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THE VALIDITY AND RELATIONSHIPS OF *PRINIA GRACILIS NATRONENSIS* (AVES: SYLVIIDAE)

Steven M. Goodman

Abstract.—Analysis of six morphological and plumage coloration characters of *Prinia gracilis* from the Nile Delta, Wadi Natroun, lower Nile Valley, and Faiyum shows that *P. g. natronensis* Nicoll of Wadi Natroun is a distinct subspecies. *Prinia g. natronensis* is more closely related to *P. g. deltae* Reichenow of the Nile Delta west of 32°E than to *P. g. gracilis* (Lichtenstein) of the Nile Valley and Faiyum. Evidence for the sequence of geological and climatic events that led to the isolation of Wadi Natroun from the Nile Delta and Valley supports this conclusion.

Five subspecies of the Graceful Warbler, *Prinia gracilis,* are currently recognized as occurring in Egypt (Meinertzhagen 1930; Vaurie 1959). One of these, *P. g. natronensis* Nicoll is confined to Wadi Natroun, a small depression in the northeastern portion of the Egyptian Western Desert. Two others important for this review are *P. g. gracilis* (Lichtenstein) of the Nile Valley south at least to Khartoum and the Faiyum, and *P. g. deltae* Reichenow from the Nile Delta. Vaurie (1959) considered *P. g. deltae* polytopic, and reoccurred up the Nile Valley at Luxor. Specimens from the Nile Delta east of 32°E to the Suez Canal were not included in the present analysis because that area appears to be a zone of intergradation between *P. g. deltae* and *P. g. palaestinae* (Zedlitz) of the Sinai and southern Israel. In Nicoll's (1917) description of *P. g. natronensis,* he characterized it as similar to nominate *P. gracilis,* but with a longer bill. In his monumental review of Palearctic passerines, Vaurie (1959) described *P. g. natronensis* as having "somewhat longer" bills and more sharply and darkly streaked upperparts than nominate *P. gracilis.* However, Vaurie measured but six adult specimens from Wadi Natroun and concluded that *P. g. natronensis* was only a "moderately well-differentiated subspecies" (1959:306). I have been able to examine 23 specimens from Wadi Natroun, including the holotype, and can offer some remarks on the systematic status of *P. g. natronensis* and its relationship to nominate *P. gracilis* and *P. g. deltae.* More material and field work is needed to evaluate the subspecific relationships of the populations inhabiting the Nile Delta east of 32°E, the Sinai, southern Israel and the Nile Valley south of the Faiyum area.

Materials and Methods

The following six measurements were taken (all in mm): Exposed culmen.—Measured from base of feathering on the forehead to maxilla tip. Bill from anterior edge of nostril.—Measured from anterior edge of nostril to maxilla tip. Gonys.—Measured from junction of rami to mandible tip. Wing.—Measured from bend of flattened wing at carpal joint to longest primary tip. Tail.—Measured from insertion of longest rectrices (always middle pair) to distal tip. Tarsus.—Measured

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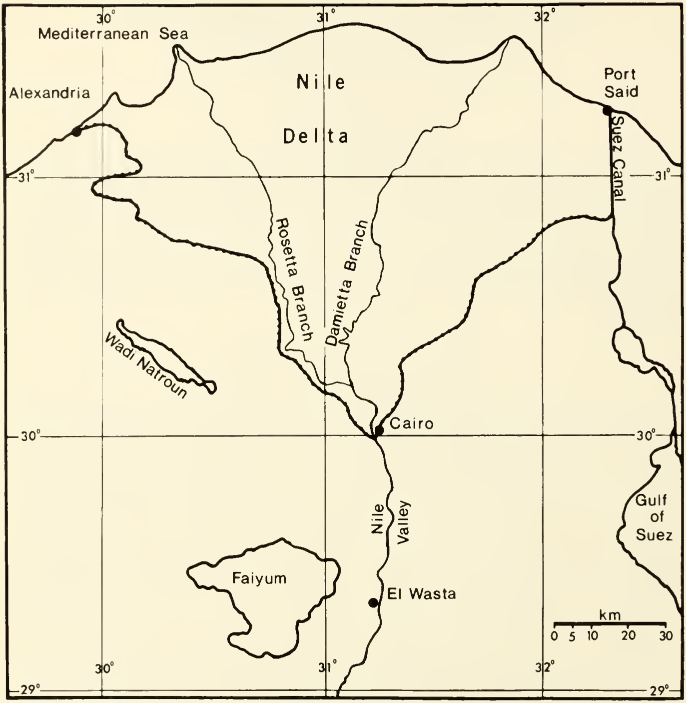

Fig. 1. Map of Egypt north of the Faiyum, including Wadi Natroun.

from junction of tibiotarsal-tarsometatarsal joint to distal edge of distalmost undivided scute overlying toes (little variation was found in the scutellation pattern of the feet). In cases when the sex designation on the specimen tag was lacking, ambiguous, or suspected of being inaccurate the specimen was classified as unsexed. Vernier calipers were used to measure the bill and tarsus to the nearest 0.1 mm, and a rule for the wing and tail to the nearest 1.0 mm.

Graceful Warbler specimens were examined from 33 localities in the Nile Delta and Valley, the Faiyum and Wadi Natroun (Appendix 1). Since adequate samples were not available from several localities, specimens were pooled into four Operational Taxonomic Units (OTUs) representing broader geographical areas (Fig. 1). These include: 1) Cairo—the environs of Cairo including Abu Rawash, south along the Nile Valley to El Wasta; 2) Wadi Natroun; 3) Nile Delta—areas of the Nile Delta west of 32°E; 4) Faiyum.

Statistical tests used MIDAS programs, written by the University of Michigan Statistical Research Laboratory. Differences among means and variances were tested by Student's *t*-test or analysis of variance (ANOVA), as appropriate. When the ANOVA showed significant variation, a Scheffé test was used to determine which means were significantly different. The Scheffé tests were also used in pairwise combinations to test differences between OTUs. Principal component analyses used a correlation matrix between unstandardized characters. Probabilities of 0.05 or less are considered statistically significant and sufficient to reject the null hypothesis.

Description of Wadi Natroun

Wadi Natroun is a narrow depression, approximately 250 km^2 in area, located southwest of the Nile Delta, from 30°17′ to 30°38′N and 30°2′ to 30°30′E. The depression is completely separated from the Nile Delta by barren desert, and its eastern edge is approximately 40 km from the Nile Delta. The lowest point is at Umm Risha, 21.9 m below sea-level.

Towards the center of the depression are a series of salt-water lakes aligned parallel to its main axis. The dominant vegetation along the edges of these lakes is *Cyperus* (cf. *laevigatus*), *Typha, Scirpus,* and *Phragmites.* The ground tends to be very muddy and encrusted with salts, principally Na_2CO_3 and $NaHCO_3$ (Abdel Salim 1966). It is interesting to note that the only known stand of wild Papyrus (*Cyperus papyrus*) in Egypt is along the edge of Lake Umm Risha (El Hadidi 1971).

Wadi Natroun has a very arid climate. The following meteorological data were compiled from Abdel Salim (1966). Between 1946–1955 the annual mean temperature was 22.8°C with the absolute extremes of 46.7°C in July (mean range 36.4°C–20.6°C) and 1.0°C in January (mean range 20.6°C–7.2°C). Depending on the season the prevailing winds come from just about every compass direction, and range in mean velocity from 10.9 km/hr in December to 19.8 km/hr in June. The average rainfall is 55.1 mm with 80% falling in November and December.

In the Pliocene Wadi Natroun was the western swampy edge of the Paleonile (Said 1975). It has been proposed that the post-Pliocene extreme western edge of the Nile extended from Abu Rawash (northwest of Cairo) to the eastern end of Wadi Natroun (Sandford and Arkell 1939). If this was the case, then at least up until the early Pleistocene Wadi Natroun and the former Nile Delta would have been connected by a vegetated zone.

The upper geological strata of the area between Wadi Natroun and the western edge of the modern Nile Delta can be divided into two distinct groups. Along the northeastern edge of the depression is a terraced slope that rises to +35 m and gently slopes towards the central lakes (Shata and El Fayoumy 1967). Running along the eastern edge of this marginal slope in a NW-SE direction and transversing the area to the western edge of the Nile Delta is a gravel ridge of the Tahreer or El Tahrir soil type (Abdel Samie 1967; Shata and El Fayoumy 1967). This ridge is endogenous in nature and is composed of nilotic gravels laid down in the early Pleistocene (Shata and El Fayoumy 1967). In the early Pleistocene a series of declines in the water table resulted in the gradual retreat of an ancient Wadi Natroun lake and the terracing of the marginal slope. This lake dried up in the late Sebilian (post-Middle Paleolithic, Sandford and Arkell 1939), by which time

Wadi Natroun was completely separated from the Nile Delta (Shata and El Fayoumy 1967). During the Holocene the water table rose, flooding some of the lower areas of the former Wadi Natroun Lake (Shata and El Fayoumy 1967), but never resulting in a "green-connection" between Wadi Natroun and the Nile Delta.

Brief Notes on the Habitat and Natural History of *P. gracilis*

Prinia gracilis is a characteristic bird of the vegetated portions of the Nile Delta and Lower Valley. This species is common and conspicuous in low vegetation, particularly matted-grass and reed-clumps. In Wadi Natroun the Graceful Warbler is a common nesting bird in the reed-beds along the marshy margins of the lakes. Loat (1905) described them as "not uncommon" in Wadi Natroun "amongst the *bourdy*" (generic for *Typha* and *Cyperus,* fide Täckholm, 1974).

At Wadi Natroun in early May 1981 Mr. Sherif Tewfik and I found pairs of *Prinia gracilis* in various stages of breeding, from nest construction to feeding young. Singing males were more common along the lakes in the very marshy spots than in the somewhat drier upland areas. Cows, donkeys, and a few goats roamed free around the lakes and grazed on the vegetation, but because they tended to limit their grazing to the drier areas, they probably interfere very little with *Prinia.*

Although no detailed study of marked individuals has been conducted, Simmons (1954) found that near Suez paired adults remain in the general vicinity of the breeding area throughout the year, while juveniles disperse from the natal territory soon after fledging. Graceful Warblers are primarily ground foragers and insectivorous (Simmons 1954; pers. obs.).

There is good evidence that Graceful Warblers do not disperse over expanses of barren desert. Although similar habitats exist in the oases of the Egyptian Western Desert, as in portions of the Nile Valley and Delta, Graceful Warblers have never been recorded in the former (Moreau 1934; Al-Hussaini 1959; pers. obs.). Thus, the desert acts as a physical barrier to dispersal and limits genetic exchange between disjunct populations. The dispersal of juvenile Graceful Warblers recorded by Simmons (1954) in the Nile Delta was probably local.

This species is sexually monomorphic (Meinertzhagen 1954), and the recorded variation in bill color is seasonal and age related (Ali and Ripley 1973; pers. obs.) rather than sexual (cf. Simmons 1954). In all of the Egyptian populations that I have looked at, breeding adult males and females have black bills. Meinertzhagen (1930) described immatures as duller than adults; while Ali and Ripley (1973) characterized immatures as more shadowy and broadly streaked on the upperparts and with a distinct yellow tinge to the sides of the neck and upper breast. These characters are difficult to discern and I know of no plumage color characters that allow reliable separation of immatures and adults. Further, I was unable to separate immatures from adults using feather wear or molt sequence. In almost all cases nothing was noted on the specimen labels about skull ossification, and consequently immatures could not be readily distinguished from adults.

Results

Of the 23 specimens examined from Wadi Natroun, two were not measured and 10 were unsexed. Descriptive statistics of male, female and unsexed Graceful

Table 1.—Measurements (mm) of *Prinia gracilis natronensis* collected in Wadi Natroun.

	Female	Male	Unsexed
Culmen			
n	5	6	10
Range	9.6–10.9	9.7–11.3	10.0–11.1
Mean	10.26	10.36	10.60
SD	0.49	0.66	0.33
Bill from ant. edge nostril			
n	5	6	10
Range	6.3–7.3	6.2–7.7	6.5–7.3
Mean	6.84	7.00	7.04
SD	0.42	0.50	0.21
Gonys			
n	4	4	10
Range	5.7–6.9	5.2–7.2	6.2–7.3
Mean	6.30	6.57	6.69
SD	0.51	0.92	0.35
Wing			
n	4	6	10
Range	42–46	42–47	42–44
Mean	44.25	45.33	42.90
SD	1.70	1.75	0.87
Tail			
n	3	6	2
Range	50–66	55–64	53–60
Mean	57.6	60.5	56.5
SD	8.02	3.39	4.94
Tarsus			
n	5	6	8
Range	18.3–19.2	18.5–19.7	17.3–18.9
Mean	18.76	19.06	17.90
SD	0.36	0.47	0.52

Warblers from Wadi Natroun are summarized in Table 1. A series of *t*-tests comparing males and females for each of the six characters revealed no significant sexual dimorphism. No significant differences were found between the unsexed birds and males and/or females. A similar series of tests was run for the sex classes of specimens from the other three OTUs. In no case was a significant difference found in intra-OTU variation of single characters, so the three sex classes (males, females and unsexed) were combined in further tests.

Since immature and adult Graceful Warblers could not be separated by plumage differences, it was not possible to take ontogenetic variation directly into account. However, if significant ontogenetic differences exist for any character within an OTU and different age classes are represented in the sample, then such characters should have a multi-modal distribution. Only uni-modal distributions for each character were found, and it is assumed that immatures cannot be separated from

Table 2.—Measurements (mm) of *Prinia gracilis* from four areas in Lower Egypt.

	Cairo to El Wasta	Wadi Natroun	Nile Delta W of 32 E	Faiyum
Culmen				
n	25	21	8	6
Range	8.1–11.2	9.6–11.3	10.1–11.5	9.1–9.7
Mean	10.06	10.45	10.45	9.40
SD	0.68	0.48	0.43	0.25
Bill from ant. edge nostril				
n	25	21	8	7
Range	5.2–7.1	6.2–7.7	6.3–7.2	6.0–6.5
Mean	6.46	6.98	6.70	6.31
SD	0.42	0.35	0.26	0.22
Gonys				
n	25	18	8	7
Range	5.8–7.0	5.2–7.3	6.1–7.0	5.5–6.7
Mean	6.45	6.57	6.53	6.17
SD	0.38	0.53	0.36	0.47
Wing				
n	25	20	8	7
Range	41–46	42–47	42–49	41–46
Mean	43.36	43.90	44.75	43.71
SD	1.41	1.68	2.43	1.88
Tail				
n	24	11	7	7
Range	44–66	50–66	53–67	48–63
Mean	57.41	59.00	60.71	56.42
SD	5.61	4.91	4.78	5.79
Tarsus				
n	24	19	8	7
Range	16.5–19.3	17.3–19.7	17.4–18.9	16.8–18.4
Mean	18.02	18.49	18.46	17.81
SD	0.66	0.69	0.50	0.58

adults by size. Descriptive statistics of the six characters for the four OTUs with sex classes combined are presented in Table 2.

Of the six characters measured only the culmen, bill from anterior edge of nostril and tarsus showed significant inter-OTU variation ($F = 6.54$, $P = 0.007$; $F = 9.95$, $P = 0.00001$; $F = 3.12$, $P = 0.03$, respectively). When all six characters were individually compared in pairwise combinations between OTUs several distinct patterns were found (Table 3).

The mean culmen length of Wadi Natroun birds was significantly different from the Cairo and Faiyum OTUs, whereas this was not the case between the Delta and Wadi Natroun OTUs. Further, the Faiyum birds were significantly different from those of the Delta and Cairo OTUs. The mean length of the bill from the anterior edge of the nostril showed a similar pattern, in that birds from Wadi Natroun were highly significantly different from the Faiyum and Cairo OTUs.

Table 3.—Matrices of F-statistics by OTUs for each character[1]

	Culmen/bill from ant. edge of nostril				Gonys/wing				Tail/tarsus			
OTU	1	2	3	4	1	2	3	4	1	2	3	4
1		22.94***	0.92	2.53		1.10	0.23	3.98		5.52*	0.56	2.71
2	5.42*		17.55***	3.43	0.76		0.06	1.40	0.65		5.58*	0.01
3	6.94*	16.62***		4.17*	2.19	4.12*		1.36	0.18	0.97		3.70
4	2.84	0.00	12.16**		0.14	0.04	2.09		2.02	0.43	2.21	

[1] Character to the left of slash is on bottom half of matrix, character to the right of slash is on the top half of matrix. See Materials and Methods for identification of numerical OTUs. One asterisk $P < 0.05$, two asterisks $P < 0.01$, three asterisks $P < 0.001$.

Also, the Faiyum and Delta OTUs showed a significant difference. The only significant interlocality difference in the mean gonys measurement was between the Wadi Natroun and the Faiyum OTUs. For the wing no distinct differences were found between OTUs, although the Delta and Cairo OTUs were border line ($F = 3.98$, $P = 0.051$). The variance of the tail length was relatively large (Table 2), and this character revealed no significant differences or information on relationships between the OTUs. The mean tarsus length showed a similar pattern as the first two characters; birds from Wadi Natroun were significantly different from the Faiyum and the Cairo OTUs.

The results of the inter-OTU Scheffé pairwise comparisons for the six characters can be summarized as follows:

1) The wing and tail revealed no significant patterns and can be excluded as characters yielding information on inter-OTU relationships.
2) The Wadi Natroun OTU was significantly different in 3 of the remaining 4 characters from the Cairo OTU, and in 4 of 4 characters from the Faiyum OTU.
3) No significant differences were found between the Wadi Natroun and Nile Delta OTUs.
4) The Faiyum and Cairo OTUs are more closely related to one another than either is to the other two OTUs.

For the Principal Components (PC) analysis only the four characters that showed inter-OTU differences were used (culmen, bill from anterior edge of nostril, gonys and tarsus). The loadings of these four characters for the first three PCs are presented in Table 4. PC I accounts for 46.3% of the phenetic variation. All loadings for PC I are positive and it is presumed to be primarily a size component. The highest loading for PC I is the bill from anterior edge of nostril. PC II explains an additional 25.2% of the phenetic variation. The highest positive loading for this component is the tarsus, while the culmen and gonys have negative loadings.

The four OTUs separate into two groups over the two-dimensional projection of the first two principal components (Fig. 2). The Wadi Natroun birds tend to cluster in the upper portion of the projection, with those from the Delta, but are somewhat separate. The Cairo OTU is widely distributed in the bottom half of the projection. The Faiyum OTU is spread throughout the Cairo OTU.

Table 4.—Character loadings and explained variances of the first three principal components.

Character	I	II	III
Culmen	0.45	−0.57	0.53
Bill from ant. edge of nostril	0.67	0.02	0.06
Gonys	0.48	−0.07	−0.79
Tarsus	0.33	0.82	0.30
% of total variance explained	46.3	25.2	20.7

Discussion

Historically in passerine systematics a combination of differences in plumage coloration and morphological measurements has been used to separate distinct populations into subspecies. It is important to distinguish between types of geographical variation and their use in interpreting infraspecific relationships. In many cases characters show smooth clinal variation within the contiguous range of a species, and arbitrary designations are drawn to separate portions of the cline into subspecies. This typological approach to subspecies has come under a considerable amount of criticism, for no real taxonomic information is presented by subspecific names used in this way (see Wilson and Brown 1953, for an early review of this misuse). However, for some characters which show clinal patterns, abrupt changes in morphology or plumage coloration occur between continuous populations; in this case they can be separated in a non-arbitrary way. These stepped clines may be the result of interspecific competition or some abrupt change in ecological parameters such as climate, soil types or vegetation cover. In other cases insular or geographically disjunct forms show distinct color or morphological differences which are not part of a broad clinal pattern. Such allopatric populations may experience different ecological restraints and have little genetic exchange with other populations. Both for stepped clines and distinct allopatric populations taxonomic information on infraspecific relationships and divergence between populations is useful to acknowledge and can be represented by a trinomial.

The results of the Scheffé and Principal Component analyses indicate that at least two distinct groups are present in the sample; birds from the Cairo and Faiyum OTUs, and birds from the Wadi Natroun and Delta OTUs. The ranges of measurements for these two groups overlap to such an extent they cannot solely be used to separate them. The only exception is the length of the bill from anterior edge of nostril, which shows only a small amount of overlap. Thus two morphologically distinct groups can be recognized in Egypt.

Size variation between the OTUs has a distinct pattern. For four of the six characters, the Wadi Natroun OTU is larger than or equal to the Delta OTU in mean character lengths, and for all six characters is larger than the Cairo and Faiyum OTUs. Excluding the Wadi Natroun OTU, the Delta OTU is always the largest, followed by the Cairo, then the Faiyum OTUs, except in one case (wing) when the Faiyum OTU is larger than the Cairo OTU.

No distinct plumage differences are apparent between Graceful Warblers from the Cairo and Faiyum OTUs. However, these birds are distinguishable from specimens collected in Wadi Natroun by having lighter brown and less sharply streaked upperparts. Specimens from the Delta OTU are generally discernable

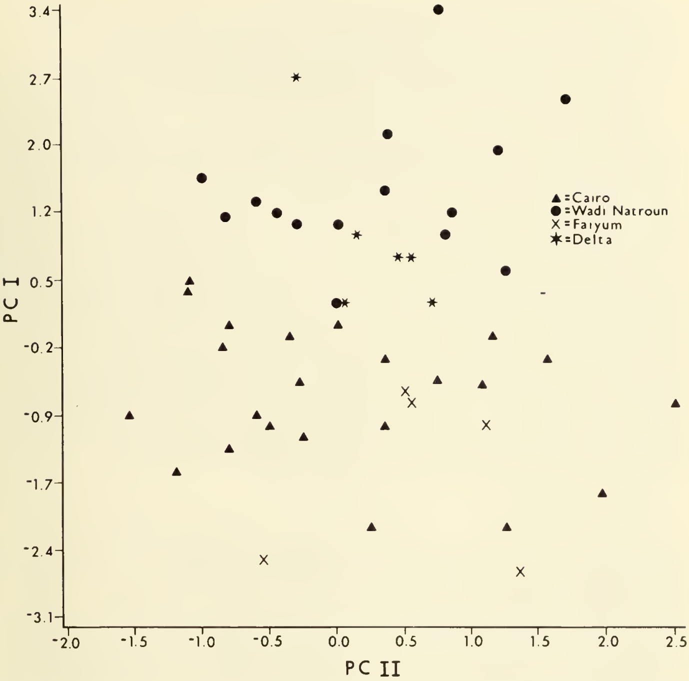

Fig. 2. Two-dimensional projection of the first two principal components (PC) for four morphological characters.

from Wadi Natroun birds by their darker and more broadly streaked upperparts. The trend in plumage coloration runs from the Delta where birds are the darkest, to Wadi Natroun, and then to the lower Nile Valley and Faiyum where birds are the lightest.

The patterns in measurements and plumage coloration differ between the OTUs. Based on the combination of the two types of characters the following subspecies are recognized:

P. g. deltae.—Occurring in the Nile Delta west of approximately 32°E. Morphologically similar to *P. g. natronensis* but separable by the distinctly darker and more saturated brown upperparts with broader streaks. Larger and slightly darker than *P. g. gracilis.*

P. g. natronensis.—Restricted to Wadi Natroun. Similar to *deltae* except as noted above. Separable from *P. g. gracilis* by having slightly darker and more broadly streaked upperparts. It should be noted that the type of *natronensis* (BMNH 1917.1.12.2) is an exceptionally light individual and does not properly represent the typical coloration of this species from Wadi Natroun.

P. g. gracilis.—Occuring from the Cairo region south along the Nile Valley and in the Faiyum. Smaller and lighter than *deltae* and *natronensis* as noted above.

The geological history of the area indicates that continuous vegetation existed during the post-Pliocene between Wadi Natroun and the Nile Valley and Delta. Presumably if *Prinia gracilis* occurred in the region at this time, the populations were probably not differentiated because of genetic exchange across the vegetated zones. In the Pleistocene, as the area experienced desiccation (Butzer 1975), Wadi Natroun was first cut off by desert from the Nile Valley and subsequently from the Nile Delta. Thus the patterns of geographic variation in the forms under consideration parallel the sequence of events that led to the complete separation of Wadi Natroun from the Nile Valley and Delta. However, it is possible that during the high water periods of the Holocene when the distance across the desert barrier would have been reduced *Prinia gracilis* dispersed from the Nile Delta to Wadi Natroun. The importance of vegetated zones between populations can be further supported by the fact that the Faiyum is a virtually disjunct oasis, but is still linked to the Nile Valley by a vegetated corridor, presumably through which genetic exchange takes place, accounting for the lack of differentiation between the populations of *P. gracilis* in the Faiyum and lower Nile Valley.

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Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, 48109.

Appendix 1.—Localities of *Prinia gracilis* material examined. *Cairo OTU*—Abu Rawash BMNH 2, FMNH 2, USNM 8; Cairo BMNH 2, ZFMK 2; Giza AMNH 3, BMNH 4, MCZ 2.

Wadi Natroun OTU—Wadi Natroun BMNH 8 (including holotype), FMNH 15.

Nile Delta OTU—Alexandria BMNH 2; Bahig DMNH 1; Bir Shams BMNH 1; Damietta BMNH 1; El Merg ZFMK 1; Idku, Rosetta FMNH 1.

Faiyum OTU—Faiyum BMNH 2; Kom Oshim FMNH 2; Lake Qarun (Moeris) BMNH 2; Tamiya AMNH 1.

Other Egyptian localities—Abu Simbil ZFMK 1; Amada DMNH 1; Armena YPM 10; Aswan USNM 1; "Balauyeh, Nubia" FMNH 1; Ismaliya USNM 2; Lake Menzala AMNH 1; "Luchess" or "Euchess" BMNH 1; Luxor AMNH 1, UMMZ 2; Port Said BMNH 7, FMNH 1, ZFMK 7, USNM 1; Qantara AMNH 1, BMNH 1; "Siout, E. of" FMNH 1; "Tartah" FMNH 2; Toshka YPM 2.

Sudan localities—Berber BMNH 1; Kaweimat ZFMK 1; Kerma AMNH 6; "Niakala" AMNH 1; Shendy AMNH 6, BMNH 1.

