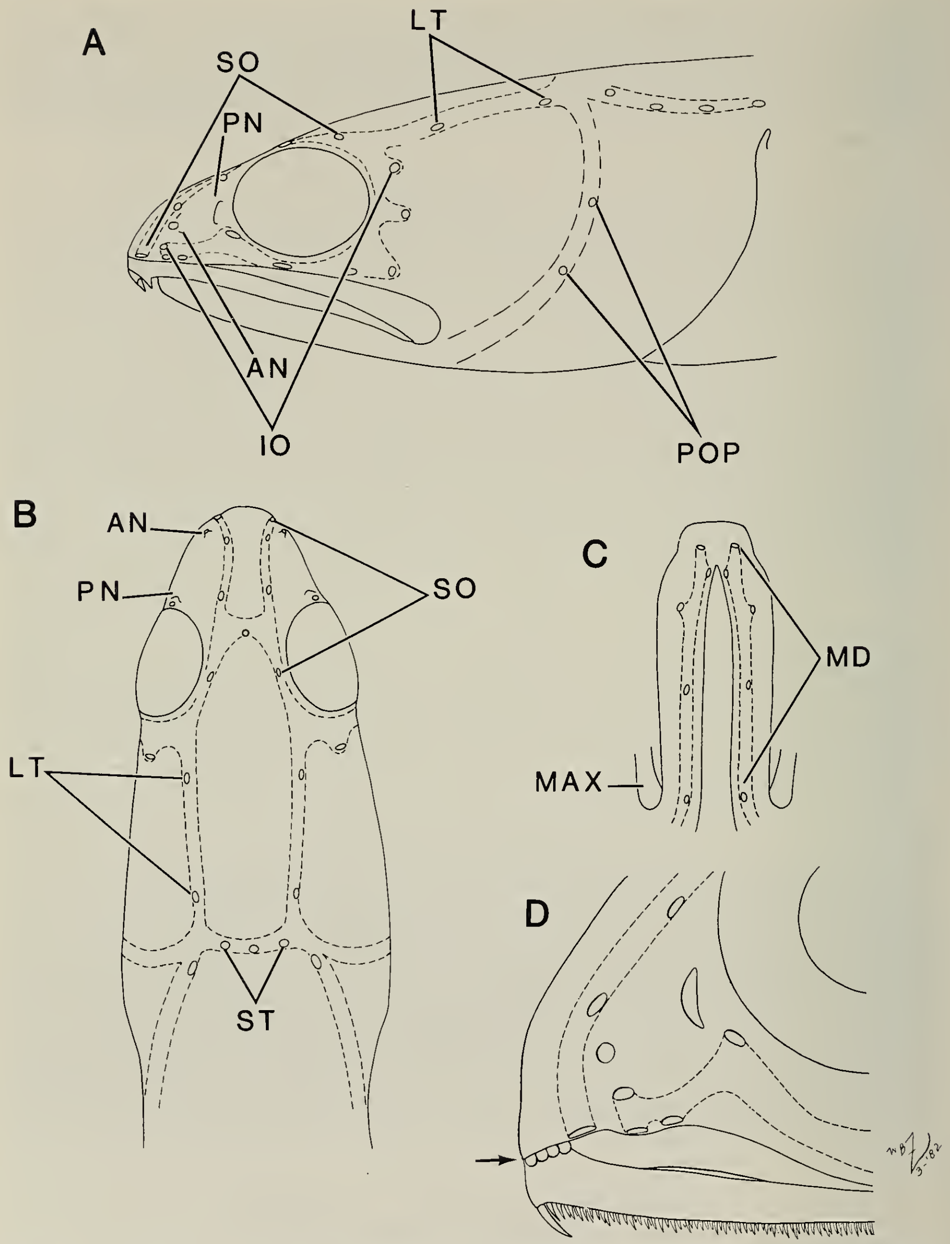


Fig. 2. *Echiodon cryomargarites,* LACM 10985-6, diagrammatic illustration of cephalic lateralis pores and upper lip lobes. A, left lateral view; B, Dorsal view; C, Ventral view of lower jaw; D, Magnified snout region showing lobes under upper lip. Prepared by W. Zomlefer.

LACM 10984-3, three specimens, ca. 210 mm TL (female), ca. 220 mm TL (female), 255 mm TL (male), 16.0–22.7 mm HL; "*Eltanin*" sta 1419, 54°32′–31′S, 159°02′–01′E, 10 Feb 1965, 3 m Blake trawl, 494–714 m.

Off Argentina and Brazil: ISH 317/71, 280 mm TL, 20.5 mm HL, female;

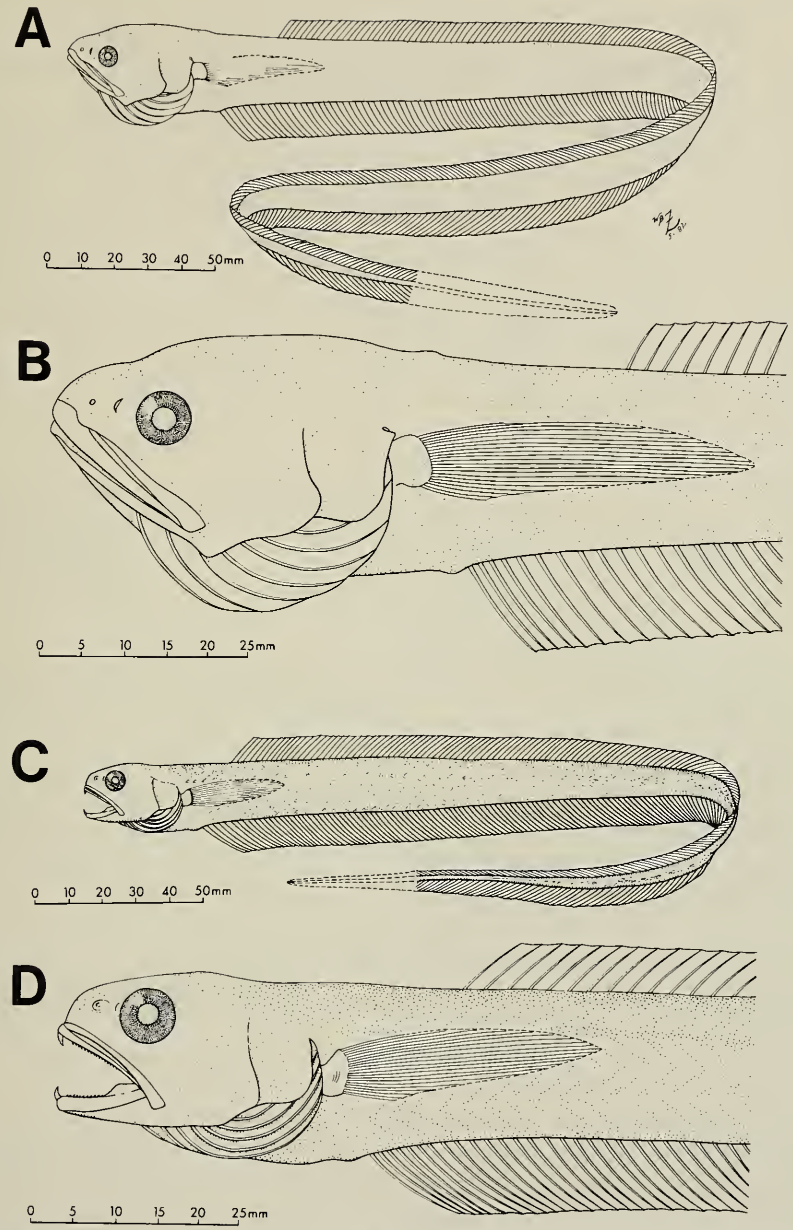


Fig. 3. *Echiodon cryomargarites,* A, B. Drawings of male holotype, LACM 10985-6, from off New Zealand. C, D. Drawings of female paratype ISH 300/71 from off Falkland Islands. Prepared by W. Zomlefer.

"*Walther Herwig*" sta 312/71, 46°53′S, 60°00′W, 18 Feb 1971, bottom trawl, 800 m. ISH 1108/66, four specimens, 181–243 mm TL, 12.3–17.0 mm HL, females; "*Walther Herwig*" sta 230/66, 35°04′S, 52°15′W, 12 Jun 1966, bottom trawl, 600 m. ISH 1554/66, 113+ mm TL, 12.3 mm HL, male; "*Walther Herwig*" sta 428/

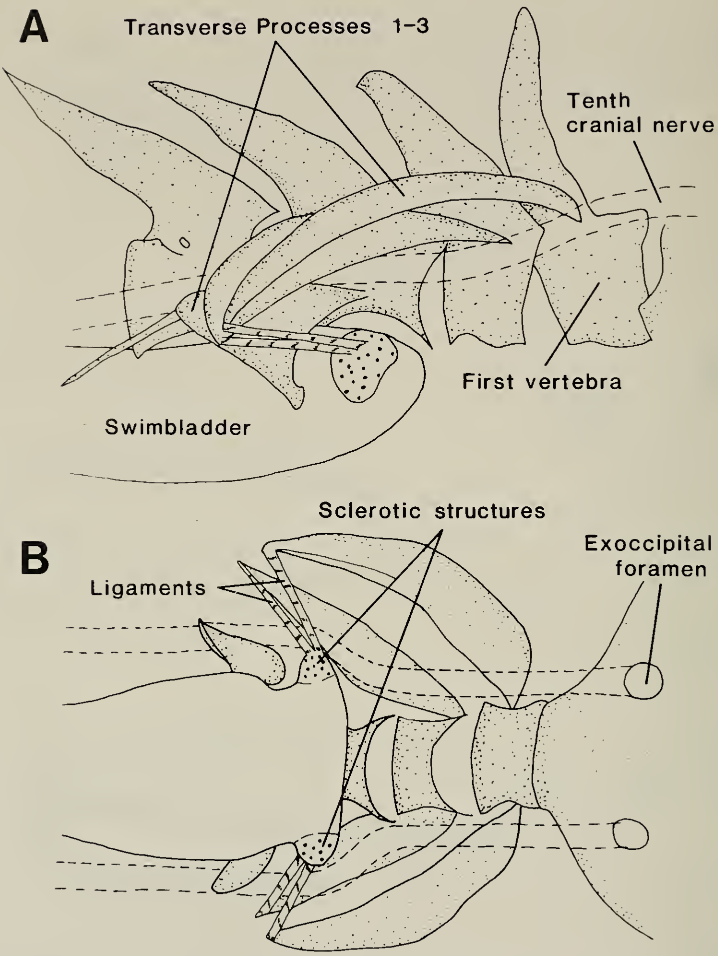


Fig. 4. *Echiodon cryomargarites,* LACM 10984-3. A, Right lateral view of first four centra illustrating modified transverse processes of first three centra, position of tenth cranial nerve, and swimbladder modifications; B, Ventral view of A.

66, 34°48′S, 52°02′W, 28 Jul 1966, bottom trawl, 400 m. ISH 1229/66, 209 mm TL, 12.0 mm HL, female; "*Walther Herwig*" sta 268/66, 39°56′S, 55°58′W, 19 Jun 1966, bottom trawl, 600 m. ISH 1580/66, three specimens, 188–245 mm TL, 12.7–20.0 mm HL, females; "*Walther Herwig*" sta 438/66, 33°41′S, 51°12′W, 31 Jul 1966, bottom trawl, 600 m. ISH 1818/68, two specimens, 268–302 mm TL, 22.3–23.3 mm HL, males; "*Walther Herwig*" sta 65/68, 29°57′S, 47°35′W, 27 Feb 1968, bottom trawl, 1200 m. Off South Georgia Is.: ISH 334/76, 255 mm TL, 19.8 mm HL, male; "*Walther Herwig*" sta 33/76, 53°36′S, 35°40′W, 11 Dec 1976, bottom trawl, 800 m.

Off Falkland Is.: ISH 300/71, two specimens, 310–315 mm TL, 25.7–27.8 mm HL, females; "*Walther Herwig*" sta 241/71, 55°00′S, 57°50′W, 4 Feb 1971, bottom trawl fished in midwater above a bottom of 775–850 m.

Diagnosis.—A species of *Echiodon* from southern oceans with a relatively flac-

Table 2.—Selected measurements and counts of *E. cryomargarites* larvae. All measurements as percent head length.

	ZMUC Dana 3641 I	USNM 257747	LACM 42592-1	LACM 11505	ZMUC P7710
Head length	4.6 mm	4.4 mm	7.9 mm	3.6 mm	7.0 mm
Snout length	26	23	20	—	28
Eye diameter	22	27	22	—	24
Upper jaw length	44	—	51	—	—
Lower jaw length	56	55	58	64	57
Vexillum length	236	218	311	492	—
Snout to vexillum	196	198	233	227	220
Snout to dorsal	203	207	247	238	236
Snout to anal	169	171	184	151	156
Snout to anus	155	155	186	153	200
A_{30}	45	45	48	45	—
D_{30}	39	40	36	34	—
Vertebrae to vexillum	10	10	12	13	11
Vertebrae to dorsal	11	11	13	14	12
Vertebrae to anal	8	8	9	8	8
Precaudal vertebrae	—	27	—	—	—

cid body, caught over depth range 400–1200 m, D_{30} 36–40, two pores in POP canal.

Description.—Morphometric data are summarized in Table 1. Meristic data are as follows, holotype in parentheses: D_{30} 36–40 (38), A_{30} 46–50 (47), pectoral fin rays on left side 19–21 (21), anal fin origin under vertebrae 6–8 (6), dorsal fin origin over vertebrae 11–12 (11), precaudal vertebrae 25–29 (28), developed gill rakers 3, olfactory rosette with seven pairs of lamellae (clear and virtually uncountable in holotype and paratypes of LACM 10985), pores of cephalic lateralis system: SO-5, IO-9, LT-2, ST-3, POP-2, MD-5 (generally difficult to see), upper lip bears three or four small lobes (Fig. 2). Sensory papillae arranged in a single row along most sensory canals, and, although difficult to discern, on snout and top of head.

The general appearance of *E. cryomargarites* is shown in Figs. 1 and 3. The body is flaccid, overall color in ethanol is tan with relatively uniform distribution of small melanophores, more concentrated along myosepta and bases of vertical fins; tongue ranging from pale cream colored to black; skin lining mouth and branchial cavity ranging from tan with scattered melanophores to uniform brown (dense melanophores); outer surface of stomach black; outer surface of intestine usually black, sometimes tan; peritoneum tan with scattered melanophores.

Posterior portion of maxillary unsheathed (Figs. 1 and 3); each premaxillary and dentary with 1–2 large canines anteriorly; teeth on premaxillaries conical, depressible, and pluriserial, tapering to one row anteriorly at the base of the canines and to two rows of shorter teeth posteriorly; dentary teeth pluriserial with innermost row fixed and outer row depressible; dentary not noticeably narrowed between anterior canines and band of conical teeth; palatines with two irregular rows of blunt conical teeth; vomer with an irregular row of small, conical teeth laterally flanking a median row of 1–5 slightly larger conical teeth; three small

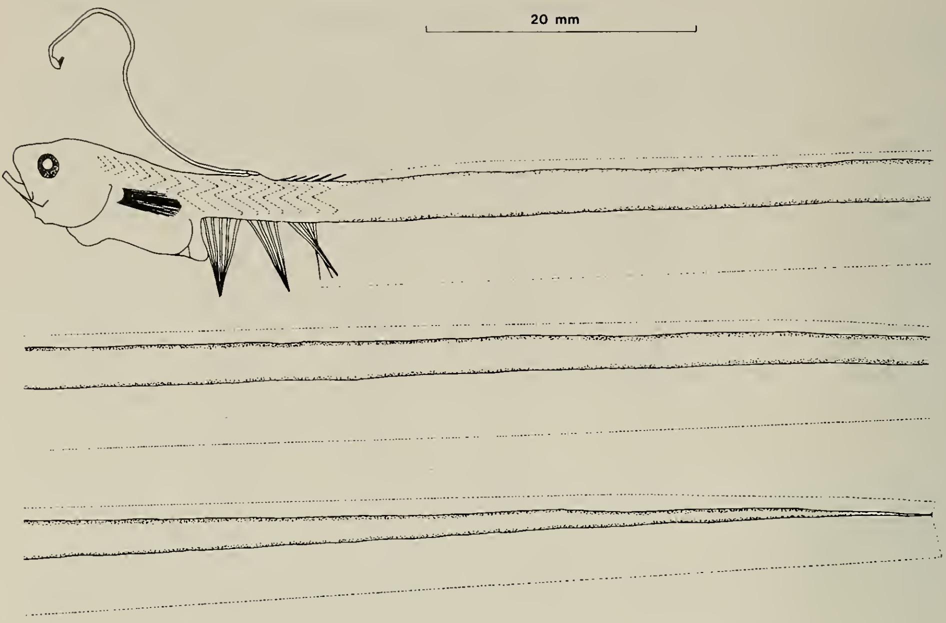


Fig. 5. *Echiodon cryomargarites* larva, LACM 42592-1. Dotted lines represent continuation of dorsal and anal fins. Stippling on body used to highlight contours and myosepta and does not represent pigmentation.

tooth patches on or associated with pharyngobranchials 2, 3 and 4; fifth ceratobranchial with medial row of small, conical teeth.

Lateral line difficult to follow, apparently restricted to anterior one third of body.

Limited osteological observations were made on three specimens cleared and counter stained for cartilage and bone (ISH 1108/66, ISH 1818/68, LACM 10985-7 and LACM 10984-3). Otoliths (sagittae) reduced relative to other carapids, their lengths about 10–15% of cranial vault length. Transverse processes of first three vertebrae with typical carapine modifications (Regan 1912; Courtenay and McKittrick 1970; Olney and Markle 1979). First two processes moveable, third and subsequent rigid (Fig. 4A). Distal tips of first two processes ligamentously attached to paired sclerified structures at anterior end of swimbladder (Fig. 4A and B). Sclerified structures stain lightly with Alcian Blue and lie anteriad of a constriction in swimbladder (Fig. 4B). (This condition may represent a precursor of the rocker bone in *Onuxodon*. If so, the rocker bone may be an ossified anterior chamber of a swimbladder that was derived from the main swimbladder.) Third process expanded, curving inward, with its posterior surface attached to the swimbladder behind the constriction (Fig. 4). Swimbladder tapers slightly posteriad and ends under vertebrae 15–16. Large tenth cranial nerve (Vagus) passes along vertebral column, under first two transverse processes and above remainder.

Etymology.—A combination of the Greek "kryos" meaning cold and "margarites," a pearl, in reference to the Antarctic distribution of this new pearlfish.

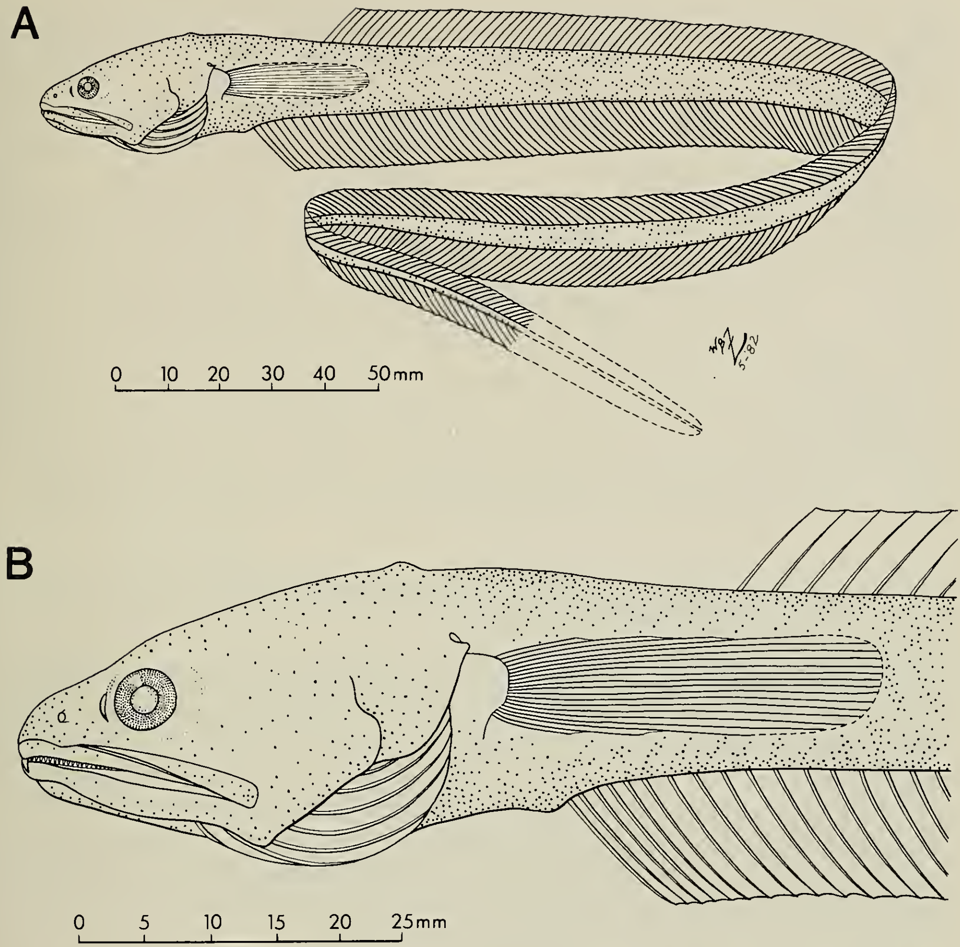


Fig. 6. *Echiodon* specimen, LACM 42593-1, 30.8 mm HL. A, Left lateral view; B, Close up of head. Prepared by W. Zomlefer.

Echiodon cryomargarites—Larvae

Material Examined.—Off New Zealand: ZMUC Dana 3641[1], 77 mm TL, 4.6 mm HL, 43°40′S, 176°36′E, 8 Jan 1929, stramin net, 300 m wire out. USNM 257747, ca. 67 mm TL, 4.4 mm HL; 43°00′S, 173°57′24″E, 7 Mar 1974, 1 m net. LACM 11505, 63+ mm TL, 3.6 mm HL; "*Eltanin*" sta 2217, 51°29.0′S, 160°13.0′E, 20 Jun 1968, IKMT. ZMUC P7710, 190 mm TL, 7.0 mm HL; ca. 42°S, 174°E, 10 Dec 1914, collected by Campbell Island shepherds on shore of Perserverance Harbor, Antarctic Convergence, mid-Pacific: LACM 42592.1, ca. 205 mm TL, 7.9 mm HL; "*Eltanin*" sta 16, 49°06-10′S, 120°13-15′W, 19 Dec 1965, IKMT, 0–200 m.

Comments.—Larvae were identified as belonging to this species on the basis of their unique combination of meristic characters (A_{30}, D_{30}, precaudal vertebrae,

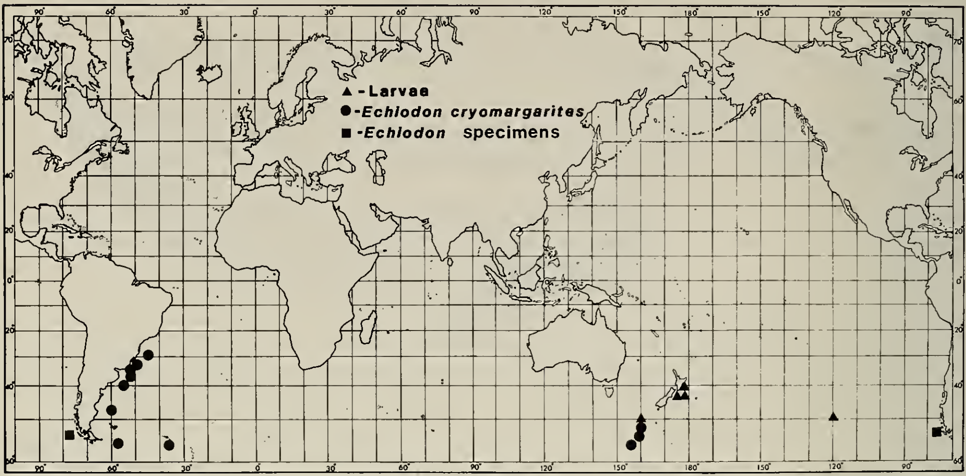


Fig. 7. Chart showing distribution of adults and larvae of *E. cryomargarites* and *E.* specimens.

and fin positions), distributional data, and gross similarity to larvae of *E. drummondii* and *E. dentatus* (Maul 1976, personal observation). Selected measurements and counts are shown in Table 2.

The general appearance of the largest larva is illustrated in Fig. 5. Noteworthy features are the sac-like drooping gut (Rendahl 1926) to which the first anal fin ray is attached, the relatively long anal fin rays, and the absence of pigment. In the three smallest specimens, 3.6–4.6 mm HL, about ten internal pigment spots were present along the vertebral column. These commence at centra 13 or 14 and are spaced about 7 to 12 centra apart. These were difficult to see even in the smallest specimen due to occlusion by epaxial musculature but were readily apparent in the 4.4 and 4.6 mm specimens after trypsin digestion.

Echiodon Specimens
Figs. 1C and D

Material Examined.—LACM 42593-1, 335 mm TL, 30.8 HL, female; "*Eltanin*" sta 21, 53°13′–16′S, 75°41′W, 5 Jan 1966, 1.5 m Blake trawl, 1500–1666 m. LACM 42593-2, 300 mm TL, 25.6 mm HL, female; same data as LACM 42593-1.

Comments.—These two specimens differed slightly in geographic distribution and morphology from *E. cryomargarites.* They have a firm body, D_{30} 35 and were caught at depths of 1500–1666 m. The general appearance of these specimens is shown in Fig. 6. Coloration, dentition, and otoliths are as for *E. cryomargarites.* The lateral line is difficult to follow but apparently extends over two thirds of the body length. Morphometric data are summarized in Table 1. Meristic data are as follows: D_{30} 35, A_{30} 46–48, pectoral fin rays on left side 20–21, anal fin origin under vertebrae 6–8, dorsal fin origin over vertebra 12, precaudal vertebrae 27–29, developed gill rakers 3, olfactory rosette with seven pairs of lamellae.

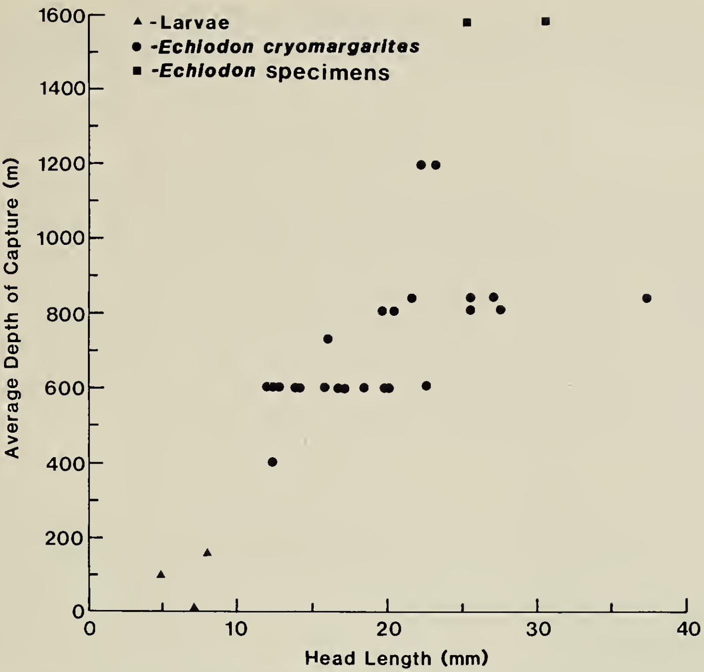


Fig. 8. Relationship between average depth of capture and size (head length) of *E. cryomargarites* adults and larvae and *E.* specimens.

These specimens described above closely resemble and may be conspecific with *E. cryomargarites.* Both forms are distinguished from *E. exsilium* and *E. dawsoni,* which have fewer precaudal vertebrae (21–24) and from *E. dentatus* and *E. drummondii,* which have slightly higher D_{30} (42–45), fewer pectoral fin rays (15–17), and fewer vertebrae to the dorsal fin origin (8–9).

Distribution

The geographic distribution of *E. cryomargarites* is shown in Fig. 7. The well established dispersal capabilities of the larvae (Olney and Markle 1979) and the West Wind Drift are sufficient to account for the wide geographic range of the species. *Antimora rostrata, Halargyreus johnsonii,* and *Merluccius australis* have similar distribution patterns (Iwamoto 1975; Cohen 1973; Inada 1981). The first two of these species co-occurred with *E. cryomargarites* in four of eleven (36%) of our adult collections (M. Stehmann, personal communication, 5 Jan 1982; LACM catalog records). In at least one case, *M. australis,* geographic variants had been described as different species but are now recognized as synonyms (Inada 1981).

There was no evidence of commensalism, and the species appear to be free living.

With one exception (ISH 300/71) all adults were caught in bottom trawls fished on continental or insular slopes. There appears to be ontogenetic descent in *E.*

cryomargarites with larger specimens being found deeper (Fig. 8). The two *Echiodon* specimens were found at about twice the depth of similar-sized *E. cryomargarites* (Fig. 8).

Acknowledgments

We are very grateful to the following curators and their institutions for making specimens available: R. Lavenberg and J. Seigel (LACM), G. Krefft and M. Stehmann (ISH), E. Bertelsen (ZMUC), Les Knapp (USNM). We thank the following for constructive review of this manuscript: E. Anderson, R. Crabtree and J. Carter (VIMS) and Drs. Bob Lavenberg and Dan Cohen (LACM). Olney and Markle were supported in part by NSF Grant DEB-81-17185. This is a joint contribution of the Huntsman Marine Laboratory, the Florida State Museum and the Virginia Institute of Marine Science (VIMS Contr. No. 1132).

Literature Cited

Andriashev, A. P. 1977. Some additions to schemes of the vertical zonation of marine bottom fauna. Pp. 351–360 *in* G. A. Llano (ed.). Adaptations within Antarctic ecosystems.—Proceedings of the Third SCAR Symposium on Antarctic Biology.

Arnold, D. C. 1956. A systematic revision of the teleost family Carapidae (Percomorphi, Blennioidea) with descriptions of two new species.—Bulletin of the British Museum (Natural History) Zoology 4:245–307.

Cohen, D. M. 1973. The gadoid fish genus *Halargyreus* (Family Eretmophoridae) in the Southern Hemisphere.—Journal of the Royal Society of New Zealand, 3(4):629–634.

Cohen, D. M., and J. G. Nielsen. 1978. Guide to the identification of genera of the fish order Ophidiiformes with a tentative classification of the order.—NOAA Technical Report NMFS Circular 417, 72 pp.

Courtenay, W. R., Jr., and F. A. McKittrick. 1970. Sound-producing mechanisms in carapid fishes, with notes on phylogenetic implications.—Marine Biology 7:131–137.

Gosline, W. A. 1960. Hawaiian lava-flow fishes, part IV. *Snyderidia canina* Gilbert, with notes on the osteology of ophidioid families.—Pacific Science 14(4):373–381.

Inada, T. 1981. Two nominal species of *Merluccius* from New Zealand and southern South America.—Japanese Journal of Ichthyology 28(1):19–30.

Iwamoto, T. 1975. The abyssal fish *Antimora rostrata* (Günther).—Comparative biochemistry and physiology 52B:7–11.

Maul, G. E. 1976. The fishes taken in bottom trawls by R. V. "Meteor" during the 1967 Seamount Cruises in the Northwest Atlantic.—Meteor Forschungsergebnisse, Reihe D-Biologie 22:1–69.

Olney, J. E., and D. F. Markle. 1979. Description and occurrence of vexillifer larvae of *Echiodon* (Pisces: Carapidae) in the western North Atlantic and notes on other carapid vexillifers.—Bulletin of Marine Science 29(2):365–379.

Regan, C. T. 1912. The classification of the blennioid fishes.—Annals and Magazine of Natural History, (8), 10:265–280.

Rendahl, H. 1926. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. XXX. Fishes from New Zealand and Aukland-Campbell Islands.—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 81:1–14.

Robertson, D. A. 1975. Planktonic stages of the teleost family Carapidae in eastern New Zealand waters.—New Zealand Journal of Marine and Freshwater Research 9:403–409.

Steyskal, G. C. 1980. The grammar of family-group names as exemplified by those of fishes.—Proceedings of the Biological Society of Washington 93(1):168–177.

Williams, J. T., and R. L. Shipp. 1982. A new species of the genus *Echiodon* (Pisces: Carapodidae) from the eastern Gulf of Mexico.—Copeia 1982(4):845–851.

(DFM) The Huntsman Marine Laboratory, St. Andrews, New Brunswick, Canada EOG 2X0; (JTW) Florida State Museum and Department of Zoology, University of Florida, Gainesville, Florida 32611; present address: Division of Fishes, NHB WG-12, Smithsonian Institution, Washington, D.C. 20560; (JEO) Virginia Institute of Marine Science and the College of William and Mary, Gloucester Point, Virginia 23062.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 658–663

TELEOSTEAN OTOLITHS FROM THE LATE CRETACEOUS (MAESTRICHTIAN AGE) SEVERN FORMATION OF MARYLAND

Richard W. Huddleston and Kurt M. Savoie

Abstract.—Approximately 1000 teleostean fish otoliths were recovered from the Severn Formation, Late Cretaceous (Early–Middle Maestrichtian) of Maryland. These otoliths represent at least 14 kinds of fishes belonging to eight families (Pterothrissidae, Argentinidae, Ariidae, Ophidiidae, Polymixiidae, Trachichthyidae, ?Pempheridae, and Apogonidae) and three unidentified families, suborders Albuloidei, Stomioidei, and Anguilloidei. Otoliths of *Vorhisia* sp. dominated the fauna, representing approximately 54 percent of the total identified otoliths. The next dominant form, represented by the Apogonidae, comprised 27 percent of the identified fauna.

Previous description of teleostean otoliths from the Late Cretaceous of North America are limited. Frizzell (1965a) described *Prealbula weileri* and *Protalbula sohli,* based on isolated sagittae from the Earliest Campanian, Eutaw Formation of Alabama. Frizzell (1965b) described *Vorhisia vulpes,* based on isolated lapilli from the Maestrichtian, Fox Hills Sandstone Formation of South Dakota. Frizzell and Koenig (1973) described asterisci from the same formation and assigned them to *V. vulpes.* These asterisci, however, do not belong to *Vorhisia* (J. E. Fitch, pers. comm.). Huddleston (1981) described *Bernardichthys zorraquinosi,* based on sagittae from the Early Cenomanian, Bernard Formation of Oregon.

The present study is based on approximately 1000 otoliths recovered from about 100 kg of fossiliferous matrix collected from an exposure at the base of the Severn Formation by one of us (KMS). All field samples were collected from LACM (Los Angeles County Museum, section of Vertebrate Paleontology) locality 4425; Beltway exit 34W, Central Avenue, Prince George County, Maryland. The locality was initially exposed by the cutting action of a small unnamed creek. Construction activities have increased the exposure. Samples were taken from a 30 cm thick section of scattered shell and small lenses of dark gray shell marl, mixed with broken shell.

The term Severn Formation was first proposed by Denton (1891) for a variety of lithologic units. Clark, Bagg and Shattuck (1897) later proposed the term Monmouth Formation for certain lithologic units occurring in New Jersey. This term also was applied to Late Cretaceous marine strata in Maryland. Recently Minard, Shol, and Owens (1978) reintroduced the term Severn Formation to replace the term Monmouth Formation in Maryland. The Severn Formation is Late Cretaceous, Early-Middle Maestrichtian and corresponds to the Navarroan Provincial stage (Brouwers and Hazal 1978).

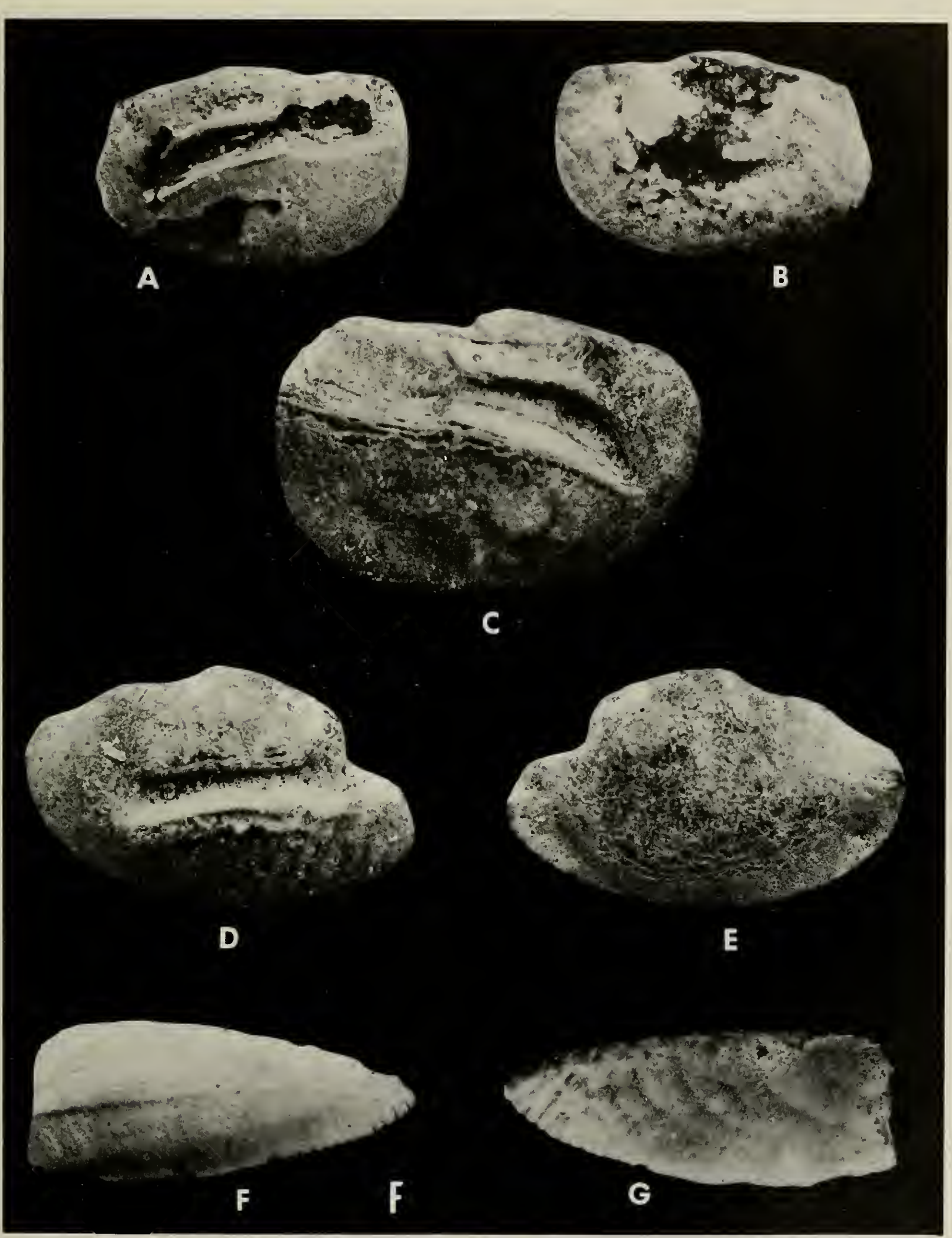


Fig. 1. A, B, Pterothrissidae, left sagitta, 15.4mm, LACM 4425/120101 (A-innerface; B-outerface); C, Pterothrissidae, right sagitta, 11.5mm, LACM 4425/116980; D, E, Anguilloidei-A, left sagitta, 10.5mm, LACM 4425/116981, (D-innerface; E-outerface); F, G, Albuloidei, left sagitta, 7.4mm, LACM 4425/116979 (F-innerface; G-outerface).

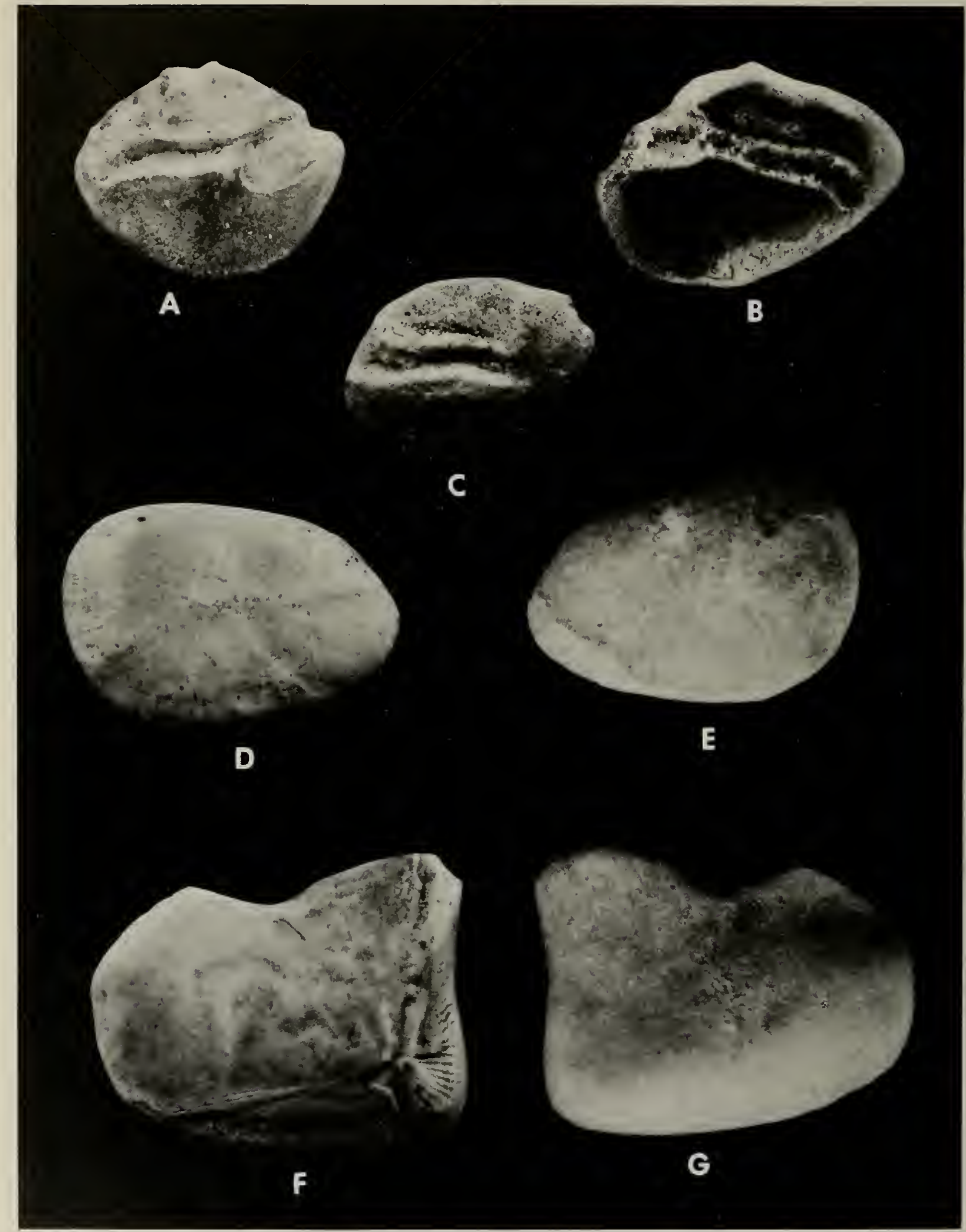


Fig. 2. A, cf. Pempheridae, left sagitta, 4.0mm, LACM 4425/116990; B, Polymixiidae, right sagitta, 4.5 mm, LACM 4425/116988; C, Anguilloidei-B, right sagitta, 6.1mm. LACM 4425/116983; D, E, Ariidae, right lapillus, 4.9mm, LACM 4425/116985 (D-innerface; E-outerface); F, G, *Vorhisia* sp., left lapillus, 25mm, LACM 4425/116984 (F-innerface; G-outerface).

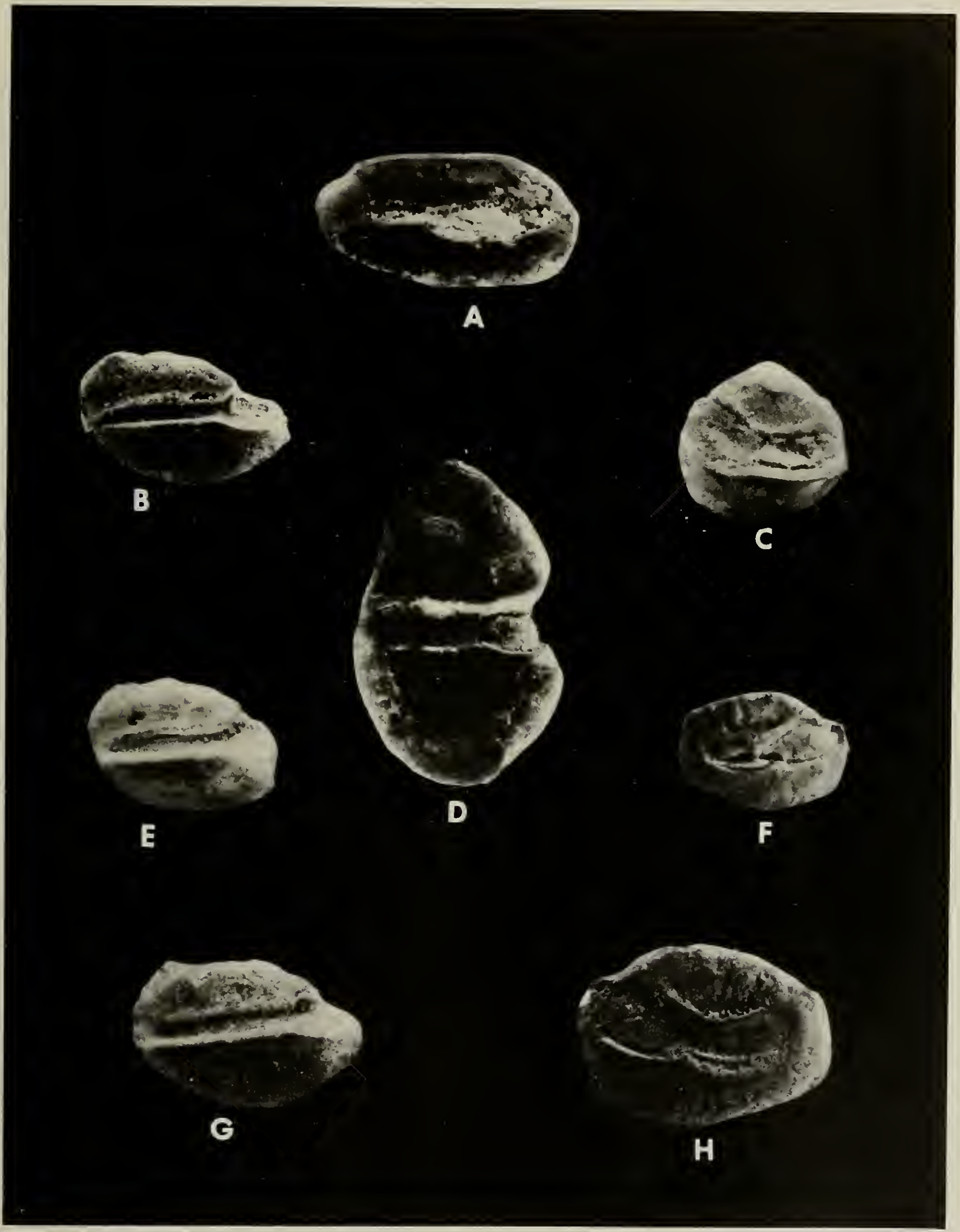


Fig. 3. A, Ophidiidae, right sagitta, 4.0mm, LACM 4425/116987; B, Argentinidae, left sagitta, 3.0mm, LACM 4425/116983; C, near-Apogonidae-B, right sagitta, 2.5mm, LACM 4425/116994; D, Stomioidei, left sagitta, 3.1mm, LACM 4425/116993; E, Argentinidae, left sagitta, 2.79mm, LACM 4425/120115; F, near-Apogonidae-A, left sagitta, 2.5mm, LACM 4425/116991; G, Argentinidae, left sagitta, 3.42mm, LACM 4425/120116; H, near-Apogonidae-A, right sagitta, 3.42mm, LACM 4425/116992.

Taxa	Number of otoliths	Figure
Pterothrissidae	12	fig. 1A–C
Albuloidei	13	fig. 1F–G
Anguilloidei-A	2	fig. 1D–E
Anguilloidei-B	2	fig. 2C
Argentinidae	3	fig. 3B, E, G
Stomioidei	4	fig. 3D
Ariidae: *Vorhisia* sp.	596	fig. 2F–G
Ariidae: unidentified	82	fig. 3A
Polymixiidae	11	fig. 2E
Trachichthyidae	63	not figured
c.f. Pempheridae	1	fig. 2A
Apogonidae-A	190	fig. 3F, H
Apogonidae-B	106	fig. 3C

Discussion

The ichthyofauna of the Severn Formation as defined by the otoliths, was dominated by the family Ariidae, with approximately 54 percent of the otoliths of a single genus, *Vorhisia* sp. Waage (1968) noted *Vorhisia* as a brackish and freshwater indicator. While *Vorhisia* sp. dominated the ichthyofauna all of these otoliths displayed varing degrees of attrition. The extent of potential postmortem transportation is not determinable. It is possible that these otoliths were washed in from a shallower area. However, it is unlikely that this *Vorhisia* sp. represented a freshwater species.

The albuloid sagittae were uncommon in the Severn samples and while the Recent Albulidae are found in warm subtropical to tropical environments it cannot be construed with any degree of certainty that the Severn albuloids occupied similar habitat without additional data. Additionally all of the albuloid otoliths displayed degrees of erosion and these otoliths may have undergone considerable postmortem transport.

The extant Polymixiidae, Apogonidae, Pempheridae, and Ariidae reflect a tropical-subtropical environment and their presence in the Severn fauna may suggest this condition. However, additional supportive data are necessary to confirm these conclusions. This late Cretaceous fauna is unusual in that its overall components more closely resemble otolith faunas observed from the Paleocene Brightseat Formation rather than the other Cretaceous age ichthyofaunas represented by otoliths (Huddleston, unpublished data).

Acknowledgments

We thank D. Haman, Chevron Oil Field Research Company for review of this manuscript and helpful comments, and D. Nolf, Belgian Museum of Natural History for his suggestions on the improvement of this study. We especially thank the late J. E. Fitch, San Pedro, California for review of this manuscript and for providing invaluable advice and comparative material throughout this study.

Literature Cited

Brouwers, E. M., and Hazel, J. E. 1978. Ostracoda and correlations of the Severn Formation (Navarroan; Maestrichtian) of Maryland.—Journal of Paleontology (Supplement)52(2):1–52.

Clark, W. B., Bagg, R. M., and Shattuck, G. B. 1897. Upper Cretaceous deposits of Maryland.—Maryland Geological Survey (Upper Cretaceous):23–110.

Denton, N. H. 1891. Mesozoic formations of Eastern Virginia and Maryland.—Geological Society of America, Bulletin 2:431–450.

Frizzell, D. L. 1965a. Otolith-based genera and lineages of fossil bonefish (Clupeiformes, Albulidae).—Senckenbergiana Lethaea 46a:85–110.

———. 1965b. Otoliths of new fish (*Vorhisia* vulpes, n. gen., n. sp. Silurioidei ?) from the Upper Cretaceous of South Dakota.—Copeia 1965(2):178–181.

———, and Koenig, J. W. 1973. Upper Cretaceous Ostariophysine (*Vorhisia*) redescribed from unique association of utricular and lagenar otoliths (lapillus and asteriscus).—Copeia 1973(4): 692–698.

Huddleston, R. W. 1981. *Bernardichthys zorraquinosi,* a new genus and species of salmoniform fish from the late Cretaceous of Oregon.—Proceedings of the Biological Society of Washington 94(1): 37–42.

Minard, J. P., Sohl, N. F., and Owens, J. P. 1978. Reintroduction of the Severn formation (Upper Cretaceous) to replace the Monmouth formation in Maryland.—U.S. Geological Survey, Bulletin 1435-A:132–133.

Waage, K. M. 1968. The type Fox Hills formation, Cretaceous (Maestrichtian), South Dakota. Part 1. Stratigraphy and paleonenvironments.—Bulletin of the Peabody Museum of Natural History, Yale University 27, 167pp.

RWH, Scientifc Research Systems, 11044 McGirk, El Monte, California 91731; KMS, 2311 Pimmit Dr. no. 702 E, Falls Church, Virginia 22043.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 664–668

A NEW SUBSPECIES OF FOX SPARROW FROM ALASKA

J. Dan Webster

Abstract.—*Passerella iliaca chilcatensis,* new subspecies, is described from the mainland of southeastern Alaska and adjacent Canada. The action represents a split of the well-known race *P. i. fuliginosa,* from which *P. i. chilcatensis* differs in being less reddish and duller in color and in having a shorter tail.

Swarth (1920) in his monograph on the Fox Sparrows and emendation of the range of *P. i. fuliginosa* (1922) intimated that the race might need subdivision. In earlier publications (Webster 1950, 1975) I, too, lumped the population of the mainland of southeastern Alaska and adjacent parts of Yukon and British Columbia with those of Vancouver Island and northwestern Washington. A similar arrangement was followed by Munro and Cowan (1947), the American Ornithologists' Union (1957), and Gabrielson and Lincoln (1959). In view of differences in color, size, and migration patterns, I now conclude that a formal description of what Swarth (1920) called "non-typical *fuliginosa*" is required.

Passerella iliaca chilcatensis, new subspecies

Holotype.—California Academy of Sciences #70787, collected 12 Jun 1981 by J. Dan Webster, 7 miles (airline) south–southwest of Klukwan, Alaska, near Tsirku River, about 250 m elevation, in alder-willow thicket near large cottonwood trees. Little body fat; 37.8 g, male, cloacal protuberance large, testes 13 and 10 mm long; adult skull.

Subspecific characters.—Blacker, less reddish than *P. i. townsendi,* both dorsally and on ventral spots; less reddish, more sepia (or yellowish), duller than *P. i. fuliginosa,* but equally dark or blackish both dorsally and on ventral spots, and with shorter tail. Dorsum of fresh-plumaged birds nearest fuscous, though slightly more olivaceous than that; compared directly with Smithe (1975).

Breeding range.—Chilkat River area of British Columbia and Alaska southeast along the mainland to the Tewart area of British Columbia. Precise localities, including those of intergradient populations, are listed below. Thickets, mostly of alder bushes but sometimes mixed with small spruces or willows, comprise the breeding habitat. These are mostly near timberline, but also occur in logging clearings, avalanche rubble, river margins, down even to sea level.

Winter range.—Most specimens I examined were from the coast of Oregon (Tillamook) and northern California south to San Francisco. However, one specimen had been taken in Alaska—Craig, Prince of Wales Island, 5 Jan 1920; and one on Puget Sound, Washington, 10 Jan 1912. Also, specimens intermediate between *chilcatensis* and one or another of the adjacent breeding races were examined. These had been taken in winter (Dec–Feb) in south coastal British Columbia and south to Tulare County, California. Swarth (1920) examined specimens of "non-typical *fuliginosa*" from the coastal counties of northern California

Table 1.—*Passerella iliaca.* Length of wing. Males, breeding populations.

Subspecies	n	r	M	SD	CV
P. i. chilcatensis	51	76–86	80.235	2.08	2.59
P. i. fuliginosa	14	79–85	82.357	1.99	2.41
P. i. altivagans	19	77–85	82.053	2.19	2.67
P. i. zaboria	50	81–92	87.220	1.65	1.89
P. i. annectens	12	78–86	82.583	2.26	2.74
P. i. townsendi	70	75–86	80.814	2.38	2.94

south to the San Francisco Bay region, plus single specimens from San Luis Obispo and San Bernardino counties farther south. Grinnell and Miller (1944), although stating that the winter range in California was concentrated in the humid northwest, cited additional specimens from Monterey, Los Angeles, Siskiyou, Shasta, and Lassen counties. It is notable that the winter range of *fuliginosa* (sensu stricto) is confined to British Columbia and Washington.

Measurements.—Tables 1–4 give a comparison of the new race with adjacent races. Wing chord, tail, and exposed culmen were measured in standard fashion, but depth of bill by Swarth's method (1920:83). Only adult male specimens taken 10 May to 8 Aug were included in the tables. In summary, *chilcatensis* differs significantly in size from adjacent races only on these points: *zaboria* has a longer wing and shorter bill; *fuliginosa* has a longer tail. While *annectens* has a deeper bill, the difference is not significant. Within the samples of the races *chilcatensis* and *townsendi* (as classified in the tables of measurements), some specimens from geographically marginal areas showed intermediacy of color characters.

Discussion.—I have listed (Tables 1–4) five races as breeding adjacent to *chilcatensis*—*annectens* to the northwest, *townsendi* to the west, *zaboria* to the northeast, *altivagans* to the east and southeast, and *fuliginosa* to the south. However, there is certainly a possibility of contact between *chilcatensis* and *olivacea* somewhere in the coast range of British Columbia, as suggested by a few winter specimens (cf. Phillips 1964).

In view of the finding by Zink (1982) of slight but significant size differences in a Califronia deme of *Passerella iliaca* in samples separated by 54 years of time, the size differences reported herein must be viewed with caution. This caution applies especially to the race *annectens,* in which 10 of the 12 male specimens I examined were collected 90 years ago, whereas for the other races a high proportion

Table 2.—*Passerella iliaca.* Length of tail. Males, breeding populations.

Subspecies	n	r	M	SD	CV
P. i. chilcatensis	49	62–75	69.306	2.53	3.66
P. i. fuliginosa	14	70–81	75.143	2.42	3.22
P. i. altivagans	18	68–72	73.556	4.21	5.72
P. i. zaboria	50	67–76	71.420	2.11	2.95
P. i. annectens	12	67–73	70.250	1.88	2.67
P. i. townsendi	69	65–78	71.072	2.75	3.87

Table 3.—*Passerella iliaca.* Length of culmen. Males, breeding populations.

Subspecies	n	r	M	SD	CV
P. i. chilcatensis	51	11.0–13.5	12.249	0.54	4.45
P. i. fuliginosa	14	11.1–13.0	12.221	0.56	4.55
P. i. altivagans	19	11.0–12.5	11.674	0.42	3.60
P. i. zaboria	48	10.0–12.3	11.308	0.55	4.87
P. i. annectens	12	11.0–11.9	11.600	0.28	2.44
P. i. townsendi	69	10.1–13.2	11.990	0.64	5.36

were collected within the last 20 years. Gabrielson and Lincoln (1951) commented on "foxing" in Alaskan Fox Sparrow specimens; I concur that postmortem changes in color, mostly from black towards red, are considerable. Comparisons of specimens for color were made only with specimens of approximately the same museum age.

According to Gabrielson and Lincoln (1959) and earlier workers, the Fox Sparrow does not breed on the southern islands of the Alexander Archipeligo of Southeastern Alaska except for Wrangell and Forrester islands. However, I noted two singing birds near Ketchikan, Revillagigedo Island, 9 Jun 1977, and about 25 in logging clearcuts on Prince of Wales Island, 9–24 Jun 1977. While I found no nests in the latter area, I collected nine adults (of *townsendi*) in breeding condition. (The one female had a prominent brood patch and had recently laid an egg.) It is probable that the species did breed on these islands prior to the onset of major logging operations 20 years ago, but only in small numbers and at high elevations near timberline. The few observers before 1959 (see reports by Bailey, Swarth and Willett, as cited by Gabrielson and Lincoln 1959) spent little or no time at high elevations during summers. On 22 Jun 1977 my assistant, Keith Gehring, climbed a high ridge above the logging clearcut in the valley of Beaver Creek, Prince of Wales Island. He saw one singing Fox Sparrow at an elevation of about 2000 feet. Apparently, the recent clearcut logging operations on Prince of Wales and Revillagigedo islands, as on the mainland near Haines and Hyder, have allowed a great population expansion of the Fox Sparrow. Near Haines, I found the race *chilcatensis* breeding in considerable numbers (three nests found) in timberline alder thickets at several locations in Jun and Jul 1972, 1975 and 1981 (cf. Webster 1975). Banks (1970) reported expansion of range of two other subspecies of *Passerella iliaca* in Oregon after clearcut logging.

Table 4.—*Passerella iliaca.* Depth of bill. Males, breeding populations.

Subspecies	n	r	M	SD	CV
P. i. chilcatensis	51	7.8–9.6	8.745	0.48	5.45
P. i. fuliginosa	13	8.5–9.9	9.031	0.43	4.80
P. i. altivagans	19	8.5–9.5	9.021	0.28	3.08
P. i. zaboria	48	8.4–9.8	9.100	0.33	3.62
P. i. annectens	12	8.2–10.1	9.233	0.54	5.84
P. i. townsendi	69	8.0–9.7	8.809	0.40	4.55

Breeding season specimens examined.—(If a locality is marked †, specimens from there are intermediate toward the adjacent race.) *Passerella iliaca chilcatensis:* ALASKA 37—7 miles SSW Klukwan; 8 miles SSW Klukwan, on Porcupine Mountain; 4–5 miles W Klukwan, near Klehini River; Four Winds Mountain, above Mosquito Lake; Chilkat Mountain; Glacier Station, on White Pass railroad; Mountains above Juneau; 7–8 miles up (=NE) Stikine River from Point Rothsay; Berg Creek, 15 miles ESE Wrangell; 4 miles NW Hyder. YUKON 6—miles 97–98 Haines Highway†. BRITISH COLUMBIA 38—near Bear Glacier, 15 miles NE of Stewart; Snowbank Pass, 47 miles NW Meziadin Junction; 24 miles S Kinaskan Lake, near Iskut River; miles 46–56 Haines Highway, Rainy Hollow; mile 85 Haines Highway†; Doch-da-on Creek; Flood Glacier; Great Glacier, on Stikine River.

Passerella i. annectens: ALASKA 17—Yakutat; Situk River; Osier Island.

Passerella i. zaboria: ALASKA 33—Many localities in N and W Alaska; Lower Tonsina; Chistochina. YUKON 24—Several localities in N and central Yukon; Tagish†. BRITISH COLUMBIA 5—Dease Lake; Atlin. NORTHWEST TERRITORIES 1—Niultin Lake. MANITOBA 5—Churchill†.

Passerella i. townsendi: ALASKA 60—Glacier Bay†; Lemesurier Island; Chichagof Island; Admiralty Island; St. Lazeria Island; Baranof Island; Wrangell Island†; Forrester Island; Prince of Wales Island. BRITISH COLUMBIA 41—Queen Charlotte islands; Goose Island; Bella Coola.

Passerella i. altivagans: BRITISH COLUMBIA 37—Nine-mile Mountain; Hudson Bay Mountain; Mount Cronin; Driftwood Mountains; Parsnip River; Williams Lake; above Stuie; Mount Revelstoke; Glacier National Park.

Passerella i. fuliginosa: BRITISH COLUMBIA 16—Several localities on Vancouver Island; Triangle Island; Alert Bay. WASHINGTON 3—Tatoosh Island; Neah Bay; La Push.

Acknowledgments

My field work was supported by the Hanover College Faculty Research Committee and the Indiana Academy of Science. The British Columbia Provincial Museum, the National Museum of Canada, the Museum of Comparative Zoology of Harvard University, the Royal Ontario Museum of Zoology, the San Diego County Museum, and the National Museum of Natural History loaned me specimens for study. The California Academy of Sciences, the Field Museum of Natural History, the University of Michigan Museum of Zoology and the Museum of Vertebrate Zoology of the University of California allowed me to study in their collections.

Literature Cited

American Ornithologists' Union. 1957. Check-list of North American birds. 5th ed. American Ornithologists' Union, Lancaster, Pa. 691 pp.

Banks, R. C. 1970. The Fox Sparrow on the west slope of the Oregon Cascades.—Condor 72:369–370.

Gabrielson, I. N., and F. C. Lincoln. 1951. Post-mortem color changes in bird specimens.—Condor 53:298–299.

———, and ———. 1959. The birds of Alaska. Stackpole Company, Harrisburg, Pa. 922 pp.

Grinnell, J., and A. H. Miller. 1944. The distribution of the birds of California.—Pacific Coast Avifauna 27:1–608.

Munro, J. A., and I. McT. Cowan. 1947. A review of the bird fauna of British Columbia.—British Columbia Provincial Museum, Special Publications 2:1–285.

Phillips, A. 1964. Remarks on Fox Sparrows.—*In* Phillips, A., J. Marshall, and G. Monson. The birds of Arizona. University of Arizona Press, Tucson. 220 pp.

Smithe, F. B. 1975. Naturalist's color guide, part I. American Museum of Natural History, New York.

Swarth, H. S. 1920. Revision of the avian genus *Passerella,* with special reference to the distribution and migration of the races in California.—University of California Publications in Zoology 21(4):75–224.

———. 1922. Birds and mammals of the Stikine River region of northern British Columbia and southeastern Alaska.—University of California Publication in Zoology 24(2):125–314.

Webster, J. D. 1950. Notes on the birds of Wrangell and vicinity, southeastern Alaska.—Condor 52:32–38.

———. 1975. The Fox Sparrow in southwestern Yukon and adjacent areas.—Condor 77:215–216.

Zink, R. M. 1983. Evolutionary and systematic significance of temporal variation in the Fox Sparrow.—Systematic Zoology 32:223–238.

Hanover College, Hanover, Indiana 47243.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 669–674

A REVISION OF THE *GOLFINGIA* SUBGENERA *GOLFINGIELLA,* STEPHEN, 1964, AND *SIPHONOIDES,* MURINA, 1967 (SIPUNCULA)

Edward B. Cutler, Norma J. Cutler, and Peter E. Gibbs

Abstract.—The *Golfingia* subgenera *Golfingiella* and *Siphonoides* are regarded as void since all of the included species have either been transferred to other taxa (*G. immunita, G. pudica,* and *G. mexicana*) or placed on the list of species inquirenda (*G. approximata* and *G. innoxia*) or incertae sedis (*G. quadrata*).

Cutler and Murina (1977) began the process of reviewing the sipunculan genus *Golfingia* and its included subgenera; subsequent work has led to an examination of the difficult *Apionsoma/Mitosiphon/Fisherana* complex (Cutler 1979) and *Thysanocardia* (Gibbs, Cutler & Cutler, in press). The present paper continues this survey with an assessment of the *Golfingia* subgenera *Golfingiella* Stephen, 1964, and *Siphonoides* Murina, 1967. Experience has shown that many published descriptions contain serious errors and for this reason, every attempt has been made to examine type-materials. Taxa are here regarded as analogous to scientific hypotheses; if they cannot, for whatever reason, be tested (verified or falsified), then they should no longer be considered as valid entities.

The literature references under each species name are only those in which material is newly recorded. For additional references see Stephen and Edmonds (1972). Table 1 lists the currently accepted names of the species considered here with their proposed status. Four of the six species were erected on single specimens.

Genus *Golfingia* Lankester, 1885

Subgenus *Golfingiella* Stephen, 1964

Golfingiella species are characterized as having two pairs of introvert rectractor muscles, introverts without hooks, single-lobed nephridia and a posteriorly-attached spindle muscle.

The subgenus was originally established by Stephen (1964) for five little-known species of *Golfingia* which Fisher (1950) had omitted from his revision. *Phascolosoma approximatum* is named as the type-species but Stephen makes no mention of the other species included. In Stephen and Edmonds (1972) four species are listed: *G. pusilla* (Sluiter), *G. abnormis* (Sluiter), *G. innoxia* (Sluiter), and *G. approximata* (Roule); *G. trichocephala* was transferred from *Golfingiella* to *Golfingia* sensu stricto.

Cutler and Murina (1977) reviewed *Golfingia* and made a few changes in *Golfingiella: G. abnormis* was synonymized under *Phascolosoma pectinatum* Keferstein. Two species (*G. pudica* (Selenka) and *G. immunita* (Sluiter)) were moved into this subgenus after examining type-material and the literature. *Golfingia pusilla* was synonymized under *G. trichocephala* placing them in the subgenus

Table 1.—The proposed status of the species assigned to *Golfingiella* and *Siphonoides*. Species with an asterisk are based on single specimens.

Currently accepted name	Proposed status
**Golfingia* (*Golfingiella*) *approximata* (Roule, 1898)	species inquirenda
**Golfingia* (*Golfingiella*) *immunita* (Sluiter, 1902)	*Golfingia* (*Apionsoma*) *immunita*
**Golfingia* (*Golfingiella*) *innoxia* (Sluiter, 1912)	species inquirenda
Golfingia (*Golfingiella*) *pudica* (Selenka, 1885)	
sensu Selenka, Stephen	*Golfingia* (*Golfingia*) cf. *margaritacea*
sensu Wesenberg-Lund, Murina, Cutler	*Golfingia* (*Apionsoma*) (cf. *immunita*)
Golfingia (*Siphonoides*) *mexicana* Murina, 1967 (includes *A. longirhyncus*)	*Aspidosiphon* (*Aspidosiphon*) *mexicanus*
**Golfingia* (*Siphonoides*) *quadrata* (Ikeda, 1905)	incertae sedis

Mitosiphon. Subsequently *Mitosiphon* was submerged under *Apionsoma* (Cutler 1979). These actions leave the four species listed in Table 1 to consider.

Golfingia (Golfingiella) approximata (Roule, 1898)

Phascolosoma approximatum Roule, 1898:385; 1906:77–81, pl. 9, fig. 87, pl. 10, figs. 100–101.

Type-locality.—Off Moroccan coast at 1105 m depth.

The single representative of this species in the Paris museum (Cat. #V23) is not in good condition. The internal organs are somewhat disrupted and since most of the introvert is missing, nothing can be added regarding the hooks, spines, or tentacles. There are four retractor muscles. Whether or not the spindle muscle is attached to the posterior end of the trunk cannot be determined: a short piece of white thread-like tissue is at the posterior end which might be the remnant of a spindle muscle or possibly it is a fragment of the ventral nerve cord. Subsequent collections of benthic organisms in the area of the type locality have yielded no additional specimens of this species. Due to the damaged, incomplete state of the holotype and only specimen, the accuracy of Roule's description cannot be verified and therefore, *G. approximata* is placed on the list of species inquirenda.

Golfingia (Golfingiella) immunita (Sluiter, 1902)

Phascolosoma immunitum Sluiter, 1902:40–41.

Type-locality.—Indonesia, 6°N, 121°E, 275 m.

This single 8 mm worm with a 6 mm introvert (not 3 and 8 mm as reported) is in the Amsterdam museum (Cat. #V. Si. 198). As Sluiter reported, it does have a posteriorly-attached spindle muscle and lacks longitudinal muscle bands. However, introvert hooks in rings, each bearing small basal spinelets (Fig. 1) are present and there are four introvert retractor muscles (Sluiter states that it has no hooks and only two retractors). The general impression one gets from its external form

Fig. 1. Introvert hook from the holotype of *Golfingia (Apionsoma) immunita*. Scale line equals 10 micrometers.

is that of a *Phascolosoma* or a papillated *Golfingia (Apionsoma)*. As the introvert is partially withdrawn, the tentacles are difficult to discern but they appear to be arranged around the nuchal organ, as typical for *Golfingia (Apionsoma)*.

This individual clearly belongs in the subgenus *Apionsoma* and is similar to *G. capitata* in overall form but differs in hook structure. Therefore, the species name is referred to this subgenus.

Golfingia (Golfingiella) innoxia (Sluiter, 1912)

Phascolosoma innoxium Sluiter, 1912:13, text-fig. 3a–b.

Type-locality.—Azores, 35°25′N, 31°22′W, 1229 m.

As noted in Cutler and Murina (1977) the single specimen on which Sluiter based this species is housed at the Musée Océanographique in Monaco but is not available for close examination. There are no drawings of its internal anatomy and it is difficult to accept Sluiter's statements without being able to verify them. Many collections have been made in the general vicinity of the type locality over the past 70 years but no additional worms matching this description have been reported.

In view of doubts concerning the validity of this species (individual) the name is here on the list of species inquirenda until further information can be obtained to adequately determine its status.

Golfingia (Golfingiella) pudica (Selenka, 1885)

Phascolosoma pudicum Selenka, 1885:11–12, figs. 14–16.—Fischer, 1929:484.—Stephen, 1948:217–218.

Golfingia pudica.—Wesenberg-Lund, 1959:59–60, text-fig. 4.—Murina, 1976:65.—Cutler and Cutler, 1979:954–955.

Type-locality.—Kerguelen Islands, 18–225 m.

This enigmatic species has been recorded five times by five different authors. These reports and specimens (in chronological order) are as follows:

1885—Selenka's original description made no mention of the posterior attachment of the spindle muscle. Examination of the type-material (from Kerguelen) in the British Museum (Nat. Hist.) showed that this muscle is not attached to the posterior end of the trunk and, therefore, belongs in *Golfingia* sensu stricto. When Cutler and Murina (1977) moved it to *Golfingiella* they erroneously assumed Wesenberg-Lund's (1959) interpretation to be correct. Selenka compared *G. pudica* to *G. vulgaris* but maintained its distinctiveness based on hooks being in rows, not scattered, papillae distribution (on introvert as well as trunk), and number of tentacles (20 or less). The eight worms in the type collection are all less than 18 mm (trunk) and not all have hooks; these look very much like *G. margaritacea.* Smaller individuals of *G. margaritacea* from Japan do have deciduous hooks (Cutler, Cutler & Nishikawa, in preparation). Fischer's (1929) account is merely a repeat of Selenka's material with no new information.

1948—Stephen recorded over 100 specimens from Kerguelen but this material cannot be located in any British museum. Stephen comments, "In many cases, the body wall was in rather degenerate condition, so that the distinguishing characters could be made out only with difficulty." There are no figures nor additional morphological comments. Due to the poor quality of the material it is difficult to accept this record.

1959—Wesenberg-Lund reported a single 8 mm worm from Mauritius which has been examined in Copenhagen. It does have the posteriorly-attached spindle muscle as she stated and therefore cannot be *G. pudica.* It closely resembles *Golfingia (Apionsoma)* species in having hooks with small, basal spinelets.

1976—Murina reported a single 16 mm worm from the East China Sea with a posteriorly attached spindle muscle. As noted above, this indicates it cannot be *G. pudica* and must therefore be *Golfingia (Apionsoma)* species. Murina states that the hooks are in rings but makes no mention of basal spinelets.

1979—When Cutler & Cutler reported their six small (2–12 mm) specimens from the Mozambique Channel they noted that they were not in good condition and "Therefore these specimens are assigned to this taxon with reservations." Similarities of *G. pudica* to *Golfingia capitata* were pointed out, and that a clear view of the tentacular arrangements is necessary to differentiate with certainty between the two. The hooks of these specimens do have rudimentary spinelets as shown for *G. immunita* (Fig. 1).

We now propose that the three most recent collections be considered as a *Golfingia (Apionsoma)* species (possibly *G. immunita*). Those from Kerguelen should be considered as *Golfingia* sensu stricto and perhaps *Golfingia margaritacea* or *G. ohlini,* both common in the Antarctic.

Subgenus *Siphonoides* Murina, 1967

Murina (1967) established the new subgenus *Siphonoides* for four species (*G. immaniata* [sic], *G. mexicana* Murina, *G. quadrata* (Ikeda), and *G. rutilofusca*

(Fischer)), differing from other subgenera in having only one pair of introvert retractor muscles and a posteriorly attached spindle muscle. The only other taxa with this combination of characters are found in the family Aspidosiphonidae.

Stephen and Edmonds (1972) placed *G. rutilofusca* in the subgenus *Phascoloides* (now *Nephasoma*) because it was found that the spindle muscle is unattached. *Golfingia immunita* was moved to *Golfingiella* (Cutler and Murina 1977) because the type-specimen had four retractor muscles, not two (see above). The following two species thus remain to be considered.

Golfingia (Siphonoides) mexicana Murina, 1967

Golfingia mexicana Murina, 1967:1333–1334, fig. 3.
Aspidosiphon longirhyncus Cutler and Cutler, 1980:4–6, figs. 4–5.

Type-locality.—Gulf of Mexico. 19°N, 76°W, 110 m.

A close comparison of specimens kindly provided by Dr. V. V. Murina pointed to the striking similarity of *G. mexicana* to *Aspidosiphon longirhynchus* Cutler and Cutler (1980). Unfortunately no specimen of either population is preserved with tentacular crowns expanded. The diameter of the introvert is very small and attempts to dissect out the tentacular crown met with limited success; a few tentacles arranged dorsal to the mouth can be discerned in *A. longirhyncus* but for *G. mexicana* no conclusion could be reached by the authors nor by Murina.

While acknowledging that the shields are poorly developed it is concluded that these two taxa are nevertheless conspecific and belong in the genus *Aspidosiphon.* Therefore, *Golfingia mexicana* is hereby transferred to *Aspidosiphon* and now includes *A. longirhyncus* as a junior synonym.

Golfingia (Siphonoides) quadrata (Ikeda, 1905)

Phascolosoma quadratum Ikeda, 1905:170–171, pl. 8, fig. 14.

Type-locality.—South Negros, Philippines.

The single specimen Ikeda used as the basis for this species could not be located in Japan. Since some of the descriptions of Ikeda have been found to be in error, this species remains suspect. Cutler and Cutler (1981) pointed to its close similarity to *G. mexicana.* Specifically nothing is known about the tentacular array and the precise anus/nephridia location cannot be ascertained. The epidermal structures need to be reexamined but cannot be. No additional specimens have been assigned to this taxon. Ikeda (1905) compared his species to *Phascolosoma macer* which has been shown to belong to *Aspidosiphon* (Cutler and Murina, 1977:183). In view of the above, the taxonomic position of this species cannot be determined so this name is added to the list of incertae sedis. It is suspected that Ikeda's worm was an atypical *Aspidosiphon,* a common genus in the Philippines.

Acknowledgments

This work was made possible by the kind cooperation of the following persons: J. Renaud-Mornant, Muséum National d'Histoire Naturelle, Paris; S. van der Spoel, Inst. voor Taxonomische Zool., Amsterdam; G. Testa, Inst. Oceanographie, Monaco; R. Sims, Brit. Mus. (Nat. Hist.), London; J. Kirkegaard, Zool. Mus., Copenhagen; and G. Murina, Inst. of Biol. Southern Seas, Sevastopol. Funding has been provided by U.S. National Science Foundation grant #DEB-8011121.

Literature Cited

Cutler, E. B. 1979. A reconsideration of the *Golfingia* subgenera *Fisherana* Stephen, *Mitosiphon* Fisher, and *Apionsoma* Sluiter (Sipuncula).—Zoological Journal of the Linnean Society 65:367–384.

Cutler, E. B., and N. J. Cutler. 1979. Madagascar and Indian Ocean Sipuncula.—Bulletin du Muséum National D'Histoire Naturelle, Paris, 4^e ser. 1 (sec A., #4);941–990.

———, and ———. 1980. Sipuncula from Southern Brazil.—Boletim do Institut Oceanografico, São Paulo 29(1):1–8.

———, and ———. 1981. A reconsideration of Sipuncula named by I. Ikeda and H. Sato.—Publications of the Seto Marine Biological Laboratory 26:51–93.

Cutler, E. B., N. J. Cutler, and T. Nishikawa. [in prep.] Systematics and distribution of Japanese Sipuncula.

Cutler, E. B., and V. V. Murina. 1977. On the sipunculan genus *Golfingia* Lankester, 1885.—Zoological Journal of the Linnean Society 60:173–189.

Fischer, W. 1929. Die Sipunculiden, Priapuliden und Echiuriden der Arktis.—*In* Romer, F., and F. Schaudinn, Fauna Arctica 5 (II):451–490.

Fisher, W. K. 1950. The sipunculid genus *Phascolosoma.*—Annals and Magazine of Natural History (12) 3:547–552.

Gibbs, P. E., E. B. Cutler, and N. J. Cutler. [in press] A review of the sipunculan genus *Thysanocardia* Fisher.—Zoologica Scripta.

Ikeda, I. 1905. Gephyreans collected by Professor Dean at Manjuyodi, Southern Negros (Philippine Islands).—Annotations Zoologicae Japonenses 5:169–174.

Murina, V. V. 1967. Report on the sipunculid worms from the sublittoral zone of Cuba and the Mexican Gulf.—Zoologicheskii Zhurnal 54(9):1329–1339.

———. 1976. New and rare species of sipunculids from the East China Sea.—Vestnik Zoologii 2: 62–67.

Roule, L. 1898. Note préliminaire sur les espèces de gephyriens recueillies dans les explorations sous marines du 'Talisman' et du 'Travailleur'.—Bulletin du Muséum National D'Histoire Naturelle, Paris 4:384–387.

Selenka, E. 1885. Report on the Gephyrea collected by H.M.S. 'Challenger' during the years 1873–1876.—Report of Scientific Research of the Challenger 13(36):1–25.

Sluiter, G. P. 1902. Die Sipunculiden und Echiuriden der Siboga-Expedition, nebst Zusammenstellung der Uberdies aus den indischen Archipel bekannten Arten.—Siboga Expeditie, Monographie 25:1–53.

———. 1912. Gephyriens (Sipunculides et Echiurides) provenant des campagnes de la Princesse Alice. 1898–1910.—Resulats des Campagnes Scientifiques de Prince Albert 1 36:1–36.

Stephen, A. C. 1948. Sipunculids.—Report of B.A.N.Z. Antarctic Research Expedition 1929–1931, (5B)4:213–220.

———. 1964. A revision of the classification of the phylum Sipuncula.—Annals and Magazine of Natural History (13)7:457–462.

Stephen, A. C., and S. J. Edmonds. 1972. The phyla Sipuncula and Echiura. London: British Museum (Natural History) 528 pp.

Wesenberg-Lund, E. 1959. Sipunculoidea and Echiuroidea from Mauritius.—Videnskabelige Meddelelser fra Danske Naturhistorisk Forening i Kjobenhavn 121:53–73.

(EBC, NJC) Utica College of Syracuse University, Utica, New York 13502, U.S.A.; (PEG) Marine Biological Association U.K., The Laboratory, Citadel Hill, Plymouth, PL1 2PB, United Kingdom.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 675–683

TWO SPECIES OF *TYLOS* AUDOUIN FROM CHILE, WITH NOTES ON SPECIES OF *TYLOS* WITH THREE FLAGELLAR ARTICLES (ISOPODA: ONISCOIDEA: TYLIDAE)

George A. Schultz

Abstract.—Two species of *Tylos* Audouin are described from Chile including a new species, *T. chilensis,* based on specimens formerly called *T. spinulosus* Dana. New specimens which more nearly match the description of *T. spinulosus* are redescribed under that name. The two species, both with three flagellar articles on the flagellum of antenna 2, are compared with each other and with the three other species of *Tylos* which also have three flagellar articles.

Roman (1977:110) listed 24 species of *Tylos* Audouin (1826) (see Ferrara and Taiti, 1979:91, for explanation of use of *Tylos* Audouin, 1826), three of which have three flagellar articles on antenna 2. To Roman's list can be added *T. marcuzzii* Soika, and *T. wegeneri* Vandel (see Schultz 1974) making a total of at least 26 species in the genus (possible synonyms among them are not considered here). *Tylos wegeneri* has three flagellar articles and *T. marcuzzii* has four. The new species described herein and *T. wegeneri* bring to five the total number of known species of *Tylos* with three flagellar articles on the flagellum of antenna 2. With length and location they are: *T. spinulosus* Dana (1853), to 27 mm, central and southern Chile; *T. neozelanicus* Chilton (1901), to 14 mm, New Zealand; *T. exiguus* Stebbing (1910), to 4.5 mm, Red Sea; *T. wegeneri* Vandel (1952), to 22 mm, West Indies and west coast of Costa Rica; and *T. chilensis,* new species, to 12 mm, central Chile.

Only slight morphological differences separate most species of *Tylos* (except *T. wegeneri* which has a unique pleotelson) and the species with three flagellar articles on antenna 2 (except *T. wegeneri*) are no exceptions.