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REVISION OF THE GENUS *LEPTOSOMATIDES* FILIPJEV, 1918 (NEMATODA: ENOPLIDA)

Tom Bongers

Abstract.—The results of a study of *Leptosomatides* type-material are given. *Leptosomatides conisetosus* Schuurmans Stekhoven and Mawson, 1955 is transferred to *Deontostoma; L. antarcticus* Mawson, 1956 is considered a good species although more information is desired regarding the presence of odontia and onchia.

Leptosomatides brevisetosus Platonova, 1976, and *L. acutipapillosus* Platonova, 1976 are synonymized with *L. marinae* by Platonova (this paper). *L. caucasiensis* Sergeeva, 1973 is synonymized with *L. euxinus* Filipjev, 1918. *Leptosomatides crassus* Platonova, 1967, *L. steineri* sensu Filipjev, 1946 and *Leptosomatum elongatum* sensu Platonova, 1967 are considered identical to *L. grebnickii* (Filipjev, 1916).

Leptosomatides steineri Filipjev, 1922, and *Leptosomatum tetrophthalmum* sensu Platonova, 1967 are synonymized with *L. arcticus* (Filipjev, 1916). *L. microlaimus* (Allgén, 1957) Platonova, 1976, and *L. filiformis* (new rank) (=*L. steineri* subsp. *filiformis* Filipjev, 1946) are considered *species inquirendae. Leptosomatides inocellatus* Platonova, 1967 does not belong to *Leptosomatides* and is considered a species *incertae sedis.*

Additional descriptions are given in this paper. Arguments are given for transferring *Leptosomatides* to the Thoracostomatinae. In fact, the only difference from *Deontostoma* is the absence of odontia and onchia in *Leptosomatides.*

In a previous paper (Bongers 1983) the confusion concerning the separation of the genera *Leptosomatum* Bastian, 1865 and *Leptosomatides* Filipjev, 1918 was discussed, and *Leptosomatum tetrophthalmum* sensu Platonova, 1967 (*nec* Ssaweljev, 1912), *L. arcticum* Filipjev, 1916, *L. grebnickii* Filipjev, 1916 and *L. elongatum* sensu Platonova, 1967 (*nec* Bastian, 1865) were transferred to *Leptosomatides.* Based on the literature it is almost impossible to distinguish the species of *Leptosomatides*; I therefore studied the type-material of the species assigned to it. Results and additional descriptions are presented in this paper.

Material

Type-material was available for study of the following species: *Leptosomatum arcticum* Filipjev, 1916; *L. grebnickii* Filipjev, 1916; *L. tetrophthalmum* sensu Platonova, 1967; *L. elongatum* sensu Platonova, 1967; *Leptosomatides steineri* sensu Filipjev, 1946; *L. steineri* subsp. *filiformis* Filipjev, 1946; *L. crassus* Platonova, 1967; *L. inocellatus* Platonova, 1967; *L. caucasiensis* Sergeeva, 1973; *L. acutipapillosus* Platonova, 1976; *L. brevisetosus* Platonova, 1976 and *L. marinae* Platonova, 1976. In addition, the Smithsonian Institution, Washington, D.C., U.S.A. put unidentified material at my disposal.

Methods and Differential Characteristics

The specimens, many of which were in poor condition, were compared with their descriptions. In several cases the literature was almost inaccessible. Recommendations 4 and 5 appendix E of the International Code of Zoological Nomenclature (hereafter termed the Code), in which it is advised to accompany the description of a new taxon by a translation into English, French, German, Italian, or Latin, if the description is not written in one of these languages, have often not been followed. In two cases the summaries contradicted the text.

The specimens from the Smithsonian Institution had been mounted in glycerin between coverslips in aluminum frames. The other specimens had been mounted on glass slides in glycerin-gelatin and could be observed from only one side. The coverglasses on the latter slides were not supported and the nematodes were severely flattened. Several slides contained more than one species. The way in which paratypes were designated for *Leptosomatides marinae, L. brevisetosus, L. acutipapillosus* and *L. caucasiensis,* for example, does not conform to the Code and leads to confusion.

The flattening of the specimens made relative measurements valueless in so far as body width is one of the components. Often the cuticle was swollen, and the hypodermal tissue had shrunken, pulling the cervical sensilla into small craters. In my opinion, cuticle thickness is valueless as a differential character in these cases; the same holds for ratio "a" and other relative measurements. When the tail is curved strongly to the ventral side (e.g., in the males of *L. marinae*; Fig. 3) the index "c" is also valueless.

The cephalic sensilla (sensu Lorenzen 1981) are setiform in *L. antarcticus, L. euxinus,* and *L. reductus,* and papilliform in the remaining species. A sensillum is considered setiform when its length is twice or more its basal breadth. Cervical sensilla were present in all species examined.

The cephalic capsule is uniform in *Leptosomatides* spp. The posterior suture undulates but is never more posterior than the anterior margin of the amphid. On the outer side of this capsule a refractive layer in the cuticle can be observed, which is homologous to the lunula in the tail. Both are present in *Leptosomatides* and related genera but absent in *Leptosomatides inocellatus,* which is removed from this genus.

The amphids are uniform in structure throughout the genus *Leptosomatides*; only some size differences occur between sexes and species. The fovea, of which the diameter is presented in this paper, is circular in lateral view and the posterior margin is clearly visible, in contradiction to the fovea in female *Leptosomatum* specimens.

The ocelli are provided with a lens-like body, here termed lens, of which the diameter, in lateral view, is used in this paper. Additional pigment, posterior to the ocelli, is present in the pharynx of a number of specimens and is not species-specific. In general, the distance from lens to anterior body end varies within about 10%. The left lens lies more anterior in two-thirds of the specimens. In two aberrant specimens, belonging to *L. euxinus* and *L. marinae,* one of the ocelli lies half as far from the anterior end as the other, but this phenomenon is not characteristic for *L. euxinus* as stated by Platonova (1976).

The renette was observed in one female of *L. tetrophthalmum* sensu Platonova, 1967 and in one female of *L. marinae.* This gland is restricted to the pharyngeal region but the position of the pore has not yet been located.

The vulva lies slightly anterior to the middle of the body; a strongly developed vaginal musculature is present in all specimens throughout *Leptosomatides* and is a differentiating character from *Leptosomatum,* in which this radial musculature is absent. This ovejector, as defined by Filipjev (1916:23), is also present in *Thoracostoma* and *Deontostoma.*

Intra-cuticular granula, anterior and posterior to the vulva, and lateral vulvar glands, are present; in *L. euxinus,* however, the granula are fewer in number but distributed over a larger area. The ducts of the lateral vulvar glands were difficult to observe. Hope (1967a) described these granula and vulvar glands in, amongst others, *Thoracostoma trachygaster.* He stated that they are absent in pre-adults but in a pre-adult of *L. crassus,* slide 7016, both are present. In *L. arcticus* five to seven glands are developed, in the remaining species two to four. A small overlap exists for which I refer to the discussion of *L. marinae.* I realize that the number of glands is a doubtful distinguishing character but it is one of the few that distinguishes females of *L. marinae* and *L. arcticus.*

Filipjev (1916) described a well-developed system of sensory papillae near the vulva of *Thoracostoma denticaudatum,* and Hope (1967b) reported comparable unevennesses anterior and posterior to the vulva of *Corythostoma triaulolaimus*; these sensilla are also present in *L. marinae.*

In my opinion, Filipjev and Platonova attach unwarranted importance to the number and size of the eggs. According to Platonova (1976) *Leptosomatides crassus* can be distinguished from *L. steineri* sensu Filipjev, 1946 by the number of eggs; up to eight in the former and four in the latter. It is my opinion that size and number of eggs depend on the season and developmental stage of the female.

When males are present, the spiculum and gubernaculum shape are useful to separate the species. The gubernaculum, and to a lesser degree the spicules, may be obscured by the opaqueness of the surrounding tissue. It was impossible to ascertain if there was any difference in length between the left and right spiculum. In this paper the length of the chord is given.

Males of *L. marinae* possess two ventromedian supplements, one precloacal with alae and one postcloacal without. The anterior and posterior alae (as termed by Hope 1967a) are also present in a number of species assigned to the Thoracostomatinae.

The term "alae" to describe the refractive ribs in the ventromedian supplement is confusing. Both Hope and I agree that the introduction of another term should be postponed until more information becomes available regarding its function. Often the number of pre- and postcloacal subventral papillae shows intraspecific variability.

Historical Review

The genus *Leptosomatides,* with *L. euxinus* as type-species, was erected by Filipjev in 1918 and described as being intermediate between *Leptosomatum,* which it resembles in the structure of the anterior end, and *Deontostoma,* which it resembles in the structure of the posterior end of the male. He remarked that

Leptosomatum arcticum and *L. grebnickii,* both described by himself in 1916, might also belong to *Leptosomatides* but preferred to wait until their males should be found.

Filipjev (1921:563) transferred *Leptosomatum gracile* sensu Steiner, 1916 *nec* Bastian, 1865 to *Leptosomatides* and in 1922 he renamed it *Leptosomatides steineri.* In 1922, the radial musculature of the vagina wall, here termed the vaginal ovejector, was added to the generic diagnosis.

Filipjev (1946) reported *L. steineri* from the New Siberian Islands; because of its more slender body, two of the specimens were described as *L. steineri* var. *filiformis.* In 1955, Schuurmans Stekhoven and Mawson added *L. conisetosus*; one year later *L. antarcticus* was described by Mawson. Both are Antarctic forms. In 1959 Timm described the only subtropical member of this genus from the Arabian Sea as *L. reductus.*

Platonova (1967) added two species from the Kara Sea, *L. inocellatus* and *L. crassus*; Sergeeva published the description of a species from the Black Sea in 1973. Three species with papilliform cephalic sensilla from the Kuril Islands, *L. acutipapillosus, L. brevisetosus,* and *L. marinae,* were described by Platonova in her thesis (1976), and in the same paper, *Leptosomatum microlaimum* Allgén, 1957 was transferred to *Leptosomatides.*

Leptosomatum arcticum Filipjev, 1916, *L. grebnickii* Filipjev, 1916, *L. tetrophthalmum* sensu Platonova, 1967 *nec* Ssaweljev, 1912, and *L. elongatum* sensu Platonova, 1967 *nec* Bastian, 1865 were transferred to *Leptosomatides* by Bongers (1983).

Leptosomatides Filipjev, 1918

Leptosomatides Filipjev, 1918:50–51; 1922:98.—Platonova, 1976:69–70 [Key].

Diagnosis.—Leptosomatidae Filipjev, 1916. No sexual dimorphism in amphid structure; fovea round. Cephalic capsule weakly developed, posterior suture undulating; lobes never reaching beyond anterior margin of amphids. Onchia and odontia absent. Labial sensilla intracuticular; cephalic and cervical sensilla papilliform or setiform. Ocelli provided with distinct lens. Dorsal pharyngeal gland opens into pharyngeal lumen; ventrosublateral glands open at anterior end, ducts cuticularized. Renette in pharyngeal region. Caudal glands long, overlapping intestine. Lunula present. Ortho- and loxometanemes-I present.

Female gonads amphidelphic, antidromic. Vaginal ovejector present, lateral vulvar glands and intra-cuticular vulvar granules usually present. Gonads located left of intestine. Male diorchic, testes opposed and outstretched; ventral precloacal papilla and 2 subventral rows of accessory sensilla present in cloacal region. Gubernaculum with cuneus, crura present or reduced. Copulatory muscles strongly developed.

Remarks.—Discussing the labial orifices of the ventrosublateral pharyngeal glands in *Leptosomatum bacillatum,* Platonova (pers. comm.) stated that one of her students previously described these orifices in *Leptosomatides marinae.* I have also observed these orifices on the anterior end of *Syringonomus typicus* Hope and Murphy, 1969, and *Leptosomatum* species. According to Hope (1982) these openings in the mandibular grooves might be characteristic for the Leptosomatidae. The glands, as present in the lateral hypodermal chord of, amongst others, *Cyclicolaimus* are absent in *Leptosomatides*; only in the vulvar region are such glands present. The gonads in *Leptosomatides* are situated on the left side of the intestine.

Leptosomatides antarcticus Mawson, 1956

Leptosomatides antarcticus Mawson, 1956:42, fig. 1a–e.

Diagnosis.—Cephalic sensilla setiform; 4 μm. Amphid (fovea) 10 μm in diameter. Ocelli 1.5 corresponding body diameters from anterior end. Spicula relatively short, 100 μm; crura of gubernaculum present. Tail conical in both sexes. Stoma provided with tooth (?).

Type.—Syntypes: 7 ♀, 3 ♂.

Distribution.—Antarctica: Enderby Land, MacRobertson Land.

Discussion.—I was not able to obtain material of this species for comparison. Although the vulvar region is not depicted and nothing is mentioned concerning the vagina structure, this species probably belongs to *Leptosomatides.* The small tooth at the anterior end of the pharynx, however, needs confirmation. *Leptosomatides conisetosus* Schuurmans Stekhoven and Mawson, 1955, which is provided with a tooth, may have influenced this observation.

If onchia and/or odontia are present, *L. antarcticus* must be transferred to *Deontostoma.*

Regarding the figures of *L. antarcticus* and *L. conisetosus,* some confusion exists. On page 42 (Mawson 1956), fig. 1a–c is stated to represent *L. antarcticus* and fig. 2a–d *L. conisetosus.* Five illustrations, however, are given of the former and three of the latter species. Moreover, fig. 1e probably represents *L. conisetosus.* An indication of the sex of the anterior ends is missing.

An additional description of the vulva structure, amphids, precloacal papilla in the male and indication of lectotype is needed.

Leptosomatides arcticus (Filipjev, 1916), new combination

Fig. 1A, B, D

Leptosomatum arcticum Filipjev, 1916:66–68, fig. 1.

Leptosomatum gracile sensu Steiner, 1916:610–620, fig. 27a–o, *nec* Bastian, 1865: 145–146, figs. 158–160.

Leptosomatides steineri Filipjev, 1922:98, pro *Leptosomatides gracile* sensu Steiner, 1916:610–620, fig. 27a–o.

Leptosomatum tetrophthalmum sensu Platonova, 1967:828–829, *nec* Ssaweljev, 1912:124.

Nec Leptosomatides steineri sensu Filipjev, 1946:159, 177–178, fig. 2.

Nec Leptosomatum arcticum sensu Mawson, 1958:315–316, fig. 1a–c.

Diagnosis.—Cephalic sensilla papilliform; 2–3 μm. Cephalic capsule 10–13 μm. Fovea 8 μm. Lens 10 μm. Lateral vulvar glands 5–7. Intracuticular granula numerous. Males unknown.

Type.—The only syntype of *L. arcticus* is a decapitated body; *Leptosomatum gracile* sensu Steiner, 1916 could not be located. Of *L. tetrophthalmum* sensu

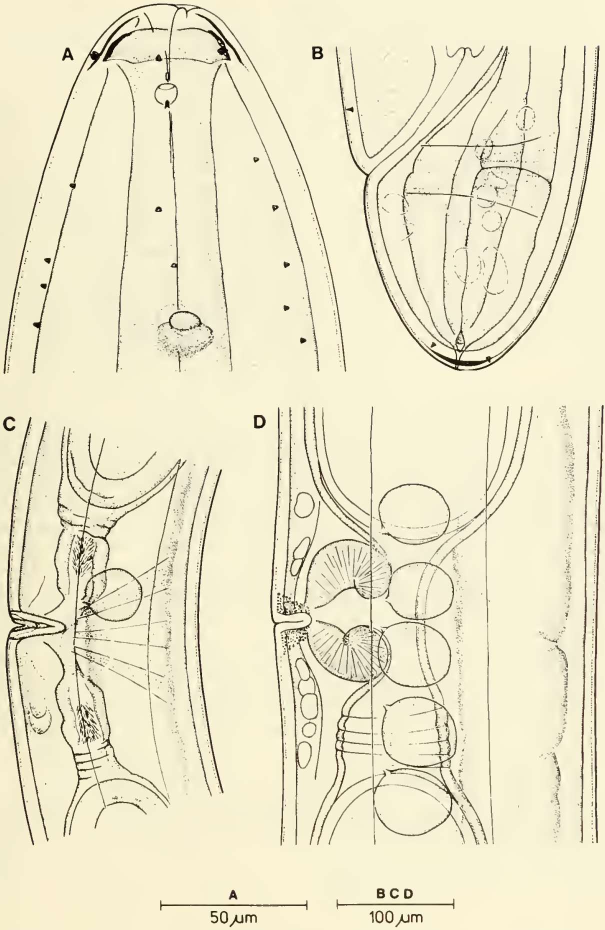

Fig. 1A, B, D. *Leptosomatides arcticus* (Filipjev, 1916) (depicted is *Leptosomatum tetrophthalmum* sensu Platonova, 1967): A, Female, anterior end; B, Female tail; C, *Leptosomatides filiformis* (Filipjev, 1946): lectotype, vulvar region; D, Vulvar region.

Platonova, 1967, 15 females are in existence. Female 5070-2, depicted in Fig. 1, whose measurements are given in the Appendix, fits the description and may be used for comparison. Slides deposited at Zoological Institute, Leningrad.

Type-locality.—Murman Coast; littoral.

Distribution.—Novaya Zemlya, Barents Sea, Kara Sea.

Discussion.—Although males are unknown, *Leptosomatum arcticum* Filipjev, 1916 has all the characters diagnostic for the females of the genus *Leptosomatides* as stated in a previous paper (Bongers 1983). The fovea comes to 8 μm, the lens 10 μm in lateral view. The only remaining syntype shows five lateral vulvar glands.

Leptosomatum gracile sensu Steiner, 1916 was transferred to *Leptosomatides* by Filipjev in 1921 (p. 563) and renamed *Leptosomatides steineri* in 1922.[1] Steiner described six pairs of cephalic sensilla in *L. gracile.* According to Hope (pers. comm.) this is probably not species-specific because in *Deontostoma* occasional specimens are found with six pairs of sensilla. Steiner depicted seven lateral vulvar glands; in Filipjev's specimens (1946) the number of glands never exceeds four. Therefore a distinction is drawn between Steiner's (1916) and Filipjev's (1946) material.

Leptosomatum tetrophthalmum sensu Platonova, 1967 was collected in 1915 and 1925 and was assigned to *Leptosomatum tetrophthalmum* Ssaweljev, 1912 by Filipjev. It seems plausible that Filipjev had seen Ssaweljev's material (Platonova pers. comm.) and that the specimens of Platonova were identical to those of Ssaweljev. Ssaweljev's description (1912) is quite superficial and incomplete and it is not possible to establish whether this species belongs to *Leptosomatum* or *Leptosomatides.* As no syntypes are present, this species was considered a *species inquirenda* in a previous paper.

The only existing material worth redescribing, although flattened, is *Leptosomatum tetrophthalmum* sensu Platonova, 1967. Two females have been restudied and dimensions and figures (Fig. 1) are presented in this paper. Slide 5070 bears two females collected 22-IX-1925.

Although more information is necessary regarding the male, the females can be distinguished from *L. euxinus* by the papilliform cephalic sensilla, from *L. marinae* and *L. grebnickii* by the number of lateral vulvar glands and the lens diameter, from *Leptosomatides* sp. A by the number of lateral vulvar glands.

Leptosomatides conisetosus Schuurmans Stekhoven & Mawson, 1955

Leptosomatides conisetosus Schuurmans Stekhoven & Mawson, 1955:98–100, figs. 20–22.—Mawson, 1956:42–43, fig. 2a–d; 1958b:320, fig. 5b.

This species known from Antarctica, Kerguelen Islands, and Macquarie Island,

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[1] Platonova (1976) probably wrongly interpreted this paper: on the one hand she considers *L. gracile* sensu Steiner, 1916, conspecific with *L. gracile* Bastian, 1865 for which she used the figures of Steiner (1916). On the other hand, however, on page 71 she accepts *L. steineri* Filipjev, 1922 and does not refer to Steiner's paper. So, according to Platonova, *Leptosomatum gracile* sensu Steiner, 1916 and *Leptosomatides steineri* Filipjev, 1922 are not congeneric. According to Filipjev (1922), however, they are objective synonyms.

was not available for re-examination, so the discussion will be based on the original description and Mawson's papers of 1956[2] and 1958b.

Leptosomatides conisetosus (lapsus *conisetosum*) is characterized by a strongly developed cephalic capsule, the presence of a small tooth at the base of the funnel-shaped buccal cavity and cuticularized lips.

The shape of the cephalic capsule varies somewhat; in the holotype the lobes are short with straight edges posteriorly and semicircular spaces between the lobes. Figure 2a of Mawson's 1956 paper, however, shows a capsule with lobes broadening posteriad.

The genus *Leptosomatides* was erected as being intermediate between *Deontostoma* and *Leptosomatum* concerning the posterior and anterior end respectively. In *L. conisetosus,* however, the anterior end shows closer affinities to *Deontostoma* than to *Leptosomatum* and I herewith transfer this species to that genus as *Deontostoma conisetosum* (Schuurmans Stekhoven and Mawson, 1955), new combination.

Leptosomatides euxinus Filipjev, 1918
Fig. 2A–D

Leptosomatides euxinus Filipjev, 1918:51–54, fig. 3a–f.
Leptosomatides caucasiensis Sergeeva, 1973:1711–1712, fig. 3a–b.

Diagnosis.—Cephalic sensilla setiform: 4–5 μm. Cephalic capsule short; 7 μm in length. Anterior part of pharynx cuticularized. Fovea 5.5–6.5 μm in diameter in both sexes. Lens 6–7 μm. Vulvar glands absent (not developed ?). Intracuticular vulvar granula finer and more dispersed than usual in the genus. Spiculum short; crura present, but reduced.

Holotype.—The holotype is on slides 5074 (body) and 5015 (head), Zoological Institute, Leningrad, U.S.S.R. The holotype of *L. caucasiensis* is also deposited at the Zoological Institute.

Distribution.—Black Sea.

Discussion.—The description and figures of slide 6565 given by Platonova (1976) are based on a specimen with an aberrant position of the ocelli; this phenomenon is also present in slide 7996 of *L. marinae.*

The type of *L. caucasiensis* is twisted; the precloacal papilla, in the summary erroneously stated to be absent, is visible at low magnification if the slide is turned over. According to Sergeeva (1973), the cervical setae are absent in *L. caucasiensis* and differences should exist in shape and development of spiculum and cephalic capsule respectively. These cervical setae are present. The development of the cephalic capsule is similar to that in *L. euxinus*; the caudal glands are longer than depicted, overlapping the intestine. *L. caucasiensis* Sergeeva, 1973 is herewith synonymized with *L. euxinus* Filipjev, 1918.

A slide (No. 8097) labelled "paratype" of *L. caucasiensis* (Coll. 1 Feb 1968),

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[2] The way in which Mawson (1956) described the body proportions is not to be recommended. On page 43: "The eyes are one-fifth to one-sixth of the distance from head to nerve ring, and this latter is1/2.7–1/3.3 of the length of the oesophagus." The length of the pharynx has to be calculated from $b = 7.2–8.8$ and $L = 14–15$. These relative measurements are almost useless.

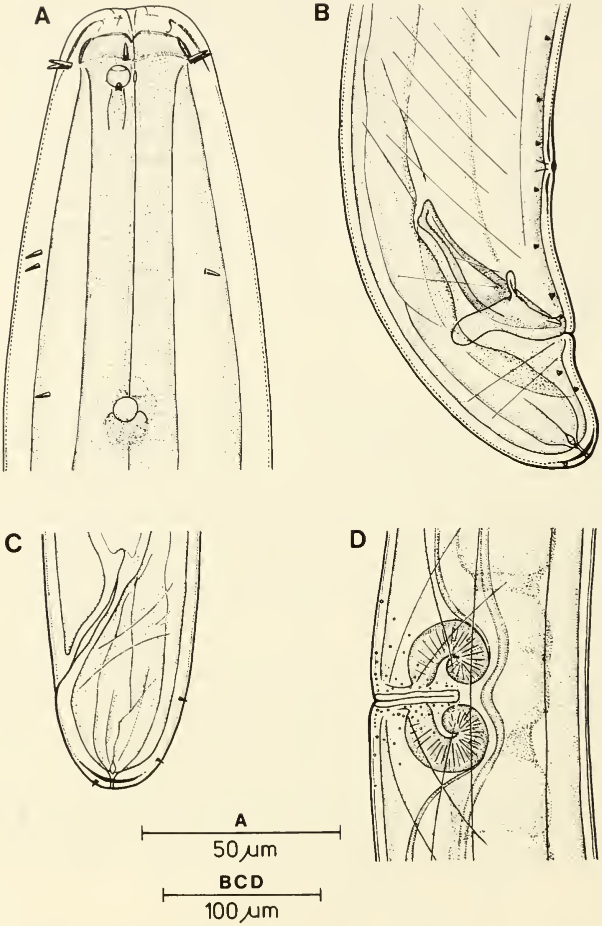

Fig. 2. *Leptosomatides euxinus* Filipjev, 1918 (depicted is *Leptosomatides caucasiensis* Sergeeva, 1973, det. Sergeeva). A, Male head; B, Male tail; C, Female tail; D, Vulvar region.

is present in the collection of the Zoological Institute, which contains a male and two female specimens in rather good condition. (The indication of slide 8097 as paratype is not valid as these specimens do not belong to the type-series.) The body dimensions of these specimens are given in the Appendix and Fig. 2 is also based on this material. The male specimen was in excellent condition and the gubernaculum structure could easily be observed. The crura are reduced; these anterior processes seem to be twisted.

In the type of *L. euxinus* I was unable to note the lateral vulvar glands. According to Filipjev (1921:405) these glands (phagocytic cells) are sometimes present, although he was unable to observe the ducts.

This species can easily be distinguished from the other species of *Leptosomatides* by the setiform cephalic sensilla, the short length of the cephalic capsule in both sexes, the ocelli, which lie at about twice the corresponding body width from the anterior end, and the c-value exceeding 120. *Leptosomatides reductus* Timm, 1959 is closely related to this species and is distinguishable by the diameter of the fovea in the male, which is about 10 μm as opposed to 6–7 μm in *L. euxinus*. Minor differences exist in the length of the cephalic setae and structure of spiculum.

Leptosomatides filiformis (Filipjev, 1946), new rank
Fig. 1C

Leptosomatides steineri filiformis Filipjev, 1946:159, 177–178.

Diagnosis.—Cephalic sensilla papilliform; 3 μm. Cephalic capsule 9–11 μm. Fovea 7 μm. Lens 8 μm. One lateral vulvar gland. Intracuticular granula almost absent. Uterine (?) ovejector present.

Type.—The specimen on slide 7010 is herewith designated lectotype. It is labelled: *L. steineri* var. *filiformis* ♀ det. I. N. Filipjev "SADKO," 80°16′N × 74°02′E, 26-8-1935 Karskoje more. Zoological Institute, Leningrad, U.S.S.R.

Distribution.—Northern Kara Sea (see coordinates).

Discussion.—Filipjev (1946) described a variety of *L. steineri* as subsp. *filiformis* on the basis of a more slender body. This female, and not a male as stated in the French summary, is characterized by the ratios 105, 8.0 and 105. In the collection of the Zoological Institute in Leningrad, two slides were present, 6999 and 7010, with aberrant females. The female on 7010, labelled as var. *filiformis,* was measured by me and the vulvar region figured (Fig. 1c). The body is twisted; anterior and posterior ends are oriented dorsoventrally, midbody laterally. The cuticle is considerably swollen.

The other female, labelled *L. steineri* var. *filiformis* (slide N-6999) has the same aberrant vagina structure. According to Platonova (pers. comm.) this female is 11.8 mm long with a pharynx length of 1700 μm, tail length of 120 μm and body width of 170 μm.

This is a doubtful species; more information is necessary regarding the torn vaginal ovejector. The difference between this species and *L. steineri* sensu Filipjev, 1946 is not less than the differences between the other short-papilloid species and, therefore, this subspecies is raised to specific level.

Leptosomatides grebnickii (Filipjev, 1916), new combination

Leptosomatum grebnickii Filipjev, 1916:68–70, fig. 2.

Leptosomatides steineri sensu Filipjev, 1946:159, 177–178, fig. 2. *Nec* Filipjev, 1922:98 pro *Leptosomatum gracile* sensu Steiner, 1916:610–620, fig. 27a–o.—*Nec Leptosomatides steineri* subsp. *filiformis* Filipjev, 1946:159, 177–178.—Platonova, 1967:829.

Leptosomatides crassus Platonova, 1967:829–831, figs. 5–7.

Leptosomatum elongatum sensu Platonova, 1967:828.—*Nec* Bastian, 1865:145, figs. 156–157.

Diagnosis.—Cephalic sensilla papilliform 2–3 μm. Cephalic capsule 10–13 μm. Fovea 10 μm in female. Lens 6 μm. Lateral vulvar glands 2–4. Intracuticular granula numerous. Spicula uniformly curved, gubernacula with paired cunei directed posteriorly at right angles to spicula.

Type.—Head on 5778 and decapitated body on 5779. Indicated by Platonova (1976) as holotype. However, as this designation was done after the original publication, the correct designation is lectotype. Zoological Institute, Leningrad, U.S.S.R.

Type-locality.—Behring Islands.

Distribution.—New Siberian Islands, Behring, Kara and Barents Sea.

Discussion.—Platonova (1976) indicated slides 5778 and 5779 as holotype; the former slide contains the head, the latter a decapitated body of a female and a complete female. Hence the head, together with the decapitated female, represent the lectotype.

According to Filipjev (1916), *Leptosomatides grebnickii* can be distinguished from *L. arcticus* (=*Leptosomatum arcticum*) by the bigger amphids. However in the description of *L. steineri* and its variety *filiformis* by Filipjev (1946), 8 μm is given for the diameter of the amphids (aperture?). From the text, it is impossible to conclude whether this diameter refers to the female, male, or amphids of the variety.

My measurements of the fovea of females of *L. steineri* sensu Filipjev, 1946 are 10 μm; for the variety *filiformis* the measurement is 7 μm; the diameter of the fovea in the male could not be stated as the anterior part of the male was twisted dorsoventrally.

Leptosomatides crassus and *Leptosomatum elongatum* sensu Platonova (det. Filipjev), both of which were described by Platonova in 1967, cannot be distinguished from *L. grebnickii.* In *Leptosomatum elongatum* sensu Platonova, the ovejector was not recorded in the more extensive description of 1976. *Leptosomatides crassus* was depicted with one short caudal gland. Both are provided with ovejector, granula, lateral vulvar glands, and long caudal glands. Slide 5761 of *L. elongatum,* collected from *Balanus porcatus* at the Murman Coast in 1923, is measured and data are presented in the Appendix.

Filipjev (1946) also described the male but as a separation is made between his *L. steineri* and its variety *filiformis,* this male might also belong to the subspecies. According to Filipjev the length of spiculum and gubernaculum are 210 and 90 μm respectively, whereas Platonova (1976) gave 137 and 25 μm. In both specimens, the gubernaculum and spiculum are of the *Pseudocella* type and 16–17 subventral precloacal papillae are present.

Leptosomatides grebnickii can be distinguished from *L. euxinus* by the papil-

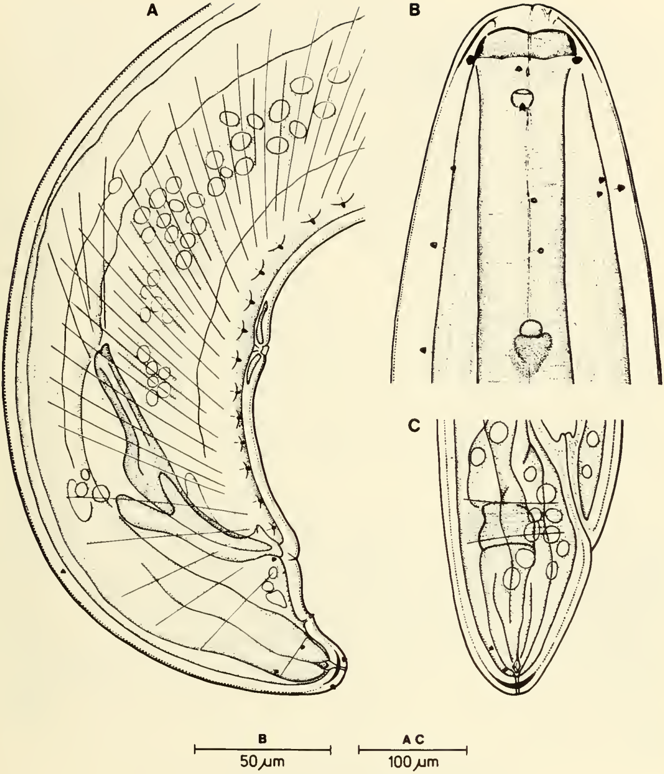

Fig. 3. *Leptosomatides marinae* Platonova, 1976. A and B, Posterior and anterior end; male paratype of *L. brevisetosus* Platonova, 1976; C, Posterior end paratype *L. marinae.*

liform cephalic sensilla; from *Leptosomatides arcticus, L. marinae* and *L.* sp. A by the size of the amphids and lens. The male is characterized by the uniformly curved spicula with paired apophyses directed posteriad at right angles to the spicula, as in *Pseudocella,* which is unique in the genus *Leptosomatides.*

Leptosomatides inocellatus Platonova, 1967

Leptosomatides inocellatus Platonova, 1967:829, figs. 3–4.

The material, on which this description was based, was collected in 1935; the nematodes were mounted in glycerin-gelatin and are rather flattened.

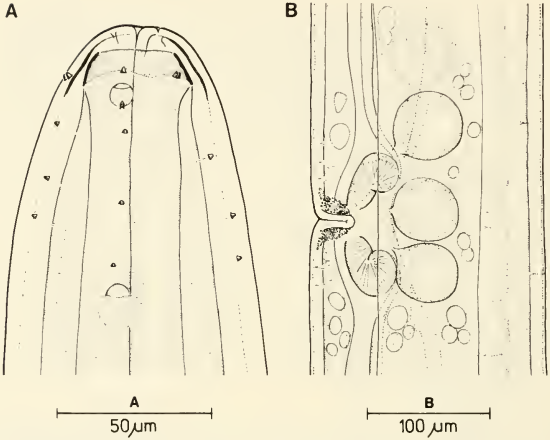

Fig. 4. *Leptosomatides marinae* Platonova, 1976. A, Anterior end, female; B, Vulvar region.

Diagnosis.—Diameter of amphidial aperture exceeds diameter of cup-shaped fovea. Vaginal musculature inconspicious. Ocelli, intracuticular vulva granula, and lateral vulvar glands absent. Caudal glands short. Distinct glands in lateral hypodermal chord. Head structure complex; stoma probably wide.

Holotype.—Slide 7026; Zoological Institute, Leningrad.

The paratypes of *L. inocellatus* are rather variable; slide 7028 contains a nematode, provided with rather long setae compared with 7027. *Leptosomatides inocellatus,* which resembles *Leptosomatum groenlandicum* Allgén, 1954, might belong to the Platycominae. At present, however, I consider it a species *incertae sedis.*

Leptosomatides marinae Platonova, 1976
Figs. 3A–C, 4A–B

Leptosomatides marinae Platonova, 1976:70, 77–79, fig. 29.
Leptosomatides acutipapillosus Platonova, 1976:70, 75–76, fig. 27.
Leptosomatides brevisetosus Platonova, 1976:70, 76–77, fig. 28.

Diagnosis.—Cephalic papilliform sensilla 3 µm long. Cephalic capsule 10–12 µm in females, 7–9 µm in males. Fovea 8–9 µm in both sexes. Lens 8 µm in diameter. Lateral vulvar glands 2–4. Intracuticular granula numerous. Spiculum robust, gubernaculum with crura. Ventromedian precloacal papilla provided with alae. Ventral postcloacal papilla present, vulva sensilla present.

Type.—Holotype 7880, by original designation. Zoological Institute, Leningrad, U.S.S.R.

Type-locality.—Iturup Island. Kasapka Bay, 4–5 m, in sponge.

Distribution.—Kuril Islands to East Kamchatka.

Discussion.—The holotypes of *L. acutipapillosus* and *L. brevisetosus* were provided by Platonova with an extra label with the name *L. marinae.* Therefore, in the (unpublished) opinion of Platonova, these three species are identical, with which I agree.

Following recommendation 24(A) of the Code, the name *L. marinae* is selected since it has line priority in the key on page 70.

It was impossible to decide on which specimens the description was based since the slides, labelled paratypes, contain more than 120 specimens, 40% of them provided with a question mark. These paratypes originate from 30 locations, and were collected between 1910 and 1975 from *Cystoseira, Laminaria, Balanus, Corallina, Alaria, Agrarum,* and sponges in the littoral zone. No slides were labelled as paratypes of *L. acutipapillosus.*

Dr. T. A. Platonova kindly gave permission to deposit one male and one female at each of the following nematode collections: Nematology Dept., Wageningen, The Netherlands; National Museum of Natural History Smithsonian Institution, Washington, D.C., U.S.A., and the South Australian Museum, Adelaide, Australia. The males, slide 6133, were labelled as paratypes of *L. brevisetosus,* collected at 9-VIII-1957, Chimushir Is. Kitabujnaja Bay from littoral rhizoids of *Laminaria,* mud, sand. The females, slide 7909, collected at Kunashir Is. 13-VII-1969 from sponges with shells, 9–10 m. The figures and dimensions given in this paper are based on these six specimens.

In 23 females of *L. marinae* the number of lateral vulvar glands was found to be 2–5 ($\bar{x} = 3.22$; $\sigma = 0.83$) in each body half.

The caudal part of the male is strongly curved; the length of the tail, the anal body width and ratio c are almost useless in this case. Of the subventral cloacal papillae, one or two are situated postcloacal, six to nine between cloaca and median precloacal papilla and 10–12 anteriad to the ventral papilla; in general they were not conspicuous.

In one of the females, a cervical gland was present, but the pore could not be found.

Although *Leptosomatum gracile* sensu Allgén, 1954 is insufficiently described and figures of head and tail region are useless, the dimensions, placement of ocelli and number of lateral vulvar glands agree with *L. marinae.* The cephalic sensilla, capsule and amphids, however, are not described or illustrated.

The males of *L. marinae* can easily be distinguished by the precloacal papilla provided with alae. The females differ from *L. arcticus* in the number of lateral vulvar glands and the position of the ocelli; from *L. grebnickii* by the diameter of the lens and fovea, from *L.* sp. A by the diameter of the lens and tail length.

Leptosomatides microlaimus (Allgén, 1957)

Leptosomatum microlaimum Allgén, 1957:7, fig. 1a–b.

Discussion.—This species was collected at a depth of 1750 m near Spitzbergen; the type-material could not be located. It appears in the key of *Leptosomatides,* given by Platonova (1976) where it is designated *L. microlaimum* Allgén, 1957.

The absence of justification, the inappropriate gender ending, and the fact that the author's name is not enclosed in parentheses may lead to confusion. Judging from the figure, I agree with this transfer. The discrepancy in Allgén's calculations of ratio "C" and the description, which cannot be taken seriously, are reason to consider it a *species inquirenda.*

Leptosomatides reductus Timm, 1959

Leptosomatides reductus Timm, 1959:207–209, fig. 2d–e.

Diagnosis.—Cephalic setiform sensilla 6.5 μm long. Ocelli twice corresponding body diameter from anterior end. Fovea in male 9–10.5 μm; in female 7–7.5 μm. Gubernaculum without crura.

Type.—Syntypes: 10 ♀, 10 ♂.

Type-locality.—Manora Island, Karachi, Arabian Sea.

Type-habitat.—Algae growing on rocks.

Discussion.—I was not able to study this material, which is deposited at the slide collection of the Pakistan Zoological Survey, Karachi. According to the description, this species resembles *L. euxinus,* but differs by the greater amphidial diameter in the male, the greater length of the cephalic setae and the absence of crura on the gubernaculum. In my opinion this is a good species.

Leptosomatides species A

Material.—Three females from the Atlantic Ocean SW of Nova Scotia. Two of them (76074 and 76075) collected at 43°40′N, 66°07′W on 10 Aug 1963 in 60 m, one female (76076), collected at 40°21′N, 67°48′W on 8 Aug 1963. These specimens are deposited in the collection of the USNM, Smithsonian Institution, Washington, D.C., U.S.A.

Description.—For general body proportions refer to the Appendix. Cephalic sensilla papilliform; 3–4 μm. Cephalic capsule 11–13 μm. Diameter fovea 7 μm, lens 10 μm. Lateral vulvar glands 3–4. Intracuticular granula numerous. Male unknown. No figures are given since the only features in which it was found to differ from *L. arcticus* are the lens diameter and the number of vulvar glands. These specimens are not named specifically as no males are present.

Key to the Species of *Leptosomatides*

1.	Length of cephalic sensilla twice their basal width (setiform)	2
–	Length of cephalic sensilla less than twice basal width (papilliform) ...	4
2.	Ocelli 1.5 corresponding body diameters; setae 4 μm	*L. antarcticus*
–	Ocelli 2 corresponding body diameters	3
3.	Setae 6 μm. Fovea in male 10 μm	*L. reductus*
–	Setae 4–5 μm. Fovea in male 6 μm	*L. euxinus*
4.	Intracuticular vulva granula present	5
–	Intracuticular vulva granula absent	*L. filiformis*
5.	Lateral vulvar glands 5–7 on each side	*L. arcticus*
–	Lateral vulvar glands 2–4 on each side	6
6.	Lens diameter 10 μm	*L.* sp. A
–	Lens diameter 8 μm or less	7

7. Lens diameter 6 μm, crura absent, precloacal papilla without alae .... *L. grebnickii*
– Lens 8 μm, crura present, precloacal papilla with alae .... *L. marinae*

Status of Nominal Species of *Leptosomatides*

Species	Present status[1]
Leptosomatides acutipapillosus Platonova, 1976	Synonym of *L. marinae*
L. antarcticus Mawson, 1956	Good species
L. brevisetosus Platonova, 1976	Synonym of *L. marinae*
L. caucasiensis Sergeeva, 1973	Synonym of *L. euxinus*
L. conisetosus Sch. Stekh. & Mawson, 1955	To *Deontostoma*
L. crassus Platonova, 1967	Synonym of *L. grebnickii*
L. euxinus Filipjev, 1918	Good species
L. inocellatus Platonova, 1967	Species *incertae sedis*
L. marinae Platonova, 1976	Good species
L. microlaimus (Allgén, 1957) Platonova, 1976	*Species inquirenda*
L. reductus Timm, 1959	Good species
L. steineri Filipjev, 1922	Synonym of *L. arcticus*
L. steineri sensu Filipjev, 1946	Synonym of *L. grebnickii*
L. steineri Subsp. *filiformis* Filipjev, 1946	*L. filiformis, species inquirenda*
Leptosomatum arcticum Filipjev, 1916	*Leptosomatides arcticus*
L. elongatum sensu Platonova, 1967	Synonym of *L. grebnickii*
L. grebnickii Filipjev, 1916	*Leptosomatides grebnickii*
L. tetrophthalmum sensu Platonova, 1967	Synonym of *L. arcticus*

[1] The indication "good species" does not mean that these species are sufficiently described; more information, regarding all species is desired.

General Discussion

As far as can be determined, the genus *Leptosomatides* forms a group that includes all species with the combination of characters given in the generic diagnosis. This genus is regarded as related to *Deontostoma.* The only distinguishing characters are the reduction of the cephalic capsule and absence of onchia and/or odontia in *Leptosomatides.* More information regarding all species is needed; especially males of some species are not known. Special attention should be given to the structure of the spiculum, gubernaculum, and cloacal papillae in the male, and the intracuticular vulvar granula, lateral glands, ovejector, and sensilla in the vulvar area of the female.

Until now, the genus *Leptosomatides* has been placed in the Leptosomatinae Filipjev, 1916. In fact the only argument for this placement is the presence of a reduced cephalic capsule. *Leptosomatides* differs from the Leptosomatinae sensu stricto (*Leptosomatum* and *Syringonomus typicus* Hope and Murphy, 1969) by the structure of the cephalic capsule, amphids, spiculum, gubernaculum, metanemes, and the presence of vulva granula, ovejector, lateral vulvar glands, median precloacal papilla, and subventral cloacal papillae. The typical sexual dimorphism in the amphids of the Leptosomatinae is absent in *Leptosomatides.* Therefore, *Leptosomatides* must be removed to the Thoracostomatinae and the diagnosis of the latter emended. The genus *Paraleptosomatides* probably also belongs to the Thoracostomatinae. In a separate paper attention will be paid to this rearrangement.

Acknowledgments

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I express my gratitude to Dr. W. D. Hope for constructive criticism, discussions and correcting the text, and to Dr. T. A. Platonova for her hospitality and valuable discussions.

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Appendix; Measurements of Species of *Leptosomatides*

Abbreviations: S—Sex, SN—slide number, L—body length, DF—distance to fovea, DRL—distance to right lens, DLL—to left lens, DNR—distance to nerve ring, PL—pharyngeal length, CL—caudal length, CW—cephalic width, OW—body width at level of lens, NW—width at level of nerve ring, PW—width at base of pharynx, MW—maximum width, AW—anal body width and the ratio's of de Man are expressed in a, b, c and V. Dimensions are given in μm.

S	SN	L	DF	DRL	DLL	DNR	PL	CL	CW	OW	NW	PW	MW	AW	a	b	c	V
Leptosomatides arcticus (*Leptosomatum tetrophthalmum* sensu Platonova, 1967)																		
F	5070-2	14,860	25	112	114	485	2531	179	54	114	168	216	279	187	53	5,9	83	67
F	5070-1	15,110	23	116	119	493	2554	181	57	104	–	239	277	185	55	5,9	83	65
Leptosomatides euxinus (*L. caucasiensis* Sergeeva, 1973)																		
M	8097-1	9190	15	110	102	477	1878	73	38	67	107	127	148	92	62	4,9	126	
F	8097-3	9430	17	121	131	469	1944	77	40	68	103	129	156	81	91	6,3	186	53
F	8097-2	12,450	16	125	114	481	1989	67	38	65	107	121	137	87	60	4,9	122	60
Leptosomatides filiformis (*L. steineri* subsp. *filiformis* Filipjev, 1946)																		
F	7010	13,930	21	112	121	526	2305	–	57	108	135	137	160	–	87	6,0	–	62
Leptosomatides grebnickii (*Leptosomatum elongatum* sensu Platonova, 1967)																		
F	5761	13,370	28	110	112	575	2734	178	52	95	132	170	204	152	66	4,9	75	65
Leptosomatides marinae (males as *L. brevisetosus* Platonova, 1976)																		
F	7909-2	13,790	16	85	89	409	2350	144	41	77	111	141	177	121	78	5,9	96	67
F	7909-3	13,860	22	89	92	409	2305	131	47	76	116	146	202	119	69	6,0	106	66
F	7909-1	14,280	17	83	81	411	2509	139	49	80	112	143	185	133	77	5,7	103	65
M	6133-3	17,950	32	121	116	617	3661	112	37	91	154	218	281	150	64	4,9	160	
M	6133-1	18,810	27	135	139	658	3277	121	52	98	160	196	260	152	72	5,7	155	
M	6133-2	19,740	29	123	125	682	3864	112	49	93	162	227	270	187	73	5,1	176	
Leptosomatides sp. A.																		
F	76074	10,650	33	96	100	460	2441	135	45	64	106	114	135	100	79	4,4	79	69
F	76075	11,290	29	96	108	485	2554	139	47	67	102	139	177	106	64	4,4	81	68
F	76076	11,410	32	98	112	486	2418	129	52	77	116	125	185	123	62	4,7	88	65

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REDISCOVERY AND REDESCRIPTION OF *CIROLANA OBTRUNCATA* RICHARDSON, 1901 (PERACARIDA: ISOPODA: CIROLANIDAE) FROM THE EAST COAST OF MEXICO

Joel W. Martin and Darryl L. Felder

Abstract.—The cirolanid isopod *Cirolana obtruncata* is reported and described from near Chompoton, Mexico. The single male collected is the third existing specimen; this report extends the known range of the species westward from Jamaica to Chompoton, Mexico. The slightly abnormal specimen is compared to earlier descriptions of the same species.

In 1901, Richardson described a new species of the isopod genus *Cirolana, C. obtruncata,* from a single specimen collected from shallow waters off Kingston, Jamaica. An additional specimen was reported on the following year by H. F. Moore; that specimen was collected at Fajardo, Puerto Rico (Moore 1902). Since that time no other collections have yielded any additional material. In her 1905 monograph on the isopods of North America, Richardson mentioned a third specimen in the U.S. National Museum of Natural History; however, this specimen lacked locality data.

In an ongoing study of the isopod fauna of the east coast of Mexico, one of us (DLF) collected a single male *Cirolana obtruncata* from a site approximately 16 km northeast of Chompoton, Mexico. The specimen measures 10.4 mm length by 4.6 mm width, and is therefore slightly larger than Moore's specimen (6 × 2.9 mm). Richardson's two specimens were not measured. Our specimen agrees closely with the original description of *C. obtruncata* by Richardson (1901, 1905) but not with that given by Moore (1902). Some useful morphological characters were not described by Richardson or Moore; below we describe our specimen of *C. obtruncata* from Mexico and comment on discrepancies between our specimen and the descriptions of Richardson (1901, 1905) and Moore (1902).

Cirolana obtruncata Richardson, 1901
Figs. 1–2

Cirolana obtruncata Richardson, 1901:514.—Moore, 1902:167, pl. 8, figs. 9–12.—Richardson, 1905:108–109, figs. 87–89.

Material examined.—USNM 23901, Kingston, Jamaica (Holotype); USNM 204419, Chompoton, Mexico (present study, male, 10.4 × 4.6 mm), coll. D. Felder and USL Tropical Field Expedition II-B, Univ. Southwestern Louisiana, 7 January 1978. From less than 1 m in *Thalassia* beds approximately 16 km northeast of Chompoton, State of Campeche, Mexico.

Distribution.—Previously known from Kingston, Jamaica (Richardson 1901). Our specimen extends the range westward into the southwestern Gulf of Mexico.

Description.—The following description is based upon our single male. Setal or

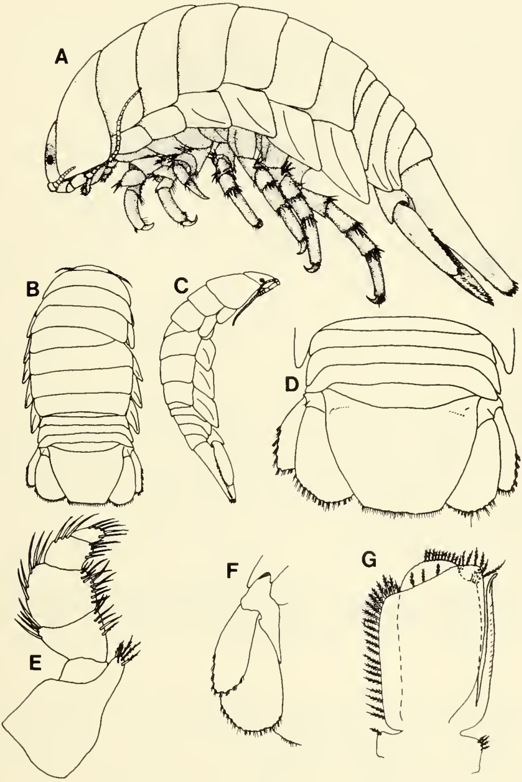

Fig. 1. *Cirolana obtruncata,* male, 10.4 × 4.6 mm. A, Lateral view; B, Dorsal view; C, Lateral view of right (abnormal) side; D, Pleotelson; E, Maxilliped; F, Uropods, ventral view; G, Pleopod 2.

segmental counts which differ in the descriptions by Richardson (1901, 1905) and Moore (1902) are set apart from our observations by brackets [ ] and parentheses ( ) respectively.