The new species described here is based on the specimens called *T. spinulosus* (Dana) by Schultz (1970). Specimens of a different species (also with three flagellar articles) kindly sent to me by Dr. Eduardo Jaramillo, Universidad Austral de Chile, proved to be more nearly like *T. spinulosus* Dana than the specimens described by Schultz under that name, and they are described here as *T. spinulosus.* I thank Dr. Eduardo Jaramillo for sending me the specimens so that accurate identifications could be made of the two species of *Tylos* from Chile. I also thank Jersey City State College for separately Budgeted Research funds.

Tylos spinulosus Dana, 1853

Figs. 1A–J, 2A–F, 3A–E

Tylus spinulosus Dana, 1853:717, pl. 47, fig. 1a–c.

Tylos spinulosus Dana.—Miers 1877:675.—Budde-Lund 1879:9; 1885:279; 1908: 78.—Stebbing 1893:424.—Chilton 1901:121; 1910:288.—Van Name 1924:192; 1936:415, 416, fig. 257.

nec *Tylos spinulosus* (Dana).—Schultz 1970:302, figs. 18–27.

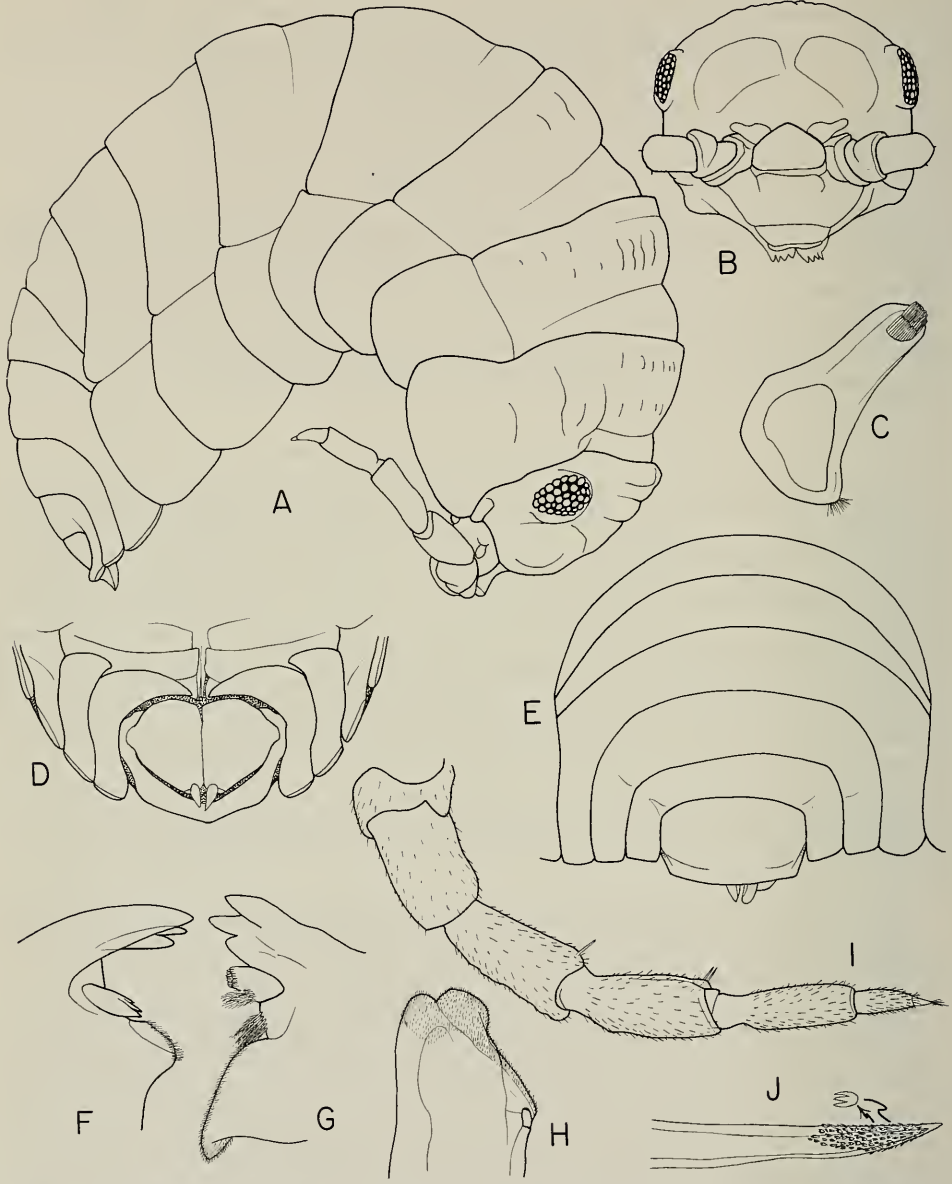


Fig. 1. *Tylos spinulosus,* male 20 mm long: A, Lateral view; B, Frontal view; C, Antenna 1; D, Underside pleon; E, Posterior View, F, Right mandible; G, Left mandible; H, Maxilla 1; I, Antenna 2; J, Endopod male pleopod 2.

Specimens have not been recorded since Dana's record. Van Name (1936:415, Fig. 257) quoted Dana's (1853) description in full and reproduced all of his illustrations. The specimens described here have a flagellum with the lengths of the articles more nearly matching those of the specimen illustrated by Dana (cf. Fig. 1I here with Pl. 47, Fig. 1b of Dana, also in Van Name 1936:415, Fig. 257).

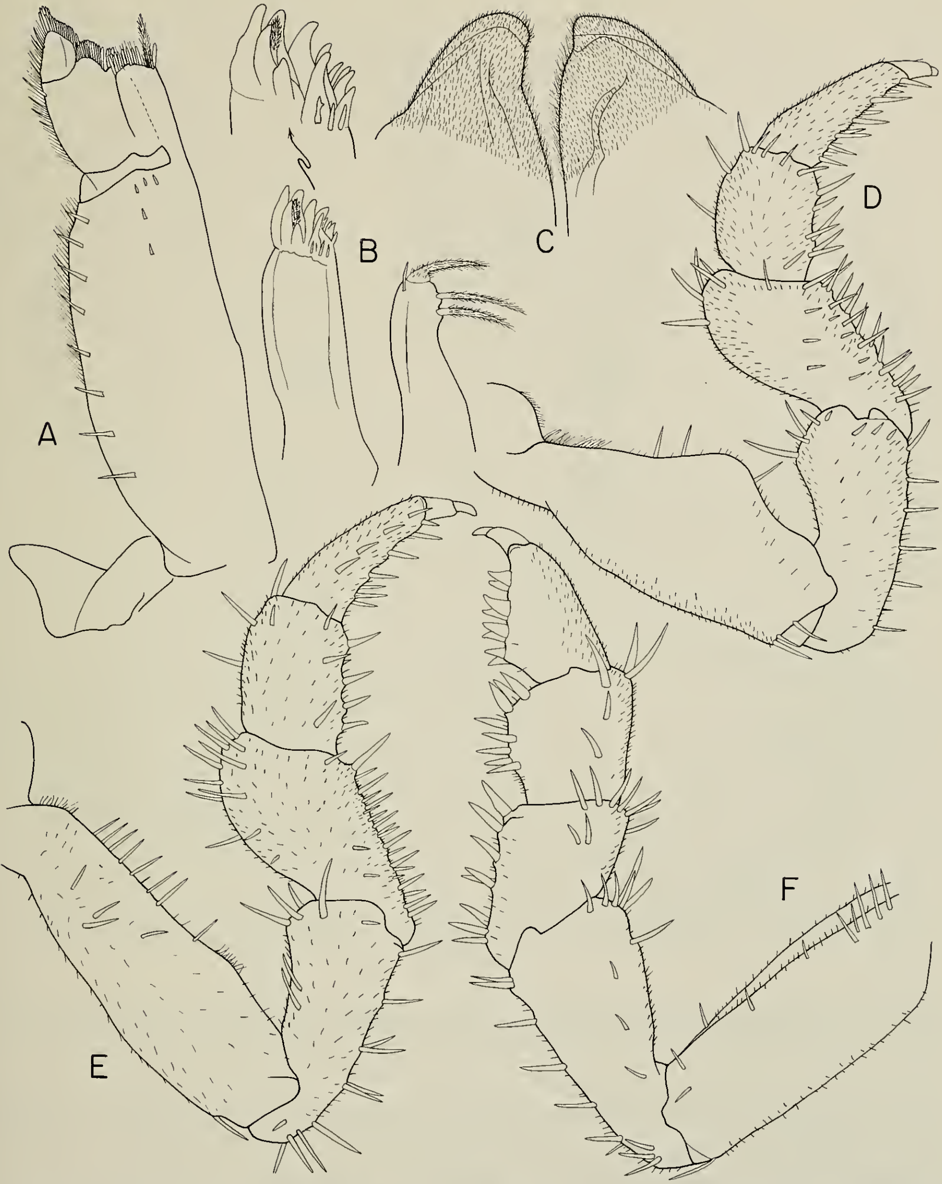


Fig. 2. *Tylos spinulosus*: A, Maxilliped; B, Maxilla 2 with detail of exopod; C, Hypopharynx; D–F, Male peraeopods I, II and VI.

They also lack the notch in the posterolateral corner of peraeonal segment I as shown by Schultz (1970). Dana did not illustrate or record such a notch. It probably would have been noted by Dana if it had been present as it is large and not characteristic of the other species of *Tylos* known at the time. *Tylos spinulosus* sensu Schultz (1970) is herein considered a new species.

Description.—Eyes large with many ocelli. Body with anterior peraeonal seg-

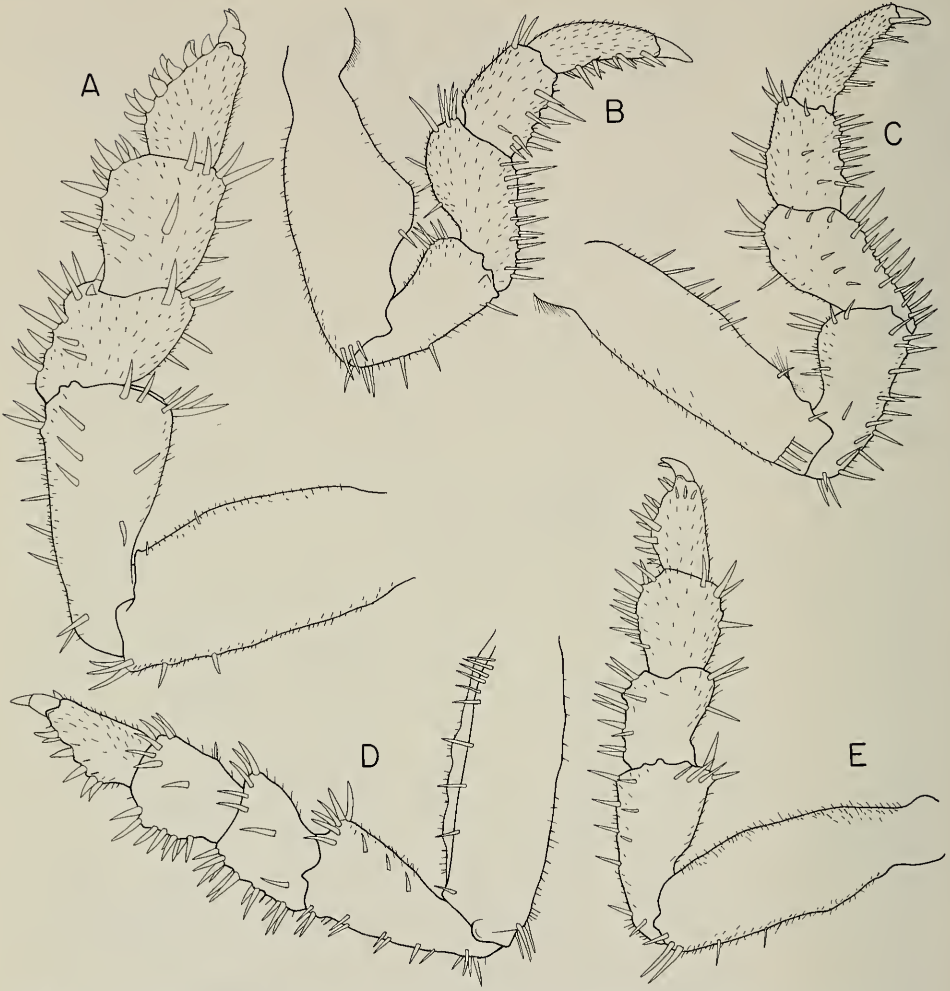


Fig. 3. *Tylos spinulosus*: A, Male peraeopod VII; B–E, Female peraeopods I, II, VI and VII.

ments with low tubercules; dorsum covered with minute hairlike scales. Frontal plate of cephalon with length of lateral margins less than half width of plate; dorsal margin obtusely rounded. Antenna 1 pear-shaped with many aesthetascs near tip. Antenna 2 short; flagellum of 3 articles, longer than last peduncular segment. Article 1 of flagellum about twice as long as articles 2 and 3 combined; article 3 tiny. Clypeus rounded. Mandibles each with 3 cusps on incisor process. Lacinia mobilis on right mandible with 3 teeth and no compound setae. Lacinia mobilis on left mandible with many small apical teeth arranged in crown; small setae present. Five setae in setal row on right mandible. Molar process of each mandible broad and fringed with many tiny setae. Exopod of maxilla 1 with many large and small teeth and one compound seta present on tip; endopod with 3 long medially pointing setae and small seta on tip. Hypopharynx bilobed.

Peraeonal segment I with broadly rounded posterolateral margin. Edge of pe-

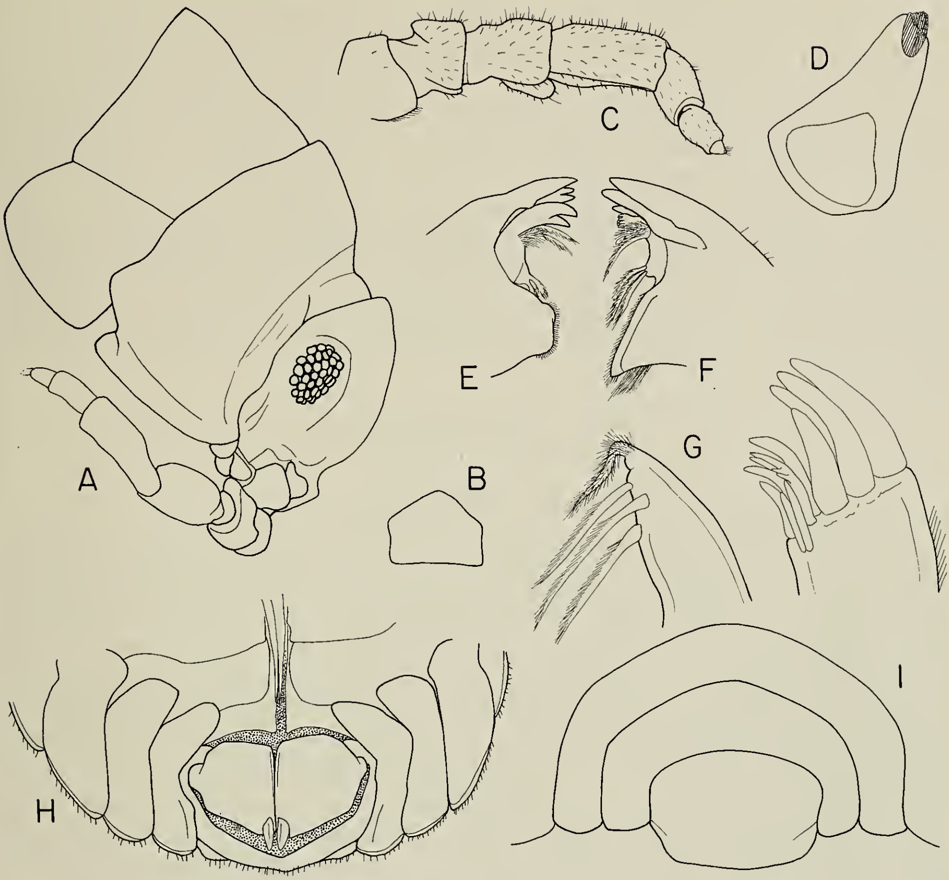


Fig. 4. *Tylos chilensis*: A, Lateral view anterior part; B, Frontal process; C, Antenna 2; D, Antenna 1; E, Right mandible; F, Left mandible; G, Maxilla 2; H, Underside of pleon; I, Posterior end.

raeonal segment II broadly rounded. Edges of peraeonal segments III–VII somewhat squarish. Peraeopods of male and female with very similar pattern of setae on inner margins. Posterior peraeopods of male (see VI and VII of male here, Figs. 2F and 3A) with very broad, short setae when compared to those on respective peraeopods of female (see VI and VII of female, Figs. 3D and 3E).

Pleon with edges of all segments reaching to general body margin. Pleotelson projecting slightly beyond general body margin, with rounded posterior border and shallow lateral notches receiving edges of pleonal segment 5. Inner edges of right and left pleonal segment 5 extensions pointed and almost touching medially; inner edges of pleonal extensions of segment 4 pointed and wide apart.

Measurements.—Males to 27 mm long; females to 26 mm long.

Etymology.—The name *spinulosus*—"with spinules,"—refers to the minute spines on the dorsum.

Type-locality.—Nassau Bay, Fuegia (Terra del Fuego), Chile. The species lives on beaches where it burrows into the sand.

Distribution.—Playa Punta Choros (29°53′S, 71°19′W), north of Coquimbo, Chile, south to Terra del Fuego. The specimens mentioned by Van Name (1936: 416) (AMNH 7120) from Toto, near Valparaiso are definitely of this species and not as recorded by Schultz (1970).

Disposition of specimens.—Specimens have been deposited in the United States National Museum—USNM 204417. Others have been retained by Dr. Jaramillo at the Universidad Austral de Chile.

Affinities.—The species is unique among the members of the genus with three flagellar articles in that the posterolateral corner of peraeonal segment I is broadly rounded (see below under *T. chilensis,* on how it differs from that species). Apparently the two species are separated ecologically. *Tylos spinulosus* is present on the beach where it burrows, and the new species described below lives high up on the shore in the spray zone.

Tylos chilensis, new species

Figs. 4A–I, 5A–H

Tylos spinulosus non Dana, Schultz 1970:302, figs. 18–27.

Description.—Eyes large with many ommatidia. Body smooth; dorsum covered with minute hairlike scales. Frontal plate of cephalon with 5 sides, height laterally about half width, with obtusely pointed dorsal side. Antenna 1 pear-shaped with many aesthetascs near tip. Antenna 2 short; flagellum of 3 articles about as long as peduncular segment. Flagellar article 1 about twice as long as 2 and very tiny 3 combined. Inner margins of long peduncular segments with grooves along lengths. Clypeus rounded. Mandibles each with 3 sharp cusps on incisor process. Lacinia mobilis on right mandible with 2 sharp teeth and compound setae. Lacinia mobilis on left mandible with crown of small teeth on tip; compound setae present. Setal row with 2 setae and broad flattened molar process with many tiny setae on right and left mandibles. Exopod of maxilla 1 with 4 large and several small teeth on tip; endopod with 4 long medially pointing setae on tip. Hypopharynx bilobed.

Peraeonal segment I (lateral view) with deeply notched posterolateral margin. Posterior margin (lateral view) obtusely pointed just above posterolateral notch. Lateral margins of peraeonal segments II–IV with squarish borders. Peraeonal segments V–VII with rounded lateral borders. All peraeopods of male and female similar, with similar patterns of many long setae on inner margin of each.

Pleon with edges of all pleonal segments reaching general body margin. Pleotelson projecting slightly beyond general body margin; posterior margin produced medially with deep grooves laterally placed to receive pleonal segments 5. Inner edges of right and left medially projecting pleonal segments 3, 4 and 5 rounded and wide apart medially.

Measurements.—Specimens to 12 mm long.

Etymology.—The name *chilensis* refers to the country in which the species was collected.

Type-locality.—Montemar, Chile (a few kilometers north of Valparaiso). Under rocks and in crevices high on a cliff facing the sea in the spray zone.

Distribution.—Known only from the type-locality.

Disposition of types.—Type-specimens have been deposited in the National Museum of Natural History (Smithsonian Institution): holotype male USNM

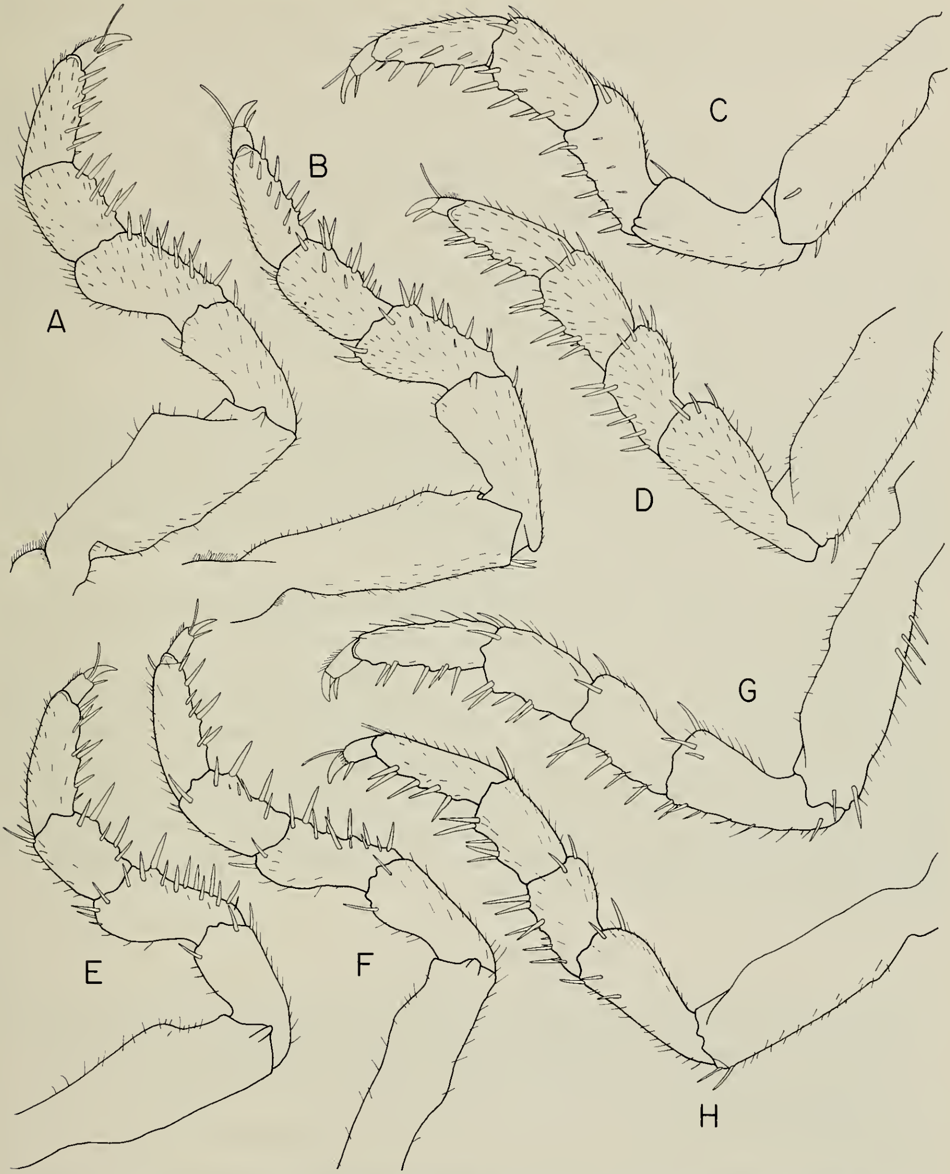


Fig. 5. *Tylos chilensis*: A–D, Male peraeopods, I, II, VI and VII; E–H, Female peraeopods I, II, VI and VII.

204144; allotype female USNM 204415; paratypes male and females USNM 204416.

Affinities.—The new species differs from all other members of the genus with three flagellar articles in that is the only one with a notch on the posterolateral edge of peraeonal segment I. It differs from *T. spinulosus,* as redescribed here, in that there is less of a protrusion or process on the posterior margin of the pleotelson. There are also differences in the shapes of, and the space between the tips of the internal ventral extensions of pleonal segments 3, 4 and 5.

Other Species of *Tylos* with Three Flagellar Articles

Tylos sp. De Borre (Three flagellar articles?) The status of this species from Peru remains unknown (Van Name 1936:416; Schultz 1970:302).

Tylos neozelanicus Chilton (1901:120, pl. 13, fig. 2). The species from Lyall Bay, New Zealand, was well described and illustrated by Chilton, but it has not been recorded since (Hurley 1961). The relative length of the flagellar articles on antenna 2 (they are each about the same length) and the regularly rounded (not produced) posterior margin on peraeonal segment I (lateral view) sets the species apart from *T. spinulosus* and *T. chilensis.*

Tylos exiguus Stebbing (1910:228, pl. 23). The species, based on tiny specimens from the Red Sea, was adequately illustrated by Stebbing who stated that it might be a young individual. So far *T. exiguus* is the only species of the genus with three flagellar articles recorded from or near the Red Sea. The three flagellar articles are each about the same length. The posterior margin of peraeonal segment I is smooth and the posterolateral angle is obtuse.

Tylos wegeneri Vandel (1952:74, figs. 4–10). Vandel described the species in some detail on specimens from Isla Margarita, Venezuela. It was further recorded by Schultz (1974) who extended its range to Tobago and St. Martins in the West Indies, and compared it to other species in the genus from the New World. Several specimens collected on 21 September, 1957, from Puntarenas, Costa Rica, were identified by the author from the collections of arthropods of the Department of Agriculture, Florida State Museum, Gainesville, Florida. The location is on the west or Pacific coast of Costa Rica so the range of the species is extended from Caribbean to Pacific shores. The unique configuration of the pleotelson sets the species apart from all others in the genus.

Literature Cited

Audouin, J.-V. 1826. Description de l'Égypte, ou recueil des observations, et des recherches qui ont été fêtes on Égypte pendant l'expédition de l'armée française. Explication sommaire des planches de crustacés de l'Égypte et de la Syrie. Histoire naturelle, J.-C. Savigny, Paris 1(4):77–98.

Budde-Lund, G. 1879. Prospectus generum specierumque Crustaceorum Isopodum terrestrium. Copenhagen pp. 1–10.

———. 1885. Crustacea Isopoda terrestria per familias et genera et species descripta. Hauniae pp. 1–319.

———. 1908. Die Landisopoden der deutschen Südpolar-Expedition 1901–1903, mit Diagnosen verwandter Arten.—Deutsche Südpolar-Expedition 9(Zool. I):69–92.

Chilton, C. 1901. The terrestrial isopods of New Zealand.—Transactions of the Linnean Society of London (2) 8(4):99–152.

———. 1910. Additions to the terrestrial Isopoda of New Zealand.—Transactions of the New Zealand Institute 42:286–291.

Dana, J. D. 1853. Report on the Crustacea of the United States Exploring Expedition. Part II. United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N. 14. Crustacea (Isopoda pp. 696–805). Sherman, Philadelphia.

Ferrara, F., and S. Taiti. 1979. A check-list of terrestrial isopods from Africa (South of the Sahara).—Monitore Zoologico Italiano (N.S.) Supplemento 12(10):89–215.

Hurley, D. E. 1961. A checklist and key to the Crustacea Isopoda of New Zealand and the subantarctic islands.—Transactions of the Royal Society of New Zealand 1(20):259–292.

Miers, E. J. 1877. On a collection of Crustacea, Decapoda and Isopoda, chiefly from South America, with descriptions of new genera and species.—Proceeding of the Zoological Society of London 1877:653–679.

Roman, M.-L. 1977. Les Oniscoides halophiles de Madagascar (Isopoda, Oniscoidea).—Beaufortia 26(334):107–152.

Schultz, G. A. 1970. A review of species of *Tylos* Latreille from the New World (Isopoda, Oniscoidea).—Crustaceana 19(2):297–305.

———. 1974. Terrestrial isopod crustaceans (Oniscoidea) mainly from the West Indies and adjacent regions. I. *Tylos* and *Ligia.*—Studies on the fauna of Curaçao and other Caribbean Islands 45: 162–173.

Stebbing, T. R. R. 1893. A history of Crustacea: Recent Malacostraca. International Science Series 74, London pp. xvii–466.

———. 1910. Isopoda from the Indian Ocean and British East Africa.—Transactions of the Linnean Society of London (2) 14:83–122.

Vandel, A. 1952. Étude des isopodes terrestres récoltes au Vénézuela par le Dr. G. Marcuzzi, suivie de considérations sur le peuplement deu Continent de Gondwana.—Memoire del Museo Civico di Storia Naturale di Verona 3:59–203.

Van Name, W. G. 1924. Isopods from the Williams Galapagos Expedition.—Zoologica, New York 5(18):181–210.

———. 1936. The American land and fresh-water isopod Crustacea.—Bulletin of the American Museum of Natural History 71:1–535.

15 Smith St., Hampton, New Jersey 08827.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 684–685

BONADUCECYTHERIDAE McKENZIE, 1977: A SUBJECTIVE SYNONYM OF PSAMMOCYTHERIDAE KLIE, 1938 (OSTRACODA: PODOCOPIDA: CYTHERACEA)

K. G. McKenzie

Abstract.—Comparison of material described from the Galapagos with that described earlier from Malta indicates that Bonaducecytheridae McKenzie 1977, is a junior synonym of Psammocytheridae Klie 1938.

Recently, Gottwald (1980) described *Psammocythere hartmanni* from Santa Cruz in the Galapagos Islands. He noted that while confident of the family in which the species belonged (Psammocytheridae Klie 1938) he was hesitant about the generic determination but did not intend to establish a new genus because he had only one specimen (a mature male).

Earlier, McKenzie (1977) had described the new family Bonaducecytheridae, type-species *Bonaducecythere hartmanni* McKenzie, 1977, on the basis of material collected from the island of Malta, in the Mediterranean.

Comparing the Maltese and Galapagos taxa it is clear that they have many characters in common. In both, the shells are small and flattened ventrally with an anterior gape; the line of concrescence is irregular; muscle scars include 3 adductors plus 1 frontal scar; antennules are 6-segmented, with the 4th segment carrying 4 dorsomedial and 6 dorso-distal bristles, while the 5th segment is bare; the antennae have 3 terminal endopodial claws and 3-jointed flagella; the mandibles have epipods with only 1–2 Strahl(en); maxillae epipods have 2 downward-pointing setae; the male P1's have curved club-like clasping ungues; P2s and P3s are slender with 4-segmented endopods. However, there are some differences in the respective hemipenes, in the P1 chaetotaxy and Gottwald (1980) did not record whether the seminal vesicles of his specimen were coiled within the duplicature as is the case in *Bonaduceythere*. Reference to more Galapagos material is needed before it can be placed in *Bonaducecythere*. If this were done, then *Psammocythere hartmanni* Gottwald, 1980, would become a junior homonym of *Bonaducecythere hartmanni* McKenzie, 1977.

On shell characters, *Bonaducecythere* is easily separated from *Psammocythere* which is broadly rounded both anteriorly and posteriorly and has a cigar-like shape (Klie 1938:214, figs 733, 734). However, it does share several characters of the soft anatomy, notably, 6-segmented antennules with identical chaetotaxy; 3-segmented antennal exopods; mandible epipods with a reduced (1–2) number of Strahl(en); maxillae with reduced epipods, bearing 2–3 downward pointing setae; strongly dimorphic P1s, with the terminal ungues being curved and club-shaped in males; and slender P2s and P3s with 4-segmented endopods. No other cytheracean family has this complex of characters (Hartmann and Puri 1974). Therefore, Bonaducecytheridae should be considered a junior synonym of Psammocytheridae.

Psammocytheridae are now held to include at least *P. remanei* Klie, 1936; *P. hartmanni* Gottwald, 1980; and *B. hartmanni* McKenzie, 1977—from Helgoland, Galapagos and the Mediterranean respectively. There are two Mediterranean records for *Bonaducecythere*—that by McKenzie (1977) from Malta; and an earlier record of n. gen., n. sp. from the island of Naxos, Greece, which, although not described, was sufficiently well illustrated (Barbeito-Gonzales 1971, Plate 43b) to identify it with *B. hartmanni.*

The preferred habitats for these three small ostracode species are all interstitial.

Literature Cited

Barbeito-Gonzalez, P. J. 1971. Die Ostracoden des Küstenbereiches von Naxos (Griechenland) und ihre Lebensbereiche.—Mittelungen Hamburger Zoologisches Museum und Institut 67:255–326.

Gottwald, J. 1980. Systematik, postembryonale Entwicklung, Evolution und Zoogeographie interstitieller Ostracoda (Crustacea) aus dem Pazifik. Dissertation zur Erlangung des Doktorgrades der Mathatmatisch-Naturwissenschaftlichen Fakultat der Georg-August-Universität zu Göttingen, 260 pp.

Hartmann, G., and Puri, H. S. 1974. Summary of Neontological and Paleontological Classification of Ostracoda.—Mitteilungen Hamburger Zoologisches Museum und Institut 70:7–73.

Klie, W. 1938. Krebstiere oder Crustacea III: Ostracoda, Muschelkrebse.—Die Tierwelt Deutschlands 34:1–230.

McKenzie, K. G. 1977. Bonaducecytheridae, a new family of cytheracean Ostracoda, and its phylogenetic significance.—Proceedings of the Biological Society of Washington 90:263–273.

Riverina College of Advanced Education, P.O. Box 588, Wagga Wagga, New South Wales 2650, Australia.

Note: Recently, Gottwald (1983) renamed *T. hartmanni* Gottwald, 1980, as *P. santacruzensis* Gottwald, 1983. For the reasons given above, this species becomes *Bonaducecythere santacruzensis* (Gottwald 1983).

Gottwald, J. 1983. Interstitielle Fauna von Galpagos XXX. Podocopida 1 (Ostracoda).—Mikrofauna des Meeresdodens 90:621–805.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 686–692

HETEROPYRAMIS ALCALA AND *THALASSOPHYES FERRARII*, NEW SPECIES OF CLAUSOPHYIDAE (CALYCOPHORAE: SIPHONOPHORAE) FROM THE SOUTH PACIFIC

Angeles Alvariño and Kenneth R. Frankwick

Abstract.—Two new species, *Heteropyramis alcala*, and *Thalassophyes ferrarii* are described and compared with the other species of their genera, *Heteropyramis maculata* Moser, 1925, and *Thalassophyes crystallina* Moser, 1925. The material was obtained in the plankton collections made in the South Pacific during the U.S. Antarctic Research Program.

The family *Clausophyidae* Totton and Bargmann, 1965, is characterized by the presence of the somatocyst in both anterior and posterior necotophores. This family includes 5 genera: *Clausophyes*, with two species, *C. ovata* (Kefferstein and Ehlers, 1860), *C. galeata* Lens and van Riemsdijk, 1908; *Chuniphyes*, with two species, *C. multidentata* Lens and van Riemsdijk, 1908; *C. moserae* Totton, 1954; *Crystallophyes* (*C. amigdalina* Moser, 1925); *Heteropyramis* (*H. maculata* Moser, 1925); and *Thalassophyes* (*T. crystallina* Moser, 1925).

The two new Clausophyidae described herein belong to the genera *Heteropyramis* and *Thalassophyes*.

Heteropyramis alcala, new species
Figs. 1–3

Material.—From cruises of R/V *Eltanin* in 1965 and 1966 (see Table 1). Holotype: Polygastric form (nectophore), and eudoxid form (bract + gonophore) from *Eltanin* cruise 25, sta 1697, off Chile, USNM 61064. Paratypes: 1 nectophore, 1 bract, 2 gonophores, from *Eltanin* cruise 16, sta 895, S of New Zealand, USNM 61065.

Etymology.—Named in honor of San Diego de Alcala, patron of the University of San Diego, and the sister city in Spain of San Diego, California.

Description.—Polygastric phase (Fig. 1): The anterior nectophore forms a high pyramid, with a height slightly more than twice its width. It is about 5 mm high and 2.2 mm wide, with 5 ridges. The dorsal and 2 lateral ridges reach the apex of the nectophore, but the 2 ventral ridges only reach a point close to the apex.

The hydroecium is not as deep as in *H. maculata*. It extends up to midlength of the nectophore and is closed by the 2 incomplete ventral ridges which are wider at the inferior part. These ridges have crests of roundish contour at the inferior part.

A series of white triangular spots appear on the lateral ridges and the apex of the nectophore. The ventral ridges and the dorsal ridge have no opaque white spots. In *H. maculata* there are 9 of these spots, one at the apex, another at the

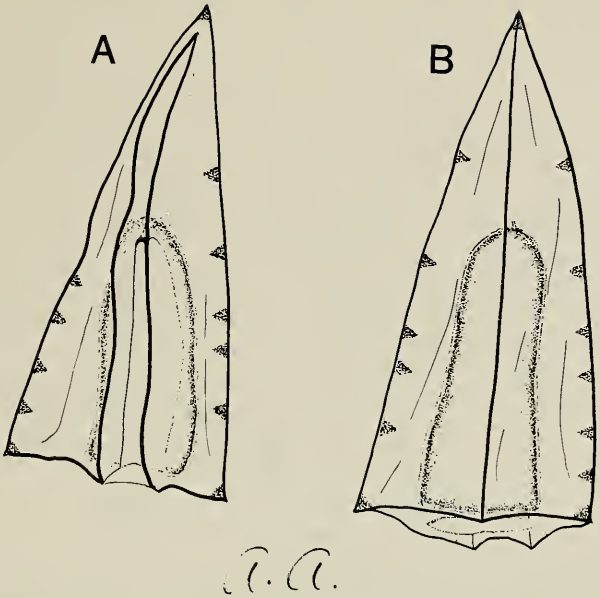


Fig. 1. *Heteropyramis alcala,* nectophore 5 mm high: A, Ventral view; B, Dorsal view.

marginal edge of the lateral ridges, and 2–4 intermediate along those ridges (Totton 1954; Totton and Bargmann 1965).

In *Heteropyramis alcala* the right lateral ridge has 6 opaque white spots, one at the marginal edge, another at midlength of the ridge, 3 about equally spaced between the other 2, and another at midlength of the upper half of the ridge. The left lateral ridge has 7 opaque white spots, one at the marginal inferior corner, another at about midlength of the ridge, and 4 about equally spaced between those 2, plus one at the midpoint of the upper half of the ridge. Another opaque white spot appears at the apex of the nectophore, bringing the total number of opaque white spots to 14.

The nectosac occupies the center of the pyramid, is less than half the width of the nectophore and reaches higher than the midlength of the nectophore. The ostium, opening of the nectosac, is equal in size to the diameter of the nectosac, and the space from the wall of the nectophore to the opening of the nectosac is

Table 1.—Records of *Heteropyramis alcala* in the South Pacific region.

Eltanin cruise	Station	Gear/ tow	Location	Depth	Date	Local time
16	895	MPS[1]	49°17′S, 162°00′E	500–250 m	7 Feb 1965	1110–1124
25	1697	BPS[2]	39°56′S, 85°54′W	1000–500 m	30 Sep 1966	0732–0753
26	1794	BPS	41°58′S, 160°06′E	1000–500 m	7 Dec 1966	1425–1449
26	1803	BPS	47°37′S, 161°49′E	1000–500 m	13 Dec 1966	1052–1112

[1] Multiple plankton sampler.

[2] Bathypelagic plankton sampler.

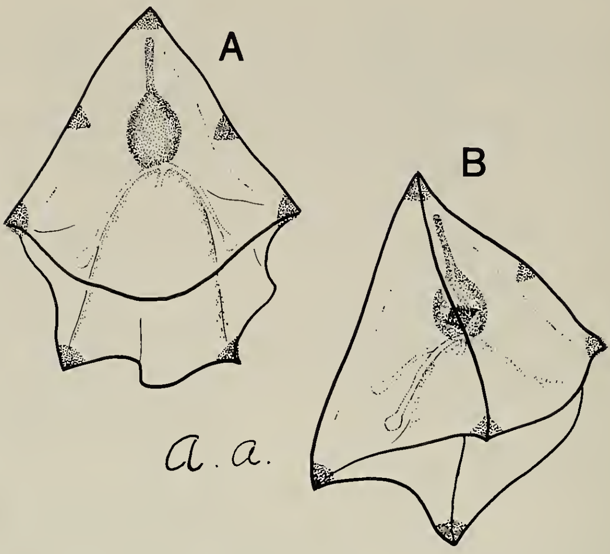


Fig. 2. *Heteropyramis alcala,* bract 3 mm high: A, Dorsal view; B, Left view.

a wide velum. In *H. maculata* the nectosac has a height less than half but more than ⅓ of the nectophore's length.

Eudoxid phase: The bract (Fig. 2) is pyramid-shaped, with 4 triangular sides. It is about 3 mm in height, and 3 mm wide at the base. The ridges of the bract present thin laminar extensions.

White opaque spots in the bract of *Heteropyramis alcala* are distributed as follows: one at the vertex of the bract, one at the base of the ridge of the pyramid, and one at the midlength of each of the 2 ridges which form the dorsal side of the bract. This distribution of the white spots differs from that of *Heteropyramis*

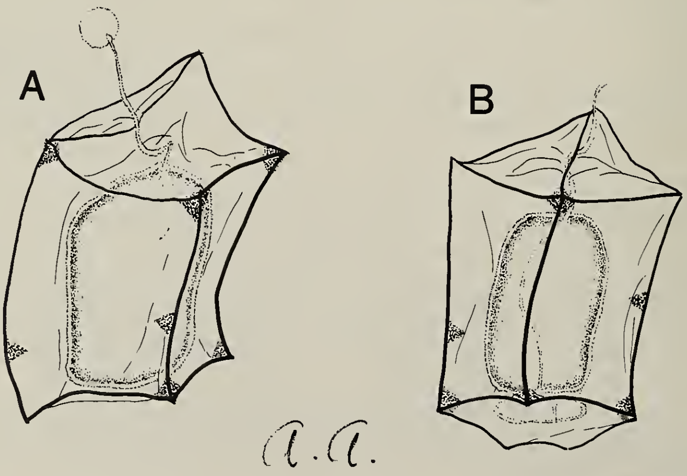


Fig. 3. *Heteropyramis alcala,* gonophore 2.5 mm high: A, Lateral view; B, Dorsal view.

maculata, which displays one apical white spot and one spot at the base of each dorsolateral ridge.

The phylocyst of *Heteropyramis alcala* is in form of a little bottle, quite different from the shape of that of *H. maculata.*

The hydroecial canals are shorter than those of *H. maculata.*

The gonophore (Fig. 3) is pentagonal-prismatic in shape, has 5 ridges, and the top forms a short pyramid. One ridge has opaque white spots at the inferior margin and the upper margin, and the other has 3 equidistant spots along the ridge, from the inferior to the upper margins. Another ridge has one spot at the inferior margin and at midlength of the ridge, and the fourth ridge has one spot at the upper corner and one at the inferior part, at about ¼ of the distance to the inferior margin. The fifth ridge has no opaque white spots.

The closely related species *H. maculata* Moser, 1925 is found mainly in the tropical oceanic regions (Alvariño 1971), and was obtained by Leloup and Hentschel (1938) west of South Georgia Islands.

Thalassophyes ferrarii, new species
Figs. 4–5

Material.—From cruises of R/V *Eltanin* in 1966 (see Table 2). Holotype: 1 superior nectophore and 1 inferior nectophore from *Eltanin* cruise 25, sta 1710, off Chile, USNM 61066. Paratype: 1 superior nectophore and 4 inferior nectophores from *Eltanin* cruise 26, sta 1794, Tasman Sea, USNM 61067.

Table 2.—Records of *Thalassophyes ferrarii* in the South Pacific region.

Eltanin cruise	Station	Gear/ tow	Location	Depth of haul	Date	Local time
25	1710	BPS	42°11′S, 86°03′W	2000–1000 m	5 Oct 1966	2020–2051
26	1794	BPS	41°58′S, 160°06′E	1000–500 m	7 Dec 1966	1425–1449
26	1803	BPS	47°37′S, 161°49′E	1000–500 m	13 Dec 1966	1052–1112

Etymology.—Named for Dr. Frank Ferrari in appreciation of his dedication and encouragement in behalf of plankton studies and his valuable assistance in developing this research.

Description.—Polygastric phase: The superior nectophore (Fig. 4) is about 7 mm high and 2 mm wide, or less than half as wide as its height. It has 5 ridges, all reaching to the apex of the nectophore, and each displaying crests. The crest of the dorsal ridge is the narrowest, and the crests of the ventral ridges the widest; widest at about the posterior third of the nectophore, forming a roundish contour of serrate edges. The lateral ridges have wide crests at the low part of the ridge, close to the ostium, ending at that region in a round edge.

The hydroecium is shallow, reaching less than half the height of the nectophore.

The long narrow nectosac reaches near the top of the nectophore. The space at the lowest part of the nectophore, between the wall of the nectophore and the opening of the nectosac is closed by the velum, which is wide.

In *Thalassophyes crystallina* Moser, 1925, the hydroecium is deep and extends up to more than half the height of the nectophore. The ridges with crests are quite different in *T. crystallina* and *T. ferrarii.* In the former, the crests are narrow or

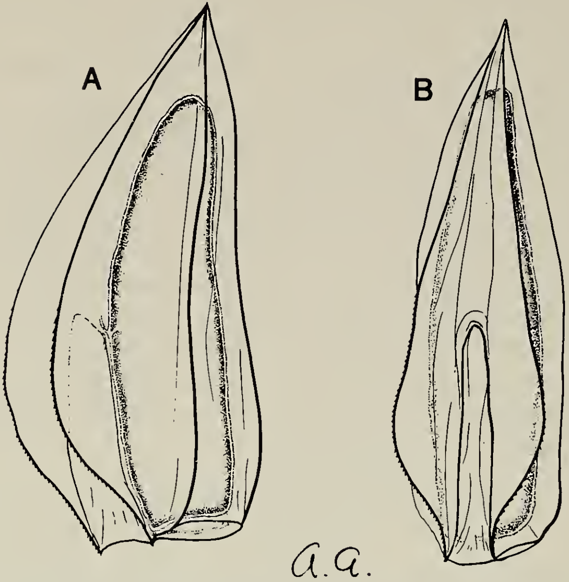


Fig. 4. *Thalassophyes ferrarii,* superior nectophore 7 mm long: A, Lateral view; B, Ventral view.

absent; in the latter they are wide and roundish at the lowest part, presenting serrate edges along the crests of the ventral ridges. The nectosac in *T. crystallina* reaches up to half the height of the nectophore, whereas in *T. ferrarii* it nearly reaches the apex of the nectophore.

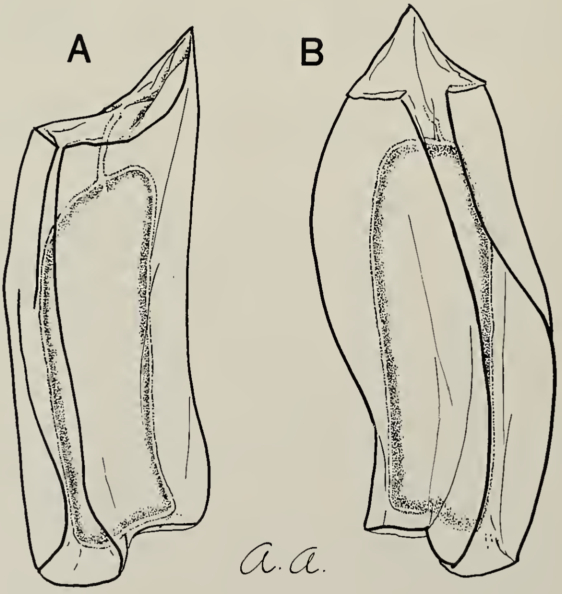


Fig. 5. *Thalassophyes ferrarii,* inferior nectophore 6 mm long: A, Lateral view; B, Ventral view.

The inferior nectophore (Fig. 5) is prismatic with an apical triangular prolongation at the dorsal side. The dorsal ridge has no crest. The lateral ridges develop a wing-like crest at the upper part, diminishing toward the low region, to end with no crest at the ostium level. The ventral ridges are pleated at the top, like two doors or flaps, forming the hydroecial folds, and covering the hydroecial tunnel-like cavity; at the low part, the ridges with crests are united by a round flap extending down from the region of the ostium.

Eudoxid phase: None observed.

The closely related species *T. crystallina* is found mainly in the Antarctic and adjacent regions (Alvariño 1971).

The scarcity and erratic distribution of most of the species of Siphonophorae, Medusae and Chondrophorae is not strange to scholars working on these groups. This peculiar phenomenon, pointed out by Alvariño (1971, 1981), Biggs (1977), Biggs, Bidigare and Smith (1981), and Sears (1953) is due to the particular behavior of these coelenterates. The resulting scattered aggregations of populations, the speed and swimming characteristics enable these animals to avoid capture by plankton nets.

Acknowledgments

We would like to express our appreciation to Drs. Izadore Barret, John R. Hunter, and Reuben Lasker for reading the manuscript. We are grateful to Dr. Frank Ferrari and Dr. Betty Landrum for their valuable assistance in providing additional collections. Special thanks are due to Dr. Thomas E. Bowman and Ms. Martha Brown for their careful editing of the paper.

Literature Cited

Alvariño, A. 1971. Siphonophores of the Pacific, with a review of the world distribution.—Bulletin Scripps Institution of Oceanography, University of California San Diego, La Jolla, California 16:1–432.

———. 1981. Siphonophorae. Atlas del Zooplancton del Atlántico Sud-occidental.—Publicación del Instituto Nacional de Investigación y Desarrollo Pesquero [INIDEP]. Ministerio de Comercio e Intereses Marítimos. Subsecretaría de Intereses Marítimos. Argentina, pp. 383–441.

Biggs, D. C. 1977. Field studies of fishing, feeding and digestion in siphonophores.—Marine Behavior and Physiology 4(4):261–274.

———, R. R. Bidigare, and D. E. Smith. 1981. Population density of gelatinous macro-zooplankton: *In situ* estimation in oceanic surface waters.—Biological Oceanography 1(2):157–175.

Kefferstein, W., and E. Ehlers. 1860. Auszug aus den Beobachtungen über die Siphonophoren von Neapel und Messina angestellt in Winter 1859–60.—Nachrichten von der Gessellschaft, Göttingen (23):254–262.

Leloup, E., and E. Hentschel. 1938. Die Verbreitung der Calycophoren Siphonophoren im Südatlantischen Ozean.—Wissenschaft Ergebnissen der deutschen Atlantischen Expedition auf dem Forschung und Vermessunsschiff "Meteor," 1925–1927, Biologische Sonderuntersuchungen 12(2):1–31.

Lens, A. D., and T. van Riemsdijk. 1908. The Siphonophora of the SIBOGA Expedition.—Siboga-Expeditie, monographie 38:1–130.

Moser, F. 1925. Die Siphonophoren der Deutschen Süd-Polar Expedition 1903–1904. Zugleich eine neue Darstellung der ontogenetischen und phylogenetischen Entwicklung der Calycophoren und Physophoren.—Deutschen Süd-Polar Expedition 17, zool. 9:1–541.

Sears, M. 1953. Notes on Siphonophores. 2. A Revision of the Abylinae.—Bulletin of the Museum of Comparative Zoology at Harvard College 109(1):1–119.

Totton, A. K. 1954. Siphonophora of the Indian Ocean together with systematic and biological notes on related species from other oceans.—Discovery Reports 27:1–161.

———, and H. E. Bargmann. 1965. A synopsis of the Siphonophora.—British Museum of Natural History, pp. 1–250.

(AA) National Marine Fisheries Service, NOAA, Southwest Fisheries Center, P.O. Box 271, La Jolla, California 92038; (KRF) University of San Diego, Alcala Park, San Diego, California 92110.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 693–697

CAECIDOTEA FILICISPELUNCAE, A NEW TROGLOBITIC ASELLID ISOPOD FROM OHIO

Thomas E. Bowman, III, and H. H. Hobbs, III

Abstract.—*Caecidotea filicispeluncae* is described from Fern Cave, Adams Co., Ohio. The endopod of the male pleopod 2 lacks terminal processes except the cannula. Affinities with other *Caecidotea* species are obscure.

Records of troglobitic asellids from Ohio are rare. Fleming (1972:252) listed *Asellus alabamensis* from Cedar Fork Cave, Adams Co. This is very probably a misidentification; as pointed out by Lewis and Bowman (1981:55), the identity of *A. alabamensis* Stafford (1911) is uncertain and its resolution awaits the collection of topotypes. A second record is that of *Caecidotea stygia* Packard from three intermittent streams near Cincinnati, Hamilton Co. (Bowman and Beckett 1978). We report herein the occurrence of a new troglobitic species of *Caecidotea* from Adams Co., southern Ohio.

Caecidotea filicispeluncae, new species
Figs. 1–2

Material.—Ohio, Adams Co., Fern Cave (38°42′23″N, 83°22′06″W). 12 Jun 1980, leg. M. Flynn and H. H. Hobbs, III: 7.5 mm holotype male (USNM 195368); 4 paratypes (USNM 195369), 4.7 mm male, ? mm male (pleon and telson missing), 7.1 mm female (small oostegites), 4.5 mm female (small oostegites). 11 Sep 1982, leg. H. H. Hobbs, III: 3 paratypes (USNM 195370), 6.2 mm female (no oostegites), 5.3 mm female (small oostegites), 4.4 mm female (small oostegites).

Etymology.—From the Latin "filix, -icis" (fern) plus "spelunca" (cave), referring to the type-locality, Fern Cave.

Diagnosis.—Blind, unpigmented. Body narrow, elongate, sides subparallel. Antenna 1 esthete formula 4-0-1. Pereopod 1 proximal palmar process a robust articulated spine; mesial and distal processes unicuspate, narrowly separated, distal process smaller. Pereopod 4 sexually dimorphic. Male pleopod 1 larger than pleopod 2, with short apical setae; lateral margin concave with short distal setae and long proximal setae. Male pleopod 2 endopod tip with subapical cannula, but no other processes. Pleopod 3 exopod apex truncate. Pleopod 4 exopod with single false suture (pattern B of Lewis and Bowman 1981).

Description.—Length of largest specimen, male holotype, 7.5 mm. Sides of body nearly straight; pereonites successively wider, greatest body width 1.7 mm at pereonite 7. Head slightly more than ⅓ wider than long; anterior margin shallowly concave; postmandibular lobes moderately developed. Pereonite 1 subequal in length to pereonites 6 and 7, about ⅓ longer than the subequal pereonites 2–5; coxa visible dorsally on pereonites 5–7. Telson ⅓ longer than wide in female, ½ longer in male; sides subparallel; posterior margin broadly angular in male, with low but distinct caudomedial lobe in female.

Antenna 1 reaching slightly beyond proximal margin of 4th segment of antenna

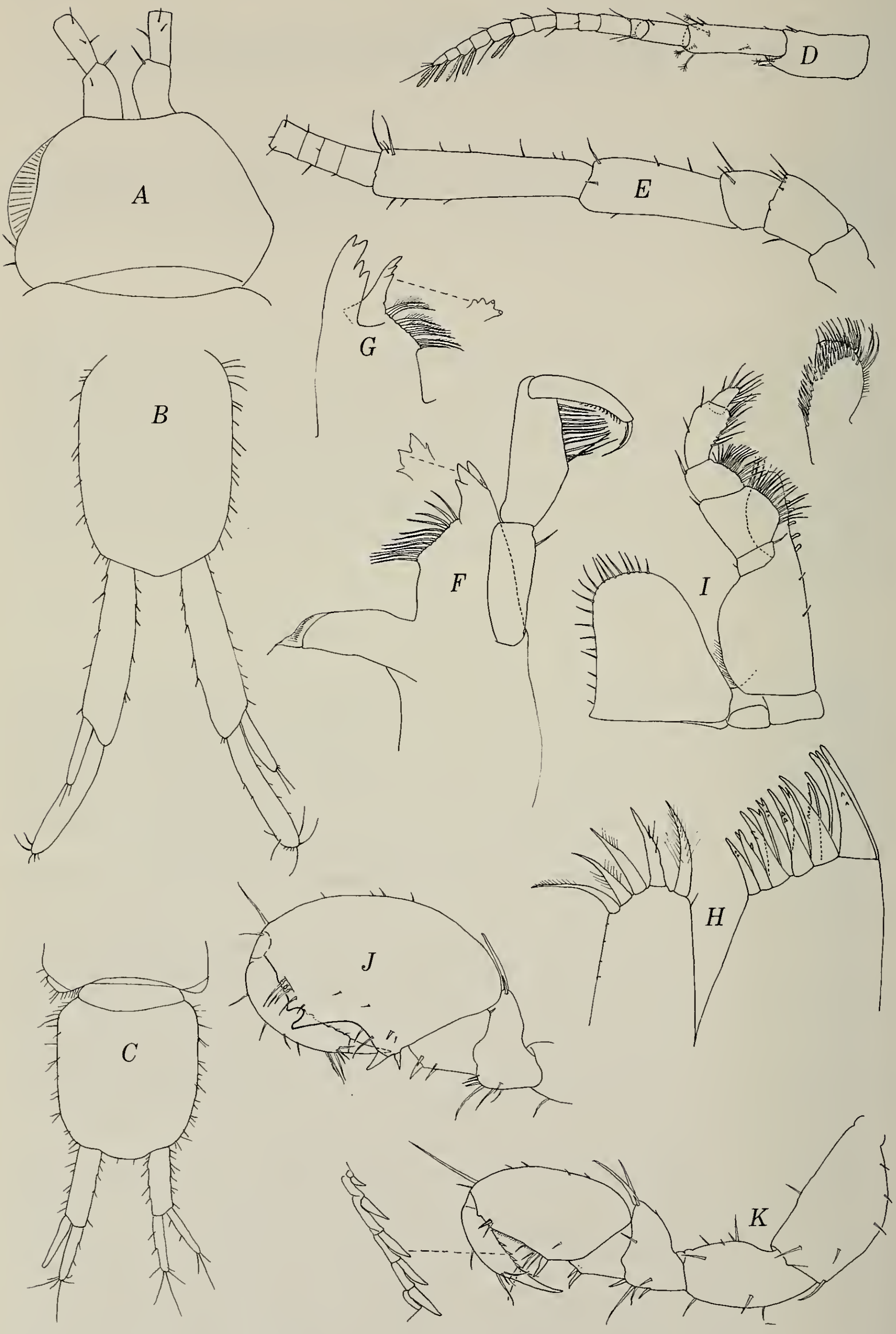


Fig. 1. *Caecidotea filicispeluncae*: *A*, 4.7 mm male; *B*, *D–J*, 7.5 mm male holotype; *C*, 6.2 mm female; *K*, 7.1 mm female. *A*, Head, dorsal; *B*, *C*, Telson and uropods, dorsal; *D*, Antenna 1; *E*, Antenna 2; *F*, *G*, Right and left mandibles; *H*, Maxilla 1; *I*, Maxilliped, with posterior view of endite; *J*, *K*, Pereopod 1.

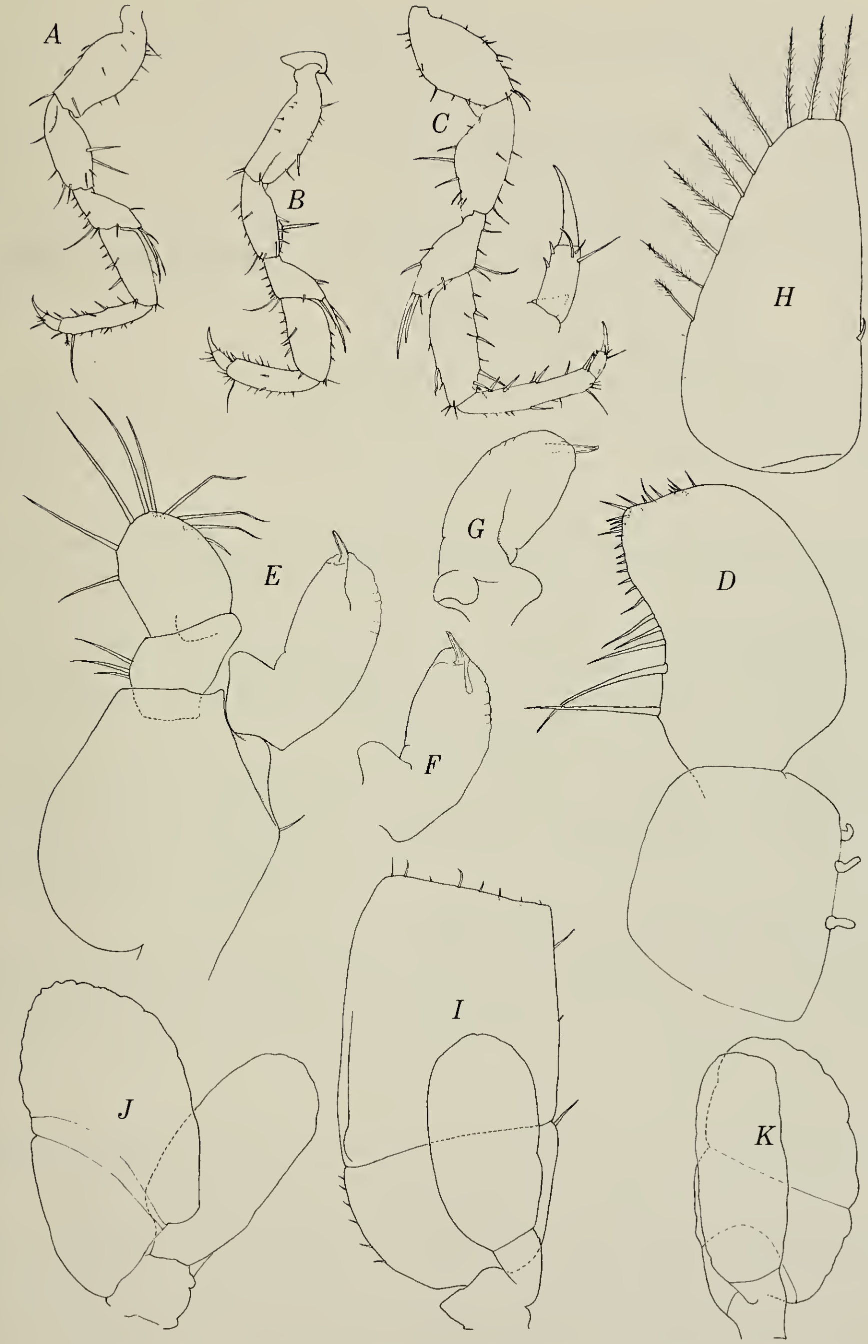


Fig. 2. *Caecidotea filicispeluncae*: *A, H,* 6.2 mm female; *B–G, I–K,* 7.5 mm male holotype. *A, B,* Pereopod 4; *C,* Pereopod 6; *D,* Pleopod 1; *E,* Pleopod 2, anterior; *F, G,* Endopod of pleopod 2, oblique and posterior views; *H,* Pleopod 2; *I,* Pleopod 3; *J,* Pleopod 4; *K,* Pleopod 5.

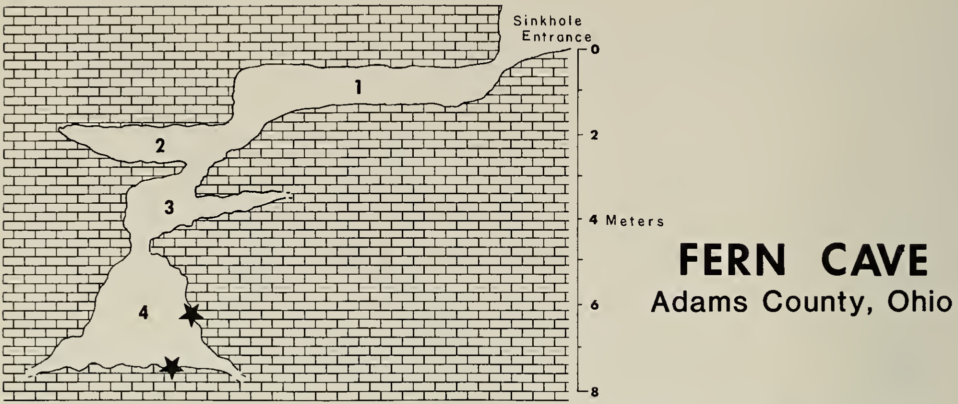


Fig. 3. Fern Cave, vertical profile, showing the 4 levels and the sites (stars) where *Caecidotea filicispeluncae* was collected.

2 peduncle; flagellum with up to 10 segments, esthete formula 4-0-1. Antenna 2 0.8× as long as body (6 mm in holotype); flagellum with up to 41 segments (in holotype).

Mandibles with 4-cuspate incisors and lacinia; spine-row with 9 and 12 spines in left and right mandibles. Maxilla 1 with 5 and 13 apical spines on inner and outer lobes, as in other species of *Caecidotea.* Maxilliped with 5 retinacula on right and left members, endite densely setose.

Male pereopod 1 propus about 0.6 as wide as long; palm defined by robust articulated spine representing proximal process; mesial process oblique, triangular, its pointed apex slightly distal to midlength of palm; separated by narrow U-shaped cleft from shorter distal process. Female pereopod 1 propus smaller, mesial and distal processes absent, palm armed with dense fringe of setules; dactyl with row of oblique teeth on flexor margin.

Pereopod 4 sexually dimorphic, modified in male for clasping female during amplexus. Femur narrow and with smaller muscles, presumably since function of limb in ambulation is reduced. Carpus and propus shorter and wider to accommodate larger muscles used in clasping female; spines on flexor margins reduced for more efficient clasping.

Male pleopod 1 protopod with 3 retinacula; endopod about ⅔ as wide as long, medial margin convex, apical margin slightly convex, armed with short naked setae, lateral margin concave for half its length in central part, armed with naked setae, setae on distal part short, those on proximal part long.

Male pleopod 2, protopod with 1 medial seta, exopod proximal segment with 3 lateral setae, distal segment oval, ¼ longer than wide, with 9 marginal setae; endopod with rounded lateral basal apophysis, tip with moderately long, narrow cannula arising subapically medial to fissure, distal third of medial margin with raised striae. Female pleopod 2 with about 10 plumose marginal setae and a curved spine at proximal third of medial margin. Pleopod 3 with about 8 setae on truncate distal margin. Pleopod 4 exopod pattern B, without proximal spines.

Uropods of male holotype nearly ⅓ longer than telson; peduncle nearly ¼ longer than exopod; rami linear, exopod about twice as long as endopod, latter narrower than exopod.

Relationships.—The combination of three characters sets *C. filicispleluncae* apart from all known species of *Caecidotea.* (1) Male pleopod 1 with short apical setae and concave lateral margin with long setae proximally. At least nine species share this character. (2) Male pleopod 2 endopod tip with cannula, but no other processes. None of the above nine species share this character. (3) Pleopod 4 with single false suture. Three of the nine species agree; pleopod 4 is undescribed for four of the nine species.

Further discussion of relationships at this time would be fruitless, since so many species of *Caecidotea* are inadequately known.

Habitat

Fern Cave is located in SE Adams Co. (38°42′23″N, 83°22′06″W). The cave is small (total horizontal length 18 m), yet it consists of four levels, making it vertically one of the most complex caves in Ohio. The passages are developed in dolomite (Peebles Formation of the Niagaran Series).

The entrance to Fern Cave opens from the bottom of a prominent sinkhole east of Blue Creek Road between Southdown Fork and Copperas Rock Hollow, at an elevation of 230 m. The cave name is derived from the dense growth of Christmas ferns (*Polystichum acrostichoides*) within the sinkhole. There is no stream in the cave, but it is a "wet" cave because of the considerable drip input and the presence of small rimstone pools. The location of the entrance at the bottom of a sinkhole suggests that the cave receives water draining into the sink. There is no significant development of speleothems in Fern Cave.

Caecidotea filicispeluncae occurs in the lowest (fourth level) of Fern Cave. Water trickles down the southeastern wall of the terminal room, resulting in a flowstone coating and several small mini-rimstone pools. *Caecidotea filicispeluncae* occurs in these pools and also on the floor of the room among gravel and allochthonous debris (see stars in Fig. 3).

Some physicochemical data were taken from cave water on 16 April 1963. The water had been diluted by heavy runoff from recent rains, but the following results were obtained: Temperature 10.5°C; O_2 10.9 mg/l; Specific conductance 142 μmhos/cm; pH 7.4; Iron 0.78 mg/l; PO_4-P 0.17 mg/l; NO_3-N 2.4 mg/l; Methyl orange alkalinity 2.4 meq; Total hardness 110 mg/l $CaCO_3$.

Literature Cited

Bowman, Thomas E., and David C. Beckett. 1978. A redescription of the troglobitic isopod, *Caecidotea stygia,* from the environs of Cincinnati, Ohio (Crustacea: Isopoda: Asellidae).—Proceedings of the Biological Society of Washington 91(1):294–302.

Fleming, Laurence E. 1972. The evolution of the eastern North American isopods of the genus *Asellus* (Crustacea: Asellidae). Part I.—International Journal of Speleology 4:221–256.

Lewis, Julian J., and Thomas E. Bowman. 1981. The subterranean asellids (*Caecidotea*) of Illinois (Crustacea: Isopoda: Asellidae).—Smithsonian Contributions to Zoology 335: 1–66.

Stafford, Blanche E. 1911. A new subterranean freshwater isopod.—Pomona Journal of Entomology 3(3):572–575.

(TEB) Department of Invertebrate Zoology (Crustacea), NHB 163, Smithsonian Institution, Washington, DC 20560; (HHH) Department of Biology, Wittenberg University, Springfield, Ohio 45501.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 698–714

PYCNOGONIDA OF THE WESTERN PACIFIC ISLANDS
II. GUAM AND THE PALAU ISLANDS

C. Allan Child

Abstract.—Nine species of Pycnogonida are reported from the western Pacific islands of Guam, Saipan, and the Palau Islands. These are: *Ammothella tippula,* new species, and *Anoplodactylus chamorrus,* new species, both from Guam; *Achelia nana* (Loman) from Saipan; and *Achelia* sp., *Ammothella elegantula* Stock, *Tanystylum rehderi* Child, *Anoplodactylus pycnosoma* (Helfer), *Anoplodactylus* sp., *Callipallene novaezealandiae* (Thomson), *Seguapallene micronesica,* new species, and *Austrodecus palauense,* new species, from the Palau Islands. No particular distributional patterns can be discerned because of the scarcity of records from islands of the western Pacific.

This is the second report in a series on the virtually unknown pycnogonids of the Western Pacific islands. In it are described two new species, *Ammothella tippula* and *Anoplodactylus chamorrus,* from Guam in the Marianas, and six species, two of which are new; *Seguapallene micronesica,* and *Austrodecus palauense,* plus at least three species identified only to genus for lack of appropriate material, from the Palau Islands in the western Carolines. A single record from Saipan Island in the Marianas is included here to complete the records for all specimens known to me.

There are no pycnogonid records to my knowledge from the Marianas and only two records from the Caroline Islands, both from Stock's (1968:10, 49) report on the collections made by the *Galathea* and the *Anton Bruun.* One records Hilton's *Ammothella pacifica* from Ifaluk Atoll, and the other is a record of *Anoplodactylus digitatus* (Böhm) from Koror, Palau Islands. Neither species was found among the specimens reported herein. Little microfaunal sampling has been done in Micronesia, Polynesia, or Melanesia, and it is safe to say that many new species of the small littoral and shallow-water genera remain to be discovered among these hundreds of islands and atolls.

Few distributional patterns are worthy of note, mainly due to the scarcity of collecting records for pycnogonids throughout the islands of the entire Pacific basin. The majority of known species reported herein have been collected at other Pacific island localities or at least from several Indo-Pacific localities. *Achelia nana* (Loman) has been recorded in Indonesia in addition to the Philippines and Japan. *Ammothella elegantula* Stock is known from the Straits of Malacca and *Tanystylum rehderi* was recorded from the Society Islands. *Anoplodactylus pycnosoma* (Helfer) has been recorded from Japan to Madagascar and from a number of intermediate localities, while *Callipallene novaezealandiae* (Thomson) has recently been noted at Enewetak Atoll, Marshall Islands (Child 1982:277), and was known previously from New Zealand, Australia, and off East Africa.

The new species have their closest affinities with related species of the Pacific basin, as would be expected. *Ammothella tippula* is closest to *A. pacifica* Hilton, noted above from Ifaluk, Caroline Islands, along with other Indo-Pacific distribution. *Anoplodactylus chamorrus* is closest to two other compact species; *A. derjugini* Losina-Losinsky, from the Sea of Japan, and *A. compactus* Hilton, a species from the California coast and islands. *Seguapallene micronesica* has no close distributional relations as the genus is known only from one other species in the subantarctic Îles Crozet of the Indian Ocean. *Austrodecus* is a predominantly Subantarctic and Antarctic genus, but with a proposed "corridor" of species carrying north from New Zealand and the Kermadec Islands to Japan. The closest morphological relation to *A. palauense,* new species, is *A. elegans* Stock, a species known only from the subantarctic Prince Edward Islands. It is less closely related to its New Zealand, Kermadec, and Japanese congeners. There is therefore no particular pattern to the distribution of the species in this report except perhaps a reinforcement to the congeneric corridor theory for *Austrodecus.*

The specimens in this report originated from the George Vanderbilt Foundation (Stanford University, California) Expedition to the Palau Islands, sponsored by the U.S. Office of Naval Research (G.V.F.), a short survey trip to Guam and Palau by J. L. Barnard and the author, and from the Bernice P. Bishop Museum (BPBM), Honolulu, Hawaii. All specimens except the Bishop specimen are deposited in the U.S. National Museum of Natural History under the catalog numbers of the old U.S. National Museum (USNM).

Family Ammotheidae

Achelia nana (Loman)

Ammothea nana Loman, 1908:60–61, pl. 1, figs. 1–13.
Achelia nana.—Stock, 1953a:300–301, fig. 14; 1954:97; 1965:14–15, figs. 1–3; 1968:16; 1974:13–14.—Utinomi, 1971:329–330.

Material examined.—Saipan, from test block immersed in sea 90 days, 24 Feb 1950, 1 ♂ (BPBM).

Remarks.—There is little difference between this specimen and published figures of males. There is a hint of a segmentation line between the first and second trunk segments, but none between the second and third. The sixth oviger segment has the strong recurved spine mentioned by Stock (1965:15).

This specimen extends the distribution slightly to the east from the known Indo-West-Pacific habitats of *Achelia nana.*

Achelia, species indeterminate

Material examined.—Palau, SE Koror Island, Iwayama Bay, E side of mouth of Raki-Swido (Oyster Pass), from sponge in 2 to 15 ft. (0.6–4.6 m), 7°18′57″N, 134°30′09″E, 22 Oct 1955, G. V. F. sta 220A, 1 juvenile. Palau, Koror Island, sea reef inside cove next to cave at SE end of Island, wash of 4 kinds of sponges in 0.1 m, 2 Jul 1974, J. L. Barnard, 1 ♀.

Remarks.—The juvenile specimen has some characters of *Achelia assimilis* (Haswell), but this variable species demands an adult with a full set of characters for assignment. The female from the cave cove is possibly a new species. The trunk is semi-triangular in dorsal aspect and has no tubercles except at the anterolateral corners of the cephalic segment. The first coxae have 2 small laterodistal

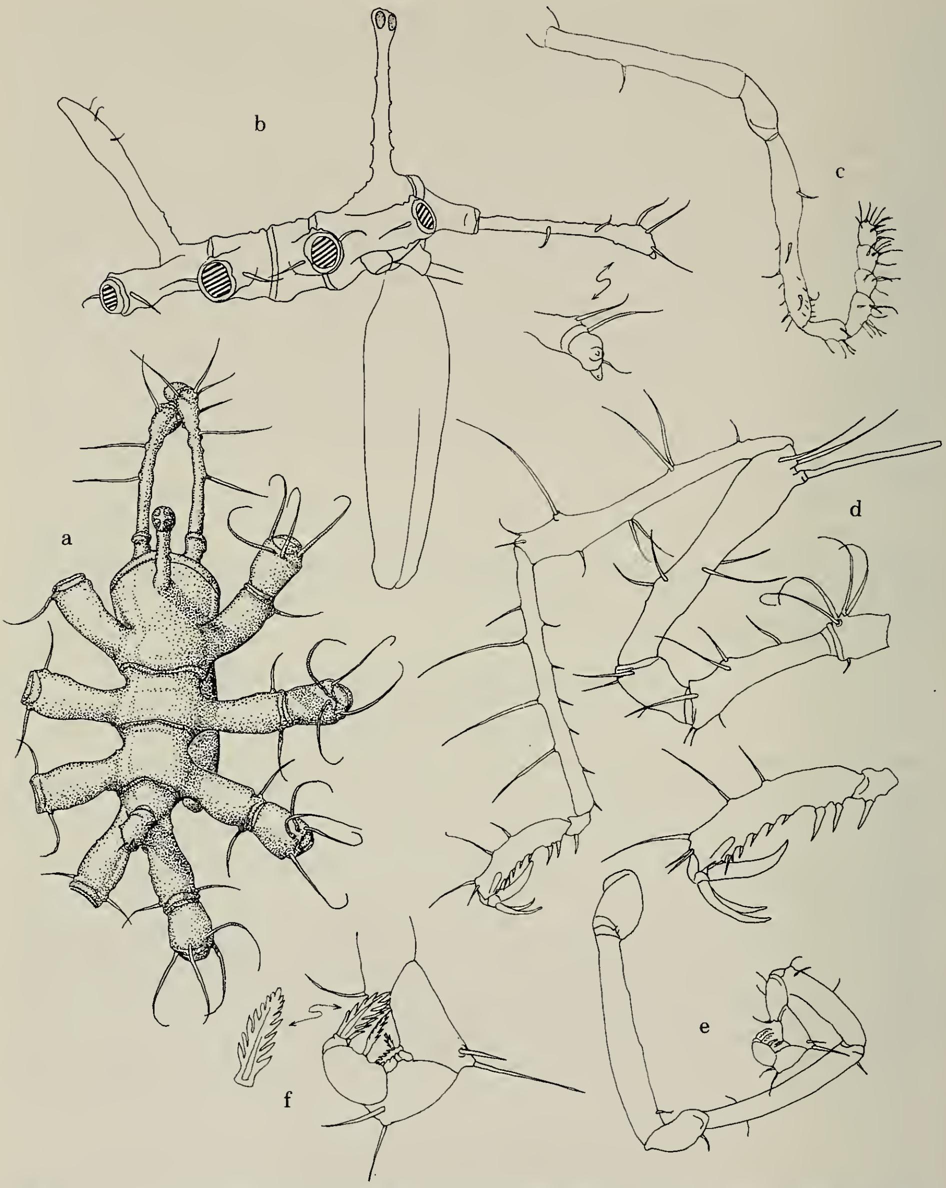


Fig. 1. *Ammothella elegantula,* male: a, Trunk, dorsal view; b, Trunk, lateral view, with distal chelifore enlargement; c, Palp; d, Third leg, with distal segments enlargement; e, Oviger; f, Strigilis, with terminal denticulate spine enlarged.

tubercles, but the trunk and appendages are otherwise without tubercles. The distal 4 palp segments are almost circular in outline and the second segment is only twice as long as its diameter. Without a male, I refrain from naming this specimen rather than add another name to this confusing group of extremely variable species.

Ammothella elegantula Stock
Fig. 1

Ammothella elegantula Stock, 1968:11–12, fig. 2a–c.

Material examined.—Palau, Koror Island, sea reef inside cove next to cave at SE end of island, wash of 4 kinds of sponges in 0.1 meter, 2 Jul 1974, J. L. Barnard, 1 ♂, 2 larvae.

Remarks.—This very distinctive species is reported here only for the second time. It was described from a juvenile specimen taken in the Straits of Malacca in 77 meters. The present material fortunately includes a male from which the adult characters may be described.

The chelae, as in all adults of *Ammothella,* are reduced to rounded knobs having 2 short stubs as fingers. The ocular tubercle does not have the 2 posterior tubercles of the type-specimen, but has many tiny low papillae over most of its surface. The abdomen does not have any of the long setae or tubular spines common to species of this genus, but has a few short distal setae. The setae of the lateral processes and first coxae are distinctive. They are longer than the segment diameter and occur distally on the posterior of the first lateral processes and on the anterior and posterior of the remaining 6 lateral processes. Those of the first coxae are longer, fully twice the segment diameter or slightly longer, and are 4 in number, placed dorsodistally.

In the adult, palp segments 2 and 4 are subequal and are the longest segments. Segments 5 and 6 are twice as long as wide and subequal in length, and the terminal 3 segments are small, only slightly longer than wide.

The male oviger is typical of *Ammothella*; second segment longest, fourth segment slightly shorter, fifth about two-thirds the length of the fourth, the seventh with a slight distal apophysis bearing 2 long setae ectally and 1 denticulate spine endally, eighth and ninth with 1 denticulate spine each, and tenth a tiny segment bearing 2 larger denticulate spines having 5 to 8 marginal serrations.

The leg is long and very slender, as described, and has a few very long setae per segment, some 4 or 5 times longer than the segment diameter. The femur and first tibia are swollen distally, or club-shaped, while the second tibia is cylindrical. The cement gland appears as a dorsodistal tube over twice as long as the femur diameter. The terminal leg segments agree very much with those of the juvenile with 2 heel spines and a similar tarsus spine. The second tibia is slightly shorter than the first in the adult and the femur is slightly shorter than either tibia. Most other measurements differ only slightly from the juvenile holotype.

The capture of this species in Palau extends its distribution well out into the Western Pacific islands from the Straits of Malacca, and its depth range is extended from 77 meters to the littoral.

Ammothella tippula, new species
Fig. 2

Material examined.—Guam, Anae Island, just E in deep channel, wash of coralline and other algae from 11 m, 13°21′25″N, 144°38′20″E, C. A. Child, 27 Jun 1974, 1 ♂ holotype (USNM 195374), 1 ♀, 1 juvenile paratypes (USNM 195375).

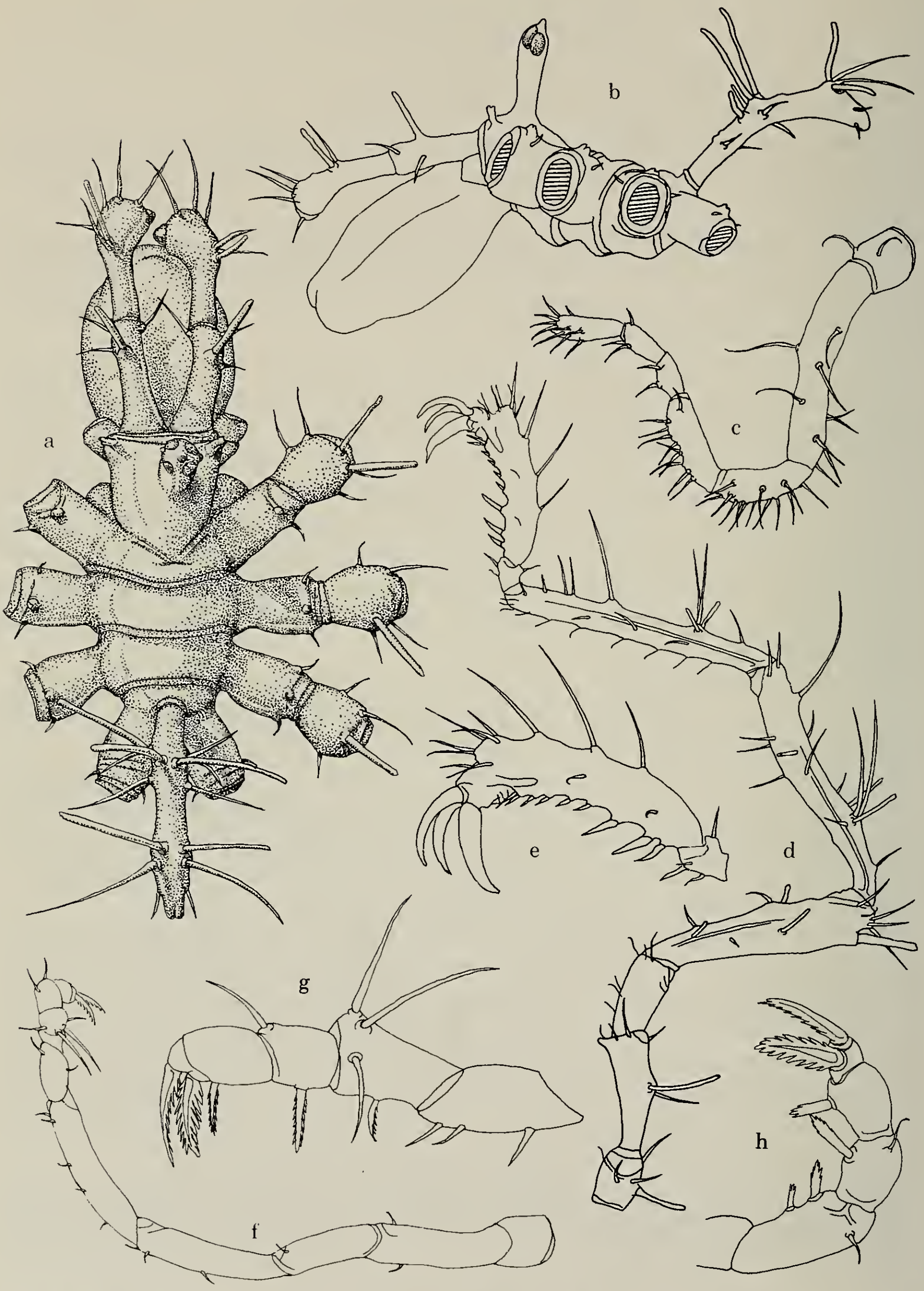


Fig. 2. *Ammothella tippula,* holotype male: a, Trunk, dorsal view; b, Trunk, lateral view; c, Palp, distal 7 segments; d, Third leg; e, Terminal segments of third leg enlarged; f, Oviger; g, Strigilis. Female: h, Strigilis.