Body (Fig. 1A–D) approximately 2.3 times longer than wide, slightly abnormal; fourth pereonite on right side extending anteriorly beneath third pereonite, not reaching lateral right border (Figs. 1B, C). Coxae of pereonites as shown (Fig. 1A) with oblique groove stronger on coxae of pereonites 3–7. Cephalon transversely oval, with slight anterior medial projection between first antennae and frontal lamina. Frontal lamina (Fig. 2D) diamond-shaped; clypeus narrowly rhomboidal;

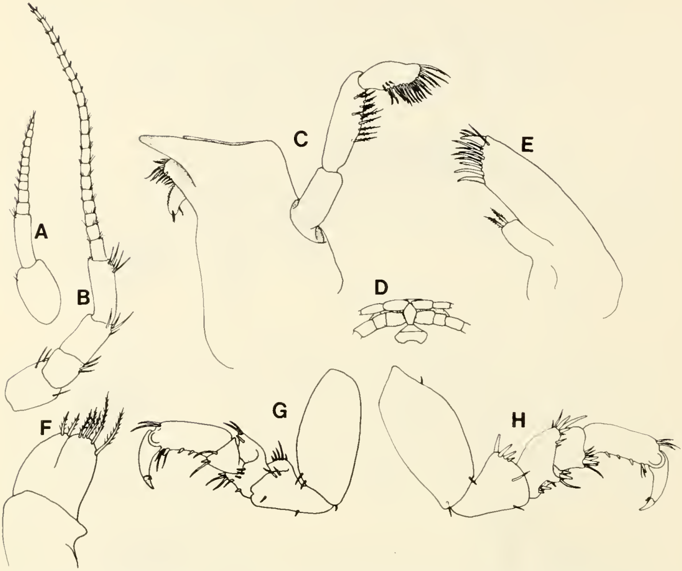

Fig. 2. *Cirolana obtruncata.* A, First antenna; B, Second antenna (proximal segment of peduncle not shown); C, Left mandible; D, Frontal lamina, clypeus, and labrum with bases of antennae; E, Maxilla 2; F, Maxilla 1; G, Pereopod I; H, Pereopod 3.

labrum wide with shallow medial posterior indentation. Eyes small, lateral. First antennae (Fig. 2A) short, extending posteriorly just beyond posterior margin of cephalon; peduncle 2-segmented, flagellum with 11 [12] (8) segments. Second antennae (Fig. 2B) extending to midlength of third thoracic segment; peduncle 5-segmented (only 4 segments illustrated), flagellum with 20 [21] segments. Left mandible (Fig. 2C) tricuspidate; molar process narrow, directed posteriorly, with 2 terminal setae and an anterior row of rounded denticles; lacinia wide, with 10–12 serrate spines and plumose setae. Mandibular palp (Fig. 2C) 3-segmented; setation 0, 12, 19. Maxilla 1 (Fig. 2F) narrow; exopod with 12–13 serrate apical spines; endopod with 2 plumose setae. Maxilla 2 (Fig. 2E) poorly developed; exopod with 5, endopod with 2 plumose setae. Maxilliped (Fig. 1E) broad; endite with 5 lightly plumose setae and no coupling hooks; palp 5-segmented, setation 10, 16, 8, 5.

Pereopods (Figs. 2G, H) stout; distal border of all segments armed with thick blunt spines and setae as shown (only 1 and 3 illustrated).

Pleopod 1 (not illustrated) endopod broadly truncated distally with 10 plumose setae on distal margin, otherwise unarmed; exopod rounded distally, bordered with 59 lightly plumose setae, with complete transverse suture more obvious toward lateral and medial borders. Exopods of pleopods 3–5 (not illustrated) larger than endopods, with complete transverse suture; exopods 3–5 bordered with 50–60 setae, endopods of pleopods 3, 4, and 5 bordered with 10, 11, and 0 plumose setae, respectively.

Pleopod 2 (Fig. 1G) with appendix masculina arising basally, extending to distal edge of endopod; endopod with many medial plumose setae and scattered setae on slightly convex and slanting distal margin; exopod minutely crenulate distally, with slight curved notch on ventromedial corner.

Uropods (Figs. 1D, F) extending to distal telson margin; posterolateral and posterior borders crenulate with short setae arising from small emarginations. Outer branch narrower, distal portion not as rounded as inner branch. Telson (Fig. 1D) posteriorly truncate, with shallow medial depression on posterior surface; weak row of tubercles on anterolateral dorsal surface. Posterior margin minutely crenulate, fringed with short setae.

Color.—Pale tan in alcohol (chromatophores not apparent), brown according to Richardson (1905).

Remarks.—Our description differs from that of Moore (1902) and Richardson (1901, 1905) as indicated above, and in the following characters. Richardson's (1905) illustration of the second maxilla shows a more complex structure, with what appears to be a 2-segmented exopod. Unfortunately, Richardson did not describe the mouthparts other than illustrating them, and Moore (1902) stated that the mouthparts are "as usual in the genus." Moore also described small spines in addition to the setae on the margins of the uropods and telson; the spines were not observed in our specimen. The telson in our specimen appears more truncate than in Richardson's or Moore's illustration. Moore's figure of the first pereopod does not show the strong ventral spination evident in our illustration (Fig. 2G). However, overall similarities between our specimen and the holotype convince us that these discrepancies are insufficient to question the specific status of our single male specimen.

There is reason to question the identity of the species described by Moore (1902). In the type-specimen, our single male, and Richardson's (1905) specimen from an unknown locality, the telson lacks spines and the telsonal setae are numerous and closely spaced. In contrast, the specimen described by Moore is much smaller, and the posterior margin of the telson is armed with small spines separated by groups of short setae (T. E. Bowman, National Museum of Natural History, Washington, D.C., personal communication). It is very likely that the Puerto Rican specimen is not *Cirolana obtruncata,* but an undescribed species. Thus, our specimen represents only the third collection of *Cirolana obtruncata.*

It should also be noted that in the description of the genus *Cirolana* restricted by Bruce (1981), one character of the genus is the presence of spines and setae on the margin of the telson and uropodal rami. The fact that this character is lacking in *C. obtruncata* may necessitate generic reassignment.

The isopod fauna of the east coast of Mexico is poorly known. Reports of the genus *Cirolana* from the east coast of Mexico are restricted to those of Richardson (1905), Dexter (1976), and Bruce and Bowman (1982) for *C. parva* Hansen, 1890. In addition, we have collected *Cirolana diminuta* Menzies, 1962, from Laguna de Terminos, Mexico and from near Chompoton, Mexico. Several workers (e.g., Menzies and Frankenberg 1966) have listed *Cirolana mayana* Ives, 1891 from Mexico. However, this species was transferred to the genus *Excirolana* by Richardson (1912), although this transfer has been largely overlooked in the literature. *Cirolana obtruncata* is easily distinguished from both *C. parva* and *C. diminuta* in having a truncate telson, diamond-shaped frontal lamina, and a distally twisted appendix masculina.

Our Mexican specimen of *C. obtruncata* is only the third one discovered and extends the known range of this species westward from Jamaica to waters off the State of Campeche, Mexico.

Acknowledgments

We thank Beverly S. Williams for help in the field and in sorting through the University of Southwestern Louisiana Museum collections, and T. E. Bowman for constructive criticism of the manuscript. This study was partly funded by a grant from the USL Graduate Student Organization and the USL Foundation.

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ON SOME BRANCHIOBDELLIDS (ANNELIDA: CLITELLATA) FROM MEXICO WITH THE DESCRIPTION OF NEW SPECIES OF THE GENERA *CAMBARINCOLA* AND *OEDIPODRILUS*

Perry C. Holt

Abstract.—A new species, *Cambarincola speocirolanae,* is described from an isopod host inhabiting a cave-like pit in San Luis Potosi, and *Oedipodrilus cuetzalanae* is described from a cambarid host in Puebla as the first member of its genus to be known from Mexico, likewise from a cave-like pit. New localities for *Sathodrilus villalobosi* Holt, 1968, are recorded from Hidalgo and Puebla.

Through the kindness of Dr. Horton H. Hobbs, Jr., I recently acquired some specimens of branchiobdellid worms from Mexico. Many were too decomposed to allow any positive identifications or adequate descriptions, but some can be recognized as specimens of *Sathodrilus villalobosi* Holt, 1968, and of new species of *Cambarincola* Ellis, 1912, and *Oedipodrilus* Holt, 1967. Since the Mexican branchiobdellid fauna is poorly known and these animals are mostly from caves or sinkhole-like habitats and one is from a non-astacoidean host, the new locality records and species descriptions are presented here.

The scanty literature pertaining to Mexican and Central American branchiobdellids was reviewed by Holt (1973a) in a paper in which he recorded fourteen species of the genera *Bdellodrilus* Moore, 1895, *Cambarincola* and *Sathodrilus.* With the addition described below, there are 46 nominal species of *Cambarincola* inhabiting all the major portions of the North American continent, eleven of which occur in Mexico. Fifteen species of the likewise wide ranging genus *Sathodrilus* have been named and described, two of which are Mexican. The species described below is the first of the genus *Oedipodrilus* (two are known from the southern Appalachians) to be recorded from Mexico.

Cambarincola speocirolanae, new species, is the second branchiobdellid to be associated with *Speocirolana pelaezi* (Bolivar y Pieltain, 1950). The quite dissimilar *C. acudentatus* Holt, 1973a, infests this isopod (Holt 1973a:12) or its congener *S. bolivari* (Rioja, 1953). The new localities recorded below for *Sathodrilus villalobosi* include caves or cave-like sinkholes.

Three points from the above may be noted: *Oedipodrilus cuetzalanae* strengthens by its presence in Mexico the opinion that the Mexican branchiobdellid fauna is not distinct from that of more northern regions (Holt 1973a:7); at the limits of their range, branchiobdellids are more likely to be found on non-astacoidean hosts, a point which may have relevance for the question of the origin of the branchiobdellid-astacoidean symbiosis; the occurrence of *S. villalobosi* in Mexican caves is consonant with Holt's (1973b:219) view that most branchiobdellids found in caves are members of epigean species.

The holotypes are deposited in the collections of the National Museum of

Natural History (USNM); the remaining material (identified by the initials "PCH") is kept in my collections in Blacksburg.

My thanks are extended to Dr. Hobbs for making this material available to me and for reading the manuscript.

Cambarincola speocirolanae, new species
Fig. 1

Type-specimens.—Holotype, USNM 80221, and one paratype, PCH 4054, taken on *Speocirolana palaezi* from Sótano del Arroyo, San Luis Potosí, by Peter Sprouse, 22 Feb 1980.

Diagnosis.—Medium-sized worms (holotype 3.2 mm in length), lips entire; no oral papillae; no dorsal ridges; jaws subequal in size, dental formula 5/4; bursa subspherical, about ⅜ body diameter in length, without atrial fold; penis muscular, blunt; spermiducal gland reflexed, subequal to bursa in length, no deferent lobes; prostate large, subequal to spermiducal gland in length and diameter, densely granular, nondifferentiated, no ental bulb; spermatheca with long, slender ectal duct.

Etymology.—For the host isopod.

Description.—The holotype has the following dimensions: total length, 3.2 mm; greatest diameter, 0.6 mm; head length, 0.7 mm; head diameter, 0.4 mm; diameter, segment I, 0.4 mm; diameter, sucker, 0.3 mm. The paratype is of similar size, and in size and body proportions, *C. speocirolanae* is typical of members of the genus.

The lips appear to be without lobes, though this is not easily determined, since both types, mounted entire, can only be viewed in lateral aspect. There are no oral papillae. The head bears one shallow external sulcus other than the prominent peristomial one; there is one internal pharyngeal sulcus. There are no obvious dorsal ridges; the supernumerary muscles are absent, but thin slips of the longitudinal segmental muscles insert on the inner edge of the sulcus that delimits the posterior, minor annuli of the anterior segments.

The jaws are subequal in size. The dental formula is 5/4, the teeth are sharp and distinct.

The spermiducal gland is proportionately small, bent in a broad u-shape alongside the gut. The prostate is larger than the spermiducal gland, lacks an ental bulb and is composed of densely granular cells, rather than the vacuolated ones of species described as having a differentiated prostate.

The ejaculatory duct is difficult to see in the type-specimens, but apparently is in no wise unusual.

The bursa, subspherical in shape, lacks an atrial fold or an externally delimited penial sheath region. The retracted penis is densely muscular, short and blunt: clearly of the type referred to as protusible.

The male reproductive system as a whole is rather small, extending dorsad hardly beyond the mid-point of its segment's diameter and in the slightly differently orientated paratype seeming to lie entirely underneath the gut.

The spermatheca has a long, slender ectal duct, but the bulb is totally obscured by gut contents in both specimens.

Variations.—The paratype is more fully extended than the holotype and as

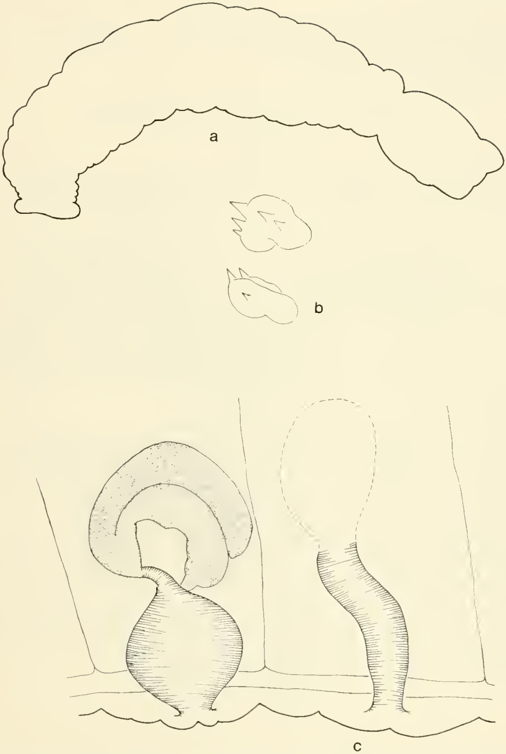

Fig. 1. *Cambarincola speocirolanae,* new species; holotype. a, Outline of entire animal; b, Jaws; c, Lateral view of reproductive systems.

noted the male efferent apparatus appears to lie beneath instead of alongside the gut.

Affinities.—Cambarincola speocirolanae has *C. jamapaensis* Holt, 1973a, as its closest relative. The latter is somewhat smaller, approximately 2.0 mm instead of 3.0 mm in length, and has lobed instead of entire lips, jaws with less prominent teeth, dorsal ridges produced by prominent supernumerary muscles, a straight instead of a reflexed spermiducal gland and a smaller prostate with an ental bulb. Although only two mature specimens of each species are known, the prostatic ental bulb and dorsal ridges of *C. jamapaensis* effectively separate them.

Host.—*Speocirolana palaezi.*

Distribution.—Known only from the type-locality. A *sótano* is a "word applied to a vertical shaft" (Reddell 1981:4).

Material examined.—The types.

Oedipodrilus cuetzalanae, new species

Figs. 2, 3b

Type-specimens.—Holotype, USNM 80223, and eight paratypes, PCH 4050, taken on *Procambarus* (*Villalobosus*) *cuetzalanae* Hobbs from Sima Zoquiapan, 1.1 km north of Cuetzalan, Puebla, by L. Wilk, J. Hooper and M. Minton, 2 Jan 1980.

Diagnosis.—Small worms (holotype 1.6 mm in length); lips entire; no oral papillae; no dorsal ridges; jaws slight, delicate, dental formula 5/4; bursa, including penial sheath, slightly greater than body diameter in length, with atrial fold; penis eversible tube furnished with hooks; spermiducal gland small, less than ½ body diameter in length; prostate obscure ental protuberance of spermiducal gland; spermatheca greater than body diameter in length, with long ectal duct, cylindrical bulb, no ental process.

Etymology.—Of Cuetzalan, a town in Puebla.

Description.—*Oedipodrilus cuetzalanae* is composed of small worms. The holotype and four paratypes have the following average dimensions: total length, 1.6 mm; greatest diameter, 0.4 mm; head length, 0.3 mm; head diameter, 0.2 mm; diameter segment I, 0.2 mm; diameter, sucker, 0.2 mm.

The lips apppar to be without lobes or indentations, but the upper and lower lips are separated by wide indentations on each side that produce low lateral lobes. No oral papillae are apparent. The peristomial sulcus is prominent; there is one other shallow external sulcus of the head and one internal pharyngeal sulcus. There are no dorsal ridges or supernumerary segmental muscles, though because of variations in the extent of contraction, segment VIII sometimes appears to have a dorsal ridge. The clitellum is inconspicuous.

The jaws are thin and delicate; the upper bears five small sharp teeth, the lower four.

The bursa is marked externally by two shallow constrictions; one setting off the bursal atrium, the other at the mid-length of the penial sheath. The atrium is proportionately small and there is an atrial fold. The penial sheath is an elongate, thin-walled structure with the penis loosely looped inside. A slender tube, the penis is provided with numerous hooks along its ectal portion, from about the external constriction of the penial sheath, and acquires a thicker wall along the more numerous loops of its ental portion. The penis is connected with the inner wall of the penial sheath by strands of tissue at the juncture of its outer and inner portions. There can be no doubt that it is eversible to at least this connection with the penial sheath (though no specimens with everted penes have been seen), carrying the many cuticular hooks which come to lie outside as it everts.

The ejaculatory duct is a short muscular tube.

The spermiducal gland is small, about ⅖ of the body diameter in length. The prostatic protuberance is an ill-defined, minute lobe at the ental end of the spermiducal gland that is not histologically different from the latter.

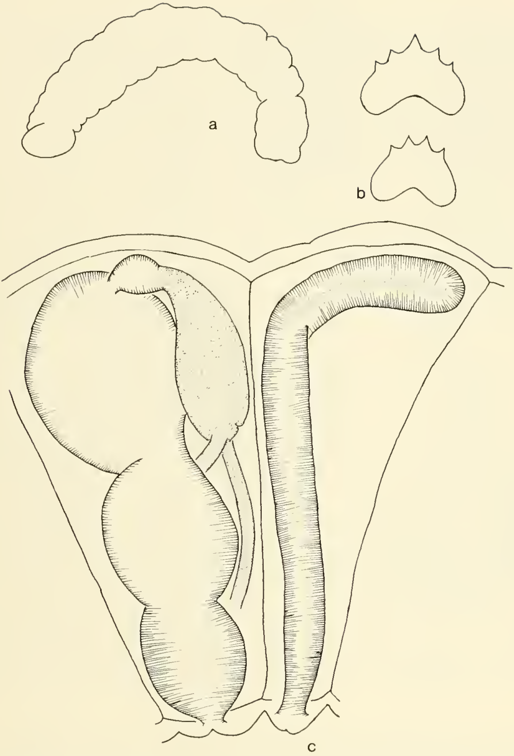

Fig. 2. *Oedipodrilus cuetzalanae,* new species; holotype. a, Outline of entire animal; b, Jaws; c, Lateral view of reproductive systems.

The spermatheca is notable for its long, slender ectal duct. The spermathecal bulb is thick-walled, resembling in this respect, the ental process of the spermatheca of some species.

Variations.—None, other than the usual ones produced by differences in contraction of the body at death, were noted.

Affinities.—Only two species of *Oedipodrilus, O. oedipus* Holt, 1967, and *O. macbaini* (Holt, 1955), have been described as of now. *Oedipodrilus cuetzalanae* is composed of slightly larger worms than its congeners: 1.6 mm in length as opposed to 1.3 mm and 1.2 mm respectively. *Oedipodrilus oedipus* has distinct,

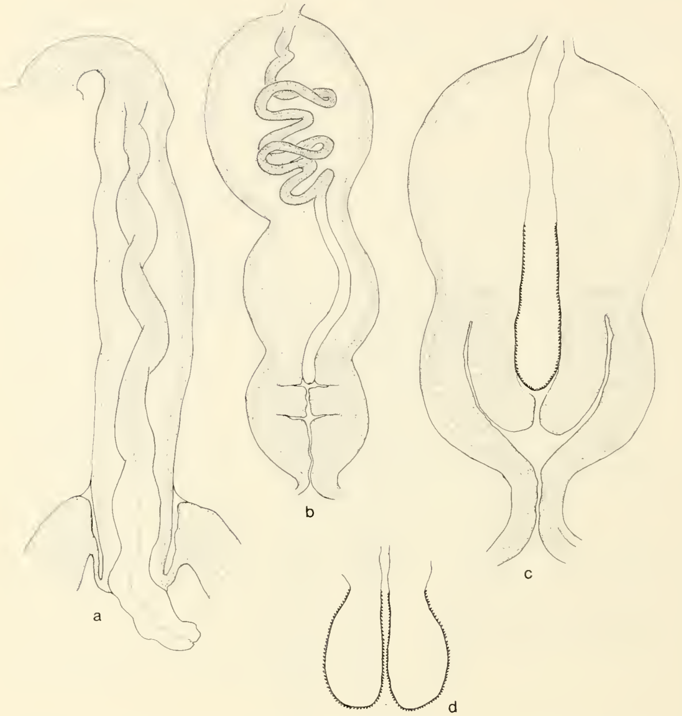

Fig. 3. Optical sections through penes of some branchiobdellid worms. a, *Sathodrilus villalobosi,* specimen from Sima Zoquiapan, Cuetzalan, Puebla; b, *Oedipodrilus cuetzalanae,* holotype; c, *Oedipodrilus oedipus,* paratype; d, *O. oedipus,* tip of partially everted penis, paratype.

well marked, dorsal ridges, absent in *O. macbaini* and *O. cuetzalanae.* The bursae, including penial sheaths, are more robust in the other species than in *O. cuetzalanae.* The prostate is small and obscure in all three species, but so much so in *O. cuetzalanae* that its very existence was almost overlooked—in the limited and only moderately well preserved material available, it would not have been noticed except that its presence in the other species occasioned a very careful search. The ectal duct of the spermatheca of *O. cuetzalanae* is longer and much more slender than in *O. oedipus*; the spermatheca is more slender in its entirety than in *O. macbaini.* The three known species of the genus form a coherent group and it is futile at this stage to speculate about which is more closely related to the other.

Host.—Procambarus (*Villalobosus*) *cuetzalanae* Hobbs.

Distribution.—Known only from the type-locality, which is a *sima* ". . . a vertical or nearly vertical pit" (Reddell 1981:4), hence a cave or cave-like sinkhole. It may be noted that the epigean *O. macbaini* is also found in caves (Holt 1973b).

Material examined.—Twenty-one specimens.

Remarks.—The comments in Holt (1967:58–60) as to the affinities of the genus *Oedipodrilus* still hold. But at that time some specimens later assigned to *Sathodrilus* were confused with *Oedipodrilus*, which is not known from Veracruz or the Pacific Northwest of the United States. The confusion resulted from a misunderstanding of the structure of the penis.

The penis of species of *Oedipodrilus* is a chitinoid tube, clearly eversible, provided with many small recurved hooks, which may vary from species to species in proportionate length and diameter (Fig. 3b–c), while that of *Sathodrilus* lacks hooks, is attached by thin strands of tissue to the inner wall of the penial sheath throughout the extent of the latter and everts as a wider, membranous tube similar to that of species of *Ceratodrilus* (Holt, 1960:69–70, 75, Fig. 7).

Sathodrilus villalobosi Holt, 1968
Fig. 3a

Sathodrilus villalobosi Holt, 1968:299–302; 1973a:36–38; 1977:119.

Nothing new can be added to the previous accounts of *S. villalobosi* except the drawing (Fig. 3a) of an optical section of the penial sheath and penis which complements that given with the original description (Holt 1968:300, Fig. 3) and the following locality records which mostly are from caves or cave-like pits.

New locality records.—Sima Zoquiapan, 1.1 km north of Cuetzalan, Puebla. Twenty-three specimens taken on *Procambarus* (*Villalobosus*) *cuetzalanae* Hobbs, 1982, by L. Wilk, J. Hooper and M. Minton 2 Jan 1980. PCH 4050.

Cueva de Guayateno, Jonotla, Puebla. Two specimens (host *P.* (*V.*) *cuetzalanae*) taken by S. Robertson, 27 Dec 1980. PCH 4057, 4063.

Sumidero de Tzitzihualayoll, Cuetzalan, Puebla. One specimen (host *P.* (*V.*) *cuetzalanae*) taken by J. Reddell *et al.*, 26 Mar 1981. PCH 4060.

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DENDROGASTER ARGENTINENSIS, NEW SPECIES, A SOUTH AMERICAN SEA-STAR PARASITE (CRUSTACEA: ASCOTHORACIDA)

Mark J. Grygier and Mariana B. Salvat

Abstract.—Dendrogaster argentinensis is a coelomic parasite of the subantarctic sea-star *Anasterias minuta* Perrier at Puerto Deseado, Argentina. Mature and juvenile females, and males, are described. This species resembles *D. fisheri* Grygier and *D. arctica* Korschelt from the northern Pacific Ocean, but is distinguished by the extreme reduction of the antennular claw guard in females. Presence of the parasite sometimes is obviously detrimental to the host. *Dendrogaster argentinensis* is the first ascothoracid described from the South American coast.

Resumen.—Dendrogaster argentinensis es un parásito de la cavidad celómica de la estrella de mar subantártica *Anasterias minuta* Perrier en Puerto Deseado, Argentina. Se describen hembras juveniles y maduras, y también machos. Esta especie es semejante a *D. fisheri* Grygier y a *D. arctica* Korschelt, ambas del Pacífico Norte, pero se distingue de ellas por la extrema reducción del proceso guardián de la uña antenular en las hembras. La presencia del parásito es a veces obviamente perjudicial para el huésped. *Dendrogaster argentinensis* es el primar ascotorácido citado para las costas de América del Sur.

The Ascothoracida are crustacean parasites of echinoderms and coelenterates, the most recent review being Wagin's (1976) monograph. The genus *Dendrogaster* Knipowitsch, the most specialized in the subclass, are endoparasites of sea-stars (Asteroidea). They have replaced most of the structure and function of their segmented body with a greatly enlarged and elaborated, branched carapace or mantle (Wagin 1954). About 20 species of *Dendrogaster* were described or reviewed by Wagin (1950, 1976), and Grygier (1981, 1982) added three more species.

Few ascothoracids are known from the South Atlantic. *Waginella sandersi* (Newman) was collected on the bottom (5200 m) at 43°33.0′S, 48°58.1′W (Newman 1974, Grygier 1983a). *Ascothorax bulbosus* Heegaard, which infests two species of the ophiuroid *Amphiura* at 110–175 m near South Georgia (Heegaard 1951), actually represents two species (Grygier 1983b). *Ascothorax gigas* Wagin parasitizes *Ophionotus victoriae* Bell along the Antarctic Peninsula and in the South Sandwich Islands (Wagin 1968, Grygier and Fratt 1984). An undescribed species of *Ascothorax* lives in *Ophiurolepis inornata* (Lyman) at 800 m off the Patagonian shelf (Bartsch 1982, Grygier 1983b). *Dendrogaster* has been recorded twice in the South Atlantic. Le Roi (1905, 1907) described *D. arborescens* from *Dipsacaster sladeni* Alcock off Cape Town, and Fisher (1940) noted *Diplasterias meridionalis* (Perrier) from 27 m at South Georgia infested with as yet unstudied *Dendrogaster* specimens.

This report is the description of the first ascothoracid from the shores of the South American continent, a new species of *Dendrogaster* parasitic in the asteroid *Anasterias minuta* Perrier. This is a middle-sized, brooding, asteriid sea-star that inhabits rocky shores (0–80 m) in subantarctic waters: southern Argentina in Santa

Cruz province and Tierra del Fuego, southern Chile, and the Falkland Islands (Islas Malvinas) (Bernasconi 1964). The *Dendrogaster* specimens were discovered by one of us (Salvat, thesis in prep.) during a study of seasonal changes in the gonads of a population of *A. minuta* at Puerto Deseado, Santa Cruz province.

Dendrogaster argentinensis, new species

Figs. 1–12

Diagnosis.—Females: Middle piece and main branches short; 4 approximately equal primary branches usually with short, alternate, lobular side branches. Antennular claw guard vestigial, its 3 setae arising directly from article; usually 1 seta proximal to these; no fusion seam on third article. Males: Strap-like testes in long, tubular, posterior protrusions. Anterodorsal spines on third antennular article with comb-rows of teeth; no fusion seam. Short aesthetasc on fourth article; 1 seta at base of claw. Furcal rami with 4 mediobasal setae.

Etymology.—Named for country of origin.

Methods and materials.—Three hundred and twenty-six specimens of *A. minuta,* collected by I. Zizich in 1973 and by H. Bello and I. Zizich in 1979 at Puerto Deseado, Argentina (47°45′S, 65°55′W), were examined for *Dendrogaster* parasites. Five infested sea-stars were found (infestation rate 1.5%). Parts of some specimens were embedded in paraffin for histological examination, the results of which are not discussed here. Antennules and mouthparts of 2 females were mounted in glycerine jelly, and a male was examined whole in lactic acid.

Holotype and 2 paratypes deposited in Museo Argentino de Ciencias Naturales, Buenos Aires (Cat. nos. 31708–10), other paratype (4, below) in National Museum of Natural History, Washington, D.C. (USNM 195246).

1) *Holotype,* mature ♀ brooding eggs, with 2 ♂♂ (♀ and ♂♂ ready to molt), coll. 6 Jun 1973; 3 complete primary branches and middle piece in ethanol, fourth primary branch in paraffin with some sections, appendages mounted. It filled an arm of host sea-star, pyloric caeca in that arm almost totally atrophied. 2) *Paratype,* mature ♀ brooding eggs, with ♂, coll. 15 Oct 1973; part in ethanol broken into many pieces, including 2 reasonably complete primary branches and a ♂ posterior protrusion; part in paraffin with some sections. Host was ♂, no data on its condition. 3) Not a type, mature ♀ with ♂, coll. 7 May 1973; parts of ♀ and ♂ in paraffin with some sections, rest of animal lost. It occupied ♀ host's disc. 4) *Paratype,* juvenile ♀, coll. 23 May 1979; complete in ethanol except for mounted appendages. It was tangled in proximal part of pyloric caeca of one arm of ♂ host. 5) *Paratype,* juvenile ♀, coll. 19 Dec 1979; complete in ethanol. Host was ♀, no data on its condition.

Description.—Females. Carapace or mantle consists of short middle piece little longer than wide, short, lateral main branches at base of middle piece, 2 more or less laterally directed primary branches on each side. In juveniles (Figs. 1, 2), middle pieces 1.8 mm and 0.6 mm long, carapace breadth 13.2 mm and 6.0 mm, respectively. Anterior primary branches little longer than posterior ones, 2 rows of bumps on each branch.

Mature females too broken up to measure carapace breadth, but primary branches (Figs. 3, 4) 17.0–22.4 mm long, 2.5–3× longer than larger juvenile. Axis of each branch narrows distally, giving off alternate side branches (in one exceptional case branches occur oppositely (Fig. 3)). Carapace viscera (gut and ovary diverticula), which follow mantle branching, also branch alternately (Fig. 4). Side

Figs. 1–12. *Dendrogaster argentinensis*: 1–7 ♀♀, 8–12 ♂. 1, Juvenile (MACN 31710); 2, Juvenile (USNM 195246); 3, Holotype fragment (MACN 31708), middle piece and one primary branch with unusual opposite side branching; 4, MACN 31709, primary branch with typical alternate branching; 5, Antennule of 2; 6, Antennule of 3; 7, Tip of maxilla of 2; 8, ♂ from mantle cavity of holotype; 9, Main body of 8, cutaway view; 10, Antennule, lateral view; 11, Thoracopod (T2), lateral view; 12, Furcal ramus, lateral view, only bases of some medial setae shown. Abbreviations: a, aesthetasc; b, main branch; g, midgut diverticulum (dashed); m, adductor muscle; mp, middle piece; n, thoracic ganglion; o, oral cone; p, primary branch; s, stomach (midgut); x, maxillary gland. Scale bars in mm.

branches irregular or, more usually, 3-lobed, with comparatively narrow pedicel; proximal ones little larger and more elaborate than distal ones.

Antennules of larger juvenile 0.32 mm long, 4-segmented (Fig. 5). First and second articles broader than long, second one smaller. Third article little narrower than these, longer than wide with oblique distal edge; 2 small, anterodistal spines but no appreciable anterobasal fusion seam (Wagin 1950). Fourth article rhomboidal with distal claw that forms subchela with third article, claw positioned opposite 2 spines. Small seta at anterior base of claw, spine to one side in at least 1 antennule; posterior edge with 1 or 2 small sensilla, posterodistal angle with 3 setae (no claw guard).

In holotype, antennules about 0.41 mm long, 50% wider than in juvenile (Fig. 6). First article comparatively shorter and wider than before, with curved basal edge. Second and third articles unchanged in proportion, spines on latter more setiform than before, with row of setules in 1 antennule. Large apodeme at anterior junction of third and fourth articles. Fourth article has tiny posterior sensillum, seta at anterior base of claw, and 3 posterodistal setae.

In both females, oral cone triangular in cross section; labrum pointed, its rear margins not meeting. Only mouthparts are maxillae (Fig. 7), fused medially for most of length, bifid tips with lightly curved posterior points.

Both mature type-females were brooding subspherical to oval eggs averaging 465×390 μm in holotype, 414×353 μm in paratype (20 from each measured).

Males. Typical for *Dendrogaster,* dwarfs living in female mantle cavity. Bivalved carapace gives rise to pair of long, tubular, posterior processes containing branch of gut and strap-like testes (Fig. 8). Protrusions up to about 16.5 mm long, 0.65 mm wide, cuticle weakly annulated. Main body (Fig. 9) with pair of antennules, oral cone, 6 thoracomeres (last 5 bearing limbs), and 5-segmented abdomen with furca. Limbs and furca bear natatory setae. Anteroventral part of thorax grossly swollen below internal organs to link hypertrophied valves.

Antennules about 0.23 mm long (Fig. 10). First 2 articles short and broad, third article as large as them together. Anterodistal spines on third article very short, with distal-facing row of comb-like teeth; no fusion seam. Fourth article more elliptical than in females; claw sickle-shaped, with short seta at base; distal edge with, progressively closer to claw, a short, strap-like aesthetasc, long seta, and short process (claw guard) with terminal seta and 2 basal setae. Oral cone shorter than antennules, constructed as in females.

Limbs only on thoracomeres 2–6, called T2–6 accordingly (Fig. 11). Each with elongate coxa, shorter oblong basis, biarticulate exopod, triarticulate endopod (biarticulate in T6). T2 and T3 with laterodistal coxal seta, T5 lacking it, T4 impossible to see clearly. Exopod with 4 terminal setae, possibly 3 in T6, endopod with 2. Medial setae, if any, not visible in whole mount. T6 shorter than T2–5.

Thoracomeres progressively less high posteriorly (Fig. 9). In abdomen, fifth segment (telson) longest, third and fourth segments shortest. Furcal rami (Fig. 12) almost square, with 4 long, mediobasal setae, 1 mediodorsal seta, 4 distal setae, second from top as long as medial setae, other 3 less than half as long.

Discussion

Affinities.—Dendrogaster argentinensis differs from all known species of the genus in having a vestigial antennular claw guard in the female, its three setae arising directly from the body of the fourth article. Otherwise, it closely resembles *D. fisheri* Grygier, 1982, which parasitizes *Pedicellaster magister megalabis* Fisher in deep California waters. Both species have a short middle piece and main branches, and two pairs of primary branches with short, alternating side branches that may have a few terminal lobes. However, *D. fisheri* is smaller at maturity (largest specimen only 26 mm across), and the axes of its primary branches are broad, distended by eggs; the branch axes do not get swollen in *D. argentinensis. Dendrogaster fisheri* has a claw guard, and there are two setae posterior to it, not just one. It has a lateral seta at the base of the claw and an isolated distal seta on the third article, both lacking in *D. argentinensis.* Lastly, the third article is wider than long and has a distinct fusion seam in *D. fisheri.* These antennular distinctions must be viewed with caution, because antennular armament can be ontogenetically variable in *Dendrograster* (Karande and Oguro 1981).

Dendrogaster argentinensis also resembles *D. arctica* Korschelt, which lives in *Leptasterias groenlandica* (Lütken) in the Bering Sea, and whose juveniles have four simple primary branches with lobular side branches (Fisher 1930, Wagin 1950). The side branches, however, are not subdivided. The antennular armament illustrated by Wagin (1950) is close to the present specimens, but there is a long, cylindrical claw guard. The male antennule of Wagin's (1950) *D. arctica* is very similar to that of the new species. Both have a short aesthetasc, similar proportions of the articles, and no lateral seta at the base of the claw. However, Wagin draws the two subterminal setae on the claw guard close to the tip, and shows no comb-like array of teeth on the third article's spines. The third article also has an evident fusion seam.

The hosts of *D. argentinensis, D. fisheri,* and *D. arctica* are all members of the Asteriidae, but this is not a strong argument for their close relation. Other asteriids of the genera *Leptasterias, Coscinasterias, Allostichaster,* and *Diplasterias* are infested with *Dendrogaster* species exhibiting a variety of morphologies (Wagin 1976, Inaba 1963, Hickman 1959, Fisher 1940). It is tempting to recognize a species group containing *D. argentinensis, D. fisheri,* and perhaps *D. arctica* on the basis of a mantle with four relatively simple, equal primary branches. But it remains to be shown how and whether the mantle branching pattern in *Dendrogaster* can be used to interpret interspecific relationships.

Host-parasite relations.—Dendrogaster argentinensis seems to have a variable impact on its host. In one case the host's gonads were undeveloped, suggesting parasitic castration, but in the other hosts the gonads were as well developed as other sea-stars from the same samples. Perhaps the questionable host was at an inactive point in its reproductive cycle. The atrophy of the pyloric caeca in the same sea-star is probably due to crowding rather than feeding, because *Dendrogaster* is reported to feed on the coelomocytes that attempt to encapsulate it (Wagin 1976).

Biogeography.—Dendrogaster argentinensis expands the range of its already widespread genus to include South American shores. The lack of ascothoracids from that continent till now is certainly the result of oversight, not of absence. The find of an ascothoracid parasitic on a gorgonian at bathyal depths off Colombia (Grygier 1984), as well as the records listed in the Introduction from the South American sector of the subantarctic, indicate that South America is likely to be a rich source of Ascothoracida.

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THREE NEW SPECIES OF *LENSIA*, AND DESCRIPTION OF THE EUDOXIA STAGES OF *LENSIA RETICULATA* AND *LENSIA LELOUVETEAU* (CALYCOPHORAE: SIPHONOPHORAE)

Angeles Alvariño and Joan Marie Wojtan

Abstract.—Three new species of *Lensia* are described and illustrated: *Lensia eugenioi, L. eltanin,* and *L. landrumae,* their diagnostic characteristics are discussed and compared with those of other closely related species of *Lensia.* The previously unknown eudoxid stages of *Lensia reticulata* Totton, 1954, and *L. lelouveteau* Totton, 1941, are also described and illustrated. The specimens were observed in plankton collections obtained during the U.S. Antarctic Research Program.

Lensia Totton

Diagnosis.—The genus *Lensia* Totton, 1932 includes diphyid Calycophorae in which the anterior nectophores of the polygastric stage are pentagonal in cross section, but may exhibit 3, 5, 7, 15, or more longitudinal ridges, with or without crests or wings. The somatocyst is usually short. The hydroecium is shallow, and is closed by short, divided mouth plates. The radial canals have no commissures. The nectosac reaches to near the top of the nectophore.

The posterior nectophore is known for only a few species. It is truncate at the top, has a rounded mouth plate, and no conspicuous teeth. The lateral radial canals are not looped, but run in an open S course.

Only a few eudoxid stages of *Lensia* have been described.

There are 24 previously described species of the genus *Lensia,* and with the three new ones there will be 27. The known species of *Lensia* are: *Lensia achilles* Totton, 1941; *L. ajax* Totton, 1941; *L. bary* Totton, 1965; *L. campanella* (Moser, 1925); *L. challengeri* Totton, 1954; *L. conoidea* (Kefferstein and Ehlers, 1860); *L. cordata* Totton, 1965; *L. cossack* Totton; 1941; *L. exeter* Totton, 1941; *L. fowleri* (Bigelow, 1911); *L. grimaldii* Leloup, 1933; *L. hardy* Totton, 1941; *L. havock* Totton, 1941; *L. hostile* Totton, 1941; *L. hotspur* Totton, 1941; *L. hunter* Totton, 1941; *L. leloupi* Totton, 1954; *L. lelouveteau* Totton, 1941; *L. meteori* Leloup, 1934; *L. multicristata* (Moser, 1925); *L. reticulata* Totton, 1954; *L. subtilis* (Chun, 1886); *L. subtiloides* (Lens and van Riemsdijk, 1908); *L. tottoni* Daniel and Daniel, 1963. (See Alvariño 1971 for distributions.)

Material.—Collections in which the new species here described were found, were obtained during the *Eltanin* cruises of the U.S. Antarctic Research Program, using plankton nets: BPS (bathypelagic plankton sampler), MPS (multiple plankton sampler), vertical (V) or oblique (OBL) plankton tows (see Tables 1–5).

Lensia eugenioi, new species
Fig. 1

Material.—(See Table 1.) Holotype: 1 superior nectophore and 1 inferior nectophore, *Eltanin* cruise 26, sta. 1785, USNM 61058: paratype, 2 superior nectophores and 2 inferior nectophores, *Eltanin* cruise 26, sta. 1803, USNM 61059.

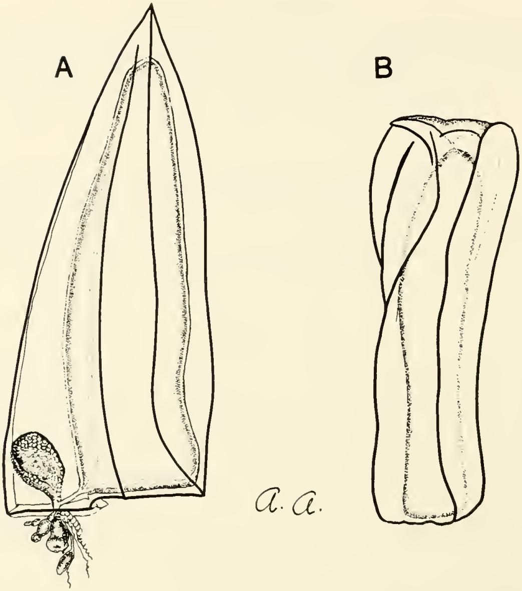

Fig. 1. *Lensia eugenioi*: A, Lateral view of superior nectophore (5 mm long); B, Ventrolateral view of inferior nectophore (4.5 mm long).

Etymology.—Named for Captain Eugenio Leira, the husband of the senior author.

Description.—The length of the superior nectophore is approximately 3 times its width. The nectosac reaches close to the top of the nectophore. There are 5 complete ridges with crests extending from the opening of the nectosac (the ostium), to the top of the nectophore: 2 ventral and 2 lateral (one at each side, corresponding to the dorsoventral), and one dorsal. In addition, 2 other lateral ridges, the ventrolateral, extend from the ostium to near the top of the nectophore, up to the level of the top of the nectosac, but do not reach the top of the bell. These incomplete ventrolateral ridges are similar to those in *L. multicristata,* although in the latter the ridges do not reach either the apex or the marginal base of the nectophore. In *L. eugenioi* they reach to the basical margin of the ostium, but not to the apex. The dorsolateral ridges of *L. eugenioi* bend sharply at the low part near the ostium region, reaching the dorsal edge of the nectophore at this point joining the dorsal ridge.

The hydroecium is very shallow, tapering to the ventral side. Two very small flaps close the opening of the hydroecium at the side of the ostium.

Table 1.—Distribution of *Lensia eugenioi* in the Antarctic-Subantarctic region.

Cruise	Station	Gear/tow	Location	Depth of haul	Date	Local time
26	1785	MPS	39°47′S, 160°30′E	250–100 m	5 Dec 1966	1112–1117
	1790	V	41°58′S, 160°06′E	200–0 m	7 Dec 1966	1351–1412
	1794	BPS	41°58′S, 160°06′E	1000–500 m	7 Dec 1966	1425–1449
	1803	BPS	47°37′S, 161°49′E	1000–500 m	13 Dec 1966	1052–1112

The somatocyst is thick, short, and pear-shaped.

The radial canals extend along the dorsal and ventral edges of the nectosac to join the circular canal, and other branches extend along each of the sides of the nectosac, from the pedicular canal to near the top of the nectosac. These branches probably bend, to run down to reach the circular canal (Fig. 1A).

The inferior nectophore (Fig. 1B) is prismatic, with 5 longitudinal ridges. The region of the hydroecium is closed at the upper part by the flaps extending from the ridges, which cover each other to form the hydroecial tunnel. There are no teeth or prolongations at the ostium region. The lateral radial canals follow a sigmoid course.

Eudoxid phase: Unknown.

Lensia eltanin, new species
Fig. 2

Material.—(See Table 2.) Holotype: 1 superior nectophore, 1 inferior nectophore, *Eltanin* cruise 11, sta. 263, USNM 61060; paratype: 1 superior nectophore and 2 inferior nectophores, *Eltanin* cruise 11, sta. 263 and 308, USNM 61061.

Etymology.—Named for the USNS *Eltanin,* which for many years has surveyed the Antarctic Ocean and adjacent oceanic regions; the present collections were obtained during this vessel's cruises in Antarctic and Subantarctic waters.

Description.—This species also belongs to the group of the previously described species, based on the characteristics of the lateral ridges.

The superior nectophore (Fig. 2A) reaches a length of about 6 to 7 mm, with a maximum width of 3 mm at the ostium. It has 5 complete ridges extending from the tip of the nectophore to the ostium. All the ridges have a narrow crest. The dorsal ridge forms a small tooth at the margin of the ostium, but does not form a marked tooth-like projection, due in part to the crest of the ridge covering that area. The lateral ridges bend sharply to the ventral side and then to the dorsal side at the lowest part of the nectophore, and reach the margin of the nectophore at about midlength of the ostium opening, between the hydroecium and the dorsal ridge.

The nectosac reaches close to the top of the nectophore.

The hydroecium is deeper than in *Lensia conoidea.* The hydroecial cavity is large, reaching to a point slightly higher than the level of the ostium, and wide, as in *L. conoidea.* The hydroecium is slightly shallower than a hemisphere, and is closed at the dorsal side, adjacent to the ostium, by 2 flaps. There is a wide distance from the ventral edge of the nectosac to the ventral edge of the nectophore, as is seen in *L. conoidea.*

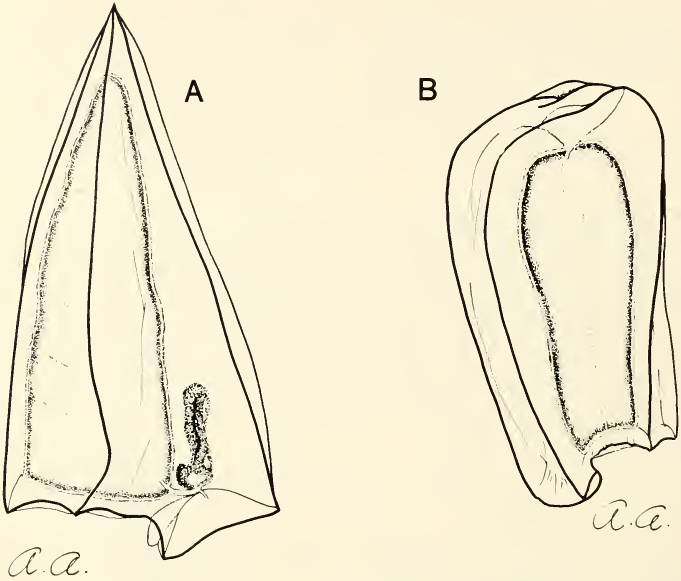

Fig. 2. *Lensia eltanin*: A, Lateral view of superior nectophore (6–7 mm long); B, Lateral view of inferior nectophore (4.7 mm long).

The somatocyst is of medium length, reaching about ⅕ of the total length of the nectophore. The somatocyst is wider at the base, and the branch that goes up is about ½ the width of the basal part of the somatocyst.

The posterior nectophore (Fig. 2B) presents 5 ridges: 2 ventral, 1 dorsal, and 2 lateral. Those forming the hydroecium are wide, wing-like; they bend, closing that area, and extend down to the level of the ostium, where they are connected

Table 2.—Distribution of *Lensia eltanin* in the Antarctic-Subantarctic region.

Cruise	Station	Gear/tow	Location	Depth of haul	Date	Local time
11	257	MPS	60°56′S, 114°43′W	500–250 m	5 Jan 1964	1451–1532
	263	BPS	61°58′S, 115°11′W	1000–500 m	7 Jan 1964	0835–0949
	308	MPS	70°07′S, 102°55′W	500–250 m	20 Jan 1964	2019–2044
	309	BPS	70°07′S, 102°52′W	1000–500 m	20 Jan 1964	2202–2308
	310	OBL	70°25′S, 99°21′W	550–0 m	22 Jan 1964	0332–0435
15	864	BPS	54°00′S, 145°17′W	1000–500 m	18 Nov 1964	~1000
16	900	MPS	51°09′S, 162°00′E	500–250 m	8 Feb 1965	1525–1535

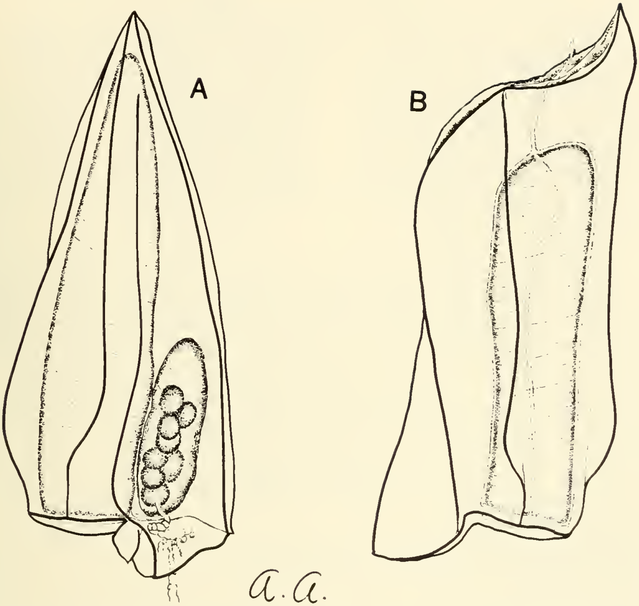

Fig. 3. *Lensia landrumae*: A, Lateral view of superior nectophore (6 mm long); B, Lateral view of inferior nectophore (4.8 mm long).

by the basal wing which is slightly lower than the ostium level. The posterior and lateral ridges are also crested, and end in small, tooth-like formations.

The radial canals follow the typical sigmoid pattern for the genus, and join the circular canal.

The apex of the posterior nectophore is roundish, with the dorsal side higher than the ventral, fitting perfectly in the hydroecium of the first nectophore.

Eudoxid phase: Unknown.

Lensia landrumae, new species
Fig. 3

Material.—(See Table 3.) Holotype: 1 superior nectophore and 1 inferior nectophore, *Eltanin* cruise 21, sta. 1403, USNM 61062; paratype: 2 superior nectophores and 2 inferior nectophores, *Eltanin* cruise 16, sta. 925, and cruise 26, sta. 1794, USNM 61063.

Etymology.—Named for Elizabeth Landrum, in recognition of her dedication throughout the years to advancing plankton studies, and her encouragement and valuable assistance to this research.

Table 3.—Distribution of *Lensia landrumae* in the Antarctic-Subantarctic region.

Cruise	Station	Gear/tow	Location	Depth of haul	Date	Local time
10	192	V	56°57'S, 74°58'W	992–0 m	11 Nov 1963	1651–1739
16	884	BPS	44°21'S, 162°00'E	1000–500 m	4 Feb 1965	1350–1406
	895	MPS	49°17'S, 162°00'E	500–250 m	7 Feb 1965	1110–1124
	925	MPS	52°26'S, 166°42'E	250–100 m	18 Feb 1965	1552–1558
21	1403	MPS	54°06'S, 119°54'W	500–250 m	20 Dec 1965	0035–0045
26	1794	BPS	41°58'S, 160°06'E	1000–500 m	7 Dec 1966	1425–1449
	1803	BPS	47°37'S, 161°49'E	1000–500 m	13 Dec 1966	1052–1112

Description.—The superior nectophore (Fig. 3A) is about 6 mm high and 2.5 mm in width. There are 5 complete ridges extending from tip of the nectophore to the region of the ostium: 2 ventral, 1 dorsal, and 2 dorsolateral. Another pair of ridges, the ventrolateral, extend from the region of the pedicel (where the margin of the nectosac is adjacent to the hydroecium), up to near the top of the nectophore. The ventrolateral ridges do not reach the top of the nectophore. The dorsal ridge and the dorsolateral ridges have crests, which are widest at the low part of the ridge, but the crests disappear from this region to the level of the ostium. This low portion of the ridge has no crest; the portion with no crest is about ⅛ of the length of the nectophore. The ventrolateral ridges present a round crest at the lowest part, that is, at the ostium region, diminishing in width as they reach the upper part of the nectophore.