Description.—Very small, holotype leg span slightly more than 5 mm. Trunk broad, robust, fully segmented, without median tubercles or spines, armed with 2 small slender anterolateral tubercles on ocular segment. Lateral processes 1.5 times longer than wide, separated by half their diameters or less, armed with tiny low dorsodistal tubercles bearing papillae and short distal setae on posterior and anterior of all lateral processes except first where anterior setae are missing. Ocular tubercle tall, over 3 times taller than maximum diameter, swollen at apex with large darkly pigmented eyes, capped with tiny papilla. Abdomen a long posterior-curing cylinder with median and distal swellings armed with 2 groups of very long tubular spines and 2 very long distal setae, 2 short median setae and 2 short laterodistal setae.

Proboscis ovoid, massive, with broad flat lips having ventral cleft just distal to marked constriction.

Chelifores 3-segmented, robust, almost as long as proboscis, second segment only slightly longer than first. First segment armed with long dorsal tubular spine and 3 lateral and distal setae. Second segment armed with long dorsal tubular spine, 1 long seta of equal length just proximal to spine, and 5 long dorsodistal and laterodistal setae, each longer than segment diameter. Chela small, ovoid, vestigial, with crease for movable finger.

Palp 9-segmented, slender, segments 3 to 9 increasingly setose distally. Segment 2 little longer than segment 4, both armed with several lateral and ventrodistal setae longer than segment diameter; segments 5 and 6 subequal, over 3 times longer than their diameter; segment 7 shortest, less than twice longer than its diameter; segment 8 twice its diameter in length; terminal segment slightly less than 3 times longer. Most setae longer than segment diameter.

Oviger 10-segmented, segments 2 and 4 subequal, segment 5 slightly longer. Seventh segment swollen distally with apophysis bearing 3 long setae. Seventh, eighth and ninth segments armed with single denticulate spine each, bearing many marginal denticulations. Terminal segment tiny, wider than long, armed with 2 denticulate spines larger than preceding ones.

Third leg: first coxa armed with 2 long tubular spines on first pair of legs, 1 similar spine on posterior 6 legs, 2 dorsodistal long setae and 1 lateral short seta on anterior and posterior of all first coxae. Coxa 2 with dorsal bulge bearing 1 long tubular spine and 1 long seta, several setae distally. Coxa 3 with several ventral and ventrodistal setae. Femur shorter than tibiae, armed with 4 lateral long tubular spines and 2 long lateral setae, ventrally with 2 short setae, and distally with 4 or 5 long setae. Cement gland tube dorsodistal, longer than segment diameter, inserted on low tubercle. Tibia 2 slightly longer than tibia 1, both armed with 2 dorsal long tubular spines, 2 long setae proximally and 1 long seta distally measuring more than 3 times segment diameter, several short lateral setae and 2 or 3 tubular spines, and several short ventral setae. Tarsus tiny, armed with 1 dorsal, 2 lateral, and 1 ventral setae and 1 ventrodistal spine. Propodus moderately slender, well curved, without heel but with 3 large heel spines and 5 or 6 small sole spines, dorsally armed with several setae longer than segment diameter and few short distal setae. Claw moderately long, slightly curved with well curved auxiliaries only slightly shorter than main claw.

Female (paratype) at least 25 percent larger in all measurements except oviger which is smaller than that of male. Oviger segment lengths similar to male but strigilis without seventh segment apophysis and setae. Denticulate spines arranged 2:1:1:2 from seventh to tenth segments. Fewer tubular spines on most appendages.

Measurements of holotype (in mm).—Trunk length (chelifore insertion of tip 4th lateral processes), 0.51; trunk width (across 2nd lateral processes), 0.46; proboscis (laterally), 0.39; abdomen (laterally), 0.38; 3rd leg: coxa 1, 0.13; coxa 2, 0.23; coxa 3, 0.16; femur, 0.44; tibia 1, 0.48; tibia 2, 0.51; tarsus, 0.07; propodus, 0.27; claw, 0.11.

Distribution.—Known only from the type-locality, Anae Island, Guam, in 11 m.

Etymology—The species name is Latin and refers to a water spider. It is sometimes spelled *tipula.*

Remarks.—There are a number of *Ammothella* species which share many characters with *A. tippula,* all of which appear to form a discrete species group within the genus: the *appendiculata* group. The Pacific members of this group are *A. appendiculata* (Dohrn), *A. indica* Stock, *A. pacifica* Hilton, *A. schmitti* Child, *A. dawsoni* Child and Hedgpeth, *A. spinifera* Cole, *A. symbius* Child, *A. setacea* (Helfer), and *A. elegantula* Stock. These species are all characterized by having a more or less slender appearance, long abdomen, slender legs bearing long setae and sometimes long spines, long chelifores with long setae or spines, fairly long ocular tubercle, and typical terminal leg segments with long claws. Most of these species bear some form of tubular, clubbed, or spatulate spines on the appendages, and it is often the presence or absence of these "special" spines that distinguishes a particular species. In relating these species to *A. tippula, A. elegantula* (reported on elsewhere in this report) is probably the most distantly related due to its lack of tubular spines, its very long slender proboscis, chelifores and ocular tubercle, and other dissimilar arrangements of setae and spines. The very long ocular tubercle and slender proboscis also disqualify *A. setacea* as a close relation. In addition, *A. setacea* has very long tubular spines on the cephalic segment and lateral processes, unlike *A. tippula.*

The remaining species all have a long curved abdomen bearing long setae, and most also have the long abdominal tubular spines as in *A. tippula,* but *A. appendiculata, A. indica,* and *A. symbius* have first scape segments much shorter than the second, unlike *A. tippula,* and have other characters such as spine arrangement which disagree with those of the new species. *Ammothella spinifera* has middorsal tubular spines on the trunk (in most but not all specimens) and tall slender lateral process tubercles unlike *A. tippula. Ammothella dawsoni* has many more spines on the chelifores and has many bristled or plumose spines on the appendages which are not found on *A. tippula,* while *A. schmitti* has similar plumose spines in a different arrangement, a short ocular tubercle and more robust propodus with shorter claws.

The closest relation to *A. tippula* is *A. pacifica,* another Pacific island species. The new species differs from *A. pacifica* in having small tubercles at the anterolateral corners of the ocular tubercle, tiny low lateral process tubercles, three heel spines instead of four, an ocular tubercle placed well posterior to the rim of the ocular segment instead of adjacent to the rim, and a generally more robust appearance. The size of these two species offers further contrast. The leg span of an adult male of *A. pacifica* is 8.24 mm, while that of *A. tippula* is only 5.26 mm.

Ammothella pacifica is known from several localities in the Indo-West Pacific, including the Caroline Islands at Ifaluk Atoll, and is very close to the new species in spination and the segment lengths of its appendages.

Tanystylum rehderi Child

Tanystylum rehderi Child, 1970:302–306, fig. 5.

Material examined.—Palau, 8 mi NW of Koror, on inner margin of barrier reef, 7°24′30″N, 134°21′18″E, from octocoral *Clavularia* sp., with sand and coral in 1–2 m, 19 Jul 1955, G.V.F. sta 25-865, 2 ♂ with eggs, 1 ♀, 1 juvenile.

Remarks.—These specimens differ little from the type-specimens, 2 males from Bora Bora and Moorea, Society Islands. The ocular tip tubercle is a larger cone in the Palau specimens. Most of the other tubercles and segment lengths agree with the types.

The female was unknown until this Palau record. The lateral process and the first coxa tubercles are reduced in the female and those of the first coxa anterior are not bifurcate as in the male. The female oviger is typical of the genus and has spines which are only distally denticulate on the terminal 3 segments in the ratio 1:1:2.

This species is related to *Tanystylum acuminatum,* as discussed by Child (1970: 305), but the shape of the proboscis is quite different in *T. rehderi,* being a low-shouldered, long-necked bottle shape, while in *T. acuminatum,* the proboscis is like a broad oval flask having a narrow and shorter neck.

The Palau specimens extend the distribution of *T. rehderi* from the Society Islands westward to the western Caroline Islands and increase its depth range to 2 meters from the intertidal of the type-specimens.

Family Phoxichilidiidae

Anoplodactylus chamorrus, new species
Fig. 3

Material examined.—Guam, Anae Island, just E in deep channel, wash of coralline and other algae from 11 m, 13°21′25″N, 144°38′20″E, C. A. Child, 27 Jun 1974, 1 ♂ holotype (USNM 195376).

Description.—Very small, leg span slightly less than 4.5 mm. Trunk unsegmented, robust, broadly oval in dorsal aspect. Lateral processes touching proximally, slightly separated distally, little longer than their diameters, each armed with single low, broad, dorsodistal tubercle, glabrous. Ocular tubercle short, cylindrical proximally, a rounded cone distally, with large darkly-pigmented eyes at tubercle midlength. Neck short, narrow, glabrous. Abdomen erect, cylindrical, tapering distally to rounded point, armed with 2 posterolateral short setae.

Proboscis ovoid with slight proximal constriction, tapering distally to flat lips.

Palps represented by tiny buds on anterior of first lateral processes.

Chelifores robust, overhanging proboscis, scape armed with several short lateral and distal setae. Chela palm longer than fingers, oval, armed with 3 or 4 endal and ectal setae. Fingers short, well curved, without teeth, armed with 2 or 3 short setae ectally on movable finger.

Oviger moderately long, first segment broad, distal half with anterior expansion,

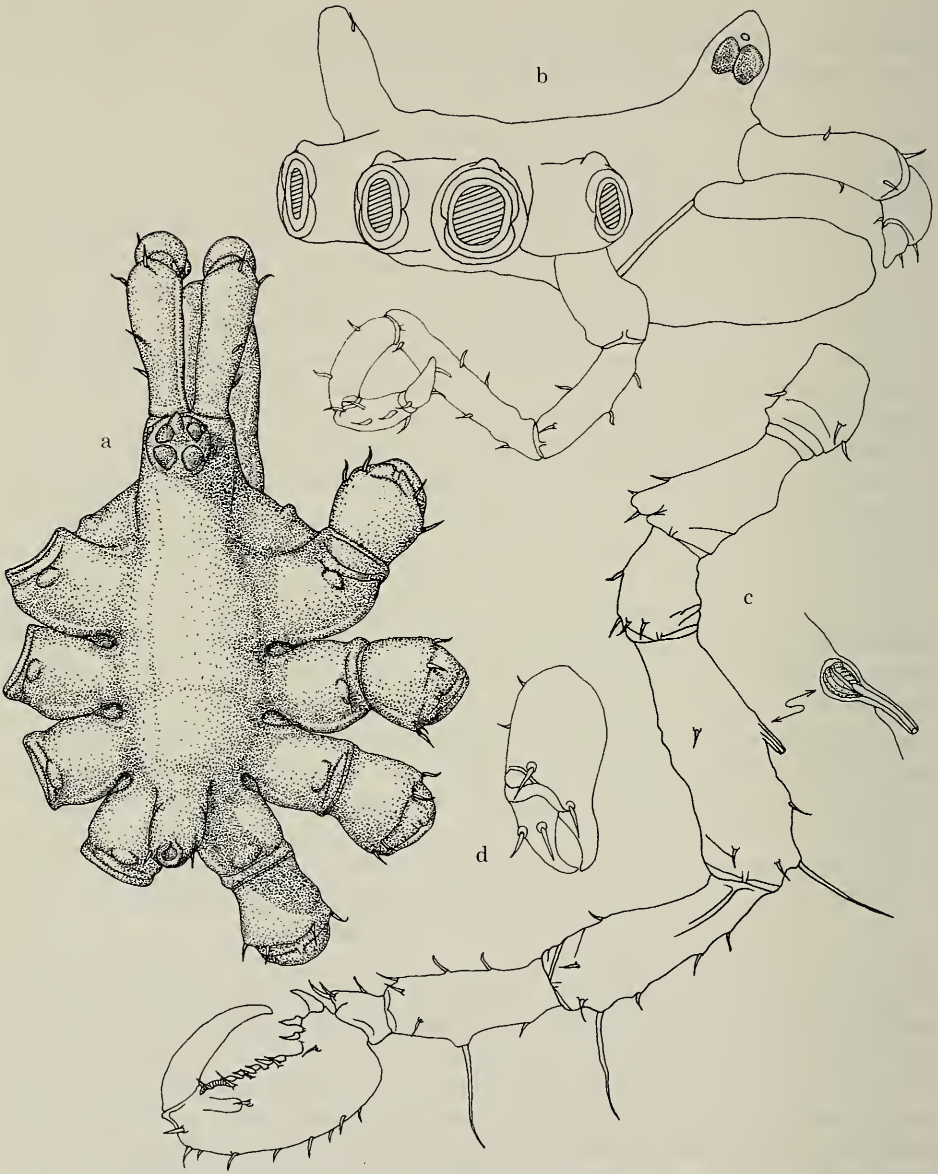


Fig. 3. *Anoplodactylus chamorrus,* holotype male: a, Trunk, dorsal view; b, Trunk, lateral view, with oviger attached; c, Third leg, with cement gland enlarged; d, Chelifore.

third segment longest, about 1.2 times as long as second segment, both second and third armed with several short setae. Strigilis with few setae; fourth with 2 or 3 ectal setae, fifth with 6 or 7 recurved short setae, terminal segment a curved cone with 3 or 4 short setae.

Leg moderately short, robust, armed with 1 dorsodistal seta almost twice as long as segment diameter of each major segment, few short setae on all segments. Femur longest segment, single cement gland a small oval terminating in slender distally-pointing tube about 0.3 as long as segment diameter. Second coxa with small ventral sexual spur not extending beyond distal end of segment, terminating in tiny sex pore. Tarsus semi-rectangular, without long ventrodistal extension, armed with 2 ventral setae. Propodus robust, with marked heel bearing 1 heel spine and 2 smaller spines, sole straight, armed with 5 curved spines, several tiny setae and small propodal lamina only 0.25 as long as sole. Claw massive, moderately curved, auxiliaries absent.

Measurements of holotype (in mm).—Trunk length (chelifore insertion to tip 4th lateral processes) 0.6; trunk width (across 1st lateral processes), 0.45; proboscis (lateral), 0.38; abdomen (lateral), 0.15; third leg: coxa 1, 0.12; coxa 2, 0.28; coxa 3, 0.13; femur, 0.35; tibia 1, 0.3; tibia 2, 0.22; tarsus, 0.08; propodus, 0.29; claw, 0.19.

Distribution.—Known only from the type-locality, Anae Island, Guam, in 11 meters.

Etymology. Named for the ancient settlers of Guam and the Mariana Islands, the Chamorros, whose friendliness is immediately evident to modern travellers in these islands.

Remarks.—This tiny species resembles several other *Anoplodactylus* species having crowded lateral processes, short neck, and short robust legs. These are; *A. anarthrus* Loman, *A. aragaoi* Sawaya, *A. arescus* d-B. R. Marcus, *A. compactus* (Hilton), *A. derjugini* Losina-Losinsky, *A. haswelli* (Flynn), *A. marcusi* Mello Leitao, *A. minusculus* Clark, *A. tarsalis* Stock, and *A. viridintestinalis* (Cole), several of which were described in the now junior synonym *Halosoma.*

The new species is perhaps least related to *A. minusculus,* which has extremely short oviger segments, a long propodal lamina, and large chela fingers with teeth. The presence or absence of chela teeth is not always a good diagnostic character. Sometimes with a good series of one species, some specimens may not have chela teeth while others will have them. *Anoplodactylus haswelli* has three heel spines, no propodal lamina, a triangular-shaped trunk, auxiliary claws and chela finger teeth, while *A. aragaoi* has slightly separated lateral processes, longer appendage segments, a longer neck, and a longer cement gland tube. This new species is unlike *A. tarsalis* and *A. arescus,* both of which have a projecting tarsus of a long triangular-shape and differing leg segment lengths.

Anoplodactylus chamorrus is more closely related to *A. anarthrus,* except that the proboscis of the latter is smaller and of a different shape, the ocular tubercle is a more rectangular shape, and the cement gland is placed more proximally on the femur. The propodus of *A. viridintestinalis* has a lamina over the full sole and has longer appendage segments than *A. chamorrus.* The figures of *A. marcusi* (Mello Leitão, 1949:167–173, figs. 1–4) are inconclusive in detail, but they show a smaller proboscis, shorter leg segments, and different oviger segment lengths than those of *A. chamorrus.*

The new species appears to be closest to *A. derjugini* and *A. compactus.* The differences are that these two species have a non-tubular cement gland, full propodal lamina, auxiliary claws, and in *A. compactus,* larger lateral process tubercles, and with A. derjugini, a differently shaped chela with longer fingers, different ocular tubercle length, two heel spines, and many more setae on the terminal oviger segment. The combination of characters in *A. chamorrus* are thus unlike those of any known species.

Anoplodactylus pycnosoma (Helfer)

Peritrachia pycnosoma Helfer, 1938:176–177, fig. 7.
Halosoma pycnosoma.—Marcus 1940:45–46.
Anoplodactylus pycnosoma.—Stock 1953:41, fig. 5; 1954:75–77, fig. 33; 1974:16; 1975:132.—Utinomi 1971:326.—Child 1975:20.

Material examined.—Palau, Ngaremediu District, Urukthapel Island, fringing coral reef around first rock cape W of sand beach, 7°15′18″N, 134°26′48″E, on red algae in 0–2 m, 31 Jul 1955, G.V.F. sta 53-980, 1 ♀. Palau, Urukthapel Island, small bay at E end of N shore, around remains of stone pier, 7°15′57″N, 134°26′55″E, in 0.6–1.3 m, 2 Nov 1955, G.V.F. sta 258, 1 ♀.

Remarks.—These two females differ only slightly from the published figures for this species. The lateral processes of the Palau specimens are further apart and the propodus is slightly longer, but the specimens agree in other characters including the brown lines at the trunk segmentation and lateral process-first coxa segmentation.

The Palau Islands are added to the Indo-West Pacific distribution for this species. It is apparently confined to littoral depths.

Anoplodactylus, species indeterminate

Material examined.—Palau, SE Koror Island, Iwayama Bay, E side of mouth of Raki-Swido (Oyster Pass), on sponge in 2–15 ft (0.6–4.6 m), 22 Oct 1955, G.V.F. sta 220A, 7°18′57″N, 134°30′09″E, 1 larva. Palau, SE Koror Island, sea reef inside cove next to cave, 7°18′34″N, 134°30′35″E, wash of 4 kinds of sponges in 0.1 m, J. L. Barnard, 2 Jul 1974, 3 larvae.

Remarks.—There are at least two species represented in the three larvae collected by Barnard, but none of these specimens is of sufficient age to be determined.

Family Callipallenidae

Callipallene novaezealandiae (Thomson)

Pallene novae-zealandiae Thomson, 1884:246–247, pl. 14, figs. 1–4.
Callipallene sp. cf. *C. novaezealandiae.*—Child 1982:277 [literature].

Material examined.—Palau, unnamed islet between Amoi and Eil Malk islands, 7°11′35″N, 134°23′00″E, from hydroid-ascidian-sponge complex in 2 m, C. A. Child, 30 Jun 1974, 2 ♂ with eggs, 1 ♀, 6 juveniles. Palau, SE Koror Island, sea reef inside cove next to cave, 7°18′34″N, 134°30′35″E, wash of 4 kinds of sponges in 0.1 m, 2 Jul 1974, J. L. Barnard, 1 ♀.

Remarks.—These specimens agree in all respects with those reported (Child 1982:277) from Enewetak Atoll. One of the males has more strigilis denticulate spines than the Enewetak specimens, which decreases the gap of differences between these specimens and Thomson's original description of the species. I therefore propose to assign both the Enewetak and the Palau specimens to Thomson's species.

The Enewetak and Palau records extend the previously known distribution of this species from east Africa, Australia and New Zealand, to the northern hemisphere in Micronesia.

Seguapallene Pushkin, 1975

This genus was designated (Pushkin 1975:1404–1405, fig. 2) to contain a species of pycnogonid from the subantarctic Îles Crozet: *Seguapallene insignatus* Pushkin. This species is without palps, has well developed 2-segmented chelifores with regular teeth on the fingers, auxiliary claws, and an oviger with strigilis claw. The principal difference between this species and the new one described herein is teeth on the strigilis claw in the latter, lacking in Pushkin's species.

Seguapallene micronesica, new species

Fig. 4

Material examined.—Palau, SE Koror Island, sea reef inside cove next to cave, 7°18′34″N, 134°30′35″E, wash of 4 kinds of sponges in 0.1 m, 2 Jul 1974, J. L. Barnard, 1 ♂ holotype (USNM 195379), 3 ♀, 2 juveniles, paratypes (USNM 195380).

Description.—Moderately small, male leg span less than 9 mm. Trunk fully segmented, stout, without median tubercles, glabrous. Lateral processes short, not longer than wide, separated by half their diameter or less, glabrous. Neck short, only as long as width of oviger bases. Ocular tubercle implanted over oviger bases, short, rounded, only as tall as basal diameter, with tiny posteromedian bump and small lateral "horn" tubercles slightly longer than their basal widths. Eyes large, darkly pigmented. Abdomen moderately short, not extending beyond first coxae tips of fourth pair of legs, cylindrical anteriorly, tapering posteriorly, armed with pair of posterolateral setae.

Proboscis short, ovoid, tapering to small flat lips, without fringe of oral setae.

Chelifore 2-segmented, scape as long as proboscis, armed with 2 short ectal setae, 2 midlateral setae longer than segment diameter and 2 or 3 dorsodistal setae as long as segment diameter. Chela palm shorter than fingers, armed with several long dorsal and lateral setae. Fingers straight, curved only at tips, armed with short broad teeth, 11 on immovable finger and 10 on movable finger.

Oviger fourth and fifth segments long, fourth 7 times longer than its diameter, fifth over 8 times its diameter, armed with several ectal setae slightly longer than segment diameter. Fifth segment with distal apophysis shorter than segment diameter, armed with distal seta. Four strigilis segments cylindrical, each segment shorter than preceding, armed with denticulate spines having 4 lobes on each margin, arranged in the formula 5:5:4:5, well curved terminal claw bearing 5 large teeth.

Third leg; first coxa armed with anterodistal seta as long as coxa diameter, coxa 2 with 4 lateral setae longer than segment diameter, coxa 3 with several shorter ventral and ventrodistal setae. Femur and tibiae with several long lateral setae and from 1 to 4 longer dorsal setae, longer than twice segment diameter. Cement glands a series of tiny ventral pores along most of femur length. Tibia 2 longest segment. Tarsus quadrilateral, short, armed with 2 ventral setae longer than tarsus diameter. Propodus slender, moderately curved, without heel or heel spines, armed with 5 or 6 sole setae as long as segment diameter and several dorsal and distal setae, dorsodistal 2 over twice propodus diameter. Main claw short, not as long as segment diameter, well curved. Auxiliary claws more than twice main claw length, strongly curved.

Female (paratype) slightly larger in all measurements. Oviger segments 4 and

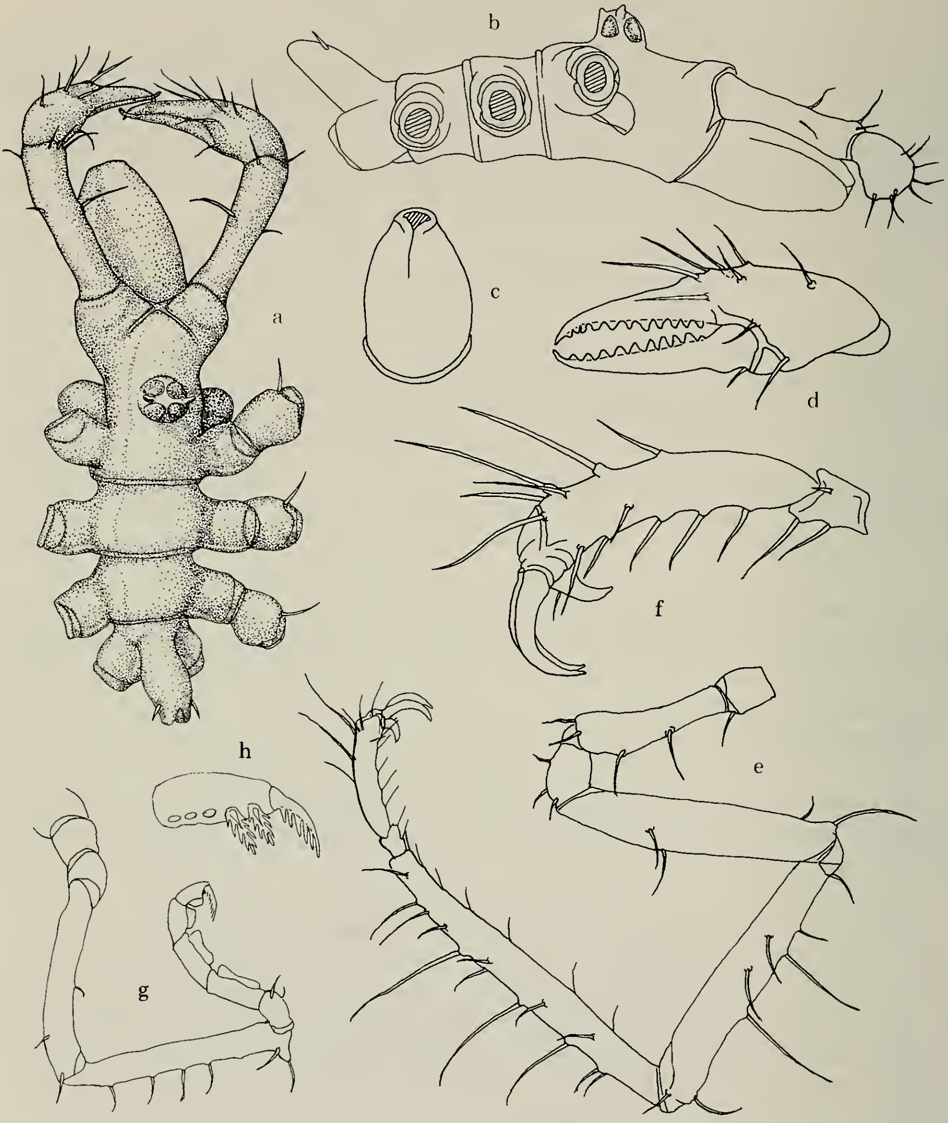


Fig. 4. *Seguapallene micronesica,* holotype male: a, Trunk, dorsal view; b, Trunk, lateral view; c, Proboscis, ventral view; d, Chela; e, Third leg; f, Terminal segments of third leg enlarged; g, Oviger; h, Strigilis terminal segment enlarged.

5 shorter, length only 3 times diameter, apophysis absent, strigilis with fewer denticulate spines and only 3 teeth on terminal claw. Main claw of propodus slightly shorter than in male.

Measurements of holotype (in mm).—Trunk length (chelifore insertion to tip 4th lateral processes), 0.95; trunk width, 0.41; proboscis (lateral), 0.38; abdomen (lateral), 0.23; third leg, coxa 1, 0.23; coxa 2, 0.46; coxa 3, 0.2; femur, 0.83; tibia 1, 0.96; tibia 2, 1.02; tarsus, 0.09; propodus, 0.36; main claw, 0.07; auxiliary claws, 0.15.

Distribution.—Known only from the type-locality, Koror Island, Palau Islands, in the intertidal.

Etymology.—Named for Micronesia, of which Palau and the Caroline islands form a major part.

Remarks.—The only other known species in this genus, *Seguapallene insignatus* Pushkin (1975:1404–1405, fig. 2), is quite different from this new species. Pushkin's species has pointed tubercles on the lateral processes, a much longer abdomen, a major ventral spine on the tarsus and three major heel spines, a large normal-size claw with two smaller auxiliaries, and marked differences in the oviger. Pushkin (1975:fig. 2f, g) illustrates what appears to be a female oviger while labeling it that of a male. The fourth and fifth segments are much shorter than those of *S. micronesica* and lack the fifth segment apophysis. His figure "g" is of the oviger terminal segments and shows a smooth claw without teeth. The denticulate spines differ greatly from the new species in having two long proximal serrations and many short distal serrations per side, similar to those common to the genus *Callipallene.* The denticulate spines of *S. micronesica* are more like those of many of the ammotheids.

The discovery of *S. micronesica* gives the genus an extraordinary distribution pattern. *Seguapallene insignatus* was described from specimens found in the cold Îles Crozet of the Subantarctic in 3 to 30 meters. The new species, found in tropical Palau, shows that the genus is not confined to particular thermal habitats, but that it is perhaps only confined to littoral and sublittoral habitats. There is a somewhat similar distribution pattern in the genus *Austrodecus* (see following species). This genus has a predominantly Antarctic and Subantarctic distribution, but several species are known to occur from New Zealand and the tropical west Pacific to Japan.

Family Austrodecidae

Austrodecus palauense, new species

Fig. 5

Material examined.—Palau, SE Koror Island, sea reef inside cove next to cave, 7°18'34"N, 134°30'35"E, wash of 4 kinds of sponges in 0.1 m, 2 Jul 1974, J. L. Barnard, 1 ♀ juvenile holotype (USNM 195377), 1 juvenile paratype (USNM 195378).

Description.—Holotype very tiny, leg span only 2.05 mm. Trunk slender, elongate, completely segmented, with 4 slender median tubercles shorter than trunk diameter, anterior tubercle longest, those posterior increasingly shorter. Lateral processes separated by their diameters or slightly more, armed with tiny laterodistal tubercles on posterior of first pair, anterior and posterior of second and third pairs, and absent from last pair. Ocular tubercle an obliquely anterior-pointing tapered cone, placed at extreme anterior of neck, bulging distally with well pigmented small eyes, over 3 times longer than its maximum diameter, apex armed with 2 tiny lateral papillae. Proboscis typical of the genus, long, tubular with distal annulations. Abdomen a long cylinder tapering distally, extending to distal tip of second coxae of fourth pair of legs, armed with 2 small lateral subapical setae.

Palp 5-segmented, second segment longest, armed with few short setae, 1 longer

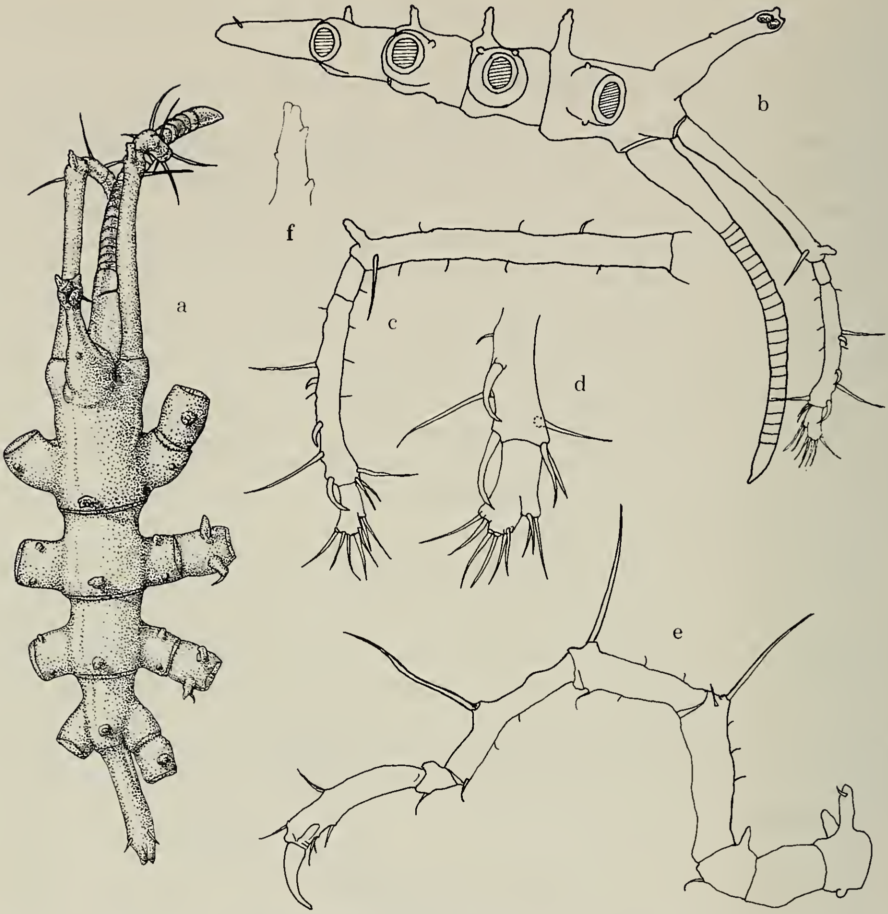


Fig. 5. *Austrodecus palauense,* holotype juvenile female; a, Trunk, dorsal view; b, Trunk, lateral view; c, Palp; d, Palp terminal segments enlarged; e, Third leg; f, Mid-dorsal tubercle of ocular segment enlarged.

ventrodistal seta and 1 slender dorsodistal tubercle not as long as segment diameter. Fourth segment curved, 0.6 as long as second, armed with several short setae, 3 long dorsal and ventral setae, and 3 stout curved spines dorsodistally. Fifth segment subrectangular with ventral tubercle giving appearance of slight bifurcation of segment, armed distally with dense setae longer than segment diameter.

Ovigers represented only by rudimentary buds ventrally on cephalic segment.

First coxae with dorsolateral tubercles slightly shorter than segment diameter, some with distal setae, arranged with 1 posteriorly on coxae of first pair of legs, 2 on second and third pair, and 1 anteriorly on fourth pair of legs. Third coxae with small dorsal tubercle not as long as segment diameter. Major leg segments armed with few short setae and single large dorsodistal setae longer than 3 times segment diameter. Propodus moderately curved, as long as femur, armed with 2 or 3 short sole setae, 2 dorsodistal setae and well curved claw slightly more than 0.3 propodus length. Sexual characters undeveloped.

Measurements of holotype (in mm).—Trunk length (palp insertion to tip 4th lateral processes), 0.59; trunk width (across 2nd lateral processes), 0.25; proboscis, 0.63; abdomen, 0.16; ocular tubercle, 0.22; 3rd leg, coxa 1, 0.05; coxa 2, 0.07; coxa 3, 0.06; femur, 0.16; tibia 1, 0.15; tibia 2, 0.17; tarsus, 0.03; propodus, 0.15; claw, 0.06.

Distribution.—Known only from Koror Island, Palau Islands, in 0.1 meter.

Etymology.—Named for the type-locality, the Palau Islands.

Remarks.—The discovery of this new species in a genus with predominantly Antarctic distribution tends to reinforce the theory that there is a western Pacific "corridor" of species from New Zealand to Japan, to account for the known temperate and tropical species development in this area. There is no known counterpart for this corridor along the eastern coast of South America or the east African coast. Several (at least five) species are known from New Zealand, two from the Kermadec Islands, the new species reported on herein from the Palau Islands, and the single known species from Japan all point toward this northern corridor. It may be possible, in future collecting, to discover other species in this corridor in the New Hebrides, Solomons, New Guinea, Marianas, and the Bonin Islands, as many species of *Austrodecus* appear to be endemic or at least are confined to restricted areas or corridors of distribution (see Stock 1957:figs. 7, 8, 12).

Austrodecus palauense appears closely related to *A. elegans,* a species from near the Subantarctic Prince Edward Islands. Both have well separated lateral processes, mid-dorsal trunk tubercles, slender laterodistal coxa 1 tubercles, and a very similar abdomen. The ocular tubercle of *A. elegans* is much longer and anterior-pointing, the leg segments are much longer, and it has auxiliary claws. How the new species will appear as an adult is conjecture, but it would already have developed auxilary claws at this stage of growth if it were to have them. It is not likely that the lateral processes would be spaced closer together in the adult than in the juvenile (or sub-adult). In all other known species of *Austrodecus,* the lateral processes are more closely spaced than in *A. palauense.*

Acknowledgments

I wish to thank the late Dr. Dennis M. Devaney for loaning the Bishop Museum material, and my colleagues, J. L. Barnard, for his infectuous collecting enthusiasm, and T. E. Bowman, both of the Department of Invertebrate Zoology (Crustacea), National Museum of Natural History, for reviewing the manuscript.

Literature Cited

Child, C. A. 1970. Pycnogonida of the Smithsonian-Bredin Pacific Expedition, 1957.—Proceedings of the Biological Society of Washington 83(27):287–308.

———. 1975. Pycnogonida of Western Australia.—Smithsonian Contributions to Zoology 190:1–28.

———. 1982. Pycnogonida of the Western Pacific Islands I. The Marshall Islands.—Proceedings of the Biological Society of Washington 95(2):270–281.

Helfer, H. 1938. Einige neue Pantopoden aus der Sammlung des Zoologischen Museums in Berlin.—Sitzungsberichte Gesellschaft Naturforschungs Freunde (Berling) 1937:162–185.

Loman, J. C. C. 1908. Die Pantopoden der Siboga-Expedition.-Siboga Expedition, Monographie 40: 1–88.

Marcus, E. 1940. Os Pantopoda brasileiros e os demais Sul-Americanos.—Boletim Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo, series 19 (Zoologia) 4:3–179.

Mello Leitão, A. de. 1949. Nova Espécie de *Halosoma* Cole, 1904 (Pantopoda, Phoxichilidiidae Sars, 1891).—Anais da Academia Brasileira de Ciencias 21(2):167–173.

Pushkin, A. F. 1975. [New Species of Callipallenidae (Pantopoda) from the Subantarctic.]—Zoologicheskii Zhurnal 54(9):1402–1406, 2 figures. [In Russian plus English Summary].

Stock, J. H. 1953. Re-description of some of Helfer's pycnogonid type-specimens.—Beaufortia 4(35): 33–45.

———. 1953a. Contribution to the knowledge of the pycnogonid fauna of the East Indian Archipelago. Biological Results of the Snellius Expedition 17.—Temminckia 9:276–313.

———. 1954. Pycnogonida from Indo-West-Pacific, Australia, and New Zealand waters.—Videnskabelige Meddelser fra Dansk Naturhistorisk Forening (Copenhagen) 116:1–168.

———. 1957. The Pycnogonid family Austrodecidae.—Beaufortia 6(68):1–81.

———. 1965. Pycnogonida from the southwestern Indian Ocean.—Beaufortia 13(151):13–33.

———. 1968. Pycnogonida collected by the "Galathea" and "Anton Bruun" in the Indian and Pacific Oceans.—Videnskabelige Meddeleser fra Dansk Naturhistorisk Forening (Copenhagen) 131:7–65.

———. 1974. Medio- and infralittoral Pycnogonida collected during the I. I. O. E. near Landbase on Nossi-Be, Madagascar.—Bulletin of the Zoological Museum, University of Amsterdam 4(3): 11–22.

———. 1975. Infralittoral Pycnogonida from Tanzania.—Travais du Muséum d'Histoire Naturelle "Gr. Antipa", Bucharest 16:127–134.

Thomson, G. M. 1884. On the New Zealand Pycnogonida with descriptions of new species.—Transactions and Proceedings of the New Zealand Institute 16(1883):242–248.

Utinomi, H. 1971. Records of Pycnogonida from shallow waters of Japan.—Publications of the Seto Marine Biological Laboratory 18(5)317–347.

Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C., 20560.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 715–718

RECOGNITION OF TWO SPECIES OF DOUBLE-LINED MACKERELS (*GRAMMATORCYNUS*: SCOMBRIDAE)

Bruce B. Collette

Abstract.—*Grammatorcynus* has been considered to be monotypic by recent authors. Electrophoretic work by A. D. Lewis indicates the presence of two species in Australia. These are identified herein as: (1) *G. bilineatus* (Rüppell, 1836); type-locality: Red Sea; "scad"; a wide-spread species (Red Sea to Tonga); with many gill rakers (19–24), large eye (7–9% of fork length), and smaller maximum size (60 cm FL, 3 kg); and (2) *G. bicarinatus* (Quoy and Gaimard, 1844); type-locality: Shark Bay, Western Australia; "shark mackerel"; limited to the northern coasts of Australia and the Gulf of Papua; few gill rakers (12–15), small eye (3–5% of FL), and larger maximum size (110 cm FL, 13.5 kg).

Most recent authors (e.g., Silas 1963; Collette 1979) have considered *Grammatorcynus* to be monotypic. In correspondence with me and in his doctoral dissertation, Lewis (1981) presented electrophoretic evidence that there are two species in Australia: a small species, the "scad," that is unspotted, and a larger one, the "shark mackerel," that frequently has dark spots on its lower sides. This brief paper presents morphological evidence for recognition of two species: the widely distributed scad, *G. bilineatus* (Rüppell) and the shark mackerel *G. bicarinatus* (Quoy and Gaimard), restricted to Australia and southern New Guinea. This evidence supports inclusion of both species in the FAO World Catalogue of scombrids (Collette and Nauen, in press). A revision of *Grammatorcynus* with discussion of its relationships to other scombrids is in progress.

Grammatorcynus bilineatus (Rüppell, 1836) Scad
Fig. 1A

Thynnus bilineatus Rüppell, 1836:39–40, pl. 12, fig. 2 (original description, Red Sea).

Grammatorcynus bilineatus Gill, 1862:125 (*T. bilineatus* type-species of new genus).

Nesogrammus piersoni Evermann & Seale, 1907: 61–62, pl. 1, fig. 3 (original description; Bulan, Sorsogon Province, Luzon, Philippine Is.).

Diagnosis.—A species of *Grammatorcynus* with many gill rakers, (3–5) + 1 + (13–18) = 19–24 on the first arch (Table 1); a large eye, 7–9% of FL (see Fig. 2); matures at a small size, about 430 mm FL; maximum size about 600 mm FL, 3 kg. Seldom with dark spots on the lower sides of the body.

Range.—Widespread in the Indo-West Pacific. Based on the literature and material examined, known from the Red Sea, Andaman Sea, East Indies, Philippines, Ryukyu Islands, New Guinea (New Britain, New Ireland, New Hanover, and the Louisiade Archipelago), Australia (Scott Reef off northern Western Aus-

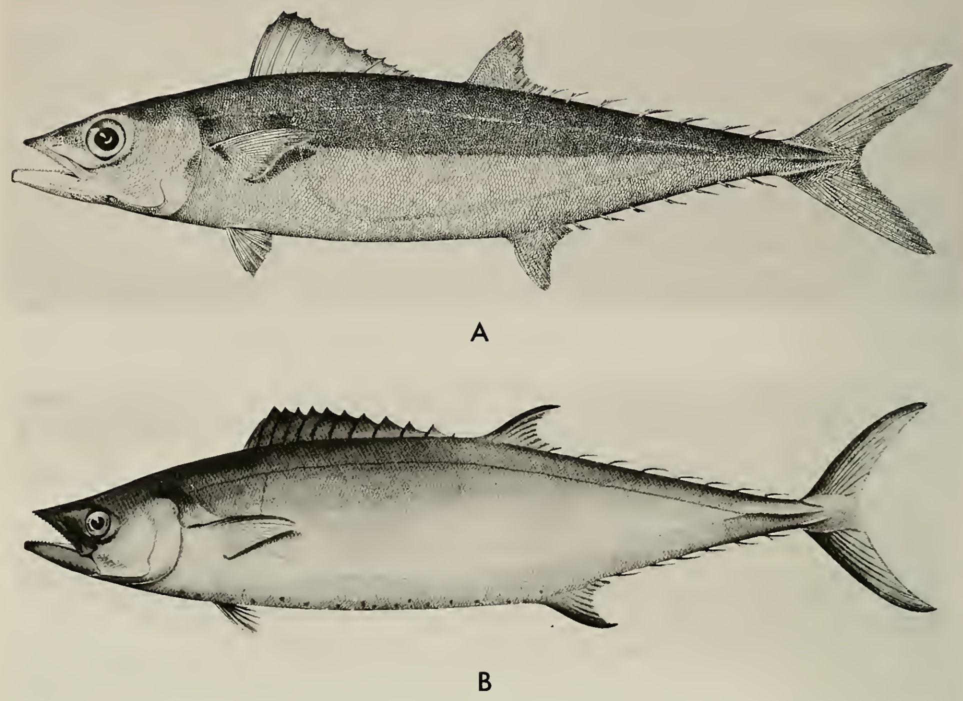


Fig. 1. Two species of *Grammatorcynus.* A, *G. bilineatus* (from Evermann and Seale 1907, fig. 3, holotype of *Nesogrammus piersoni,* 372 mm FL, Philippine Islands); B, *G. bicarinatus* (from McCulloch 1915, pl. 1, fig. 1, 925 mm FL, New South Wales, Australia).

tralia, eastern Queensland), the Solomon Islands, New Caledonia, the Caroline Islands, Marshall Islands, Fiji, and Tonga.

Material examined.—52 specimens (23.5–575 mm FL) from 36 lots: Red Sea (13 specimens including Senckenburg Museum 2755, the stuffed holotype of *Thynnus bilineatus*), Andaman Sea (4), Celebes (2), Philippines (5 including USNM 55899, the holotype of *Nesogrammus piersoni*), New Guinea (7), Australia (7), Solomons (1), Carolines (3), Marshalls (8), and Fiji (2).

Grammatorcynus bicarinatus (Quoy and Gaimard, 1824) Shark Mackerel

Fig. 1B

Thynnus bicarinatus Quoy and Gaimard, 1824:357, pl. 61, fig. 1 (original description; Baie des Chiens-Marins = Shark Bay, W. Australia).

Grammatorcynus bicarinatus McCulloch, 1915:266–269, pl. 1, fig. 1 (description; off Cook Is., near Tweed River Heads, New South Wales; 925 mm FL, 18.75 lbs.).

Diagnosis.—A species of *Grammatorcynus* with few gill rakers, (1–2) + 1 + (10–12) = 12–15 on first arch (Table 1); a small eye, 3–4% of FL (see Fig. 2); reaches large size, probably 1100 mm FL, 13.5 kg. Frequently has dark spots on the lower sides of the body (Fig. 1B).

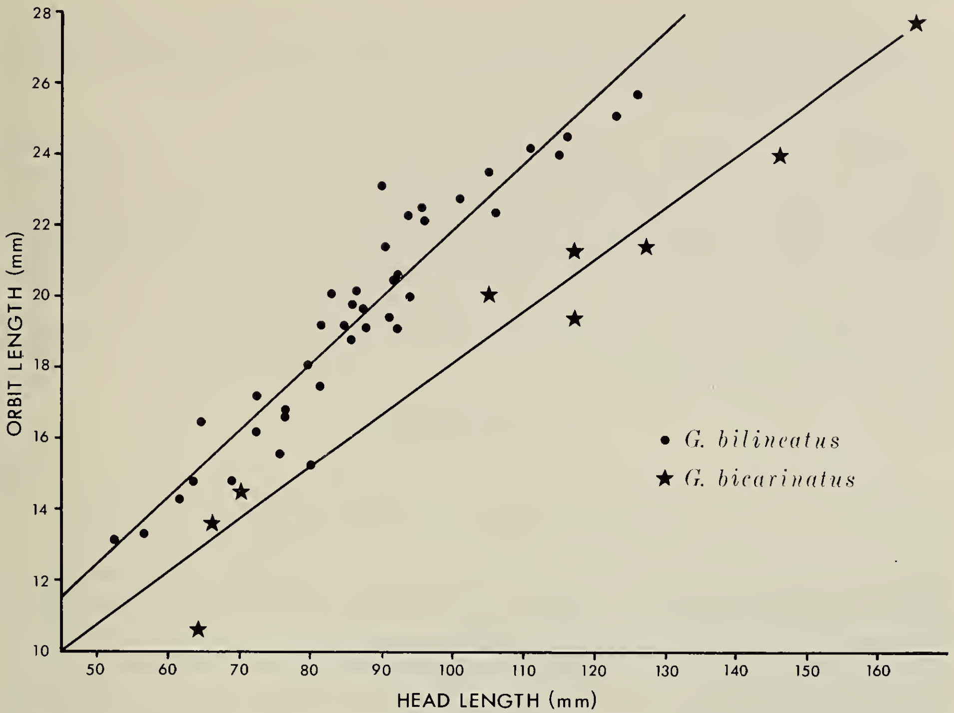


Fig. 2. Regression of orbit length on head length in two species of *Grammatorcynus*. Regression equation for *G. bilineatus* (n = 44), Y = 2.923 + 0.189X; for *G. bicarinatus* (n = 9), Y = 3.593 + 0.144X. Probability that regressions are the same (by ANCOVA), $P < 0.0000001$; that the slopes are equal, $P = 0.0032$; and that the intercepts are equal, $P < 0.0000001$.

Table 1.—Total number of gill rakers in the species of *Grammatorcynus*.

Species and area	12	13	14	15	16	17	18	19	20	21	22	23	24	N	$\bar{x}$
G. bilineatus															
Red Sea									1	6	2	2	1	12	21.7
Andaman Sea											3	1		4	22.3
Celebes Islands									2					2	20.0
Philippine Islands								1	—	2	1			4	20.8
New Guinea								1	3	1	—	1		6	20.5
Australia								1	2	1	1			5	20.4
Solomon Islands										1				1	21.
Caroline Islands										1	1	1		3	22.0
Marshall Islands								1	1	6				8	20.6
Fiji Islands									1	1				2	20.5
Total								4	10	19	8	5	1	47	21.1
G. bicarinatus	1	—	6	2										9	14.0

Range.—Positively known only from the northern coasts of Australia with occasional stragglers south to 30°S on both east (Cook Is., N.S.W.) and west (Shark Bay, W.A.) coasts and in the Gulf of Papua off southern New Guinea (A. D. Lewis, pers. comm.).

Remarks.—The original description of *bicarinatus* is not detailed enough to tell which species is involved, the figure is poor, and there is no type-material. I use the name because the shark mackerel extends further south on the coasts of Australia than does the scad, to Cook Island, N.S.W. on the east (McCulloch 1915) and to Exmouth Gulf, W.A. (USNM uncat.) and, presumably Shark Bay on the west.

Material examined.—9 specimens (300–825 mm FL) from 8 lots: Western Australia (4); Queensland (5).

Acknowledgments

I thank Dr. A. D. Lewis (Department of Agriculture and Fisheries, Fiji) for informing me of this problem and for providing frozen specimens of both species for me to dissect. Sally Rothwell spent the month of February 1983 working in my laboratory on *Grammatorcynus* on a Careers in Biology Program from Colgate University. Her efforts have made early completion of this preliminary paper possible. I thank the curators of the collections housing material of *Grammatorcynus* for permission to study their material and I will acknowledge their help individually in the revision of the genus. Ruth Gibbons ran the analysis of covariance and prepared the figures. Drafts of the manuscripts were read by Robert H. Gibbs, Jr., A. D. Lewis, Victor G. Springer, and Austin B. Williams.

Literature Cited

Collette, B. B. 1979. Adaptations and systematics of the mackerels and tunas.—*In* The physiological ecology of tunas, Gary Sharp and Andrew Dizon, eds.; Academic Press, N.Y., pp. 739.

Collette, B. B., and C. Nauen. (In press). Scombrids of the world. FAO Species Catalogue, vol. 3, Food and Agriculture Organization of the United Nations Fisheries Synopsis No. 125.

Evermann, B. W., and A. Seale. 1907. Fishes of the Philippine Islands.—Bulletin of the [U.S.] Bureau of Fisheries 26:49–110.

Gill, T. N. 1862. On the limits and arrangement of the family of scombroids.—Proceedings of the Academy of Natural Sciences of Philadelphia 14:124–127.

Lewis, A. D. 1981. Population genetics, ecology and systematics of Indo-Australian scombrid fishes, with particular reference to skipjack tuna (*Katsuwonus pelamis*). Australian National University, Ph.D. thesis.

McCulloch, A. R. 1915. Notes on, and descriptions of Australian fishes.—Proceedings of the Linnean Society of New South Wales 40:259–277.

Quoy, J. R. C., and J. P. Gaimard. 1824. Voyage autour du Monde, . . . Exécuté sur les corvettes de S.M. l'Uranie et la Physicienne, pendant les années 1817, 1818, 1819 et 1820. 3, Zoologie, 712 pp.

Rüppell, E. 1836. Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Fische des rothen Meeres, 6:29–52. Frankfurt am Main.

Silas, E. G. 1963. Synopsis of biological data on double-lined mackerel *Grammatorcynus bicarinatus* (Quoy and Gaimard) (Indo-Pacific).—Food and Agriculture Organization of the United Nations Fishery Report No. 6, 2:811–833.

National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 719–724

TWO NEW SPECIES OF CORAL TOADFISHES, FAMILY BATRACHOIDIDAE, GENUS *SANOPUS*, FROM YUCATAN, MEXICO, AND BELIZE

Bruce B. Collette

Abstract.—*Sanopus reticulatus,* new species, is described from three specimens collected at Progreso, Yucatan, Mexico. It differs from the other species of *Sanopus* in its reticulate body pattern and shorter distance from snout to second dorsal fin origin (403–419 versus 420–487 thousandths of standard length). It is most closely related to *S. barbatus* and *S. johnsoni,* species with mottled bellies, branched chin barbels, and high numbers of fin rays and vertebrae. *Sanopus greenfieldorum,* new species, is described from three specimens collected at Carrie Bow Cay, Belize. It is most closely related to *S. astrifer* but has light lines on its head instead of light spots.

While examining fishes in the Zoological Museum of the University of Hamburg (ZMH) in September 1982, I was surprised to discover a fine specimen of toadfish collected in Yucatan in 1893 that was identified as *Opsanus tau.* It was clearly a specimen of *Sanopus* with a distinctive pattern and was from the Gulf of Mexico, beyond the known range of the genus (Cozumel Is., Quintana Roo, south to Panama); I suspected it represented an undescribed species. Subsequently, two additional specimens of this species were located at the Museum of Comparative Zoology (MCZ) at Harvard that had been misidentified as *Opsanus pardus* by Barbour and Cole (1906). A second new species was discovered first by David W. and Teresa A. Greenfield on the barrier reef near Carrie Bow Cay, Belize, in 1974 about the time my (1974) revision of *Sanopus* was published. Another specimen of this species was collected at Carrie Bow Cay in 1980, and a juvenile in 1983.

The purpose of this paper is to describe these two new species and to compare them with the four known species in the genus: *S. barbatus* (Meek and Hildebrand), *S. astrifer* (Robins and Starck), *S. splendidus* Collette, Starck, and Phillips, and *S. johnsoni* Collette and Starck (see Collette 1974).

Counts and measurements follow those given in my review of *Sanopus.* Tables of meristic data presented there are not repeated here. Material of the four previously treated species housed at the National Museum of Natural History (USNM) was compared with the new species. Specimens of *S. astrifer* and *S. barbatus* from the Field Museum of Natural History in Chicago (FMNH) collected subsequent to 1974 were examined to increase the sample size of comparative material.

Sanopus reticulatus, new species
Figs. 1A–B

Opsanus pardus non Goode and Bean, Barbour and Cole, 1906:159 (two specimens from Progreso).

Holotype.—ZMH 20930, male, 236 mm SL, Mexico, Yucatan, Progreso; Weiss, 25 Jan 1893.

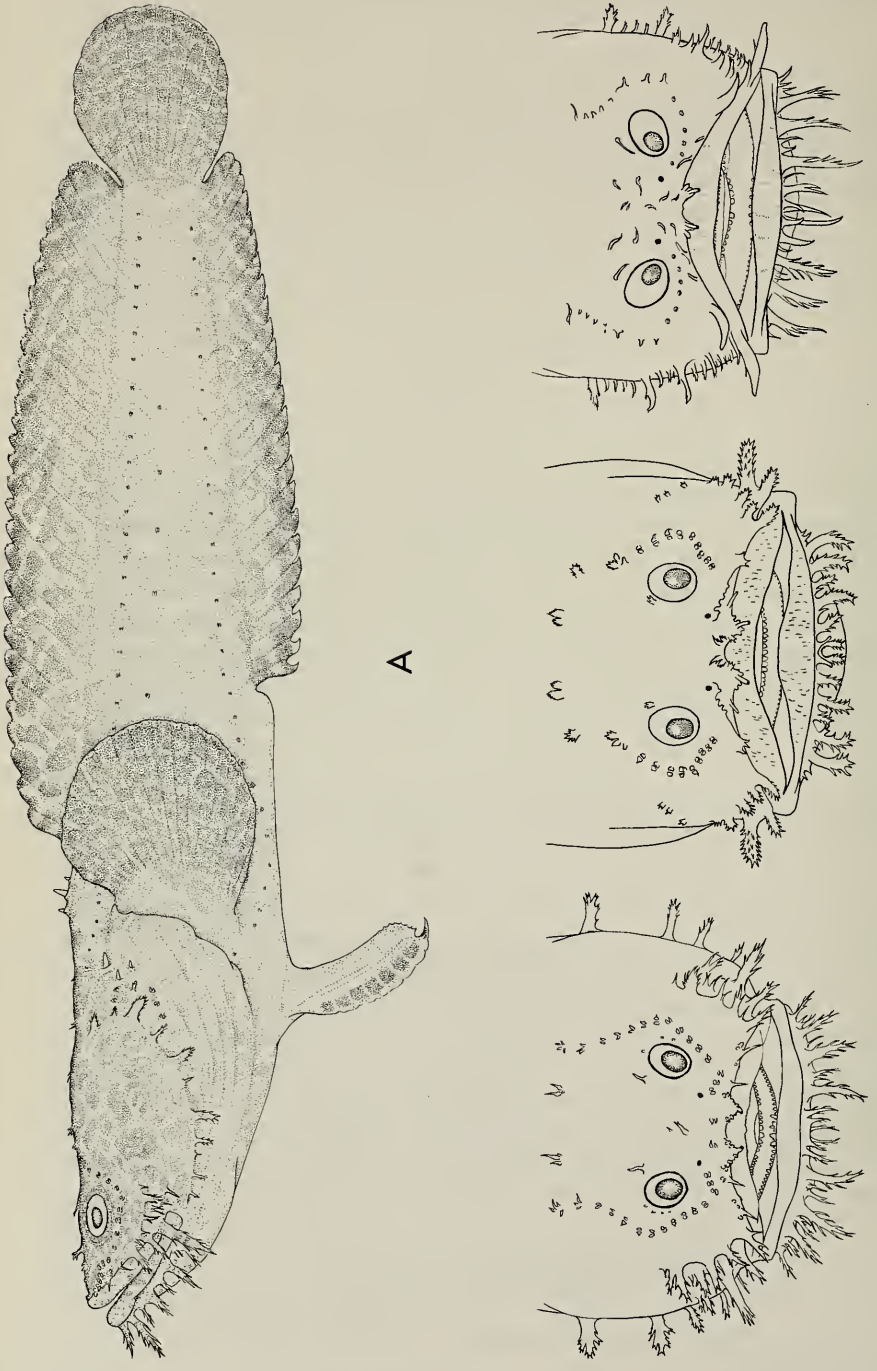


Fig. 1. A, *Sanopus reticulatus* (holotype, ZMH 20930, 236 mm SL, Progreso, Yucatan, Mexico); B–D, Diagrammatic anterodorsal views of heads of three species of *Sanopus*: B, *S. reticulatus* (holotype, ZMH 20930, 236 mm SL, Progreso, Yucatan, Mexico); C, *S. barbatus* (USNM 211322, 250 mm SL, Bonacca, Honduras); D, *S. johnsoni* (holotype, USNM 205945, 253 mm SL, Cozumel Is., Mexico).

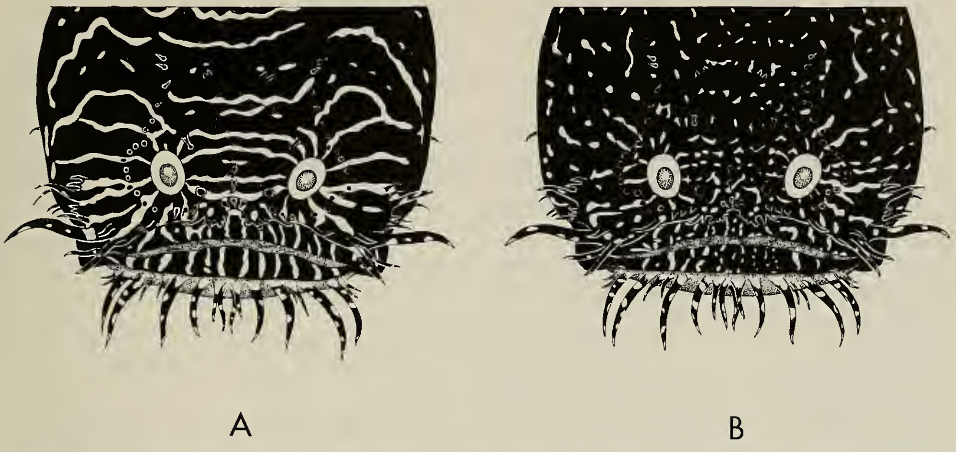


Fig. 2. Diagrammatic anterodorsal views of heads of two species of *Sanopus.* A, *S. greenfieldorum* (holotype, USNM 213555, 280 mm SL, Carrie Bow Cay, Belize); B, *S. astrifer* (USNM 209720, 245 mm SL, Glovers Reef, Belize).

Paratypes.—MCZ 32889 (233 mm SL) and USNM 258111 (225 mm), Mexico, Yucatan, Progreso, Leon J. Cole, early 1904.

Diagnosis.—Differs from the other five species of *Sanopus* in having a reticulate pattern on the body and head (Fig. 1A). Similar to *S. barbatus* and *S. johnsoni* and different from *S. astrifer, S. greenfieldorum,* and *S. splendidus* in having branched chin barbels. Maxillary barbel branched as in the first two species but more deeply divided than in either of them (Fig. 1B–D). Distance from tip of snout to origin of second dorsal fin (Table 1) shorter (403–419 thousandths of SL, $\bar{x}$ 413.7) than in the other species (420–487, means 432.5–451.0). No cirri present in interorbital region as are present in *S. johnsoni* (Fig. 1D).

Description.—Dorsal fin rays III, 31–32; anal fin rays 25–26; pectoral fin rays 19–20; vertebrae 11 + (27–29) = 38–40; upper lateral line papillae 34–36; lower lateral line papillae 30–32; dentary teeth 18–19; palatine teeth 9–14; total vomerine teeth 8–10; and premaxillary teeth 34–41 in one or two rows on each jaw. Body proportions given in Table 1.

Etymology.—Named in reference to its diagnostic color pattern.

Biology.—The holotype is a male with well-developed gonads. Both paratypes are immature. The holotype had a specimen of majid crab in its stomach, *Macrocoeloma trispinosum* (Latreille). There was a snail in the intestine of one of the paratypes.

Sanopus greenfieldorum, new species
Fig. 2A

Holotype.—USNM 213555, male, about 280 mm SL, Belize, 2 mi. S of Carrie Bow Cay; D. W. and T. Greenfield, G74-21; 24 Jul 1974.

Paratypes.—FMNH 94575, ripe female, about 270 mm SL, Belize, between Carrie Bow Cay and South Water Cay; E. Reynaud; 10 Mar 1980. USNM 261601, 29.3 mm, Carrie Bow Cay; G. Hendler; 2 Apr 1983.

Diagnosis.—Similar to *S. astrifer* in having a dark body with prominent light markings. Differs from *S. astrifer* in having many light lines on head (Fig. 2A)

Table 1.—Morphometric comparison (in thousandths of standard length) between adults of the six species of *Sanopus.*

	S. reticulatus (n = 3)			*S. barbatus* (n = 12)			*S. johnsoni*
Character	Range		$\bar{x}$	Range		$\bar{x}$	
SL (mm)	225	236	231.3	213	370	309.5	253
Head length	326	363	340.0	341	397	375.5	352
Head width	245	303	265.3	295	322	310.9	295
Orbital	40	45	43.3	34	52	43.2	42
Interorbital	61	77	71.0	85	108	95.3	89
Snout–2 dorsal fin origin	403	419	413.7	427	471	447.5	439
Snout–anal fin origin	587	592	589.3	572	647	604.9	581
Pectoral fin length	162	183	172.3	157	199	172.3	175
Pelvic fin length	132	157	140.7	131	159	146.6	153

	S. greenfieldorum (n = 2)			*S. astrifer* (n = 4)			*S. splendidus* (n = 6)		
	Range		$\bar{x}$	Range		$\bar{x}$	Range		$\bar{x}$
SL (mm)	270	280	275.0	233	263	244.3	217	252	237.0
Head length	361	415	388.0	354	368	360.5	338	356	345.8
Head width	318	356	337.0	323	333	327.3	290	314	299.5
Orbital	41	41	41.0	41	50	46.0	40	52	46.2
Interorbital	92	113	102.5	84	97	90.3	69	77	73.5
Snout–2 dorsal fin origin	439	575	507.0	420	487	444.8	423	439	432.5
Snout–anal fin origin	467	659	563.0	570	597	585.5	583	604	594.0
Pectoral fin length	190	202	196.0	193	219	206.8	158	203	178.6
Pelvic fin length	157	166	161.5	144	180	162.0	154	203	170.0

instead of small light spots (Fig. 2B). About 4 continuous light lines between eyes, several more on top of head posterior to these, and 6–8 more lines radiating out from lower part of orbit. Eye slightly smaller than in *S. astrifer* (41 thousandths of SL, 99–115 thousandths of head length compared to 41–50 and 116–139).

Description.—Dorsal fin rays III, 30–32; anal fin rays 24–25; pectoral fin rays 22; vertebrae (11–12) + (26–27) = 37–39; upper lateral line papillae 36–40; lower lateral line papillae 30–33; dentary teeth 22–28; palatine teeth 14–16; total vomerine teeth 10–16; and premaxillary teeth 31–35 in one or two rows on each jaw. Body proportions given in Table 1; both adult type specimens bent, therefore, measurements of SL, snout to second dorsal, and snout to anal could not be made with accuracy.

Underwater photographs of a specimen larger than the types taken by James Bohnsack show a pattern similar to that in Fig. 2A but with a few more and slightly wider lines on the head. The lines are white on a gray-black background.

Etymology.—Named for David W. and Teresa Arambula Greenfield who collected the holotype, suspected it was undescribed, and sent it to me for examination. The Greenfields have been working actively on the fish fauna of Belize for more than a decade and described a new toadfish, *Triathalassothia gloverensis,* from Glovers Reef in 1973 (but it also occurs at Carrie Bow Cay).

Biology.—The holotype was taken by spear from a depression in the sand under a large coral head (*Montastrea*) in one meter of water on the reef flat behind the barrier reef. The fish was facing out so only the front of the head was seen. This is the same type of habitat in which *S. astrifer* has been taken at Glovers Reef (D. W. Greenfield, pers. comm.). The adult paratype was also taken by spear from under a dead coral clump in slightly deeper water on the reef flat behind the barrier reef between Carrie Bow Cay and South Water Cay. James Bohnsack (pers. comm.) photographed an *S. greenfieldorum* in the spur and groove zone of the fore reef at Carrie Bow Cay at a depth of about 6 m at about 9:30 PM during the last week of April 1982. It was under a coral head facing out with a little more of the fish showing than in Fig. 2A. The juvenile paratype was taken with rotenone at 24.4 m over an area of *Montastrea* on the fore reef crest.

The holotype is a male with slightly developed testes. The gut contents consist of fragments of two specimens of the portunid crab, *Portunus vocans* (A. Milne Edwards), one specimen of a majid crab, *Mithrax,* probably *M. pleuracanthus* Stimpson, and a few fish bones. The adult paratype has two large ovaries that occupy much of the body cavity. There are 191 eggs in the left ovary, 178 in the right. The eggs are mostly 5 or 6 mm in diameter. The teeth of the adult paratype are pink and the stomach and intestine were filled with spines and broken pieces of the test of *Diadema antillarum* Philippi. Two crabs were among the gut contents, a female *Portunus vocans* and a chela and carpus from a xanthid crab. There were also fragments of a skull and a few vertebrae of a small fish. The juvenile paratype contained the carapace of an alpheid shrimp, an undescribed species of the isopod *Stenetrium,* and a small snail, *Tricolia* cf. *affinis* (C. B. Adams) of the family Phasianellidae.

Discussion

In my 1974 diagnosis of *Sanopus,* I noted that it lacked the discrete glands on the posterior surface of the pectoral fin between the bases of the upper fin rays that are present in *Opsanus.* I did not point out that there is a well-developed glandular area inside the gill cavity anterior to the pectoral girdle. This shared specialization is characteristic of adults and subadults of all six species of *Sanopus.*

Description of two more species of *Sanopus* raises the toadfish fauna of the western Atlantic to 30 (including three freshwater species in rivers draining into the western Atlantic) in 7 genera (Collette and Russo 1981: table 13). The New World batrachoid fauna now comprises 43 out of a total of about 66 species in the family, confirming the New World as the center of diversity for the family.

Crabs are an important component of the diet of the two new species of *Sanopus* as they are in other species of toadfishes (Collette and Russo 1981). *Diadema* was present in the gut of the adult paratype of *S. greenfieldorum,* in the recently collected specimen of *S. astrifer* from Glovers Reef (FMNH 91034) and in the holotype of *S. johnsoni* (Collette 1974). Randall et al. (1964) reported 15 species from 7 other families as *Diadema* predators.

Egg number and size in *S. greenfieldorum* are comparable to other toadfishes, i.e., relatively few large eggs. Females of 9 species of *Batrachoides* ranging from 106–352 mm SL had 88–588 eggs, 3–6 mm in diameter (Collette and Russo 1981: table 10) compared to *S. greenfieldorum,* 270 mm SL with 369 eggs, 5–6 mm in diameter.

Comparative Material Examined

See Collette (1974) for data on *Sanopus* examined up to that time. Additional material, all from FMNH, is as follows. *S. astrifer*: 91034 (1, 263), Belize, Glovers Reef; 20 June 1978. *S. barbatus*: 91030(1, 330, Honduras, Brus Lagoon; 7 May 1975. 91031(2, 295–330), Honduras, Big Hog Is.; 21 May 1975. 91032(1, 328), Honduras, Big Hog Is.; 20 May 1975. 91033(1, 300), Honduras, Little Hog Is.; 18 May 1975.

Acknowledgments

I thank Dr. H. Wilkens (ZMH) and Mr. Karsten Hartel (MCZ) for loaning me the specimens of *S. reticulatus*. Dr. Karel Liem (MCZ) and Mr. Hartel kindly permitted me to retain one MCZ specimen for the USNM collections. Dr. David W. Greenfield collected the holotype of *S. greenfieldorum,* called my attention to it, and permitted me to retain it for the USNM collections. Dr. Donald Stewart (FMNH) loaned material of *S. greenfieldorum, S. astrifer,* and *S. barbatus.* The drawings are by Keiko Hiratsuka Moore. Dr. James Bohnsack provided me with color underwater photographs of a specimen from a night dive at Carrie Bow Cay. Radiographs of the types were made by Ruth Gibbons. Dr. Austin B. Williams identified crustaceans and Dr. Richard S. Houbrick identified the snail in the stomachs of the types. Dr. David W. Greenfield and Dr. Williams read drafts of the manuscript.

Literature Cited

Barbour, Thomas, and Leon J. Cole. 1906. Reptilia, Amphibia, and Pisces. *In* Vertebrata from Yucatan.—Bulletin of the Museum of Comparative Zoology 50:146–159.

Collette, Bruce B. 1974. A review of the coral toadfishes of the genus *Sanopus* with descriptions of two new species from Cozumel Island, Mexico.—Proceedings of the Biological Society of Washington 87:185–204.

———, and Joseph L. Russo. 1981. A revision of the scaly toadfishes, genus *Batrachoides,* with descriptions of two new species from the Eastern Pacific.—Bulletin of Marine Science 31(2): 197–233.

Greenfield, David W., and Terry Greenfield. 1973. *Triathalassothia gloverensis,* a new species of toadfish from Belize (=British Honduras) with remarks on the genus.—Copeia 1973(3):560–565.

Randall, John E., Robert E. Schroeder, and Walter A. Starck. 1964. Notes on the biology of the echinoid *Diadema antillarum.*—Caribbean Journal of Science 4(2+3):421–433.

National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Washington, D.C., 20560.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 725–757

A REVISION OF THE SEGUENZIACEA VERRILL, 1884 (GASTROPODA: PROSOBRANCHIA). I. SUMMARY AND EVALUATION OF THE SUPERFAMILY

James F. Quinn, Jr.

Abstract.—A summary of the superfamily Seguenziacea is compiled from the literature and unpublished observations, and a complete bibliography is presented. A taxonomic resumé of seguenziacean genera is given. A preliminary classification of the superfamily includes 74 nominal species and subspecies in seven genera and four species-groups within *Seguenzia.* The known characters of the shells and anatomy are reviewed. The superfamily Seguenziacea is shown to be distinct from any other known archaeogastropod or mesogastropod superfamily. This superfamily is characterized by: nacreous shells of archaeogastropod ultrastructure, often complexly sculptured with 0–3 (usually 2 or 3) labral sinuses; modified rhipidoglossate radula (formula 12-4.1.1.1.4-12); paucispiral corneous operculum; epipodial tentacles; monopectinate ctenidium; long intestine with an anterior loop; specialized structures in the reproductive tract (e.g., a well developed penis); and modification of the mantle edge to form distinct incurrent and excurrent siphons. Contents of the intestine of *Seguenzia* sp. cf. *S. eritima* Verrill indicate that *Seguenzia* is a detritivore.

Ancistrobasis is known from the Eocene, Pliocene, and Recent; *Seguenzia* occurs from the Miocene to the Recent; all other genera are unknown as fossils. Although probably derived from the Trochacea, no direct link with any known fossil or living prosobranch group has yet been established. The superfamily Seguenziacea is here considered to be an isolated offshoot of the Trochacea, independently acquiring advanced anatomical features of a mesogastropod nature as a consequence of extremely small body size and in response to a deep-water habitat.

The enigmatic superfamily Seguenziacea comprises a group of very small (usually 5 mm or less in height), trochoid-like prosobranchs of world-wide distribution. Although a few species have been recorded from outer continental shelf or abyssal plain depths, by far the majority of known species have been described from the continental slopes. Because of their deep-water habitats, information concerning seguenziacean species has been largely confined to original species descriptions and records published in reports of major national exploratory expeditions. Very few species are represented in collections by large series of specimens, and even fewer have been collected alive. As a result, the taxonomy and systematic position of the Seguenziacea have remained in states of confusion and debate. As a first step towards resolving the status and relationships of this group, a review of all information in the literature is presented, augmented by original observations.

The observations summarized here suggest that seguenziaceans are archaeogastropods which have acquired anatomical specializations more typical of a mesogastropod organization. Archaeogastropod affinity is indicated by the nacreous shell, protoconch, epipodial tentacles, anterior loop of the intestine, and modified rhipidoglossate radula. Features in common principally with mesogastropods include a monopectinate ctenidium, specialized reproductive system including development of a penis, and functional modification of the mantle edge to form distinct incurrent and excurrent siphons. A similar combination of characteristics is not found in any other known gastropod group, and the argument for a separate superfamily, the Seguenziacea, as suggested by Keen (1971), Golikov and Starobogatov (1975), Goryachev (1979), Quinn (1981, 1983a, b), McLean (1981), and Marshall (in press), is supported. Although a probable origin within the Trochacea is postulated, phylogenetic relationships of the Seguenziacea are still unclear.

Seventy-four nominal species are here assigned to seven genera plus four species-groups within *Seguenzia* within the Seguenziacea and a preliminary classification is presented (Table 1). No attempt to determine species synonymies was made since that task is properly the province of a full monographic review. Such a monograph will be published as time and material permit. However, consideration of shell morphology and radular characters indicates that several rather discrete species-groups exist within *Seguenzia* sensu lato. These species-groups, not formally defined here, are referred to in the text and Table 1 as *Seguenzia* Groups I–IV, designations used here for convenience of discussion and as an indication of areas requiring close attention in future studies. Species names are used in the text without citation of date of description as this information may be found in Table 1. A synopsis of the history of the supraspecific taxa is presented and a complete bibliography is included in the Literature Cited.

Taxonomic Resumé

Seguenzia was proposed almost simultaneously in 1876 by the British malacologist J. G. Jeffreys and the Italian paleontologist G. Seguenza. It appears that Jeffreys' paper (15 June 1876) was published prior to Seguenza's (May–June 1876), but there is still some doubt as I have been unable to determine an exact date of publication for Seguenza's paper; therefore, pending acquisition of further information, Jeffreys is here considered the author of *Seguenzia.* Although Jeffreys and Seguenza agreed on the name for the genus, they disagreed strongly on its supposed systematic position. Seguenza (1876) assigned the group to the Trochidae. Jeffreys (1876), on the other hand, thought that *Seguenzia* was most closely related to the Solariidae (=Architectonicidae) and later emphatically restated that opinion (Jeffreys 1879) after Watson (1879a) erected the second seguenziacean genus, *Basilissa,* and allocated it, along with *Seguenzia,* to the Trochidae on the basis of the nacreous shells.

Verrill (1884) was the first to examine the radula of *Seguenzia,* which he described as taenioglossate. On that evidence he erected the family Seguenziidae, included both *Seguenzia* and *Basilissa,* and placed the family near *Aporrhais* (Strombidae). Based on specimens from the collections of the *Blake* Expedition, Dall (1889b) defined *Ancistrobasis* as a subgenus of *Basilissa,* and placed both in the Trochidae. Dall assigned *Fluxina discula* to the Solariidae (=Architectonicidae) and placed the Seguenziidae near the Trichotropidae, approximating Tryon's (1887) allocation of *Seguenzia.* Dautzenberg and Fischer (1897a) defined *Basi-*

lissopsis for a small, distinctively shaped seguenziacean which they included in the Trochidae.

Schepman (1908, 1909) contributed perhaps the most information of any author to date to the understanding of the Seguenziacea. In his 1908 report, Schepman described and illustrated radulae of *Basilissa* and his new genus, *Guttula,* and although he retained these two genera in the Trochidae, he commented on the uniqueness of their radular formulae. In the second part of his report (1909), he illustrated the radula of *Seguenzia melvilli,* the first accurate description and clear illustration of a radula of *Seguenzia.* He speculated that *Seguenzia* would eventually be recognized as belonging to a rhipidoglossate group also encompassing *Basilissa,* although he followed Tryon (1887), Dall (1889b), and explicitly Pelseneer (1906), in placing the Seguenziidae near the Trichotropidae. Dall (1925) included his new subgenus, *Orectospira,* in *Basilissa,* but Habe (1955a, b) has shown that *Orectospira* is turritellid rather than seguenziid.

Reflecting the hiatus in research on the deep sea, it was not until 1971 that another generic taxon was established. *Thelyssa* Bayer, 1971, was erected for a species described from University of Miami collections of deep-water Caribbean molluscs. *Thelyssa* is very similar to, and may eventually be considered a subgenus of, *Basilissa.* The most recently defined genus, *Mioseguenzia* Nordsieck, 1973, was introduced for *Janthina cimbrica* Sorgenfrei, a Miocene fossil from Denmark, and two new taxa, *M. cimbrica recens* and *M. conica.* Dr. Philippe Bouchet (in litt.) has informed me that his examination of Nordsieck's specimens revealed them to be larval shells of the Cypraeacea. From Sorgenfrei's illustration, it appears that *M. cimbrica* is also a larval form, thus excluding *Mioseguenzia* from the Seguenziacea.

The genus *Fluxina* Dall, 1881, has been used for a number of seguenziaceans (Dall 1889b; Schepman 1909; Bayer 1971) and recently included in a list of seguenziacean genera (Boss 1982); however, Merrill (1970a) has shown that the type-species of *Fluxina, F. brunnea* Dall, is a *Calliostoma* (Trochidae). *Fluxiella* (Okutani, 1968, 1974) is a nomen nudum, and *F. vitrea* Okutani, is here assigned to *Seguenzia* Group IV. Quinn (1983b) recently erected *Carenzia* for the *Seguenzia carinata* species-group, and Marshall (in press) is treating the species-groups referred to herein as *Seguenzia* Groups II and IV, as well as three other new genera.

Shell Morphology

Species of the Seguenziacea, although not uncommon in collections of deep-water molluscs, are rarely represented by large suites of shells, and even fewer by live-collected specimens. Resulting identifications and classifications have been based almost solely on shell characters. The taxonomic value of shell characters has not been critically evaluated, and authors have labored under considerable uncertainty as to which variations are merely intraspecific, and which actually represent specific differences. This inadequacy is perhaps best illustrated by the following comments of W. H. Dall (1889b:269): "In examining the specimens of *Seguenzia* . . . I find myself in a dilemma. Either each separate individual is to be regarded as a species or the variability of the shells is very great. Persistent

Table 1.—Preliminary classification of the Seguenziacea.

Seguenziacea Verrill, 1884	
Seguenziidae Verrill, 1884	
Seguenzia Jeffreys, 1876	
Type-species.—*Seguenzia formosa* Jeffreys, 1876; by monotypy.	
Group I (*Seguenzia* s.s.)	
S. formosa Jeffreys, 1876	NE Atlantic Ocean
S. formosa var. *lineata* Watson, 1879	W Atlantic Ocean
S. formosa var. *nitida* Verrill, 1884	NW Atlantic Ocean
†*S. monocingulata* Seguenza, 1876	Pliocene, Italy
†*S. monocingulata* var. *elegans* Seguenza, 1876	Pliocene, Italy
†*S. monocingulata* var. *elata* Seguenza, 1876	Pliocene, Italy
S. eritima Verrill, 1884	NW Atlantic Ocean
S. elegans Jeffreys, 1885	NE Atlantic Ocean
S. elegans var. *bicarinata* Locard, 1898	NE Atlantic Ocean
S. occidentalis Dall, 1908	NE Pacific Ocean
S. stephanica Dall, 1908	NE Pacific Ocean
S. costulifera Schepman, 1909	Celebes, Indonesia
S. dautzenbergi Schepman, 1909	Celebes, Indonesia
S. melvillii Schepman, 1909	Celebes, Indonesia
S. certoma Dall, 1919	NE Pacific Ocean
S. giovia Dall, 1919	NE Pacific Ocean
S. cervola Dall, 1919	NE Pacific Ocean
S. caliana Dall, 1919	NE Pacific Ocean
S. antarctica Thiele, 1925	S of Kerguelen, Southern Ocean
S. sumatrensis Thiele, 1925	SW of Sumatra, Indian Ocean
S. orientalis Thiele, 1925	E of Kenya, Indian Ocean
S. floridana Dall, 1927	W Atlantic Ocean
†*S. hapala* Woodring, 1928	Miocene-Recent, W Atlantic Ocean
S. hosyu Habe, 1953	Tosa Bay, Shikoku, Japan
S. louiseae Clarke, 1961	SE Atlantic Ocean
?*S. fatigans* Barnard, 1963	S of Madagascar, SW Indian Ocean
S. soyoae (Okutani, 1964)	Off Torishima Is., Japan
S. mirabilis Okutani, 1964	Off Aoga-shima Is., Japan
S. nipponica Okutani, 1964	Sea of Enshu-Nada, Japan
S. megaloconcha Rokop, 1972	NE Pacific Ocean
†*S. donaldi* Ladd, 1982	Pleistocene, New Hebrides
Group II	
S. ionica Watson, 1879	NW Atlantic Ocean
S. lampra (Watson, 1879)	E of Japan, NW Pacific Ocean
S. polita Verco, 1906	S of South Australia
S. sykesi Schepman, 1909	Banda Sea, Indonesia
S. cazioti Dautzenberg, 1925	NE Atlantic Ocean
S. rushi Dall, 1927	NW Atlantic Ocean
Group III	
S. siberutensis Thiele, 1925	SW of Sumatra, Indian Ocean
S. simplex Barnard, 1963	Off Cape Point, South Africa
Group IV	
S. discula (Dall, 1889)	NW Atlantic Ocean
?*S. dalliana* (Melvill and Standen, 1903)	N Indian Ocean
S. marginata (Schepman, 1909)	Banda Sea, Indonesia

Table 1.—Continued.

S. trochiformis (Schepman, 1909)	Ceram Sea, Indonesia
S. stenomphala (Melvill, 1910)	N Indian Ocean
S. gelida (Barnard, 1963)	W of Cape Point, South Africa
?S. solarium (Barnard, 1963)	S of Madagascar, SW Indian Ocean
S. vitrea (Okutani, 1968)	S of Boso Peninsula, Honshu, Japan
Carenzia Quinn, 1983	
Type-species.—*Seguenzia carinata* Jeffreys, 1877; by original designation.	
C. carinata (Jeffreys, 1877)	W and NE Atlantic Ocean
C. trispinosa (Watson, 1879)	W Atlantic Ocean
C. inermis (Quinn, 1983)	NE Pacific Ocean
Basilissa Watson, 1879	
Type-species.—*Basilissa superba* Watson, 1879; by subsequent designation, Cossmann, 1888.	
B. alta Watson, 1879	NW Atlantic Ocean
B. alta var. *oxytoma* Watson, 1879	NW Atlantic Ocean
B. simplex Watson, 1879	SW Atlantic Ocean
B. munda Watson, 1879	E Atlantic Ocean
B. superba Watson, 1879	N of Australia, SW Pacific Ocean
B. sibogae Schepman, 1908	Celebes, Indonesia
B. watsoni Dall, 1927	NW Atlantic
Ancistrobasis Dall, 1889	
Type-species.—*Basilissa costulata* Watson, 1879; by subsequent designation, Dall, 1927.	
†*A. reticulata* (Philippi, 1844)	Pliocene, Italy; ?Recent, NE Atlantic
A. costulata (Watson, 1879)	NW Atlantic Ocean
A. lusitanica (Fischer, 1882)	NE Atlantic Ocean
A. depressa Dall, 1889	NW Atlantic Ocean
?†*A. radialis* (Tate, 1890)	Eocene of South Australia
†*A. cossmanni* (Tate, 1894)	Eocene of South Australia
A. compsa Melvill, 1904	N Indian Ocean
?†*A. bilix* (Hedley, 1905)	E of Australia, SW Pacific Ocean
A. bombax (Cotton and Godfrey, 1938)	S of Australia
†*A. pacifica* Ladd, 1970	Eocene of Tonga, SW Pacific Ocean
Basilissopsis Dautzenberg and Fisher, 1897	
Type-species.—*Basilissopsis watsoni* Dautzenberg and Fischer, 1897; by monotypy.	
B. oxytropis (Watson, 1879)	S Atlantic Ocean
B. watsoni Dautzenberg and Fisher, 1897	NE Atlantic Ocean
B. rhyssa (Dall, 1927)	NW Atlantic Ocean
Thelyssa Bayer, 1971	
Type-species.—*Thelyssa callisto* Bayer, 1971; by original designation.	
T. callisto Bayer, 1971	NW Atlantic Ocean
Guttula Schepman, 1908	
Type-species.—*Guttula sibogae* Schepman, 1908; by monotypy.	
G. sibogae Schepman, 1980	N of New Guinea, W Pacific Ocean
G. blanda Barnard, 1963	Off Cape Point, S. Africa
G. galatheae Knudsen, 1964	Kermadec Trench, SW Pacific Ocean

† = species described from fossil material.
? = provisional placement.

study of the specimens has convinced me that the latter is the true solution, and that the most evident characters, such as the umbilicus (in some adult specimens) may be present or absent; that the number of spiral threads, their strength and sharpness on the basal disk, are entirely inconstant, and, while in the typical *formosa* the ridge next to the suture is waved or granulate, in many it is perfectly plain."

Indeed, this is the impression obtained when only a few specimens are examined, especially within *Seguenzia* Group I. However, my examination and comparison of a large number of specimens and species indicate that shell characters are not as variable as thought; indeed, several appear to be of considerable importance in separating species.

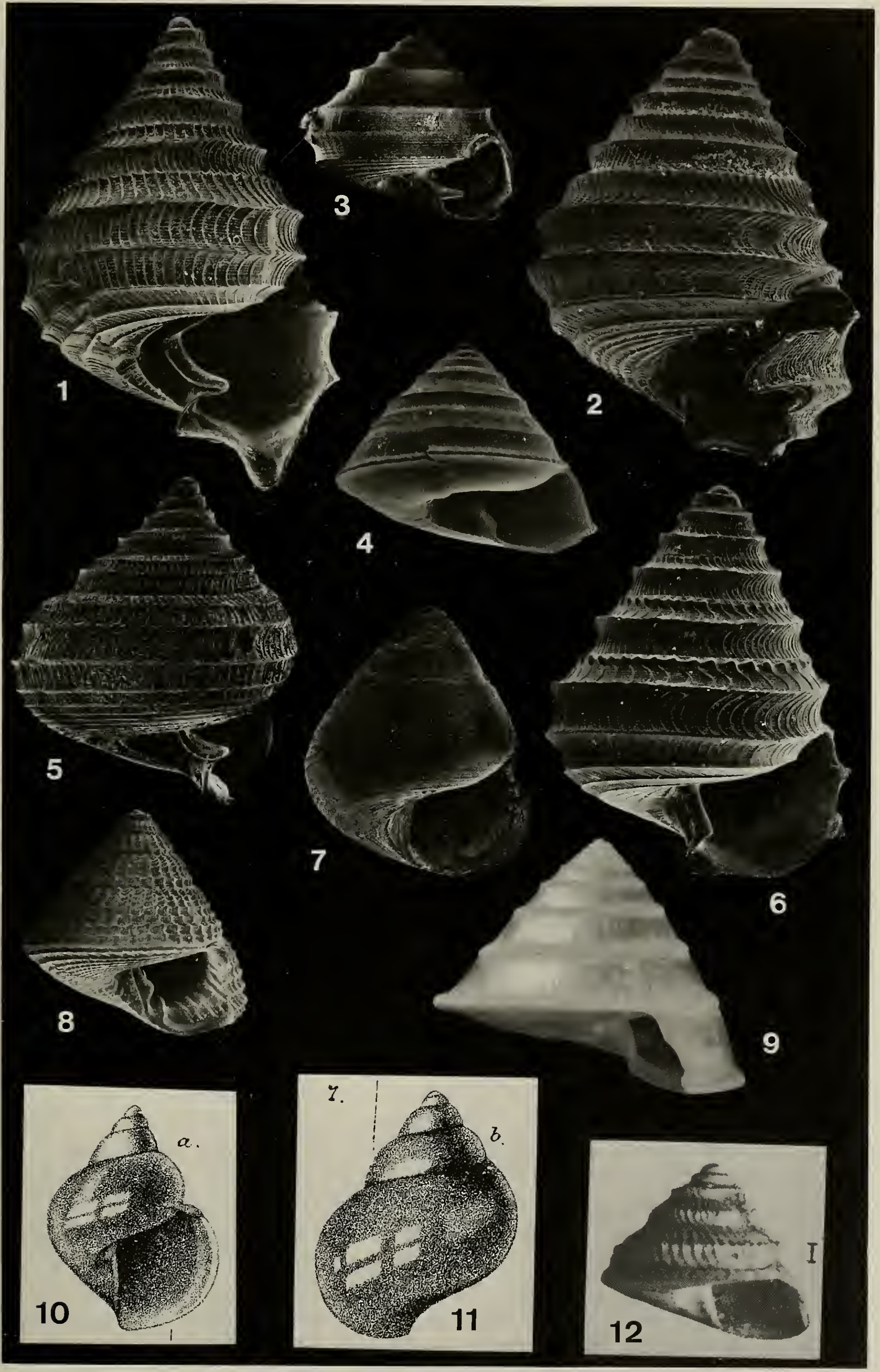
Shell shape.—Shell shapes may be trochoid, turbinate, conoid, or lenticular. Outlines of some major species-groups are given in Figs. 1–14. All seguenziacean groups except *Seguenzia* Group III, *Ancistrobasis,* and *Guttula* are distinctly carinate, at least at the periphery. *Carenzia* and *Basilissopsis* often have a mid-whorl ridge or angulation marking the abapical edge of the posterior labral sinus (Figs. 4, 12), which may approach the strength of the corresponding carina of *Seguenzia* Groups I and II (Figs. 1–3, 5, 6). The latter two species-groups, in addition to peripheral and medial carinae, have a basal, and often a subsutural, carina. Major intraspecific variation in shell shape is conferred by changes in height-width ratio with a concomitant increase or decrease in relative spire height.

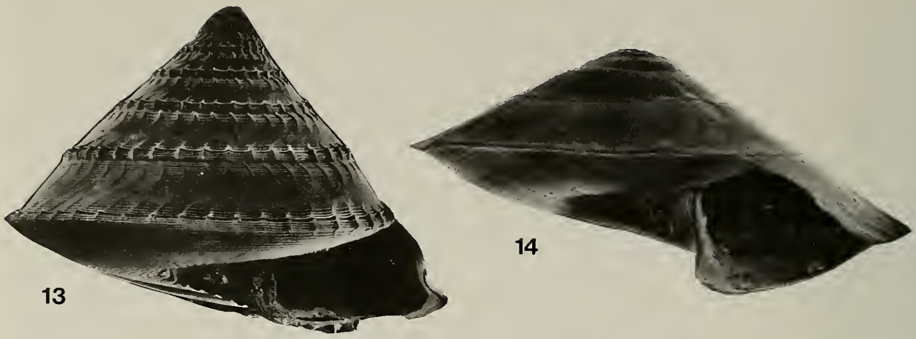
Sculpture.—*Guttula* and *Seguenzia* Groups III and IV, and *Carenzia* are almost devoid of sculpture, having at most fine spiral striae (Figs. 4, 7, 10, 11, 14). *Basilissa, Thelyssa,* and *Basilissopsis* usually have collabral growth lines slightly thickened at regular intervals, producing weak, sigmoid, axial riblets, often crossed by fine spiral threads (Figs. 9, 12, 13). Continuation of axial sculpture onto the peripheral carina often produces a crenulated or scalloped periphery. *Seguenzia* Group II species usually have rather strong spiral basal cords in addition to carinae and fine spiral striae (Fig. 3).

Only *Seguenzia* Group I and *Ancistrobasis* exhibit strong sculptural patterns (Figs. 1, 2, 5, 6, 8). *Ancistrobasis* has reticulate sculpture of subequal axial and spiral cords with nodules produced at the intersections, and the base bears strong, obscurely nodulous or undulate spiral cords. The intricate sculpture of *Seguenzia* Group I is by far the most striking of all seguenziaceans. In addition to the three or four spiral carinae previously described, the shell bears strong basal cords, fine spiral threads between carinae, and collabral riblets. The abrupt changes in di-

→

Figs. 1–12. Seguenziacean shells: 1, 2, 5, 6, *Seguenzia* Group I; 3, *S.* Group III; 4, *Carenzia*; 7, *S.* Group IV; 8, *Ancistrobasis*; 9, *Thelyssa*; 10, 11, *Guttula*; 12, *Basilissopsis*. 1, *Seguenzia* n. sp., Philippines, USNM, SEM, 20×; 2, *S. hapala,* off West Florida, FDNR, SEM, 33.5×; 3, *S. rushi,* off Puerto Rico, USNM, SEM, 13.4×; 4, *Carenzia carinata,* Straits of Florida, UMML, SEM, 13.4×; 5, *Seguenzia* sp. cf. *S. elegans,* off Yucatan, UMML, SEM, 13.4×; 6, *S. lineata,* off Yucatan, UMML, SEM, 20×; 7, *S. siberutensis,* Philippines, USNM, SEM, 13.4×; 8, *Ancistrobasis* n. sp., off West Florida, FDNR, SEM, 13.4×; 9, *Thelyssa callisto,* W of Great Inagua Is., Bahamas, USNM, height 5.8 mm; 10, 11, *Guttula sibogae* (from Schepman 1908, pl. II, fig. 7); 12, *Basilissopsis watsoni* (from Dautzenberg 1927, pl. VI, fig. 36). (USNM = U.S. National Museum of Natural History; FDNR = Florida Department of Natural Resources, Marine Research Laboratory; UMML = Rosenstiel School of Marine and Atmospheric Science, University of Miami.)

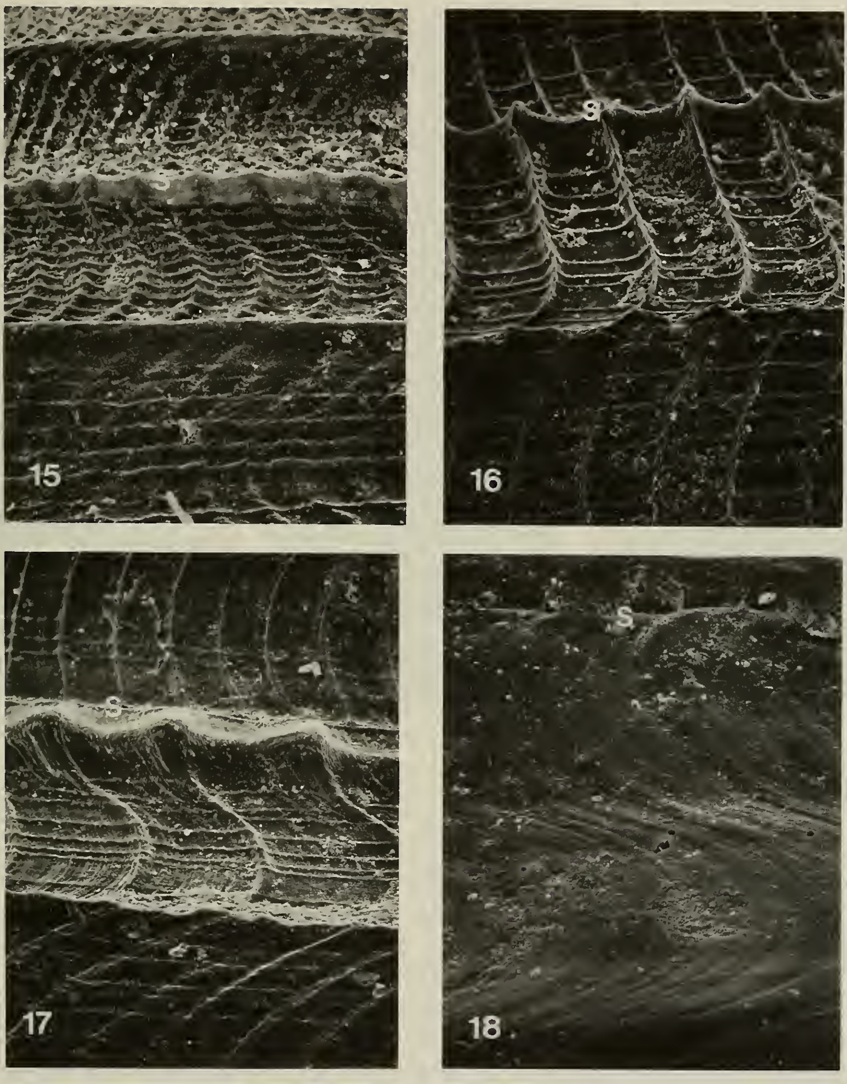

1
2
3
4
5
6
7
8
9
7.
a.
b.
10
11
12



Figs. 13, 14. Seguenziacean shells: 13, *Basilissa alta,* Straits of Florida, UMML, SEM, 6.5×; 14, *Seguenzia* Group IV, *Seguenzia discula,* Straits of Florida, UMML, SEM, 6.5×. (UMML = Rosenstiel School of Marine and Atmospheric Science, University of Miami).

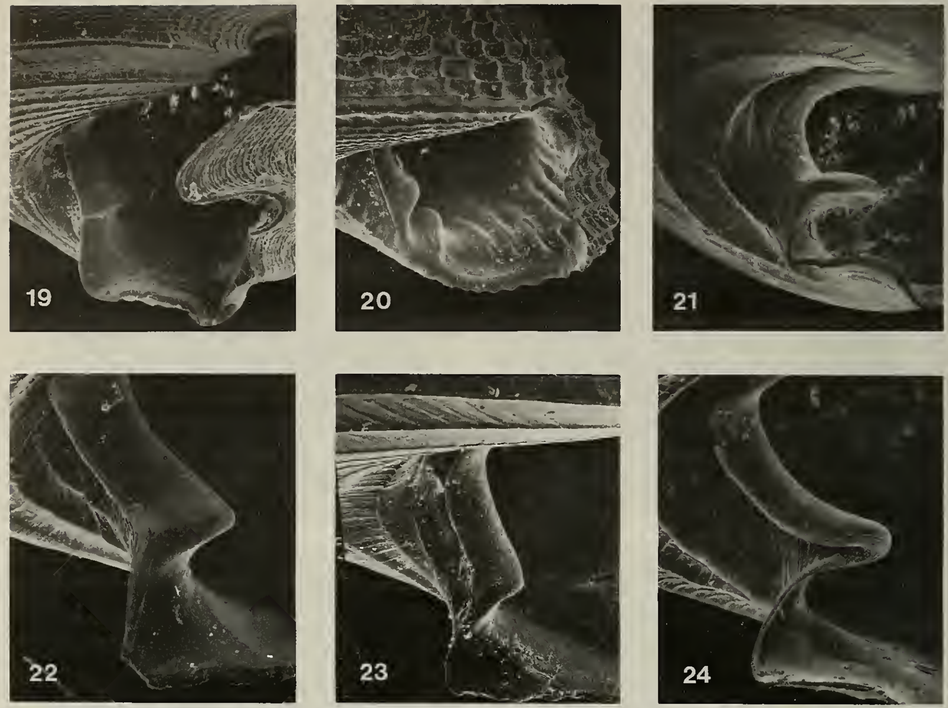
rection of the collabral lirae reflect the positions of the three labral sinuses characteristic of this group.

Labral sinuses.—Reminiscent of many Pleurotomariacea and Turridae, almost all Seguenziacea are characterized by the presence of usually two, often three, sinuses in the outer lip. *Guttula* alone exhibits an entire lip (Fig. 10). All other groups have a shallow to deep subsutural (=anal) sinus and a shallow sinus in the peripheral part of the basal lip. A third, very narrow sinus occurs in the anterolateral part of the lip of *Seguenzia* Group I, corresponding to the peripheral carina, and has been reported to occur in *Seguenzia* Group II (Watson 1879a; 1886). In groups with a strong, flange-like peripheral carina (*Seguenzia* Group IV and *Carenzia, Basilissa, Basilissopsis,* and *Thelyssa*), the anterolateral sinus is represented by a channel corresponding to the carina. The outer lip descends from the suture, defining the edge of the subsutural sinus which may be J- (Figs. 15, 17), reversed L- (Fig. 16), or V- or U-shaped (Fig. 18), then abruptly swings forward perpendicular to the axis of coiling (as far as ¼ whorl in some species of *Seguenzia* Group I), retreats to the anterolateral sinus, advances again for a short distance, retreats again to form the basal sinus, and finally arcs forward slightly to the columellar region. In undamaged specimens of species of *Seguenzia* so far examined, the edges of the three sinuses are usually distinctly flared and often strongly produced into a spout-like process, especially the anal sinus. The "sinus" at the base of the columella may be more an artifact of development of the columellar tooth rather than primarily of functional significance, although there is a shallow, papillate embayment of the mantle edge in *Seguenzia* sp. cf. *S. eritima* (see *Anatomy* section). The basal sinus is analogous to the anterior (inhalent) siphonal canal of many higher gastropods, and the subsutural sinus corresponds to the anal, or excurrent, sinus of many prosobranchs, most notably the pleurotomariaceans and the Turridae. The subsutural sinus apparently appears immediately after termination of the protoconch (Figs. 25–29 herein; see also Bandel 1979, pl. 1, Figs. 2, 4). The slightly sinuous or straight subsutural riblets descend almost perpendicularly before abruptly swinging forward to become confluent with the mid-whorl carina. This configuration is very similar to that seen in adult shells (Figs. 15–17), and seems to contradict Bandel's statement that no subsutural sinus is present prior to the third teleoconch whorl (Bandel 1979:52).



Figs. 15–18. SEM micrographs of surface sculpture of *Seguenzia* and *Carenzia* species, 134× (s = suture): 15, *S. hapala*; 16, *Seguenzia* n. sp.; 17, *S. lineata*; 18, *C. carinata.*

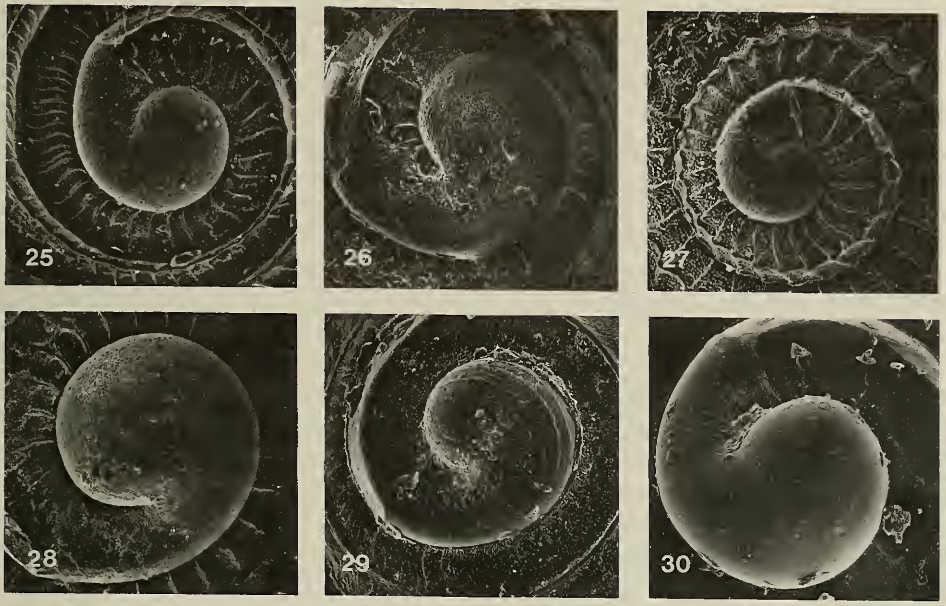
Columellar tooth.—Although the columellae of several seguenziacean groups end in blunt, obscure denticles, only *Seguenzia* Groups I and II, and some *Ancistrobasis* species, have prominent tooth development. The teeth in these groups are basically of three types. The Type I tooth, present in *Ancistrobasis* and a few *Seguenzia* Group I species (Figs. 19, 20), appears as a low to moderate ridge or swelling midway down the columella. This ridge may represent the true termination of the columella, with the vertical part of the basal lip thickened to form an effective continuation of the columellar structure. The Type II, or patulous, tooth (Fig. 21) occurs in *Seguenzia* Group II and occasionally in Group I. It forms a very strong, tongue-like projection extending into the aperture and terminating a strongly concave columella. In some species the projection is not so pronounced



Figs. 19–24. SEM micrographs of apertures of *Seguenzia* and *Ancistrobasis*: 19, *S. hapala,* 50×; 20, *Ancistrobasis* n. sp., 25×; 21, *S. floridana,* 25×; 22, *Seguenzia* sp. 50×; 23, *S. lineata,* 50×; 24, *Seguenzia* n. sp., 50×.

(Figs. 22, 23). The basal lip descends from the outer edge of the tooth well back from the tip (Fig. 21). The Type III tooth (Fig. 24) is also strongly projecting, but forms a fairly acute tooth rather than a broad shelf. In this type, the basal lip joins along the inner side of the tip. Although usually easily distinguishable in specimens in which they are fully developed, teeth of Types II and III are often indistinguishable during ontogeny. In addition, the tooth may appear at different times within the same species, or even within the same population. This usually presents little problem in identification; however, it does pose problems in making accurate and consistent measurements of shell height, since the collumellar tooth is more often preserved than any part of the fragile basal lip.

Protoconch.—The seguenziacean protoconch is perhaps the most conservative shell feature within the group, varying only in size and relative prominence. It is very similar to the trochacean protoconch, consisting of about one whorl, sometimes smooth, but usually sculptured with microscopic granules that usually coalesce into irregular ridges, and ending in a slightly thickened rim (Bandel 1979; Figs. 25–30 herein). Bandel (1979) also showed that the mineralogical ultrastructure of the protoconch was typically archaeogastropodan (see discussion of shell structure below). Size (between 275 μm and 400 μm in all specimens so far examined) and morphology of the seguenziacean protoconch indicate direct or lecithotrophic development (see Bouchet 1976; Bouchet and Warén 1979). Size



Figs. 25–30. SEM micrographs of protoconchs of *Seguenzia, Carenzia, Ancistrobasis,* and *Basilissa,* 100×: 25, *S. hapala*; 26, *Seguenzia* sp. cf. *S. elegans*; 27, *Ancistrobasis* n. sp.; 28, *B. alta*; 29, *C. carinata*; 30, *C. trispinosa.*

of the protoconch is very consistent within a species, and may be used with some confidence to distinguish between morphologically similar species.

Shell structure.—Two studies of the ultrastructural organization of *Seguenzia* have been published recently (Bandel 1979; Barskov et al. 1980). Bandel's study investigated all aspects of shell structure from all parts of the shells of *S. megaloconcha* Rokop and *S. floridana* Dall (as *S. monocingulata* Seguenza), while Barskov *et al.* concentrated on the nacreous layer near the aperture of a shell of *Seguenzia* "sp. 3" from the Pacific [possibly the species cited as *S. ellegans* (sic) in Barsanova (1966)].

Protoconchs of *S. megaloconcha* and *S. floridana* have a very thin periostracum through which crystallites of the outer acicular prismatic layer protrude, forming nodules and irregular ridges, an organization typical of most archaeogastropods (except the Neritacea), but not found in mesogastropods or neogastropods (Bandel 1979). Beneath the acicular prismatic layer are added, in order from outer to inner: granular, dendritic, dissected crossed acicular, and blocky prismatic layers. The granular and dendritic layers disappear in the post-protoconch shell, with the dissected crossed acicular layer forming the entire outer prismatic structure beneath the outer acicular layer in *S. floridana*; in *S. megaloconcha* the dissected crossed acicular organization is replaced by "spherulite sectors with marginal needles dissecting each other" (Bandel 1979:51).

The nacreous layer appears only after the first two post-protoconch whorls, and is sandwiched between the outer dissected crossed acicular (or spherulitic) and inner blocky prismatic layers, except in the last whorl of actively growing individuals where the inner blocky prismatic layer is absent. The nacreous layer comprises numerous lamellae of closely packed, generally rhomboidal tablets (Bandel 1979; Barskov et al. 1980), and forms the major structural unit of the adult shell (Barskov et al. 1980). Insertion of the nacre tablets into the outer prismatic layer may be of two types: a stair-step arrangement found in the whorl walls, and columnar stacks of tablets found on the columellar wall (Bandel 1979). Fully developed nacre, however, is the columnar nacre typical of the Pleurotomariacea and Trochacea (Bandel 1979).

Barskov et al. (1980) reported that the shell of *Seguenzia* "sp. 3," which from their Fig. 1 appears very similar to *S. megaloconcha,* was constructed in two layers: 1) an outer prismatic layer with a thickness of about 0.02 mm, the structure of which they did not describe, and 2) an inner nacreous layer about 0.20 mm thick. Absence of an inner prismatic layer indicates that the specimen was not fully grown because the last whorl of actively growing specimens examined by Bandel (1979:52) also lacked the inner layer. Barskov et al. (1980) described in some detail the structural arrangement of the nacreous layer: generally rhomboidal tablets, 20–30 μm long, 15–20 μm wide, and 4–6 μm high, closely packed into lamellae, with the edges of a tablet offset from those above and below it. This arrangement results in a stair-step, or "brickwork," pattern of tablet stacking which is similar to that characteristic of some bivalves, but not previously known in gastropods (Barskov et al. 1980; also see Wise 1970, and Erben 1972). Barskov et al. interpreted this as distinguishing *Seguenzia* from all other known gastropods. However, the "brickwork" pattern described and figured by Barskov et al. appears virtually identical to the transitional stair-step nacre described and illustrated by Bandel (1979:51, pl. 3, fig. 7) which he found near the edge of the aperture. Since the shell chip examined by Barskov et al. was taken from near the outer lip of their specimen, it seems more probable that they only observed Bandel's transition nacre and missed the typical gastropod type of nacre found by Bandel. Also, if the fracture plane is not just right, it is very difficult to distinguish between the different types of nacre constructions (Dr. Roger Batten, pers. comm.). Therefore, rather than *Seguenzia* being totally different in shell structure from all other gastropod groups, as claimed by Barskov et al., it bears strong similarity to the shell structures of the Pleurotomariacea and Trochacea as demonstrated by Bandel (1979).

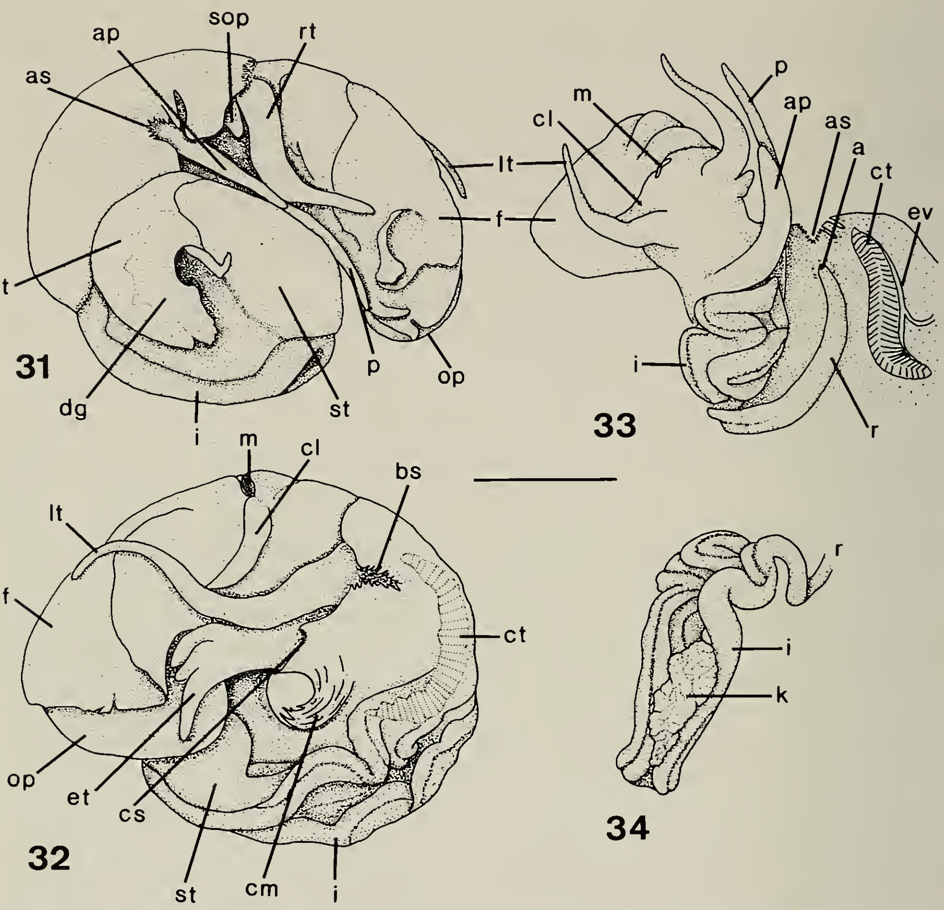
Aperture.—The aperture in *Seguenzia* Group I is roughly auriculate, that of *Guttula* ovate, and in the other seguenziacean genera more or less quadrate. The basic shape of the aperture is often distorted by relative development of, or lack of, a columellar tooth, and by the claw-like extension of the outer lip, especially in *Seguenzia. Ancistrobasis* is the only defined seguenziacean group which develops apertural lirae, consisting of a thickened ridge crenulated by several short, low, rounded ridges, and located at the abapertural edge of the posterior labral sinus (Fig. 20). However, several species of *Seguenzia* develop a ridge similar to that in *Ancistrobasis,* but without the crenulations.

Operculum and Anatomy

Operculum.—In all species for which the operculum has been described (e.g., Bayer 1971: 124, 126, Fig. 7A), it has been characterized as thin, corneous, paucispiral with subcentral nucleus, and auriculiform. Figure 35 shows the operculum of an undescribed *Seguenzia* species. Superficially, it appears more similar to many mesogastropod opercula than to the multispiral opercula of most operculiferous archaeogastropods. However, it is perhaps unwise to attribute phylogenetic significance to this structure since there are some archaeogastropods with similar opercula (e.g., *Euchelus* Philippi), and mesogastropods with multispiral opercula (e.g., *Echininus* Clench and Abbott). Moreover, the oligogyrous condition may be the result of the extremely small size of seguenziaceans.

Anatomy.—Although most shell characters of apparent phylogenetic significance (e.g., nacreous layer, protoconch) indicate that seguenziaceans are archaeogastropod in affinity, the incompletely known anatomy of these animals shows an intriguing combination of characters often used to distinguish archaeogastropods from mesogastropods. There is only one published account of the anatomy of a seguenziacean (*Guttula galatheae*; Knudsen 1964); however, Dr. Philippe Bouchet (in litt.) has informed me that anatomical work on *Carenzia carinata* (Jeffreys) is in progress. To Knudsen's remarks, Dr. James McLean has generously allowed me to add observations he made on a partial dissection of *Seguenzia megaloconcha* Rokop from the eastern Pacific, and I have added a commentary on my own dissection of *Seguenzia* sp. cf. *S. eritima* Verrill (hereafter *S.* "*eritima*"). Knudsen's description of the external anatomy is as follows (Knudsen 1964:128): "The foot is broad and has a distinct median ridge. A well developed propodium is present. The posterior part of the foot is rounded. An epipodium is present, having 3–4 tentacles. The cephalic tentacles are well developed, and pointed. No eyes could be observed. The mantle edge has a finger-shaped tentacle located on the right side. The anus is situated on a rounded lobe projecting from the extreme right side of the mantle edge. The penis is extremely well developed." McLean adds the following commentary on *Seguenzia megaloconcha*: "The foot is contracted so that its shape cannot be described nor the epipodial tentacles counted, though there seem to be six on the right and at least three, probably 6, on the left. In the terminology of Crisp (1981) the epipodial tentacles are papillate like the cephalic tentacles. The foot is too contracted to tell whether or not there are epipodial sense organs. Eyes and optic tentacles are lacking; the cephalic tentacles are long, papillate, and evenly tapered, the greatest diameter at the base 4 times broader than the blunt tips, the attachment to the head constricted to half the maximum basal diameter. The right cephalic tentacle has the right subocular peduncle projecting from the thickened basal area. There are no neck lobes or cephalic lappets. The penis is longer than the cephalic tentacles, not papillate, evenly tapered, the tip narrower in diameter than the tips of the cephalic tentacles, the basal diameter exceeding the diameter of the bases of the cephalic tentacles. The snout is ⅓ the length of the cephalic tentacles, the mouth a vertical slit under an upper lip. The gill is attached to the mantle skirt and is pectinibranch with about 30 triangular filaments, with no evidence of a free bipectinate tip or the transverse pallial vein of the Trochacea. The edge of the mantle skirt is finely fringed, but the pallial tentacle on the right side of the mantle skirt is relatively small."

The following description is based on my study of a male specimen of *S.* "*eritima*": Although strongly contracted, the foot appears to be truncated anteriorly, tapering gradually to a broadly rounded, possibly bilobed, posterior; there



Figs. 31–34. Animal of *Seguenzia "eritima"*: 31, animal removed from shell, right side; 32, same, left side; 33, mantle reflected to right showing head and anterior portion of pallial cavity; 34, dorsal view of intestine and kidney. Scale bar = 1 mm for Figs. 31, 32; 1.5 mm for Figs. 33, 34. Abbreviations: a, anus; ap, accessory cephalic process; as, anal sinus; bs, basal sinus; cl, lateral processes of snout; cm, columellar muscle; cs, columellar sinus; ct, ctenidium; dg, digestive gland; et, epipodial tentacle; ev, efferent branchial vein; f, foot; i, intestine; k, kidney; lt, left cephalic tentacle; m, mouth; op, operculum; p, penis; r, rectum; rt, right cephalic tentacle; sop, subocular peduncle; st, stomach; t, testis.

is a small, short tentacle at each anterolateral corner. There appear to be four pairs of epipodial tentacles which increase in size from anterior to posterior. Epipodial sense organs appear to be lacking. Epipodial tentacles (Fig. 32, et) are like those described by Crisp (1981). The operculum is very thin, corneous, with a subcentral nucleus and about four or five rapidly expanding whorls.

The snout is very short, but provided with long, triangular, lateral extensions (oral lappets?; Figs. 32, 33, cl). The mouth is transversely elongate, surrounded by an outer lip which is interrupted mid-ventrally. The cephalic tentacles (Figs. 31–33, rt, lt) are long, papillate, and tapered from a broad base to a blunt tip. The right tentacle bears a prominent subocular peduncle (Figs. 31, 33, sop) on the base. There are no eyes or optic tentacles. A very long, slender penis (Figs. 31, 33, p) arises from the right side of the head lateral and posterior to the right cephalic tentacle; a ciliated sperm groove runs along the ventral side of the free part of the penis, becoming lateral at the base where the seminal duct opens into the groove. Two small accessory tentacles are situated just posterior to the base of the penis. A large cephalic process (Figs. 31, 33, ap) arises dorsal and posterior to the left cephalic tentacle, crosses the head obliquely to the right, and curves forward to the right of the right cephalic tentacle. It is attached to the head for about half its length, becomes free behind the right tentacle and projects forward between the tentacle and penis.

The mantle edge bears two deep and two shallow papillate embayments, or mantle sinuses, which correspond in position to the shell sinuses. One of the major embayments, corresponding to the basal sinus of the shell, is located over the base of the left cephalic tentacle and undoubtedly acts as the primary incurrent siphon (Fig. 32, bs). This embayment is papillate along the entire edge, and a ridge of muscle is located just back of the edge, indicating that this area can be expanded to some extent. The other large embayment functions as the excurrent, or anal, siphon, and is in the extreme right part of the mantle edge (Figs. 31, 33, as). It too is papillate, but only along the posteriormost edge. The medial edge of this mantle sinus is strongly folded, indicating that considerable extension is possible, forming a baffle or pseudosiphon directing the exhalent current to the right. The two smaller embayments, one located on the extreme left (Fig. 32, cs) and the other mid-dorsally, are both papillate; the other areas of the mantle edge are smooth. There are no pallial tentacles.

The ctenidium (Figs. 32, 33, ct) is monopectinate, with about 30 triangular lamellae, extending in a curve from a posterolateral position medially and anteriorly to end just to the right of the large left mantle sinus. Neither osphradium nor hypobranchial gland was observed. The intestine (Figs. 31–34, i) is prominent, convoluted, arising from the style sac of the stomach, running forward to about the accessory cephalic process, turning to the left and running back to the middle part of the stomach, and finally turning forward along the right to the anus which is on a small papilla. The intestine was filled with fine detrital material (mostly mud, foraminiferan tests, and diatom frustules) which was consolidated into a continuous fecal string which had an ovoidal cross section and a generally dorsal longitudinal groove. The preservation of the large, thin-walled stomach (Figs. 31, 32, st) was not adequate for detailed study of the internal morphology. The left kidney (Fig. 34, k) is located above the stomach, above and within the posterior bight of the intestine. There appears to be no right kidney. The circulatory system is apparently of monotocardian layout. The heart is located dorsolaterally to the right of the anterior end of the stomach. The single auricle receives the long efferent branchial vein and the ventricle is not penetrated by the intestine. The aortae emerge and run along the right side of the body.

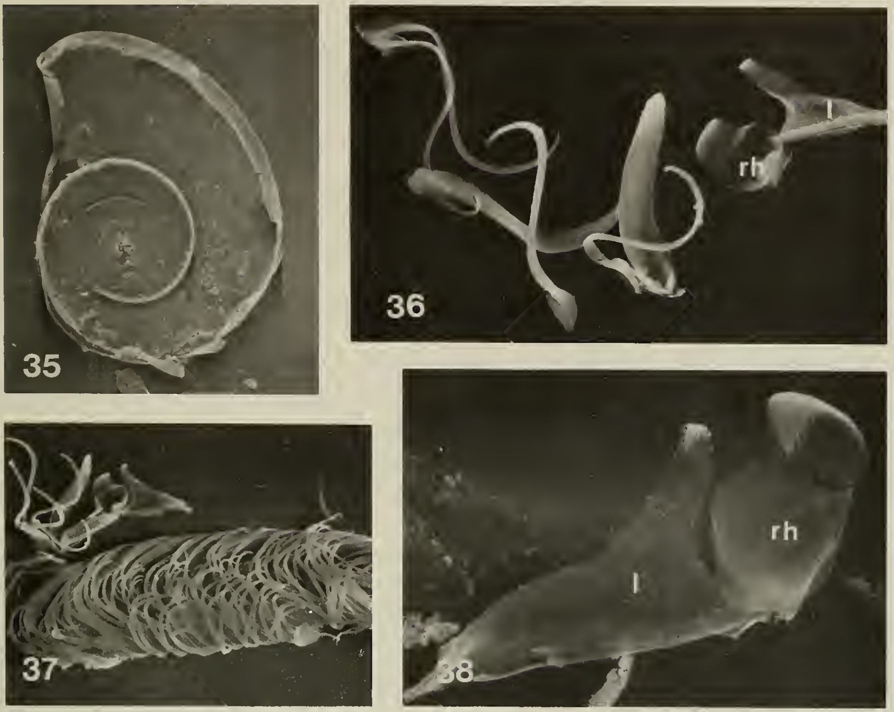
The above descriptions, although of differing completeness, have several elements in common. The epipodium, epipodial tentacles, and penis are shared by all three species. A pallial tentacle is present in both *Guttula galatheae* and *Seguenzia megaloconcha*. Although by no means conclusive, these similarities, along with radula and shell characters, tend to support my inclusion of *Guttula* in the Seguenziacea.

The descriptions of *Seguenzia megaloconcha* and *S.* "*eritima*" agree in most respects, but there are a few obvious differences in external morphology between the two species. The pallial tentacle of *S. megaloconcha* is absent in *S.* "*eritima,*" and there is no basal constriction of the cephalic tentacles in *S.* "*eritima.*" Presence of pallial tentacles in one and not another species of the same genus is also seen in the rissoacean genera *Cingula* and *Onoba* (Fretter and Graham 1978b). This situation may also be found in individuals of the same species (e.g., *Onoba semicostata*; Fretter and Graham 1978b:165). The basal constriction of the cephalic tentacles in *S. megaloconcha* may not have any significance but bears investigation in other species. The lateral extensions of the snout in *S.* "*eritima,*" not found in *S. megaloconcha,* are of functional importance but are of unknown taxonomic significance at present. The extensions are probably primarily sensory in nature, supplementing the cephalic tentacles, but may be used in feeding, either by stirring up the substrate, or by aiding in the movement of food into the mouth.

The most striking difference between *S. megaloconcha* and *S.* "*eritima*" is the large accessory cephalic process which lies obliquely across the head of *S.* "*eritima,*" but is totally absent in *S. megaloconcha.* It is a conspicuous structure, arising from the head behind the left tentacle, remaining attached to the dorsum behind the right tentacle, and finally projecting forward as a finger-like process to the right of the right tentacle. The internal structure of this process has not yet been determined, although it appears to be solid and muscular; its function is not immediately evident, and I have not been able to locate any reference in the literature to a similar structure occurring in any other prosobranch. The penes of *S. megaloconcha* and *S.* "*eritima*" originate at different positions. That of *S. megaloconcha* arises from the dorsum of the head near the midline, and that of *S.* "*eritima*" arises from the right side. The significance of this difference is unclear to me. The location of the anterior and posterior aortae, on the right side of the animal, is apparently unique among coiled gastropods. All accounts I have been able to locate have described the aortae being on the left side. Knowledge of the anatomy of other seguenziacean species is needed before the systematic significance of these anatomical structures can be inferred.

Radula

The distinctive seguenziacean radula combines features of rhipidoglossate and taenioglossate radular types, but fits neither type. All seguenziaceans for which radulae have been illustrated (Figs. 39–48) have the central part of the radula comprised of a rhachidian (Figs. 37, 38, rh) flanked by a single pair of laterals (Figs. 37, 38, l), and the outer part of 4–12 pairs of marginals which completely cover the central portion in the folded, non-working condition (Fig. 36). It thus appears to be a modification of the rhipidoglossate radula, derived by reduction of number of laterals and marginals to the point where, in *Seguenzia* Group I, the radula bears a strong superficial similarity to the taenioglossate state (Fig. 46). In fact, many of the species in the family Triphoridae have radular formulae (Triphorinae, 30-9.1.1.1.9-30; Mastoniinae, 8-5.1.1.1.5-8; see Kosuge 1966) which are similar to that of the seguenziaceans (12-4.1.1.1.4-12). However, the teeth of the two radular types are totally different structurally, and there is little resemblance in shell or anatomy between triphorids and seguenziaceans. There is little



Figs. 35–38. SEM micrographs of operculum and radula of *Seguenzia* sp.: 35, operculum, 47×; 36, intact radular ribbon with marginals folded over central part, 268×; 37, individual teeth teased out of ribbon, 570×; 38, rhachidian and lateral teeth, 1340×.

doubt that these two groups are unrelated, and further comparisons are unnecessary. There are a large number of modified radular types in the archaeogastropods, especially in deep-water groups, and use of this structure to infer relationships should be made with care.

Seguenzia.—(Figs. 36–38, 46–48). The *Seguenzia* radula consists of the rhachidian, a single pair of laterals, and (as far as is known) four pairs of marginals per row. The rhachidian is pyriform with a basal attachment process and a single, denticulate cusp. The lateral has a broad, rather triangular base with a long, slender, finely denticulate cusp near the proximal corner. The first marginal is larger than the rest, blade-like, and denticulate on both sides near the tip. The remaining marginals are long, very slender, with a few fine, spinular teeth slightly removed from the tip, and a rhomboidal base. Both Schepman (1909) and Barnard (1963c) illustrated *Seguenzia* radulae (*S. melvilli* and *S. simplex*; Figs. 47 and 48, respectively) showing rhachidians without the basal process and cuspless laterals. In *S. melvilli,* Schepman may have simply missed the basal process of the rhachidian, and the cusp of the lateral may have been worn or broken off. Barnard's species, *S. simplex,* may not be congeneric with *Seguenzia* sensu stricto, although the same considerations as those mentioned for *S. melvilli* may also apply here. Scanning electron micrographs presented by Bandel (1979) and Hickman (1980) of the radula of *S. megaloconcha* are almost indistinguishable from those presented here (Figs. 36–38, 46) of the radula of an undescribed species from the Philippines. Schepman (1908) also described the radula from a syntype of *Basilissa lampra* Watson, which he mistakenly considered the type of *Basilissa.* However, that radula (Fig. 45) is more similar to those described for *Seguenzia* (Figs. 46–48) than to those of true *Basilissa* (Figs. 40, 41). The shell shape of *B. lampra* is similar to those of *Seguenzia* Group III, so it is probable that this species is a *Seguenzia* sensu lato rather than a *Basilissa.* Thiele (1925) described the radula of *Fluxina trochiformis* Schepman, in which he found a single, broad lateral, a single, rather wide inner marginal, and five outer marginals denticulate on the distal edges. Thiele therefore transferred *F. trochiformis* to *Basilissa.* This species bears a strong conchological resemblance to *F. discula* Dall, which has recently been assigned to *Basilissa* (Merrill 1970b; Quinn 1979). However, *F. discula* and *F. trochiformis* are here referred to *Seguenzia* Group IV pending description of that group as a new genus by Marshall (in press).

Basilissa.—(Figs. 40, 41). The radula of *Basilissa* differs from that of *Seguenzia* sensu stricto in having 6–7 marginal teeth (Bayer 1971) and a larger, more triangular cusp on the lateral tooth.

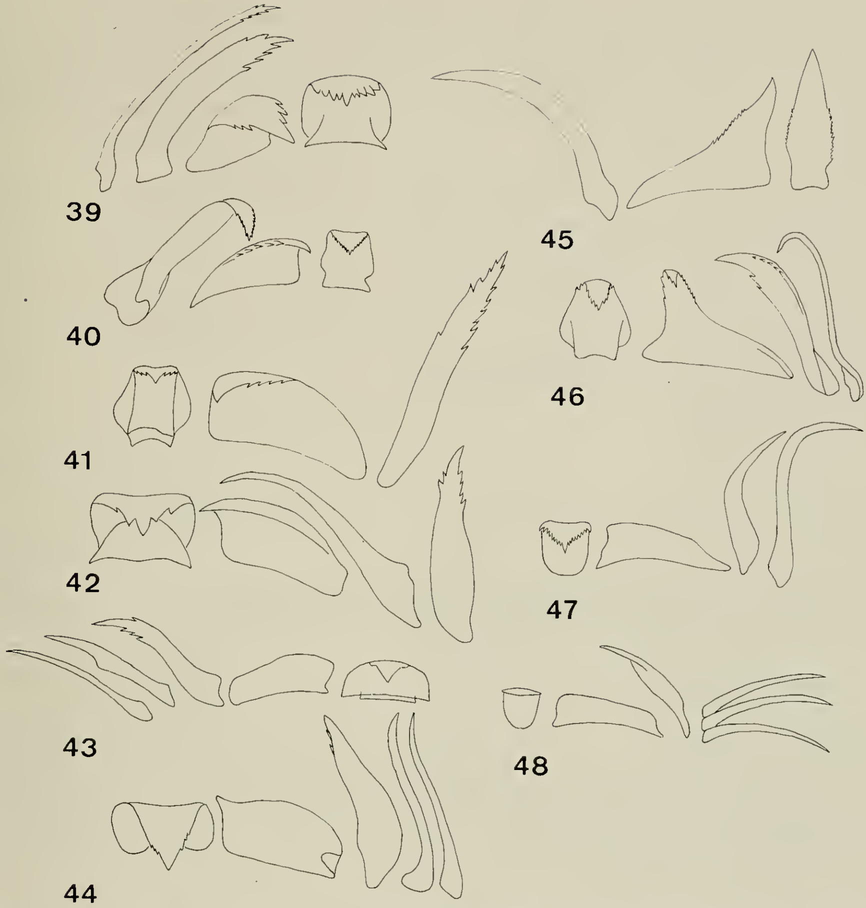
Ancistrobasis.—(Fig. 39). The radula of *Ancistrobasis* has not been previously illustrated or described. It is more trochoid than that of either *Seguenzia* or *Basilissa,* having a rather large, rectangular rhachidian with denticulate cusp, a large, subquadrate lateral with an inwardly directed cusp denticulate on both sides, and twelve slender marginals finely denticulate near the tip.

Guttula.—(Figs. 42–44). The radulae of all three nominal species of *Guttula* have been described and illustrated, and indicate an affinity with more typical seguenziaceans. The rhachidian is broad, rather rectangular, with a denticulate cusp. The lateral is large, broad, and rectangular, with or without a cusp. There are a "few" marginals (no one has given a specific number, although Barnard (1963c:266) states "not more than ten"). The length of the radula of *G. sibogae* Schepman is about 1 mm and its width about 0.3 mm (Schepman 1908). Schepman counted about 20 rows of teeth, Barnard (1963c) about 22.

Fossil Record

As far as is known, the Seguenziacea are relatively young, possibly originating sometime during the late Cretaceous or early Tertiary, and at least one group (*Ancistrobasis*) attained its modern form by the Eocene. Over 20 fossil species have been described, most of which were assigned to *Basilissa,* but less than half of these taxa are true seguenziaceans (Tables 1, 2).

The earliest occurrences of the Seguenziacea in the geological record are *Seguenzia radialis* Tate (Tate 1888, 1890) and *Basilissa cossmanni* Tate (Tate 1894) from the Eocene of South Australia, and *Basilissa* (*Ancistrobasis*) *pacifica* Ladd (Ladd 1970) from the Eocene of Tonga. All three taxa are here considered *Ancistrobasis* species. *Ancistrobasis* also occurs in the Pliocene of Sicily (*Solarium reticulatum*; Philippi 1844; Jeffreys 1885). The first known occurrence of *Seguenzia* is *S. hapala* Woodring from the middle Miocene of southern Mexico (Perrilliat 1972). Specimens of this species have also been collected from the basal Pliocene of the Dominican Republic (Gurabo Formation; H. E. Vokes, in litt.), the upper Pliocene-basal Pleistocene of Jamaica (Bowden Formation; Woodring



Figs. 39–48. Diagramatic sketches of seguenziacean radulae, not to scale: 39, *Ancistrobasis depressa*; 40, *Basilissa alta* (after Bayer 1971); 41, *B. sibogae* (after Schepman 1908); 42, *Guttula sibogae* (after Schepman 1908); 43, *G. blanda* (after Barnard 1963); 44, *G. galatheae* (after Knudsen 1964); 45, *Seguenzia lampra* (after Schepman 1908); 46, *Seguenzia* sp.; 47, *S. melvilli* (after Schepman 1909); 48, *S. simplex* (after Barnard 1963).

1928), and the Recent throughout the Gulf of Mexico and Caribbean [Treece, 1977, 1980 (as *S. formosa*); Treece 1979 (as *S. monocingulata*); Quinn unpublished data]. Seguenza (1876, 1877, 1879) recorded *S. monocingulata* from the Pliocene of Italy. *Mioseguenzia* Nordsieck, 1973, described with a Miocene type-species, is cypraeacean (Bouchet, in litt.), not seguenziacean. Some members of the Paleozoic-Mesozoic family Omphalotrochidae Knight, 1945, bear a superficial resemblance to *Basilissa,* but, as discussed below, this similarity is probably convergent and not an indication of relationship.

Other allocations of fossil species to *Basilissa* (Cossmann 1888; Noetling 1901; Oppenheim 1906, 1923; Yokoyama 1922; Koperberg 1931; Riedel 1932; Ravn 1933, 1939) followed Cossmann's (1888) erroneous concept of the genus. Most of these species appear to be referrable to the Trochidae (Table 2).

Table 2.—Taxa rejected from, or of doubtful inclusion in, the Seguenziacea.

ORIGINAL BINOMEN	
Seguenzia tricarinata Jeffreys, 1885	Nassariid protoconch
S. laxa Jeffreys, 1885	Indeterminate
†*Basilissa boutillieri* Cossmann, 1888	?
B. patula von Martens, 1901	*Calliotropis*
†*B. lorioliana* Noetling, 1901	?
B. ottoi var. *chuni* von Martens, 1903	*Calliotropis*
†*Trochus* (*Basilissa*) *libycus* Oppenheim, 1906	?
B. babelica Dall, 1907	*Orectospira*
B. niceterium Hedley and May, 1980	*Calliostoma*
†*B. ?laeviuscula* Yokoyama, 1922	*Proconulus*?
Trochus (*Basilissa*) *lukavatzensis* Oppenheim, 1923	?
†*B. lemoinei* Koperberg, 1931	?
†*B. antiqua* Riedel, 1932	?
†*B. tricincta* Ravn, 1933	cf. *Bathybembix*
†*B. odumi* Ravn, 1939	cf. *Bathybembix*
†*B.* (*Orectospira*) *nenokamiensis* Kanno, 1958	*Orectospira*
B. bicarinata Habe, 1961	*Calliotropis*
Mioseguenzia Nordsieck, 1973	
Type-species.—*Janthina cimbrica* Sorgenfrei, 1958; by original designation.	
†*M. cimbrica* (Sorgenfrei, 1958)	Cypraeacean larval shell
M. cimbrica recens Nordsieck, 1973	Cypraeacean larval shell
M. conica Nordsieck, 1973	Cypraeacean larval shell

† = species described from fossil material.
? = affinities uncertain.

Relationships

Speculations on relationships of the Seguenziacea to other prosobranch groups have been, and remain, inconclusive. Jeffreys (1876, 1879) strongly advocated assignment of *Seguenzia* to the Solariidae (=Architectonicidae), but this view has never gained acceptance. Following Seguenza's (1876) lead, many authors have placed *Seguenzia* in the Trochidae (Watson 1879a, 1886; Thiele 1925, 1929; Wenz 1938; Cotton 1959; Keen and Cox 1960; Barnard 1963c; Knudsen 1964; Barsanova 1966; Bayer 1971; Abbott 1974). These authors also considered *Basilissa* and *Guttula* to be trochids. *Seguenzia* has also been included in the Pleurotomariidae (Tryon 1883), Haliotidae (von Martens 1881; Tate 1888), and Scissurellidae (Locard 1898), principally because of the posterior sinus in the outer lip. Verrill's (1884) establishment of the Seguenziidae, including *Seguenzia* and *Basilissa,* and placement in the Mesogastropoda near the genus *Aporrhais* was followed by Golikov and Starobogatov (1975). The Seguenziidae have also been placed near, or included in, the Trichotropidae (Tryon 1887; Dall 1889b, c; Tate 1890; provisionally by Schepman 1909), near the Triphoridae (Dall 1927; Woodring 1928; Taylor and Sohl 1962), between the Archaeogastropoda and Mesogastropoda (Keen 1971), and near the Trochidae (Clarke 1961, 1962; Bandel 1979; Quinn 1979, 1981; Boss 1982). Recently Goryachev (1979) proposed inclusion

Table 3.—Comparison of shell and anatomical features of the Trochacea, Seguenziacea, and Rissoacea. Characters of the Trochacea and Rissoacea taken from Fretter and Graham (1962).

Structure	Trochacea	Seguenziacea	Rissoacea
Shell	Nacreous or porcellaneous	Nacreous	Porcellaneous
Protoconch	Archaeogastropod	Archaeogastropod	Mesogastropod
Radula	Rhipidoglossate	Modified rhipidoglossate	Taenioglossate
Epipodium	Present, with tentacles and sense organs	Present, with tentacles	Absent
Reproductive system	No copulatory organs; gametes shed through right kidney; fertilization external	Penis and closed gonoduct present; fertilization internal	Penis present; glandular gonoducts with accessory structures in female; fertilization internal
Ctenidium	Bipectinate (rarely monopectinate)	Monopectinate	Monopectinate
Pallial tentacles	Absent	Present in at least 2 species	Often present
Circulatory system	Diotocardian, with transverse pallial vein	Monotocardian (?), without transverse pallial vein	Monotocardian
Kidneys	Both right and left present	Right kidney lost (?)	Right kidney lost
Intestine	Long, with anterior loop; rectum passing through ventricle	Long, with anterior loop; rectum free of ventricle	Short, without anterior loop; rectum free of ventricle

of the Seguenziidae in the Protopoda Fisher, 1884 [sensu Golikov and Starobogatov (1975) = Turritellacea + Vermetacea] or possibly in a separate order. In view of data presented here, both proposals seem very unlikely. These assignments were made principally on the evidence of shell and, occasionally, radular characters. Therefore, features of the anatomy and shell morphology detailed in this paper permit a more critical examination of the possible affinities of the Seguenziacea than has yet been possible.

The first problem in assessing the probable relationships of the Seguenziacea is to determine the proper prosobranch suborder, Archaeogastropoda or Mesogastropoda, to which the group should be assigned. Table 3 presents a summary of the known characters of the Seguenziacea in comparison with corresponding traits of the Trochacea and Rissoacea, as representatives of the Archaeogastropoda and Mesogastropoda, respectively. If the use of the term "mesogastropod" is restricted to describe a certain level of anatomical organization rather than as a discrete taxonomic entity (Fretter et al. 1981), the Seguenziacea must be interpreted as mesogastropodan. However, as will be argued below, most of the *Seguenzia*-mesogastropod (the taxon) similarities are probably convergent, and may not be indicative of any phytogenetic relationship. Therefore, I propose that the Seguenziacea are highly modified and specialized archaeogastropods whose anatomical advances are consequences of extremely small body size and adaptation to life in the deep-sea.

Two seguenziacean characters which are the most indicative of archaeogastropod affinity are the shell and radula. Nacreous shells are known in the Monoplacophora and some lower groups of the Bivalvia, Cephalopoda, and Gastropoda, leading to the assumption that nacre is a primitive character within the Mollusca. Besides the Seguenziacea only two groups of living gastropods, the Pleurotomariacea and most Trochacea (both archaeogastropod), have nacreous shells. Nacre has not been noted in any mesogastropod or higher group. The seguenziacean radula seems to be a modification of the rhipidoglossate radula. Verrill's (1884) description of the radula of *S. eritima* as taenioglossate has induced many authors to assign *Seguenzia* to the Mesogastropoda. The seguenziacean radula does resemble the taenioglossate radula superficially, principally in having only a single lateral and a reduced number of marginals in each radula half-row. Of the mesogastropod families discussed by Boss (1982), only two were recorded as having more than two marginal teeth, the Turritellidae (3-0.1.1.1.0-3) and the Triphoridae (30-9.1.1.1.9-30 or 8-5.1.1.1.5-8), and neither family is in any way similar to seguenziaceans in shell or anatomy. Moreover, the two marginals of the typical taenioglossate radula are very similar to each other in shape and size. Seguenziacean marginals are morphologically different, the innermost tooth being rather large and robust and the outer whisker-like, a situation reminiscent of several rhipidoglossate ground plans in which the marginals may be divided into two or more distinct morphological groups, with the innermost usually much stronger than the outer. It has been suggested to me that the multiple marginals of the seguenziacean radula might have been produced by repeated splitting of the taenioglossan marginals. While this remains a possibility, especially in view of the observations of Shimek and Kohn (1981) on the Turridae, the apparent affinity of the Seguenziacea with archaeogastropods such as the Trochacea (discussed below) suggests that the seguenziacean radula is merely a modification of the rhipidoglossate radula, and is adapted for sweeping particulate matter from the bottom and conveying it to the esophagus.

Other traits of the Seguenziacea which suggest archaeogastropod affinity are a long intestine with an anterior loop, a subocular peduncle on the base of the right cephalic tentacle, and an epipodium with epipodial tentacles. The intestine follows a course similar to that of the Trochacea, but the seguenziacean anterior loop (perhaps not homologous with that of the Trochacea?) is much longer, and the intestine does not penetrate the ventricle. The subocular peduncle has been noted in several species of Trochidae (Crisp 1981), but to my knowledge is not known in any other prosobranch group, except, perhaps, the Fissurellacea (McLean, in litt.). The epipodium and associated tentacles have been generally considered an archaeogastropod trait (Fretter and Graham 1962), but epipodial tentacles are also known in some mesogastropods [e.g., Litiopidae and Dialidae (Houbrick 1980; see also Thiele 1929)]. Even the fecal string of *Seguenzia* resembles that of the Trochacea, although there is no liver string (see Fretter and Graham 1962).

Several seguenziacean features show progression into an advanced grade of organization. However, most of the advancement may be attributed to adaptation to a small body size and for increased functional efficiency. The radula has already been discussed. The other principal modifications include the development of an advanced reproductive tract, a monopectinate ctenidium, and functional inhalent and exhalent pallial siphons.

Although no in-depth anatomical examination of the seguenziacean reproductive system has yet been made, presence of a well-developed penis suggests other modifications of the tract, such as possible accessory structures in the female oviduct. I have not examined any females, but Dr. Anders Warén (pers. comm.) has indicated that such modifications may be present in female *Carenzia carinata* from the northeastern Atlantic. My examination of the male of *S.* "*eritima*" indicates a simple sperm duct, without prostate gland, which opens into a ciliated sperm groove on the penis. Penial structures, either as modifications of a cephalic tentacle or de novo structures, are rare, but not unknown in the archaeogastropods. Perhaps the best known situation is in the Neritacea, in which a true cephalic penis has been developed (see Fretter and Graham 1962; Fretter 1965). Several other archaeogastropod groups also have been reported to have a penis: Cocculinacea (*Cocculina* and *Addisonia*; see Dall 1889b, 1890); Trochidae [*Solariella* (=*Calliotropis*) and *Turcicula* (=*Bathybembix*); Dall 1889a, b, 1890]; Fissurellacea (*Rimula* and *Fissurella*; Dall 1889b); and the recently described Neomphalacea (*Neomphalus*; McLean 1981; Fretter et al. 1981). The Cocculinacea and Neomphalacea each have a modified cephalic tentacle (the former the right, and the latter the left tentacle), but the function as a penis is undoubted. The "penis" described by Dall (1889b) in the Fissurellacea was found to be solid by Odhner (1932) who referred to the structure as a "sexual cirrus." The rudimentary "penis" reported in the Trochidae (Dall 1889a, b, 1890) has not been investigated subsequently. McLean (in litt.) considers the penis-like structures of the fissurellaceans and trochids to be the right subocular peduncle. Since all archaeogastropod groups with an undoubted penis except the Neritacea (Cocculinacea, Neomphalacea, and Seguenziacea) are principally deep-sea forms, and most are extremely small (less than 10 mm, except *Neomphalus fretterae* McLean, 1981, which may be as much as 30 mm in diameter and which lives in a unique situation, the Galápagos Rift), energy conservation is a primary concern. Internal fertilization severely reduces the wastage of gametic products, and evolution of copulatory structures would be the most efficient solution to that problem.

A monopectinate ctenidium is generally associated with a mesogastropod, or higher, grade of organization, and has not been reported previously in any archaeogastropod except *Umbonium* (Fretter 1975; McLean 1981). Presence of such a ctenidium in the Seguenziacea may well be an adaptation for economy of space in the pallial cavity of these small animals. A monopectinate ctenidium provides more efficient use of space and eliminates any circulatory dead spots which are found in most bipectinate ctenidia. However, the change from bipectinate to monopectinate conditions must require some compensation for the decrease in strength of the ciliary currents flowing through the pallial cavity caused by reduction of the number of ctenidial leaflets; therefore, the Seguenziacea, like many mesogastropods and virtually all neogastropods, have modified the mantle edge to form inhalent and exhalent siphons. However, seguenziacean siphons are papillate embayments in, rather than extensions of, the mantle edge. The papillae may augment the ctenidial cilia in producing the inhalent and exhalent currents, and the siphons undoubtedly enhance the efficiency and directionality of the currents. The seguenziacean siphons are apparently analogous to those of mesogastropods and neogastropods, but are de novo structures derived in conjunction with evolution of a monopectinate ctenidium. In addition, in at least one species (*S.* "*eritima*"), a cephalic process forms a baffle across the opening of the mantle cavity which probably prevents water from entering or exiting the mantle cavity except through the siphons.

Since the known features of the Seguenziacea are either clearly archaeogastropod in nature or can be derived from archaeogastropod structures as adaptations for small body size and life in the deep-sea, it seems most prudent to consider the Seguenziacea the end of a long-separated evolutionary lineage of archaeogastropod derivation, which has developed mesogastropod-like adaptations independent of any mesogastropod lineage. In this regard, the Seguenziacea are similar to the Neomphalacea (McLean 1981) and Neritacea (Fretter and Graham 1962; Fretter 1965).

If Seguenziacea are indeed archaeogastropods, as argued here, then which group might be considered seguenziacean precursors? Solely on the basis of shell shapes and position of anal sinuses, two possibilities exist. First is an origin in a euomphalacean group such as the Omphalotrochidae Knight, 1945, especially *Omphalotrochus* Knight, 1945, *Orecopia* Knight, 1945, and *Babylonites* Yochelson, 1956. Earlier (Quinn 1981) I suggested that the Seguenziacea might have been derived from such omphalotrochids based on the subsutural sinus and channeled, claw-like extension of the outer lip, which are apparent homologues of the anal and basal sinuses of the seguenziacean shell. McLean (1981) has since pointed out that the Omphalotrochidae are not known to have nacreous shells, and that a reversion to the nacreous condition would be unlikely. In addition, there is a gap of about 200 million years between the extinction of the Omphalotrochidae (Middle Permian) and the earliest known seguenziacean (Eocene). Therefore, an Omphalotrochidae-Seguenziacea lineage is not supported.

The other, and more probable origin, involves a derivation from within the Pleurotomariacea-Trochonematacea-Trochacea lineage. It has been hypothesized that the Pleurotomariacea gave rise to the Trochonematacea (Knight et al. 1960), which in turn were ancestral to the Trochacea (Fretter and Graham 1962). All three superfamilies have nacreous shells and the Pleurotomariacea and Trochonematacea both have labral sinuses. We know the anatomy of living Pleurotomariacea and Trochacea from which we may infer possible relationship with the Seguenziacea, but inferences about the extinct Trochonematacea are purely speculative. The Pleurotomariacea are gastropods retaining such primitive conditions as paired pallial organs, simple reproductive system and intestine penetrating the ventricle [see Fretter and Graham (1962) and Fretter (1964, 1966) for summary of other features]. From the position of the shallow anal sinus or channel, the Trochonematacea were probably dibranchiate, with the right ctenidium possibly being lost in the later forms (Knight et al. 1960). The Trochacea have lost the right ctenidium and osphradium, but retain the other paired pallial structures, the intestine is long, with an anterior loop, but still penetrates the ventricle, and the reproductive system remains relatively unspecialized (Fretter and Graham 1962). The Pleurotomariacea and Trochacea have rhipidoglossate radulae, although comparatively reduced in the latter group, and, in most other anatomical regards, the Trochacea and Pleurotomariacea are also remarkably similar (Fretter and Graham 1962; Fretter 1964, 1966; Graham 1965). Although similar to the

Trochacea and Pleurotomariacea in having nacreous shells, rhipidoglossate radulae (although modified), epipodium and epipodial tentacles, and an anterior loop of the intestine, the Seguenziacea have highly modified reproductive and circulatory systems and a monopectinate ctenidium, which indicate a long-standing separation from the mainstream of archaeogastropod evolution. My contention that the seguenziaceans are more likely to have had their origin within the Trochacea rests primarily on the fact that it seems more plausible to derive the seguenziacean organization as modifications of a trochoid organization than of a zeugobranch condition, and secondarily on the radula, trochoid-like fecal-string, and cephalic tentacles, especially the presence of a subocular peduncle on the right tentacle. Admittedly, this is rather tenuous evidence from which to draw a conclusion, but may serve as a working hypothesis for further research.

Since the anatomy of no seguenziacean is fully known, only three having been partly described, and the fossil record is so scanty, no discussion of relationships within the superfamily is now possible, nor is it possible to determine whether the anal sinus is a primitive character which was inherited from some ancestor or an innovation of the seguenziaceans. In view of the tendency of many other prosobranchs to develop similar structures, I believe the latter to be true, thus reinforcing my belief that the seguenziaceans are derived from some holostomatous ancestor, i.e., a trochoid. It is probable that additional family-group taxa may be required as future systematic studies are completed. Indeed, the monophyly of the Seguenziacea may even now be questioned. For example, it could be argued that the genera with labral sinuses may have evolved from the Trochonematacea, *Guttula* may have arisen independently from the Trochacea, and the selective pressures of similar habitats subsequently produced similarly constructed organisms. However, the presence of a penis, epipodium and epipodial tentacles, and radulae and shells similar to some undoubted seguenziaceans, suggest that *Guttula* should be included in the Seguenziacea.

Therefore, the Seguenziacea, as here defined, comprise the genera *Seguenzia, Carenzia, Basilissa, Basilissopsis, Ancistrobasis, Thelyssa,* and *Guttula.* The superfamily is characterized by nacreous shells, generally with labral sinuses, modified rhipidoglossate radula, and an anatomy retaining some archaeogastropod traits (epipodium with tentacles, long anterior loop of the intestine, and subocular peduncle) but attaining several mesogastropod features (penis in males, monopectinate ctenidium, and monotocardian circulatory system). This combination is so different from other known prosobranchs that there can be little doubt that recognition of a separate superfamily as suggested by Keen (1971), Golikov and Starobogatov (1975), Goryachev (1979), Quinn (1981, 1983a, b), McLean (1981), and Marshall (in press) is necessary. The Seguenziacea are here retained within the Archaeogastropoda as an independent offshoot of the Pleurotomariacea-Trochonematacea-Trochacea lineage, with the Trochacea as the most probable ancestral stock.

Acknowledgments

I thank the following curators for the opportunity to examine specimens in their care: Dr. Richard S. Houbrick (U.S. National Museum of Natural History, Mollusks), Dr. Gilbert L. Voss (Rosenstiel School of Marine and Atmospheric Science, University of Miami), Dr. Kenneth J. Boss (Museum of Comparative

Zoology, Harvard University), Dr. John Peake and Ms. Kathie Way (British Museum, Natural History), Dr. Thomas R. Waller (U.S. National Museum of Natural History, Paleobiology), Mr. Granville D. Treece (Marine Science Institute, University of Texas), and Dr. Linda H. Pequegnat (Texas A&M University). I am especially indebted to Dr. Michael A. Rex (University of Massachusetts) for providing the preserved specimens of *Seguenzia* "*eritima.*"

Parts of this paper were presented at the 1980 and 1982 annual meetings of the American Malacological Union. I am grateful to those colleagues who provided numerous valuable critiques of and suggestions on those presentations. Special thanks go to Drs. James H. McLean (Los Angeles County Museum), Carole S. Hickman (University of California, Berkeley), Philippe Bouchet (Laboratoire de Malacologie, Muséum National d'Histoire Naturelle, Paris), and Boss and Houbrick who kindly read and commented on earlier versions of this manuscript. Dr. McLean also generously allowed me to incorporate some of his unpublished anatomical observations and examine specimens of *Seguenzia megaloconcha.* Dr. Bruce A. Marshall (National Museum of New Zealand) kindly provided me with advance information concerning new taxa from the New Zealand region. The manuscript also benefitted from comments by William G. Lyons, Thomas H. Perkins, and Scott A. Willis, and SEM services were provided by Lana Tester (all Florida Department of Natural Resources Bureau of Marine Research).

This paper is a scientific contribution from the Rosenstiel School of Marine and Atmospheric Science, University of Miami, and forms part of a dissertation submitted to the school in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Literature Cited and Bibliography

Abbott, R. T. 1974. American seashells. 2nd Ed. Van Nostrand Reinhold, New York, 663 pp.

Bandel, K. 1979. The nacreous layer in the shells of the gastropod-family Seguenziidae and its taxonomic significance.—Biomineralisation 10:49–61.

Barnard, K. H. 1962. New species and records of South African marine Mollusca from Natal, Zululand, and Moçambique.—Annals of the Natal Museum 15(19):247–254.

———. 1963a. Deep-sea Mollusca from the region south of Madagascar.—Department of Commerce and Industries, Investigational Report No. 44:1–19.

———. 1963b. Deep-sea Mollusca from west of Cape Point, South Africa.—Annals of the South African Museum 46:407–453.

———. 1963c. Contributions to the knowledge of South African marine Mollusca. Part IV. Gastropoda: Prosobranchiata: Rhipidoglossa, Docoglossa, Tectibranchiata, Polyplacophora, Solenogastres, Scaphopoda.—Annals of the South African Museum 47:201–360.

———. 1966. Deep-sea Mollusca from the region south of Madagascar.—International Indian Ocean Expedition, Collected Reprints 2:1–19 (reprint of Barnard, 1963a).

———. 1974. Contributions to the knowledge of South African Marine Mollusca. Part VII. Revised Fauna List.—Annals of the South African Museum 47:663–781.

Barsanova, N. G. 1966. K nachozhdeniyu glubokovodnikh predstavitelei semeistva Seguenziidae (Gastropoda, Prosobranchia) v Tikhom Okeane. [On the finding of deep-sea representatives of the family Seguenziidae (Gastropoda, Prosobranchia) in the Pacific Ocean].—Trudy Instituta Okeanologii 81:144–152.

Barskov, I. S., M. A. Golovinova, and V. N. Goryachev. 1980. [Structure of the nacreous layer of deep-water mollusks of the genus *Seguenzia* (Mollusca, Gastropoda)].—Doklady Akademii Nauk SSSR 252(4):1015–1017. [In Russian; translation in Doklady Biological Sciences 252: 312–314.]

Bayer, F. M. 1971. New and unusual mollusks collected by R/V JOHN ELLIOTT PILLSBURY and R/V GERDA in the tropical western Atlantic.—Bulletin of Marine Science 21(1):111–236.

Belyaev, G. M. 1966. Donnaya fauna naibol'shikh glubin (ul'traabissali) Mirovogo okeana. [The benthic fauna of the greatest depths (ultra-abyssal) of the world ocean.].—Izdatel'stvo "Nauka," Moscow, 248 pp.

Boss, K. J. 1982. Seguenziidae, pp. 973–974.—*In* S. P. Parker (ed.), Synopsis and Classification of Living Organisms. Vol. 1. McGraw-Hill, New York.

Bouchet, P. 1976. Mise en évidence de stades larvaires planctoniques chez des Gastéropodes Prosobranches des étages bathyal et abyssal.—Bulletin Muséum National d'Histoire Naturelle, Paris (3) 400:947–972.

Bouchet, P., and A. Warén. 1979. Planktotrophic larval development in deepwater gastropods.—Sarsia 64(1–2):37–40.

Cernohorsky, W. O. 1978. Tropical Pacific marine shells. Pacific Publications, Sidney/New York, 352 pp.

Clarke, A. H., Jr. 1959. New abyssal molluscs from off Bermuda collected by the Lamont Geological Laboratory.—Proceedings of the Malacological Society of London 33(5):231–238.

———. 1961. Abyssal mollusks from the South Atlantic Ocean.—Bulletin of the Museum of Comparative Zoology 125(12):345–387.

———. 1962. Annotated list and bibliography of the abyssal marine molluscs of the world.—National Museum of Canada, Bulletin 181:114 pp.

Cossmann, M. 1888. Catalogue illustré des coquilles fossiles de l'Eocène des environs de Paris. III.—Annales de la Société Royale Malacologique de Belgique 23:3–324.

———. 1918. Essais de Paléoconchologie comparée. Vol. 11. Paris, 388 pp.

Cotter, G. de P. 1907. Fossils from the Miocene of Burma.—Records of the Geological Survey of India, Calcutta 36:131–132.

Cotton, B. C. 1946. Australian beaded top shells.—South Australian Naturalist 23(3):6–8.

———. 1959. South Australian Mollusca. Archaeogastropoda. Handbook of the flora and fauna of South Australia. Government Printer, Adelaide, 449 pp.

———, and F. K. Godfrey. 1931. South Australian shells, including descriptions of new genera and species.—South Australian Naturalist 12(4):51–63.

———, and ———. 1938. New species of South Australian Gastropoda.—Records of the South Australian Museum, Adelaide 6(3):199–206.

Crisp, M. 1981. Epithelial sensory structures of trochids.—Journal of the Marine Biological Association of the United Kingdom 61(1):95–106.

Dall, W. H. 1881. Preliminary report on the Mollusca. Reports on the results of dredging . . . in the Gulf of Mexico, and in the Caribbean Sea, 1877–79, by the United States Coast Survey steamer "Blake". . .—Bulletin of the Museum of Comparative Zoology 9(2):33–144.

———. 1885. List of marine Mollusca comprising the Quaternary fossils and Recent forms from American localities between Cape Hatteras and Cape Roque including the Bermudas.—United States Geological Survey Bulletin 24:1–336.

———. 1889a. Notes on the soft parts of *Trochus infundibulum* Watson, with an account of a remarkable sexual modification of the epipodium, hitherto undescribed in Mollusca.—Nautilus 3:2–4.

———. 1889b. Report on the Mollusca. Part II. Gastropoda and Scaphopoda. Reports on the results of dredging . . . in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey steamer "Blake" . . .—Bulletin of the Museum of Comparative Zoology 18: 1–492.

———. 1889c. A preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the southeastern coast of the United States.—Bulletin of the United States National Museum 37:1–221.

———. 1890. Preliminary report on the collection of Mollusca and Brachiopoda obtained in 1887–88. Scientific results of explorations by the U.S. Fish Commission steamer "Albatross." No. VII.—Proceedings of the United States National Museum 12:219–362.

———. 1907. Descriptions of new species of shells, chiefly Buccinidae, from the dredgings of the U.S.S. "Albatross' during 1906, in the northwestern Pacific, Bering, Okhotsk, and Japanese Seas.—Smithsonian Miscellaneous Collection 50, pt. 2, no. 1727:139–173.

———. 1908. Reports on the dredging operations off the west coast of Central America to the Galapagos . . . XXXVI. Reports on the scientific results of the expedition to the eastern tropical Pacific . . . by the U.S. Fish Commission steamer "Albatross," from October, 1904, to March, 1905 . . . XIV. The Mollusca and Brachipoda.—Bulletin of the Museum of Comparative Zoology 43(6):205–487.

———. 1919. Descriptions of new species of Mollusca from the north Pacific Ocean in the collection of the United States National Museum.—Proceedings of the United States National Museum 56(2295):293–371.

———. 1921. Summary of the marine shellbearing mollusks of the northwest coast of America, from San Diego, California, to the Polar Sea, mostly contained in the collection of the United States National Museum, with illustrations of hitherto unfigured species.—Bulletin of the United States National Museum 112:1–217.

———. 1925. Illustrations of unfigured types of shells in the collection of the United States National Museum.—Proceedings of the United States National Museum 66(2554):1–41.

———. 1927. Small shells from dredgings off the southeast coast of the United States by the United States Fisheries steamer "Albatross" in 1885 and 1886.—Proceedings of the United States National Museum 70(2667):1–134.

Dautzenberg, P. 1889. Contribution à la faune malacologique des Iles Açores.—Résultats des Campagnes Scientifiques accomplies sur son yacht par le Prince Albert I^{er}, Prince de Monaco 1:1–112.

———. 1925. Mollusques nouveaux provenant des croisiéres du Prince Albert I^{er} de Monaco.—Bulletin de l'Institut Océanographique de Monaco No. 457:1–12.

———. 1927. Mollusques provenant des campagnes scientifiques du Prince Albert I^{er} de Monaco dans l'Ocean Atlantique et dans le Golfe de Gascogne.—Résultats des Campagnes Scientifiques accomplies sur son yacht par le Prince Albert I^{er}, Prince de Monaco 72:1–400.

———, and H. Fischer. 1897a. Campagnes scientifiques de S. A. le Prince Albert I^{er} de Monaco. Dragages effectués par l'Hirondelle et par la Princesse Alice, 1888–1896.—Memoires de la Société Zoologique de France 10:139–234.

———, and ———. 1897b. Campagnes scientifiques de S. A. le Prince Albert I^{er} de Monaco. Diagnoses d'espèces nouvelles de gasteropodes.—Bulletin de la Société Zoologique de France 22: 37–45.

———, and ———. 1906. Mollusques provenant des dragages effectués à l'ouest de l'Afrique pendant les campagnes scientifiques de S. A. S. le Prince de Monaco.—Résultats des Campagnes Scientifiques accomplies sur son yacht par le Prince Albert I^{er}, Prince de Monaco 32:1–125.

Erben, H. K. 1972. Uber die Bildung und das Wachstum von Perlmutt.—Biomineralisation 4: 15–46.