The somatocyst is large, massive and globular-oval in shape, in contact with ventral wall of the nectosac.

The hydroecium is deep, but reaches to the level of the ostium, and is closed by two flaps on the dorsal side.

The region of the somatocyst between the nectosac and the ventral ridges is filled with mesoglea, as is seen in *L. conoidea.*

The posterior nectophore (Fig. 3B) is prismatic, with 5 ridges having the same characteristic features as the superior nectophore. The upper part of the nectophore extends in a triangular peak on the dorsal side. The crests of the dorsal and lateral ridges widen near the ostial region, but the lowest part has no crest, showing a pattern similar to that of the superior nectophore. The ventral ridges are wing-like, closing the hydroecium, which resembles a tunnel.

The anterior and posterior radial canals are straight, running from the pedicel at the top of the nectophore, to the ring canal. The lateral radial canals bend in a step-like shape at the upper part of the nectosac, and run down straight to the ring canal.

Because the characteristics of the ridges and crests of this inferior nectophore are similar to those in the superior nectophore of *L. landrumae* n. sp., it is assumed that these inferior nectophores correspond to that species.

The eudoxid phase is unknown.

Discussion.—The species closely related to *L. eugenioi* and *L. eltanin* are *L. achilles, L. bary,* and *L. cordata.* In *L. achilles* the somatocyst is a somewhat elongate spindle-shaped club. The lateral ridges are just at midwidth of the lateral sides, bending ventrally and then dorsally to reach to the dorsal ⅓ of the ostium

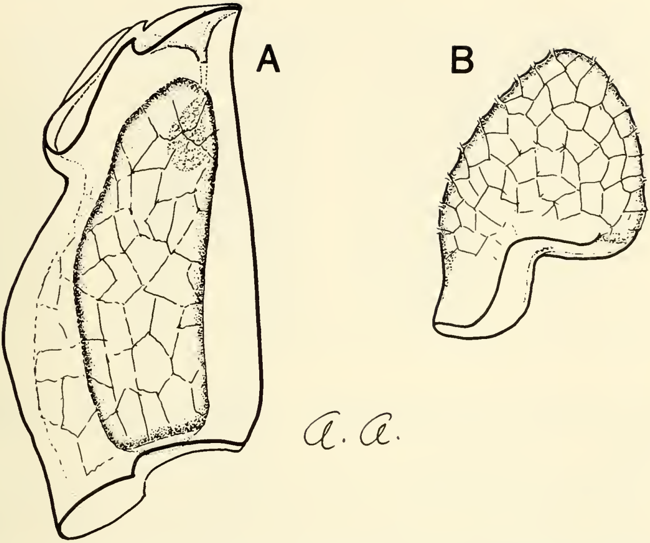

Fig. 4. *Lensia reticulata*: A, Lateral view of gonophore (2.5 mm long); B, Bract (1.6 mm high).

margin. The hydroecial cavity is deep, exhibiting the same depth from the dorsal to the ventral side of the cavity. The top of the hydroecium is level with the ostium; on the dorsal of the proximal part of the ostium, the top of the hydroecium is slightly higher than the ventral side, or distal part of the ostium.

In *Lensia bary* the somatocyst exhibits a large spindle or inverted club shape. There is an elongate globular oval with a small ampullar projection at the top. Lateral ridges are slightly bent at the ostium region (less sharply bent than in *L. achilles*), reaching the middle of the ostium region. The hydroecium is as deep as in *L. achilles,* but shallow toward the ventral side (the part far from the ostium). The top of the hydroecium is level with the ostium.

Lensia cordata has lateral ridges bending sharply to the dorsal side, reaching one-fourth of the dorsal ostium region. The somatocyst is heart-shaped, on top of a short peduncle. The heart-shaped part begins level with or slightly higher than the ostium. The hydroecium is shallower than in *L. achilles* and *L. bary,* ending just at the level of the ventral ridges.

Lensia cordata has longitudinal ridges with crests, while crests are not present in *L. bary* and or *L. achilles.*

One of the main differential characteristics of the above-mentioned group of species of *Lensia* is the position of the end of the lateral ridges at the ostium region. In *L. achilles* that point is at one-third of the dorsal side, in *L. bary* at

Table 4.—Distribution of eudoxids of *Lensia reticulata* in the Antarctic-Subantarctic region.

Cruise	Station	Gear/tow	Location	Depth of haul	Date	Local time
10	165	V	65°00′S, 74°58′W	2035–0 m	1 Nov 1963	0350–0455
11	249	BPS	58°57′S, 114°45′W	1000–500 m	3 Jan 1964	0132–0233
	253	MPS	59°56′S, 114°56′W	480–250 m	4 Jan 1964	0220–0304
	254	BPS	59°55′S, 114°56′W	1000–250 m	4 Jan 1964	0350–0502
	257	MPS	60°56′S, 114°42′W	500–250 m	5 Jan 1964	1451–1532
	262	MPS	61°56′S, 115°12′W	500–250 m	7 Jan 1964	0714–0754
	268	MPS	62°57′S, 115°16′W	500–250 m	8 Jan 1964	0738–0821
	292	BPS	68°20′S, 114°47′W	unknown	15 Jan 1964	2237–0000
	303	BPS	70°09′S, 106°40′W	1000–500 m	19 Jan 1964	1946–2103
	308	MPS	70°08′S, 102°55′W	500–250 m	20 Jan 1964	2019–2044
	320	BPS	67°58′S, 90°54′W	1000–500 m	26 Jan 1964	0822–0929
	326	BPS	65°55′S, 89°06′W	1000–500 m	28 Jan 1964	0625–0730
15	881	MPS	57°00′S, 150°08′W	500–250 m	21 Nov 1964	2112–2131
16	895	MPS	49°17′S, 162°00′E	500–250 m	7 Feb 1965	1110–1124

about the middle of the ostial opening, in *L. cordata* at one-fourth of the dorsal side, in *L. eugenioi* at the dorsal side, and in *L. eltanin* at about midlength of the ostium.

The hydroecium is different in shape and size for all five closely related species, and the shape and size of the somatocyst is also different in each of the species.

Lensia eugenioi is the only one in the group with five complete ridges and two additional ridges (ventrolateral), which go from the ostium to near the top of the nectophore, not reaching the apex.

Lensia landrumae is different from any of the previously described species of the genus *Lensia* in the shape of ridges and crests, hydroecium, and somatocyst.

Lensia reticulata Totton, 1954

Fig. 4

Diagnosis.—The nectophores are multicristate, with cross-connecting ridges forming an irregular meshwork.

The superior nectophore of the polygastric phase has been described (Totton 1954). The eudoxid phase has not been previously described.

Material.—Specimens of the eudoxid phase of *Lensia reticulata* were observed in collections from *Eltanin* cruises listed in Table 4. Voucher material of eudoxid phase, 1 bract and 1 gonophore, cruise 11, sta. 308, USNM 61068; 1 bract, 2 gonophores, cruise 11, sta. 326, and cruise 15, sta. 881, USNM 61069.

Description.—The gonophore (Fig. 4A) is an oval, with a roundish area at the top where the bract is attached. The walls of the gonophore are thin, and have a reticular pattern similar to that of the polygastric nectophore.

The bract (Fig. 4B) is like a cap, formed by two parts; the top or hemispherical cover is of thick mesoglea, covered by a thick network of ridges, like a honeycomb; the visor part is wide. The visor part attaches to the groove at the top of the gonophore.

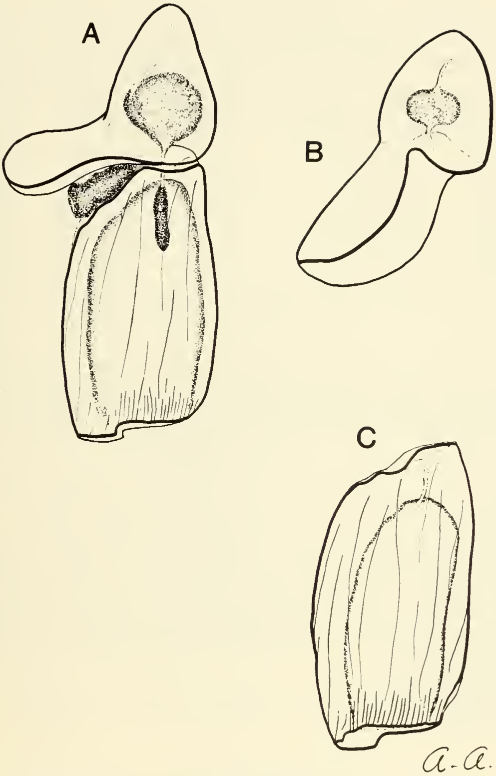

Fig. 5. *Lensia lelouveteau*: A, Complete eudoxid (5 mm long); B, Bract (2.5 mm long); C, Gonophore (3 mm long).

Lensia lelouveteau Totton, 1941
Fig. 5

Diagnosis.—The eudoxid phase of *Lensia lelouveteau* has not been previously described. The specimens found could belong to this species, based on the multicristate pattern of the ridges and the particular feature of a band of ridges at the inferior part of the gonophore, all of which makes this gonophore very similar to the description and characteristics of the superior nectophore of *L. lelouveteau* Totton, 1941.

Table 5.—Distribution of the eudoxid phase of *Lensia lelouveteau* in the Antarctic-Subantarctic region.

Cruise	Station	Gear/tow	Location	Depth of haul	Date	Local time
10	196	V	65°21'S, 75°02'W	2045–0 m	13 Nov 1963	0702–0838
11	253	MPS	59°57'S, 114°57'W	480–250 m	4 Jan 1964	0220–0304
	257	MPS	60°56'S, 114°43'W	500–250 m	5 Jan 1964	1451–1532
	268	MPS	62°58'S, 115°17'W	500–250 m	8 Jan 1964	0738–0821
	308	MPS	70°07'S, 102°55'W	500–250 m	20 Jan 1964	2019–2044
	326	BPS	65°55'S, 89°08'W	1000–500 m	28 Jan 1964	0625–0730
16	900	MPS	51°09'S, 162°01'E	500–250 m	8 Feb 1965	1526–1535
	926	MPS	52°26'S, 166°42'E	500–250 m	18 Feb 1965	1544–1552
21	1403	MPS	54°03'S, 119°54'W	500–250 m	20 Dec 1965	0035–0045
26	1794	BPS	41°58'S, 160°06'E	1000–500 m	7 Dec 1966	1425–1449
	1803	BPS	47°37'S, 161°49'E	1000–500 m	13 Dec 1966	1052–1112

Material.—Complete eudoxid specimens (bract and gonophore attached), and bracts and gonophores free, disentangled, have been observed in plankton collections obtained by *Eltanin* cruises listed in Table 5. Voucher material: 1 complete eudoxid, cruise 16, sta. 900, USNM 61070; 4 eudoxids, 3 bracts, 5 gonophores, cruise 16, sta. 926, and cruise 11, sta. 268, USNM 61071.

Description.—The bract (Fig. 5A, B) has a conical top of thick mesoglea, with wide, round, wing-like shield at the ventral side. At the union of the conical body and the laminar wing or bracteal margin, the body is contracted into a neck-like shape. This laminar wing may cover more than half the height of the gonophore. The phylocyst is globular in shape. The hydroecial cavity is conical and shallow.

The gonophore (Fig. 5C) is cylindrical, with a short top platform which adjusts to the cavity of the bract, extending at the ventral side into a flattened triangular shape, where other parts of the eudoxid are located. The walls of the gonophore are covered by ridges similar to those found in the nectophore of the polygastric form of *Lensia lelouveteau.*

It appears that there is no asexual swimming bell; gonads were observed inside the gonophore, which acts as a swimming bell.

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POSEIDONEMERTES COLLARIS, N.SP. (NEMERTEA: AMPHIPORIDAE) FROM CALIFORNIA, WITH NOTES ON ITS BIOLOGY

Pamela Roe and Daniel E. Wickham

Abstract.—The morphology of a new monostiliferous hoplonemertean, *Poseidonemertes collaris* (Amphiporidae) from Bodega Harbor, California, is described and aspects of its biology are discussed. Anterior musculature and other characteristics are those of the genus. Diagnostic specific features include a readily-contracted, pointed head, two eyes, and branched intestinal diverticula.

Specimens of a small, rather common nemertean were collected from intertidal areas of Bodega Harbor, Bodega Bay, California. Although the fauna of this area is relatively well-known, this worm was previously undescribed. Externally, the animal closely resembles a number of other small, whitish, two-eyed nemerteans. Examination of its internal structure, however, reveals it to be a new species in the genus *Poseidonemertes.*

Materials and Methods

Between June 1980 and June 1982, 23 specimens were obtained from 193 samples (200–500 cc^3 each) of surface sediments in Bodega Harbor, California. Other individuals were obtained from less quantitative sampling. The samples of sediment were washed and sorted by hand in shallow trays, and the nemerteans were removed. External morphology and some internal features were observed in living animals. Specimens were anesthetized in 7% $MgCl_2$, fixed in sea water Bouin, embedded in paraffin, cut in 10 μm sections and stained in Ehrlich's hematoxylin and eosin.

Poseidonemertes collaris, new species

Figs. 1–11

Type-material.—The following have been deposited at the National Museum of Natural History (Smithsonian Institution):

Holotype: Entire specimen, preserved in 5% formalin, collected 5 Nov 1982, length 22 mm, width 13 mm, USNM 80917.

Paratype: A complete set of transverse sections of a male, USNM 80918.

Type-locality.—Bodega Harbor, Bodega Bay, Sonoma County,. California (38°18′N, 123°2′W) in intertidal muddy sand.

Etymology.—Named for the characteristic behavior of drawing the tip of the head into the body, forming a collar of tissue around the retracted head.

Diagnostic characteristics.—Body stout, approximately 20 mm × 1.2 mm; sharply pointed anterior head region; 2 conspicuous ocelli nearly terminal; color in life ivory to apricot; rhynchocoel full length of body, proboscis at least ¾ body length; body wall longitudinal muscles divided anteriorly, inner and outer layers forming proboscis insertion; cephalic retractor muscles from inner longitudinal layer; body wall diagonal muscle layer present; intestine with unbranched caecum and bifurcated lateral diverticula.

Additional material examined.—Three series of transverse sections, 2 series of frontal sections, 2 series of sagittal sections including both males and females, plus several living animals.

External features and behavior.—Twenty measured living animals ranged in length from 7.5 mm to 37 mm (average = 20.4 mm, SD = 6.9, N = 20) and width from 0.7 mm to 2 mm (average = 1.2 mm, SD = 0.37, N = 18) when crawling. Color ranges from ivory to nearly apricot. In some specimens intestinal diverticula appear gray-green or greenish-yellow. The epidermis of some individuals contains white or brown pigment spots or granules scattered over the body.

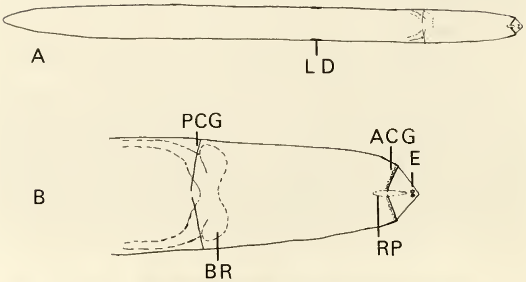
Animals tend to be stout, with the posterior end often broader than the anterior. They are highly contractile, and can easily shorten to ⅓ or ¼ their expanded length. When contracting, worms do not coil or twist, and the head remains pointed. Two large, prominent eyes are located close together near the tip of the head (Fig. 1). Pigment cups of the eyes are comma to round in overall shape. Two pairs of cephalic grooves are present. The anterior pair is distinct, both dorsally and ventrally, is far anterior to the brain, and is sometimes united dorsally. The anterior cephalic grooves vary in shape. They usually form a posteriorly directed chevron, although they can form a transverse or even an anteriorly directed curve across the head. On the dorsal surface of the head, the anterior cephalic grooves are often bordered by reddish-brown pigment spots (Fig. 1). Along the lateral margins of the head, a groove extends from the anterior cephalic grooves a short distance posteriorly. The distance from the tip of the head to the anterior cephalic groove is about 0.2 mm. Living animals frequently and characteristically retract the head to the level of the anterior cephalic grooves, forming a collar of epidermal tissue around the tip (Fig. 2). We were unable to relax animals before fixation to the point that the collar did not form. The posterior cephalic grooves, just posterior to the brain, are thin, fine lines not highly visible (Fig. 1).

The brain lies far behind the anterior cephalic grooves, the distance being about 1.5 mm in one animal measured. The brain and anterior parts of the lateral nerve cords appear light pink when viewed through the body wall. Gonads are not readily visible through the rather opaque epidermis.

In living specimens a pair of lateral epidermal depressions that are devoid of white spots is found in the region of the anterior intestine, approximately ⅓ of the body length from the anterior end (Fig. 1). We were unable to locate these areas on any of our sectioned material and do not know their function, but they might be nephridiopores.

Body wall, musculature and parenchyma.—The epidermis is 50–56 μm in height, and possesses no unusual features. The dermis is 20–22 μm thick.

Body wall musculature consists of an outer circular layer (12–14 μm thick) and inner longitudinal layer (80–136 μm thick in the anterior region of the intestine). A single layer of crossed, diagonal muscle fibers was found between the circular and longitudinal muscle layers. The longitudinal muscle layer is divided into outer and inner layers, from the region just posterior to the brain, anteriorly (Figs. 3, 1



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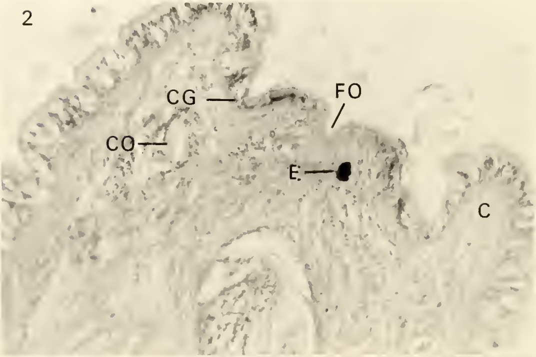

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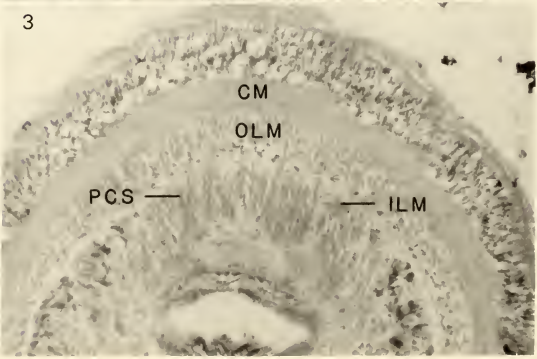

4). The outer portion continues as a distinct, compact layer, next to the circular muscles, to the tip of the head. Anterior to the brain, outer longitudinal fibers bend inward to contribute to the proboscis insertion, which is composed primarily of inner longitudinal fibers (Figs. 3, 4). Due to the contribution of the outer layer, musculature forming the proboscis insertion represents a precerebral septum. Inner longitudinal muscle fibers penetrate between the muscle bundles of the septum and continue as head retractors (Figs. 3, 4); thus the septum is of the split condition as defined by Kirsteuer (1974). Dorsoventral musculature is only weakly developed and occurs primarily in the stomach region, with muscle fibers running through the parenchyma in that area.

Parenchyma occurs in limited amount in the precerebral region and in the area between the two longitudinal muscle layers. A thick layer surrounds the proboscis sheath in the brain region, and continues to the intestinal region. Posteriorly a small amount of parenchyma surrounds the dorsal blood vessel. Parenchyma forms a rather thick cushion around the stomach and lateral nerve cords, becoming reduced posteriorly.

Nervous system.—The brain consists of 2 dorsal and 2 ventral lobes, approximately equal in size. The ventral commissure is thicker and shorter than the dorsal one. Neurochord cells were not found. Along the anterior part of the stomach and the anterior intestinal region, the lateral nerve cords send off many nerves to the epidermis (Fig. 5). Posteriorly the 2 lateral nerve cords descend ventrally and medially before joining at the posterior end of the animal. Cerebral organs and eyes are well-supplied with nerves. The proboscis has 10 proboscis nerves (counted in 1 animal, Fig. 6).

Sensory organs and cephalic glands.—The cephalic glands (Fig. 7) extend barely posterior to the ventral commissure, and empty into the frontal organ, as in *Poseidonemertes caribensis* (Kirsteuer, 1974). The frontal organ (Fig. 2) consists of a fenestrated epidermis just dorsal and anterior to the rhynchodaeal pore. The cell bodies of the cephalic glands are primarily found posterior to the cerebral organs but anterior to the brain.

The eyes are large (28 × 24 and 26 × 22 μm diameter, 1 serially sectioned specimen) (Fig. 8) with cup-shaped pigment surrounding a central nervous area.

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Figs. 1–3. *Poseidonemertes collaris.* 1. A, External features showing conspicuous eyes, anterior cephalic grooves, rhynchodaeal opening (dashed oval), posterior cephalic grooves in relation to brain and anterior lateral nerve cords (dashed lines) and pair of lateral depressions (thickened areas along sides); B, Enlargement showing details of head; 2, Frontal section of anterior head region, showing characteristic collar of posterior cephalic tissues resulting from contraction of tip of head; 3, Transverse section of the proboscis insertion or precerebral septum showing contribution of both outer and inner longitudinal muscles to the septum. Muscle bundles of split septum are also depicted.

List of Abbreviations, Figures 1–11: ACG, anterior cephalic groove; AS, accessory stylet sac; B, basis; BR, brain; C, collar; CE, columnar epithelium; CG, cephalic groove; CGL, cephalic glands; CM, circular muscles; CO, cerebral organ; DBV, dorsal blood vessel; E, eye; ES, esophagus; FO, frontal organ; GD, gonoduct; HRM, head retractor muscle; ILM, inner longitudinal muscle; IN, intestine; LBV, lateral blood vessel; LD, lateral depression; LM, longitudinal muscle; LN, lateral nerve; N, nerves; OLM, outer longitudinal muscle; OV, ovary; PCG, posterior cephalic groove; PCS, precerebral septum; PN, proboscis nerve; PR, proboscis; PY, pylorus; RH, rhynchocoel; RM, rhynchocoel muscle; RP, rhynchodaeal pore; RS, rhynchodaeal sphincter; S, stylet; VC, ventral commissure.

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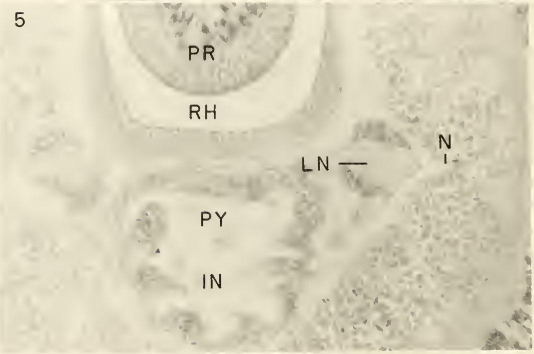

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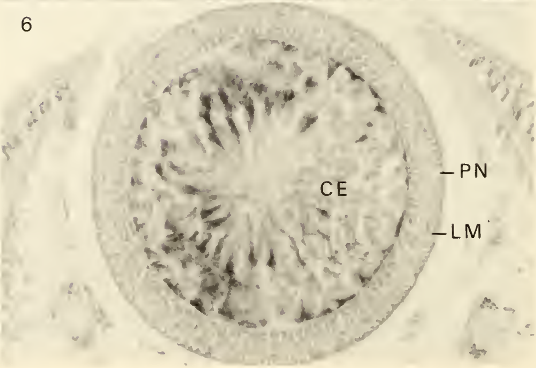

The cerebral organs are approximately 100 μm long and extend nearly to the precerebral septum. They are comprised of a median ciliated canal next to and partly surrounded by a more lateral neuroglandular tissue (Fig. 2), and are innervated by nerves that enter at an antero-medial position. The ciliated duct of each organ opens into the anterolateral corners of the anterior cephalic grooves.

Proboscis apparatus.—The large rhynchodaeal pore is subterminal. Anterior to the pore and extending to the tip of the head is a narrow, ventral, ciliated depression. The pore leads into a thin-walled rhynchodaeum. A strong rhynchodaeal sphincter muscle occurs slightly anterior to the proboscis insertion (Fig. 7). The rhynchocoel extends to the posterior end of the animal. Its wall contains 2 distinct muscle layers, an outer, thick circular layer and an inner longitudinal layer lined by thin endothelium. Posteriorly the circular muscle layer becomes much thickened (Fig. 9).

The proboscis is of the typical monostiliferan form. The anterior proboscis chamber is lined by a columnar, glandular epithelium that forms distinct papillae. The musculature is well-developed, and consists of an outer circular layer next to the columnar epithelium, a middle longitudinal layer that is divided into 2 bands by the proboscidial nervous system, and a thin (1–2 fibers) inner circular layer adjacent to a thin squamous endothelium (Fig. 6). The posterior part of the proboscis narrows and consists of columnar epithelium, a thin longitudinal muscle layer and endothelium. The proboscis and continuing proboscis retractor muscles extend approximately ¾ of the length of the animal.

The central stylet lacks ornamentation and averages 87.5 μm in length by 16.4 μm in width at its base (Table 1). In some specimens, the stylet widens in a band anterior to its proximal piece. The basis is longer than the stylet (average length = 119.4 μm, average width = 11.6 μm, Table 1). It is cylindrical in shape, has a slightly indented waist, and is rounded at its posterior end (Fig. 10). In live specimens the posterior ⅓ to ¼ (average = 29%, SD = 0.04, N = 5) of the basis is characteristically more darkly pigmented than the anterior region. Two accessory stylet sacs are present, each with 0 to 4 developing stylets (Table 1, Fig. 10).