Fischer, P. 1882. Diagnoses d'espéces nouvelles de mollusques recuillis dans le cours de expéditions scientifiques de l'aviso le Travailleur (1880 et 1881).—Journal de Conchyliologie 30:49–55.

———. 1885. Manuel de Conchyliologie et de Paléontologie conchyliologique, ou historie naturelle de mollusques vivants et fossiles. F. Savy, Paris, pp. 689–896.

Fretter, V. 1964. Observations on the anatomy of *Mikadotrochus amabilis* Bayer.—Bulletin of Marine Science 14(1):172–184.

———. 1965. Functional studies of the anatomy of some neritid prosobranchs.—Journal of Zoology 147:46–74.

———. 1966. Observations on the anatomy of *Perotrochus.*—Bulletin of Marine Science 16(3):603–614.

———. 1975. *Umbonium vestiarium,* a filter-feeding trochid.—Journal of Zoology 177:541–552.

———, and A. Graham. 1962. British Prosobranch Molluscs. The Ray Society, London, 755 pp.

———, and ———. 1977. The prosobranch molluscs of Britain and Denmark. Part 2—Trochacea.—Journal of Molluscan Studies, Supplement 3:39–100.

———, and ———. 1978a. The prosobranch molluscs of Britain and Denmark. Part 3—Neritacea, Viviparacea, Valvatacea, terrestrial and freshwater Littorinacea and Rissoacea.—Journal of Molluscan Studies, Supplement 5:101–152.

———, and ———. 1978b. The prosobranch molluscs of Britain and Denmark. Part 4. Marine Rissoacea.—Journal of Molluscan Studies, Supplement 6:153–241.

———, ———, and J. H. McLean. 1981. The anatomy of the Galapagos Rift limpet, *Neomphalus fretterae.*—Malacologia 21(1–2):337–361.

Giles, E., and J. Gosliner. 1983. Primary type specimens of marine Mollusca (excluding Cephalopoda) in the South African Museum.—Annals of the South African Museum 92(1):1–52.

Golikov, A. N., and Y. I. Starobogatov. 1975. Systematics of prosobranch gastropods.—Malacologia 15(1):185–232.

Goryachev, V. N. 1979. K sisteme glubokovodnikh mollyuskov semeistva Seguenziidae (Gastropoda). [On the system of the deep-sea molluscan family Seguenziidae (Gastropoda)]. Pp. 70–71 *in* I. M. Likharev (ed.), Molluscs. Main results of their study. Abstracts of communications. Zoological Institute, Akademiya Nauk SSSR, Leningrad.

Graham, A. 1965. Observations on the anatomy of some trochacean gastropods.—Bulletin of Marine Science 15(1):202–210.

Habe, T. 1953. Descriptions of twelve new Japanese shells.—Venus 17(3):130–144.

———. 1955a. Notes on the systematic position of the genus *Orectospira* Dall, 1925.—Zoological Magazine 64:259–260.

———. 1955b. Note on the systematic position of the genus *Orectospira* Dall, 1925.—Minutes of the Conchological Club of Southern California 147:4.

———. 1961. Coloured illustrations of the shells of Japan. Vol. II. Hoikusha Publ. Co., Osaka, 183+42 pp.

———. 1964. Shells of the western Pacific in color. Vol. II. Hoikusha Publ. Co., Osaka, [7]+ 233 pp.

Harris, G. F. 1897. Catalogue of Tertiary Mollusca in the Department of Geology, British Museum (Natural History). I. Australasian Tertiary Mollusca. London, 407 pp.

Hedley, C. 1905. Mollusca from one hundred and eleven fathoms, east of Cape Byron, New South Wales.—Records of the Australian Museum 6(2):41–54.

———. 1907. The results of deep-sea investigations in the Tasman Sea. 3. Mollusca from eighty fathoms off Narrabeen.—Records of the Australian Museum 6(4):283–304.

———, and W. L. May. 1908. Mollusca from one hundred fathoms seven miles east of Cape Pillar, Tasmania.—Records of the Australian Museum 7:108–125.

Hickman, C. S. 1980. Gastropod radulae and the assessment of form in evolutionary paleontology.—Paleobiology 6(3):276–294.

Houbrick, R. S. 1980. Review of the deep-sea genus *Argyropeza* (Gastropoda: Prosobranchia: Cerithiidae).—Smithsonian Contributions to Zoology 321:1–30.

Jeffreys, J. G. 1876. Preliminary report of the biological results of a cruise in H. M. S. 'Valorous' to Davis Strait in 1875.—Proceedings of the Royal Society of London 25:177–230.

———. 1877. New and peculiar Mollusca of the Eulimidae and other families of Gastropoda, as well as of the Pteropoda, procured in the 'Valorous' Expedition.—Annals and Magazine of Natural History (4)19:317–339.

———. 1879. Notes as to the position of the genus *Seguenzia* among the Gastropoda.—Journal of the Linnean Society of London, Zoology 14:605–606.

———. 1880a. The deep-sea Mollusca of the Bay of Biscay.—Annals and Magazine of Natural History (5)6:315–319.

———. 1880b. The French deep-sea exploration in the Bay of Biscay.—Report of the British Association for 1880:1–13.

———. 1883. Mediterranean Mollusca (No. 3) and other Invertebrata.—Annals and Magazine of Natural History (5)11:393–401.

———. 1885. On the Mollusca procured during the 'Lighting' and 'Porcupine' Expeditions, 1868–70. (Part 9).—Proceedings of the Zoological Society of London for 1885:27–63.

Johnson, C. W. 1934. List of marine Mollusca of the Atlantic coast from Labrador to Texas.—Proceedings of the Boston Society of Natural History 40(1):1–204.

Jung, P. 1975. Quaternary larval gastropods from Leg 15, Site 147, Deep Sea Drilling Project. Preliminary report.—Veliger 18(2):109–126.

Kanno, S. 1958. New Tertiary molluscs from the Chichibu Basin, Saitama Prefecture, Central Japan.—Science Report. Tokyo Bunrika Daig C6, No. 55:157–229.

Keen, A. M. 1971. Sea shells of tropical West America. 2nd Ed. Stanford University Press, Stanford, California, 1064 pp.

———, and E. Coan. 1974. Marine molluscan genera of western North America. An illustrated key. 2nd Ed. Stanford University Press, Stanford, 208 pp.

———, and L. R. Cox. 1960. [Margaritinae]. Pp. I249–I251 *in* R. C. Moore (ed.), Treatise on

Invertebrate Paleontology. Part I, Mollusca 1. Geological Society of America, University of Kansas Press.

Kensley, B. 1973. Sea-shells of southern Africa—Gastropods. Maskew Miller Ltd., Cape Town, 236 pp.

Knight, J. B. 1945. Some new genera of Paleozoic Gastropoda.—Journal of Paleontology 19(6):573–587.

———, R. L. Batten, and E. L. Yochelson. 1960. [Trochonematacea]. Pp. I224–I225 *in* R. C. Moore (ed.), Treatise on Invertebrate Paleontology. Part I, Mollusca 1. Geological Society of America, University of Kansas Press.

Knudsen, J. 1964. Scaphopoda and Gastropoda from depths exceeding 6000 meters.—Galathea Report 7:125–136.

Kobelt, W. 1878. Illustrirtes Conchylienbuch. Nürnberg, 331 pp.

———. 1886–1888. Prodromus Faunae Molluscorum Testaceorum maria Europaea inhabitantium. Nürnberg, 550 pp.

Koperberg, E. G. 1931. Jungtertiäre und Quartäre Mollusken von Timor.—Jaarboek van het Mijnwezen in Nederlandsch-Indië 59:1–165.

Kosuge, S. 1966. The family Triphoridae and its systematic position.—Malacologia 4(2):297–324.

Ladd, H. S. 1970. Eocene mollusks from Eua, Tonga.—United States Geological Survey, Professional Paper 640-C:i–iii, C1–C10.

———. 1982. Cenozoic fossil molluscs from western Pacific islands; Gastropods (Eulimidae and Volutidae through Terebridae).—United States Geological Survey, Professional Paper 1171:1–100.

Laubier, L., and P. Bouchet. 1976. Un nouveau copépode parasite de la cavité palléale d'un gastéropode bathyal dans le Golfe de Gascogne *Myzotheridion seguenziae* gen. sp. nov.—Archives Zoologie Expérimentale et Générale 117(4):469–484.

Locard, A. 1886. Prodrome de Malacologie française. Catalogue général des Mollusques vivants de France (Mollusques marins). Lyon, Paris, 779 pp.

———. 1898. Expeditions scientifiques du "Travailleur" et du "Talisman" pendant les années 1880, 1881, 1882, 1883. Mollusques testaces. II. Paris, 515 pp.

———. 1899. Les Coquilles marines au large des Côtes de France. Paris, 198 pp.

Marshall, B. A. (In press). Recent and Tertiary Seguenziidae (Mollusca: Gastropoda) from the New Zealand region.—New Zealand Journal of Zoology.

Martens, E. von. 1881. Mollusca.—Zoological Record 16, 93 pp.

———. 1901. Neue Meeres-Conchylien von der Deutschen Tiefsee-Expedition.—Sitzungs-Berichten der Gesellschaft Naturforschender Freunde Berlin 1901:14–26.

———. 1903. Die beschalten Gastropoden der Deutschen Tiefsee-Expedition 1898–1899. A. Systematisch-geographischer Teil.—Wissenschaftliche Ergebnisse der deutschen Tiefsee Expedition auf dem Dampfer "Valdivia." 7:1–146.

Maury, C. J. 1922. Recent Mollusca of the Gulf of Mexico and Pleistocene and Pliocene species from the Gulf States. Part 2: Scaphopoda, Gastropoda, Amphineura, Cephalopoda.—Bulletins of American Paleontology 9(38):34–142.

McLean, J. H. 1981. The Galapagos Rift limpet *Neomphalus*: Relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation.—Malacologia 21(1–2):291–336.

Meek, F. B. 1864. Description of Carboniferous fossils.—Geological Survey of California, Paleontology of California 1:3–16.

Melvill, J. C. 1904. Description of twenty-eight species of Gastropoda from the Persian Gulf, Gulf of Oman, and Arabian Sea, dredged by Mr. F. W. Townsend, of the Indo-European Telegraph Service, 1900–1904.—Proceedings of the Malacological Society of London 6:158–169.

———. 1910. Descriptions of twenty-nine species of marine Mollusca from the Persian Gulf, Gulf of Oman, and North Arabian Sea, mostly collected by Mr. F. W. Townsend, of the Indo-European Telegraph Service.—Annals and Magazine of Natural History (8)7:1–17.

———, and R. Standen. 1903. Descriptions of sixty-eight new Gastropoda from the Persian Gulf, Gulf of Oman, and North Arabian Sea, dredged by Mr. F. W. Townsend, of the Indo-European Telegraph Service, 1901–1903.—Annals and Magazine of Natural History (7)12:289–324.

Merrill, A. S. 1970a. *Fluxina* Dall is a *Calliostoma* Swainson.—Nautilus 84(1):32–34.

———. 1970b. The family Architectonicidae (Gastropoda: Mollusca) in the western and eastern Atlantic.—Unpublished Ph.D. Dissertation, University of Delaware, [6] + 338 pp.

Morris, P. A., and W. J. Clench. 1973. A Field Guide to shells of the Atlantic and Gulf Coasts and the West Indies. Houghton Mifflin Co., Boston, 330 pp.

Nobre, A. 1884. Molluscos marinhos de Portugal. Porto.

———. 1932. Molluscos marinhos de Portugal. Vol. 1. Porto, 466 pp.

———. 1936. Molluscos marinhos de Portugal. Vol. 2. Porto, 381 pp.

———. 1938–1940. Fauna malacologica de Portugal: I. Moluscos marinhos e das águas salobras. Porto, 807 pp.

Noetling, F. 1901. The fauna of the Miocene beds of Burma.—Palaeontologia Indica, N. S., 1(3), 378 pp.

Nordsieck, F. 1968. Die Europäischen Meeres-Gehauseschnecken (Prosobranchia) vom Eismeer bis Kapverden und Mittelmeer. Gustav Fischer, Stuttgart, 273 pp.

———. 1973. Abyssal mollusks from the Ionic Sea.—La Conchiglia 5(11–12):4–7.

Odhner, N. H. 1932. Zur Morphologie und Systematik der Fissurelliden.—Jenaische Zeitschrift für Naturwissenschaft 67:292–309.

Okutani, T. 1964. Report on the archibenthal and abyssal gastropod Mollusca mainly collected from Sagami Bay and adjacent waters by the R. V. "*Soyo-Maru*" during the years 1955–1963.—Journal of the Faculty of Science, University of Tokyo, Sect. II, 15:371–447.

———. 1968. Bathyal and abyssal Mollusca trawled from Sagami Bay and the south off Boso Peninsula by the R/V "Soyo-Maru," 1965–1967.—Bulletin of the Tokai Regional Fisheries Research Laboratory 56:7–55.

———. 1974. Review and new records of abyssal and hadal molluscan fauna in Japanese and adjacent waters.—Venus 33(1):23–39.

———. 1982. Rediscoveries of an abyssal trochid, *Basilissa superba* Watson from the south of Japan.—Venus 40(4):237–239.

Oldroyd, I. S. 1927. The marine shells of the west coast of North America. Vol. 2. Gastropoda, Scaphopoda, and Amphineura. Part 2. Stanford University Publications, University Series, Geological Sciences, 304 pp.

Oppenheim, P. 1906. Zur Kenntnis alttertiärer Faunen in Ägypten. 2 Lieferung: Der Bivalven zweiter Teil, Gastropoda und Cephalopoda.—Paleontographica 30:163–348.

———. 1923. Über eine Eocänfauna der Polje von Lukevac bei Nevesinje in der Herzegowina. Berlin, 100 pp.

Pelseneer, P. 1906. Mollusca.—*In* E. R. Lankester (ed.), A Treatise on Zoology. Pt. V. Adam and Charles Black, London, 355 pp.

Perrilliat, M. del C. 1972. Monographía de los moluscos del Mioceno medio de Santa Rosa, Veracruz, México. Parte 1. (Gasterópodos: Fissurellidae a Olividae).—Paleontología Mexicana 32:1–232.

———. 1974. Catálogo de moluscos del terciario del sur de México (Estados de Veracruz, Oaxaca y Chiapas).—Paleontología Mexicana 38:1–66.

Philippi, R. A. 1844. Enumeratio Molluscorum Siciliae cum viventium tum tellure tertiaria fossilium, quae itinere suo observavit. Vol. 2. Halis Saxonum, 303 pp.

Popov, S. V., and I. S. Barskov. 1978. Shell structure of mollusks and its value in phylogeny and classification.—Malacological Review 11(1–2):152–153. (Abstract of report to 5th Meeting on the Investigation of Molluscs, Leningrad, Feb. 1975).

Porter, H. J. 1974. The North Carolina marine Mollusca—an atlas of occurrence. University of North Carolina, Institute of Marine Sciences, Morehead City, North Carolina, 351 pp.

Pulley, T. E. 1952. An illustrated check list of the marine mollusks of Texas.—Texas Journal of Science 2:167–199.

Quinn, J. F., Jr. 1979. Biological results of the University of Miami Deep-Sea Expeditions. 130. The systematics and zoogeography of the gastropod family Trochidae collected in the Straits of Florida and its approaches.—Malacologia 19(1):1–62.

———. 1981. A preliminary overview of the Seguenziidae Verrill, 1884.—Bulletin of the American Malacological Union for 1980:74 [abstract].

———. 1983a. The Seguenziacea: An update.—American Malacological Bulletin 1(1). [Abstract].

———. 1983b. *Carenzia,* a new genus of Seguenziacea (Gastropoda: Prosobranchia) with the description of a new species from the northeastern Pacific.—Proceedings of the Biological Society of Washington 96:355–364.

———. In preparation. A revision of the Seguenziacea Verrill, 1884 (Gastropoda: Prosobranchia). II. Systematics of the western Atlantic species.

Ravn, J. P. J. 1933. Études sur les Pélécypodes et gastropodes daniens du Calcaire de Faxe.—Kongelige Danske Videnskabernes Selskabs Skrifter (9)5(2):3–74.

———. 1939. Études sur les Mollusques du Paléocène de Copenhague.—Biologiske Skrifter utgitt av Det Kongelige Danske Videnskabernes Selskabs 1(1):1–106.

Rex, M. A. 1972. Species diversity and character variation in some western North Atlantic deep sea gastropods.—Unpublished Ph.D. Dissertation. Harvard University, 178 pp.

———. 1976. Biological accommodation in the deep-sea benthos: comparative evidence on the importance of predation and productivity.—Deep-Sea Research 23(10):975–987.

Riedel, L. 1932. Die Oberkreide vom Mungofluss in Kamerun und ihre Fauna.—Beiträge zur geologischen Erforschung der deutschen Schutzgebeite, 16:1–154.

Rios, E. C. 1975. Brazilian marine mollusks iconography. Fundacáo Universidade do Rio Grande, Rio Grande-RS, 331 pp.

Rokop, F. J. 1972. Notes on abyssal gastropods of the eastern Pacific, with descriptions of three new species.—Veliger 15(1):15–19.

Schepman, M. M. 1908. The Prosobranchia of the Siboga Expedition. Part 1. Rhipidoglossa and Docoglossa.—Siboga Expedition, Monographie 49^1a:1–107.

———. 1909. The Prosobranchia of the Siboga Expedition. Part 2. Taenioglossa and Ptenoglossa.—Siboga Expedition, Monographie 49^1b:109–231.

Seguenza, G. 1876. Studii stratigrafici sulla Formazione pliocenica dell'Italia Meridionale. Elenco dei Cirripedi e dei Molluschi della zona superiore dell'antico plioceno.—Reale Comitato Geologico Italiana, Bolletino 7(5–6):180–189.

———. 1877. Brevissimi cenni intorno le Formazioni Terziarie della provincia di Reggio-Calabria. Messina, 31 pp.

———. 1879. Le formazione Terziarie nella provincia di Reggio (Calabria).—Atti Reale Accademia dei Lincei, Memorie (3)1:1–446.

Shimek, R. L., and A. J. Kohn. 1981. Functional morphology and evolution of the toxoglossan radula.—Malacologia 20(2):423–438.

Sorgenfrei, F. 1958. Molluscan assemblages from the marine Middle Miocene of South Jutland and their environments.—Danmarks Geologiske Undersogelse (II) 79:1–503.

Tate, R. 1888. Census of the fauna of the older Tertiary of Australia.—Journal and Proceedings of the Royal Society of New South Wales 22:240–253.

———. 1890. The gastropods of the older Tertiary of Australia.—Transactions of the Royal Society of South Australia 13:185–235.

———. 1894. Unrecorded genera of the older Tertiary fauna of Australia.—Journal of the Royal Society of New South Wales 27:169–191.

Taylor, D. W., and N. F. Sohl. 1962. An outline of gastropod classification.—Malacologia 1(1): 7–32.

Thiele, J. 1903. Die beschalten Gastropoden der Deutschen Teifsee-Expedition 1898–1899. B. Anatomisch—systematische Untersuchungen einiger Gastropoden.—Wissenschaftliche Ergebnisse der deutschen Tiefsee Expedition auf dem Dampfer "Valdivia" 7:147–180.

———. 1925. Gastropoda der Deutschen Tiefsee-Expedition. II.—Wissenschaftliche Ergebnisse der deutschen Tiefsee Expedition auf dem Dampfer "Valdivia" 17(2):36–382.

———. 1929–35. Handbuch der systematischen Weichtierkunde. 2 vols. Gustav Fischer, Jena, 1134 pp.

Treece, G. D. 1977. Bathymetric records of marine shelled Mollusca from the northern shelf of Yucatan, Mexico.—Unpublished M.S. Thesis, Texas A&M University, 212 pp.

———. 1979. Living marine mollusks from the south Texas continental shelf.—Texas Journal of Science 31(3):271–283.

———. 1980. Bathymetric records of marine shelled Mollusca from the northeastern shelf and upper slope of Yucatan, Mexico.—Bulletin of Marine Science 30(3):552–570.

Tryon, G. W. 1883. Structural and systematic conchology: An introduction to the study of the Mollusca. Vol. 2. Philadelphia, 430 pp.

———. 1887. Manual of Conchology. Vol. 9. Solariidae, Ianthinidae, Trichotropidae, Scalariidae, Cerithiidae, Rissoidae, Littorinidae. Philadelphia, 488 pp.

Verco, J. C. 1906. Notes on South Australian marine Mollusca, with descriptions of new species—Part IV.—Transactions and Proceedings and Report of the Royal Society of South Australia 30:205–224.

Verrill, A. E. 1884. Second catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded.—Transactions of the Connecticut Academy of Science 6:139–294.

———. 1886. Results of the explorations made by the steamer "Albatross," off the northern coast of the United States in 1883.—Report of the Commissioner of Fish and Fisheries for 1883: 503–699.

Warén, A. 1980. Marine Mollusca described by John Gwyn Jeffreys, with the location of the type material.—Conchological Society of Great Britain and Ireland, Special Publication 1:1–60.

Watson, R. B. 1879a. Mollusca of H.M.S. 'Challenger' Expedition. III. Trochidae, viz. the genera *Seguenzia, Basilissa, Gaza* and *Bembix.*—Journal of the Linnean Society of London, Zoology 14:586–605.

———. 1879b. Mollusca of H.M.S. 'Challenger' Expedition. IV. Trochidae continued, viz. the genera *Basilissa* and *Trochus,* and the Turbinidae, viz. the genus Turbo.—Journal of the Linnean Society of London, Zoology 14:692–716.

———. 1886. Report on the Scaphopoda and Gasteropoda collected by H.M.S. Challenger during the Years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger, 1873–1876, Zoology 15:1–680.

Wenz, W. 1938. Gastropoda. Allgemeine Teil und Prosobranchia.—*In* O. Schindewolf, Handbuch der Paläozoologie, Band 6, Teil 1, Leif. 1 & 2:1–480.

Wise, S. W., Jr. 1970. Microarchitecture and mode of formation of nacre (mother-of-pearl) in pelecypods, gastropods and cephalopods.—Eclogae Geologicae Helvetiae 63:775–797.

Woodring, W. P. 1928. Miocene mollusks from Bowden, Jamaica. Part II. Gastropods and discussion of results.—Carnegie Institution of Washington, Publication 385:1–564.

Yochelson, E. L. 1956. Permian Gastropoda of the southwestern United States: I. Euomphalacea, Trochonematacea, Pseudophoracea, Anomphalacea, Craspedostomatacea, Platyceratacea.—Bulletin of the American Museum of Natural History 110(3):173–276.

Yokoyama, M. 1922. Fossils from the Upper Murashino of Kazusa and Shimosa.—Journal of the College of Science, Tokyo 44:1–200.

Florida Department of Natural Resources, Bureau of Marine Research, 100 Eighth Avenue S.E., St. Petersburg, Florida 33701.

NOTE: While this paper was in press, the monograph cited as "Marshall in press" was published (New Zealand Journal of Zoology 10:235–262, September 1983). In that report, Marshall recognizes 22 new species in eight genera, five of which were new. Since Marshall provided names for *Seguenzia* Groups II and IV (*Seguenziella* and *Fluxinella,* respectively), and modified the composition of several other taxa of my Table I, the reader is urged to consult his paper for further information.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 758–769

OBSERVATIONS ON SPECIES OF THE FOSSIL GENUS *AXOPORA* (COELENTERATA: HYDROZOA) AND ITS EVOLUTIONARY SIGNIFICANCE TO THE STYLASTERIDAE

Stephen D. Cairns

Abstract.—Two species of *Axopora* are redescribed and the remaining valid species are diagnosed and discussed. Three species are illustrated by scanning electron photomicrographs. Special emphasis is given to the morphology of the gastrostyles, and their supposed homology to those of the stylasterids is discussed. A hypothetical evolutionary scheme is proposed suggesting the evolution of the axoporids from a hydractiniid ancestor by the acquisition of calcification and the transformation of its protective spines to gastrostyles. An ancestor to the axoporids is suggested to have evolved into the stylasterids also, the major changes being the encasement of its gonozooids and dactylozooids in specialized calcareous structures. The Axoporidae is considered to be a family of athecate hydroids with close affinities to the Hydractiniidae and Stylasteridae.

The Axoporidae is a small family of calcified hydrozoans (13–14 nominal species in 1–2 genera), known only from the Oligocene to Eocene of Europe and South West Africa. They were originally described as Scleractinia (*Pocillopora* of Defrance (1826), and *Holaraea* of Milne Edwards and Haime (1849)) and some were even classified as tabulate corals and sponges (*Alveolites* and *Geodia* of Michelin (1844)). Michelin (1844) also identified a species as a milleporid, and, until 1963, most axoporids were assigned to the order Milleporina. Boschma (1963b) removed the axoporids from the Milleporina and created a new order, the Axoporina, for them, which, according to him, had closer affinities to the Stylasteridae than to the Milleporina.

The classification and phylogenetic position of the axoporids are based strongly on the characteristics of their gastrostyles. Until 1963, all axoporid gastrostyles were considered to be longitudinally grooved, nonspinose, fasciculate structures. However, Boschma (1963b) revealed that they are deeply ridged spinose cylinders, not at all fasciculate. Scanning electron microscopy allows an even more detailed analysis of gastrostyle morphology and a detailed comparison to other stylasterid gastrostyles.

Following a redescription of two species of *Axopora* and diagnoses of the other valid species, the interrelationships of the axoporids, stylasterids, and athecate hydroids will be discussed.

Class Hydrozoa

Order Hydroida

Family Axoporidae Boschma, 1951

Diagnosis.—Calcified hydrozoans with long spinose gastrostyles and with no skeletal evidence of dactylozooids (dactylopores) or gonophores (ampullae). Eocene to Oligocene (?Miocene): Europe, South West Africa, (?New Zealand). One or two genera.

Genus *Axopora* Milne Edwards and Haime, 1850

Diagnosis.—Characteristics of the family. Type-species: *Geodia pyriformis* Michelin, 1844. Five to seven species.

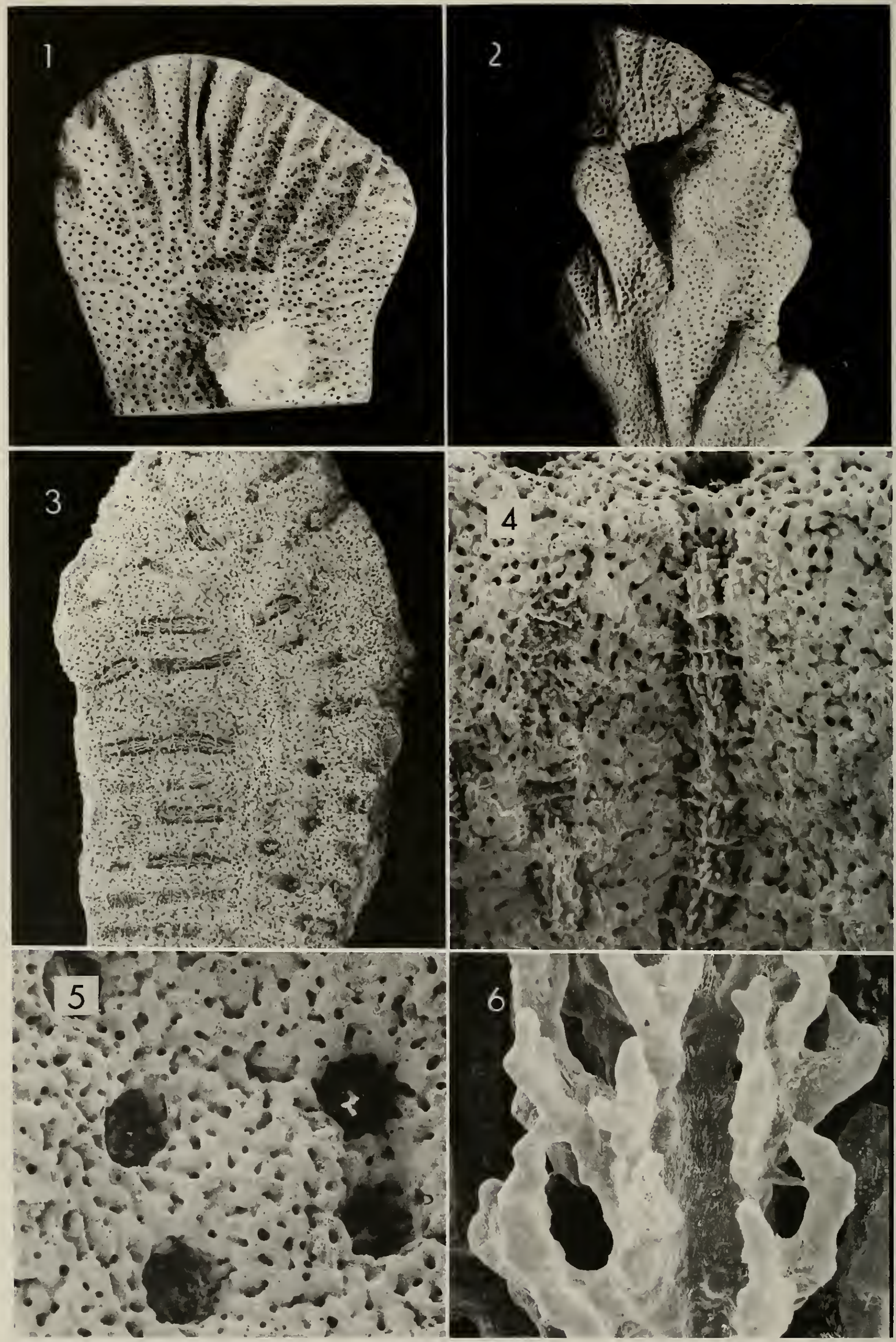
Axopora solanderi (Defrance, 1826)
Figs. 1–7

Pocillopora solanderi Defrance, 1826:48.
Palmipora solanderi.—Michelin 1844:166, pl. 45, fig. 9.
Lobopora solanderi.—Milne Edwards and Haime 1850:lix.
Axopora solanderi.—Milne Edwards and Haime 1851:151; 1857:243–244, pl. F3, fig. 2.—Boschma 1951:25, fig. 3; 1961:F94, fig. 78–1, 2; 1963a: 107, figs. 2a–b, d; 1963b:122, 125, pl. 1, fig. 1, pl. 2, figs. 1–2, pls. 3–8.
Axopora michelini Duncan, 1866:50, pl. 7, figs. 11–15.—Boschma 1963b:124, 126.
Axopora fisheri Duncan, 1866:64, pl. 10, figs. 20–22.—Boschma 1963b:124–125, 126.
Millepora mamillosa d'Archiardi, 1867:11.
Axopora mamillosa.—Steinmann 1903:5.—Boschma 1963b:125–126.

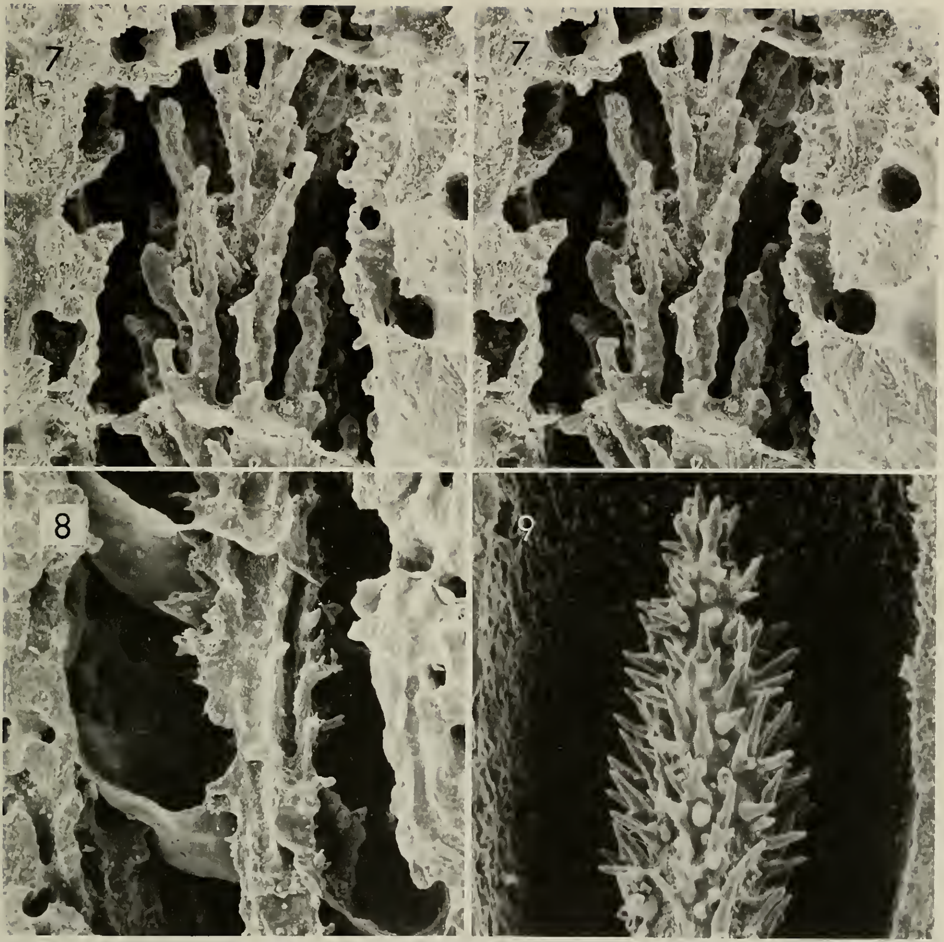
Description.—Corallum composed of flattened lobes (typical form) (Figs. 1–2) or lumpy masses (*michelini* form), but never forming laminar encrustations. In both lumpy and lobate forms, gastrostyles originate on both sides of a midline (Fig. 3), a plane in center of lobe or lump, not differing in porosity from rest of corallum. Surface coenosteum usually smooth but may be ridged, especially at tips of lobate specimens. Coenosteal ridges subparallel and roughly perpendicular to lobe edge, up to 1 mm tall and 1.5 mm broad. Lower relief ridges sometimes cross between adjacent parallel ridges producing reticulate pattern (Fig. 1). Coenosteal texture appears to be reticulate-granular, but preservation of specimens examined did not allow a definitive categorization.

Gastropores round, 0.15–0.35 mm in diameter, flush with coenosteal surface (Fig. 5). Gastropores randomly arranged, occurring at a density of 1.6–2.2 pores per mm^2. Very diffuse ring palisade occurs in upper part of gastropore tube, elements measuring about 25 μm in diameter. Gastrostyles extend almost to coenosteal surface and occupy most of space within gastropores, unlike in the stylasterids, where there is always considerable space around the style.

Length of gastrostyles and number of tabulae per gastrostyle vary with width of lobe or lump in which they occur (Figs. 4, 7). In thick coralla, gastrostyles up to 3.8 mm long and have over 18 tabulae. Styles rarely exceed 0.21 mm in diameter; maximum H:W observed was 23.5. According to Boschma (1963b: 121), gastrostyles sharply ridged, with spines occurring on ridges; however, scanning electron microscopy reveals that base of styles definitely not ridged, but spinose. Above base of style, spines vertically aligned, sometimes 1–3 across, and separated from adjacent rows by shallow groove. Spines so long, and sometimes bifurcate, that it is difficult to distinguish actual ridges on style (Figs. 6, 7). Gastrostyle spines cylindrical, up to 0.13 mm long and about 30 μm in diameter.



Figs. 1–6. *Axopora solanderi* from Valmondois (USNM 68437). 1–2, distal lobes, ×1.8, ×1.3, respectively; 3, Cross section of lobe showing midline and gastrostyles, ×6; 4, A gastrostyle and tabulae from colony of Fig. 3, ×27; 5, Coenosteum and gastropores, ×40; 6, Detail of gastrostyle, ×250.



Figs. 7–9. Gastrostyles. 7, Stereo view of gastrostyle and tabulae of *Axopora solanderi,* British Museum R 50812, ×140; 8, Gastrostyle and tabulae of *Sporadopora dichotoma* from the Drake Passage (*Hero* 715–895), ×100; 9, Gastrostyle tip of *Lepidopora granulosa* from Drake Passage (*Eltanin* sta 740), ×190.

Tabulae invariably present, occurring at irregular intervals, averaging about every 0.25 mm. Tabulae about 6 μm thick, completely sealing off lower gastropore tube from upper tube.

Discussion.—*Axopora solanderi* is distinguished from the other species in the genus by its nonencrusting growth form and massive corallum. Its gastrostyles are superficially similar to those of *Sporadopora dichotoma,* particularly with regard to the high H:W, similar tabulae, and apparent ridges (Fig. 8); however, the gastrostyles of *S. dichotoma* are distinctly ridged and bear much smaller and sharper spines. The characteristics of the tabulae are quite variable and not usually considered to be of generic or even specific value. Of all the stylasterines, *Lepidopora granulosa* (Fig. 9) has gastrostyles most similar to those of *A. solanderi.*

Distribution.—Eocene to Oligocene: England, France, Italy.

Material examined.—Auvers-sur-Oise, Seine et Oise, France, 7 fragments (*michelini* form), USNM 80889 (Invertebrate Paleontology Series); Valmondois, France, 2 fragments (typical form), USNM 68437; Sands of Beauchamps, Auvers, France, 2 fragments (*michelini* form), USNM 68438; Parnes, Beavoir, France, 1 fragment (*michelini* form), USNM 80891 (Invertebrate Paleontology Series); Le Bois Gouet, Lutecien, France (typical form), USNM 68439; Paris Basin, France, 1 fragment (*michelini* form), British Museum R 50812.

Axopora parisiensis (Michelin, 1844)
Figs. 10–15

Alveolites parisiensis Michelin, 1844:166, pl. 45, fig. 10.

Holaraea parisiensis.—Milne Edwards and Haime 1849:259; 1850:1vi, 40, pl. 7, fig. 2.

Axopora parisiensis.—Milne Edwards and Haime 1851:151; 1857:244.—Boschma 1951:25; 1963a:107–109, fig. 1; 1963b:122–123, 126.

Description.—Corallum always encrusts an elongate cylindrical object, such as a gorgonian stem, which, when the stem is lost, produces a cylindrical corallum with a hollow center (Figs. 10–11). Largest specimen examined 14 mm long and 6.5 mm in diameter, with hollow center 2.5 × 2.0 mm in diameter. Coenosteal encrustation always thin, with no side branches or lobes. Coenosteum papillose (Fig. 13), producing spongy coenosteal texture.

Gastropores round, 0.45–0.55 mm in diameter, surrounded by round to polygonal, infundibuliform calices (Fig. 12). Otherwise constant-diameter cylindrical gastropore becoming flared near coenosteal surface. Calices closely packed in honeycomb arrangement, each calice measuring about 1.2 mm in diameter. The density of gastropores therefore less than one pore per mm^2. Diffuse ring palisade present, similar to that of *A. solanderi.* Tips of gastrostyles extending only to base of funnel-shaped section of gastropore and thus each occupying only about one-half of gastropore (Figs. 14–15).

Because the corallum is never thick, gastrostyles are relatively short and rarely have tabulae. A large gastrostyle is 0.9 mm long and 0.18 mm in diameter (H:W = 5); however, H:W ratios usually lower than 5. Spination of gastrostyle is similar to that of *A. solanderi,* with cylindrical spines up to 1.25 mm long and 19–26 μm in diameter arranged in poorly defined vertical rows. The "ridges" of these styles are virtually nonextant.

Discussion.—*Axopora parisiensis* is easily distinguished by its large infundibuliform calices and its cylindrical encrusting growth form.

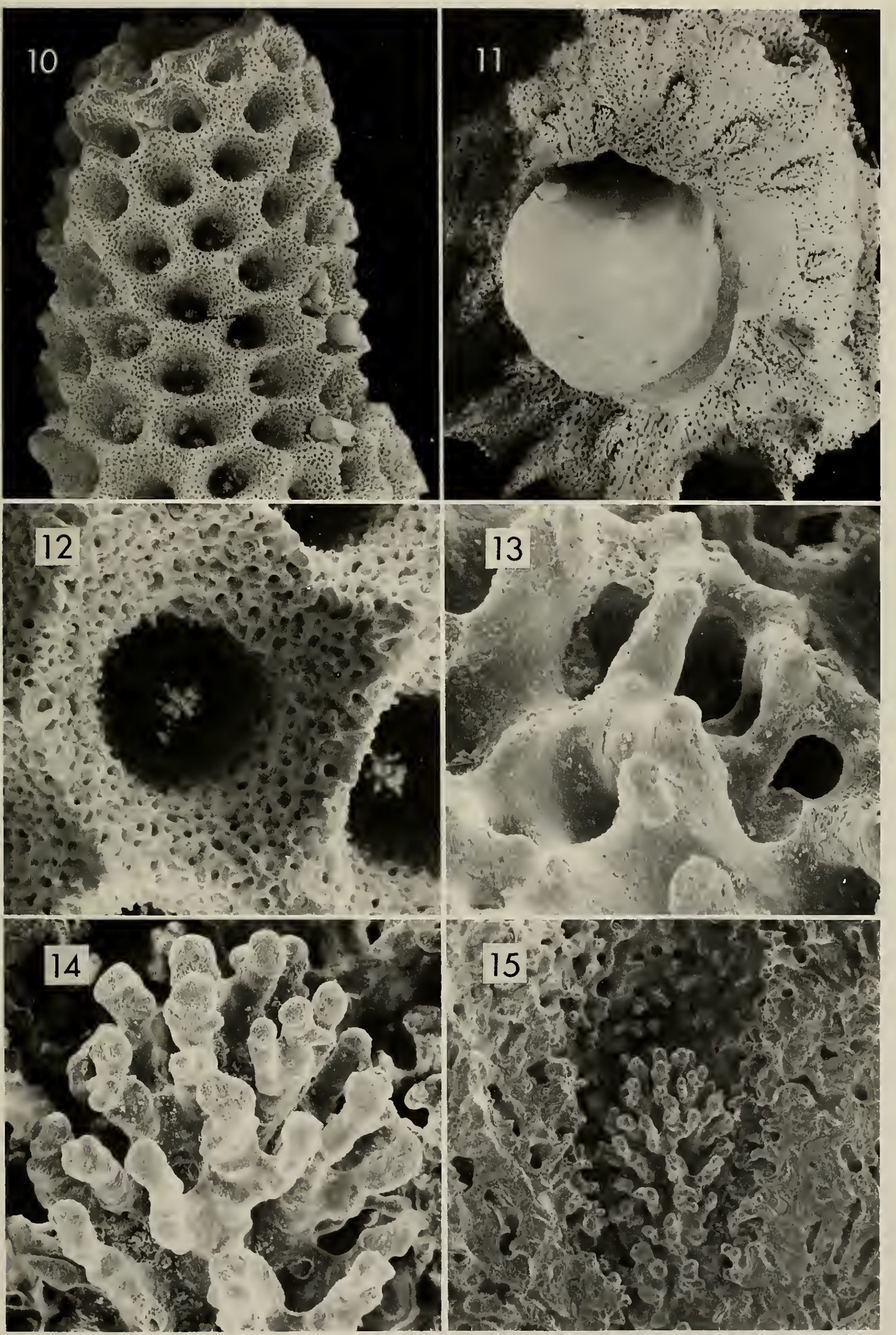
Distribution.—Eocene: France and England.

Material examined.—Vandane, France, 3 fragments, USNM 68440; Parnes, France, 2 fragments, USNM 68441; Campbon, France, 15 fragments, USNM 68442; Cuise, France, 2 fragments, USNM 68443; St. Lucien de la Haye, France, 1 fragment, USNM 68444; Grignon, Seine-et-Oise, France, 35 fragments, USNM 68445.

Axopora kolosvaryi (Boschma, 1954)
Figs. 16–17

Axopora ramea.—Kolosváry 1949:189, pl. 20, fig. 2.

Axoporella kolosváryi Boschma, 1954:101–103, figs. 2a–c; 1956:F-94, fig. 78-3a–c; 1963a:114–115.



Figs. 10–15. *Axopora parisiensis* from Parnes (USNM 68441). 10, encrusting piece of colony, ×9; 11, Cross section of encrustation, ×13; 12, Infundibuliform calice, ×50; 13, Papillose coenosteal texture within a calice, ×385; 14–15, Gastrostyle, ×230, ×60, respectively.

Axopora kolosváryi.—Boschma 1963b:127.

Diagnosis.—Corallum encrusting (Boschma 1963b:127). Gastropores round, about 0.35 mm in diameter, flush with surface. Gastrostyle 80–90 μm in diameter, extending almost to surface of coenosteum. Style covered with short clawlike spines, curved both upwards and downwards on style (Fig. 16). Spines only about 35 μm long, tapering to point from broad base up to 20 μm in diameter (Fig. 17). Spines not aligned in rows; gastrostyles not ridged. Tabulae present.

Discussion.—Axopora kolosvaryi is distinguished from the other species of *Axopora* by its very short clawlike gastrostyle spines, which are not arranged in rows. Only one tiny specimen was available for examination, inadequate for a redescription of the species.

Distribution.—Lower Eocene: Hungary.

Material examined.—One fragment from Gánt, Hungary (topotypic), USNM 68447.

Axopora pyriformis (Michelin, 1844)

Geodia pyriformis Michelin, 1844:178, pl. 46, fig. 2.
? *Millepora parasitica* Catullo, 1856:79, pl. 18, fig. 4.
Axopora pyriformis.—Milne Edwards and Haime 1850:lix; 1857:244.—Boschma 1951:25; 1956:F94; 1963a:123, 126, pl. 1, figs. 2–5, pl. 2, figs. 3–4.

Diagnosis.—Corallum always encrusting, usually on gastropod shells. Gastropores 0.25–0.40 mm in diameter, occurring with a density of 1.4–1.5 per mm^2. Otherwise similar to *A. solanderi.*

Discussion.—Boschma (1963b:126) noted that the only difference between *A. pyriformis* and *A. solanderi* was in growth form, which may in itself be a variable character. This allows for the possibility that *A. pyriformis* is a junior synonym of *A. solanderi.* Unfortunately, no specimens of *A. pyriformis* were available for study.

Distribution.—Eocene: France.

Axopora arborea Keferstein, 1859

Axopora arborea Keferstein, 1859:381, pl. 15, fig. 9.—Boschma 1951:26; 1963b: 124, 126.
? *Axopora paucipora* Keferstein, 1859:382, pl. 15, fig. 10.—Boschma 1963b:124, 126.
Axopora ramea d'Archiardi, 1867:11.—Not Kolosváry 1949:189 (=*A. kolosvaryi*).—Boschma 1963b:125, 126.

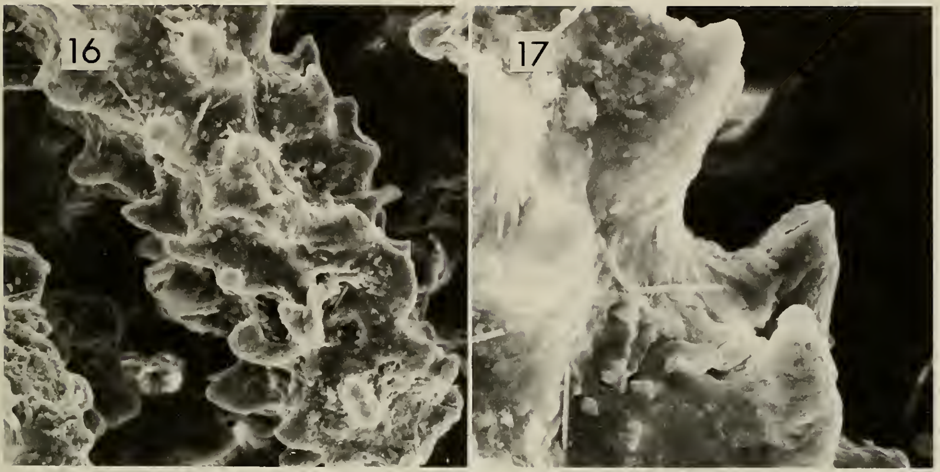
Diagnosis.—Corallum delicately branched; branches 3–6 mm in diameter. Details of gastrostyles unknown.

Discussion.—The poorly known *A. arborea* is distinguished from other species by its delicately branching growth form. No specimens were available for study.

Distribution.—Oligocene: Germany.

Axopora cleithridium (Squires, 1958), new combination

Sporadopora cleithridium Squires, 1958:25–27, pl. 1, figs. 8–12.
Axoporella cleithridium.—Squires, 1962:136–137.



Figs. 16–17. *Axopora kolosvaryi* from Gánt, Hungary (USNM 68447), details of gastrostyle spination, ×310, ×925, respectively.

Diagnosis.—Corallum with thick branches, up to 14 mm in diameter. Gastropores irregular in shape, 0.1–0.2 mm in diameter. Gastrostyles up to 5 mm long; tabulae present.

Discussion.—This is the only known *Axopora* with thick branches. Squires (1958) originally described it as a stylasterine, *Sporadopora,* and even described its dactylopores. When he (Squires 1962) later transferred it to *Axoporella* he did not mention the lack of dactylopores. Those referred to in 1958 were probably the superficial expression of coenosteal canals.

Only one specimen was available for study, a paratype from NZGS 5170. It does not appear to have dactylopores nor does it have any gastrostyles or tabulae. Perhaps the lack of styles and tabulae in this particular specimen is a result of poor preservation, but it does cast doubt on the placement of this species in the Axoporidae. Its occurrence in the Kapitean (Upper Miocene) of New Zealand would make it by far the youngest member of the family.

Apparently Boschma (1963b) overlooked this species in his revision of *Axopora.*

Distribution.—Upper Miocene: New Zealand.

Material examined.—Whata, Rowallon, S. D., Southland, New Zealand, NZGS 5170, USNM 68446 (Paratype).

Other Species

Axopora microspora and *A. alpina,* both originally described by d'Orbigny (1850) in the genus *Holaraea,* were considered as *species dubiae* by Boschma (1963b) because of insufficient data. Both species are known from Faudon, France.

Diamantopora lotzi Weissermel, 1913, is the only species in its genus, and *Diamantopora* is the only other genus in the Axoporidae. It was distinguished from *Axopora* by its nongrooved gastrostyles (Boschma 1956); however, this characteristic was subsequently shown to be variable within *Axopora. Diamantopora lotzi* may therefore represent a seventh valid species of *Axopora,* but until specimens can be examined in detail, its position will remain in doubt. It is known only from the Eocene of South West Africa.

Discussion

Although traditionally allied with the milleporids (from 1844 to 1963) several authors had noted the similarities of axoporids and stylasterids, particularly with regard to their gastrostyles. Römer (1863) was perhaps the first to point this out when he observed the similarity of the gastrostyle of the fossil stylasterine *Dendracis multipora* (subsequently synonymized with *Allopora compressa*) with those of *Axopora arborea.* Reuss (1865) made a similar observation based on the same species. Steinmann (1903) was the foremost advocate of this point of view when he remarked that *Axopora* was undoubtedly the ancestor of the three Recent stylasterid genera *Sporadopora, Errina* (now *Errina, Lepidopora, Lepidotheca,* and *Inferiolabiata*) and *Spinopora* (now *Stellapora*). Boschma (1954) mentioned the resemblance of the gastrostyles of *A. kolosvaryi* with those of other stylasterids and finally he (Boschma 1963b) removed the axoporids from the Milleporina, creating a separate order for them, the Axoporina. He stated that the axoporids were more closely related to the stylasterids than to the milleporids because of their similar gastrostyles, and noted that the gastrostyles of *Distichopora* were most similar to those of *Axopora.*

I agree that the axoporids are closely related to the stylasterids, but most closely to the genus *Lepidopora.* Points of similarity and presumed homology between *Lepidopora* and *Axopora* include: 1) a structurally similar gastrostyle; including size, H:W, and spination, 2) a diffuse ring palisade, 3) a calcium carbonate skeleton with anastomosing coenosteal canals, and 4) a random (nonlinear) arrangement of gastropores on the corallum. Points of difference are that *Axopora*: 1) lacks dactylopores, 2) lacks ampullae, 3) has a less spacious gastropore, 4) has tabulae, 5) has a different coenosteal texture, and 6) has both an encrusting and branching growth form. The major differences are the first two: that *Axopora* lacks dactylopores and ampullae; however, this does not necessarily mean that *Axopora* lacked dactylozooids or gonozooids, only that it lacked skeletal evidence of these features. For instance, the Recent calcified hydroid *Janaria* has both dactylozooids and gonozooids but has no skeletal evidence of these structures because they are composed of tissue that projects above the coenosteum, as in *Hydractinia* and most other athecate hydroids. Thus, *Axopora* may well have had dactylozooids and gonozooids but they were not housed in specialized calcareous structures. Most assuredly *Axopora* did have gonozooids, which were probably superficial structures as in *Hydractinia.*

In a phylogenetic analysis of the stylasterine genera (Cairns, in press), I chose the athecate hydroid *Hydractinia* as the out-group, or sister taxon, to the stylasterine corals. The most plesiomorphic (primitive) genus of stylasterine resulting from this analysis was *Lepidopora,* particularly *L. granulosa. Axopora,* because of its lack of skeletal evidence of dactylozooids and gonozooids and its encrusting growth form for some species, shows similarities to *Hydractinia.* On the other hand, of all the stylasterines, *Axopora* is most similar to *Lepidopora,* the most primitive stylasterine genus. I therefore propose that *Axopora* evolved from a hydractiniid ancestor in the early Tertiary (?Oligocene) and that a common ancestor gave rise to the stylasterines through *Lepidopora.* Furthermore, I consider the axoporids to be a family of athecate hydroids closely related to the Stylasteridae and Hydractiniidae.

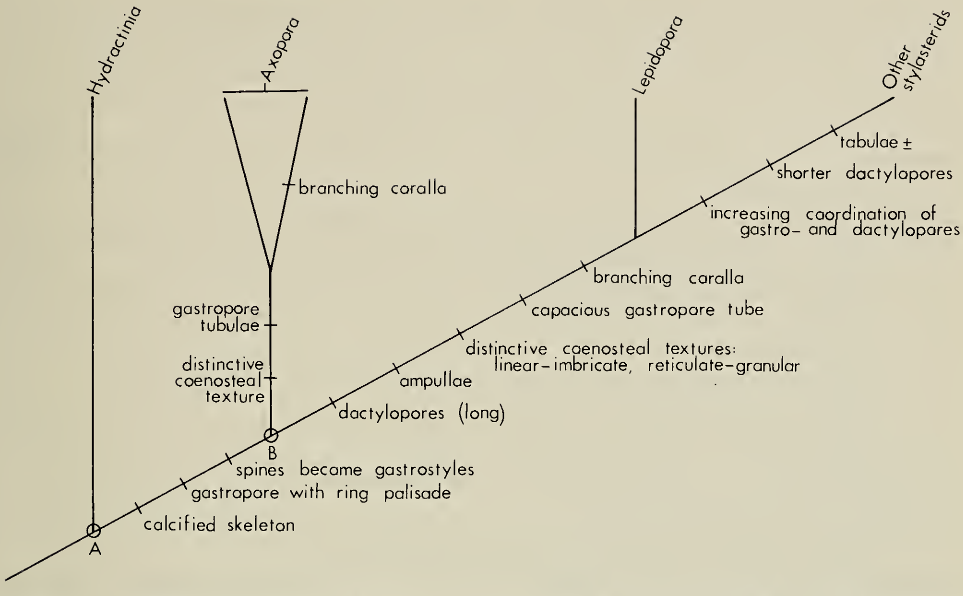


Fig. 18. Suggested evolution of the axoporids and stylasterids indicating significant character state changes. A and B are hypothetical ancestors.

As a hypothetical scenario I suggest the following (Fig. 18). In the Paleocene or Late Cretaceous a hydractiniid ancestor (A), which was encrusting and already had the gastrostyle homolog in the form of a chitinous spine, evolved the ability to calcify its skeleton and to protect its gastrozooids by enclosing them in rudimentary tubes: the gastropores. The chitinous spine transformed into the calcareous gastrostyle. The resultant hypothetical ancestor (B), with little further modification became the stem that resulted in *Axopora.* This evolutionary line developed a distinctive coenosteal texture, tabulae to stabilize its long gastrostyles, and, for some species, the ability to take advantage of the branching mode. *Axopora* became extinct in the Eocene (? Miocene), perhaps because it did not develop the further safeguards characteristic of the stylasterines: a protected gonozooid (ampullae) and a protected dactylozooid (dactylopores). (Stylasterines eventually evolved quite elaborate structures to protect their zooids, including fixed and hinged gastropore lids and dactylopore spines). In addition to the dactylopores and ampullae, the line leading to the stylasterines also evolved distinctive coenosteal textures (imbricate platelets and reticulate-granular coenosteum, among others), a more capacious gastropore tube, and an exclusively branching form. The characteristic of gastropore tabulae was probably independently acquired by several genera, such as *Sporadopora, Distichopora,* and *Errina,* and is therefore considered a convergent character.

The fossil record produces an apparent contradiction to the proposed scenario in that the earliest known stylasterids occur before the earliest known axoporids: the Paleocene (Danian of Denmark) and Eocene, respectively. As a test of my hypothesis, but not necessarily a confirmation, I predict the eventual discovery of *Axopora* from the Paleocene. An alternative explanation would be that the axoporids evolved through an intermediate Paleocene ancestor, which did not evolve *Axopora* until the Eocene and for which there is no known fossil record.

Literature Cited

d'Archiardi, A. 1867. Coralli fossili del terreno nummulitico dell'Alpi Venete. Catalogo delle specie e breve note. Pisa.

Boschma, H. 1951. Notes on Hydrocorallia.—Zoologische Verhandelingen, Leiden 13:49 pp., 2 pls.

———. 1954. De famile Axoporidae.—Verslag van de Koninklijke Nederlandse Akademie van Wetenschappen 63(4):99–104, 2 text-figs.

———. 1956. Milleporina and Stylasterina. Pp. F90–F106, text-figs. 75–85 *in* R. C. Moore (ed.), Treatise on Invertebrate Paleontology. Part F. Coelenterata.—University of Kansas Press, Lawrence, Kansas.

———. 1963a. The generic name *Axopora.*—Proceedings Koninklijke Nederlandse Akademie van Wetenschappen (B)66(3):107–117, 2 figs.

———. 1963b. Notes on species of the genus *Axopora.*—Proceedings Koninklijke Nederlandse Akademie van Wetenschappen (B)66(3):118–129, 8 pls.

Cairns, S. D. [in press.] A generic revision of the Stylasteridae. Part 2. Phylogenetic revision.—Bulletin of Marine Science 34(2).

Catullo, T. A. 1856. Dei terreni di sedimento superiore delle Venezie e dei fossili Bryozoari, Anthozoari e Spongiari ai quali danno ricetto. Padova, 88 pp., 19 pls.

Defrance, M. J. L. 1826. *Pocillopore* (Foss.). P. 48 *in* F. G. Lavrault (ed.), Dictionnaire des Sciences Naturelles 42. Strasbourg and Paris.

Duncan, P. M. 1866. A monograph of the British fossil corals. Part 1. Introduction; Corals from the Tertiary formations.—Palaeontographical Society, London, iii + 66 pp., pls. 1–10.

Keferstein, W. 1859. Die Korallen der norddeutschen Tertiärgebilde.—Zeitschrift der Deutschen geologischen Gesellschaft 11:354–383, pls. 14–15.

Kolosváry, G. 1949. The Eocene corals of the Hungarian Transdanubian Province.—Földtani Közlöny, Bulletin de la Société Geologique de Hongrie 78:141–242, pls. 1–22.

Michelin, J. L. H. 1844. Pp. 149–178, pls. 43–46 *in* Iconographie Zoophytologique. C. P. Bertrand, Paris.

Milne Edwards, H., and J. Haime. 1849. Mémoire sur les Polypiers appartenant aux groupes naturels des Zoanthaires perforés des Zoanthaires tabulés.—Compte Rendu hebdomadaire des Séances de l'Académie des Sciences, Paris 29:257–263.

———, and ———. 1850. A monograph of the British fossil corals. Part 1. Introduction. Corals from the Tertiary and Cretaceous formations.—Palaeontographical Society, London, lxxxv + 71 pp., 11 pls.

———, and ———. 1851. Monographie des Polypiers fossiles des terraines palaeozoiques, précédée d'un tableau général de la classification des Polypes.—Archives du Muséum National d'Histoire Naturelle, Paris 5:502 pp., 20 pls.

———, and ———. 1857–1860. Histoire Naturelle des Coralliaires ou Polypes proprement dits. Volume 2, 633 pp. (1857), atlas, 31 pls. (1860). Roret, Paris.

d'Orbigny, A. D. 1850. Prodrome de Paléontologie stratigraphique universelle des Animaux Mollusques et Rayonnés 2. V. Masson, Paris.

Reuss, A. E. 1865. Zur Fauna des deutschen Oberoligocäns. II. Anthozoen.—Sitzungsberichte der Akademie der Wissenschaften in Wien 50:614–690, pls. 6–15.

Römer, F. A. 1863. Beschreibung der norddeutschen tertiären Polyparien.—Palaeontographica 9: 199–245, pls. 35–39.

Squires, D. F. 1958. The Cretaceous and Tertiary corals of New Zealand.—New Zealand Geological Survey Paleontology Bulletin 29:105 pp., 16 pls.

———. 1962. Additional Cretaceous and Tertiary coral from New Zealand.—Transactions of the Royal Society of New Zealand 1(9):133–150, 4 pls.

Steinmann, G. 1903. Nachträge zur Fauna von Stramberg. II. *Milleporidium,* eine Hydrocoralline aus dem Tithon von Stramberg.—Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients 15:1–8, 2 pls.

Weissermel, W. 1913. Tabulaten und Hydrozoen.—Beiträge zur geologischen Erforschung der deutschen Schutzgebiete 5:84–111, pl. 14.

Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 770–779

ON A SMALL COLLECTION OF ENTOCYTHERID OSTRACODS WITH THE DESCRIPTIONS OF THREE NEW SPECIES

Horton H. Hobbs, Jr. and Auden C. McClure

Abstract.—Three new entocytherid ostracods, *Ascetocythere jezerinaci, Ankylocythere carpenteri,* and *Ornithocythere thomai,* infesting burrowing crayfishes, are described from Lee County, Virginia, Elmore County, Alabama, and Washington County, Alabama, respectively. Reports of the ostracods infesting crayfishes from nine additional collections containing burrowing crayfishes from Kentucky, Indiana, Ohio, Virginia, and West Virginia are also presented.

This report is based upon ostracods gleaned from 12 containers in which crayfishes from Alabama, Kentucky, Indiana, Ohio, Virginia, and West Virginia had been preserved. In each container, at least one of the crayfish (either *Cambarus* (*Jugicambarus*) *dubius* Faxon, 1884, or *C.* (*Lacunicambarus*) *diogenes* Girard, 1852) that had been placed in it had been captured from a burrow. In five containers, only representatives of one of these two burrowing species had been placed in the jars. Twelve species of ostracods, three of which are previously undescribed, were among the specimens found. Following the descriptions of the new species, new locality records are listed together with remarks concerning the ostracods and their host crayfishes.

Previous records of the hosts of ostracods belonging to the genera *Ascetocythere* and *Ornithocythere* provide evidence that these ostracods are probably restricted to crayfishes that are recognized as primary burrowers. The same crayfishes, however, frequently have been found to harbor members of the other entocytherid genera encountered in the collections reported here. Thus we are reasonably certain that among those specimens from jars in which more than one host crayfish species was preserved, the members of *Ascetocythere* and *Ornithocythere* were symbionts of the burrowing crayfish; the other ostracods could have been using any or all of the crayfishes present as hosts.

Ascetocythere jezerinaci, new species
Fig. 1a–d

Description.—Male: Eye pigmented, located approximately 0.28 shell length from anterior margin. Shell (Fig. 1*a*) subovate, about 1.7 times as long as high and margins lacking prominences and emarginations. Submarginal setae more abundant anteriorly and posteriorly than ventrally; none observed on dorsal margin.

Copulatory complex (Fig. 1*b*) with peniferum bearing 2 prominences extending anteriorly from subterminal expansion. More dorsal (anterior) process heavy, its length about half minimum anterior-posterior diameter of peniferum, tapering, and flanking anterodorsally directed penis. Ventral process shorter, more heavily

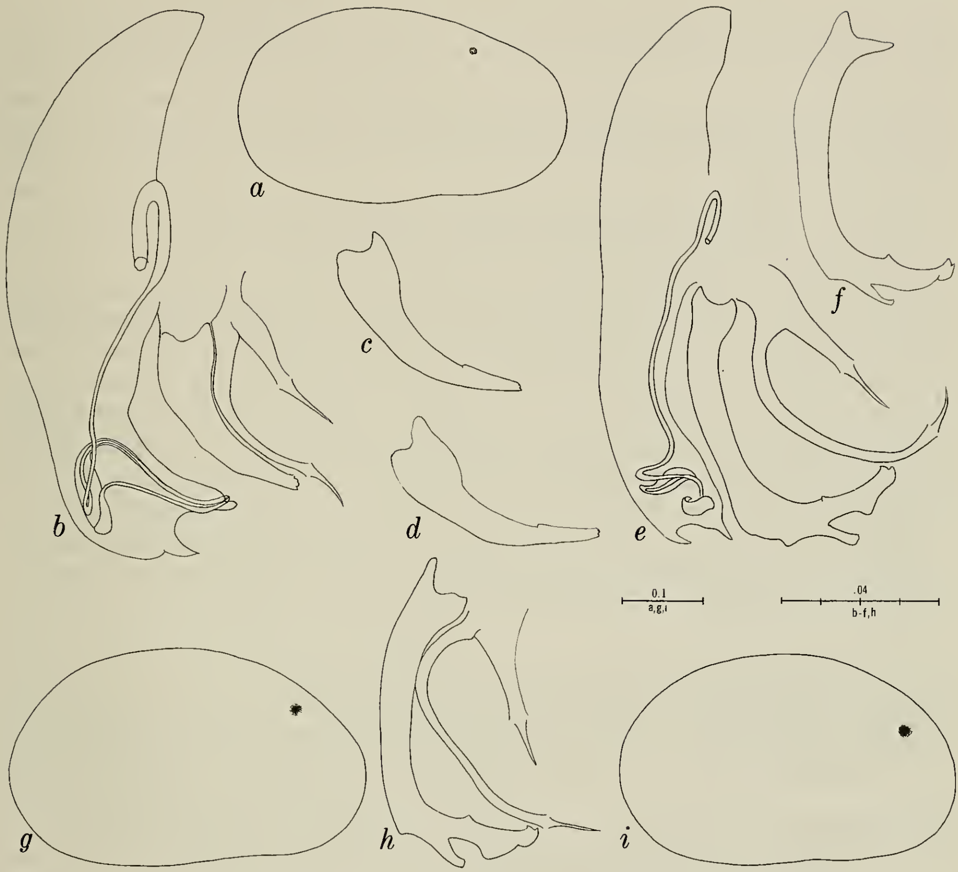


Fig. 1. *Ascetocythere jezerinaci* (*a–d*) and *Ankylocythere carpenteri* (*e–i*): *a, g,* Dextral view of shell of holotype; *b, c, d, e,* Copulatory complex; *c, d, f,* Clasping apparatus; *h,* Clasping apparatus and fingers; *i,* Dextral view of shell of allotype. (Scales in mm.)

sclerotized, acute, and slightly arched. Penis complex long and extending anteriorly, emerging on anterior surface of ventral expansion near tip of anterior process; 2 elements contiguous only along distal third of prostatic duct. Clasping apparatus (Fig. 1*c, d*) arched but not clearly divisible into horizontal and vertical rami, massive basally, and tapering along distal four-fifths of its length; postaxial border entire, preaxial border with notch at base of distal third; apex with 3 or 4 rounded denticles. Both dorsal and ventral fingers moderately robust, latter gently curved from base and directed anteroventrally.

Measurements.—Holotype: length of shell 392 μ; height of shell 217 μ; corresponding measurements of the paratypic male 399 μ and 217 μ, respectively.

Type-locality.—Creek and burrows 2.2 air kilometers (1.3 miles) north of Stickleyville, Lee County, Virginia (36°33'N, 82°55'W). The specimens on which this description is based were removed from debris in a jar that had contained specimens of the crayfishes *C.* (*J.*) *dubius, C.* (*Cambarus*) *bartonii* (Fabricius, 1798), and *C.* sp. Also infesting these crayfishes were the entocytherids *Donnaldsoncythere donnaldsonensis* (Klie, 1931) and *Uncinocythere simondsi* (Hobbs and Walton, 1960).

Disposition of types.—The holotypic and paratypic male are deposited in the National Museum of Natural History, Smithsonian Institution, numbers 204400 and 204401, respectively.

Range and specimens examined.—This ostracod is known only from the type-locality, from which we have seen only the two type-specimens.

Host and entocytherid associates.—See "Type-locality."

Relationships.—*Ascetocythere jezerinaci,* a member of the Asceta Group (Hobbs and Hart 1966:39), has its closest affinities with *As. didactylata* Hobbs and Hart (1966). Although the processes borne on the ventral extremity of the peniferum of the latter are directed ventrally and those of *As. jezerinaci* are disposed anteriorly, the relative positions of the processes made them readily comparable. Moreover, except for fewer, only one, denticles on the preaxial border of the clasping apparatus in *As. jezerinaci,* this structure is strikingly similar in the two species, as are most other features.

Hobbs and Walton (1975:6–7) presented a key to the then-known members of the genus. To include the new species described here in it, the following is offered to replace couplet 12 in their key.

12(3′). Ventral part of peniferum with angular flange 13
12′. Ventral part of peniferum lacking angular flange 16
16(12′). Processes on ventral extremity of peniferum directed ventrally; preaxial border of clasping apparatus with more than one denticle .... *As. didactylata* Hobbs and Hart, 1966:43
16′. Processes on ventral extremity of peniferum directed anteriorly; preaxial border of clasping apparatus with single denticle .... *As. jezerinaci,* new species

Etymology.—This entocytherid is named in honor of Raymond F. Jezerinac of Ohio State University at Newark, a student of crayfishes and one of the collectors of most of the material examined in this study.

Ankylocythere carpenteri, new species

Fig. 1e–i

Description.—Male: Eye pigmented, located about 0.2 shell length from anterior margin. Shell (Fig. 1*g*) subovate, about 1.6 times as long as high, margins lacking prominences and emarginations. Submarginal setae present anteriorly and posteriorly, sparse ventrally, and absent dorsally.

Copulatory complex (Fig. 1*e*) with arched peniferum moderately deeply excavate ventrally resulting in acute, anteroventrally directed prominences anteriorly and posteriorly, posterior prominence distinctly curved anteriorly. Penis complex situated in ventral sixth of peniferum but exhibiting no distinctive features. Clasping apparatus (Fig. 1*e, f, h*) L-shaped with vertical ramus 1.6 to 1.9 times as long as horizontal ramus. Former slightly arched, and neither preaxial nor postaxial borders armed; preaxial border of horizontal ramus with single tooth near midlength; postaxial margin with (1) distinct angular bend at or near junction of vertical and horizontal rami, in some views appearing rounded and slightly produced (Fig. 1*e*); (2) prominent slender talon, situated slightly proximal to level of tooth on preaxial border, directed anteroventrally and somewhat mesially; and (3) well defined excrescence slightly proximal to midway between distal base of talon and two apical denticles. Dorsal finger prominent, straight, and bearing simple apical seta; ventral finger moderately slender, curved throughout length or along proximal and distal fourths, and directed anteroventrally.

Female: Eye located about 0.14 shell length from anterior margin. Shell (Fig. 1*i*) subovate, 1.6 times as long as high, and shallowly excavate ventrally anterior to midlength. Shell margin otherwise entire. Submarginal setae present but rather widely spaced anteriorly, ventrally, and posteriorly.

Genital apparatus, like that of other members of genus, consisting of simple, slightly tapering papilla.

Measurements.—The length of five males ranges from 378 to 399 μ, mean 388 ± 7.98 μ; the height ranges from 238 to 252 μ, mean 244 ± 5.9 μ; corresponding measurements of five females are 399 to 413 μ, mean 405 ± 8.6 μ, and 245 to 252, mean 248 ± 3.83 μ.

Type-locality.—Small stream entering Coosa River 1.7 kilometers upstream from Bibb Graves Bridge at Wetumpka, Elmore County, Alabama (T.18N, R.18E, Sec. 13). The host was *C.* (*L.*) *diogenes.*

Disposition of types.—The holotypic male, allotypic female, and a dissected paratypic male are deposited in the National Museum of Natural History, Smithsonian Institution, numbers 204402, 204403, and 204404, respectively. Paratypic males are in the collections of the British Museum (Natural History) and that of H. H. Hobbs III, Wittenberg University.

Range and specimens examined.—*Ankylocythere carpenteri* is known only from the type-locality where 11 specimens were obtained from five crayfish.

Host and entocytherid associates.—See "Type-locality."

Relationships.—*Ankylocythere carpenteri* is allied to those members of the genus that have a well developed talon on the horizontal ramus of a clasping apparatus that does not have a conspicuously long vertical ramus. Among its closer relatives are *Ankylocythere freyi* Hobbs III, 1978; *Ank. krantzi* Hobbs III, 1978; *Ank. tiphophila* (Crawford, 1959); and *Ank. sinuosa* (Rioja, 1942). It differs from all other members of the genus, in possessing a distinct angle on the postaxial surface of the clasping apparatus at, or immediately adjacent to, the junction of the horizontal and vertical rami.

Etymology.—This ostracod is named for Michael R. Carpenter of the Smithsonian Institution who collected the specimens on which the above description is based and who has assisted one of us (HHH) in the laboratory on numerous occasions during the past decade.

Ornithocythere thomai, new species

Fig. 2

Description.—Male: Eye pigmented, located about one-sixth shell length from anterior margin. Shell (Fig. 2*a*) subovate, 1.8 times as long as high, and greatest height about 1.4 times that at level of eye, margins entire; submarginal setae closer

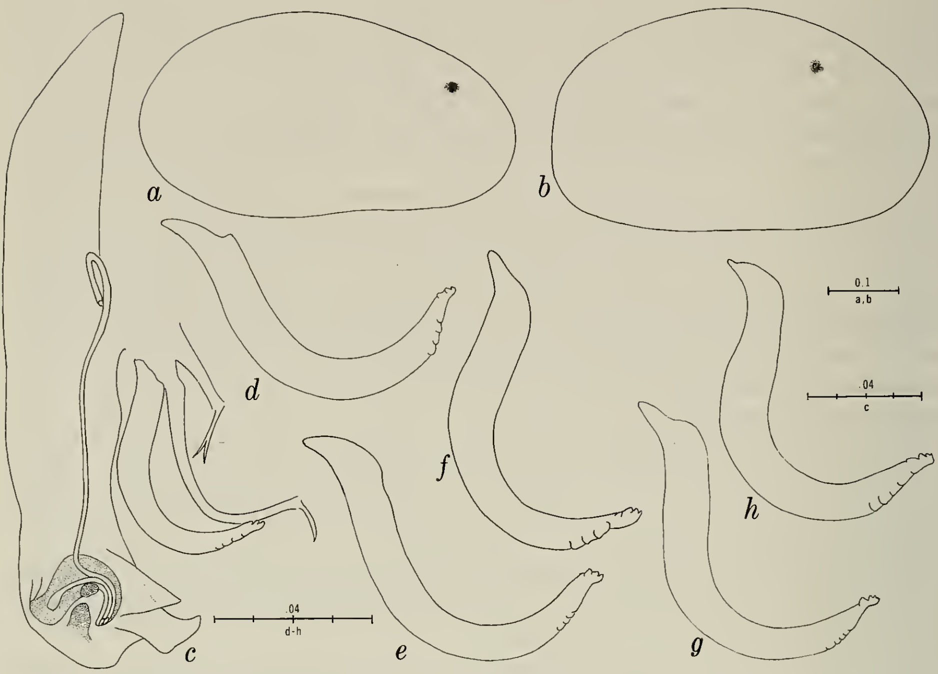


Fig. 2. *Ornithocythere thomai*: *a,* Dextral view of shell of holotype; *b,* Same of allotype; *c,* Copulatory complex of dissected male paratype; *d–h,* Clasping apparatus. (Scales in mm.)

together anteriorly and posteriorly than ventrally and dorsally, very few along latter margin.

Copulatory complex (Fig. 2*c*) with peniferum extending ventrally clearly beyond clasping apparatus, ventral part strongly sclerotized, and anterodorsally directed beaklike prominence with ventral subangular knob near midlength. Hyaline, triangular, lamelliform process situated at proximal base of beaklike prominence, its apex directed anteriorly. Penis conspicuous, U-shaped, and situated in ventral fifth of peniferum, its two components contiguous for about half length of prostatic element. Penis guides strongly sclerotized. Clasping apparatus (Fig. 2*d–h*) broadly C-shaped, not clearly divisible into vertical and horizontal rami, gently tapering in diameter almost from base. Preaxial border entire almost to apex, there bearing 4 apical denticles; postaxial border also entire except for series of 4 or 5 rounded to subangular prominences on distal fourth. Ventral finger (excluding apical setae) about 4 times length of dorsal finger, straight along proximal two-thirds, distal third bent anteriorly at 90 degrees, bearing simple seta; dorsal finger straight, directed anteroventrally, and terminating in apparently bifurcate seta.

Triunguis female: Eye situated about one-third shell length from anterior margin. Shell (Fig. 2*b*) about 1.7 times as long as high, truncate posteriorly, greatest height 1.4 times that at level of eye. Submarginal setae distributed as in male.

Genital apparatus consisting of short, sclerotized, conical papilla; apparently flexible hyaline rod, coated with detritus, extending pendant from apex.

Measurements.—The length of the shells of seven males ranges from 455 to 504 μ, mean 487 ± 15.6 μ, the height from 252 to 273 μ, mean 266 ± 7.0 μ; corresponding measurements of the two females are 504 μ and 287 to 294 μ.

Type-locality.—Burrows along drainage ditch adjacent to Crosbys Creek at Millry on State Route 17, Washington County, Alabama (T.8N, R.3W, Sec. 25). The host crayfish was *C.* (*L.*) *diogenes,* which harbored no other entocytherids except *Ank. freyi.*

Disposition of types.—The holotypic male, allotype, and a dissected paratypic male are deposited in the National Museum of Natural History, Smithsonian Institution, numbers 204405, 204406, and 204407, respectively. Paratypic males are in the British Museum (Natural History), in the collection of H. H. Hobbs III, Wittenberg University, and in the Smithsonian Institution.

Range and specimens examined.—Known only from the type-locality. A total of eight males and four triunguis females were obtained from the six crayfish collected.

Host and entocytherid associates.—See "Type-locality."

Relationships.—*Ornithocythere thomai* has its closest affinities with *O. aetodes* Hobbs III, 1970. The two are remarkably similar in most features, particularly in the structure of the ventral part of the peniferum; however, the translucent triangular element is much more prominent in *O. thomai,* as is obvious since this structure has been overlooked previously in *O. aetodes.* The two species may be distinguished most readily by the rounded, as opposed to the angular, clasping apparatus of *O. thomai.*

Etymology.—This ostracod is named in honor of Roger F. Thoma of the Ohio Environmental Protection Agency, a student of crayfishes, and the other collector of most of the specimens that are mentioned in this study.

New Locality Records for Entocytherids and Their Hosts

ALABAMA:

1. Crosbys Creek and drainage ditch at Millry on State Route 17, Washington County, 22 Apr 1970; Horton H. Hobbs, Jr., collector.

Entocytherids: *Ank. freyi* Hobbs, and *O. thomai,* new species.

Host: *C.* (*L.*) *diogenes* Girard, 1852.

Remarks.—*Ankylocythere freyi* was described from specimens that were infesting the same host species as that reported herein from Crenshaw County, Alabama. Whereas the new locality falls within the range of the species recorded by Hobbs III, it lies slightly to the north of those records plotted by him (1978: Fig. 3) west of the Tombigbee River. Information relative to *O. thomai* is presented following its description above.

2. Branch entering the Coosa River 1.7 kilometers upstream from Bibb Graves Bridge at Wetumpka, Elmore County, 12–13 Aug 1976; Michael R. Carpenter, collector.

Entocytherid: *Ank. carpenteri,* new species.

Host: *C.* (*L.*) *diogenes.*

Remarks.—As noted above, this ostracod is known only from the type-locality, where no other entocytherids were found infesting the host.

INDIANA:

Roadside ditch 6.1 air kilometers west of New Point, just north of State Route 46, Decatur County, 14 June 1980; John A. Thoma, Roger F. Thoma, and Raymond F. Jezerinac, collectors.

Entocytherid: *Dactylocythere crawfordi* Hart, 1965.

Host: *C.* (*L.*) *diogenes.*

Remarks.—This is the third record of the occurrence of *Dt. crawfordi* in Indiana; the other two are in the basins of the Wabash and West Fork of the White rivers. The locality cited above lies in the watershed of the East Fork of the White River, some 85 kilometers southeast of that in Marion County listed by Hart and Hart (1974:55).

KENTUCKY:

1. Patton's Creek (Ohio River basin), 3.4 kilometers northwest of Sligo on County line road, Oldham-Trimble counties, 19 Apr 1980; J.A.T., R.F.J., and Mathew McClusky, collectors.

Entocytherids: *Dactylocythere exoura* Hart and Hart, 1966, *Dt. ungulata* (Hart and Hobbs, 1961), and *Donnaldsoncythere donnaldsonensis* (Klie, 1931).

Hosts: *Cambarus* (*C.*) *ortmanni* (Williamson, 1907), *C.* (*Erebicambarus*) *ornatus* Rhoades, 1944a, *C.* (*L.*) *diogenes,* and *Orconectes rusticus* (Girard, 1852).

Remarks.—Hart and Hart (1974:58) recorded only two localities for *Dt. exoura,* one each in Grant and Oldham counties. The new locality is no more than six or seven kilometers north of that in Oldham County cited by the Harts, and the hosts are among those previously cited. Although the Oldham-Trimble locality does not alter the limits of the range of *Dt. ungulata* depicted by Hart and Hart (Fig. 49), it does provide a new county record and a precise locality on the northwestern boundary. Neither this nor any of the following records for the wide-ranging *Dn. donnaldsonensis* is noteworthy.

2. Big Creek (tributary to Levisa Fork, Big Sandy River basin), 3.4 kilometers northeast of Dunlap on State Route 194, Pike County, 18 Jun 1981; R.F.T., Raymond J. Jezerinac, and R.F.J., collectors.

Entocytherids: *Ascetocythere sclera* Hobbs and Hart (1966) and *Dn. donnaldsonensis.*

Hosts: *Cambarus* (*C.*) *sciotensis* Rhoades, 1944b, *C.* (*J.*) *dubius, Cambarus* sp., and *Orconectes* sp.

Remarks.—To our knowledge, this is the first record of the occurrence of *As. sclera* in Kentucky; however, having been found in neighboring parts of Virginia and West Virginia (Hart and Hart 1974:41), its occurrence in the extreme southeastern part of Kentucky is not a surprise. Our specimens exhibit no variations that set them apart from those from elsewhere.

OHIO:

Vernal pond, 6.9 kilometers northeast of Hebron on Licking Twp. Road 305, Licking County, 9 Apr 1981; R.F.T. and Craig Ciola, collectors.

Entocytherid: *Dt. crawfordi.*

Host: *C.* (*L.*) *diogenes.*

Remarks.—This record extends the known range of *Dt. crawfordi* about 60 kilometers to the east into the Muskingum River basin.

VIRGINIA:

1. Along Hobbs Branch (tributary of Levisa Fork, Big Sandy River basin), about 1.0 kilometer southeast of State Route 35, 5.1 kilometers east of Grundy, Buchanan County, 18 Jun 1981; R.F.T., R.F.J., and R.J.J., collectors.

Entocytherids: *As. sclera* and *Dn. donnaldsonensis.*

Hosts: *C.* (*C.*) *sciotensis, C.* (*J.*) *dubius,* and *Cambarus* sp.

2. 2.2 air kilometers north of Stickleyville, along tributary to Wallen Creek, Powell River basin, Lee County, 20 Jun 1981; R.F.J. and R.F.T., collectors.