Digestive tract.—The esophagus, which is narrow and not highly folded, opens into the anterior end of the rhynchodaeum, anterior to the rhychodaeal sphincter (Fig. 7). The columnar epithelial cells of the esophagus have cilia that are shorter and more sparsely distributed than in the stomach. The esophagus extends posterior to the brain, where it gradually widens and empties dorsally into the capacious, highly folded stomach. Neither the esophagus nor the stomach appears to be highly glandular. Posteriorly the stomach becomes a flattened, non-folded pylorus. The pylorus is lined by non-ciliated cells, and empties dorsally and broadly into the intestine (Fig. 5). The shape of the pylorus is influenced by longitudinal muscles which ensheath the entire foregut.

At the junction of the pylorus and intestine, the intestinal epithelium contains

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Figs. 4–6. *Poseidonemertes collaris.* 4, Frontal section at level of proboscis insertion and precerebral septum, showing contribution of outer longitudinal muscles to septum (arrow) and inner longitudinal muscles continuing as head retractor muscles; 5, Transverse section near pyloric-intestine junction. Section shows nerves to body wall, characteristic throughout anterior intestinal region; 6, Transverse section of anterior chamber of proboscis, showing 10 proboscidial nerves.

Table 1.—Measurements of the stylet apparatus of *Poseidonemertes collaris.*

Animal number	Basis length, µm	Basis width, µm	Central stylet length, µm	Central stylet width, µm	Ratio of central stylet length to basis length	Number of accessory stylets per sac
1	—	—	—	—	—	3, 3
2	100	50	100	—	1.0	2, 0
3	122	25.5	91.8	—	0.75	3, 2
4	137	46	80.5	15	0.59	3, 3
5	115	37	76.5	20.4	0.67	3, 3
6	124.5	27	102	18	0.82	3, 4
7	118	22	74	12	0.63	4, 4
Range	100–137	22–50	74–102	17–20.4	0.59–1.0	0–4
Number	6	6	6	4	6	14
Average	119.42	34.58	87.47	16.35	0.74	2.86
Standard Deviation	12.17	11.59	12.14	36.46	0.15	1.03

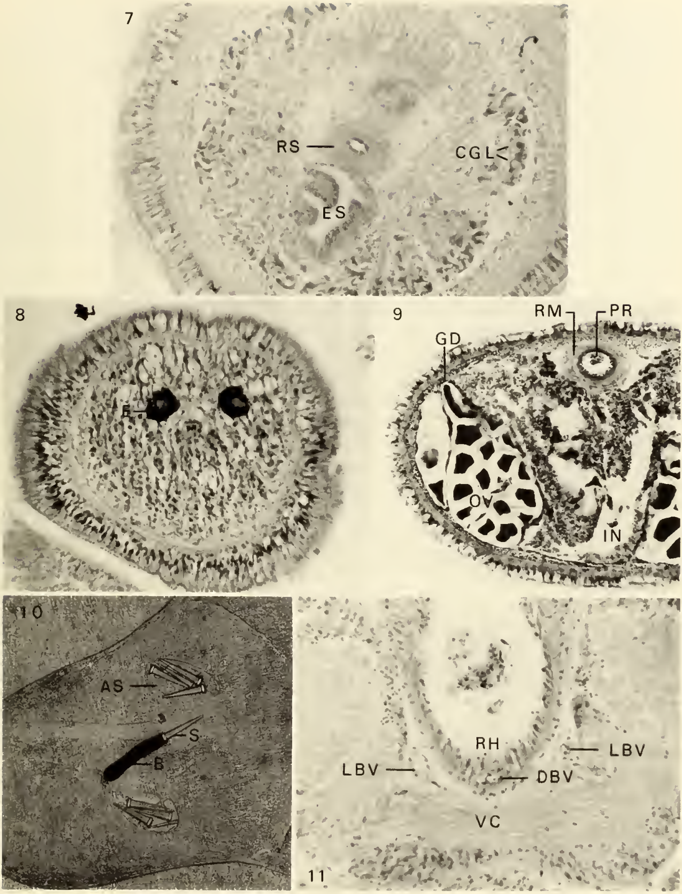
both blue- and red-staining cells, indicating secretory diversity in this area. Both types of cells continue through much of the length of the intestine although the blue-staining cells are far more restricted in distribution, being found mainly in the mid-dorsal lining.

The intestinal caecum is broad and shallowly indented, but without diverticula, and occasionally extends to the posterior end of the brain. The anterior lateral diverticula of the intestine sometimes bend forward and their tips occasionally extend beyond the caecum anteriorly. Lateral intestinal diverticula are often bifurcated and the tips of the bifurcations may branch even more. The anus is terminal.

Circulatory system.—The 2 cephalic blood vessels form an anterior loop behind the eyes at the level of the anterior cephalic grooves, and in the region of the ventral brain commissure they converge with the dorsal blood vessel which runs within the rhynchocoel wall for a short distance (Fig. 11). It could not be determined from our material whether the dorsal vessel joins both or only one of the lateral vessels anteriorly. Posterior to the convergence, the 2 lateral vessels lie above the lateral nerve cords for a short distance, then descend medially to a position ventral to the lateral cords. The blood vessels in the anterior part of living worms lie medial to the lateral nerve cords and can be seen to weave in and out next to the tips of the lateral intestinal diverticula. The dorsal blood vessel is contractile and the blood is colorless. Near the posterior end of the body the 3 vessels appear to unite dorsal to the intestine.

Excretory system.—In the anterior intestinal region is a poorly-defined duct dorsal to each lateral nerve cord that may represent the excretory system, which latter does not appear to be well-developed. Living specimens did, however, display large, lateral, rectangular to oval areas approximately 0.1 to 0.8 mm long (depending on contraction state of the animal) and about ⅓ of the body length posterior to the head which might be nephridiopores (Fig. 1). These areas were not visible on any sectioned material.

Reproductive system.—Sexes are separate. Gonads lie between and ventral to the lateral intestinal diverticula, from close to the anterior end of the intestine to



Figs. 7–12. *Poseidonemertes collaris.* 7, Transverse section at level of rhynchodaeal sphincter just anterior to proboscis insertion. Part of the insertion can also be seen dorsal to sphincter; 8, Transverse section of tip of head showing prominent eyes; 9, Transverse section through posterior region showing ovary, gonoduct, structure of intestinal diverticulum and posterior intestine, and strong circular musculature of posterior region of rhynchocoel wall; 10, Stylet apparatus in partly everted proboscis from living specimen; 11, Transverse section at level of brain, showing dorsal blood vessel within rhynchocoel wall.

the posterior tip of the animal. Both ovaries and testes are arranged in a single row on each side of the intestine, each mature gonad extending from the ventrum to the dorsum of the animal. Gonoducts are dorsolateral (Fig. 9). Mature ovaries typically contain about 25 oocytes, but can contain up to 50 oocytes each.

Remarks on biology.—Specimens were found in the samples we collected most months of the year, although they seemed to be more abundant (or at least easier to locate) during summer months. The animals are rapid burrowers and live in mucus burrows covered with sand grains and other sediment. From observations of the microhabitats where most individuals were collected, these worms seem to prefer sandy mud rather than finer sediments, and tend to occur where there are moderate amounts of algae (primarily ulvoids). They were not found in anoxic mud.

Sexually mature animals were collected in June, July, and August, and one mature female was found in November. One female released eggs in August. The eggs were fertilized with sperm taken from a mature male, and early development was observed. Fertilized eggs are oval, 92 × 112 μm diameter (with fertilization membrane included, 173 × 204 μm in diameter) and are white to barely pink in color. Both unfertilized, but extruded, and fertilized eggs are covered by a thick transparent membrane. Fertilized eggs released swimming larvae within 18 hours in water kept at approximately 60°F. Eyespots became visible by day three. Larvae were of the typical hoplonemertean oval form, except that they were rather depressed dorsoventrally. They were rapid swimmers in comparison to larvae of *Carcinonemertes* species (pers. obs.). Three day old larvae have functioning musculature, as witnessed by the fact that one individual changed its dimensions from 122 × 82 μm to 163 × 61 μm by stretching.

Discussion

Several small, pale, marine, two-eyed monostiliferans have been described from various parts of the world (e.g., *Amphiporus bioculatus, Correanemertes bioculatus* and *Poseidonemertes gondwanae* as discussed in Kirsteuer (1967); *Paranemertes biocellatus* Coe, 1944; *Tetrastemma worki* and *T. hansi* as discussed in Corrêa (1961); *Poseidonemertes caribensis* Kirsteuer, 1974). The animals described in this paper superficially resemble many of the above worms. The arrangement of musculature in the anterior body region, however, places the present specimens firmly within genus *Poseidonemertes.* Kirsteuer (1974) provided diagnostic descriptions of several nemertean genera with split longitudinal musculature. The genus *Poseidonemertes* is characterized by members having split longitudinal musculature, with contributions from both outer and inner layers forming the proboscis insertion. Due to the contribution of the outer layer, the insertion represents a precerebral septum, which in this genus is characteristically split into muscle bundles (Kirsteuer 1974). Inner longitudinal muscle fibers continue past the septum as head retractors (Kirsteuer 1974). In addition, other features, such as musculature of proboscis sheath consisting of separate layers, rhynchocoel having no appendages and extending into the posterior part of the body, presence of intestinal caecum, lack of extracerebral blood vessels, cerebral organs being anterior to the brain and the dioecious condition of the animals agree with the generic diagnosis for *Poseidonemertes,* as defined by Kirsteuer 1974. Some of our specimens did show diagonal body wall musculature and thus differ from the generic diagnosis of *Poseidonemertes.* However, the single-fiber layer of diagonal musculature can be easily overlooked. Since this was the only minor generic feature in which our specimens differed from other described *Poseidonemertes,* we consider our specimens to belong to the genus *Poseidonemertes.*

Three species of *Poseidonemertes* have previously been described, all from tropical waters (*P. gondwanae* Kirsteuer, 1967; *P. caribensis* Kirsteuer, 1974; *P. bothwellae* Gibson, 1982). The present animals differ from the other members of *Poseidonemertes* in sufficient features to warrant recognizing them as a new species. The differences include the following: The sharply pointed, elongated head, as well as the characteristic contracting of the tip of the head into more posterior parts of the head, forming a collar of tissue around the tip, are apparently unique among described members of the genus *Poseidonemertes.* However, the ability to retract the head is not unusual among amphiporids (Jon Norenburg, pers. comm.); similar behavior was described by Coe (1904) for *Paranemertes californica,* and Berg (1972) for *Nipponnemertes pulcher.* The head of *P. gondwanae* is pointed, but the cephalic grooves of that species are not prominent, nor does the animal retract the head tip back to the grooves (Kirsteuer 1967). In the other two species the head is rounded (Kirsteuer 1974; Gibson 1982), and in disturbed animals of *P. caribensis* the head widens posterior to its tip (Kirsteuer 1974), a behavior much different from that observed in the present animals. The presence of lateral depressions approximately ⅓ the body length posterior to the anterior end, as occurs in the California animals, has not been described for other species of *Poseidonemertes.* In addition, the numerous nerves leading from the lateral nerve cords to the body wall in the anterior intestinal region in *P. collaris,* have not been described for other species of the genus. The lateral gut diverticula of *P. collaris* are at least bifurcate and may show even more branching; lateral gut diverticula are missing in *P. bothwellae* (Gibson 1982) and are unbranched in *P. gondwanae* and *P. caribensis* (Kirsteuer 1967, 1974), and in *P. caribensis* the intestinal caecum is provided with branches (Kirsteuer 1974).

Poseidonemertes collaris differs from the previously described species in other ways as well. In *P. gondwanae* the stylet is nearly as long as the basis, the basis is truncated, the dorsal blood vessel does not enter the rhynchocoel wall, and *P. collaris* averages twice the length of *P. gondwanae* (Kirsteuer 1967). In *P. caribensis* the proboscis sheath does not extend to the posterior end of the body (Kirsteuer 1974). Specimens of *P. bothwellae* are dark brown in color, and the dark color obscures the four eyes in living animals (Gibson 1982). In addition, whereas the stylets of the Australian and Californian specimens are similar in size, the stylet basis in the new species is approximately twice the length of that for *P. bothwellae* (Gibson, 1982).

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CLARIFICATION OF THE MONOTYPIC GENERA *CHIRISCUS* AND *SYMMIUS* (CRUSTACEA: ISOPODA: IDOTEIDAE)

Gary C. B. Poore

Abstract.—*Chiriscus australis* Richardson, 1911, has been re-examined and placed in the older genus *Macrochiridothea* Ohlin of which *Chiriscus* becomes a junior synonym. *Symmius caudatus* Richardson, 1904, is redescribed. Both *Symmius* and *Macrochiridothea* are diagnosed and a list of non-idoteine genera of the Idoteidae is given.

In the early part of this century Harriet Richardson described two monotypic genera in the isopod family Idoteidae: *Symmius* (1904) and *Chiriscus* (1911). As part of an examination of non-idoteine genera present in southern Australia it was thought desirable to re-examine the type and only species of the two genera in order to establish their continued validity.

Brusca (1984) has revised in detail the genera of the Idoteinae. The remaining genera of the family, a group which Brusca referred to as the "glyptonotine-group," are listed in Table 1. They comprise four subfamilies the relationships of which are far from clear and receive more attention by Poore (in press).

Richardson's description of *Chiriscus australis* was in part incorrect. It may now be safely placed in the older genus *Macrochiridothea* Ohlin, 1901. The genus *Chiriscus* becomes a junior synonym of the larger genus for which an amended generic diagnosis is given.

Symmius caudatus clearly does not belong to any other genus and is here redescribed in more detail and the genus diagnosed. Richardson's (1904) description contained numerous errors and omissions.

Family Idoteidae

Macrochiridothea Ohlin

Macrochiridothea Ohlin, 1901:286.—Nordenstam, 1933:105.—Sheppard, 1957: 168–173.—Menzies, 1962:98.—Hurley & Murray, 1968:244.—Moreira, 1973: 12.—Jones & Fenwick, 1978:619.

Chiriscus Richardson, 1911:169–170.—Sheppard, 1957:168–169.

Diagnosis.—Head immersed partly in pereonite 1, laterally expanded, margins incised or entire. Eyes dorsal if present. Pereonites 5–7 only with coxal plates distinct dorsally. Pereonite 7 much narrower than pereonite 6. Pleonites 1–3 completely free; pleonite 1 much narrower than following pleonites; no partial sutures on the remaining pleotelson. Pereopod 1 subchelate, propodus grossly expanded. Pereopods 2 and 3 subchelate; elongate-ovate propodus cupped by triangular or lobed fifth article; dactyl well developed, minute or absent. Pereopods 4–7 ambulatory, pereopod 6 the longest; all pereopods with dactyl, usually minute.

Table 1.—Non-idoteine genera of the Idoteidae (see Brusca, 1984, for genera of Idoteinae and Poore, in press, for one additional genus).

Austridotea Nicholls, 1937
Austrochaetilia Poore, 1978
Chaetilia Dana, 1853
Chiridotea Harger, 1878
Chiriscus Richardson, 1911 (junior synonym of *Macrochiridothea*)
Glyptonotus Eights, 1852
Macrochiridothea Ohlin, 1901
Maoridotea Jones & Fenwick, 1978
Mesidotea Richardson, 1905 (junior synonym of *Saduria*)
Notidotea Nicholls, 1937 (may be a synonym of *Euidotea* (Idoteinae)—Hurley, 1961)
Parachiridotea Daguerre de Hureaux & Elkaim, 1972
Proidotea Racovitza & Sevastos, 1910 (Oligocene fossil)
Saduria Adams, 1852
Saduriella Holthuis, 1964
Symmius Richardson, 1904

Mandible with toothed incisor, large lacinia mobilis and substantial setal row, molar absent (except for single seta). Maxillipedal palp of 4 articles, about 3 times as long as endite, penultimate article proximally broad. Pereopods and antennae ornamented with numerous clubbed setae. Uropods overlapping in midline, enclosing pleopods except anteriorly; rami unequal.

Remarks.—This diagnosis modifies those of Menzies (1962) and Moreira (1973) to include *Macrochiridothea australis* which differs from species previously known in two respects. Pereopods 2 and 3 of *M. australis* do not possess dactyls although in all other respects they are similar. The state in *M. australis* is the final step in a trend shown in the genus toward loss of dactyls; in at least two species the dactyls are minute (Moreira 1973). Only *M. australis* lacks a lateral incision on head. The incision ranges from well developed (e.g., *M. stebbingi*) to only slight (*M. robusta*) (Moreira 1973). In all other respects Richardson's species conforms with *Macrochiridothea* which must therefore be broadened to include it.

The figures of *M. australis* enable it to be distinguished from other species in the genus. Moreira (1973), Hurley & Murray (1968), and Bastida & Torti (1969) have figured several species in more detail. This enables an assessment of the mouthparts and pleopods, which may all be important in generic relationships within the family.

Macrochiridothea australis (Richardson), new combination

Figs. 1a, 2

Chiriscus australis Richardson, 1911:170–171, figs. 1–5.

Diagnosis.—Body smooth except for broad dorsolateral bosses on pereonites 1–4. Body 2.3× as long as wide. Head laterally expanded but without lateral incisions. Eyes present, minute. Antenna 2, peduncle article 4 lobed to shield article 5. Pereopods 2 and 3 without dactyls, article 5 strongly lobed. Pereopods 4 and 7 each with an extremely minute dactyl.

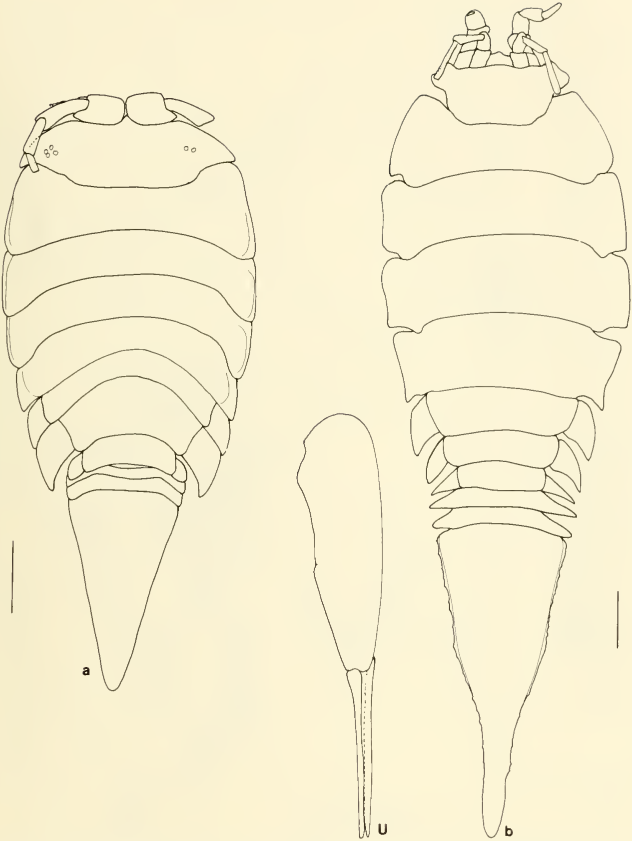

Fig. 1. a, *Macrochiridothea australis*, holotype; b, *Symmius caudatus*, ♀ syntype; u, uropod of *S. caudatus* (scales 1 mm).

Material.—Holotype, USNM 42092, ovigerous ♀, 7.9 mm; Argentina, off Rio de la Plata, 21 m, 12 Jan 1888 (U.S. Fisheries Commission Steamer *Albatross* station 2764).

Remarks.—Only the holotype, an adult female, is known. The diagnosis given enables the species to be distinguished from the eight listed by Moreira (1973).

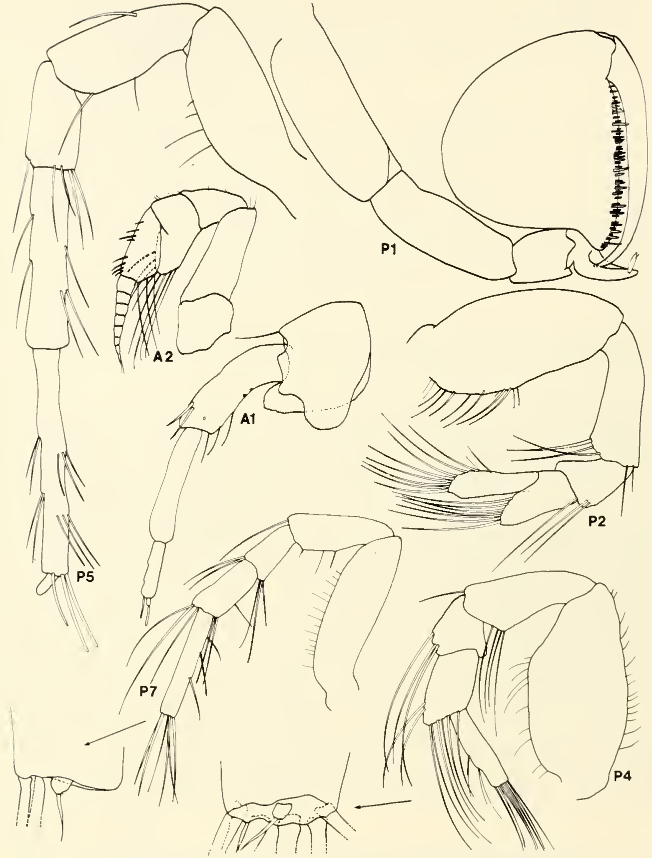

Fig. 2. *Macrochiridothea australis,* holotype: P1, P2, P4, P5, P7, pereopods 1, 2, 4, 5 and 7; A1, A2, antennae 1 and 2.

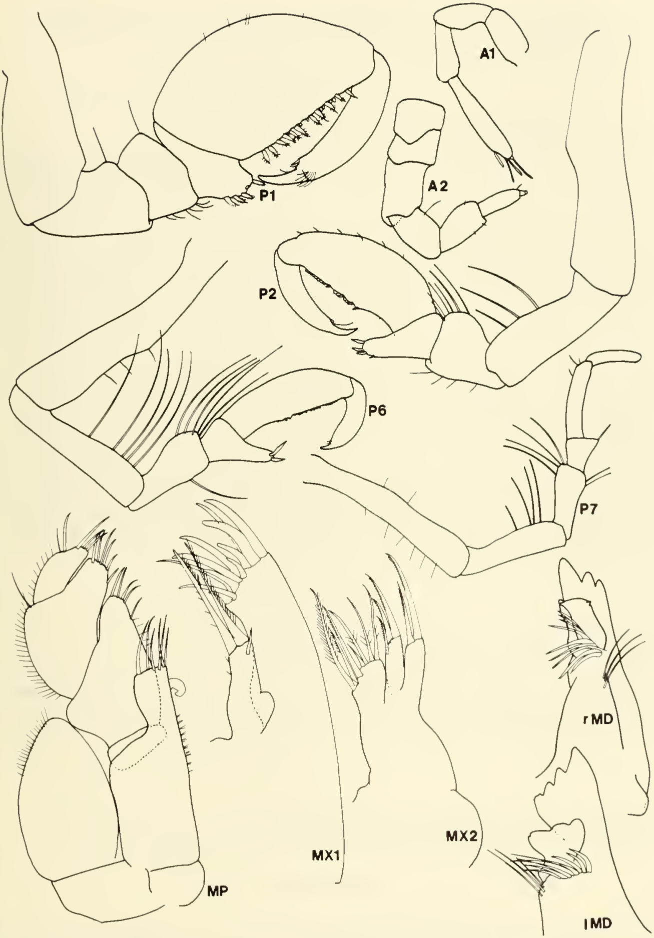

Fig. 3. *Symmius caudatus* ♀ syntype: P1, P2, P6, P7, pereopods 1, 2, 6 and 7; A1, A2, antennae 1 and 2; MD, mandibles (left & right); MX1, MX2, maxillae 1 and 2; MP, maxilliped.

Macrochiridothea australis is most similar to *M. lilianae* in body shape and form of the pereopods.

Symmius Richardson

Symmius Richardson, 1904:39–40.—Nordenstam, 1933:103.

Diagnosis.—Head partly immersed in pereonite 1, laterally expanded slightly, margins entire. Eyes dorsal. Pereonites 5–7 only with coxal plates distinct dorsally. Pereonite 7 little narrower than pereonite 6. Pleonites 1 and 2 completely free, of similar width and laterally acute; no partial sutures on the remaining pleotelson. Pereopods 1–6 prehensile; propodus of pereopod 1 swollen, those of pereopods 2–6 cylindrical, decreasing in size posteriorly and cupped by a triangular lobed fifth article. Pereopod 7 ambulatory, of similar size to pereopod 6; dactyl without an unguis. Mandible with toothed incisor, large lacinia mobilis and substantial setal row, molar absent (except for 3 distal long setae). Maxillipedal palp of 4 articles, about 3 times as long as endite, articles 2 and 3 mesially lobed. Pereopods and antennae ornamented with simple or plumose setae. Uropods overlapping in midline, enclosing pleopods except anteriorly; rami equal and narrow.

Remarks.—The format of this and the previous diagnosis enables the genus to be distinguished from others in the non-idoteine group (Poore, in press). Richardson (1904) did not illustrate the mouthparts of *S. caudatus* which are shown here in some detail. The relationships of *Symmius* to other non-idoteines are not clear. The genus is unique in that pereonite 7 reaches full width of the body, in having only two free pleonites, and in possessing six pairs of prehensile limbs.

Symmius caudatus Richardson
Figs. 1b, 3

Symmius caudatus Richardson, 1904:40–41, figs. 11–15.

Diagnosis.—As given for genus.

Material.—3 syntypes (of 9 reported by Richardson): USNM 29081; ovigerous ♀, 12.6 mm; juveniles, 8.8 mm and 12.2 mm. Oxe Zaki, Japan, 109–127 m (U.S. Fisheries Commission Steamer *Albatross* station 3715).