Entocytherids: *As. jezerinaci,* new species, *Dn. donnaldsonensis,* and *Uncinocythere simondsi.*

Hosts: *C.* (*C.*) *cavatus* Hay, 1902, *C.* (*J.*) *dubius,* and *Cambarus* (*C.*) sp.

Remarks.—All of the information available to us concerning *As. jezerinaci* is presented immediately following the description of this entocytherid. The presence of *U. simondsi* here represents a new state record.

3. Spring seep along State Route 871, 0.7 kilometer north of the junction with Route 646, Scott County, 9 Jul 1981; collectors (?).

Entocytherids: *Ascetocythere ozalea* Hobbs and Hart, 1966; and *Dn. donnaldsonensis.*

Host: *Cambarus* (*J.*) *dubius.*

Remarks.—This is the third locality reported for *As. ozalea* which, insofar as we are aware, is endemic in the Tennessee River basin in Virginia; the other two localities are in Scott and Russell counties, Virginia (Hart and Hart 1974:40).

4. Mud Fork (Bluestone-New River basin), about 0.9 kilometer north of the town of Mud Fork (17.9 kilometers west southwest of Bluefield, West Virginia), on County Road 643, 19 Jun 1981; R.F.T., R.F.J., and R.J.J., collectors.

Entocytherid: *Dn. donnaldsonensis.*

Hosts: *C.* (*C.*) *sciotensis, C.* (*J.*) *dubius,* and *Cambarus.* sp.

WEST VIRGINIA:

1. Panther Creek State Forest (Tug Fork-Big Sandy River basin), 10 kilometers south of Panther, McDowell County, 19 Jun 1981; R.F.T., R.F.J., and R.J.J., collectors.

Entocytherids: *Dn. donnaldsonensis, Phymocythere phyma* (Hobbs and Walton, 1962), and *U. simondsi.*

Hosts: *Cambarus* (*C.*) *sciotensis, C.* (*J.*) *dubius, Cambarus* sp., and *Orconectes* sp.

Remarks.—The presence of *P. phyma* at this locality represents the southwesternmost record for the species, also the first report of its presence in the Guyandot drainage system. *Uncinocythere simondsi* has not been previously reported from West Virginia.

2. Tributary of West Fork of Twelve Pole Creek (Ohio River basin), Cabwaylingo State Forest, 4.3 kilometers northwest of Wilsondale, Wayne County, 18 Jun 1981; R.F.T., R.F.J., and R.J.J., collectors.

Entocytherids: *As. sclera* and *Donnaldsoncythere donnaldsonensis.*
Hosts: *C.* (*J.*) *dubius* and *Cambarus* sp.

Acknowledgments

We are grateful to Michael R. Carpenter, Raymond F. Jezerinac, and to Roger F. Thoma for donating most of the specimens reported here to the Smithsonian Institution, and to Messrs. Jezerinac and Thoma for supplying us with the identifications of the hosts of the entocytherids collected by them and for their comments on the manuscript. Thanks are also extended to C. W. Hart, Jr., of the Smithsonian Institution and to H. H. Hobbs III of Wittenberg University for their criticisms of the manuscript, and to Margaret Webb of the Madeira School, Greenway, Virginia, for assistance in preparing the illustrations.

Literature Cited

Crawford, E. A. 1959. Five new ostracods of the genus *Entocythere* (Ostracoda, Cytheridae) from South Carolina.—University of South Carolina Publications, Series III, Biology, 2(4):149–189, 37 figures.

Fabricius, Johann C. 1798. Supplementum Entomologiae Systematicae, 572 pages. Hafniae et Storch.

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.

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.

Hart, C. W., Jr. 1965. New entocytherid ostracods and distribution records for five midwestern states.—Transactions of the American Microscopical Society 84(2):255–259, 5 figures.

———, and Dabney G. Hart. 1966. Four new entocytherid ostracods from Kentucky, with notes on the troglobitic *Sagittocythere barri.*—Notulae Naturae of the Academy of Natural Sciences of Philadelphia 388:1–10.

———, and Horton H. Hobbs, Jr. 1961. Eight new troglobitic ostracods of the genus *Entocythere* (Crustacea, Ostracoda) from the eastern United States.—Proceedings of the Academy of Natural Sciences of Philadelphia 113(8):173–185, 32 figures.

Hart, Dabney G., and C. W. Hart, Jr. 1974. The ostracod family Entocytheridae.—Academy of Natural Sciences of Philadelphia Monograph 18:ix + 239 pages, 49 figures, 52 plates.

Hay, William Perry. 1902. Observations on the crustacean fauna of Nickajack Cave, Tennessee, and vicinity.—Proceedings of the United States National Museum 25(1292):417–439, 8 figures.

Hobbs, Horton H., Jr., and C. W. Hart, Jr. 1966. On the entocytherid ostracod genera *Ascetocythere, Plectocythere, Phymocythere* (gen. nov.), and *Cymocythere* with descriptions of new species.—Proceedings of the Academy of Natural Sciences of Philadelphia 118(2):35–61, 37 figures.

———, and Margaret Walton. 1960. Three new ostracods of the genus *Entocythere* from the Hiwassee drainage system in Georgia and Tennessee.—Journal of the Tennessee Academy of Science 35(1):17–23, 20 figures.

———, and ———. 1962. New ostracods of the genus Entocythere from the Mountain Lake region, Virginia (Ostracoda, Entocytheridae).—Virginia Journal of Science 13(2):42–48, 13 figures.

———, and ———. 1975. New entocytherid ostracods from Tennessee with a key to the species of the genus *Ascetocythere.*—Proceedings of the Biological Society of Washington 88(2):5–20, 2 figures.

Hobbs III, H. H. 1970. New entocytherid ostracods of the genus *Ornithocythere* and the description of a new genus.—Proceedings of the Biological Society of Washington 83(15):171–182, 2 figures.

———. 1978. New species of ostracods from the Gulf Coastal Plain (Ostracoda: Entocytheridae).—Transactions of the American Microscopical Society 97(4):502–511, 6 figures.

Klie, W. 1931. Campagne spéologique de C. Bolivar et R. Jeannel dans l'Amérique du Nord (1928), 3:Crustaces Ostracodes.—Biospeologica: Archives de Zoologie Expérimentale et Générale 71(3): 333–344, 20 figures.

Rhoades, Rendell. 1944a. The crayfishes of Kentucky, with notes on variation, distribution and descriptions of new species and subspecies.—American Midland Naturalist 31(1):111–149, 10 figures.

———. 1944b. Further studies on distribution and taxonomy of Ohio crayfishes and the description of a new subspecies.—Ohio Journal of Science 44(2):95–99.

Rioja, Enrique. 1942. Estudios carcinologicos. XIV, Consideraciones y datos acerca del género *Entocythere* (Crus. Ostrácodos) y algunas de sus especies, con descripción de una nueva.—Anales del Instituto de Biología, Universidad Autónoma de Mexico 13(2):685–697, 21 figures.

Williamson, E. B. 1907. Notes on the crayfish of Wells County, Indiana, with description of new species.—31st Annual Report of the Department of Geology and Natural Resources, Indiana 1906:749–763, plate 35.

(HHH) Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C. 20560; (ACM) 823 Bulls Neck Road, McLean, Virginia 22102.

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 780–806

SEVEN NEW SPECIES OF THE INDO-PACIFIC GENUS *EVIOTA* (PISCES: GOBIIDAE)

Susan L. Jewett[1] and Ernest A. Lachner

Abstract.—Seven new species of gobiid fishes of the genus *Eviota* Jenkins from Indo-Pacific marine waters are described as: *E. albolineata* (a member of Group I, Lachner and Karnella 1980:113); *E. japonica, E. latifasciata, E. punctulata* (Group II); *E. cometa, E. sigillata* (Group III); and *E. sparsa* (Group VII, the characters of which are discussed herein). The available evidence does not indicate that these species form a natural group. A table of characters for Groups I, II, III, and VII is given. Illustrations of the seven new species and a table of pertinent characters and meristics are provided.

As part of our continuing study of the systematics and zoogeography of the gobiid genus *Eviota* Jenkins (Lachner and Karnella 1978, 1980; Karnella and Lachner 1981), we present descriptions of seven new species. In our earlier study (1980:113) we discussed six species groups of *Eviota.* We herein define a seventh species group, and relate each of the new species to Groups I, II, III, or VII. A summary of species group characters is presented in Table 1.

The new species and their species group allocations are as follows: *Eviota albolineata,* Group I (containing 17 nominal species); *E. japonica, E. latifasciata* and *E. punctulata,* Group II (11 nominal species); *E. cometa* and *E. sigillata,* Group III (7 nominal species); and *E. sparsa,* Group VII (2 species, one to be described subsequently). The salient characters of the seven new species are given in the diagnostic accounts under each species, and some are summarized in Table 2.

Methods

The methods of obtaining counts and measurements and the presentation of these data, as well as the description of the cephalic sensory pore and cutaneous papillae systems, follow that of Lachner and Karnella (1978, 1980), and Karnella and Lachner (1981) with the following modifications:

1. "Pelvic fin membrane" refers to the membrane connecting the third and fourth rays of the pelvic fin. It is considered to be reduced when its length does not extend to the first branch of the fourth pelvic fin ray and to be well developed when it exceeds that point (Fig. 1, Lachner and Karnella 1980).
2. "Postanal midline spots" refers to the dark spots, composed at least in part of subcutaneous pigmentation, that occur along the posteroventral midline of the trunk. These spots begin at, or just posterior to, the origin of the anal fin, and extend to a vertical drawn 2 to 3 scale rows anterior to the hypural joint, otherwise referred to as the "midcaudal peduncle." There are usually 4 to 6 postanal midline

---

[1] Formerly Susan J. Karnella.

Table 1.—Characters distinguishing four species groups of *Eviota.*

Characters	Groups			
	I	II	III	VII
Cephalic sensory pore pattern	1	2	2	5
Vertebrae	26	26	25	26
Some pectoral fin rays branched	yes[1]	yes	no	yes
Male genital papilla	nonfimbriate	nonfimbriate, fimbriate or cup-shaped	nonfimbriate	nonfimbriate
Pelvic fin membrane	reduced to well developed	reduced	reduced to well developed	well developed
Length of fifth pelvic fin ray relative to fourth fin ray	absent to 2/10	absent to 1/10	1/10 to 5/10	6/10–9/10
Spinous dorsal fin elongation	Yes or no	yes or no	yes	yes

[1] Except some specimens of *E. monostigma* and *E. pseudostigma.*

spots. An additional spot, usually smaller and less intense, may occur more posteriorly, near the insertion of the ventral procurrent rays. This spot is not included when counting the postanal midline spots.

3. "Midcaudal peduncle spot" refers to a dark spot on the caudal peduncle, usually centered on the lateral midline, 2 to 3 scale rows anterior to the insertion of the caudal fin. The spot may be composed entirely of subcutaneous pigment or may be a combination of surface and subcutaneous pigmentation. It is in line with the last subcutaneous trunk bar when a series of trunk bars occurs.

Three cephalic sensory pore patterns are found in the species described in this paper. Pore pattern 1 represents the full complement of sensory pores for the genus *Eviota* and includes the paired nasal (NA) pores, the single anterior interorbital (AITO) and posterior interorbital (PITO) pores, the paired supraotic (SOT), anterior otic (AOT), and intertemporal (IT) pores, as well as two pairs, an upper and lower, of preopercular (POP) pores (Fig. 4, Lachner and Karnella 1980). Pore pattern 2 lacks only the IT pores, and pore pattern 5 lacks the IT and both pairs of POP pores. Cutaneous papillae patterns A, B and B-1 (Lachner and Karnella 1980:7) correspond to pore patterns 1, 2 and 5, respectively.

Presentation of material examined for holotypes and paratypes is of the following format: catalog number, size range, abbreviated locality data, depth of capture, collector and field number. Non-type material is summarized by geographic locality rather than listed by individual museum lot.

Abbreviations: the following museum acronyms are used to designate institutions and collections cited:

AMNH	American Museum of Natural History, New York
AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BPBM	Bernice P. Bishop Museum, Honolulu

Table 2.—Summary of diagnostic characters of seven new species of *Eviota*. (Pectoral fin rays are numbered sequentially from 1 to 18, beginning with uppermost ray. Figures given refer to numbered fin rays, and list the maximum branching for each species.)

	Species						
Characters	*albolineata*	*japonica*	*latifasciata*	*punctulata*	*cometa*	*sigillata*	*sparsa*
Group (after Lachner and Karnella 1980)	I	II	II	II	III	III	VII
Cephalic sensory pore pattern	1	2	2	2	2	2	5
Number of vertebrae	26	26	26	26	25	25	26
Dorsal/anal fin ray formula	9/8	9/8	8/8	9/8	9/8 or 8/7	9/8 or 8/7	9/8
Spinous dorsal fin elongation	uncommon, males only	well developed, both sexes	none	uncommon, males only	well developed, males only	well developed, both sexes	uncommon
Limits of pectoral fin ray branching	4–18	8–17	10–18	8–16	none	none	8–17
Length of fifth pelvic fin ray relative to fourth fin ray	1/10–2/10	1/10–2/10	rudiment	1/10–2/10	1/10	1/10–2/10	6/10–8/10
Development of pelvic fin membrane	well developed	reduced	reduced	reduced	reduced to well developed	well developed	well developed
Number of branches on fourth pelvic fin ray	6–12	8–16	7–11	8–18	4–9	3–7	3–5
Number of postanal midline spots	undeveloped	6	undeveloped	6	undeveloped (or 5)	7	5

CAS	California Academy of Sciences, San Francisco
FMNH	Field Museum of Natural History, Chicago
ROM	Royal Ontario Museum, Toronto, Canada
RUSI	Rhodes University, J.L.B. Smith Institute of Ichthyology, Grahamstown, South Africa
USNM	Former United States National Museum, now National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C.
WAM	Western Australian Museum, Perth
YCM	Yokosuka City Museum, Yokosuka, Japan

Eviota albolineata, new species

Figs. 1–2

Material examined.—998 specimens from numerous localities, ranging from the east coast of Africa to the Tuamotu Archipelago; total size range 7.7–24.7; gravid females 11.1–21.1.

Holotype: USNM 227140, (22.2), male; Tahiti, shallow patch south of Tapueraha Pass, 0–3.0 m, 21 Apr 1970, C. L. Smith, S70-45.

Paratypes: TAHITI: AMNH 43023, 2 (16.2, 21.3); same data as holotype. AMNH 43022, 1 (16.4); north side of Passe Tiamahana, 10.7–13.7 m, S70-11. AMNH 43025, 1 (18.9), off Papeari, 0–2.1 m, S70-53. AMNH 43024, 13 (15.6–19.3); south of Tapueraha reef, 0–3.6 m, S70-41. USNM 227166, 11 (14.1–22.0); south of Tapueraha, 0–7.6 m, S70-44. CAS 52829, 4 (16.4–21.6); off Papeari, 6.1–10.7 m, S70-51. BPBM 29191, 1 (19.4); off Papeari, 0–3.6 m, S70-55. AMS I.24025-001, 6 (16.0–19.4); south of Tapueraha Pass, 0–2.4 m, S70-43. ANSP 151994, 6 (16.9–19.8); same data as previous. CAS 48471, 4 (14.4–19.5); Atimaono, Teauaraa Pass, 0.9–13.7 m, sta 18, GVF Reg. 1350. HUAHINI NUI: AMNH 43034, 45 (13.2–20.9); 0.5 mi. south of Fare, 10.7–12.2 m, S70-8. The following five lots with same data as previous: USNM 227165, 5 (15.4–19.9); ANSP 151995, 5 (13.5–22.0); BPBM 29192, 5 (14.6–20.6); CAS 52830, 5 (13.7–21.1); AMS I.24026-001, 5 (13.2–22.9). AMNH 43033, 1 (17.9); 0.5 mi. south of Passe Avapeihi, 0–1.8 m, S70-6. AMNH 43020, 2 (14.4, 19.9); ca. 2 mi. south of Fare, 0–1.8 m, S70-7. BORA BORA: AMNH 43027, 5 (12.7–19.0); lagoon channel south of Topua Is., 0–7.6 m, S70-19. AMNH 43028, 1 (13.5); ca. 2 mi. southwest of Topua Is., 0–1.8 m, S70-16. AMNH 43026, 1 (19.7); 2 mi. southwest of Topua Is., 0–1.8 m, S70-15. USNM 227167, 7 (13.5–19.3); lagoon channel south of Topua Is., 0–10.7 m, S70-18.

Non-type Material: Numerous specimens from the following localities: OCEANIA: Society Islands, Tuamotu Archipelago, Tubuai Islands, Cook Islands, Samoa Islands, Fiji, New Hebrides, Santa Cruz Islands, Solomon Islands, Gilbert Islands, Marshall Islands, Marianas Islands, Caroline Islands, Palau Islands; PAPUA NEW GUINEA; AUSTRALIA: Lord Howe Island, Great Barrier Reef; TAIWAN; PHILIPPINE ISLANDS; INDONESIA; INDIAN OCEAN: India, Sri Lanka, Chagos Archipelago, Agalega Islands, Mauritius, Seychelles Islands, Amirantes Islands, Aldabra Atoll, Comoro Islands, Mozambique.

Diagnosis.—Cephalic sensory pore system complete; pectoral fin rays numerous, modally 18, with most rays branched; dorsal/anal fin ray formula typically 9/8; elongation of spines in first dorsal fin uncommon; pelvic fin typically I, 4 1/10–

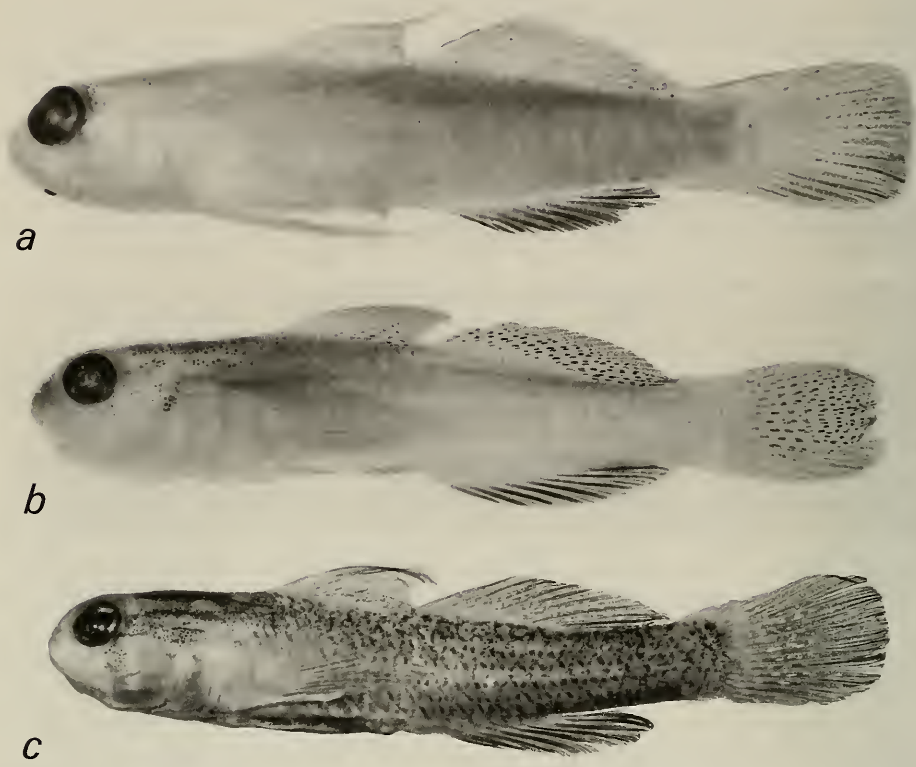


Fig. 1. *Eviota albolineata.* a, 16.4 mm SL, male, Seychelles Islands, USNM 227132; b, 20.3 mm SL, male, Tuamotu Archipelago, BPBM 14048; c, Holotype, 22.2 mm SL, male, Tahiti, USNM 227140.

2/10 with well developed membrane between rays; branches on fourth pelvic fin ray 6–12; trunk lacking both dark spot on middle portion of caudal peduncle and well developed postanal midline spots although some tiny spots or dark streaks may be present; body generally pale with dark dusky anal fin and scattered speckling on second dorsal and caudal fins; when color pattern highly developed, as in eastern Oceania populations, head with weak alternating dark and light horizontal stripes dorsolaterally and trunk moderately to distinctly dusky.

Description.—Dorsal fin VI-I, 8(1), VI-I, 9(*20*); anal fin I, 8(*21*); pectoral fin rays 16(2), 17(5), 18(7), 19(*6*), 20(1); pectoral fin rays 4–18 may be branched, 7–17 usually branched; pelvic fin I, 4 plus a rudiment (1), I, 4 1/10(*16*), I, 4 2/10(4); branches on fourth pelvic fin ray 6–12, average 8.4; segments between consecutive branches of fourth pelvic fin ray 1–4, average 2.1; pelvic fin membrane well developed; branched caudal fin rays 11(8), 12(8), 13(*2*), 14(1); segmented caudal fin rays 16(1), 17(*20*); lateral scale rows 23(4), 24(*13*), 25(2); transverse scale rows 6(*2*), 7(11); breast scaleless; vertebrae 10(13) precaudal plus 16(*12*), 17(1) caudal, total 26(*12*), 27(1).

Dorsal fin elongation uncommon, observed only in males, usually involving

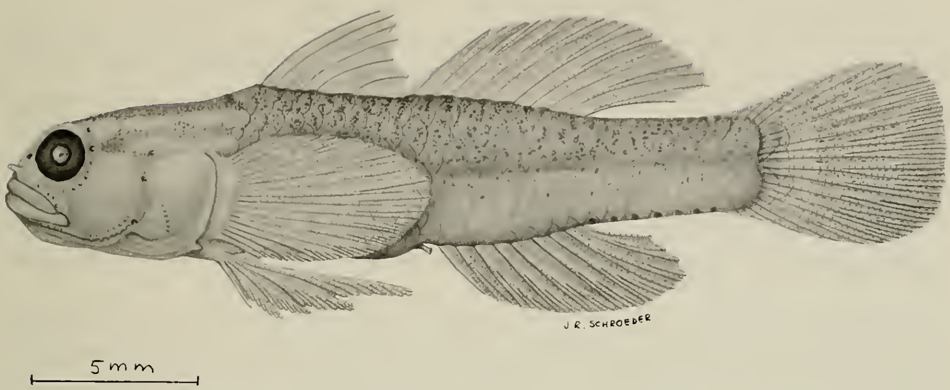


Fig. 2. *Eviota albolineata,* 22.2 mm SL, male, Moorea, Society Islands, CAS 48469.

first spine, occasionally second spine; maximum length of depressed first spine extending to end of base of second dorsal fin. Pelvic fin usually not extending beyond origin of anal fin. Cephalic sensory pore system pattern 1; cutaneous papillae system pattern A. Male genital papilla not fimbriate.

Slender species, trunk beneath spinous dorsal fin not very deep relative to depth of head and caudal peduncle. Distal margin of nonfilamentous spinous dorsal fin straight or slightly concave and approximates a vertical line perpendicular to horizontal axis of body, in contrast to a straight margin forming acute angle with horizontal axis, as in most other *Eviota.*

Color of preserved specimens.—This species is a complex of two color forms, one highly pigmented, represented in part by the type material from the Society Islands and Tuamotu Archipelago (eastern Oceania population) and a pallid form that is more widespread, occurring more to the west in Oceania, the Indo-Australian Archipelago, the Great Barrier Reef, and the Indian Ocean (western Oceania-Indian Ocean population). Within the geographic ranges of each color form are irregularly distributed intermediate color forms which are not typically clinal.

The coloration typical of the highly pigmented specimens of eastern Oceania (see Figs. 1c, 2) follows. Dorsolateral portion of head behind eyes with 2 or 3 narrow dark horizontal stripes composed of moderately dense scattered brown chromatophores, upper 2 stripes extending to anterior section of trunk, lower stripe extending to anterior portion of opercle. Lowermost dark stripe commonly obscure, other 2 varying in intensity and length. Dark stripes separated by 3 pale bands equal to or wider than stripes, upper pale band most prominent but sometimes masked by pigmentation on dorsal portion of head and nape. Pale bands often indistinct, uppermost may be limited to a large pale spot dorsolaterally behind eye at about position of supraotic pore. Striped pattern variously reduced or absent in some specimens. Head and nape dorsally variably pigmented, either with chromatophores scattered uniformly over predorsum, with weak to moderately developed saddles traversing midline, or with reticulated pattern; predorsal midline with 2 elongate spots evenly spaced between eyes and dorsal fin origin; head laterally with 3 small dusky spots, 1 at upper preopercular pore, 2 bordering margin of eye at four o'clock and two o'clock, latter at about anterior otic pore;

3 spots most apparent when dark horizontal stripes faint or absent; spot at upper preopercular pore most persistent of 3. Central portion of chin pale or rarely with small discrete spot in line with vertical through middle of eye, or with 2 to 4 small spots lateral to this position. Tip of snout and region around anterior nasal tubes dusky. Remainder of head mostly pale.

Fleshy base of pectoral fin variously pigmented with scattered chromatophores: most commonly, upper third with pale round to horizontally elongate spot more or less surrounded by faint chromatophores, or, uncommonly, with faint scattered chromatophores throughout or pale spots on both upper and lower portions of base.

Trunk often with rather uniformly scattered brown chromatophores, somewhat more dense dorsolaterally, in some specimens chromatophores absent ventrally. Dorsal portion of trunk, especially along insertions of dorsal fins, may have small clusters of chromatophores. Lateral midline of trunk with pale horizontal stripe about a half scale in width, stripe often obscure or lacking; rarely, a weak pale horizontal stripe along middorsolateral portion of trunk.

Tiny dark spots usually present along ventral midline of trunk posterior to origin of anal fin; spots number up to 14, not integrated with any subcutaneous pigment; spots sometimes joined to form variously developed elongate streaks. Subcutaneous postanal midline spots and bars and midlateral caudal peduncle spot typical of many *Eviota* absent in this species. However, subcutaneous pigmentation present in belly region as 1 to 3 large dark patches.

First dorsal fin pale to dusky, usually with some dusky pigmentation posteriorly on distal portion of membrane, and sometimes with narrow dark basal band; in some specimens, fin dusky throughout. Second dorsal and caudal fins with discrete, fine, scattered, brown chromatophores on otherwise pale membrane; in some very darkly pigmented specimens (including holotype) second dorsal and caudal fins dusky brown throughout, lacking distinct dark spots, but with discrete small pale spots interspersed over membrane. Anal fin uniformly very dark brown. Pectoral and pelvic fins usually pale except on very dark specimens where finely dusky.

Coloration of widespread pallid form (see Fig. 1a), found primarily in Indian Ocean and western Oceania, consisting of very pale head and trunk, with traces of most of diagnostic marks listed above for eastern Oceania form. Remnants of light and dark horizontal stripes on head may persist; upper pale band may be represented by pale spot near the supraotic sensory pore and lower dark stripe by narrow band of chromatophores. Three small dark spots at upper preopercular sensory pore and at the margin of the eye at two o'clock and four o'clock, usually persist. Chin usually with small dark spot on middle portion, nearly in line with vertical through eye, sometimes replaced or supplemented by 2 to 4 dark lateral spots. Predorsal midline with scattered chromatophores anteriorly, 1, or less frequently 2, elongate dark streaks mesially and weak remnants of transverse bar posteriorly. Fleshy base of pectoral fin most often pale, sometimes with weak scattered chromatophores in midsection. Trunk usually entirely pale, at most with scattered brown chromatophores on upper portion; sometimes pale midlateral band faintly discernible. Ventral midline of posterior trunk with tiny dark spots or continuous streak, as in dark color form, but intensity of pigmentation somewhat reduced; some specimens have this pigmentation segmented into 6 or fewer elongate dark spots, but pigment never as extensive as in species of *Eviota* with well developed postanal midline spots.

First dorsal fin largely pale, distal portion with some faint scattered speckling and some specimens with weak narrow dusky basal band. Second dorsal fin pale in anterior basal region, remainder of fin pale to light dusky with fine dark spots scattered over midportion. Caudal fin pale to dusky with fine dark spots scattered over upper two-thirds of fin. Anal fin in males moderate to dark dusky throughout; in females fin may be somewhat lighter and pigmentation restricted to distal or middle portion of fin or, occasionally, lacking. Pectoral and pelvic fins pale.

The heavily pigmented color form, with well developed dark and light stripes on head, is found in the Society Islands and Tuamotu Archipelago, and is also represented by a few specimens from the Cook and Santa Cruz Islands, and the Great Barrier Reef. Specimens with only traces of this pattern are found in a wider geographic area, but occur irregularly in a non-clinal distribution. Specimens from all localities in the Indian Ocean other than Sri Lanka, and most specimens from Australia show no traces of the head stripes. When the dark stripes are not discernible the species may be recognized by the characteristic dark spots on the side of the head, by the dark anal fin, the characteristically spotted second dorsal and caudal fins, the lack of subcutaneous ventral midline trunk spots and bars, and the generally pale trunk. The single dark spot on the chin is more common in specimens from the Indian Ocean than in those from western Oceania, and is almost entirely lacking in eastern Oceania.

Color in life.—Indian Ocean color form. The following observations were made by Thomas H. Fraser at Inhaca Island, Mozambique (RUSI 1856): Specimen taken from hole in rocky substrate at base of coral head; "brilliant solid green, very conspicuous," observed under water at distances of about 4.5–6 m.

Western Oceania color forms. The following color notes were recorded by R. Wass. Specimens taken at Tutuila Island, Samoa Islands (USNM 222522): "Body pale, edges of scales orange, yellow spot on pectoral base, yellow spots on anal base, dusky distally, orange spots on head and lips, seven orange internal blotches behind anus." (USNM 222520): "Seven internal orange marks behind anus, body orange especially dorsally, nape with four orange saddles, lips orange, snout yellow, upper pectoral base red, trailing edges of fins dusky." The following color was described for a specimen from Guam (UG 4324): "when live—transparent with pink and green patches along back and lower sides."

Geographic distribution.—A widely distributed and abundant species, ranging from the east coast of Africa eastward through the Indo-Pacific region to the Tuamotu Archipelago. This species is not known from the Red Sea, Japan, and the Hawaiian Islands.

Etymology.—The specific name is a Latin combination meaning white line, in reference to the pale stripes situated laterally on the head.

Remarks.—The existence of two color forms of *Eviota albolineata* presents a systematic problem that is further compounded by the close relationship of *E. albolineata* with the allopatric species *E. guttata*. Our recognition of *E. albolineata* as a wide ranging species distinct from *E. guttata* of the Red Sea and Gulf of Oman, is based on the examination of hundreds of specimens and the appraisal of several specific color marks. Yet, we regard our interpretation of these species as tentative because of the great differences between the pallid and the heavily pigmented forms of *E. albolineata,* and the close relationship between *E. guttata* and *E. albolineata.* A summary of the basis for our decision follows.

Eviota albolineata is a member of Group I (Lachner and Karnella 1980:113), closely resembling *E. guttata* in general color pattern and meristic characters. In addition to Group I characters these two species share the following: three spots laterally on the head, at two and four o'clock behind the eye, and one at the upper preopercular pore; a uniformly dark anal fin; small, discrete dark spots on the second dorsal and caudal fins; one or more spots on the chin; and varying amounts of speckled pigmentation on the trunk.

Eviota albolineata differs primarily from *E. guttata* in lacking the 6–7 enlarged, dark ventral midline spots and associated dark subcutaneous marks on the posterior trunk. Other differences are the pale body of the western Oceania-Indian Ocean form, the head stripes of the eastern Oceania form and the lack of a well developed dark bar along base of the spinous dorsal fin in both color forms of *E. albolineata.* There are minor differences in the pectoral fin ray counts: *E. guttata,* average 16.6 range (15–18); *E. albolineata,* Indian Ocean, 17.1 (16–18); eastern Oceania, 18.7 (18–20).

The data reported by us for color in life for the Indian Ocean color form of *E. albolineata* (Mozambique) and the western Oceania color forms (Samoa and Guam) are strikingly different, adding to the confusion in interpreting this species.

Eviota japonica, new species

Figs. 3–4

Material examined.—67 specimens from several localities in Japan and the Ryukyu Islands; total size range 10.6–24.1; gravid females 13.9–17.7.

Holotype: USNM 221758, (17.5), female; Ryukyu Is., Kohamajima Is., 9 Apr 1974, M. Hayashi and T. Itoh, sta 9, formerly YCM-P1420.

Paratypes: RYUKYU ISLANDS: YCM-P1459, 1 (17.7); Ishigakijima Is., Kabira Bay, M. Hayashi and T. Itoh. YCM-P2841, 4 (10.9–13.9); Ishigakijima Is., Kabira Bay, M. Hayashi and T. Itoh. YCM-P2615, 1 (15.0); Ishigakijima Is., Shitafukigawa River, M. Hayashi and T. Itoh. USNM 221752, 6 (10.6–16.8); N'afa Okinawa, Luchu Is., *Albatross.* JAPAN: USNM 221745, 26 (12.1–21.3); Tanegashima Is., *Albatross.* USNM 221748, 28 (11.4–24.1); Tanegashima Is., *Albatross.* FMNH 94179, 19 (9.6–20.9); Aikawa Rikuzen, *Albatross.*

Diagnosis.—Cephalic sensory pore system lacks IT pore; pectoral fin with some branched rays; dorsal/anal fin ray formula typically 9/8; spinous dorsal fin may contain filamentous spines in both sexes; pelvic fin I, 4 1/10–2/10 and with reduced membrane between rays; branches on fourth pelvic fin ray 8–16; trunk with 6 dark postanal midline spots contiguous with subcutaneous bars, last of which aligned with dark midcaudal peduncle spot; 4 narrow dark bars on belly; 2 prominent dark occipital spots in addition to many smaller and less intense spots elsewhere on head and fleshy base of pectoral fin.

Description.—Dorsal fin VI-I, 8(1), VI-I, 9(*18*), VI-I, 10(1); anal fin I, 8(*20*); pectoral fin 15(1), 16(*14*), 17(5); pectoral fin rays 8–17 may be branched, 11–16 usually branched; pelvic fin I, 4 1/10(*19*), I, 4 2/10(10); branches on fourth ray

Fig. 3. *Eviota japonica.* a, b, Paratype, 21.0 mm SL, female, Aikawa Rikuzen, Japan, FMNH 94179; c, Holotype, 17.5 mm SL, female, Ryukyu Islands, USNM 221758.

of pelvic fin 8–16, average 11.2; segments between consecutive branches of the fourth pelvic fin ray 0–5, average 1.4; pelvic fin membrane reduced; branched caudal fin rays 13(5), 14(6), 15(4); segmented caudal fin rays 17(*20*); lateral scale rows 23(4), 24(*9*), 25(6); transverse scale rows 7(8), 8(*7*); breast scaleless; vertebrae 10(*16*) precaudal and 16(*16*) caudal, total 26.

First and second spines of spinous dorsal fin may be filamentous in both sexes, first spine longest and may extend to end of base of second dorsal fin when depressed. Pelvic fin variable in length, most often not extending to origin of anal fin, sometimes beyond. Cephalic sensory pore system pattern 2; cutaneous papillae system pattern B. Male genital papilla not fimbriate.

Color in preserved specimens.—Salient color pattern consisting of 2 prominent dark occipital spots, less intense dark spots and bars on head laterally and ventrally, 2 dark spots on fleshy base of pectoral fin, numerous small dark spots along dorsal midline, and 6 postanal ventral midline spots.

Head with 2 small dark spots on either side of dorsal midline behind eyes, followed by 2 pairs of prominent dorsolateral occipital spots; first pair almost always irregular in shape and vertically elongate, often bridged dorsally by narrow band of less dense chromatophores; second pair of occipital spots larger than first, more regular in shape, roundish to angular or triangular, and never connected to each other dorsally although sometimes a small dark spot or spots on dorsal midline midway between occipital spots; both pairs of occipital spots usually dense, dark brown, at least in lower portion of spot, dorsal portion, or in some cases whole spot, consisting of large dark chromatophores not coalesced into solid

Fig. 4. *Eviota japonica,* Paratype, 18.3 mm SL, female, Tanegashima, Japan, USNM 221745.

dark pigmentation; 3 weak spots or narrow, poorly defined, transverse bars occurring along dorsal midline posterior to second pair of occipital spots; remainder of nape pale.

Cheek and opercle with irregularly shaped spots and bars, those on cheek less intense than those on opercle, but neither as dark as occipital spots; consistently present pigmentation includes elongate bar below the eye at six o'clock to below rictus, mark from eye at about seven-thirty, across lips to chin; snout weakly pigmented with small spots; lower opercle, branchiostegal membranes and lower portion of head with many small dark irregularly shaped elongate spots, equal in intensity or darker than opercle spots, sometimes approaching intensity of occipital spots.

Fleshy base of pectoral fin with 2 dark oval or elongate spots composed of loose aggregates of large dark chromatophores, spots clearly separated in midportion of base, both spots about equal in intensity to opercle spots. Dorsal midline with approximately 13–14 small dark spots or narrow bars from origin of spinous dorsal fin to procurrent rays of caudal fin. Six small, dark postanal midline spots, integrated with 6 subcutaneous bars on lower portion of trunk; upper portion of postanal trunk with 5 subcutaneous bars, third upper bar contiguous with third and fourth lower bars, last upper bar forming small, circular, entirely subcutaneous central caudal peduncle spot; upper, and to lesser extent, lower subcutaneous bars may be obscure. Four subcutaneous bars ventrolaterally on belly, not joined across ventral midline, bars narrow except in gravid females where broader in upper portion; anteriormost belly bar just posterior to pectoral fin base and lower portion of fourth bar terminating at anus; first 2 belly bars merging dorsolaterally, merged bar followed posteriorly by another dorsolateral subcutaneous bar aligned with the third lower belly bar; fourth belly bar lacking dorsal extension; 2 additional subcutaneous bars in nape region. Trunk mostly pale, faintly pigmented with fine scattered chromatophores; scale pockets usually unpigmented, rarely with fine peppery pigmentation along margins.

Dorsal fins usually uniformly pale to dark dusky although occasionally spinous dorsal fin pale with dusky bands; second dorsal fin irregularly dusky, sometimes with pale spots; anal fin uniformly moderate to dark dusky, often slightly darker than dorsal fins; caudal fin irregularly pigmented, usually pale or light dusky, sometimes with small dark spots on rays; pectoral and pelvic fins very slightly pigmented if at all.

Geographic distribution.—Known from several localities in southern Japan and the Ryukyu Islands.

Etymology.—The specific name *japonica* is based on the occurrence of this species in Japanese waters.

Remarks.—*Eviota japonica* is a member of Group II (Lachner and Karnella 1980:114) and is most closely related to *E. queenslandica* in that they share similar meristic characters, cephalic sensory pore patterns, and prominent patterns of dark spots on the head and pectoral base. They differ in the following details of the color pattern: the dark occipital spots of *E. japonica* tend to be irregular and angular in shape, and the spots on remainder of head somewhat elongate, but in *E. queenslandica* all spots are usually roundish; occipital spots of *E. japonica* are very dark, usually solid brown, at least in lower portions of spots, and usually darker than spots on cheek, opercle and sometimes pectoral base, whereas all spots in *E. queenslandica* are about equal in intensity to each other, the occipital as well as other spots composed of clusters of large, dark chromatophores rather than solid brown pigmentation; the branchiostegal membranes, lower margins of opercles, and the chin in *E. japonica* are usually heavily pigmented with elongate or angular dark marks, sometimes nearly as dark as occipital spots, but in *E. queenslandica* these areas have faint to moderate spots or scattered pigmentation, similar to the remainder of the head but less intensely pigmented; the trunk is mostly pale in *E. japonica,* at most with faint peppery chromatophores marking scale pockets, whereas the trunk in *E. queenslandica* is brownish due to heavier scale and scale pocket pigmentation; *E. japonica* has four subcutaneous bars in belly region, five subcutaneous bars above and six below on trunk posterior to anal fin origin, and with six postanal midline spots, and *E. queenslandica* has three bars or scattered chromatophores on belly region, four subcutaneous bars above and five below on posterior trunk, and with 5 postanal midline spots; the subcutaneous caudal peduncle spot in *E. japonica* is small, very faint and entirely subcutaneous whereas spot in *E. queenslandica* is small to moderate in size, somewhat more pronounced, and mostly subcutaneous, but often with a slight surface pigmentation as well.

The above color characters distinguishing these two species show no intergradation in the Ryukyu Islands where the two species are sympatric. We now report *E. queenslandica* for the first time from the Ryukyu Islands (YCM-P2523, 2 specimens, YCM-P4166, 2, YCM-P4069, 8, all from Ishigakijima Island; YCM-P2926, 2, from Taketomijima Island).

Eviota latifasciata, new species

Fig. 5

Material examined.—88 specimens from 4 localities in the western Pacific and Indian Oceans, total size range 7.7–14.7, gravid females 10.7–13.2.

Holotype: AMS I.18051-001, (12.4), female; Gilbert Islands, Abaiang Atoll, off Bolton Point, 7.6–10.7 m, 10 Nov 1973, D. F. Hoese.

Fig. 5. *Eviota latifasciata,* Paratype, 10.9 mm SL, juvenile, Abaiang Atoll, USNM 260079.

Paratypes: GILBERT ISLANDS, ABAIANG ATOLL: AMS I.18051-073, 17 (9.4–14.0); BPBM 28959, 2 (11.4, 12.9); AMNH 55062, 2 (11.2, 12.3); same data as holotype. USNM 260079, 4 (10.3–13.0); Lagoon side of Teirin Is., D. F. Hoese. AMS I.18043-001, 15 (8.4–13.8); CAS 52737, 2 (11.6, 12.4); ANSP 151949, 2 (12.4, 13.4); Lagoon off Teirin Is., 7.6 m, D. F. Hoese. CAROLINE ISLANDS: USNM 225034, 2 (11.7, 12.8); Ponape, 7°35′N, 158°11′50″E, 0–15.2 m, V. G. Springer 80-8. USNM 225033, 6 (11.1–12.6); Ponape, 7°01′59″N, 158°14′02″E, 0–4.6 m, V. G. Springer 80-11. USMN 225032, 4 (9.5–13.0); Ponape, 7°01′N, 158°19′E, 0–18.3 m, V. G. Springer 80-22. USNM 225037, 15 (7.7–12.0); Senyavin Is., Ant Atoll, 6°47′N, 157°54′24″E, 0–24.4 m, V. G. Springer 80-17.

Non-type material: 8 specimens from Christmas Island in the Indian Ocean (all WAM material); 10 specimens from Kapingamarangi Atoll, Caroline Islands, all in poor condition and faded (all CAS material).

Diagnosis.—Cephalic sensory pore system lacking IT pore; pectoral fin with some branched rays; dorsal/anal fin ray formula typically 8/8; no filamentous spines in first dorsal fin; pelvic fin typically I, 4 plus rudiment and with reduced membrane between rays; branches on fourth pelvic fin ray 7–11; body generally pale with small dark occipital spot and 4 broad dusky subcutaneous postanal trunk bars; postanal midline spots inconspicuous; large dark midcaudal peduncle spot present. Diminutive species, all specimens less than 15 mm SL.

Description.—Dorsal fin VI-I, 7(1), VI-I, 8(*29*), VI-I, 9(2); anal fin I, 8(*30*), I, 9(2); pectoral fin rays 15(2), 16(*14*), 17(9), 18(7); pectoral fin rays 10–18 may be branched, 11–15 usually branched; pelvic fin I, 4 plus rudiment (*20*), I, 4 1/10(3); branches on fourth pelvic fin ray 7–11, average 9.3; segments between consecutive branches of fourth pelvic fin ray 0–2, average 1.0; pelvic fin membrane reduced; branched caudal fin rays 11(7), 12(*4*); segmented caudal fin rays 17(*20*); lateral scale rows 23(3), 24(*4*), 25(1); transverse scale rows 6(*6*), 7(2); breast scaleless; vertebrae 10(*8*) precaudal plus 16(*8*) caudal, total 26.

Spinous dorsal fin not elongate. Pelvic fin usually extending beyond origin of anal fin. Cephalic sensory pore system pattern 2; cutaneous papillae system not completely discernible in this small species. Male genital papilla not fimbriate.

Color in preserved specimens.—Pale body, salient pigmentation consisting of small, dark occipital spot and 4 broad, dark, subcutaneous postanal trunk bars. Head mostly pale, occipital spot located laterally on head above midopercle, of varying size and intensity, never large and pronounced. Some scattered chromatophores dorsally on head just behind eyes. Fleshy base of pectoral fin unpigmented. Trunk with 7–10 small, weak, rectangular shaped saddles over dorsum, from about middle of spinous dorsal fin posteriorly to caudal fin, better developed posteriorly, obscure in some specimens; belly with 2 broad, dusky subcutaneous patches extending dorsolaterally on trunk, and sometimes a faint subcutaneous bar dorsolaterally on nape; postanal portion of trunk with 4 broad, dusky to dark, subcutaneous bars, fourth either more intensely pigmented throughout or darker in midportion, appearing as large, dark, midcaudal peduncle spot overlying less dense subcutaneous bar. Postanal ventral midline spots inconspicuous. Spinous dorsal fin mostly pale, usually with a narrow horizontal dusky stripe basally and dusky distal margin; fin sometimes with scattered dark chromatophores throughout, never intensely dark; second dorsal fin similar to spinous dorsal fin, basal pigmentation more pronounced posteriorly. Anal fin pale to dark brown, usually darker than dorsal fin. Caudal fin pale to weakly pigmented, darker on lower half, sometimes rays with small dark spots. Pectoral and pelvic fins pale.

In specimens from Ponape and Ant Atoll the subcutaneous trunk bars are mostly obscure and in some individuals the lower portion of the third postanal bar is partially divided resulting in five bars on the lower trunk. Specimens from Kapingamarangi Atoll are very faded, showing only the occipital and caudal peduncle spots.

Geographic distribution.—This species is known from Christmas Island in the Indian Ocean, Kapingamarangi Atoll, Ant Atoll and Ponape, Caroline Islands, and from Abaiang Atoll, Gilbert Islands.

Etymology.—The specific name is formed from the Latin words *latus,* meaning broad or wide, and *fasciatus,* meaning banded, in reference to the broad subcutaneous bars on the trunk.

Remarks.—This species is a member of Group II (Lachner and Karnella 1980: 114) and can be distinguished from other members of this group by the combination of the following characters: dorsal/anal fin ray formula 8/8, no elongation of the spinous dorsal fin, a nonfimbriate male genital papilla, typically four postanal subcutaneous trunk bars, the presence of an occipital spot, and an unpigmented fleshy base of the pectoral fin. *Eviota latifasciata* shares several of the above characters with *E. bipunctata* and *E. indica* but differs from these in its coloration and reduced number of subcutaneous trunk bars.

Some variation in the pectoral fin ray count of *Eviota latifasciata* with locality was observed; Christmas Island 17(2), 18(4), Kapingamarangi Atoll 17(4), 18(3), Ponape 15(2), 16(5) and Abaiang Atoll 16(9), 17(3).

Eviota punctulata, new species
Figs. 6–7

Material examined.—255 specimens from 9 areas in Indonesia, Australia and western Oceania; total size range 7.3–23.1; gravid females 11.8–15.7.

Holotype: USNM 224550, (20.7), male; Fiji Is., Great Astrolabe Reef, reef north of Vuro Is., 8 May 1965, R. Bolin and party, *Te Vega* Exp., Cr. 7, sta 278.

Paratypes: FIJI ISLANDS: USNM 224543, 18 (18.0–23.1); same data as holotype. USNM 224542, 3 (15.5–19.9); same locality as holotype, *Te Vega* Exp.,

Fig. 6. *Eviota punctulata,* Paratype, 17.0 mm SL, male, Papua New Guinea, USNM 224548.

Cr. 7, sta 279. PAPUA NEW GUINEA: USNM 224548, 18 (11.2–18.2); Ninigo Is., 0–9.1 m, V. G. Springer 78-3. USNM 224545, 1 (13.3); Hermit Is., 0–0.9 m, V. G. Springer 78-9. USNM 224547, 7 (11.6–17.8); Hermit Is., 0–7.6 m, V. G. Springer 78-18. USNM 224549, 17 (10.8–16.1); Hermit Is., 0–12 m, V. G. Springer 78-19. CAS 47909, 5 (13.0–17.0); AMS I.22213-001, 5 (11.2–16.9); above two lots with same data as USNM 224549. USNM 224544, 1 (17.8); New Ireland, Nusa Is., 0–10 m, T. Roberts. GREAT BARRIER REEF, AUSTRALIA: Lizard Is.: AMS I.18740-107, 11 (14.8–18.0); Yonge Reef, D. F. Hoese, LZ 75-17. AMS I.18739-102, 3 (12.5–15.8); Palfrey Is., 3–10 m, D. F. Hoese, LZ 75-49. AMS I.20762-045, 1 (17.1); S. of Rocky Point, 1.5–4.6 m, D. F. Hoese 75-38. AMS I.21539-082, 1 (12.6); between Bird and South Is., 1.5–7.6 m, D. F. Hoese 75-113. AMS I.21343-008, 4 (10.1–13.8); Palfrey Is., 3 m, D. F. Hoese 75-5. USNM 224546, 4 (11.4–20.4); Palfrey Is., 2–6 m, G. Anderson and B. Russell, FT 74-2. Endeavour Reef, collected by C. L. Smith and J. Tyler: ANSP 146495, 1 (16.4); 13.7–18.3 m, TS,A-15. ANSP 146494, 4 (12.9–18.6); 7.6–18.3 m, TS,A-3. CAS 47911, 3 (11.0–18.9); 13.7–15.2 m, TS,A-16. ANSP 146492, 4 (13.2–15.3); 13.7–19.8 m, TS,A-11. AMNH 42919, 7 (11.1–22.8); 0–13.7 m, S69-16. Little Hope Island, collected by C. L. Smith and J. Tyler: AMNH 42918, 1 (15.1); S69-28. AMNH 42920, 1 (18.8), 0–4.6 m, S69-30. PHILIPPINE ISLANDS: collected by the Smithsonian BFAR, and Silliman University teams, and Alcala: CAS 47910, 3 (13.9–16.0); Palawan Prov., Bararin Is., 0–13.7 m, SP 78-20. USNM 224541, 4 (15.3–18.3); Palawan Prov., Cuyo Is., Tagauayan Is., 0–2.4 m, SP 78-25. AMS I.22209-001, 2 (15.1, 18.3); Palawan Prov., Cuyo Is., 0.6–1.2 m, SP 78-17.

Non-type material: Numerous specimens from the following general localities: INDONESIA; GREAT BARRIER REEF, AUSTRALIA; OCEANIA: Palau Islands; Kapingamarangi Atoll; Ponape Islands.

Diagnosis.—Cephalic sensory pore system lacking IT pore; pectoral fin with some branched rays; dorsal/anal fin ray formula typically 9/8; elongation of spines in first dorsal fin rare; pelvic fin I, 4 1/10–2/10 with reduced membrane between rays; branches on fourth pelvic fin ray 8–18; trunk with 6 dark postanal midline spots; head with dark, somewhat teardrop-shaped, postocular spot; midportion of fleshy base of pectoral fin with oblique streak of dusky pigmentation; scale pocket pigmentation on trunk well developed, more so posteriorly; dorsal and caudal fins with numerous prominent small dark spots.

Description.—Dorsal fin VI-I, 8(1), VI-I, 9(*23*), VI-I, 10(1), VII-I, 9(1); anal fin

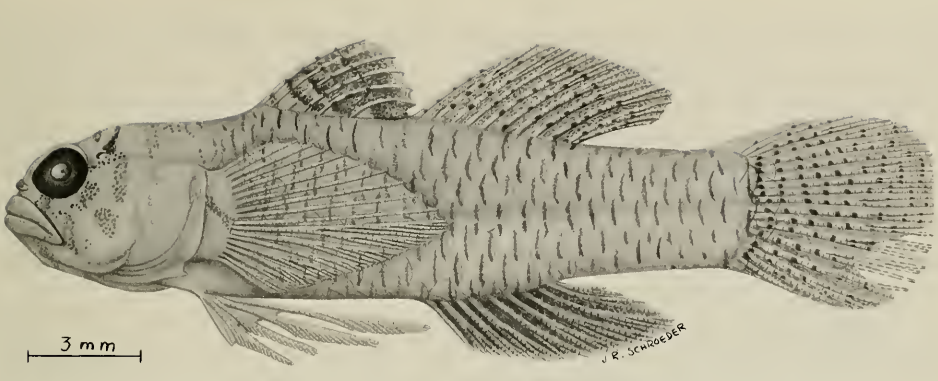


Fig. 7. *Eviota punctulata,* Holotype, 20.7 mm SL, male, Fiji Islands, USNM 224550.

I, 7(2), I, 8(*24*); pectoral fin 15(5), 16(16), 17(4), 18(*1*); pectoral fin rays 8–16 may be branched, 10–15 usually branched; pelvic fin I, 4 1/10(9), I, 4 2/10(*15*); branches on fourth pelvic fin ray 8–18, average 13.7; segments between consecutive branches of fourth pelvic fin ray 0–4, average 1.2; pelvic fin membrane reduced; branched caudal fin rays 12(14), 13(6), 14(*2*); segmented caudal fin rays 16(2), 17(*24*); lateral scale rows 23(7), 24(8), 25(*5*), 26(1); transverse scale rows 6(6), 7(*13*); breast scaleless; vertebrae 10(*10*) precaudal plus 16(*10*) caudal, total 26.

Spinous dorsal fin elongation rare and not well developed, only observed in males; first spine may be filamentous, and extending, when depressed, to base of fifth dorsal fin ray. Pelvic fin usually extending beyond origin of anal fin. Cephalic sensory pore system pattern 2; cutaneous papillae system pattern B. Male genital papilla not fimbriate.

Color in preserved specimens.—Salient coloration of *Eviota punctulata* consisting of dark, boldly marked scale pockets, small distinct dark spots on dorsal and caudal fins, and oblong to teardrop-shaped mark dorsolaterally on head behind upper portion of eye.

Cheek and preopercle with about 4–5 irregularly shaped patches of chromatophores, one of which always more or less vertically elongate and occurring just posterior to rictus; opercle mostly pale, faint brownish patch on upper portion; snout more or less dusky; usually faint bar from eye to upper lip at about seven o'clock; chin and branchiostegal area with faint patches of chromatophores or dusky. Dark, more or less teardrop-shaped spot dorsolaterally on head behind upper portion of eye, spot darkest ventrally; spot extending obliquely toward dorsal midline, nearly meeting contralateral mark. Two smaller dark marks anterior to these, on dorsal portion of head immediately behind eyes. Three or 4 irregular transverse bars on nape, bars meeting at midline posterior to teardrop mark; bars less intense than teardrop spot and sometimes subdivided into irregular marks.

Fleshy base of pectoral fin usually with oblique dusky mark through midlateral portion; pale areas above and below mark may be encircled by chromatophores; pectoral fin base frequently uniformly pigmented or with fine chromatophores above and below larger chromatophores in midlateral portion. Trunk characteristically pigmented with dark, vertically elongate, rather wide marks on scale pockets, these smaller on belly and most intensely pigmented posteriorly on trunk.

Belly with 3 dark, narrowly separated subcutaneous patches aligned with fainter subcutaneous patches located dorsolaterally on trunk; another dorsolateral subcutaneous patch anteriorly, on nape. Six postanal ventral midline spots, spots poorly developed and sometimes obscure, occasionally followed by weaker, smaller seventh spot near procurrent caudal rays. Six postanal spots associated with short, dark, subcutaneous bars usually faint or obscure. Seventh spot, when present, not confluent with bar although sometimes associated with very small subcutaneous marking. Upper subcutaneous trunk bars indistinct and rarely perceptible, reduced in development.

First dorsal fin variable, usually dark dusky brown on membrane, sometimes darker distally, base coloration of spines pale, spines with small dense black to brown spots: 4–5 spots occurring on first spine, spots fewer and sometimes fainter on subsequent spines, spots sometimes diffuse, indistinct or wanting; spots may be arranged in rows appearing as narrow oblique bars on fin. Membrane of second dorsal fin usually uniformly dusky brown but may be darker basally and distally, rays transparent with about 3–5 small discrete dark brown spots on each element. Caudal fin membrane dusky brown, rays mostly hyaline with about 6–8 small dark spots on each element, spots sometimes arranged to form irregular, vertically linear pattern. Anal fin uniformly dark brown, darker than second dorsal or caudal fins, equal to or slightly darker than first dorsal fin. Pectoral fin pale with very fine dark chromatophores bordering rays. Pelvic fin pale.

Sexual dichromatism not pronounced. Females tending to be frayed and paler than males; most females with less pronounced spots on fins and scale pocket markings, although in some specimens marks equal in intensity to those on males.

Geographic distribution.—This species occurs in the Java Sea and northward to the Philippine Islands, eastward to Ponape and Fiji Islands, and on the Great Barrier Reef, Australia.

Etymology.—The specific name *punctulata* is derived from the Latin word *punctum,* and is used in reference to the small dark spots on the fins.

Remarks.—*Eviota punctulata* is a member of Group II (Lachner and Karnella 1980:114) and is easily distinguished from other members of the group in having a unique color pattern, extensive branching on the fourth pelvic fin ray and little or no elongation of the spinous dorsal fin.

Eviota cometa, new species

Figs. 8–9

Material examined.—71 specimens from 4 general areas; total size range 10.3–18.5; gravid females 11.6–14.8.

Holotype: USNM 235817, 1 (15.7); Fiji Islands, Totoya Is., 18°58′57″S, 179°52′12″W, 30 m, 27 Apr 1983, V. G. Springer, VGS 82-8A.

Paratypes: FIJI ISLANDS: AMS I.24027-001, 1 (14.5); Naviti Is., 17°06′S, 177°13′E, 16.8–30 m, V. G. Springer 82-32. USNM 235832, 8 (10.3–13.7); ANSP 151996, 2 (11.7, 13.3); CAS 52831, 2 (13.2, 14.9); 18°42′S, 178°29′E, 0–39.1 m, VGS 82-25. USNM 235863, 1 (13.0); Kandavu, 19°04′S, 178°02′E, 0–13.7 m, VGS 82-22. USNM 260328, 1 (16.4); N of Vuro Is., 18°52′S, 178°30.5′E, R. Bolin.

Non-type material: Numerous specimens from four regions in the Pacific Ocean, the Ponape, Gilbert, Phoenix and Line Islands.

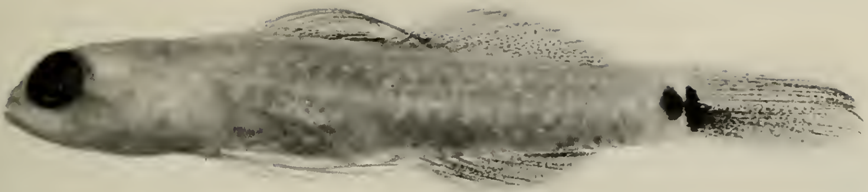


Fig. 8. *Eviota cometa,* 11.6 mm SL, male, Northern Escape Reef, Great Barrier Reef, Australia, ANSP 152010.

Diagnosis.—Cephalic sensory pore system lacking IT pore; pectoral fin rays unbranched; dorsal/anal fin ray formula usually 8/7 or 9/8; spinous dorsal fin may contain filamentous spines, uncommon in females; pelvic fin typically I, 4 1/10 with reduced to well developed membrane between rays; branches on fourth pelvic fin ray 4–9; body pale with prominent dark double mark at base of caudal fin and dark streak from mark along lower portion of caudal fin; subcutaneous bars and postanal midline spots absent in almost all specimens.

Description.—Dorsal fin VI-I, 7(1), VI-I, 8(22), VI-I, 9(*21*), VI-I, 10(1); anal fin I, 6(2), I, 7(21), I, 8(*22*); pectoral fin rays 13(1), 14(2), 15(7), 16(*12*), 17(4); pelvic fin I, 4 plus rudiment (*3*), I, 4 1/10(17), I, 4 2/10(2); branches on fourth pelvic fin ray 4–9, average 6.7; segments between consecutive branches of fourth pelvic fin ray 1–5, average 1.7; pelvic fin membrane reduced to well developed, most often reduced; branched caudal fin rays 11(*14*), 12(3), 13(1); segmented caudal fin rays 16(2), 17(*24*); lateral scale rows 21(1), 22(8), 23(2); transverse scale rows 5(7), 6(3), 7(1); breast scaleless; vertebrae 10(14) precaudal plus 15(14) caudal, total 25.

First 3 spines of spinous dorsal fin in males may be filamentous, first longest, maximum extension to midcaudal peduncle; females rarely with slight elongation of first spine. Pelvic fin almost always extending beyond origin of anal fin. Cephalic sensory pore system pattern 2; cutaneous papillae pattern not well developed in this species. Male genital papilla not fimbriate.

Color in preserved specimens.—Head and trunk mostly pale with dusky anterior nostrils, few scattered chromatophores above and behind eye, large scattered subcutaneous chromatophores on belly. Prominent dark, basicaudal mark consisting of 2 portions: roundish spot, about size of pupil, midlaterally at end of caudal peduncle, touching or nearly so, a dark, elongate, vertical mark at base of caudal rays; vertical mark extending from slightly above midline nearly to ventral margin of fin. Dark, dusky streak extending posteriorly from lower half of dark vertical mark to distal margin of fin; remainder of caudal fin mostly pale. Spinous dorsal fin with dusky band basally, otherwise pale. Second dorsal fin with dusky band basally and distally, or in large males, dusky throughout. Anal fin dusky on lower half or dusky throughout, slightly darker than other fins. Pectoral and pelvic fins pale, except in large males where they are faintly dusky.

Postanal midline of trunk pale or with many tiny subcutaneous spots, usually

Fig. 9. *Eviota cometa,* 15.6 mm SL, male, Palmyra, CAS 52852.

not forming distinct large spots; few specimens from Line Islands having 5 distinct postanal midline spots. Belly with large scattered chromatophores, lacks distinct bars or pigment patches.

In specimens from Fiji, scale pockets along ventroposterior portion of trunk weakly pigmented, pigmentation consisting of single row of chromatophores bordering each scale pocket; this pigmentation may also occur more dorsally on trunk, but less well developed.

Large male specimens having darker fins and somewhat enlarged, more diffuse, basicaudal mark. Males may also have broad faint dusky band through lower two-thirds of head and trunk; band consisting of fine, widely scattered, dark chromatophores. Males from Abaiang Atoll having enlarged basicaudal spot, anterior portion of which deeper than in other populations and nearly merging with posterior portion, latter also broader than typical. Females from Abaiang having more typically shaped mark.

Color in life.—The following description is from a color slide of a 16.1 mm SL male specimen, collected at Fanning Island, 20 Sep 1978, by P. S. Lobel (Northern Territory Museum, Australia). Body pale with reddish-brown pigmentation through most of lower portion of trunk, pigmentation beginning at eye, extending across upper cheek and opercle, over belly region where intensity greatest, terminating at end of caudal peduncle where coloration weakest; eye and anterior nostrils with some reddish pigmentation. Lower half of head with some scattered, fine, dark chromatophores. White spots within reddish-brown coloration on body: 3 or 4 spots laterally on head, 5 or 6 on belly, 6 on postanal ventral midline of trunk, those on belly most distinct, on posterior trunk most diffuse. Six elongate white spots bordering upper limit of reddish-brown coloration just above midlateral body septum. Large black basicaudal mark at hypural joint, anterior roundish part merging somewhat with posterior bar-like portion, margins of both sections diffuse. Weak dusky streak extending from lower portion of basicaudal spot horizontally through lower portion of caudal fin to distal margin of fin. Second dorsal and anal fins with slight dusky pigmentation posteriorly, otherwise pale. All other fins pale, lacking prominent pigmentation.

Geographic distribution.—This species occurs in the Great Barrier Reef, Australia, and Oceania at Fiji, Ponape and the Gilbert, Phoenix and Line Islands.

Etymology.—The specific name *cometa* is Latin for comet and is used in reference to the basicaudal spot and the trailing dark streak.

Remarks.—*Eviota cometa* is a member of Group III (Lachner and Karnella 1980:114). Of the species in this group it most closely resembles *E. zebrina.* Both species share a variable dorsal/anal fin ray formula of 8/7 or 9/8, have a pelvic fin membrane that ranges in development from reduced to well developed, and have similar prominent basicaudal spots. *Eviota cometa* differs from *E. zebrina* in lacking well developed body pigmentation, other than the basicaudal mark, and lacking vertical bars on the caudal fin. *Eviota cometa* has a dark horizontal streak on the lower portion of the caudal fin not found in specimens of *E. zebrina* from Oceania and Australia.

Eviota cometa and *E. zebrina* are sympatric at Fiji and the Great Barrier Reef. At Fiji most specimens of both species have a dorsal/anal fin ray formula of 9/8 but on the Great Barrier Reef *E. zebrina* has a formula of 9/8 and *E. cometa* 8/7.

No pattern emerges when the dorsal/anal fin ray formula of *Eviota cometa* is plotted against geographic locality. The formula varies within and between localities.

Eviota sigillata, new species

Fig. 10

Material examined.—490 specimens from several areas extending from the Indian Ocean to Oceania; total size range 9.0–21.0; gravid females 12.4–15.0.

Holotype: USNM 223836, (18.3), male; Indian Ocean, St. Brandon Shoals, south of Raphael Is., 0–3.7 m, 8 Apr 1976. V. G. Springer, VGS 76-12.

Paratypes: INDIAN OCEAN, ST. BRANDON SHOALS: USNM 223834, 31 (10.3–17.7); CAS 47938, 5 (14.0–18.1); AMS I.22205-001, 5 (13.6–18.0); ANSP 146761, 5 (13.1–16.8); BPBM 26538, 4 (14.1–18.6); WAM P.27053-001, 3 (12.0–17.7); ROM 36923, 3 (14.8–17.7). Preceding seven lots from same collection as holotype. USNM 223830, 1 (14.6); Albatross Is., 0–18.3 m, VGS 76-22. USNM 223827, 4 (15.6–19.6); N of Frigate Is., 15.2–21.3 m, VGS 76-5. USNM 223831, 29 (12.3–20.3); S of Raphael Is., 0–9.1 m, VGS 76-20. USNM 223835, 16 (9.6–19.0); southern part of Shoals, 15.2 m, VGS 76-18. USNM 223828, 25 (10.1–19.7); E of Raphael Is., 7.6–9.1 m, VGS 76-8. USNM 223833, 1 (14.4); E of Raphael Is., 0.2–1.1 m, VGS 76-7. USNM 223829, 12 (10.9–18.1); 0–2 m, VGS 76-1. USNM 223832, 7 (16.6–21.0); NE of Siren Is., 16.8–21.3 m, VGS 76-19. RUSI 1888, 2 (13.6, 16.1); W of Tortue Is., T. H. Fraser, SA-35.

Non-type material: Numerous specimens from the following general areas: INDIAN OCEAN: Seychelles Islands, Chagos Archipelago, Sri Lanka; INDONESIA; GREAT BARRIER REEF, AUSTRALIA; OCEANIA: Yap Island, Kapingamarangi Atoll, Ponape Islands.

Diagnosis.—Cephalic sensory pore system lacking IT pore; pectoral fin rays unbranched; dorsal/anal fin ray formula typically 9/8 with some geographic variation to 8/7; spinous dorsal fin may contain filamentous spines in both sexes;

Fig. 10. *Eviota sigillata.* a, 13.0 mm SL, female, Sri Lanka, USNM 223841; b, 17.4 mm SL, male, Seychelles Islands, ANSP 146506.

pelvic fin I, 4 1/10–2/10 and with well developed membrane between rays; branches on fourth pelvic fin ray 3–7; trunk with 7 dark postanal midline spots; coloration variable with age and sex: females and small males with chromatophores somewhat clustered laterally on head, 2 dark spots basally on upper and lower portions of caudal fin and additional weaker spots on fin membrane, and with dusky pigmentation basally in dorsal fins; large males, frequently more robust in body shape, having uniformly distributed chromatophores on head, more diffuse spotting on caudal fin, lower basicaudal spot more prominent, and dorsal fins with more extensive dusky pigmentation.

Description.—Dorsal fin VI-I, 8(7), VI-I, 9(*23*), VI-0 10(1); anal fin I, 7(7), I, 8(*24*); pectoral fin rays 14(1), 16(9), 17(*10*), 18(10), 19(1); pelvic fin I, 4 1/10(*15*), I, 4 2/10(16); branches on fourth pelvic fin ray 3–7, average 5.3; segments between consecutive branches of fourth pelvic fin ray 1–7, average 3.4; pelvic fin membrane well developed; branched caudal fin rays 11(*21*); segmented caudal fin rays 17(*31*); lateral scale rows 21(*6*), 22(4), 23(3), 24(1); transverse scale rows 5(1), 6(*5*); breast almost always scaleless, single embedded scale observed in one specimen; precaudal vertebrae 10(*20*), caudal vertebrae 15(*19*), 16(1), total 25(*19*), 26(1).

First 4 dorsal fin spines of males and first 3 spines of females may be filamentous, spines longer in males, when depressed, longest spine extending to procurrent caudal fin rays. Pelvic fin always extending beyond origin of anal fin. Cephalic sensory pore system pattern 2; cutaneous papillae system pattern B. Male genital papilla not fimbriate.

Some mature males may have deeper bodies than females and immature males. Head depth, at posterior margin of opercle, expressed as thousandths of the standard length, 213–234 (7 spec. 13.3–20.1 mm SL) for deep bodied or stout males; 201–215 (6 spec., 16.3–19.7) for nonstout males; and 209–219 (6 spec. 13.4–16.0) for females.

Color in preserved specimens.—There is markedly pronounced sexual dimorphism in coloration and body depth. In mature females and nearly all small specimens of both sexes (less than approximately 13–17 mm SL), dark color laterally on head irregular and somewhat clustered, most concentrated on anterior portion of opercle, cheek pale or with few chromatophores, and snout and nostrils very dark, prominent against pale upper jaw and chin. Head dorsally and nape with few small dark spots, usually along midline, followed by series of 11 to 13 small dark spots on midline of trunk from origin of spinous dorsal fin to end of caudal peduncle, latter series faint or obscure in many specimens. Fleshy base of pectoral fin variably pigmented, often with small oblique patch of chromatophores in central portion, or with patches on upper or lower portions, base entirely pale in many specimens. Scale pockets weakly pigmented if at all, development of pigmentation mostly restricted to upper anterior portion of trunk, remainder of trunk predominantly pale. Seven small, dark, postanal midline spots integrated with 7 narrow dark vertical subcutaneous bars extending to slightly below midtrunk, pale interspaces usually wider than dark bars; subcutaneous bars on upper trunk obscure. Two broad, oblique, dark subcutaneous patches on belly. First and second dorsal fins with dusky pigmentation basally, outer portions pale. Anal fin light dusky or pale. Caudal fin with 2 dark spots, on upper and lower basal portions, lower spot larger and more prominent; 6 to 8 smaller spots scattered over rest of fin, often weakly developed, few specimens with spots arranged in 2 or 3 wavy vertical bands; lower portion of caudal fin dusky from base to distal margin. Pectoral and pelvic fins unpigmented.

Small and some moderate sized males have pigment patterns nearly identical to females, although somewhat darker. As males mature they develop a color pattern that differs from females and all juveniles in the following ways: pigmentation laterally on head, including snout, cheek, and opercle, more or less uniformly distributed rather than clustered as on anterior portion of opercle of females and juveniles, and consisting of small evenly spaced dark brown chromatophores; upper caudal fin spot less intense and lower spot larger and more diffuse; dark basal pigmentation of spinous and second dorsal fins is broader and darker, extending to distal margins of fins in some specimens; postanal midline spots larger and more diffuse, sometimes seemingly merging with one another; dark subcutaneous bars on posterior lower trunk usually obscure.

Males also undergo dimorphism in head and body depth with maturity, evident as deepening of anterior part of body (Fig. 10b). This always correlated with mature male color pattern found in specimens that range in size from approximately 13 to 21 mm SL. Males with deep bodies much less common and usually among largest specimens in a given collection. Size at which dimorphism occurs varies among collections and with localities.

Our description of the color in preservation is based mostly on specimens from the St. Brandon Shoals. Almost all other specimens were faded to some degree and do not exhibit the full color pattern as seen on most St. Brandon Shoals specimens. The holotype is a male representing a transitional stage of color pattern between that of the juvenile and large adult male.

Color in life.—The following color description is based on a color transparency of a 14.4 mm SL female captured in the Chagos Archipelago on March 5, 1979 by R. Winterbottom and A. R. Emery (ROM 36877). Snout, excluding upper lip, orange-red; iris golden orange-red with some white in upper portion, pupil black; head from eye to end of opercle reddish-orange, becoming light golden orange dorsally on head and nape; upper and lower jaws, chin, head below eye, and fleshy base of pectoral fin pale. The two dark oblique subcutaneous marks found on belly of preserved specimens golden-orange, separated by milky-white areas. Eleven or 12 small orange spots on trunk along dorsal midline beginning at origin of spinous dorsal fin, preceded by 3 small orange spots dorsally on head and nape. Trunk dorsolaterally, especially anteriorly, light orangish; scale pockets, above midline of body, reddish-orange. Seven subcutaneous spots and bars along ventral midline reddish-orange, lower portions of bars most intense. Two reddish-orange, vertically aligned spots, basally on upper and lower portions of caudal fin, lower spot somewhat larger. Small faint orangish spots elsewhere on caudal fin and small, milky-white spots on rays with tiny whitish spots also on membrane of lower portion of fin. First and second dorsal fins with very small faint orangish spots, basal portions with tiny milky-white spots; tiny milky-white spots also on pelvic and anal fins.

Geographic distribution.—*Eviota sigillata* is known from several localities in the Indian Ocean, a single locality in Indonesia, several localities in the northern portion of the Great Barrier Reef, Australia, and from Yap, Palau and Ponape Islands of Oceania.

Etymology.—The specific name is derived from the Latin word *sigillatus,* meaning adorned with little figures or marks, in reference to the seven dark, subcutaneous ventral midline spots.

Remarks.—This species is a member of group III (Lachner and Karnella 1980: 114) and aspects of its color pattern may resemble those of *E. storthynx* and *E. zebrina,* also of this group. *Eviota sigillata* differs from *E. storthynx* in lacking a dark, postocular spot, and differs from *E. zebrina* in having dark spots on upper and lower portions of caudal fin base, rather than a single central dark spot.

Geographic differentiation occurs in two meristic characters, the dorsal/anal fin ray formula and the number of pectoral fin rays. Specimens from the Great Barrier Reef and Indonesia have a dorsal/anal fin ray formula of 8/7(6 specimens), and have 14–17(6) pectoral fin rays, whereas specimens from the Indian Ocean and Oceania typically have a formula of 9/8 (22 of 24 specimens) and have 16–19(24) pectoral fin rays.

Eviota sparsa, new species
Figs. 11–13

Material examined.—215 specimens from 5 general areas; total size range 7.3–21.3; gravid female 15.9.

Holotype: USNM 227483, 1 (16.9), male; Samoa Islands, Tutuila Is., at Utulei village, 15.2 m, R. Wass.

Paratypes: SAMOA ISLANDS: USNM 260327, 7 (8.4–18.6); CAS 52832, 2 (14.9, 16.3); ANSP 151998, 2 (13.6, 16.9); same data as holotype. PHILIPPINE ISLANDS: Collected by Smithsonian Philippine expeditions in 1978 and 1979: USNM 227485, 1 (13.4); Palawan Prov., Cuyo Is., Cocoro Is., 0–21.3 m, SP 78-

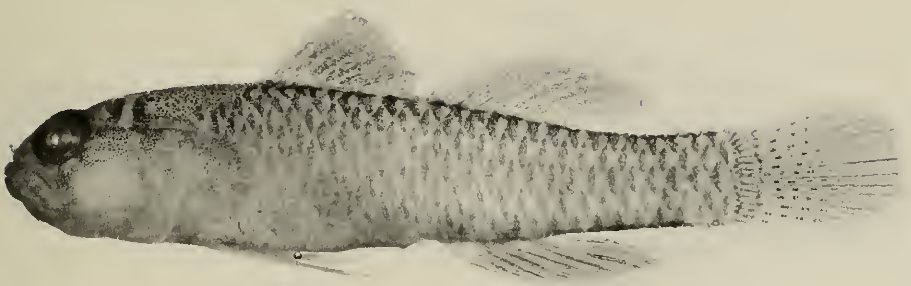


Fig. 11. *Eviota sparsa,* Holotype, 16.9 mm SL, male, Samoa Islands, USNM 227483.

27. AMS I.23987-001, 1 (17.2); Siquijor Is., 0–10.7 m, SP 78-7. AMNH 55055, 1 (16.7); Palawan Prov., Cuyo Is., Tagauayan Is., 0–13.7 m, SP 78-24. USNM 227481, 4 (15.6–17.9); Siquijor Is., 0–30.5 m, LK 79-16. INDONESIA: USNM 210070, 3 (14.2–16.6); Saparua off Kampungmahu, 13.7–16.8 m, VGS 73-12. USNM 227484, 3 (15.3–15.9); Banda Islands, VGS 74-10 or 74-11.

Non-type material: Numerous specimens from the following areas: Indonesia; Palau Islands; Great Barrier Reef, Australia.

Diagnosis.—Cephalic sensory pore system lacking IT and POP pores; pectoral fin with some branched rays; dorsal/anal fin ray formula typically 9/8; elongation of spines in first dorsal fin uncommon; pelvic fin typically I, 4 6/10–8/10 with well developed membrane between rays; branches on fourth pelvic fin ray 3–5; 5 dark postanal midline spots; body generally dusky brown; specimens from Indonesia, Philippine and Palau Islands may have prominent marks laterally on head.

Description.—Dorsal fin VI-I, 8(3), VI-I, 9(*26*), VI-I, 10(1); anal fin I, 7(2), I, 8(*27*); pectoral fin rays 14(1), 15(2), 16(*13*), 17(7), 18(6); pectoral fin rays 8–17 may be branched, 12–15 usually branched; pelvic fin I, 4 6/10(*8*), I, 4 7/10(16), I, 4 8/10(5), I, 4 9/10(1); 1 specimen in 30 with divided fifth pelvic fin ray; branches on fourth pelvic fin ray 3–5, average 4.1; segments between consecutive branches of fourth pelvic fin ray 2–8, average 4.5; pelvic fin membrane well developed; branched caudal fin rays 11(1), 12(*5*), 13(12), 14(2), 15(2); segmented caudal fin rays 16(1), 17(*28*), 18(1); lateral scale rows 23(4), 24(22), 25(3); transverse scale rows 6(10), 7(17); breast scaleless; vertebrae 10(*11*) precaudal plus 16(*11*) caudal, total 26.

Elongation of spinous dorsal fin uncommon, first 4 spines in males may be filamentous, longest spine extending to about middle of base of second dorsal fin; first 2 spines of spinous dorsal fin in females rarely slightly elongate, never filamentous. Pelvic fin usually reaching origin of anal fin or beyond. Cephalic sensory pore system pattern 5; cutaneous papillae system pattern B-1, as found in *E. storthynx* (Lachner and Karnella 1980:7). Male genital papilla not fimbriate.

Color in preserved specimens.—Body more or less uniformly dusky brown, most specimens lacking accentuated color markings. Pigmentation of head laterally ranging from scattered dark brown chromatophores to variously intense clusters

Fig. 12. *Eviota sparsa,* 15.3 mm SL, male, Northern Escape Reef, Great Barrier Reef, Australia, ANSP 148483.

of chromatophores, 2 most prominent clusters occur dorsolaterally behind eye and above preopercle. These patches more or less vertically elongate and rectangular shaped, anterior cluster smaller. Patches sometimes integrated with weaker transverse bars or spots on dorsal portion of head. These clusters usually well developed in specimens from Indonesia, Philippines and Palau Islands, moderate to weak in Samoan specimens, and weak or obscure in Australian specimens. Cheek pigmentation varying from scattered chromatophores to weak or moderately dark clusters of chromatophores; 2 to 5 clusters present, 2 of which may radiate from lower eye. Chin and snout with fine scattered chromatophores. Nape pigmentation ranging from uniformly scattered chromatophores to 2 or 3 weak, irregular transverse bars or irregular wavy clusters of chromatophores.

Fleshy base of pectoral fin with scattered chromatophores or varyingly elongate aggregations of chromatophores on lower, or lower and upper portions of base, separated by pale or less intensely pigmented area. Sometimes a weak vertical dusky band through basal portion of pectoral fin; band may be integrated with one or both elongate pigment patches. Trunk with brownish crescent shaped marks on scale pockets, marks composed of 2 or 3 rows of chromatophores; scale pocket pigmentation forms a rather uniform diamond pattern over trunk. Five somewhat

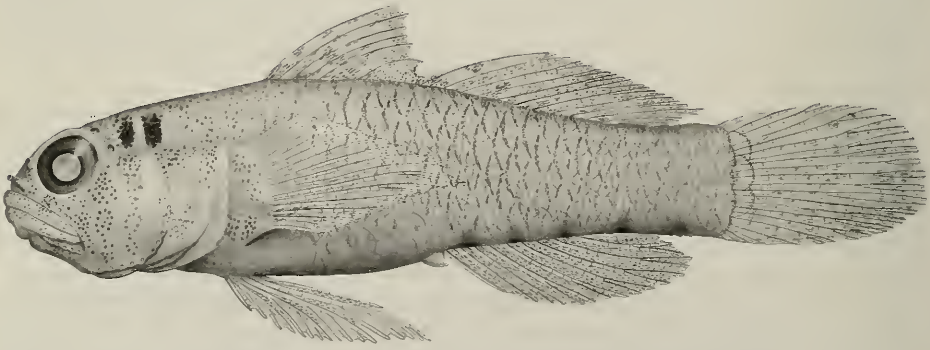


Fig. 13. *Eviota sparsa,* Paratype, 15.7 mm SL, female, Saparua, Indonesia, USNM 210070.

elongate, dark subcutaneous postanal midline spots integrated with 5 bars on posteroventral region of trunk, bars weak to moderately developed, sometimes obscure; posterodorsal portion of trunk with faint or obscure subcutaneous bars. Sixth dark ventral midline spot may occur at base of procurrent rays, often obscure. No prominent dark external or subcutaneous midcaudal peduncle spot. Belly with 3 fairly wide subcutaneous bands, first 2 extending vertically entire depth of trunk, third occurring on lower trunk only, bands usually faint to obscure.

Spinous dorsal fin most often uniform brownish but may have scattered dusky blotches or a dusky basal band. Membrane of anal and second dorsal fins uniformly light dusky, basal portions may be slightly darker, fin rays pale; some specimens with few pale circular spots on second dorsal fin; some specimens with anal fin slightly darker than dorsal fins. Caudal fin pale to light dusky, sometimes with several tiny weak dark spots on rays. Pectoral and pelvic fins pale.

Color in life.—The following color notes were recorded by Richard Wass from an undetermined specimen of the type series, collected at 15.2 meters, Utulei village, Tutuila Is., Samoa: "Background coloration pale. Posterior halves of scales covered with tiny orange and yellow spots outlined in dusky resulting in brown effect at a distance. Dorsal and caudal rays with reddish orange spots. Anal rays red. Fin membranes dusky. Three darkly pigmented (internal) areas at base of anal and three on ventral portion of caudal peduncle. Orange spots on lower lip and chin. Dusky orange spots on cheek and nape."

Geographic distribution.—This species is known from Indonesia, the Philippines, Palau Islands, the Great Barrier Reef, and the Samoan Islands.

Etymology.—The specific name *sparsa* is a Latin word meaning sprinkled or flecked, in reference to the chromatophores scattered over the body.

Remarks.—*Eviota sparsa* is a member of Group VII. It can be distinguished from the other member of this group by the following characters: a long fifth pelvic fin ray and a uniform, unaccentuated coloration in most specimens.

Acknowledgments

We wish to extend our thanks to all those who participated in making specimens available to us on loan. In addition, we thank T. H. Fraser and R. Wass for descriptive accounts of live coloration of specimens, and R. Winterbottom, A. Emery, P. Lobel, and Helen Larson for color slides that contributed to live color descriptions. The following individuals generously allowed us to make specimen exchanges in order to distribute paratypes among major museums: J. E. Böhlke, C. L. Smith, and D. F. Hoese. Finally, special thanks go to M. Hayashi (YCM), C. L. Smith (AMNH) and R. Wass (Office of Marine Resources, Government of American Samoa), for allowing us to retain specimens from their collections as holotypes at the USNM.

The specimens illustrated in Fig. 1a and Fig. 10b were photographed by Kjell Sandved. The drawings shown in Figs. 2, 5, 7 and 9 were rendered by J. R. Schroeder, and those in Figs. 4, 12 and 13 by Paul Mazer.

Literature Cited

Karnella, S. J., and E. A. Lachner. 1981. Three new species of the *Eviota epiphanes* group having vertical trunk bars (Pisces:Gobiidae).—Proceedings of the Biological Society of Washington 94(1):264–275.

Lachner, E. A., and S. J. Karnella. 1978. Fishes of the genus *Eviota* of the Red Sea with descriptions of three new species (Teleostei:Gobiidae).—Smithsonian Contributions to Zoology 286:1–23.

———, and ———. 1980. Fishes of the Indo-Pacific genus *Eviota* with descriptions of eight new species (Teleostei:Gobiidae).—Smithsonian Contributions to Zoology 315:1–127.

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

PROC. BIOL. SOC. WASH.
96(4), 1983, pp. 807–855

REVISION OF THE GENUS *LEPTOSOMATUM* BASTIAN, 1865 (NEMATODA: LEPTOSOMATIDAE)

Tom Bongers

Abstract.—The available type-material of the species of *Leptosomatum*, has been studied and compared with the type-species of the genera *Leptosomatides* (*L. euxinus* Filipjev, 1918) and *Syringonomus* (*S. typicus* Hope and Murphy, 1959).

The character complex present in *L. elongatum*, the type-species of *Leptosomatum*, sharply distinguishes the species of *Leptosomatum* from the genus *Leptosomatides*, hitherto regarded as being related to *Leptosomatum*. Females of *Leptosomatides* can be distinguished from those of *Leptosomatum* by the presence of a strongly muscularized vagina wall, here termed the vaginal ovejector. The main distinguishing character is the presence of a sexual dimorphism in the amphids of *Leptosomatum*, which is absent in *Leptosomatides*.

The species of *Leptosomatum* can be grouped into three complexes: a) The monotypic complex *L. kerguelense* Platonova, 1958 (new synonyms: *L. clavatum* Platonova, 1958 partim, *L. crassicutis* Platonova, 1958, and *L. arcticum* sensu Mawson, 1958) characterized by the presence of a cephalic capsule in both sexes. b) The *L. bacillatum*-complex composed of *L. bacillatum* (Eberth, 1863) (new synonyms: *L. elongatum* Bastian, 1865, *L. filipjevi* Schuurmans Stekhoven, 1950, and *L. tuapsense* Sergeeva, 1973), *L. sachalinense* Platonova, 1978 (new synonym: *L. diversum* Platonova, 1978), *L. acephalatum* Chitwood, 1936 and probably *L. clavatum* Platonova, 1958 partim and *L. sundaense* n.sp. for *L. sabangense* sensu Micoletzky, 1930 nec Steiner, 1915. This complex is characterized by the presence of a cephalic capsule in juveniles and females, but not in males. c) The *L. punctatum*-complex with *L. punctatum* (Eberth, 1863) (new synonyms: *L. longisetosum* Schuurmans Stekhoven, 1943 and (?) *Stenolaimus macrosoma* Marion, 1870), and *L. keiense* Micoletzky, 1930. In this complex the cephalic capsule is absent in juveniles and adults.

More information is needed regarding the species *L. abyssale* Allgén, 1951; *L. bathybium* Allgén, 1954; *L. behringicum* Filipjev, 1916; *L. breviceps* Platonova, 1967; *L. groenlandicum* Allgén, 1954; *L. indicum* Stewart, 1914; *L. pedroense* Allgén, 1947; *L. sabangense* Steiner, 1915; *L. tetrophthalmum* Ssaweljev, 1912 and *L. sundaense* new name; pro *L. sabangense* sensu Micoletzky, 1930, they are considered species inquirendae.

Leptosomatum ranjhai Timm, 1960, and *L. micoletzkyi* Inglis, 1970, do not belong to *Leptosomatum* and are, for the moment, considered species incertae sedis.

L. caecum Ditlevsen, 1923 belongs to *Pseudocella*.

L. arcticum Filipjev, 1916; *L. elongatum* sensu Platonova, 1967; *L. gracile* sensu Allgén, 1954; *L. grebnickii* Filipjev, 1916 and *L. tetrophthalmum* sensu Platonova, 1967 are transferred to *Leptosomatides* Filipjev, 1918.

The genus *Leptosomatum* Bastian, 1865, which contains large-sized marine nematodes, was last revised by Filipjev (1918). Platonova (1976) published a key and reviewed the family Leptosomatidae. According to these authors the genus is characterized by the reduced cephalic capsule and the simple gubernaculum. On this basis, females of *Leptosomatum* cannot be distinguished from those of *Leptosomatides* Filipjev, 1918. The genus now contains 31 nominal species and identification of these has become impossible.

While studying populations of a *Leptosomatum* species I observed some phenomena that appeared to be undescribed. Re-examination of type-specimens of most species revealed the presence of a character complex that clearly demarcates *Leptosomatum* from related genera. Some species that do not possess this complex had to be excluded from *Leptosomatum,* some were transferred to *Leptosomatides* and *Pseudocella,* and others must be regarded as species inquirenda.

In a series of papers, starting with the present one, I will try to raise the classification of the Leptosomatidae from the α-level and to establish a classification based on holapomorphy as proposed by Lorenzen (1981). The first step is the demarcation of the genera. Lorenzen did not succeed in basing the classification of the family Leptosomatidae on holapomorphy, partly because many species descriptions are incomplete and inadequate.

Many species are synonymized, due to poor descriptions, sexual dimorphism, and post-adult growth.

In this paper I give an historical account, call attention to artifacts, give supplementary descriptions, discuss the species, and provide a key. In another paper I shall give a phylogenetic approach.

Historical Review

The genus *Leptosomatum* was erected by Bastian (1865) who included eight species: *L. punctatum* (Eberth, 1863); *L. gracile* Bastian, 1865; *L. bacillatum* (Eberth, 1863); *L. figuratum* Bastian, 1865; *L. coronatum* (Eberth, 1863); *L. longissimum* (Eberth, 1863); *L. subulatum* (Eberth, 1863), and *L. elongatum* Bastian, 1865. The last mentioned was designated as "typical species."[1]

Marion (1870) transferred *L. coronatum* to *Thoracostoma.* Villot (1875) synonymized *L. figuratum* with *L. coronatum,* and described *L. roscovianum, L. magnum* and *L. minutum.* It was soon realized that these species did not conform to Bastian's definition of the genus: de Man (1889) made *L. magnum* type-species of his new genus *Cylicolaimus*; in 1918 Filipjev transferred *L. minutum* to the same genus and in 1927 he removed *L. roscovianum* to *Synonchus.*

Von Linstow, also, broadened the scope of *Leptosomatum*; he transferred *Thoracostoma schneideri* (Bütschli, 1874) to it and described four new species: *L. antarticum* (1892), *L. setosum* (1896), *L. papillatum* (1903), and *L. australe* (1907); of these *L. setosum* was transferred to *Thoracostoma* by de Man (1904); *L. antarticum* and *L. papillatum* were removed to *Deontostoma* by Filipjev (1916), and *L. australe* was considered species inquirenda by Filipjev (1918). In 1893 de Man synonymized *L. gracile* with *L. elongatum.*

The generic revision by Filipjev (1918) recognized only three of the above mentioned species, viz. *L. bacillatum, L. punctatum* and *L. elongatum.* In ad-

---

[1] The indication "typical species" did not orginally have the nomenclatorial meaning it has today. According to Stiles and Hassal (1905), *L. elongatum* has to be considered as type by original designation.

dition four other species were included: *L. tetrophthalmum* Ssaweljev, 1912; *L. grebnickii, L. arcticum,* and *L. behringicum,* the latter three previously described by Filipjev in 1916. In the same paper Filipjev erected the genus *Leptosomatides.* He was somewhat uncertain about the generic placement of *L. grebnickii* and *L. arcticum* because in some respects these species resembled the type-species of *Leptosomatides, L. euxinus*; but as males of these two species were still unknown, he left them in *Leptosomatum.*

In 1936 Chitwood described *L. elongatum* subsp. *acephalatum*; in 1951 he reunited this form with the nominate form, but Timm (1953), in an anatomical and morphological study, raised it to specific rank.

Allgén (1947, 1951, 1954, 1954a, and 1957) described five species, which are all doubtful, being described from single specimens. Moreover he confounded *Leptosomatum* and *Leptosomatides*; this will be discussed later.

Platonova (1958, 1967, 1978) published on specimens of *Leptosomatum* identified by Filipjev in the twenties, and described some new species. In her thesis (1976) she reviewed the genus and gave a key.

Minor contributions to the taxonomy of *Leptosomatum* were made by Stewart (1914), Steiner (1915, 1916), Ditlevsen (1923), Kreis (1928), Micoletzky (1924, 1930), Schuurmans Stekhoven (1943a, 1943b, 1950), Mawson (1958), Timm (1960), Inglis (1971), and Sergeeva (1973).

Material and Methods

The original material of the following species was studied: *L. elongatum* sensu de Man, 1893; *L. arcticum, L. grebnickii* and *L. behringicum* Filipjev, 1916; *L. bacillatum* (=*L. filipjevi* Schuurmans Stekhoven, 1950) and *L. punctatum* sensu Filipjev, 1918; *L. coecum* Ditlevsen, 1923; *L. elongatum* subsp. *acephalatum* Chitwood, 1936; *L. sabangense* sensu Allgén, 1942; *L. acephalatum* sensu Timm, 1953; *L. bathybium* Allgén, 1954; *L. groenlandicum* Allgén, 1954; *L. crassicutis, L. kerguelense* and *L. clavatum* Platonova, 1958; *L. ranjhai* Timm, 1960; *L. breviceps* Platnonova, 1967; *L. arcticum, L. elongatum* and *L. tetrophthalmum* sensu Platonova, 1967; *L. tuapsense* Sergeeva, 1973; *L. diversum* and *L. sachalinense* Platonova, 1978.

Of related genera, type-specimens of *Syringonomus typicus* Hope and Murphy, 1969 were studied, as well as the *Leptosomatides* collection of the Zoological Institute in Leningrad.

Furthermore 80 specimens in the collection of the Smithsonian Institution, Washington, were made available; as well as some hundreds of specimens from the Dutch coast, deposited in the nematode collection of the Nematology Department, Landbouwhogeschool, Wageningen. These latter specimens had mainly been collected from the sponge *Halichondria panicea* (Pallas, 1766), in which they occur in great densities; from 100 ml of sponge more than 900 specimens were collected. The sponges were taken off stones in the lower littoral, and immediately fixed in 5% formaldehyde. In the laboratory the nematodes were removed from the sponges. In some cases the sponges were kept in sea water for three hours, in order to allow the nematodes to leave them. They were then fixed and mounted in glycerin following the Seinhorst method (1959). The coverglasses were supported by splinters of broken coverglasses with a thickness of 0.11 mm.

The specimens of Filipjev, Platonova and Sergeeva, and also *L. bathybium, L. groenlandicum, L. caecum,* and *L. elongatum acephalatum* had been mounted in glycerin-gelatin; for this study the three last-mentioned species were remounted. *L. elongatum* sensu de Man, 1893 and *L. ranjhai* had been remounted some years before.

Specimens from Texel, used for the E.M.-study, were collected after they had left the sponge and were subsequently fixed in an iso-osmotic 1.5% glutaraldehyde solution buffered with sodium-cacodylate at pH 7.1 for 30 minutes. The head end was excised and embedded in 1% sea water agar. These agar pieces, measuring 1 × 1 × 3 mm, were additionally fixed for one hour. Post-fixation took place in an 1% osmium tetroxide solution in 0.1 M sodium-cacodylate.

After dehydration in ethanol, the material was transferred to monomere methacrylate in which it was kept overnight. The next day the monomer was replaced by pre-polymerized methacrylate, refreshened once and polymerized for 24 hours at 50°C. Sections were stained in uranyl acetate and lead citrate.

Notation

Cobb's formula for expressing body proportions, which was used by Filipjev (1918), is of limited use for describing dimensions of populations, because no correlations can be given. In a hypothetical case where the length of individuals in a population varies from 6 to 9 mm, information is lost when the ratio "b" is noted as 6.4–12.3. Moreover, the distribution remains indefinite. The standard deviation, which expresses the spread of the ratio, is useful only when applied to nematodes of equal length. The utility of the standard deviation is further decreased, when applied to establish significant differences between *Leptosomatum* populations, by the fact that life cycle and environmental factors influence body length.

To avoid indistinctness and to provide accurate information, body proportions are noted for each specimen separately in the Appendix. The specimens are arranged according to body length to show the relation between body length and other dimensions.

Body length was measured along the axis, which was drawn with the aid of a drawing-tube; the other, smaller measurements were taken directly with an ocular micrometer. Spicules were measured along the chord. The cephalic diameter was measured at the level of the cephalic sensilla, thickness of cuticle at level of the base of the pharynx. Pre-neural body length is distance from head end to the most anterior part of the nerve ring; length to ocelli and amphids are defined analogously. Body diameter at vulva level was measured when necessary, beside the protruding lips. The precision of the diameter of the amphid aperture is limited by focussing difficulties.

Regarding the terminology, in this paper the term "lunula" is proposed for the crescent-shaped median lamella in the tail tip, surrounding the caudal pore as described by Hope (1967:313) for *Pseudocella wieseri.* The term "vaginal ov-ejector" is used to indicate the strong musculature in the vaginal wall of *Deontostoma, Thoracostoma* and *Leptosomatides* sp. which is depicted by Steiner (1916, Taf. 30 fig. 27o, n) for what he considered to be *Leptosomatum gracile* (=*Leptosomatides steineri* Filipjev, 1922).

Artifacts

A subject that has received little attention from taxonomists is the post-mortem phenomena caused by the fixative, the mounting medium or long-term storing. These phenomena may be advantageous—the fovea becomes more clear—but often they are disadvantageous, especially when not recognized: swelling of the cuticle, and dehydration after having been mounted for decades.

Glycerin-gelatin shrinks when dried up as do the specimens mounted in this medium, and ruptures appear. This was the case in the type-material of *L. elongatum* subsp. *acephalatum* Chitwood, 1936. On rehydration of glycerin-gelatin the medium increased in volume and ruptures disappear as a result of this swelling. The length of the nematode, which has been broken into pieces by the drying gelatin, increased by about 10%, which means that the original length has been restored. After removing superfluous gelatin, the specimen and adhering medium were dehydrated and mounted in glycerin in the usual way. Although the pieces of the nematode had not been measured, it seems acceptable that the length has been decreased by the same percentage as it increased by dehydration. This aspect of remounting is probably also applicable to the material of de Man (1893) because at present, these specimens are much smaller than originally described.

I have also observed specimens, embedded in anhydrous glycerin for a considerable time, showing signs of shrinkage although they had been dehydrated sufficiently slowly to allow the glycerin to replace the water in the tissue. This phenomenon was noted in population 1–3 of *L. bacillatum* (pp. 820 and 821). The cuticula hardly changed but the pharynx and intestine decreased considerably in length, often resulting in a rupture in the intestine. The diameter of the body decreased; this can be seen quite readily when comparing the cephalic capsule, which hardly shrinks, with the more posterior tissues. This dehydration however, gives more contrast to the fovea of the male amphid.

The type-material of *L. ranjhai* Timm, 1960 showed the same artifacts, but it is not known whether this is the result of remounting from glycerin-gelatin or of the above-mentioned factors combined.

Body width is influenced by flattening more than the other dimensions. Often it was difficult to ascertain the degree of flattening, or even whether a specimen was flattened at all. For this reason body widths are considered of minor importance.

Purposely flattening in order to bring mounted specimens within focal distance of the immersion lens is to be avoided, especially when applied to type specimens. Glass rods or other supports for the coverglasses should have at least the same diameter as the nematode body. One holotype specimen studied had a body width of 130 μm, whereas the supporting rods were no thicker than 24 and 28 μm.

In contrast, to soil-inhabiting nematodes, which are usually fixed after having actively passed through a cottonwool filter, marine nematodes are generally fixed together with the substrate. The fixed sample thus may contain specimens that were dead and decaying at the moment of fixation. It is, therefore, essential to be able to recognize post-mortem artifacts. For this purpose, nematodes that had died at least one day before, were fixed using 4% formaldehyde in sea water. *Leptosomatum bacillatum* showed the following artifacts: loosening and swelling of cuticular layers; loosing and retraction of the pharyngeal tissues at the anterior end. The cuticular pores became more distinct and the spicular manubrium be-

Table 1.—Differential characteristics of type-species of *Leptosomatum* and *Leptosomatides.*

	Leptosomatum elongatum	*Leptosomatides euxinus*
Cephalic capsule	reduced in male; poorly developed in female. Posterior suture invisible	present; posterior suture visible
Sexual dimorphism in amphids	present	absent
Renette	restricted to females	wanting
Vulvar glands in lateral hypodermal chord	absent	present
Intra-cuticular vulvar granula	absent	present
Vaginal ovejector	absent	present
Atrophy of digestive system and muscles in males	present	absent
Ventromedian precloacal papillae	absent	present
Specialized subventral pre- and postcloacal sensilla	absent	present
Spicules	short and slender	robust
Gubernaculum	dorsal wall of spicule pouches slightly cuticularized	complex; crura and cuneus present
Copulatory musculature	not extensive	strongly developed
Metanemes	loxometanemes	ortho- and loxometanemes

came clearer. The turgor disappeared, resulting in longitudinal cuticular folds at both body ends.

The Separation of *Leptosomatum* and *Leptosomatides*

Leptosomatides euxinus Filipjev, 1918, and *Leptosomatum elongatum* Bastian, 1865, are the type-species of their genera. *Leptosomatum elongatum* sensu de Man, 1893 is without doubt identical with *L. elongatum* Bastian, 1865. Both type-species have been studied and compared. The two genera can be distinguished by the characters listed in Table 1.

One may wonder why Filipjev (1918) hesitated to transfer *L-um arcticum*[2] and *L-um grebnickii,* both described by him in 1916, to *Leptosomatides.* This may be explained in the following way. In 1912 Ssaweljev gave a poor description of a female, which read as follows:

> "23. *Leptosomatum tetrophthalmum* n.sp. ♀—12.7; a = 60; b = 7; c = 75. Der Bau des Kopfendes ähnlich wie bei *Leptosomatum elongatum* Bastian, 1865 (de Man, 1893). Hinter den rotbraunen, kegelförmigen mit lichtbrechenden Körperchen versehenen Augen noch ein Paar heller Pigmentflecke, ähnlich wie bei den Enoplusarten. Nervenring am Ende des vorderen Oesophagusdrittels, Vulva am Ende des zweiten Körperdrittels. Querfaserschicht der Cutis am Vorderende zu sehen. Palafjord, Mogilnojesee."

---

[2] *L-um* and *L-ides* are used in this section as abbreviations for *Leptosomatum* and *Leptosomatides* respectively.

No original material of Ssaweljev (1912) is present in the collection of the Zoological Institute in Leningrad but it is plausible that Filipjev saw this female (Platonova pers. comm.). In the collection, a slide is present (number 5267 dated 12-IX-1915), from the same locality identified by Filipjev as *L-um tetrophthalmum* Ssaweljev, 1912. Beside this specimen, some females are present, labelled *L-um tetrophthalmum* dated 22-IX-1925, and females, without additional eye pigment, labelled as *L-um elongatum* Bastian, 1865; both identified by Filipjev and published by Platonova (1967).

All these specimens resemble *L-ides euxines* closely in the structure of the vulvar region. Assuming that the ovejector was characteristic for the type-species of *Leptosomatum,* Filipjev could not use it, to separate the two genera.

Re-study of *elongatum* sensu Platonova, 1967 (sensu Filipjev), revealed that Filipjev was in error regarding the identity of *L-um elongatum* sensu Bastian, 1865 and de Man, 1893. *L-um elongatum* sensu Filipjev and Platonova has all the characters diagnostic for females of the genus *Leptosomatides* as have *L-um tetrophthalmum, L-um arcticum* and *L-um grebnickii.* These characters are absent in *L-um elongatum* sensu de Man, 1893.

This means that *L-um tetrophthalmum* sensu Platonova, 1967; *L-um elongatum* sensu Platonova, 1967 nec Bastian, 1865; *L-um arcticum* Filipjev, 1916 nec Mawson, 1958 and *L-um grebnickii* Filipjev, 1916 belong to *Leptosomatides.* They will be discussed in another paper. *L-um arcticum* sensu Mawson, 1958 will be discussed under *L. kerguelense.*

No syntypes of *L-um tetrophthalmum* Ssaweljev, 1912, are present; it must be considered a species inquirenda.

Morphological Observations

In *L. bacillatum,* a cephalic capsule is present in females but not in males. De Man (1893) and Timm (1953) gave attention to this capsule in *L. elongatum* and the closely related *L. acephalatum* respectively. I will show that the reported difference between these two species, in structure of the cephalic capsule, does not really exist.

The supposed difference in head structure between *L. elongatum* sensu de Man, 1893 and *L. elongatum* subsp. *acephalatum* Chitwood, 1936 was the main reason for Timm (1953:230) to raise the latter to species level. For females of *L. acephalatum* Timm described "six pairs of fine sclerotized pieces, symmetrically arranged around the 'cap' of oesophageal tissue," which was presumed to be homologous to "un système de deux lignes chitineuses et très minces . . . et qui font défaut dans la region dorsale" as described by de Man (1893) in *L. elongatum.* This comparison is the result of an incorrect interpretation of de Man's paper; neither de Man's nor Timm's passage concerns the cephalic capsule.

De Man in fact described the anterior end of the ventrosublateral pharyngeal glands. He described the cephalic capsule as "une sorte de charpente chitineuse, radiairement symétrique et située à la péripherie, à laquelle s'insère évidemment l'extremité anterieure de l'oesophage."

In whole mounts, the cephalic capsules seems to be a refractive structure that quickly disappears out of focus and, therefore, Mawson (1958) described sclerotized pieces in what she considers to be *L. arcticum* and Timm (1960) described

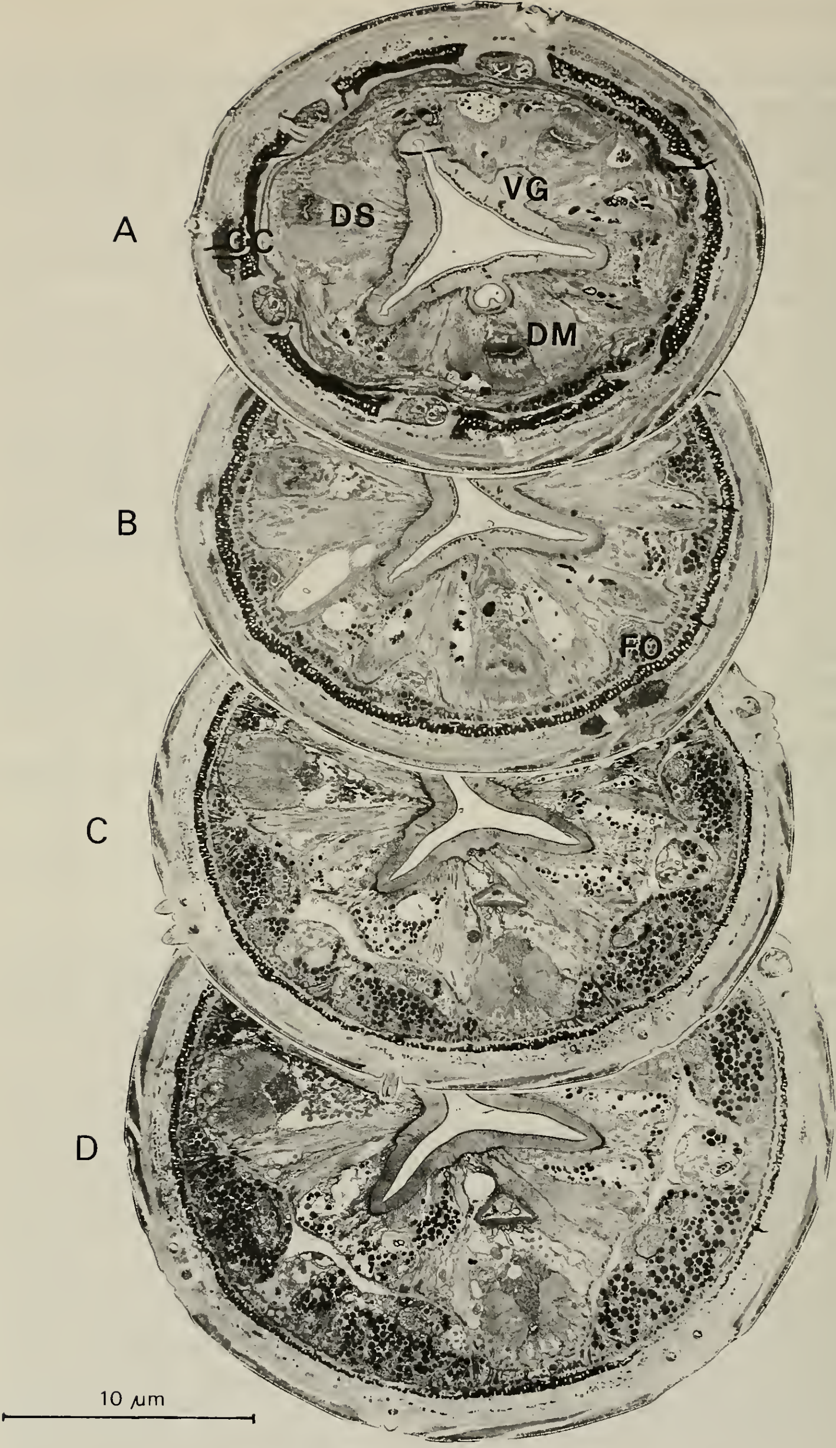


Fig. 1. Sections through cephalic capsule of female *L. bacillatum* at four different levels. A, Anterior part; B, Two microns posteriad of A; C, On level of cephalic papillae; D, Through posterior part of capsule. (CC: Cephalic capsule, LG: Ventrosublateral pharyngeal gland, DM: Dilator muscles, FO: Foramen, DS: Dorsal sector of pharynx.)

similar structures for *L. ranjhai.* Inglis (1964:289) is quite sure that what Timm (1953) is describing is the "lining of the cephalic ventricle, one component of each pair of sclerotized pieces corresponding to the musculature supplying the onchia and the other component corresponding to the radius of the oesophagus."

In Fig. 1A–D the structure of the anterior end of a female is represented spatially. Section A is cut through the anterior part of the capsule; B two microns posteriorly; C at the level of the cephalic papillae and D just in front of the posterior suture.

The cephalic capsule—the "charpente chitineuse" of de Man—is a conoid capsule; reduced but homologous to the capsule in *Leptosomatides, Syringonomus,* and the Thoracostomatinae. In pre-adult males this capsule is present; it disappears when the cuticle is shed during the last molt, so it is a part of the cuticle. In Fig. 1A–D this layer can be seen as an electron-dense layer that consists of radially arranged rods, 0.75 μm in length.

The posterior suture is almost straight; the anterior is interrupted by the inner labial sensilla, but neither suture is visible in glycerin-slides. De Man (1893) depicted this rim in his Fig. 9b.

The anterior end of the pharynx is affixed to the cephalic capsule. Each sector of the pharynx contains four dilator muscles (Fig. 1 DM), paired two by two; these muscles were termed the "sclerotized pieces" by Timm (1953). The space between these bundles, the foramen (Inglis 1964), is filled by the socket cell of the labial sensilla on the inner and the pocket cell on the outer side; the latter, which is filled with electron-dense droplets, increases posteriorly in size and is pushed aside into the body-cavity at the posterior end of the cephalic capsule. The two paired bundles are separated by the pharyngeal nerves, apodemes and associated muscles, and ventrosublaterally by the pharyngeal glands. The cephalic ventricle (Inglis 1964) is absent in *Leptosomatum.*

The "secondary capsule" as depicted by Filipjev (1916, Fig. 4a) is a space, filled with a spongy tissue, between the cuticular layers; I am not certain about its ultrastructure. This space might be homologous to the lunula. These secondary capsule and lunula have been underestimated as a diagnostic character in the Leptosomatidae. In males, if the cephalic capsule is lacking, this secondary capsule (Fig. 10b) may be confused with the cephalic capsule.

In the anterior part of the pharynx I have observed one dorsal and two ventrosublateral glands. The former empties into the pharyngeal lumen; the cuticularized duct is easily observed in glycerin specimens. The ventrosublateral glands (Fig. 1 LG) open on the lips as described by Timm (1953). These ducts are also cuticularized; de Man (1893) described them as "deux lignes chitineuses" being absent in the dorsal region.

In contrast to the amphids in females and juveniles, the amphids in males are remarkable. In males the fovea is an inverted cardiform pouch with, in *L. bacillatum,* a length of 10 μm which opens to the exterior by a small pore. The fusus is about 15 μm in diameter, fusiform, 40 μm long, and leading to the amphidial gland (Fig. 10b). Some preliminary observations are worth mentioning.

In *L. bacillatum* the amphidial glands are 600–900 μm long and extend to the pharynx base. In related species with a short pharynx, the glands overlap the intestine. The posterior part is glandular and contains secretory organelles. The duct of the amphidial gland is filled with numerous microvilli (Fig. 2) with a diameter of 0.2–0.5 μm: their number exceeds 500 in the posterior part of the

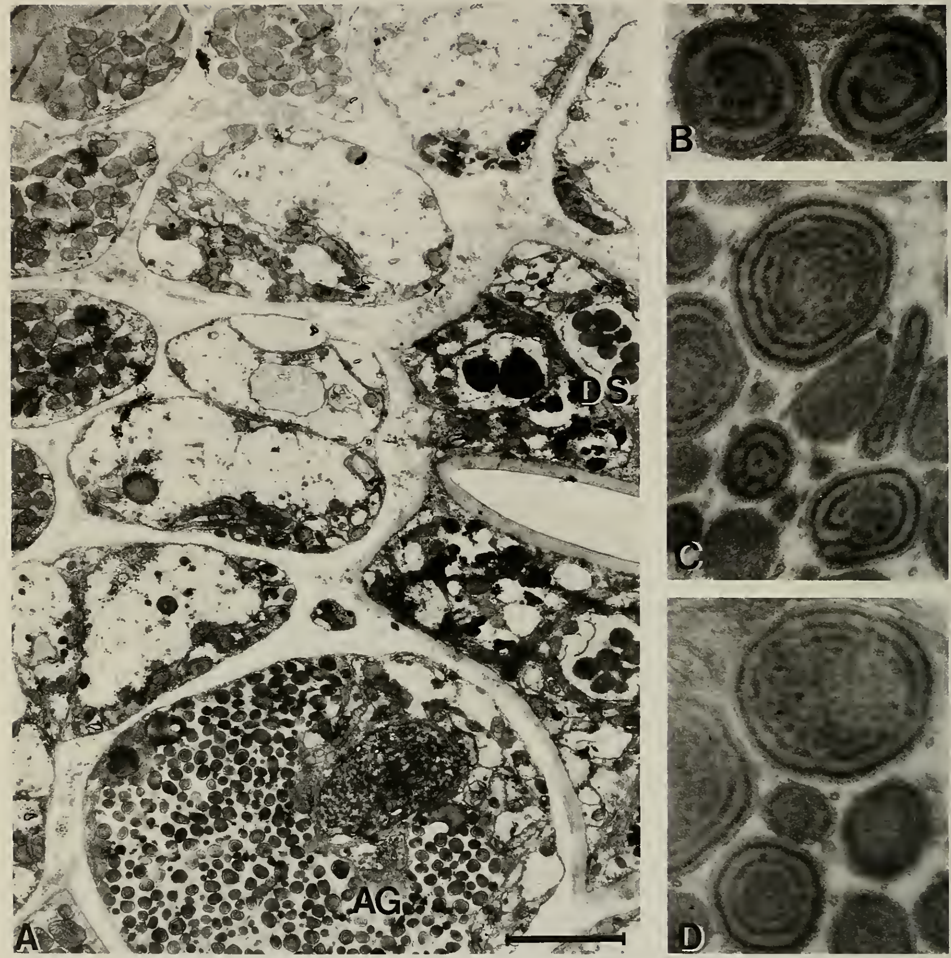


Fig. 2. A, Section through posterior end of fusus in *L. bacillatum,* male. AG: Amphidial gland, DS: Dorsal sector of pharynx. B–D, Details of microvilli. (A, 10,000×; B, 100,000×; C and D, 80,000×.)

fusus. Posteriorly the number decreases; at the level of the ganglia of the amphidial nerves, 50 could be counted.

These microvilli are composed of alternating electron-dense and transparent layers, the latter on the outer side. The outer two or three electron-dense layers are circular without interruptions; interiorly these layers become irregular and single fibers are present in the center. In the anterior part of the fusus the villi are enclosed in membraneous chambers that resemble the amphidial chambers in the male of *Meloidogyne incognita* (see Baldwin and Hirschmann 1973). In the fovea 14 modified cilia could be counted.

No features were observed that contradict the opinion that the villi originate in the anterior part of the fusus. This means that some of the villi reach a length of at least 400 μm. However, as the free-floating ends of the microvilli are extended in the direction of the amphidial gland, it is difficult to imagine that, unless actively involved in transport, the microvilli are not expelled by the excretory products of the amphidial glands. Numerous ganglia are situated anteriorly and posteriorly to the nerve ring in both sexes. In males two of them, at one corresponding body diameter behind the nerve ring, are swollen and therefore, I presume them to be the ganglia of the amphidial nerves (Fig. 9a). They are easily seen under a dissecting microscope. Under the light microscope the amphids in other species of *Leptosomatum* resemble those in *L. bacillatum.* Bastian (1865) depicted these amphidial glands in the male of *L. elongatum.*

The renette is situated ventrally in the posterior part of the pharynx and is restricted to females; in specimens with a short pharynx, "b" exceeding 8, the gland partly or wholly overlaps the intestine. The renette is not always developed, but the pore is always visible in laterally mounted females. In males I have observed neither pore nor renette, and as hundreds of males have been studied, I am certain that they are absent.

The renette in females might have been functionally replaced by the amphidial glands in males of *Leptosomatum,* although it will be difficult to prove this hypothesis.

The ventromedian cells in the pseudocoelom, here termed coelomocytes to avoid the misleading term pseudo-coelomocytes, may be present in juveniles and adults. In some populations they are developed, in others not; populations occur in which these cells are restricted to a part of the population. Further details concerning their structure and function are wanting.

Subventral pre- and postcloacal sensilla are designations for those specialized setae, often placed on hemispherical swellings of the cuticle, which differ from those in the subdorsal region, and which are functionally related to the role of the male, as depicted e.g., for *Leptosomatides inocellatus* by Platonova (1978:73). In *L. punctatum,* which is provided with cephalic setae, the setae are sparsely distributed over the whole body, just as other species with setae. They also occur in the subventral and subdorsal cloacal region.

In the lateral epidermal chords of *Cylicolaimus* (see de Man 1889a:1) glands are present; in *Pseudocella* they are more simply built, and these glands are restricted to the vulvar region in *Leptosomatides.* These glands are absent in *Leptosomatum* as are the vaginal ovejector and intra-cuticular vulva granula, which, however, are present in *Leptosomatides.*

The pre-cloacal ventromedian supplement is present in *L. punctatum* and in males of *L. keiense.* The copulatory musculature is not reduced in the former and a correlation may exist between the presence of the supplement and this musculature.

Descriptive Section

Leptosomatum Bastian, 1865

Phanoglene Eberth, 1863 nec Nordmann, 1840 (Filipjev, 1918).
Leptosomatum Bastian, 1865:144.—de Man, 1893:102–103.—Filipjev, 1918:42–44.—Platonova, 1976:58–60.

Type-species.—L. elongatum Bastian, 1865.

Diagnosis.—Leptosomatinae Filipjev, 1918, with weakly developed cephalic capsule, apparent only in optical section; reduced in male or in both sexes. Somatic tissues atrophied in males. Renette and cervical pore restricted to females, incidentally present in juveniles. Renette usually situated in pharyngeal region, but not always developed.

Sexual dimorphism expressed in structure of amphids. Males with enlarged fovea; amphidial glands strongly developed and outstretched over almost entire pharyngeal length. Pre- and postneural region of pharynx covered by numerous ganglia in both sexes. Ganglia of amphidial nerves in males much enlarged and situated at one body-diameter posterior to nerve ring.

Stoma narrow, without onchia or odontia. Labial sensilla subcuticular, cephalic and cervical sensilla seti- or papilliform. Dorsal pharyngeal gland orifice at level of amphids in pharyngeal lumen; orifices of ventrosublateral glands on anterior end; ducts cuticularized.

Ocelli provided with lens. Caudal glands long; overlapping intestine. Lunula present. Ventral row of coelomocytes usually present. Dorso- and ventrolateral orthometanemes present.[3]

Male diorchic, testes opposed and outstretched. Female amphidelphic, antidromic. Gubernaculum simply built; without appendices. Precloacal ventromedian supplement reduced or absent. Subventral pre- and postcloacal genital sensilla absent.

Leptosomatum abyssale Allgén, 1951

Allgén described a female, originating from a depth of 400 m from the Sagami Sea near Japan, which was not available for this study. He mentioned the shape or the amphids—small and transversely oval—as different from *L. elongatum.* It would be interesting to know whether *L. abyssale* has ocelli.

The description is absolutely inadequate; no details on the cephalic capsule, sensilla, or vulvar region are given. Until the slide is available for re-study, *L. abyssale* must be considered a species inquirenda.

The *Leptosomatum bacillatum* Complex

To this complex belong *L. bacillatum* (Eberth, 1863), *L. acephalatum* Chitwood, 1936, and *L. sachalinense* Platonova, 1978. These species might be conspecific, but in view of the geographical distribution and minor differences in size and ratios, I advise considering them as closely related species until well preserved material becomes available for a detailed comparison.

Leptosomatum bacillatum (Eberth, 1863) Bastian, 1865

Figs. 3–12

Phanoglene bacillatum Eberth, 1863:19–20.
L. elongatum Bastian, 1865:145.
L. filipjevi Schuurmans Stekhoven, 1950:27.
L. gracile Bastian, 1865:145–146.
L. sabangense sensu Allgén, 1942:8.
L. tuapsense Sergeeva, 1973:1710–1712.
? *L.* sp. Kreis, 1928:139.

---

[3] For terminology see Lorenzen 1978.

Nec *L. elongatum* sensu Platonova, 1967; *L. gracile* sensu Allgén, 1954. (Both belong to *Leptosomatides* and will be discussed in another paper.)

Diagnosis.—Cephalic and cervical sensilla papilliform. Cephalic capsule present in juveniles and females; absent in males. Ventromedian precloacal supplement absent. Caudal pore terminal. Ocelli relatively far posterior. Renette restricted to pharyngeal region.

Distribution.—Mediterranean, Black Sea, North Sea, (Spitsbergen ?, Vancouver Island ?, California ?, South Georgia ?, Gulf of Panama ?, Argentina ?, Lesser Antilles ?, and Falkland Islands ?).

I consider records with a question mark to be doubtful because of the numerous errors Allgén made in identifications of species of *Leptosomatum* and *Leptosomatides.* For example, *Leptosomatum microlaimum* Allgén, 1957, is a species of *Leptosomatides* and has been transferred to that genus by Platonova (1976). Specimens identified by Allgén (1954) as *Leptosomatum gracile* are doubtful as he mentions the presence of vulvar glands, which are characteristic for *Leptosomatides.* The specimens identified by Allgén as *Leptosomatum sabangense* belong, as far as can be determined, to *Leptosomatum bacillatum.* Finally, it is doubtful that Allgén has accurately identified any of the species belonging to the *Leptosomatum bacillatum*-complex, given the morphological similarity among members of that complex and the superficial nature of Allgén's work.

Synonymy.—Eberth (1863:20) described *L. bacillatum* as *Phanoglene bacillatum* from: "unter Corallen im Hafen von Nizza." Attempts were made to obtain material from the type-locality but harbor constructions had been carried out and in a letter dated 1980-1-22 Dr. A. Meinesz stated: ". . . qu'il n'y a pas de 'banc de coreaux' dans le port de Nice et il n'y en a jamais eu." Recently Marc Lavaleije (pers. comm.) suggested that Eberth might have meant the calcareous alga *Corallina.* In (1878) de Man reported *L. bacillatum* from the Mediterranean, but as he did not make permanent mounts of the nematodes collected prior to 1876 (Loof 1961), only the description can be used.

Filipjev (1918) reported *L. bacillatum* from the Black Sea. These specimens are still present in the collection of the Zoological Institute in Leningrad where I was able to study them. Filipjev mentioned the presence of the opening of the gland of the accessory organ; this could not be confirmed. The amphids of the female were vaguely perceptible; presumably Filipjev depicted the male amphid in the figure of the female (Fig. 1a). In 1922 he reported gravid females with a length of 12.8 mm.

Schuurmans Stekhoven (1950) renamed *L. bacillatum* sensu Filipjev, 1918, as *L. filipjevi* because Filipjev did not depict the cuticular pores on the tail tip. These pores are depicted by Eberth (1863) and were also present in the juvenile described by Schuurmans Stekhoven (1950). Examination of *L. filipjevi* Schuurmans Stekhoven, 1950 (=*L. bacillatum* sensu Filipjev, 1918) showed that the pores are present.

Leptosomatum elongatum Bastian, 1865, was described from Falmouth; this material has probably been lost. De Man (1893) gave a redescription based on specimens from the type-locality, and synonymized *L. elongatum* and *L. gracile.* These slides are still present in the collection of the Zoological Museum in Amsterdam, and were placed at my disposal. They are labelled:

A 57, *Leptosomatum elongatum* B. ♀ Trefusis VI-1892. Zoöl. Museum A'dam. V. As. no. 652.
A 58, *Leptosomatum elongatum* B. ♂♀ Trefusis VI '92. Zoöl. Museum A'dam. V. As. no. 653.
A 58, *Leptosomatum elongatum* B. ♂♀ Trefusis VI '92. Zoöl. Museum A'dam. V. As. no. 654.
A 59, *Leptosomatum* sp.? ♂ Wimereux 1890. Zoöl. Museum A'dam. V. As. no. 655.

The nematodes were in a rather good condition; they only showed some shrinking caused by dehydration as mentioned before, but were identical to those recently found along the Dutch coast and *L. bacillatum* sensu Filipjev, 1918.

Compared with the description, the mounted specimens of 1893 have decreased in size by approximately 30 percent. De Man was accustomed to studying specimens prior to mounting; only a part of his material was transferred to permanent slides (Loof 1961). Measurements were carried out on living specimens or on specimens recently fixed. It is known that an increase in the volume of a nematode in a hypo-osmotic environment, is expressed especially as an increase in body length. Thus de Man possibly measured his material in diluted seawater. According to Newall (1976) the length of *Enoplus brevis* increases by 40% in a 10% diluted seawater solution.

Leptosomatum tuapsense Sergeeva, 1973, was found to be identical to *L. bacillatum.* According to Sergeeva *L. tuapsense* differs from *L. elongatum* by the setae (?) and structure and length of the spicula. De Man (1893) mentioned a spiculum length of 98 μm, whereas Sergeeva gave 94 μm; the length of the cephalic sensilla is 1.5 and 1.25 μm respectively.

The holotype of *L. tuapsense* (slide N 8092), which is deposited in Leningrad, has been studied. The shape of the spicula, as depicted by Sergeeva, is not the lateral view; the manubrium is less cuticularized than depicted by her. The presence of a cephalic capsule could not be confirmed; she depicted the ducts of the ventrosublateral pharyngeal glands. The dimensions of the amphids have to be halved; the breadth of the fovea is one-sixth of the corresponding body diameter.

In the course of time, Sergeeva collected more material from the Black Sea, which was assigned to *L. bacillatum* (Eberth, 1863) and deposited at the Zoological Institute in Leningrad. I herewith synonymize *L. tuapsense* Sergeeva, 1973, with *L. bacillatum* (Eberth, 1863).

From the Swedish Museum for Natural History, Stockholm, three slides were placed at my disposal. They are labelled: "RMev Sthlm 3:13, 3:66, 3:82" and represent *L. sabangense* sensu Allgén, 1942:8. Although these juveniles are in a poor condition, I consider them identical to *L. bacillatum.*

Regarding *L.* sp. Kreis, 1928, more information is desired. It might belong to *L. bacillatum*; the length and ratio "c" however, need confirmation.

New Records

1. Den Helder, The Netherlands (52°58′N, 4°42′E); Nov 1970. 3 juv., 4 ♂ and 8 ♀, collected from *Polysiphonia* sp. and *Halichondria panicea.* Littoral. Collection Nematology Department Wageningen.
2. Kattendijke, The Netherlands (51°33′N, 3°47′E); Oct 1970. 25 juv., 15 ♂ and

19 ♀, collected from *Halichondria panicea.* Littoral. Collection Nematology Department Wageningen.

3. Burghsluis, The Netherlands (51°40′N, 3°40′E); Feb 1978. 200 specimens from *Halichondria panicea.* Littoral. Collection Nematology Department Wageningen.
4. Texel, 't Horntje, The Netherlands (53°01′N, 4°47′E); Jun 1977. 230 specimens collected by Robin den Ottolander from *Halichondria panicea.* Littoral. Collection Nematology Department Wageningen.
5. Texel, Oudeschild, The Netherlands (53°03′N, 4°50′E); Nov 1970. 55 juv. 10 ♂ and 1 ♀, collected from *Halichondria panicea.* Littoral. Collection Nematology Department Wageningen.
6. Wimereux, France (50°48′N, 1°34′E); 1 ♀, collected by de Man in 1890 and labelled "*Leptosomatum* sp." Collection Zoological Museum Amsterdam.
7. Ambleteuse, France (50°48′N, 1°34′E); Jun 1978. 2 ♀, collected by Michiel Buil from *Halichondria panicea.* Littoral. Collection Nematology Department Wageningen.
8. Banyuls, France (42°29′N, 3°07′E); 3 ♀ from unknown sponges. Jun 1976. Collection Nematology Department Wageningen.
9. N.E. England. 1 ♀ and 1 ♂; collected by R. W. Warwick from *Laminaria* holdfasts at low tide on a rocky shore. Collection Smithsonian Institution Washington, D.C.

Discussion and Description of New Records.—The general morphology has been described by de Man 1893 (*L. elongatum*), Filipjev 1918, and Timm 1953 (*L. acephalatum*). The ultrastructure of the cephalic capsule and amphids, has been described in a previous section.

The study of the life cycle revealed an annual cycle for the Dutch population (4) and it is reasonable that this cycle is also present in other populations in temperate zones. The eggs are deposited in July and August; the length and development of the nematodes are correlated with the sampling date. There are indications that populations collected at corresponding days in different years show significant differences in length. This may be caused by food supply and/or temperature effects.

The renette is maximally developed in autumn. In August 1978, more than 50% of the females showed a more or less developed renette, whereas in the autumn of 1981 at the same locality ('t Horntje) this gland was found in less than 10% of the specimens.

Pre-adult females of the February population from Burghsluis can have a body length between 4 and 6 mm; pre-adults of Texel (June) always exceed 6 mm in length, and these pre-adults reach a length of 8 mm. Schuurmans Stekhoven (1950) described a juvenile from Villefranche measuring 9.5 mm.

Females continue growing after having reached the adult stage; for males, there is no evidence for length increase in the adult stage. The ratios are length-dependent and therefore correlated with the seasons. The ratios of the Dutch population are plotted on graphs to show the length dependance and variability (Figs. 3–6, 8).

Newly hatched juveniles reach a length of 1.4 mm; the maximum length of

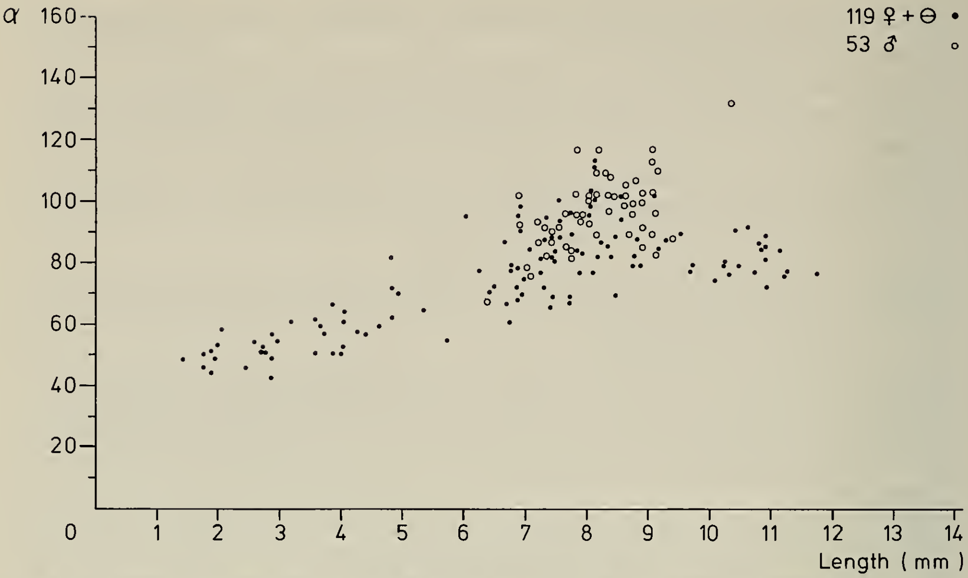


Fig. 3. Relation between ratio "a" (length/body width) and length, based on several *L. bacillatum* populations (Texel).

females from populations 2 and 3 never exceeded 12 mm. Population 4 yielded adults of 14 mm whereas one of the females from Banyuls measured 16.8 mm.

The variability of structure and length of spiculum and gubernaculum are given in Fig. 7.

The ocelli of *L. bacillatum* are placed relatively far posteriorly compared with

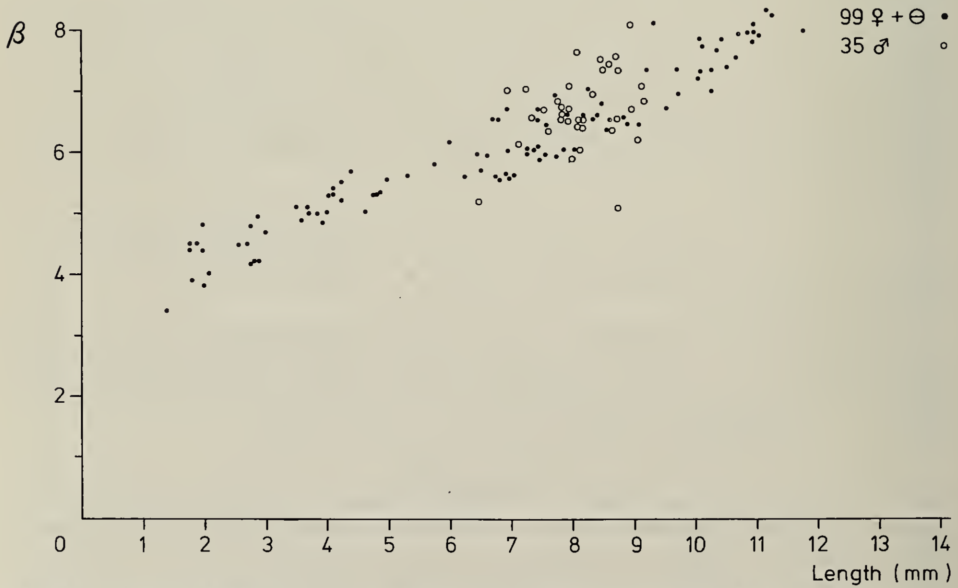


Fig. 4. Relation beween ratio "b" (=length/pharynx length) and length, based on several *L. bacillatum* populations (Texel).

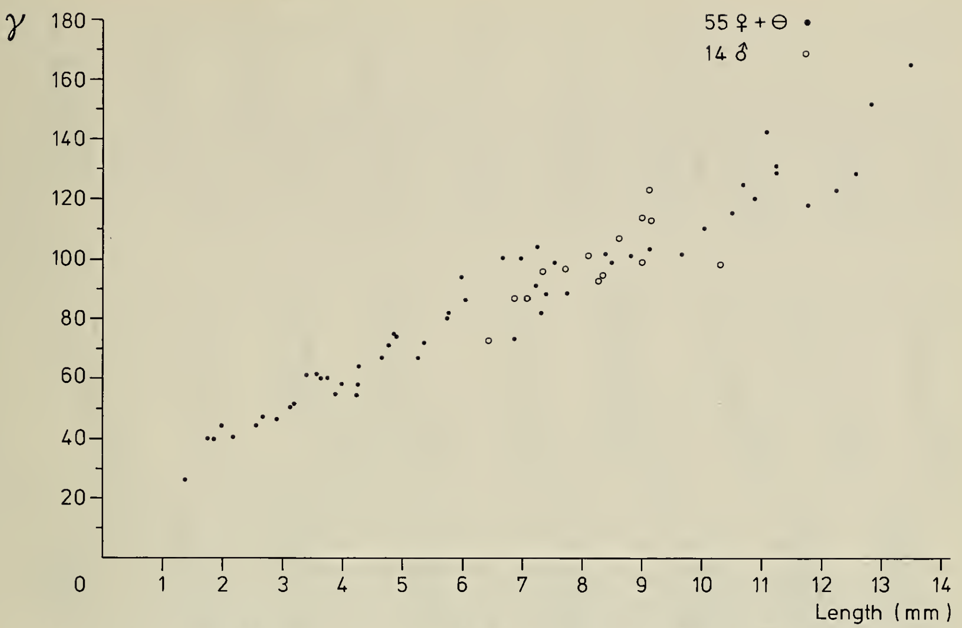


Fig. 5. Relation between ratio "c" (length/tail length) and length, based on several *L. bacillatum* populations (Texel).

L. kerguelense with which females could be confused. The distance from anterior end to ocelli, in the former species, is about 1.3 times the corresponding body diameter and up to 2.0 in the biggest females; in males it ranges from 1.4 to 1.7. In *L. kerguelense* the same calculation varies from 0.7 to 1.0 for females and

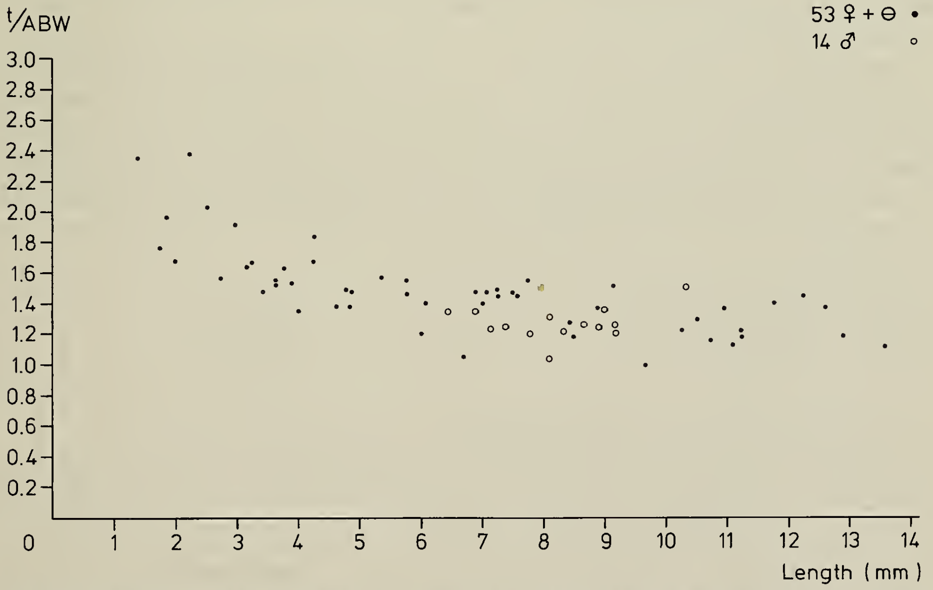


Fig. 6. Relation between "tail/anal body width" and length, based on several *L. bacillatum* populations (Texel).

Fig. 7. Variability in spicule shape of the *L. bacillatum* population from Burghsluis.

from 0.8 to 1.1 for males. Incidentally the ocelli lie at slightly different levels—one more anterior—but this phenomenon is not so common as in *Leptosomatides* sp.

The transverse oval amphid aperture, often called "amphid," measures about 1 μm in females and is situated at 13–24 μm from the anterior end; the opening leads to an almost round fovea with a diameter of 1.5–3.0 μm. The amphidial gland was never noted in females. In males, the canal through the cuticle is conical; the smaller anterior opening measures 1.0–1.5 μm; posteriorly, at the level of the epiderm, this canal appears to be circular; 5 μm in diameter. The underlying fovea

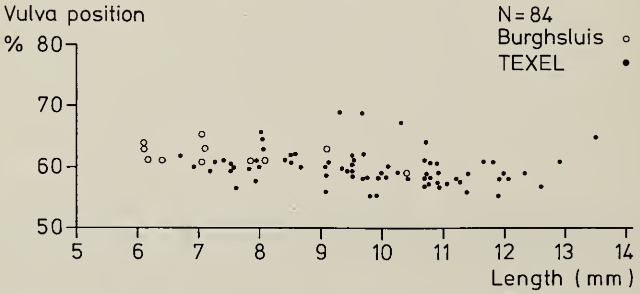


Fig. 8. Relation between V (=distance from anterior extremity to vulva × 100/body length) and length, based on several *L. bacillatum* populations from Texel.

is an inverse, obtuse cardiform pouch. The pore, especially in males, is difficult to resolve.

The cephalic and cervical sensilla are papilloid, and reduced posterior to the nerve ring. The paired cephalic papillae are of different length; those situated more laterally reaching a length of 1.5–2 μm, the more medial papillae 1–1.5 μm. They are placed in cuticular invaginations and are in a number of cases difficult to detect. The papillae near the caudal gland pore are irregular in number and position.

The cephalic capsule in females is refractive and attains a maximum length of 8 μm.

Leptosomatum acephalatum Chitwood, 1936
(*L. bacillatum*-complex)

Leptosomatum elongatum acephalatum Chitwood, 1936:
L. elongatum.—Chitwood, 1951, nec Bastian, 1865.

Diagnosis.—Same as *L. bacillatum* but lower a- and c-value.

Distribution.—East coast USA (Beaufort, North Carolina) and Mexico (?).

Discussion of status.—In 1936 Chitwood split off the variety *L. elongatum acephalatum* based on a male without cephalic capsule. In 1951 he united the variety with the nominate form after having found the female. Having studied material collected from the same sponge *Hymeniacidon heliophila,* Timm (1953) raised the variety to specific rank.

Timm's arguments were the difference in number of eggs, the fine suture around the head in de Man's specimens, the lack of sclerotized pieces in the dorsal head region, and the sexual dimorphism in head structure and size.

Regarding the number of eggs per female, in the Dutch population the number varies between zero and 55 and depends on the season. The uterus stretches with an increasing number of eggs.

The fine suture around the head—the posterior suture of the cephalic capsule—was not noted in mounted specimens of the Dutch *L. bacillatum* populations, nor could it be detected in the specimens on which the 1893 description was based. In living or newly-fixed specimens I have sometimes noted this suture.

Concerning the lack of sclerotized pieces in the dorsal region, a misunderstanding exists, which is discussed in a previous section. The sexual dimorphism, as expressed in the absence of a cephalic capsule in the male, was not described by de Man (1893), but as males were also mounted, it seems reasonable to suppose that he noted the dimorphism and considered the absence of the refractive capsule in the male as an artifact.

The material of Chitwood (1936) (one male, USNM 33973) and Timm (1953) (one male, USNM 33986) has been re-studied; they are identical in structure to *L. elongatum* sensu de Man, 1893; to *L. bacillatum* sensu Filipjev, 1918, and the material from off the Dutch coast. Both males however, are in poor condition. It is not precluded that *L. acephalatum* is conspecific to *L. bacillatum* (Eberth, 1863) but regarding the difference in ratio c and the geographical distribution, the decision to synonymize these species is postponed till more material from the type-locality becomes available.

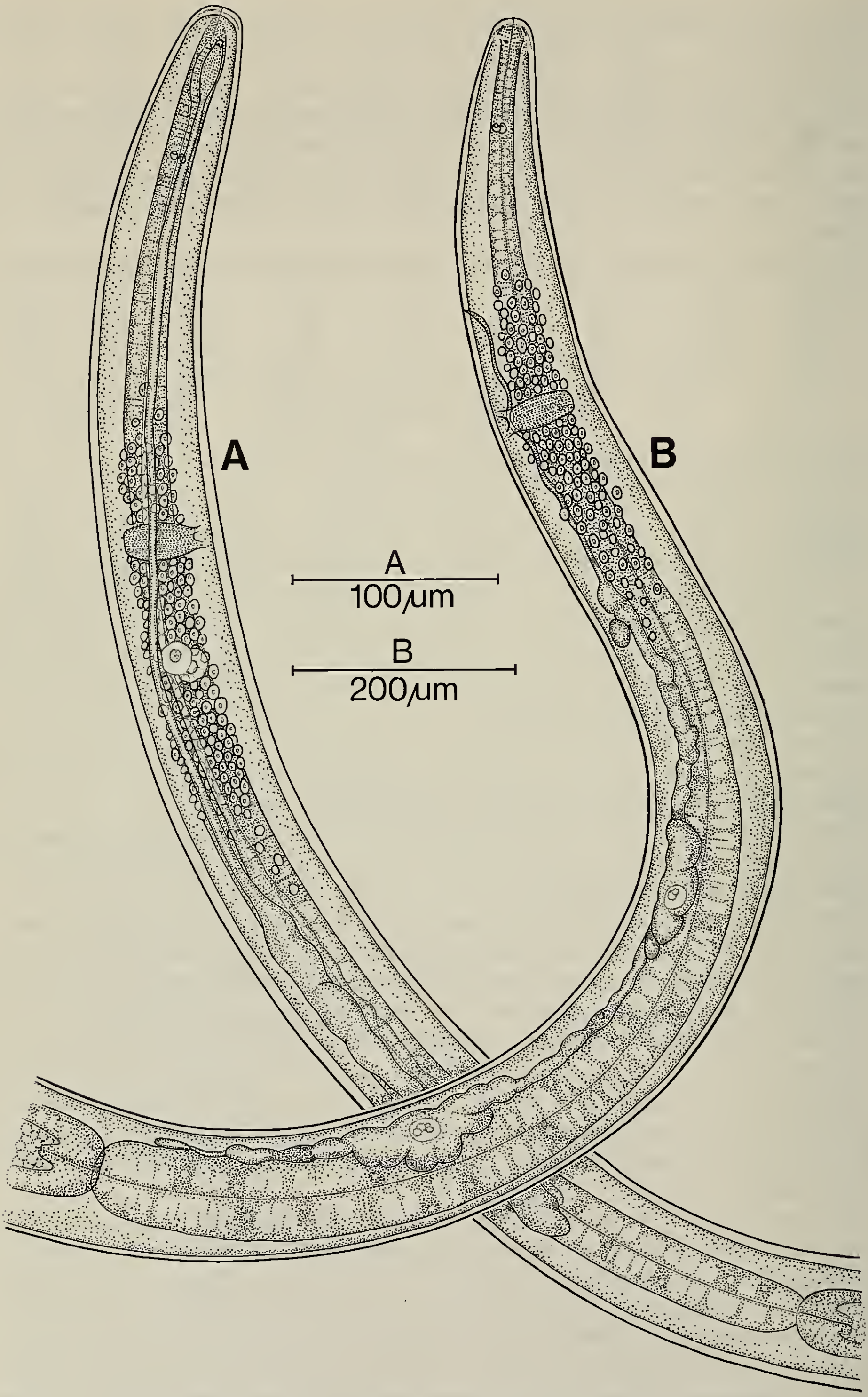


Fig. 9. *L. bacillatum* from Texel. A, Anterior end of male; B, Anterior end of female.

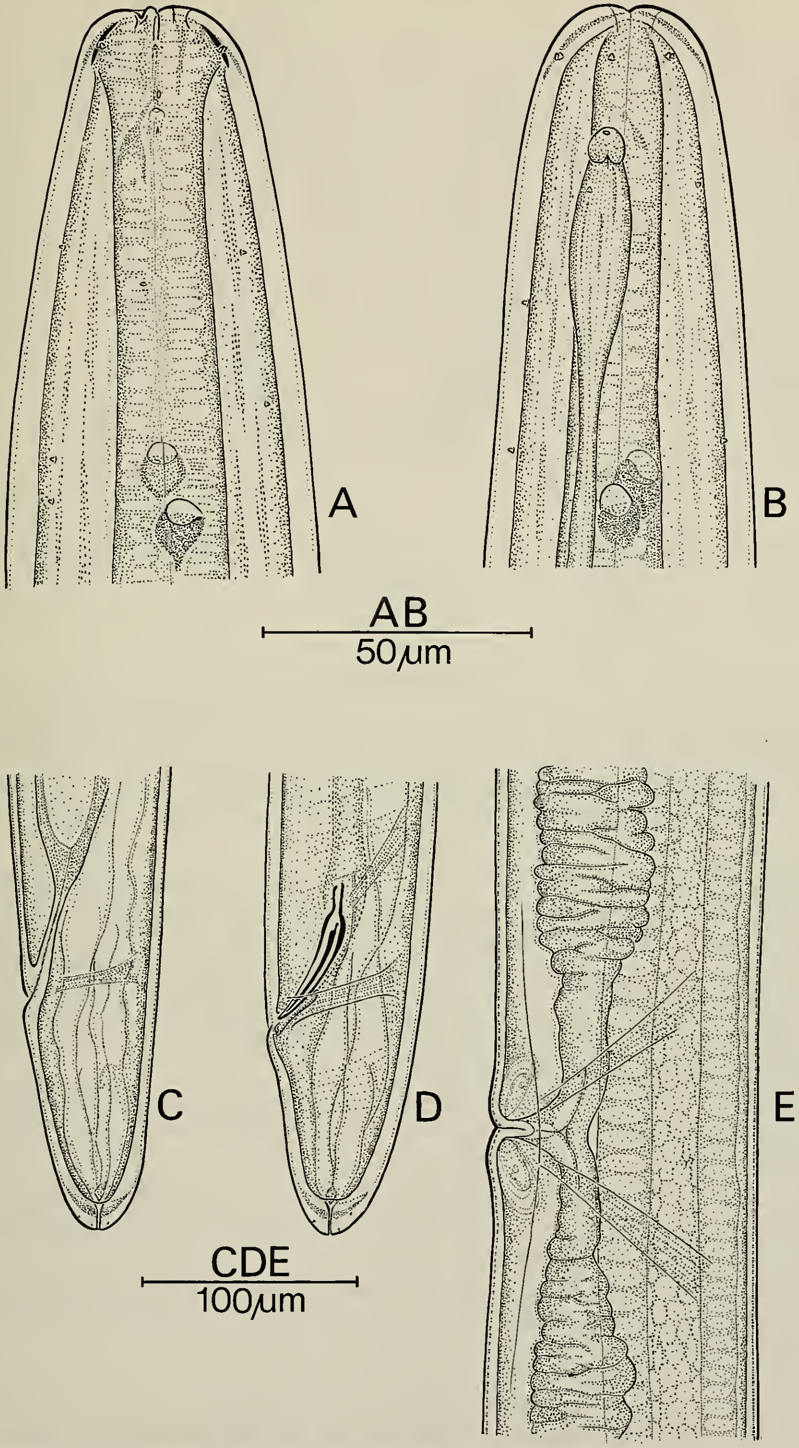


Fig. 10. *L. bacillatum.* A, Head of female, 102; B, Head of male, 76101; C, Posterior end female, 76102; D, Posterior end male, 76101; E, Vulvar region, (Burghsluis).

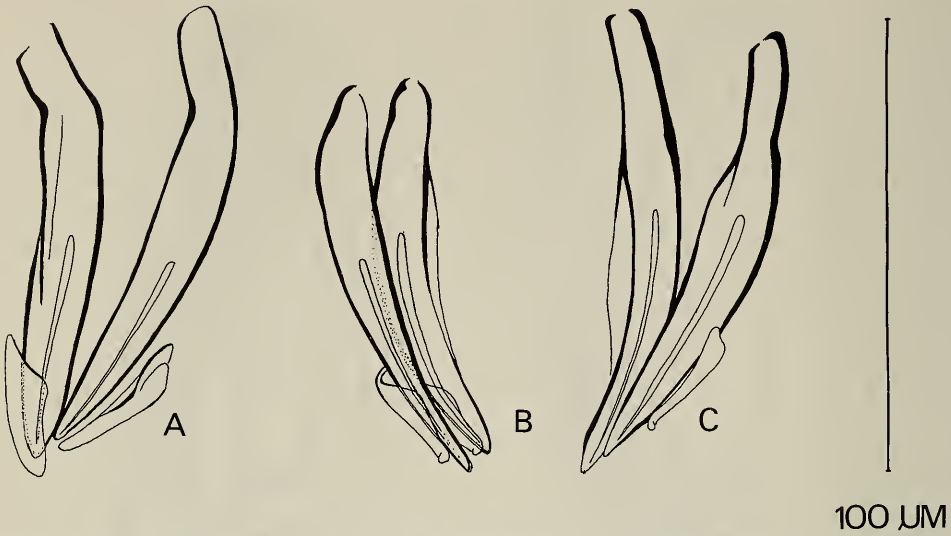


Fig. 11. A and B, Spicules *L. bacillatum* sensu Filipjev, 1918; C, Spicules holotype *L. tuapsense* Sergeeva, 1973.

New Records

1. Quintana Roo, Mexico; North end of Ascension Bay; 4 ♀, 2 ♂ and 2 juv. Collected 7 Apr 1960 by F. C. Daiber and E. L. Bousfield at inlet behind Allen Pt. On mangrove roots; *Isognomon alata, Melampus,* sponges, amphipods, fiddler crabs, and anemones. Collection Smithsonian Institution, Washington, D.C.
2. Quintana Roo, Mexico; Allen Point, Ascension Bay. 13 Apr 1960. 1 ♀, collected by W. L. Schmitt. Collection Smithsonian Institution, Washington, D.C.
3. Quintana Roo, Mexico; North end of Ascension Bay. 2 ♂, 4 ♀ and 1 juv. 15 Apr 1960 by E. L. Bousfield and H. Rehder. Shore just east of Halfway Point. Turtle grass flats off the Point to sandy beaches and mangrove roots, sand varying from a very fine sandy-mud to a coarser shell sand. Collection Smithsonian Institution, Washington, D.C.
4. Quintana Roo, Mexico; behind central part of Niccehabin Reef; 16 Apr 1960. Collected by W. L. Schmitt *et al.* 1 juv. Collection Smithsonian Institution, Washington, D.C.
5. Quintana Roo, Mexico; Ascension Bay. Along shore near Suliman Pt. 17 Apr 1960, W. L. Schmitt *et al.* 1 juv. On rocks in littoral. Collection Smtihsonian Institution, Washington, D.C.
6. Quintana Roo, Mexico; South end Cozumel Island. North of Pta. Santa Maria. 22 Apr 1960. E. L. Bousfield. 1 ♀, collected on shore. Collection Smithsonian Institution, Washington, D.C.

Remarks.—The measurements of these specimens are given in the Appendix. In general, the specimens from Mexico deviate in slenderness and tail length from the Dutch *L. bacillatum* specimens. The diameter of the lens is 8 µm, compared with 7 µm in *L. bacillatum.*

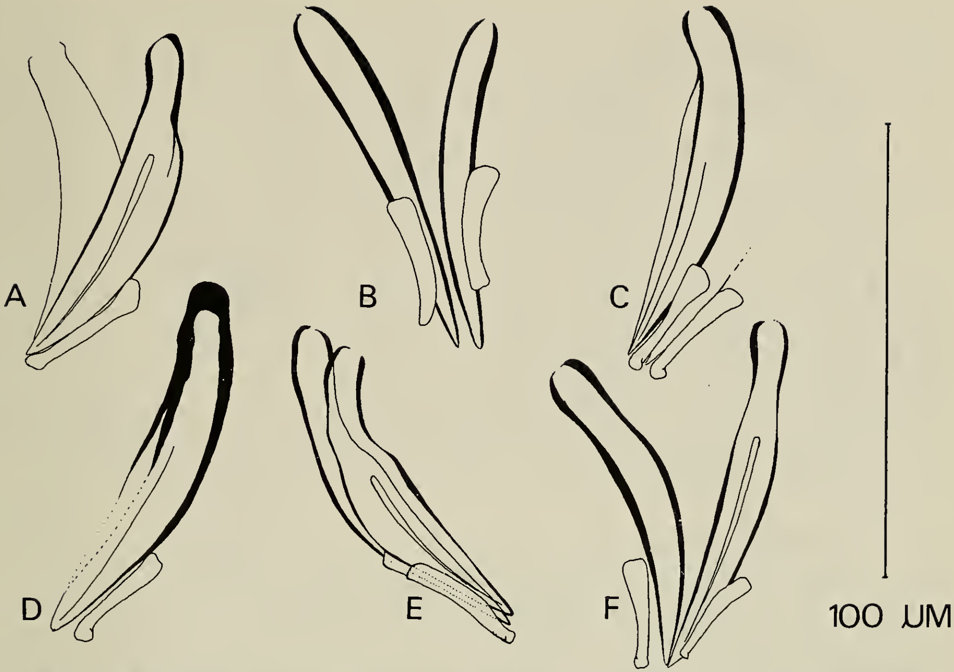


Fig. 12. Spicules. A, Holotype *L. diversum*; B, Paratype *L. diversum*; C, D and F, Paratypes *L. sachalinense*; E, Holotype *L. sachalinense*.

Leptosomatum sachalinense Platonova, 1978
(*L. bacillatum*-complex)

L. diversum Platonova, 1978:495.

Diagnosis.—Same as *L. bacillatum*; pharynx slightly shorter.

Geographical distribution.—South Sakhalin.

Leptosomatum diversum (lapsus *diversus*) and *L. sachalinense* (lapsus *sachalinensis*) Platonova, 1978, were, according to the author, fixed in alcohol. This material shows, moreover, the characteristic artifacts of a post-mortem fixation, resulting in clearance of the cuticular "pores," longitudinal folding of the body, clearing of the contours and swelling of the spicular manubrium. The alcohol caused the content of the lateral epidermal chord to dissolve as depicted for the anterior body part of *L. diversum*. This artifact is not restricted to *L. diversum* as one of the paratypes of *L. sachalinense* (slide 8013) shows the same phenomenon. The posterior body parts of the specimens are folded, the cuticle separated irregularly and the precloacal papilla, as described and depicted, has to be ascribed to this. This "papilla" is situated on one of the subventral folds and could not be confirmed in the paratypes. In both species the cuticle is pierced by small pores; this is not a diagnostic character. The caudal glands, described as equal in length for *L. sachalinense* reach a length of 880, 1090, and 1350 μm. A difference in head structure could not be noted; this structure is identical to that in *L. bacillatum*. I herewith synonymize *L. sachalinense* and *L. diversum*. The holotype and the description of *L. sachalinense* closely agree.

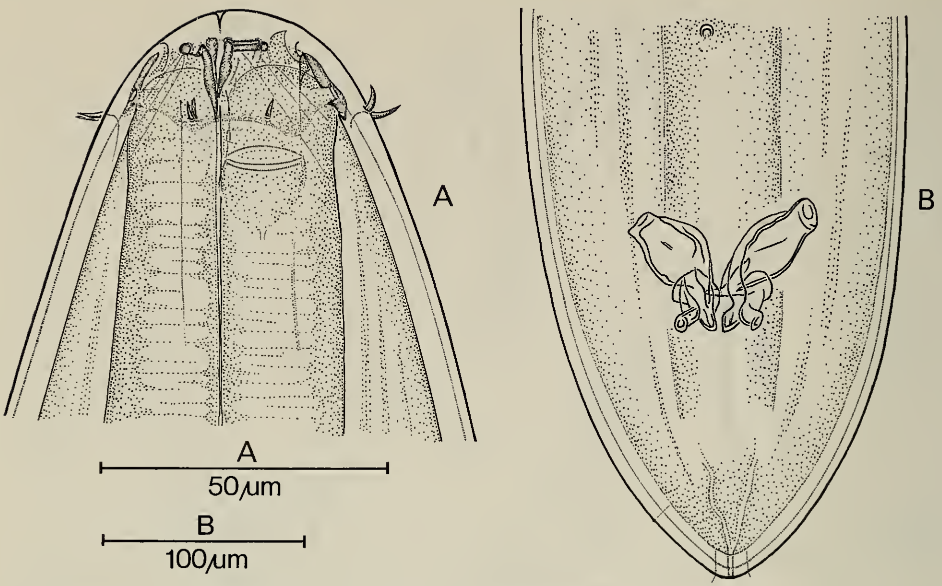


Fig. 13. *L. bathybium.* A, Head; B, Posterior end.

Ratio "b," in the original description of *L. sachalinense* (females), has a higher maximum value than in the Dutch populations of *L. bacillatum.* However, personal examination of the paratypes revealed that the maximum value of "b" (b = 6.3–12.9) is not as high as indicated by Platonova, and in personal communication with her, it has been determined that the datum is in error. The only feature in which *L. sachalinense* differs from *L. bacillatum* (Eberth, 1863), is the structure of the spicula; in some cases the manubrium is open, in some cases closed and heavily cuticularized (or swollen?). Although I am not able to distinguish this species from *L. bacillatum,* because of the poor condition of the first, I postpone the synonymization until more material becomes available for re-study.

Leptosomatum bathybium Allgén, 1954a

Fig. 13a, b

The holotype, a male from a depth of 4500 m was placed at my disposal by the Museum for Natural History at Göteborg. The type is labelled "The Swedish Deep Sea Exped. *Leptosomatum bathybium,* Allgén."

Mounted on a slide, it could only be studied from one side. The fixation or way of mounting has caused a loss of contrast; only the cuticularized structures in cephalic and caudal region could be recognized. Moreover, the structures of the anterior region and their relative proportions could not be reconstructed due to flattening.

The interpretation of the internal head structure does not conform to the description given by Allgén (1954a). Each lip bears in the transverse plane a C-shaped cuticularized structure, the concave side medial. From the middle of these C-shaped structures, a connective piece runs to three "buccal rods" (or mandibles?) in the anterior part of the lumen. A cephalic capsule is present; the posterior suture of this capsule, which curves to produce shallow lobes, is distinguishable.

The diameter of the cyathiform amphid is 16 μm, the aperture about 14 μm. The cephalic setae are vaguely visible; probably 10 setae are present; 6 μm in length. The pharyngeal part of the worm is twisted dorsally over 370°. This part is hyaline to such a degree that the nerve ring could not be found with certainty. With some reservation, it is located on 28% of the pharynx length.

Ocelli are absent. The testis could not be located, and the caudal glands probably overlap the intestine. A ventromedian pre-cloacal sensillum is situated at 150 μm. In ventral view, the "papilla" is horseshoe-shaped with the open side posteriad. The lunula is absent.

Concerning the reproductive system Allgén (1954a) states: "Wegen der Lage des Tieres im Präparat was es leider sehr schwierig das Geschlecht des jungen Tieres zu bestimmen. Bei anwendung von Ölimmersion habe ich doch im Hinterabschnitt des körpers 2 Organe entdeckt, im welchen ich mit Vorbehalt die kurzen sehr dünnen am proximalen Ende angeschwollenen Spicula und das plumpe, unregelmäszig geformte akzessorische Stück glaube gefunden zu haben."

Leptosomatum bathybium Allgén, 1954, must be considered a species inquirenda.

It may be necessary to erect a new genus for this species close to *Platycomopsis* but I prefer to await the urgently needed revision of the Leptosomatidae.

In the collection of the Smithsonian Institution, Washington, D.C., some unidentified specimens are present from the Atlantic Ocean (4500 m) that might belong to the same genus. At present these slides are labelled "cf. *L. bathybium*" and are at the disposal of the next revisor.

Leptosomatum behringicum Filipjev, 1916

The material, on which the original description was based, was collected by Grebnickii in 1880 in the Bering Sea. Platonova (1976) gave a redescription in which she indicated two holotypes: 5780 and 5781. The first contains a complete female, the other a single head. Platonova and I have agreed to exclude 5781 and to designate 5780, deposited in the Zoological Institute, Leningrad, USSR, as lectotype.

Filipjev (1916) remarked that the weak color of the eye pigment was caused by alcohol used as a fixative, and that older females show traces of disintegration.

Specimen 5780 is mounted in glycerin-gelatin, situated dorsoventrally in such a way that the structure of vulva and vagina could not be determined; this difficulty was reinforced by the filled uteri. In the anterior gonad, 9 eggs are present; the posterior contains 14 eggs that are pressed against each other and have a flattened appearance.

The type-specimen of *L. behringicum* which I have examined was in such poor condition that it was impossible to obtain additional information concerning the structure of head, vagina, vulva, and lateral epidermal chord. It is impossible, therefore, to decide whether it belongs to *Leptosomatum* or *Leptosomatides,* and it has to be considered a species inquirenda.

Leptosomatum breviceps Platonova, 1967

In 1967 Platonova described a nematode from Filipjev's collection. The slide, numbered 7383, bears the superscription: VIII-1914, Barentz Sea, Kolski'j Golf,

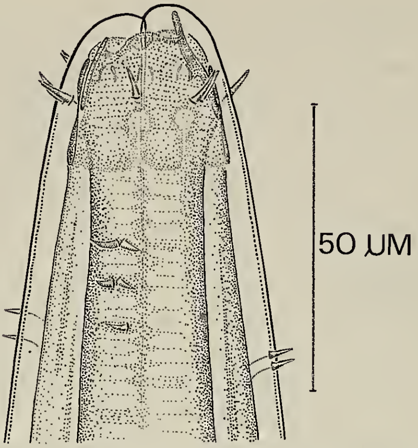


Fig. 14. Anterior end *L. caecum* Ditlevsen, 1923, Lectotype.

I. Filipjev, *L. brev.* ♀ (juv.) and is deposited in the Zoological Institute, Leningrad, USSR.

The description of 1967 and the redescription of 1976 did not mention that the description was based on a juvenile. The formation of the vulva had started, but was not completed.

The cuticular layers were split, resulting in a space of 3.5 μm at the anterior end and 2 μm at the pharyngeal base. This phenomenon might indicate that the last molt was imminent. According to Platonova's (1967) illustration, the anterior end is orientated dorsoventrally; the posterior part laterally. Both illustrations are modified. I have found that neither the anal opening nor the rectum could be observed, the tail is probably longer than described. The anterior cervical setae are slightly shorter than the cephalic setae, and they are progressively smaller posteriorly.

This specimen is extremely flattened, supported by glass-rods of 28 μm. The medial portion of the exteriormost cuticular layer is a more or less compact layer at the anterior end, comparable to the spongy layer in the male of *L. bacillatum.* This layer was incorrectly called "head capsule"; the anterior part of the space was termed "stoma ring." The setae are broken or partly invisible.

Having setiform cephalic sensilla, a ventrally orientated spinneret and no cephalic capsule, this juvenile resembles *L. punctatum.* As only one juvenile is known, I consider *L. breviceps* Platonova, 1967, a species inquirenda, the more so because it was found far outside the known area of *L. punctatum.*

Leptosomatum caecum Ditlevsen, 1923
Fig. 14

In 1923, five specimens of a nematode were collected by Ph. Dollfus near Rockall Island from a depth of 240 meters and offered to Ditlevsen for examination. Two slides were obtained from the Zoological Museum in Copenhagen, and Dr. Kirkegaard was so kind as to give permission to remount the nematodes, which had been embedded in glycerin-gelatin. One slide is labelled "Pourquoi

Pas SA 207 26 Prof. 240m. fond à Lophohelia. Dollfus. *Leptosomatum caecum* n.sp. Hj. Ditl."; the other without indication n.sp. I have added 1342 and 1343 respectively. The dimensions of the specimens (for the abbreviations see p. 852) were as follows:

S	SN	L	DNR	PL	CL	NW	PW	MW	AW	V%
F	1342	9950	416	1528	90	88	104	132	90	60
F	1343	9660	370	1340	85	82	99	143	85	63

Each specimen has little optical contrast, but slide 1343 shows, more or less, the contours of the cephalic capsule, which resembles that of *Pseudocella* and is herewith designated as lectotype; the other female, slide 1342, is too hyaline to observe the capsule.

Ditlevsen (1923) incorrectly interpretated the position of the amphids; although rather hyaline, they are slightly perceptible and situated as usual in the lateral lacunae. I did not depict them. The cephalic setae, of which 10 are present, reach a length of 9–10 μm. The cervical setae do not exceed 6 μm; their position on the left and right body halves is not alike. The lateral vulvar glands are present; the vaginal ovejector seems to be absent as are the pre- and postvulvar sensilla and groups of setae near the caudal pore. The caudal glands are short and restricted to the tail as depicted by Ditlevsen. In the lateral epidermal chord, big vacuoles or glands can be seen with a diameter of 40 μm. The cuticle thickness varies from 6 μm at the pharyngeal base to 9 μm near the anal opening.

Although Filipjev probably did not examine these specimens, he suggests in a footnote (1927:94) that *L. caecum* might belong to *Pseudocella,* with which I agree.

The transferring of *L. caecum* to *Pseudocella* makes *P. caeca* (Ditlevsen, 1923) a secondary homonym to *P. coeca* (Ssaeljev, 1912) according to art. 58 sub 1 of the Code. If not a synonym of one of the other nominal species in *Pseudocella, L. caeca* must be renamed; I propose to postpone this decision until a revision of *Pseudocella.*

Leptosomatum clavatum Platonova, 1958

Leptosomatum kerguelense Platonova, 1958:60–61, partim.

Diagnosis.—Cephalic and cervical sensilla papilliform. Cephalic capsule in female 10 μm long. Ocelli far posterior. Ratio "c" less than in *L. bacillatum* of comparable size. Male unknown.

Distribution.—Kerguelen and Macquarie islands.

Discussion.—The identity of this species, which was found at the Kerguelen Islands, is fixed by the designation of the lectotype in 1968 (see discussion of *L. kerguelense*). Only females and juveniles are known. They differ from *L. kerguelense* by the ocelli being situated far posterior at about 1.5 corresponding body diameters from the anterior end (in the type, which is severely flattened, the preocellar length hardly exceeds the corresponding body diameter), a more slender body, longer tail (T/ABW = 1.5), and the caudal pore being situated terminally.

Slides 5836, 6013, 7346, 7365, 7369, 7371, 7372 and 7377 belong to *L. clavatum* (lectotypte 5835). Because type-material of the Zoological Institute in Leningrad is not loaned, I was not able to measure the specimens in detail. The

Table 2.—Dimensions of *L. clavatum.* DF, distance to fovea; C, cuticle thickness at pharynx base. For other abbreviations see p. 852.

Sn	L	DF	DL	C	PL	CL	a	b	c	V%	Labelled as:
5835	14,420	28	109	2	1909	187	67	7.6	77	60	Allotype *L. clavatum*
5836	12,430	29	118	8	1726	129	52	7.2	96	61	Allotype *L. kerguelense*
6013	10,860	24	126	10	1411	145	46	7.7	75	59	Paratype *L. kerguelense*

measurements are presented in Table 2. Although slide 5835 is labelled as "allotype" it represents the lectotype because Platonova (1968) designated this slide as holotype.

New record

1. Macquarie Islands (54°32′S, 158°59′E); 15 Feb 1967. 3 juv., 11 ♀ and 1 ♂; 112–124 m. Collection Smithsonian Institution, Washington, D.C.

Remarks.—On morphological grounds, as far as is known, the population from the Macquarie Is. cannot be distinguished from *L. bacillatum.* It deviates by the body proportions i.e., the placement of the ocelli, ratio "c" and, to a lesser degree, the body width. The cephalic capsule comes to 10 μm, the amphidial aperture to 3 μm, the fovea to 4 μm, and the lens diameter varies from 6 to 9 μm.

In this population, mixed with *L. kerguelense* and *L.* sp. *A* (see p. 846), one male was present that also might belong to the latter. It resembles the male of *L. bacillatum.* The spiculum length is 78 μm, the gubernaculum 19 μm, and the lens diameter is 9 μm in dorsoventral view. The anterior part of the single male is twisted; dimensions of the amphids cannot be given. No figures are given since the females differ only in the above-mentioned characteristics. The redescription of the lectotype and information regarding the male are wanting.

Leptosomatum groenlandicum Allgén, 1954
Fig. 15

The male specimen, on which the description was based, was placed at my disposal by the Swedish Museum of Natural History. It is labelled: RMev Sthlm. 37.299 East Greenland King Osc.fj.N-37. The nematode, mounted in glycerin-gelatin, was remounted because air had penetrated under the coverglass.

This male was curved in the shape of a "c." The length of 14.544 mm given by Allgén (1954), is the straight distance between the extremities. The length along the body axis came to 17.5 mm. The nerve ring is situated 580 μm from the anterior end; the lengths of pharynx and tail are 2950 and 270 μm respectively. Ocelli are absent. The shortness of the gonads is remarkable; the anterior reaching a length of 478 μm, the posterior 488 μm. The junction of these gonads is situated 10.3 mm from the anterior end. The spicula are 160 μm long; they are ensheathed by a gubernaculum that is characterized by a dorsal outgrowth with a membraneous appearance. Ten cephalic setae are present; the lateral setae are broadened. Six rows of cervical setae are visible extending to the level of the nerve ring. Subdorsal of the cloacal aperture, 4 setae could be seen. The cuticle is thick, lunula absent, and the caudal glands could hardly be observed.

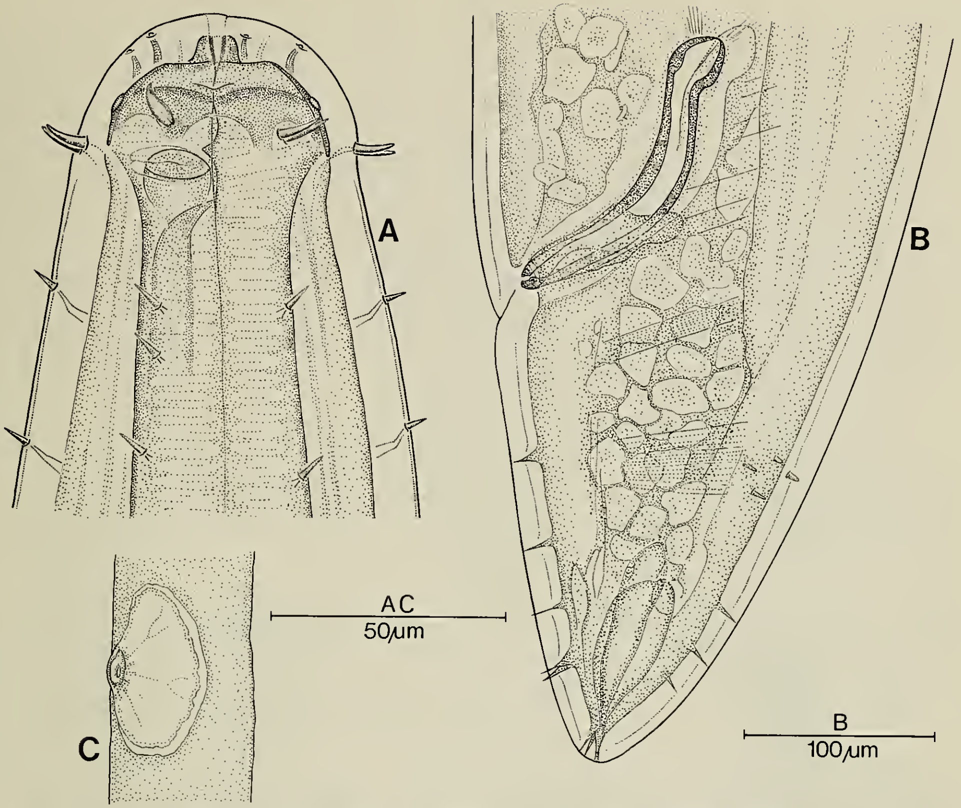


Fig. 15. *L. groenlandicum.* A, Head; B, Posterior end; C, Gland in lateral epidermal chord at level of pharynx base.

In the lateral epidermal chord, characteristic glands are present, which open to the exterior by a pore. These openings alternate dorsally and ventrally; sometimes 2 in sequence open on the same side. The presence of a coffee-bean shaped structure as described by Lorenzen (1981:136) could not be confirmed. The amphidial aperture is large and probably closed by a shield. Due to the flattening, the head structure is difficult to interpret; a cephalic capsule is present as are the cephalic ring and oesophageal capsule as termed by Inglis (1964). A tooth seems to be present in the pharyngeal lumen. More material however, is necessary for confirmation.

This male resembles *Leptosomatides inocellatus* Platonova, 1967, which differs from other *Leptosomatides* species by the absence of ocelli, lateral vulvar glands, ovejector, and lunula; and by the presence of lateral epidermal glands and amphids comparable to those of *Leptosomatum groenlandicum.* A new genus must be erected for these two species. At present I prefer to consider *Leptosomatum groenlandicum* a species inquirenda.

Leptosomatum indicum Stewart, 1914

This species was found in September 1903 near Chilka Lake in India. Filipjev (1921), in the additional notes on his revision, reported that he could not obtain

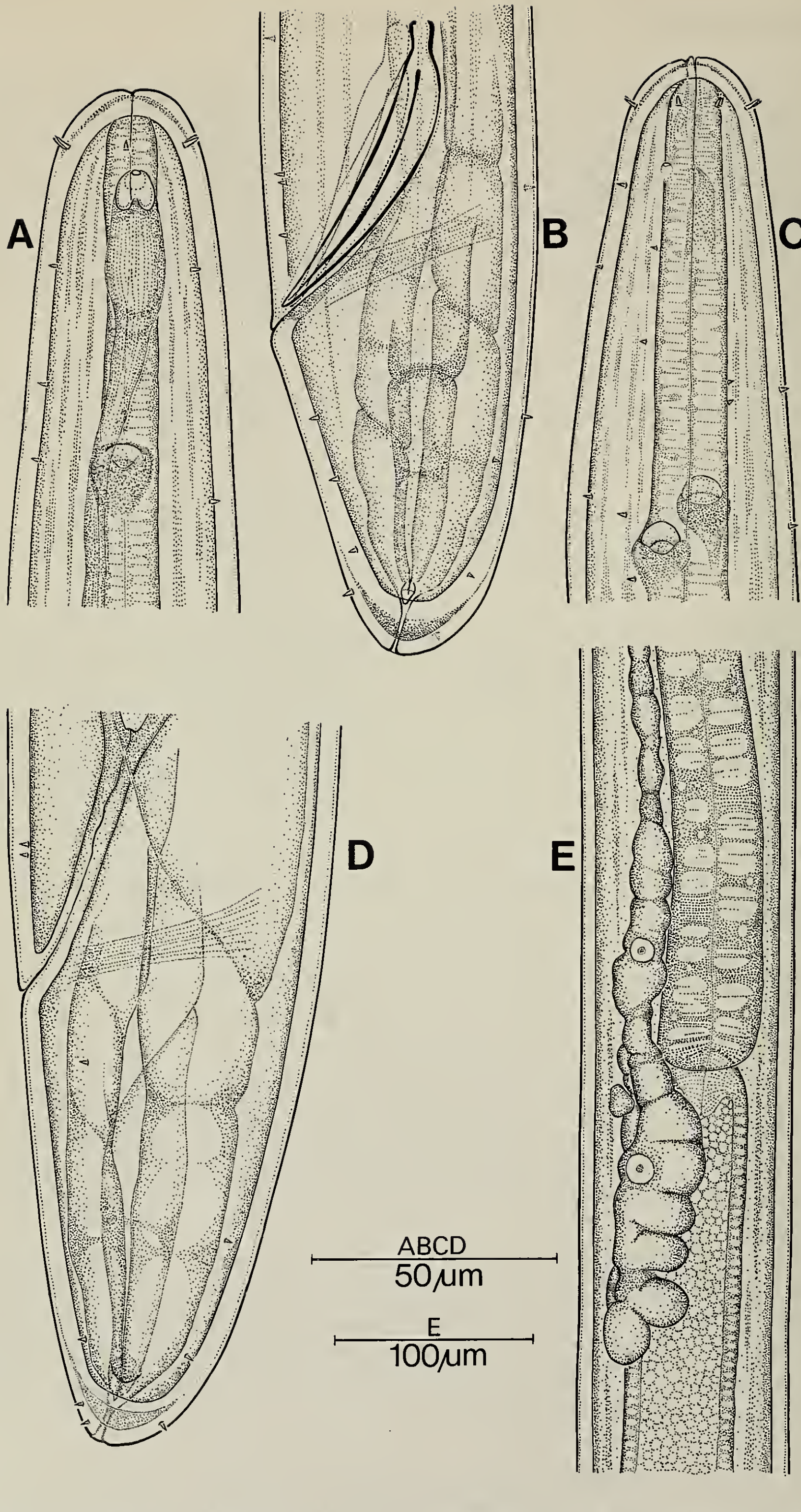


Fig. 16. *L. keiense.* A, Anterior end male; B, Posterior end male; C, Anterior end female; D, Posterior end female; E, Renette, 76047.

Stewart's paper. Although the paper was available, I did not succeed in obtaining the specimen (Indian Museum no. ZEV 6142/7) on which the description was based.

The female is mounted in "glycerin jelly-formalin" and the figures suggest a loss of contrast in the cephalic capsule. In the paper, the length of the nematode is not given but, calculated from the other data, must be 5 mm. The ocelli are situated at a distance of 0.56 mm from the anterior end; this seems questionable.

Because of the cephalic capsule structure, *L. indicum* probably belongs to *Deontostoma* despite the fact that the nematode is rather small. But prior to transfer, re-study of this specimen and collection of new material is necessary. Until more specimens become available a more precise identification cannot be attempted and *L. indicum* Stewart, 1914, must be considered a species inquirenda.

Leptosomatum keiense Micoletzky, 1930

Fig. 16

The original material could not be located. The following information is based on the description of Micoletzky (1930) and additional material from the Philippines.

Diagnosis.—Cephalic, cervical, and body sensilla setiform; cephalic capsule absent in juveniles and adults; ventromedian precloacal papilla reduced (or absent?). Caudal pore ventral to terminus. Ocelli far posterior, provided with big lenses (10–11 μm). Pharynx short. Renette may overlap intestine.

Distribution.—Indonesia and Philippines.

New records

Philippines; collected by E. G. Menez from algae (*Caulerpa* and *Eucheuma*). Sublittoral. Collection Smithsonian Institution, Washington, D.C.

1. Pangasinan; Telbang Cove (16°11′N, 120°03′E). 1 ♂, 1 ♀ and 1 juv. 3 Sep 1967.
2. Pangasinan; Cangaluyan Is. (16°22′N, 120°00′E). 2 ♂, 1 ♀ and 1 juv. 4 Sep 1967.
3. Salcedo, Bolic Is. (11°05′N, 125°39′E). 2 juv. and 1 ♂. 10 Sep 1967.
4. Great Santa Cruz Is. (5°52′N, 122°04′E). 1 juv. 18 Sep 1967.
5. Zamboanga; Sacol Is. (5°56′N, 122°11′E). 1 juv. 19 Sep 1967.

Additional description and discussion.—At first sight, this species resembles *L. punctatum* in the presence of setiform sensilla, the ventrally placed spinneret and the absence of a cephalic capsule. It can be distinguished by the greater diameter of the lens and the strong negative allometric growth of the pharynx. In some males the pre-cloacal papilla is absent.

Leptosomatum keiense, as described by Micoletzky, is probably a species-complex. According to Micoletzky (1930:280): "das präanal gelegene Ergänzungsorgan hatte ich nicht immer nachweisen können . . . die Augenlage ist veränderlich . . . Linsendurchmesser 5.8–6.7, selten bis 12 μm . . . die Ausbildung des Kopfborsten zeigt individuelle Verschiedenheiten . . . b = 4.5–12.1."

The material from the Philippines shows the same variability. Males 76044 and 76045 (pop. 2), which are mounted in lateral position, do not show any trace of an accessory organ; in male 76041, mounted dorsoventrally, a papilla is present 141 μm anterior to the cloacal vent, whereas in 76049, mounted laterally, this papilla lies at 126 μm. Moreover, female 76040 (pop. 1) seems to be provided with a ventromedian sensillum; this observation could not be confirmed in the other female (76046, pop. 2), which is twisted. The diameter of the lens is variable; 7–13 μm. Male 76049 (pop. 3) has a lens of 13 μm diameter, the two males of population 2 have a lens diameter of 7 μm, but in general it varies between 9 and 11 μm.

Notable is the short pharynx in one of the males (b = 11). According to Micoletzky (1930), this phenomenon also occurs in females. In juvenile 76048, a renette is developed that extends posteriorly 700 μm from the anterior end and overlaps the intestine. The amphidial glands in 76041, 76033, 76045 and 76049 attain lengths of 640, 800, 710 and 740 μm respectively; in the latter the glands overlap the intestine.

The ocelli, situated at 1.5 times the corresponding body diameter from the anterior end, are provided with an intensively pigmented cup. The cephalic setae are 3.5–4.5 μm long; short setae are situated over the whole body length. The amphids, 15–27 μm from the anterior end, resemble those of related species. The fovea measures 8 μm in the male and 3 μm in the female; the apertures 2 and 1 μm respectively. In one of the females (76040) the cervical pore could be detected at 227 μm from the anterior end. The spiculum length is 63–66 μm, the gubernaculum, if present, was not perceptible. Male 76045 is extensively atrophied; numerous coelomocytes of 6 × 4 μm could be seen throughout the body length of this male.

As stated above, *L. keiense* might be a mixture of at least two species. The ratio "pharnyx length/tail length" (=P/T) clearly separates the adults of population 2, in which P/T exceeds 12, from the remaining specimens in which P/T never exceeds 10. It is possible that the material of Micoletzky (1930) is still present and since the few specimens from the Philippines were collected at different localities, I postpone the separation, but I give some remarks regarding the specimens of population 2.

These males can be distinguished by their relatively small lenses (7 μm), the absence of a precloacal papilla, a slender body ("a" = 97 and 104), a short tail ("c" = 94 and 104), and the allometric trend less conspicuous than the other males. Ratio "c" of the female, that has been found in the same sample, is also rather high; the lens diameter is 12 μm in dorsoventral view. The juveniles from population 2 cannot be distinguished from those of the other localities.

Leptosomatum kerguelense Platonova, 1958
Figs. 17a, b, 18

Leptosomatum crassicutis Platonova, 1958:12–13
Leptosomatum clavatum Platonova, 1958:15–16 partim.
Leptosomatum arcticum sensu Mawson, 1965:315–316

Diagnosis.—Cephalic and cervical sensilla papilliform; cephalic capsule present in both sexes; ventromedian precloacal papillae absent. Caudal pore slightly ventral to terminus. Ocelli relatively far anterior. Renette restricted to pharyngeal region. Tail length equal to anal body width. Spicula long; gubernaculum reduced to 2 membranes.

Type.—Lectotype 5833; Zoological Institute Leningrad.

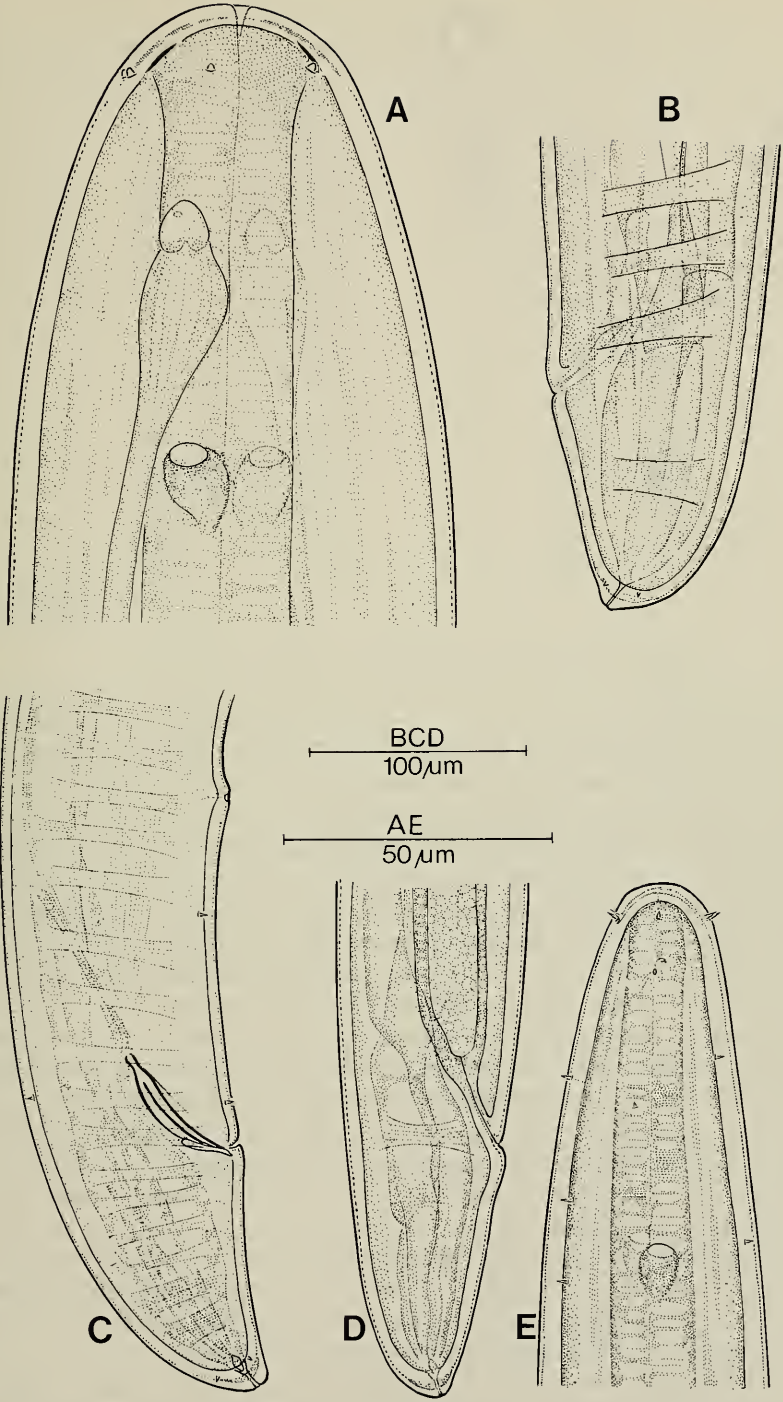


Fig. 17. *Leptosomatum kerguelense* (76056): A, Head; B, Caudal end. (C–E) *L. punctatum*: C, Caudal end of male, 1286-6; D, Caudal end of female, 1286-5; E, Anterior end of female, 76037.

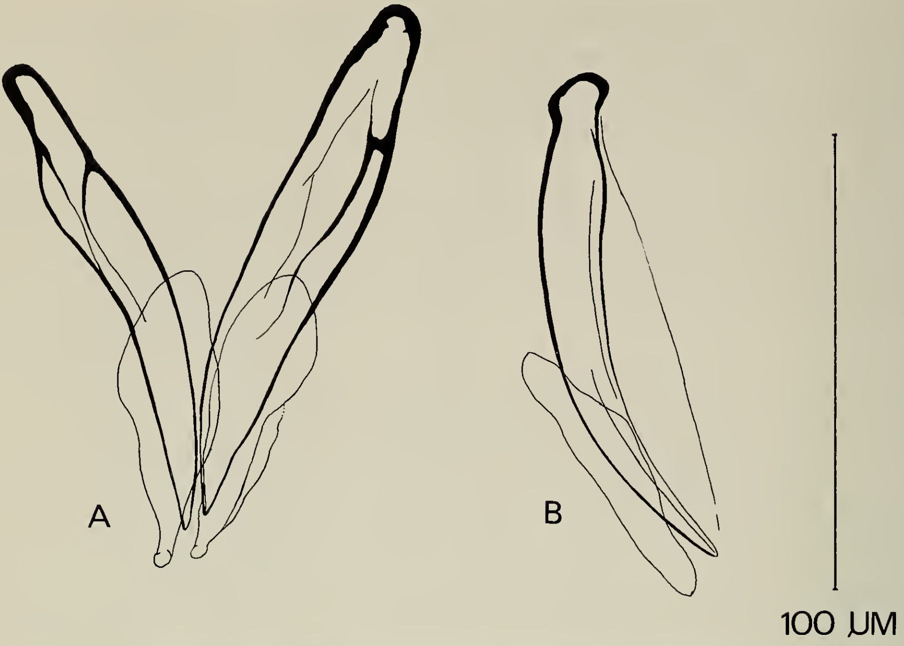


Fig. 18. Spicules *L. kerguelense.* A, Holotype; B, Paratype.

Distribution.—A subantarctic species: South Georgia, Kerguelen Islands, Heard Island, Crozet Islands, and Macquarie Islands.

Synonymy.—The three species from the Kerguelen Islands (Platonova 1958) were described from the remainder of an alcohol collection from which the macrofauna was removed. This fixation caused some particular effects of which the swelling and loosening of the cuticle are the most striking. The specimens are mounted in glycerin-gelatin, flattened, and as stated by Platonova (1958) in mediocre condition. In 1968 the species were redescribed, depicted (some shifting had taken place) and holotypes (=lectotypes) were designated.

Both papers are rather confusing; regarding *L. clavatum* for example, the lectotype (slide 5835) is called holotype and labelled as allotype. Slide 5835 does not correspond with the formula: the ratios as given in the description are also at variance with both the formula and the type. The lectotype fits neither the description nor the figures. The male on slide 7633, labelled as holotype, does not belong to the syntype and more juveniles are designated as paratypes than originally belonged to the syntypes.

In the description of *L. crassicutis* attention is given to the aberrant construction of the cephalic capsule. This feature, however, is an artifact due to the swelling of the cuticle, which can be confirmed by observing the cuticular pores, forming little holes in the cuticle surface and cones on the epidermis.

The cuticle thickness is stated to be a differentiating character for *L. crassicutis.* I have measured the cuticle at the level of the pharyngeal-intestinal junction, as did Platonova, and the pre-ocellar body length. The data are given in Table 3. The cuticle thickness, which is heavily influenced by the fixative (or post-mortem fixation?), cannot be maintained as a diagnostic character for *L. crassicutis.* The

Table 3.—Sex (S) or stage, Slide number (SN), Pre-ocellar body length (OL), Cuticula thickness (Cut.) and species assigned to Kerguelen population described by Platonova (1958).

S	SN	OL	Cut.	Spec.	S	SN	OL	Cut.	Spec.
M	5831	75	12,1	crass.	J	7346	89	4,4	kerg.
F	5832	62	8,5	crass.	J	7359	69	8,4	kerg.
M	5833	73	8,5	kerg.	F	7362	65	3,2	clav.
F	5834	89	6,1	kerg.	J	7363	32	2,4	clav.
F	5835	109	2,0	clav.	J	7364	65	1,6	clav.
F	5836	118	8,5	kerg.	J	7365	97	4,0	clav.
F	5838	73	12,1	clav.	J	7366	65	5,3	clav.
F	5840	69	2,4	clav.	J	7367	32	2,0	clav.
M	6010	69	7,7	kerg.	J	7368	57	5,7	clav.
M	6011	73	12,1	kerg.	J	7369	105	5,7	clav.
F	6012	77	12,6	kerg.	J	7370	69	4,0	clav.
F	6013	126	10,1	kerg.	J	7371	93	3,6	clav.
M	6014	77	8,9	kerg.	J	7372	105	x	clav.
F	6015	77	8,1	kerg.	J	7374	57	4,0	clav.
F	6019	69	4,9	kerg.	J	7377	81	3,2	clav.
M	7343	77	13,0	kerg.	J	7633	57	8,1	clav.
J	7345	57	4,9	kerg.	M	7634	64	2,0	clav.

lack of bristles on the surface of the cuticle is given as a distinguishing feature for all three species. Herewith I synonymize *L. crassicutis* and *L. kerguelense* as their lectotypes 5831 and 5833 are evidently conspecific. I propose the name *L. kerguelense* Platonova, 1958; Recommendation 24a is not followed because the description of *L. crassicutis,* which is based on artifacts, would only lead to confusion. The type (5833) corresponds with the formula and description; the figure, however, is of one of the paratypes as the lectotype is mounted dorsoventrally. The spicula of holo- and paratype are depicted in Fig. 18. The caudal glands, as depicted for *L. kerguelense* by Platonova, are much longer; they overlap the intestine as is usual in *Leptosomatum.*

Measuring the syntypes, another feature was found that was not previously recorded. Two types of juveniles and females occur; the first belongs to *L. kerguelense,* the other resembles *L. bacillatum.* These latter specimens are characterized by, among other features, ocelli situated far posteriorly. To this species belong slides 7346 and 5835, both labelled *L. clavatum* and slides 7365, 7369, 7371, 7372, 7377, 6013 and 5836 labelled *L. kerguelense.* Slide 5835 is the lectotype of *L. clavatum,* and 5836 the lecto-allotype of *L. kerguelense.* The lectotype of *L. clavatum* does not agree in every respect with the description of 1958. The measurements of the lectotype and discussion of its status are given in the paragraph of *L. clavatum.*

Leptosomatum arcticum sensu Mawson, 1958; nec Filipjev, 1916 is also indentical to *L. kerguelense.* Mawson's material was not available for this study. Based on the description, there is no need to assign this species to *Leptosomatides* because structure of the gubernaculum is as in other species of *Leptosomatum.* The only difference from *L. kerguelense* is that the spiculum/gubernaculum ratio is not identical. This might be caused by artifacts or the gubernaculum may be obscured by the opaqueness of the surrounding tissue.

New records

1. South Georgia (53°52′S, 37°37′W). 3 ♂, 2 ♀, 1 juv. Coll. 7 Feb 1966 at a depth of 97–101 m. Collection Smithsonian Institution, Washington, D.C.
2. Macquarie Islands (54°32′S, 158°59′E). 5 Feb 1967. One pre-adult ♀. 112–124 m. Collection Smithsonian Institution, Washington, D.C.

The above-mentioned specimens of the first population are in a poor condition which may be caused by a post-mortem fixation, but they clearly belong to *L. kerguelense.* The cephalic capsule in male and female measure 4 and 6 μm respectively. The amphidial fovea has a diameter of 5 μm in the female and 11 μm in the male. The construction of these amphids is identical to that in *L. bacillatum*; only slightly more robust. The tail is obtuse, caudal glands are long, and the caudal pore is shifted ventrally. Although this species is easily recognizable, a redescription from well preserved material is desirable.

Leptosomatum micoletzkyi Inglis, 1971

Remarks.—This species, described from one male, is distinguished from the species of *Leptosomatum* by the amphids, which lie at more than one cephalic diameter from the anterior end; the presence of subventral precloacal setae, and the absence of the lunula (?). Sexual dimorphism, comparable with *Leptosomatum,* seems to be absent. The spicules are slightly sinuous and end distally in blunt tips. The gubernaculum enfolds the spicules near their distal ends; proximally it forms large membranes.

The male, which was not available, does not fit any nominal genus. At present it would lead to confusion to erect a new genus for this species and I consider *L. micoletzkyi* Inglis, 1971, a species incertae sedis until the female is described.

Leptosomatum pedroense Allgén, 1947

Allgén (1947) described this species from a juvenile which was not available for this study. The length of this juvenile is 7120 μm with a ratio "a" of 29.06. This means that the diameter of this specimen is 240 μm, leading to the assumption that this juvenile is extremely flattened. This is supported by the figure of the tail. Being based on a juvenile and described insufficiently, *L. pedroense* Allgén, 1947, must be considered a species inquirenda.

Leptosomatum punctatum (Eberth, 1863) Bastian, 1865

Fig. 17c–e

Phanoglene punctata Eberth, 1863:20.
? *Stenolaimus macrosoma* Marion, 1870:17–18.—1870a:10.
Leptosomatum longisetosum Schuurmans Stekhoven, 1943a:4.

Diagnosis.—Cephalic, cervical and body sensilla setiform; cephalic capsule absent in juveniles and adults. Ventromedian precloacal supplement present. Caudal pore ventral to terminus. Ocelli relatively far posterior. Lens 6–7 μm. Copulatory musculature relatively strongly developed.

Distribution.—Mediterranean, Black Sea, and Red Sea.

Synonymy.—Filipjev (1918) synonymized *S. macrosoma* Marion, 1870, with *L. bacillatum* (Eberth, 1863) because of Marion's statement (1870:17), "Elle ne presente pas non plus la couronne de soies longes et robustes" in which opinion he was followed by Platonova (1976).

The argument of Filipjev, however, was based on an incorrect interpretation because Marion's (1870:17) passage had been taken out of context. The whole paragraph reads: "Le tube oesophagien se termine en effet de la même manière que celui du *Stenolaimus lepturus,* mais la tête régulièrement arrondie ne porte point de papilles. Elle ne presente pas non plus la couronne de soies longues et robustes da sa congénère; la peine si l'on remarque quelques poils courts dispersés tout le long du corps et un peu plus nombreux à la tête." In other words, *S. macrosoma* has neither papillae on its head, nor the long hairs of the proceeding species *S. lepturus* (*=Anticoma acuminata* (Eberth, 1863) op. Allgén, 1942). The latter has three protruding lips to which Marion alluded and called papillae.

Stenolaimus macrosoma was characterized (Marion, 1870:17) by: "quelques poils courts dispersés tout le long du corps et un peu plus nombreux à la tête." Therefore, it is obvious that *S. macrosoma* is more closely related to *L. punctatum,* as the sensilla are setiform. I believe *S. macrosoma* to be identical to *L. punctatum* (Eberth, 1863).

In 1943a Schuurmans Stekhoven described *L. longisetosum* and, in the same year, illustrated it in a separate paper (1943b). I was not able to locate this specimen. According to the author, *L. longisetosum* differs from *L. punctatum* in the shape of the tail. This tail however, shows the typical shape of a juvenile of *L. punctatum.* I consider *L. longisetosum* identical with the latter.

New records

1. Red Sea; Ain Sukhna (29°36'N, 32°24'E). 1 ♀. Collected by W. D. Hope on 5 Jan 1967 from the intertidal sediment on the beach at El Sokhna Hotel. Various types of corals and colonial coelenterates. Collection Smithsonian Institution, Washington, D.C.
2. Banyuls; France (43°00, 3°10'E). 1 juv., 1 ♀ and 1 ♂. Deposit of unknown sponges and *Corallina.* Jun 1976. Collection Nematology Department Wageningen.

Description and discussion.—In general this species is smaller than *L. bacillatum.* The female from the Red Sea is only 3.6 mm long; half as long as the adults from Banyuls.

The length of the cephalic setae varies among individuals. Filipjev (1918) mentioned 6 μm; longer than in this material where 3–4 μm has been measured for the juveniles, 4, 5 for the male and 4 and 5 μm for the females. Setae of 2–3 μm are sparsely present over the whole body length. Dr. Platonova was so kind as to remeasure the cephalic setae of Filipjev's material, and found 3.5 μm for the males and 4.9 μm for the females.

The amphidial aperture and fovea in the male measure 1 and 8 μm against 2 and 3 in the female. The structure of these amphids is comparable to those in *L. bacillatum.* Eberth (1863), in his original description, probably depicted one of the amphidial glands.

The ocelli, with a lens diameter of 6–7 μm, lie at 1.3 times the corresponding body width from the anterior end. The spiculum and gubernaculum length are 79 and 20 μm, respectively. The ventromedian pre-cloacal papilla is situated at 166 μm from the cloacal aperture. The tail, in both sexes, is rather long, 1.8 times the anal body width and more tapered than in *L. bacillatum.*

Leptosomatum ranjhai Timm, 1960

From the Arabian Sea Timm (1960) described a new species without sexual dimorphism in the head structure. The holo- and allotype were present in Wageningen in 1973 when a fire destroyed the laboratory and damaged a part of the collection. The types of *L. ranjhai* have been remounted but the contrast was almost lost which may be partly due to clearing in lactophenol.

The cephalic capsule in *L. ranjhai* is strongly developed; the posterior suture was clearly visible but the presence of cuticularized rods, surrounding the head, could not be confirmed.

The lateral epidermal chord in both sexes contains big vacuoles or glands, the structure of which could not be clarified; they measure from 22 × 19 to 34 × 30 μm and more than 30 could be counted in one body side. Ortho- and loxometanemes-I are present. A sexual dimorphism in the amphids is absent; the structure of vagina and vulva preclude placement in *Leptosomatides.* It is necessary to erect a new genus for this species. This will be done after having compared the other genera in the Leptosomatidae and the remaining material of *L. ranjhai.*

Leptosomatum sabangense Steiner, 1915

Fig. 19c, d

Nec *L. sabangense* sensu Micoletzkyi, 1930 (=*L. sundaense* new name).

Diagnosis.—Cephalic and cervical sensillae papilliform. Cephalic capsule present, posterior to cephalic sensilla. Tail length twice anal body width. Caudal pore terminal. Male unknown.

Distribution.—Indonesia and Red Sea.

Synonymy.—In 1915 Steiner described *L. elongatum* var. *sabangense,* which was raised to species level by Filipjev in 1921. Steiner split off the variety because of the tail length which is twice the anal body diameter.

The figures of Steiner (1915) give another characteristic in which *L. sabangense* differs from *L. elongatum,* namely that the cephalic capsule is situated posterior to the cephalic papillae. This is depicted in both Figures 5 and 6 (Taf. 22) and confirmed in the text. This phenomenon is unique in this genus and needs confirmation.

Leptosomatum sabangense sensu Micoletzky, 1930, has another type of capsule, situated as usual in this genus but longer (11–13 μm). The pharynx is variable in length (b = 6.8–12.6). In the female, the ocelli are situated far posterior, in the male at less than one corresponding body diameter from the anterior end. More information is necessary concerning *L. sabangense* sensu Micoletzky, 1930 nec Steiner, 1915 which has to be renamed. I propose the name *L. sundaense* new name.

New record

1. Red Sea; Ain Sukhna (29°36′N, 32°24′E). 1 juv. Collected by W. D. Hope 5 Jan 1967 from the intertidal sediment on the beach at El Sokhna Hotel. Various types of corals and colonial coelenterates. Collection Smithsonian Institution, Washington, D.C.

Description.—This juvenile is characterized by the placement of the cephalic capsule posterior to the cephalic papillae and the tail length, which is 2.16 times

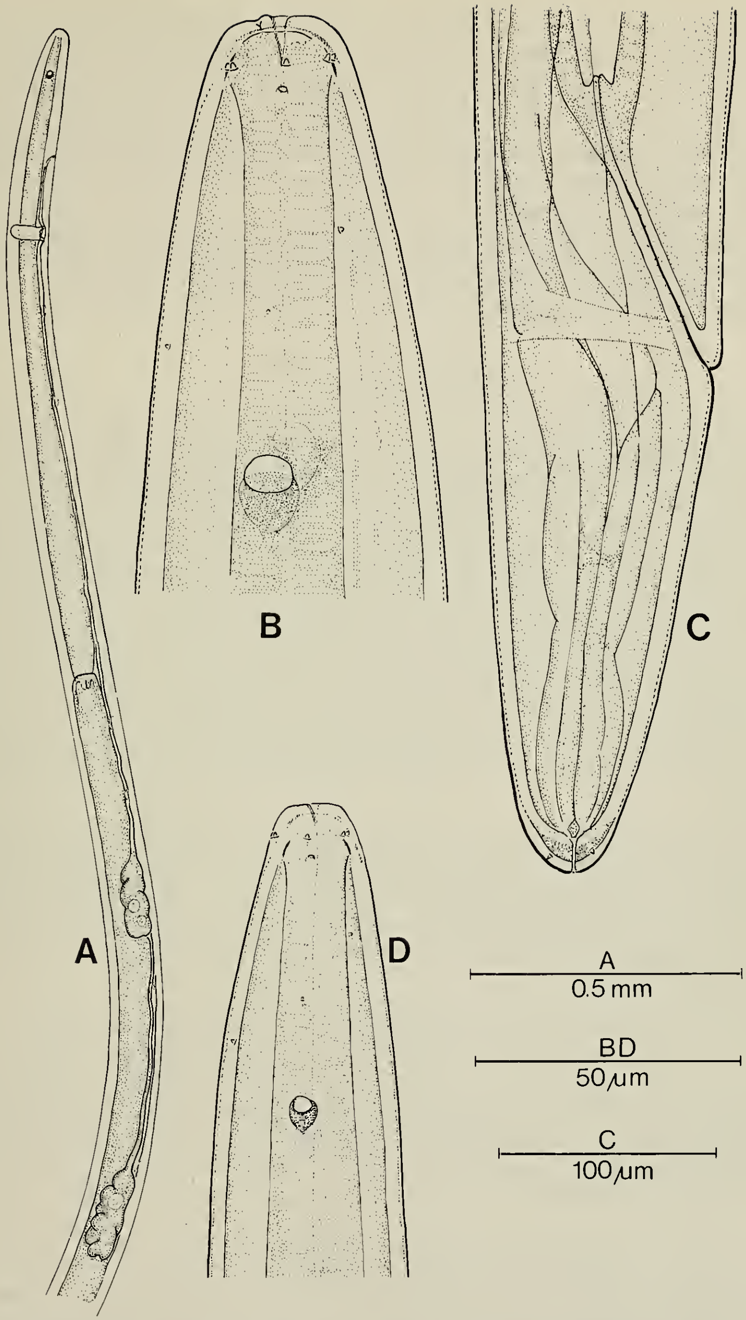


Fig. 19. Anterior end *A*, and head B, of *L.* sp. A; Tail C, and anterior and D, of *L. sabangense,* juvenile.

the anal body width. The measurements are given in the Appendix. Tail and cephalic end are depicted in Fig. 19c, d.

Discussion.—Records of *L. sabangense* which are only based on ratio c are doubtful because a correlation is necessary between this length and the anal body width resulting in a T/ABW of 2. Moreover in newly hatched juveniles this ratio may exceed 2.5 in *L. bacillatum* too. So a record of *L. sabangense* must be based on the T/ABW of adults, ratio c, and the placement of the cephalic capsule. *L. sabangense* sensu Micoletzky, 1924, a long-tailed female, also from the Red Sea, may be related to the above described juvenile. The record of Allgén (1942) is discussed under *L. bacillatum.*

Despite the fact that at a juvenile is assigned to *L. sabangense* Steiner, 1915, in this paper, more information is necessary concerning this species, which must be considered a species inquirenda.

Leptosomatum sp. A

Fig. 19a, b

Material.—Macquarie Islands (54°32′S, 158°59′E); 15 Feb 1967. 3 juv. and 6 ♀; 112–124 m. Collection Smithsonian Institution, Washington, D.C.

Description. This species, of which only juveniles and females are known, resembles *L. bacillatum* (Eberth, 1863) in the presence of a cephalic capsule, cephalic papillae and the terminal caudal pore. It can be distinguished by the short pharynx and related to this, the renette in the postpharyngeal region, the short cephalic capsule, large lens, and slenderness of the anterior body region. The male (76081) assigned to *L. clavatum* might eventually be assigned to this species.

The pharynx in the adults is relatively short, resulting in a ratio "b" of 9.8–11.8. The renette, which seems to be bilobed is developed in 76067, 76069, 76071, and 76072, and restricted to the anterior-intestinal region. The pore could not be observed.

The cephalic capsule is relatively short, 6–8 μm in length; as in the other species of this genus the posterior suture is not perceptible. The amphidial aperture and fovea measure 2 and 3 μm respectively. The ocelli lie at 70–86 μm from the anterior end, the lens varies from 8 to 10 μm. The anterior body end is very slender; the cephalic width never exceeds 30 μm, the width at the ocelli never exceeds 60 μm.

Discussion.—This species which appears to be hitherto undescribed, is not named because males are absent. Regarding the position of the renette I doubt whether this species belongs to *Leptosomatum.* An unpublished scanning study of the head of 504 and 518 however, revealed that the labial region is identical to that in *Leptosomatum.* Until more specimens become available, a diagnosis of this species cannot be given.

Syringonomus Hope and Murphy, 1969

The collection which was made available by the Smithsonian comprises 4 juveniles and 4 females of *Syringonomus typicus* Hope and Murphy, 1969. The specimens were collected 20 Feb 1967 at a depth of 943–1007 m near Recife (7°58.0′S, 34°17.0′W). This species will be discussed here as this monotypic genus is closely related to *Leptosomatum.*

Dr. W. D. Hope was so kind as to send me a male and female paratype; comparison confirmed the identification of this deep-sea species. The measurements are presented in the Appendix. Little needs to be added to the description of Hope and Murphy (1969). I wish to consider four points: (1) At the posterior end of the pharynx, in the male paratype, the amphidial glands are visible. These glands are easily overlooked as the males are not atrophied. (2) The renette is probably sexlinked; it is present in some females and absent in the male. (3) The subventral precloacal papillae are not specialized, they are comparable to the subdorsal setae. (4) Dorso- and ventrolateral orthometanemes are present.

This genus is characterized by the unique lyre-shaped pattern on, and thickening of, the cuticle in males at the level of the amphidial aperture, and the absence of ocelli. Females are distinguishable from *Leptosomatum* species by the absence of ocelli and combination of cephalic setae and presence of cephalic capsule.

General Discussion

The genus *Leptosomatum* formerly comprised all species of Leptosomatidae with a reduced cephalic capsule, but now it is one of the most distinctly demarcated genera within the family. Together *Syringonomus* and *Leptosomatum* form a taxon that may be regarded holophyletic, just as each genus is in itself holophyletic.

The presence of vaginal ovejector and lateral vulvar glands is a good character to distinguish females of *Leptosomatides* from those of the above-mentioned genera. The ovejector has been underestimated as a diagnostic character and may serve to separate *Pseudocella,* in which the ovejector is absent, from *Thoracostoma* and *Deontostoma* species. The same applies to the glands in the lateral epidermal chord, present in *Pseudocella* but restricted to the vulvar region in *Leptosomatides, Thoracostoma,* and *Deontostoma* as far as is known. In this way *Thoracostoma* species without ocelli can be distinguished from *Pseudocella* species if only females are at hand. In a separate paper I shall consider this in more detail and examine the systematic consequences.

Reviewing these characters, *Leptosomatides* shares more characters with *Thoracostoma* and *Deontostoma* than does *Pseudocella. Leptosomatum ranjhai* Timm, 1960, is closely related to *Pseudocella*; in *L. ranjhai,* lateral epidermal glands are also present, the pigment spots are situated anteriorly, the vaginal ovejector is absent and moreover, *L. ranjhai* is provided with loxometanemes, as are *Pseudocella, Thoracostoma,* and *Deontostoma* as far as is known. Although metanemes are often difficult to observe, I am confident that loxometanemes are absent in *Leptosomatum* and *Syringonomus.*

Hitherto I have been unable to study *Paraleptosomatides* Mawson, 1956; judging from literature, this genus is related to the members of the Thoracostomatinae. The type-specimen of *Leptosomella acrocerca* Filipjev, 1927, has been lost (Platonova pers. comm.), and according to Hope (pers. comm.) the type-material of *Tubolaimella* is also lost.

The present author is still interested in re-studying the above-mentioned genera as well as *Leptosomatum abyssale* Allgén, 1951; *L. indicum* Stewart, 1914; *L. keiense* Micoletzky, 1930; *L. micoletzkyi* Inglis, 1971; *L. pedroense* Allgén, 1947; *L. sabangense* Steiner, 1915; *L. sabangense* sensu Micoletzky, 1930, and *L. bacillatum, L. elongatum, L. gracile* and *L. sabangense* sensu Allgén as described in several papers.

As no syntypes are present, attempts will be made to obtain material to designate neotypes for *L. bacillatum, L. punctatum* (both from Nice) and *L. elongatum* (Falmouth), the type-species of *Leptosomatum.*

Some taxonomists have described new species of nematodes in a very unsatisfactory manner. In addition to descriptions and illustrations often being inadequate, the rules and recommendations of the International Code of Zoological Nomenclature have not been followed consistently, especially recommendations 72b, c and d; 73d, 74a, b, c and e, as well as recommendations of Appendix E of the Code, i.e., 4, 5 and 19. Indicating paratypes to serve as reference-specimens is useful because special attention has been paid to them, but they are most useful if deposited in other collections. Care has to be taken not to flatten mounted specimens; as stated previously, it is difficult to recognize flattening, and resulting artifacts may mislead the observer.

Acknowledgments

I am grateful to Mr. P. A. A. Loof under whose guidance this study was conducted and the L.E.B.-fonds and Wageningenfonds for their financial support.

Grateful appreciation is expressed to Dr. W. D. Hope for constructive criticism, discussion and correcting the text; to Dr. T. A. Platonova for her hospitality, valuable discussions and additional measurements; moreover to Dr. W. D. Hope, Washington; Dr. J. B. Kirkegaard, Copenhagen; Prof. O. Nybelin, Göteborg; Dr. R. Oleröd, Stockholm; Dr. T. A. Platonova, Leningrad; Dr. N. G. Sergeeva, Sebastopol; Prof. dr. S. v. d. Spoel, Amsterdam and Dr. R. W. Timm, Dacca for the loan of type-specimens.

I should like to thank Mr. T. S. Ie and Mr. H. Lohuis for advice and assistance regarding the E.M.-part.

Status of Nominal Species

L. abyssale Allgén, 1951	species inquirenda
L. acephalatum Chitwood, 1936	probably good species
L. arcticum Filipjev, 1916	to *Leptosomatides*
L. arcticum sensu Mawson, 1958	synonym of *L. kerguelense*
L. australe V. Linstow, 1907	species inquirenda; Filipjev, 1918
L. bacillatum (Eberth, 1863)	good species
L. bathybium Allgén, 1954	species inquirenda
L. behringicum Filipjev, 1916	species inquirenda
L. breviceps Platonova, 1967	species inquirenda
L. caecum Ditlevsen, 1923	to *Pseudocella*
L. clavatum, Platonova, 1958	probably good species
L. crassicutis Platonova, 1958	synonym of *L. kerguelense*
L. diversum Platonova, 1978	synonym of *L. sachalinense*
L. elongatum Bastian, 1865	synonym of *L. bacillatum*
L. elongatum sensu Platonova, 1967	to *Leptosomatides*
L. filipjevi Sch. Stekhoven, 1950	synonym of *L. bacillatum*
L. gracile Bastian, 1865	synonym of *L. bacillatum*
L. gracile sensu Allgén, 1954	to *Leptosomatides*
L. grebnickii Filipjev, 1916	to *Leptosomatides*
L. groenlandicum Allgén, 1954	species inquirenda
L. indicum Stewart, 1914	species inquirenda
L. kerguelense Platonova, 1958	good species
L. keiense Micoletzky, 1930	good species
L. longisetosum Sch. Stekhoven, 1943	synonym of *L. punctatum*
L. longissimum (Eberth, 1863)	species inquirenda; Filipjev, 1918
L. micoletzkyi Inglis, 1971	species incertae sedis
L. pedroense Allgén, 1947	species inquirenda
L. punctatum (Eberth, 1863)	good species

Status of Nominal Species (Continued)

L. ranjhai Timm, 1960	species incertae sedis
L. sabangense Steiner, 1915	species inquirenda
L. sabangense sensu Micoletzky, 1930	*L. sundaense* new name
L. sabangense sensu Allgén, 1942	synonym of *L. bacillatum*
L. sachalinense Platonova, 1978	probably good species
L. subulatum (Eberth, 1863)	species inquirenda; Filipjev, 1918
L. tetrophthalmum Ssaweljev, 1912	species inquirenda
L. tetrophthalmum sensu Platonova, 1967	to *Leptosomatides*
L. tuapsense Sergeeva, 1973	synonym of *L. bacillatum*

Species inquirendae; probably belonging to *Leptosomatum*:

L. abyssale Allgén, 1951; Japan, Sagami Sea, 400 m depth. Resembling *L. bacillatum.*

L. behringicum Filipjev, 1916; Bering Sea. Resembles *L. bacillatum* but tail length equal to anal body width.

L. breviceps Platonova, 1967; Barents Sea. Resembles *L. punctatum.*

L. pedroense Allgén, 1947; San Pedro, California.

L. sabangense Steiner, 1915; Indonesia. Cephalic capsule posterior to papillae. Tail length twice anal body width.

L. sundaense; new name for *L. sabangense* sensu Micoletzky, 1930; Indonesia. Tail length twice anal body width in females, long cephalic capsule (10–12 μm) placed anterior to papillae. Short pharynx. Ocelli in males far anterior.

Key to the Valid Nominal Species of *Leptosomatum*

1\. Cephalic sensilla setiform; cephalic capsule absent in all sexes and stages (*L. punctatum*-complex) 2

– Cephalic sensilla papilliform; cephalic capsule present in females and juveniles 3

2\. Lens 9–11 μm in diameter; pharynx short; ventromedian pre-cloacal papilla present or absent .... *L. keiense*

– Lens 6–7 μm in diameter; ventromedian pre-cloacal papilla present .... *L. punctatum*

3\. Ocelli at 1 corresponding diameter from anterior end, cephalic capsule present in male .... *L. kerguelense*

– Ocelli at 1.5 corresponding diameter from anterior end; males, if present, without cephalic capsule 4

4\. Cephalic capsule 10 μm; male rare; females big, never less than 10 μm in length; (Southern Hemisphere) .... *L. clavatum*

– Cephalic capsule less than 9 μm in length; males not rare; females often smaller than 10 μm 5

5\. Tail length in female twice anal body width (Indonesia) ...... *L. sundaense*

– Tail length in adults 1.5 anal body width .... *L. bacillatum*-complex: *L. bacillatum* (Europe), *L. acephalatum* (East coast USA) and *L. sachalinense* (Sakhalin Is.)

Literature Cited

Allgén, C. 1942. Die freilebenden Nematoden des Mittelmeeres.—Zoölogische Jahrbücher (Systematik) 76:1–102.

———. 1947. West American marine nematodes (Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16, 75).—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 110:65–219.

———. 1951. Pacific freeliving marine nematodes (Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16, 76).—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 113:263–411.

———. 1954. Freeliving marine nematodes from East Greenland and Jan Mayen. The Swedish Greenland-Expedition 1899.—Meddelelser om Grønland 107(6):1–44.

———. 1954a. Über zwei Tiefsee-Nematoden von der schwedischen Albatross-Expedition 1948.—Zoologischer Anzeiger 153:318–321.

———. 1957. On a small collection of freeliving marine nematodes from Greenland and some other arctic regions with reviews and analyses of the compositions of all hitherto known arctic nematode faunas.—Meddelelser om Grønland 159(3):1–42.

Bastian, H. Ch. 1865. Monograph on the Anguillilidae, or free Nematoids, marine, land, and freshwater; with descriptions of 100 new species.—Transactions of the Linnean Society of London 25:73–184.

Baldwin, J. G., and H. Hirschmann. 1973. Fine structure of cephalic sense organs in *Meloidogyne incognita* males.—Journal of Nematology 5:285–302.

Bütschli, O. 1874. Zur Kenntnis der freilebenden Nematoden, insbesondere der des Kieler Hafens.—Abhandlungen der Senckenbergischen Naturforschenden Geschellschaft 9:236–292.

Chitwood, B. G. 1936. Some marine nematodes of the superfamily Enoploidea.—Transactions of the American Microscopical Society 55:208–213.

———. 1951. North American marine nematodes.—Texas Journal of Science 3:617–672.

Ditlevsen, Hj. 1923. Sur quelques Nématodes libres (Côtes de Bretagne et Rockall).—Bulletin de la Société Zoologique de France 48:178–203.

Eberth, C. I. 1863. Untersuchungen über Nematoden.—Leipzig: W. Engelmann, pp. 1–77.

Filipjev, I. 1916. Free-living nematodes in the collection of the Zoological Museum of the Imperial Academy of Sciences in Petrograd.—Ezhigodnik Zoologicheskago Muzeya 21:59–116.

———. 1918/1921. Free-living marine nematodes of the Sebastopol area.—Trudy Osoboi Zoologischeskoi Laboratorii i Sebastopol'skoi Biologicheskoi Statsii Akademii Nauk (2) 4:1–350 (1918), 351–614 (1921). [English translation by M. Raveh, Isreal Program for Scientific Translations, Jerusalem 1968 (part 1 p. 1–255), 1970 (part 2, p. 1–203).]

———. 1922. Encore sur les Nématodes libres de la Mer Noire.—Trudy Stavropol'skogo Sel'skokhozyaistvennogo Instituta 1:83–184.

———. 1927. Les Nématodes libres des mers septentrionales appartenant à la famille des Enoplidae.—Archiv für Naturgeschichte 91A(6):1–216.

Hope, W. D. 1967. Free-living marine nematodes of the genera *Pseudocella* Filipjev, 1927, *Thoracostoma* Marion, 1870, and *Deontostoma* Filipjev, 1916 (Nematoda: Leptosomatidae) from the west coast of North America.—Transactions of the American Microscopical Society 86: 307–334.

Hope, W. D., and D. G. Murphy. 1969. *Syringonomus typicus* new genus, new species (Enoplida: Leptosomatidae) a marine nematode inhabiting arenaceous tubes.—Proceedings of the Biological Society of Washingtion 82:511–517.

Inglis, W. G. 1964. The marine Enoplida (Nematoda): a comparative study of the head.—Bulletin of the British Museum (Natural History; Zoology) 11:265–375.

———. 1971. Marine Enoplida (Nematoda) from Western Australia.—Transactions of the Royal Society of South Australia 95:65–78.

Kreis, H. 1928. Die freilebenden marinen Nematoden der Spitzbergen-Expedition von F. Römer und F. Schaudinn im Jahre 1898.—Mitteilungen aus dem Zoologischen Museum in Berlin 14: 131–197.

Linstow, O. v. 1892. Helminthen von Süd-Georgien. Nach der Ausbeute der Deutschen Station von 1882–1883.—Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten 9(2):1–19.

———. 1896. Nemathelminthen Hamburger Magalhaensische Sammelreise (Hamburg). 1896, 22 pp.

———. 1903. Entozoa des Zoologische Museums der Kaiserlichen Akademie der Wissenschaften zu St. Petersburg. II.—Ezhegodnik Zoologischeskago Muzeya 8:265–294.

———. 1907. Nematoda.—National Antarctic Expedition 1901–1904, National History 3:1–4.

Loof, P. A. A. 1961. The nematode collection of Dr. J. G, de Man.—Beaufortia 8(93):169–254.

Lorenzen, S. 1978. Discovery of stretch receptor organs in nematodes—structure, arrangement and functional analyses.—Zoologica Scripta 7:175–178.

———. 1981. Entwurf eines phylogenetischen System der freilebenden Nematoden.—Veröffentlichungen des Instituts für Meeresforschung im Bremerhaven. Suppl. 7:1–472.

Man, J. G. de. 1878. Contribution à la connaissance des Nématodes marins du Golf de Naples.—Tijdschrift der Nederlandse Dierkundige Vereeniging 3:88–118.

———. 1889. Troisième note sur les Nématodes libres de la mer du Nord et de la Manche.—Mémoires de la Société Zoologique de France 2:182–216.

———. 1889a. Espèces et genres nouveaux de Nématodes libres de la mer du Nord et de la Manche.—Mémoires de la Société Zoologique de France 2:1–10.

———. 1893. Cinquième note sur les Nématodes libres de la mer du Nord et de la Manche.—Mémoires de la Société Zoologique de France 6:81–125.

———. 1904. Nématodes libres (Expédit. Antarctique Belge).—Résultats du Voyage S.Y. Belgica: 1–51.

Marion, A. F. 1870. Rescherches zoologiques et anatomiques sur des Nématoides non parasites, marins.—Annales des Sciences Naturelles 13(14):1–100.

———. 1870a. Additions aux recherches sur les Nématoides libres du Golf de Marseille.—Annales des Sciences Naturelles 14(1):1–16.

Mawson, P. M. 1958. Free-living nematodes section 3: Enoploidea from subantarctic stations.—Report of the British Australian New-Zealand Antarctic Research Expedition (B) 6:407–358.

Micoletzky, H. 1924. Weitere Beiträge zur Kenntnis freilebender Nematoden aus Suez.—Sitzungsberichte der Akademie der Wissenschaften in Wien (I) 132:225–262.

———. 1930. Freilebende marine Nematoden von den Sunda-Inseln. I. Enoplidae. (Papers from Dr. Th. Mortensen's Pacific Expedition (1914–16, 53), (edited by H. A. Kreis).—Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn 87:243–339.

Newall, D. R. 1976. Volume and ionic regulation in *Enoplus communis, Enoplus brevis* (Bastian) and *Heterodera rostochiensis* Wollenweber. Ph.D. Thesis: University of Newcastle upon Tyne.

Platonova, T. A. 1958. Contribution to the nematode fauna of the family Leptosomatidae from Kerguelen Island [in Russian].—Informatsionnyi Byulleten' Sovetskoi Antarkticheskoi Ekspeditsii 1955–58, 3:59–61.

———. 1967. Free-living marine nematodes of the family Leptosomatidae from the European arctic [in Russian].—Zoologicheskii Zhurnal 46:828–839.

———. 1968. Marine free-living nematodes of the family Leptosomatidae from Kerguelen Island [in Russian]. Resultaty Biologitscheskich Issledowanij Sowjetskoi Antarkitscheskoi Expeditsii 1955–1958.—Issledovanija Fauny Morjei 6(14):5–24.

———. 1976. New Enoplida (free-living marine nematodes) of the U.S.S.R.-seas [in Russian]. In: Akad. Nauk. CCCP, Zool. Inst.—Issledovanija Fauny Morjei 15(23):3–164.

———. 1978. Marine nematodes of the order Enoplida from the coastal waters of South Sachalina [in Russian].—Zoologicheskii Zhurnal (57)4:495–498.

Schuurmans Stekhoven, J. H. 1943a. Einige neue freilebende marine Nematoden der Fischereigründe vor Alexandrien.—Note dell' Istituto italo-germanico di biologia marina di Rovigno d'Istria 2(25):1–15.

———. 1943b. Freilebende marine Nematoden des Mittelmeeres. IV. Freilebende marine Nematoden der Fischereigründe bei Alexandrien.—Zoologische Jahrbücher (Systematik) 76:323–380.

———. 1950. The free-living marine nemas of the Mediterranean I. The bay of Villefranche.—Mémoires de l'Institut Royal des Sciences Naturelles de Belgique (2)37:1–220.

Seinhorst, J. W. 1959. A rapid method for the transfer of nematodes from fixative to anhydrous glycerin.—Nematologica 4:67–69.

Sergeeva, N. G. 1973. New species of free-living nematodes of the order Enoplida from the Black Sea [in Russian].—Zoologicheskii Zhurnal 52(11):1710–1714.

Ssaweljev, S. 1912. Zur Kenntnis der freilebenden Nematoden des Kolafjords und des Relictensee Mogilnoje.—Trudy Imperatorskago St Peterburgskago Obshchestva Estestroispytatelei 43:108–126.

Steiner, G. 1915. Freilebende marine Nematoden von der Küste Sumatras.—Zoologische Jahrbücher (Systematik) 38:222–244.

———. 1916. Freilebende Nematoden aus der Barentssee.—Zoologische Jahrbücher (Systematik) 39:511–676.

Stewart, F. H. 1914. Report on a collection of freeliving nematodes from the Chilka Lake on the East Coast of India.—Record of the Indian Museum 10:245–254.

Stiles, C. W., and A. Hassal. 1905. The determination of generic types and a list of roundworm genera, with their original and type species.—Bulletin of the Bureau of Animal Industry United States Department of Agriculture 79:1–150.

Timm, R. W. 1953. Observations on the morphology and histological anatomy of a marine nematode, *Leptosomatum acephalatum* Chitwood, 1936, new combination (Enoplidae: Leptosomatinae).—American Midland Naturalist 49:229–248.

———. 1960. A new species of *Leptosomatum* (Nematoda) from the Arabian Sea.—Journal of Helminthology 34:217–220.

Villot, A. 1875. Recherches sur les Helminthes libres ou parasites des côtes de la Bretagne.—Archives de Zoologie Expérimentale et Générale (1) (4):451–482.

Department of Nematology, Agricultural University, P.O.B. 8123; 6700 ES, Wageningen, The Netherlands.

Appendix.—Numerical data new records.

Abbreviations: Sex (S) or stage; specimen number (SN); length (L); distance to lens (DL); distance to nerve ring (DNR); pharynx length (PL); caudal length (CL); cephalic width (CW); width at level of ocelli (OW); at nerve ring level (NW); pharynx base (PW); vulva or midbody width if not applicable (MW) and anal body width (AW).

S	SN	L	DL	DNR	PL	CL	CW	OW	NW	PW	MW	AW	a	b	c	V
L. bacillatum, pop. 1; Den Helder																
J	1072-b	2960	48	182	730	61	17	28	35	41	39	28	72	4.1	49	
F	1063-b	6760	92	303	1214	77	31	58	75	83	86	53	79	5.6	88	60
F	1064-a	7250	80	311	1214	80	30	55	70	83	89	55	81	6.0	91	56
M	1065	7880	86	297	1216	96	29	52	64	67	66	53	118	6.5	82	
M	1073-b	7940	84	283	1118	83	31	53	72	83	88	66	90	7.1	96	
M	1073-c	8590	88	296	1166	86	31	58	74	83	83	59	103	7.4	100	
M	1062	8690	84	324	1157	99	30	52	74	78	86	64	101	7.5	88	
F	1070	8760	88	327	1345	86	34	66	89	110	135	66	65	6.5	102	59
F	1074	10,230	102	333	1476	91	36	66	86	106	127	68	81	6.9	112	64
F	1069	10,870	108	342	1378	94	34	64	91	114	128	67	85	7.9	116	57
L. bacillatum, pop. 2; Kattendijke																
J	1082-a	2470	50	199	669	58	17	30	36	38	37	30	65	3.7	43	
J	1082-c	2730	55	172	567	64	16	31	41	47	41	28	58	4.8	43	
J	1084-a	3140	61	200	709	63	22	41	52	56	52	39	56	4.4	50	
J	1054	5340	81	292	1115	74	25	45	59	64	64	47	83	4.8	72	
M	1055	7300	78	269	1112	78	28	50	71	74	80	56	91	6.6	94	
F	1052	7540	75	271	1181	81	31	55	77	81	81	56	93	6.4	93	75
F	1056	8130	83	283	1345	88	33	59	72	81	83	55	98	6.0	92	61
M	1045	9080	89	245	1287	84	31	53	70	78	80	59	114	7.1	108	
F	1050	9120	78	286	1378	88	31	53	74	89	89	58	102	6.6	104	62
M	1049	10,370	75	306	1378	86	28	52	67	78	78	56	133	7.5	121	
L. bacillatum, pop. 3; Burghsluis																
F	2152	6270	82	288	1123	81	33	68	75	81	81	58	77	5.6	77	59
F	2165	7040	89	283	1251	89	34	64	87	100	96	62	70	5.6	79	65
M	2037	7550	90	333	1192	93	31	56	72	83	79	65	91	6.3	81	
F	2162	7570	78	331	1281	81	33	58	78	86	81	61	88	5.9	93	58
M	2008	7870	82	330	1138	101	30	54	70	73	76	67	104	6.9	78	
M	2047	8050	82	321	1288	87	33	53	75	79	82	75	98	6.3	93	
M	2026	8330	78	327	1225	89	33	56	81	86	81	73	97	6.8	94	
M	2077	9060	79	345	1417	93	30	51	65	73	78	68	116	6.4	97	
F	2018	9160	87	311	1254	84	37	72	99	109	110	64	83	7.3	109	59
F	2064	10,440	101	322	1336	98	34	64	90	106	115	72	91	7.8	107	64

Appendix.—Continued.

Abbreviations: Sex (S) or stage; specimen number (SN); length (L); distance to lens (DL); distance to nerve ring (DNR); pharynx length (PL); caudal length (CL); cephalic width (CW); width at level of ocelli (OW); at nerve ring level (NW); pharynx base (PW); vulva or midbody width if not applicable (MW) and anal body width (AW).

S	SN	L	DL	DNR	PL	CL	CW	OW	NW	PW	MW	AW	a	b	c	V
L. bacillatum, pop. 4; Texel, 't Horntje																
M	3108	6430	84	316	1242	89	30	55	77	89	95	66	68	5.2	72	
F	3074	7480	74	286	1112	86	34	63	89	99	109	66	72	7.1	91	61
F	3158	7790	78	297	1177	78	34	58	79	87	93	61	84	6.6	100	60
M	3106	8040	88	302	1057	81	31	58	75	81	86	65	93	7.6	99	
F	3024	8330	94	347	1273	91	35	67	84	97	97	67	86	6.5	92	60
M	3056	8750	89	310	1196	86	32	58	80	90	92	70	95	7.3	102	
F	3101	11,130	92	314	1335	78	31	67	93	124	132	70	84	8.3	143	57
F	3046	11,780	92	330	1483	101	34	70	96	132	152	72	78	7.9	117	61
F	3053	12,820	91	337	1464	83	35	61	91	118	146	70	88	8.8	154	61
F	3014	13,570	91	326	1446	82	34	60	91	124	136	73	100	9.4	165	65
L. bacillatum, pop. 5; Texel, Oudeschild																
J	1012-c	1370	47	149	407	52	13	23	28	25	24	22	55	3.4	26	
J	1011-b	3850	74	219	773	72	27	50	67	77	72	47	50	5.0	53	
J	1061	4260	63	227	896	66	23	41	53	53	53	36	80	4.8	65	
J	1003-a	5330	70	247	952	74	28	50	74	83	81	47	64	6.0	72	
J	1010-b	6690	78	277	1062	66	27	56	84	102	99	62	66	6.5	101	
M	1004	7080	90	288	1155	81	31	56	77	90	92	66	77	6.1	87	
M	1006	7770	89	312	1195	80	33	56	88	94	92	66	83	6.5	97	
M	1035	8040	86	335	1378	86	31	55	70	77	84	64	96	5.8	93	
M	1033	8920	95	336	1336	78	32	58	91	102	105	63	85	6.7	114	
F	1009	9350	78	274	1148	78	33	63	88	103	107	64	87	8.1	120	58
L. bacillatum, pop. 6; Wimereux																
F	A-59	11,560	89	279	1420	83	27	62	87	116	156	71	74	8.1	139	
L. bacillatum, pop. 7; Ambleteuse																
F	1277-1	7980	83	284	1048	79	25	52	74	95	114	64	70	7.6	101	60
F	1277-2	8570	109	329	1284	77	30	63	76	96	101	61	85	6.7	111	59
L. bacillatum, pop. 8; Banyuls																
F	1286-1	7620	102	288	1155	89	33	68	96	112	134	73	57	6.6	86	60
F	1286-2	13,490	109	376	1741	89	35	61	82	93	94	64	144	7.7	152	59
F	1286-3	16,890	135	415	1892	106	33	66	85	96	119	67	142	8.9	159	61
L. bacillatum, pop. 9; N.E. England																
M	76101	8720	82	324	1342	93	29	45	71	76	85	69	103	6.5	94	
F	76102	10,190	91	294	1305	108	32	60	83	92	113	66	90	7.8	94	59
L. acephalatum, pop. 1; Mexico, N.E. Asc. Bay																
J	76103	4700	69	227	779	76	25	47	64	74	73	52	64	6.0	62	
F	76104	7200	95	272	997	133	38	75	95	98	107	68	67	7.5	54	58
J	76105	7290	101	300	1070	91	31	58	82	88	112	81	65	6.8	80	
F	76113	7780	97	303	1088	95	32	59	91	122	115	76	64	7.2	82	57
F	76106	7790	108	220	1178	90	37	68	94	121	110	69	66	6.8	89	60
M	76107	8030	75	337	1132	98	35	58	81	96	118	73	68	7.1	82	
M	76108	8430	101	360	1142	92	32	60	90	90	98	66	86	7.4	92	
F	76109	8970	112	316	1124	96	34	73	98	130	140	77	64	8.0	93	57
L. acephalatum, pop. 2; Mexico, Allen Point																
F	76110	7720	82	298	1106	103	37	71	102	118	121	72	64	7.0	75	56

Appendix.—Continued.

Abbreviations: Sex (S) or stage; specimen number (SN); length (L); distance to lens (DL); distance to nerve ring (DNR); pharynx length (PL); caudal length (CL); cephalic width (CW); width at level of ocelli (OW); at nerve ring level (NW); pharynx base (PW); vulva or midbody width if not applicable (MW) and anal body width (AW).

S	SN	L	DL	DNR	PL	CL	CW	OW	NW	PW	MW	AW	a	b	c	V
L. acephalatum, pop. 3; Mexico, N.E. Asc. Bay																
J	76092	4660	86	188	852	77	29	54	73	79	77	52	59	5.5	61	
M	76093	7630	106	326	1051	90	32	60	77	85	92	60	83	7.3	85	
F	76094	7790	102	333	1178	89	37	70	103	130	153	77	51	6.6	88	56
M	76095	7810	110	343	924	92	34	62	81	100	99	67	78	8.5	85	
F	76096	8090	118	341	1106	109	34	70	98	123	123	74	66	7.3	73	50
F	76097	8700	87	358	1250	96	32	65	90	113	139	74	63	7.0	91	58
F	76091	9860	110	343	1215	91	30	62	96	126	147	81	67	8.1	108	54
L. acephalatum, pop. 4; Mexico, Niccehabin Reef																
J	76098	7320	95	286	979	85	26	52	81	107	120	71	61	7.5	86	
L. acephalatum, pop. 5; Mexico, Suliman Pt.																
J	76099	3430	65	322	562	70	22	45	65	87	95	53	36	6.1	49	
L. acephalatum, pop. 6; Mexico, S.E. Cozumel Is.																
F	76100	10,170	87	316	1178	108	40	79	117	164	193	91	53	8.6	94	51
L. clavatum, Macquarie Islands																
J	76078	6050	106	337	1115	106	25	69	87	87	89	73	68	5.4	57	
J	76079	6520	85	271	1014	94	25	58	81	85	102	67	64	6.4	69	
J	76080	8420	116	370	1352	128	37	64	110	125	162	99	52	6.2	66	
M	76081	8570	81	312	1014	112	27	52	73	79	87	67	99	8.5	77	
F	76082	11,050	132	427	1386	125	36	81	106	119	133	89	83	8.0	88	62
F	76083	12,120	113	374	1589	121	31	82	89	102	114	74	106	7.6	100	63
F	76084	12,510	133	452	1673	100	33	83	110	125	144	88	87	7.5	125	62
F	76085	12,780	141	419	1606	142	38	85	110	127	154	92	83	8.0	90	63
F	76086	13,030	146	444	1741	146	40	85	108	125	158	94	82	7.5	89	63
F	76087	13,490	131	436	1639	152	35	79	123	146	171	99	79	8.2	89	60
F	76088	13,960	121	374	1758	142	33	83	110	134	162	93	86	7.9	98	62
F	76089	14,230	150	469	1656	139	37	85	114	150	168	92	85	8.6	102	61
L. keiense, pop. 1; Philippines, Telbang Cove																
J	76039	3540	65	196	544	77	19	46	61	72	79	52	45	6.5	46	
F	76040	4970	84	256	834	90	24	44	71	87	95	58	52	6.0	55	49
M	76041	5780	71	213	689	90	32	53	71	77	74	62	75	8.4	64	
L. keiense, pop. 2; Philippines, Cangaluyan Is.																
J	76042	1710	42	148	406	46	16	32	44	47	48	38	36	4.2	37	
J	76043	4550	74	229	592	81	27	59	78	85	102	67	45	7.7	56	
M	76044	6180	80	273	834	66	25	44	58	64	61	55	97	7.4	94	
M	76045	6580	68	278	888	63	27	45	60	60	63	55	104	7.4	104	
F	76046	7870	67	280	979	69	25	48	71	90	114	54	69	8.0	114	
L. keiense, pop. 3; Philippines, Bolic Is.																
J	76047	4830	76	222	558	82	27	49	69	77	85	56	57	8.7	59	
J	76048	5610	92	256	642	98	27	64	89	105	121	71	46	8.7	57	
M	76049	7620	89	260	689	108	37	62	81	88	93	66	82	11.0	71	
L. keiense, pop. 4; Philippines, Gr. Santa Cruz Is.																
J	76050	4870	59	212	523	64	22	46	66	79	92	60	53	9.3	76	

Appendix.—Continued.

Abbreviations: Sex (S) or stage; specimen number (SN); length (L); distance to lens (DL); distance to nerve ring (DNR); pharynx length (PL); caudal length (CL); cephalic width (CW); width at level of ocelli (OW); at nerve ring level (NW); pharynx base (PW); vulva or midbody width if not applicable (MW) and anal body width (AW).

S	SN	L	DL	DNR	PL	CL	CW	OW	NW	PW	MW	AW	a	b	c	V
L. keiense, pop. 5; Philippines, Sacol Is.																
J	76051	3770	63	182	490	75	27	53	69	78	84	59	43	7.7	50	
L. kerguelense, pop. 1; South Georgia																
M	76052	7150	64	452	1031	87	29	59	102	108	116	79	62	5.9	82	
J	76053	7420	69	386	1166	73	37	81	129	152	156	114	48	6.4	102	
M	76054	8530	68	345	1169	100	40	85	112	125	145	91	59	7.3	85	
F	76055	9350	67	408	1268	125	46	86	116	160	168	119	56	7.4	75	56
M	76056	10,210	77	431	1082	106	37	80	112	124	134	92	76	9.4	96	
F	76057	15,840	73	469	2315	116	36	89	141	162	201	135	79	6.8	137	59
L. kerguelense, pop. 2; Macquarie Islands																
J	76058	10,710	64	366	1470	107	38	68	112	146	162	106	66	7.3	100	
L. punctatum, pop. 1; Red Sea																
F	76037	3660	67	213	816	81	21	41	58	66	63	44	55	4.5	45	54
L. punctatum, pop. 2; Banyuls																
J	1286-4	2940	58	214	608	69	17	40	57	69	61	45	43	4.8	43	
F	1286-5	7600	79	321	1065	114	29	60	87	99	111	70	68	7.1	67	56
M	1286-6	7830	85	319	991	106	35	72	99	105	114	89	69	7.9	74	
L. sabangense; Red Sea																
J	76038	6490	58	213	761	95	16	31	48	52	61	44	106	8.5	68	
L. sp. *A*; Macquarie Islands																
J	76067	7610	71	267	879	98	23	46	67	77	92	62	83	8.7	78	
J	76068	8720	70	275	896	95	25	54	71	81	99	62	88	9.7	92	
J	76069	8790	74	292	930	96	21	48	67	77	83	58	106	9.5	92	
F	76070	11,100	71	284	1048	115	28	49	77	102	139	71	80	10.6	97	58
F	76071	11,830	75	366	1166	116	27	50	108	102	112	76	106	10.1	102	61
F	76072	12,150	86	325	1031	120	26	56	85	112	139	77	87	11.8	101	59
F	518	12,290	81	370	1200	116	28	52	79	94	133	71	92	10.2	106	61
F	504	12,440	87	370	1268	114	27	52	73	85	110	67	113	9.8	109	64
F	76073	14,090	75	362	1301	129	27	56	76	94	108	78	130	10.8	109	63
Syringonomus typicus; Recife, Brazil																
J	76059	3310	—	239	667	79	22	—	56	66	78	60	42	5.0	42	
J	76060	3330	—	241	666	65	26	—	61	73	81	65	41	5.0	51	
F	76061	4450	—	280	881	101	34	—	70	81	95	x	47	5.1	44	68
F	76062	5050	—	321	952	104	31	—	71	88	113	90	45	5.3	49	63
F	76063	5240	—	313	904	118	34	—	74	89	116	81	45	5.8	44	60
J	76064	5360	—	297	762	95	29	—	71	82	95	79	56	7.0	56	
J	76065	5570	—	305	928	110	27	—	63	74	89	75	63	6.0	51	
F	76066	6880	—	453	1227	110	23	—	66	84	100	65	69	5.6	63	50

BIOLOGICAL SOCIETY OF WASHINGTON PROCEEDINGS

110th Annual Meeting, 10 May 1983

The meeting was called to order at 2:35 PM by President Paul Spangler. It was moved and passed to dispense with the reading of the minutes of the previous meeting.

The Treasurer's Report was offered by David Pawson for Treasurer Leslie Knapp. Pawson noted that the Society's net worth is now increasing because of the increased page charges and the reduction in the number of free pages. The discrepancies between the 1981 and 1982 items on the balance sheets are attributable mainly to calendar differences, i.e., timing of payments and receipt of income. A motion to approve the Report was passed unanimously.

The Editor's Report by Editor Brian Kensley was offered by Acting Editor Stephen Cairns. Cairns added that we have received 43 MSS so far in 1983. Volume 96(2) is in galley and 96(3) will be sent to Allen Press shortly. Ten MSS have been scheduled for 96(4). A motion to approve the report was passed unanimously.

The President announced the results of the annual elections: President, David Pawson; Vice-president, Donald Davis; Treasurer, Leslie Knapp; Secretary, Cathy Kerby; Councilors Daryl Domning, Carl Ernst, C. W. Hart, Robert P. Higgins, David A. Nickle. He then turned the chair over to incoming-president Pawson, who led a round of applause in appreciation of the services of outgoing-president Spangler.

The meeting was adjourned at 3:01 PM.

Thomas E. Bowman,
Substitute Secretary

INFORMATION FOR CONTRIBUTORS

Content.—The *Proceedings* of the Biological Society of Washington contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers will be published in English (except for Latin diagnosis/description of plant taxa which should not be duplicated by an English translation), with a summary in an alternate language when appropriate.

Publication Charges.—Authors will be asked to assume publication costs of page-charges, tabular material, and figures, at the lowest possible rates.

Submission of manuscripts.—Manuscripts should be sent to the Editor, *Proceedings* of the Biological Society of Washington, National Museum of Natural History, 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 will be reviewed in order of receipt by a board of associate editors and appropriate referees.

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. Synonymy of abbreviated style (author, date, page) (except in botanical papers), with full citations of journals and books (no abbreviations) in the Literature Cited is required.

The establishment of new taxa must conform with the requirements of the appropriate international codes of nomenclature. Authors are expected to be familiar with these codes and to comply with them. New species-group accounts must designate a type-specimen deposited in an institutional collection.

The sequence of material should be: Title, Author(s), Abstract, Text, Acknowledgments, Literature Cited, Author's (s') Address(es), Appendix, List of Figures (entire figure legends), Figures (each numbered and identified), Tables (each table numbered with an Arabic numeral and heading provided).

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 a facsimile with the original, and retain an author's copy. Pages must be numbered on top. One manuscript page = approximately 0.5 printed page. Underline singly scientific names of genera and lower categories; leave other indications to the editor.

Figures and tables with their legends and headings should be self-explanatory, not requiring reference to the text. Indicate their approximate placement by a pencil mark in the margin of the manuscript.

Illustrations should be planned in proportions that will efficiently use space on the type bed of the *Proceedings* (12.5 × 20 cm) and should not exceed 24 × 15 inches. Figures requiring solid black backgrounds should be indicated as such, but not masked.

Art work will be returned only on request.

Proofs.—Galley proofs will be submitted to authors for correction and approval. Reprint orders will be taken with returned proof.

Costs.—Page charges @ $60.00, figures @ $10.00, tabular material $3.00 per printed inch.

All authors are expected to pay the charges for figures, tables, changes at proof stage, and reprints. Payment of full costs will probably facilitate speedy publication.

CONTENTS