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REVISION OF THE LUMBRICULID OLIGOCHAETE *ECLIPIDRILUS* EISEN, 1881, WITH DESCRIPTIONS OF THREE SUBGENERA AND *ECLIPIDRILUS* (*LEPTODRILUS*) *FONTANUS* N. SUBG., N. SP. FROM PENNSYLVANIA

James T. Wassell

Abstract.—A division of seven species of *Eclipidrilus* into the three subgenera *Eclipidrilus, Premnodrilus,* and *Leptodrilus* is based on characteristics of the reproductive systems. *Eclipidrilus fontanus* n. sp. is similar to *E. lacustris* (Verrill, 1871), but has paired reproductive structures. A key to species of *Eclipidrilus* and records of recent collections are included.

Microdrile oligochaetes of the genus *Eclipidrilus* have a holarctic freshwater distribution. Six species occur in North America, one of which is also known from the British Isles, and a single species is restricted to Asiatic U.S.S.R. In the United States *Eclipidrilus* species are found in the Great Lakes and Mississippi River drainages, in waters of both the Rocky and Appalachian mountains, and in streams of the southeastern states. They have been found in both river and lake habitats and some species are restricted to unpolluted locations. Specimens are rare, in some places locally abundant, and current information suggests a restricted distribution. An accurate generic diagnosis has not appeared in the literature since the discovery of *E. levanidovi* Sokolskaya, 1977, which has reproductive structures more anterior than other species. For an historical review of the literature pertaining to this genus see Wassell (1981). A revised diagnosis is provided here.

Eclipidrilus Eisen, 1881

Diagnosis.—Prostomium prolobous, rounded or produced into proboscis-like extension. Preclitellar segments biannulate. Setae simple pointed with nodulus distal, similar throughout. Two pairs of posterior lateral blood vessels present. Male pores paired on VIII or X; or single median on X. Ovarian pores paired on IX or XI. Spermathecal pores paired on VII or IX; one or two median on IX; single median on VIII and IX. Testes: one pair in VIII or X; two pairs in IX and X; always present in segment bearing male pores. Vasa deferentia one or two pairs. Atria: tubular, with thick muscular walls of spirally arranged fibers; an outer layer of longitudinal fibers may be present. Prostatic cells surrounding the atria may be compact or sparse. Penes paired or single, of three general types: small protrusible; long muscular eversible; retractile with thin cuticularized sheaths. Ovaries: one pair in IX or XI, always present in segment immediately posterior male pores. Spermathecae: paired in VII or IX; one or two median in IX; one in both VIII and IX; always present in segment immediately anterior male pores.

Type-species.—*Eclipidrilus frigidus* Eisen, 1881, by original designation.

Eclipidrilus (*Eclipidrilus*) Eisen, 1881

Diagnosis.—*Eclipidrilus* with long muscular eversible penis. Penis without cuticular sheath and contained in muscle layer. Atrium with wide lumen posteriorly. Atrium constricted anteriorly with narrow lumen, before widening to contain penis. Penis formed from tissue lining anterior inside of atrium, which is continuous with atrium posteriorly and with longitudinal body wall muscle anteriorly. Penial structure not attached to dorsal body wall by retractor muscles. Atrium and male structures paired or single.

Type-species.—*Eclipidrilus frigidus* Eisen, 1881.

Remarks.—This is the nominate subgenus which in addition to *E.* (*E.*) *frigidus* Eisen, 1881, includes *E.* (*E.*) *asymmetricus* (Smith, 1896). The latter species was originally described as *Mesopodrilus* due to its singular penis and atrium. Because of the morphological similarity of the reproductive structures these two species are included in this subgenus.

In addition to its unpaired atria, *E.* (*E.*) *asymmetricus* has a prostomial extension. This species has not been collected since its original description. A recent attempt by the author to obtain it from samples taken at the type-locality (Quiver Lake, Illinois) was unsuccessful. Paratype material examined (NMNH 24588) is a post-reproductive specimen.

Eclipidrilus (*E.*) *frigidus* has paired reproductive structures and a blunt prostomium. Lectotype material was examined (NMNH 25565, 32911). This species has been recently collected from the Salmon River, Veil Falls, Idaho in 1976 by R. L. Denton. I am grateful to the collector and D. R. Spencer for these specimens, which are placed in the museum of the Louisiana State University (LSU 3176).

Eclipidrilus (*Premnodrilus*) Smith, 1900, new rank

Diagnosis.—*Eclipidrilus* with long retractile penis with cuticularized sheath and contained in muscle layer. Atrium with wide lumen posteriorly, constricted anteriorly to form duct attached to penis. Penis surrounded by muscle layer anteriorly continuous with longitudinal body wall muscle and may be attached to dorsal body wall posteriorly by retractor muscles. Atria and male structures paired.

Type-species.—*Premnodrilus palustris* Smith, 1900.

Remarks.—The subgenus (*Premnodrilus*) is designated for the generic name chosen by Smith in 1900 for species which possess a reproductive system of this type. An important characteristic of this subgenus is the thin cuticularized penis sheath, which has been described previously only by Sokolskaya (1977). Three species in this subgenus are distinguished by segmental location of reproductive structures, by condition of the prostomium, and dimensions of the atria. This subgenus includes: *E.* (*P.*) *palustris* (Smith, 1900), *E.* (*P.*) *daneus* Cook, 1966, and *E.* (*P.*) *levanidovi* Sokolskaya, 1977.

Eclipidrilus (*P.*) *daneus* has a prostomial extension and the atria have comparatively thin walls so that the lumen comprises about two-thirds of the diameter of the atria. This species has been collected from seven Louisiana parishes during 1979–1981; specimens are in the museum of the Louisiana State University (LSU 3178–3186). The holotype and paratypes have been examined (NMNH 32907, 32908).

Eclipidrilus (*P.*) *palustris* has a prostomial extension and atria have thicker walls than *E.* (*P.*) *daneus* so that the lumen comprises about one-third of the atrial diameter. This species has recently been collected from three counties in Florida (LSU 1490, 1949, 2156). A study of sagittal sections of one of these specimens reveals a glandular material in X, similar to that described for *Spelaedrilus multiporus* Cook, 1975, and a slight elaboration of the spermathecal duct, similar to that in *E.* (*E.*) *frigidus*, but less extensive. An additional pair of testes in IX was observed in this specimen. The cotype (NMNH 25509) was examined.

Eclipidrilus (*P.*) *levanidovi* is placed in this subgenus because of the cuticular penis sheath evident in the description. The reproductive structures are displaced anteriorly by two segments in contrast to all other *Eclipidrilus* species. No specimens were available for examination. The original description is in Russian.

Eclipidrilus (*Leptodrilus*), new subgenus

Diagnosis.—*Eclipidrilus* with short protrusible penis without cuticularization and not contained in muscle layer. Atrium with wide lumen posteriorly, constricted anteriorly to become the penis. Penis formed from papilla structure of body wall muscles, no retractor muscles attached dorsally. Atrium and male structures paired or single.

Type-species.—*Lumbricus lacustris* Verrill, 1871.

Remarks.—This new name is derived from the Greek "leptos" meaning slender, thin, small and weak. This refers to the small thin penis with weak musculature. The two species in this subgenus differ in the paired or unpaired condition of the reproductive systems. The unifying characteristic of this subgenus is the morphology of the atria and penes. This subgenus includes: *E.* (*L.*) *lacustris* (Verrill, 1871), and *E.* (*L.*) *fontanus*, new species.

Eclipidrilus (*L.*) *lacustris* has a single median atrium. It is reported from Lake Superior, where the type-collection was made, and recently from Cayuga Lake, New York (Spencer 1978) and Quebec, Canada (Cook in Brinkhurst and Cook, 1966). The Cayuga Lake specimen was made available to me for study and is placed in the museum of the Louisiana State University (LSU 3177). Lectotype and paralectotype specimens were examined (NMNH 15587, 17947, 32667).

Eclipidrilus (*Leptodrilus*) *fontanus*, new species
Figs. 1, 2

Material examined.—HOLOTYPE: NMNH 068641, Pennsylvania: Somerset County, Forbes State Forest, Wild Cat Spring, 22 Jul 1978, 1 whole mount specimen. PARATYPES: NMNH 068642, same locality and date, 10 whole specimens in formalin. NMNH 068643, same locality and date, 7 whole mount specimens. NMNH 068644, same locality and date, 1 specimen, 7 slides, transverse sections 20 μm thick. NMNH 068645, same locality, 29 May 1979, 1 specimen, 4 slides sagittal sections and 1 slide whole mount of posterior end. NMNH 068646, same locality, 29 May 1979, 1 specimen, 3 slides sagittal sections and 1 slide whole mount of posterior end. LSU 3053, same locality, 22 Jul 1978, 9 whole mount specimens and 1 sagittal sectioned specimen. ADDITIONAL SPECIMENS (all from Pennsylvania): LSU 3188, same locality, 22 Jul 1978, 1 transverse sectioned specimen. LSU 3046, same locality, 3 Oct 1976, 4 whole specimens. LSU 3047,

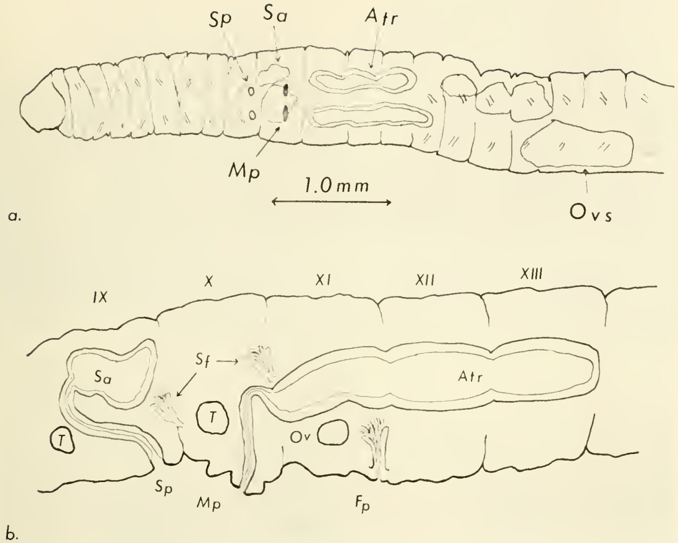

Fig. 1. *Eclipidrilus fontanus*: a, Holotype, drawing of whole mount from prostomium to XX; b, Diagram from sagittal sections of IX–XIII. Atr = atrium, Mp = male pore, Ovs = ovisacs, Sa = spermathecal ampulla, Sp = spermathecal pore, Fp = female pore, Ov = ovary, Sf = sperm funnel, t = testes.

same locality, 28 May 1978, 1 whole specimen. LSU 3048, Somerset County, Tub Mill Run, Forbes State Forest, 22 Jul 1978, 5 whole specimens. LSU 3049, Fayette County, Bear Run, 24 Sep 1976, 5 whole specimens, coll. Dr. W. P. Coffman. LSU 3050, same information, 9 Sep 1976, 5 whole specimens. LSU 3051, Fayette County, Dunbar Creek near Dunbar, Limestone Run at Game Commission Road, 23 Feb 1975, coll. J. Duncan, 2 whole specimens. LSU 3052, Somerset County, Powdermill Creek, Youghiogheny drainage, 28 Jan 1975, coll. Dr. J. Sykora, 2 whole specimens. (All specimens collected by author unless otherwise noted.)

Etymology.—From the Latin adjective "fontanus" relating to spring. This refers to the type-locality.

Diagnosis.—64 to 108 segments. Length up to 31 mm, preserved; diameter 0.6 mm at II, 0.8 mm at X. Prostomium rounded, as long as wide at peristomial junction. II–VIII with secondary annulations. Setae 93–253 μm long, ratio of point to node setal length to total setal length 0.28–0.30.

Testes paired, present in X, present or absent in IX. Two pairs male funnels present anterior septa 9/10 and 10/11. Atria paired, 0.3–1.4 mm long, cylindrical,

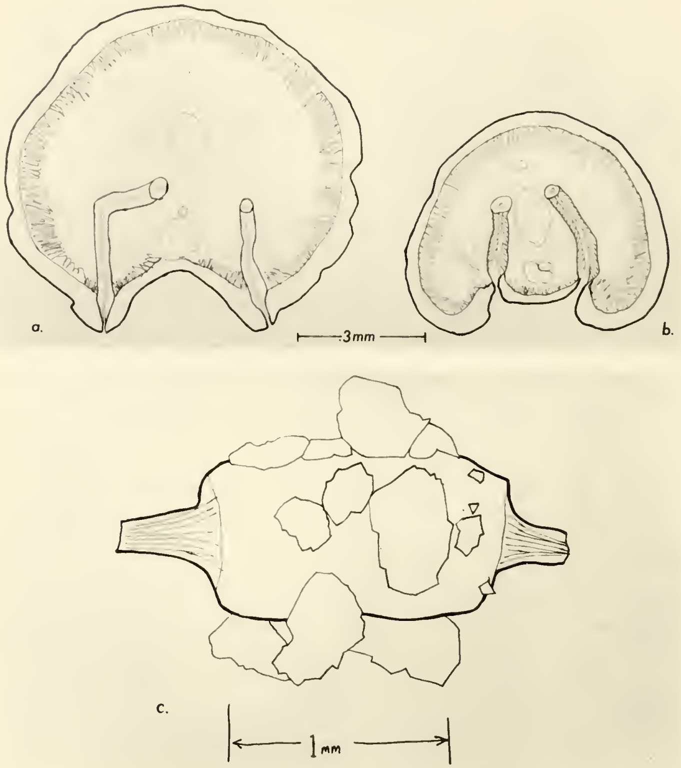

Fig. 2. *Eclipidrilus fontanus*: A, Transverse section of X through penial ducts and penis; B, Transverse section through spermathecal pores and ducts; C, cocoon with sand grains attached.

may extend to XIII, consisting of spiral muscles ca. 45 μm thick, diameter range 132–379 μm. Ratio of diameter of lumen to external diameter of atrium 0.60–0.75. Penes paired on X, protrusible extensions of distal duct of atrium without cuticularization.

Ovaries paired in XI, ovarian funnels open anterior 11/12. Spermathecae paired in IX, may extend into X, ampulla pear-shaped to ovoid, ca. 275 μm long, 200 μm wide. Spermathecal ducts distinct with uniform diameter ca. 25 μm, no muscular thickening of the duct, ca. 300 μm long, open on IX.

Table 1.—Comparison of species characteristics in *Eclipidrilus.*

Species	Penes	Atrium (diameter)	% lumen	Testes; funnels	Spermathecae	Ovaries	Prostomial extension
E. asymmetricus	Long eversible	Single	80	X; 10/11	IX, paired	XI	Present
E. frigidus	Long eversible	Paired (170–200 μm)	80	IX, X; 9/10, 10/11	IX, paired	XI	Absent
E. daneus	Long cuticularized retractile	Paired (120–220 μm)	80	X; 9/10, 10/11	IX, paired	XI	Present
E. levanidovi	Long cuticularized retractile	Paired (177–190 μm)	70	VIII; 8/9	VII, paired	IX	Absent
E. palustris	Long cuticularized retractile	Paired (270–300 μm)	30	(IX), X; 9/10, 10/11	IX, paired	XI	Present
E. lacustris	Small protrusible	Single (200–300 μm)	80	IX, X; 9/10, 10/11	IX, single or paired; VIII and IX, single	XI	Absent
E. fontanus n. sp.	Small protrusible	Paired (130–380 μm)	80	(IX), X; 9/10, 10/11	IX, paired	XI	Absent

Remarks.—This new species resembles *E.* (*L.*) *lacustris* except for the paired arrangement of reproductive structures. Two pairs of vasa deferentia occur in this species and one pair of testes is always present in X. A second pair of testes has been observed in IX in some specimens. The presence of anterior testes is probably not as strong a taxonomic character as previously thought. The occurrence of testicular tissue in IX in this species is indicative of an early maturity state and loss of gonad material in IX may result from sexual activity.

This species has been collected only from very clean, cold mountain streams. The type-locality is a cold, sandy bottom bubbling spring. The cocoon is barrel-shaped with sand grains attached.

Discussion.—This study reinforces the genus *Eclipidrilus* as a valid taxon. All species of *Eclipidrilus* are united because of the spiral arrangement of muscle fibers which comprise the atrium. The loss of bilateral symmetry in the reproductive system is an advanced condition in this genus and has occurred in two species. (Table 1). It has been suggested (Holmquist 1976) that the occurrence of unpaired reproductive organs is so unique within the Lumbriculidae (except *Tatriella* Hrabě, 1936) that the two species of *Eclipidrilus* with unpaired systems are deserving of generic rank. These species were originally in *Mesopodrilus* Smith, 1896, which was made a junior synonym of *Eclipidrilus* by Hrabě (1936) after Michaelsen (1901). The discovery of *E.* (*L.*) *fontanus* (with paired reproductive structures), which is similar to the unilateral *E.* (*L.*) *lacustris,* provides evidence that the bilateral arrangement is ancestral. Consequently, undesirable polyphyletic taxa would result from the elevation of these two species to a genus separated from *Eclipidrilus.*

Key to species of *Eclipidrilus*

1\. Single atrium 2

– Atria paired 3

2\. Atrium with constriction. Penis muscular, elongate. Spermathecae paired with pores median. Prostomial extension present. Illinois (unreported since 1896) .... *E.* (*E.*) *asymmetricus* (Smith, 1896)

– Atrium not constricted. Penis simple. Single spermatheca with median pore. Prostomium rounded. Cayuga Lake, New York; Lake Superior; Quebec, Canada; British Isles .... *E.* (*L.*) *lacustris* (Verrill in Smith and Verrill, 1871)

3\. Male pores on VIII. Spermathecae open on VII. U.S.S.R., Chukotski Peninsula .... *E.* (*P.*) *levanidovi* Sokolskaya, 1977

– Male pores on X. Spermathecal pores on IX 4

4\. Penes with lightly cuticularized sheaths. Prostomial extension present 5

– Penes without cuticularized sheaths. Prostomium rounded 6

5\. Atrial muscle 60–100 μm thick, lumen comprises ca. one-third of atrial diameter. Florida, South Carolina .... *E.* (*P.*) *palustris* (Smith, 1900)

– Atrial muscle 6–20 μm thick, lumen comprises ca. two-thirds of atrial diameter. Louisiana, Montana, South Carolina .... *E.* (*P.*) *daneus* Cook in Brinkhurst and Cook, 1966

6\. Atria constricted, extending to XV. Penes muscular, elongate. Spermathecal ducts elaborate. California, Idaho .... *E.* (*E.*) *frigidus* Eisen, 1881

– Atria not constricted, extending to XII. Penes simple. Spermathecal ducts simple. Pennsylvania .... *E.* (*L.*) *fontanus* n. sp.

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HYPSELOSTOMA LATISPIRA, A NEW PUPILLID LAND SNAIL FROM THE PHILIPPINE ISLANDS

Fred G. Thompson and Kurt Auffenberg

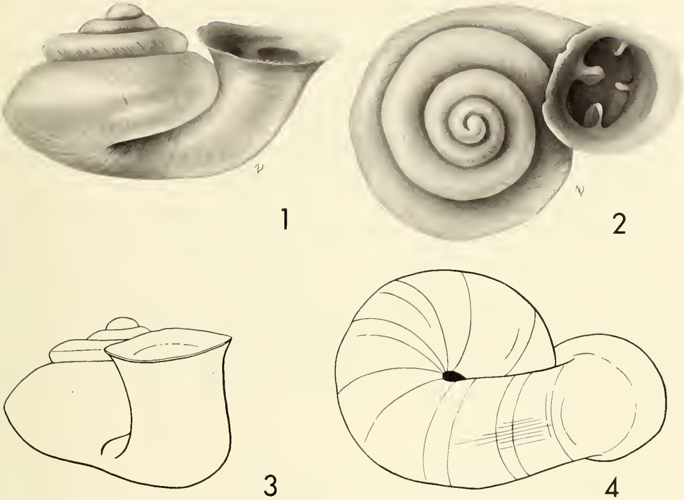
Abstract.—Hypselostoma latispira, new species (Gastropoda: Pulmonata, Pupillidae) is described from Luzon Island. It is most closely related to *H. roebeleni* Moellendorff from Coron Island. The Philippine species of *Hypselostoma* appear to be monophyletic and closely related to the type species, *H. tubiferum* (Benson), from the Malay Peninsula.

The genus *Hypselostoma* Benson, 1856, is widely deployed from Burma and the Malayan peninsula eastward to Vietnam, the Ryukyu Islands, and the Philippine Islands. The genus was monographed by Pilsbry (1917). Haas (1937), Tomlin (1939), and Benthem Jutting (1949, 1950, 1962) described additional species and subspecies. Von Moellendorff (1888), Quadras and von Moellendorff (1894, 1896), Pilsbry (1917), and Haas (1937) discuss the Philippine fauna.

Hypselostoma has a reduced aperture barrier, derived from a more generalized state, such as occurs in *Gyliotrachela* Tomlin, 1930 (see Solem 1981). In *Hypselostoma* the angular lamella and the parietal lamella are fused into a single sinuous tooth. In this respect the aperture barrier is similar to that of *Boysidia* Ancey, 1881. *Hypselostoma* differs from *Boysidia* by having the aperture projecting free from the last whorl and by having spiral sculpture. *Boysidia* has an adnate aperture and lacks spiral sculpture (Thompson and Dance 1983). *Hypselostoma*-type shells could have been derived from both *Gyliotrachela*-type and *Boysidia*-type ancestors. Considering the diverse assortment of shells classified as *Hypselostoma,* it is apparent that the genus as presently conceived is polyphyletic. The Philippine species are conchologically very similar. Apparently they are a monophyletic group, which appears to be closely related to the type-species, *H. tubiferum* Benson, 1856, from the Malayan Peninsula. This relationship is presumed on the basis of similar shell shapes and aperture barriers.

Hypselostoma latispira, new species
Figs. 1–4

Description.—Shell medium-sized for genus, 4.2–4.4 mm wide. Brown with white peristome. Depressed-conical in shape; about 0.51–0.56 times as high as wide. Whorls 4.3. Spire very depressed; first 4 whorls rapidly expanding laterally to form wide cone of about 90° (Fig. 1). Body whorl becomes more ventral in position so that penultimate whorl is scalariform (Figs. 1, 3). Last whorl projecting strongly to side and upward above periphery with plane of aperture lying at 15–30° to the horizontal axis. Minor diameter of shell 0.67–0.71 times major diameter. Base of last whorl obtusely convex. Umbilicus (Fig. 4) narrowly perforate or rimate with sides of umbilical wall evenly rounded onto base, not forming an obtuse angle. Last whorl angulate at periphery; usually not furrowed above or below (2 paratypes have very weak supraperipheral furrow). Sculpture consisting of low



Figs. 1–4. *Hypselostoma latispira*, holotype.

irregularly spaced growth striations and wrinkles that give surface fine, undulating appearance. Base of last whorl with fine longitudinal striations which are most prominent on last half of whorl. Peristome widely expanded; broadly triangular and nearly rounded in shape. Aperture slightly constricted in area of upper palatal plica. Internal barrier consisting of 4 teeth deeply inserted within aperture forming a cross-like configuration. Parietal lamella largest, about as high as wide, weakly sinuous and slightly arched toward upper palatal plica, forming rounded sinus in upper right corner and triangular sinus in upper left. Columellar lamella about as long as parietal lamella but about half as high. Upper palatal and lower palatal plica about equal-sized, small, and tubercular.

Measurements in mm of five specimens follow. Ratios are calculated from ocular micrometer units and not from converted mm measurements.

	Length	Major width	Lesser width	Aperture width	Length/maj. width	Les. width/maj. width
Holotype	2.3	4.5	2.9	1.7	0.51	0.65
Paratype	2.3	4.2	2.8	—	0.55	0.67
Paratype	2.4	4.2	3.0	1.8	0.56	0.71
Paratype	2.2	4.4	3.0	1.7	0.51	0.68
Paratype	2.4	4.4	3.0	1.9	0.54	0.68

Type-locality.—Philippine Islands, Luzon Island, Benguet Province, Baguio City (16°25′N, 120°37′E). HOLOTYPE: UF 39912; collected 16 Jun 1981 by Kurt

Auffenberg. PARATYPE: UF 39913 (4); same data as holotype. Non-paratypic specimens are UF 39914 (3); preserved in 70% alcohol. Specimens were found in the late morning during a rainstorm while they were crawling on damp algae covering huge limestone boulders approximately 10 m in diameter. The boulders were in an abandoned limestone quarry cut into a hillside. The area is forested with *Pinus* sp. Choyote, *Sechium edule,* formed a ground cover in the area of the quarry, but was not on the limestone boulders.

Remarks. —Seven other species of *Hypselostoma* occur in the Philippine Islands (Pilsbry 1917:183–188; Haas 1937:5–7). Five are monotypic. *Hypselostoma polyodon* Moellendorff, 1896 has two subspecies, and *H. luzonicum* Moellendorff, 1888 has five. The following two taxa are known from Luzon Island: *H. l. luzonicum* Moellendorff, 1888 and *H. l. major* Moellendorff, 1890. Both differ conspicuously from *H. latispira* by having high conical shells in which the height is about equal to the major width, and by having three palatal plica. *Hypselostoma latispira* is most similar in shape to *H. roebeleni* Moellendorff, 1894 from Coron Island in the Calamianes group. *Hypselostoma roebeleni* differs from *H. latispira* by having a broad umbilical perforation, which is about one-fourth the lesser width of the shell, and by having a strong peripheral keel, which is accentuated above by a deeply impressed furrow extending nearly to the peristome and a similar but weaker furrow below.

Etymology.—The species name *latispira* is derived from the Latin *latus,* meaning broad, and *spira,* a coil. The name alludes to the low, wide spire that characterizes the species, and is a noun in apposition.

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REVISION OF THE MILLIPED GENUS *DYNORIA* (POLYDESMIDA: XYSTODESMIDAE)

Rowland M. Shelley

Abstract.—The milliped genus *Dynoria* is unique in the tribe Apheloriini by lacking torsion in the acropodites of the male gonopods. Thus, the prostatic groove does not cross from the medial to the lateral surfaces but runs entirely along the former until it reaches the distal solenomerite. *Dynoria* is comprised of two species, *D. icana* Chamberlin and *D. medialis* Chamberlin, which differ chiefly in the configuration of the solenomerite and the presence (*icana*) or absence (*medialis*) of a parasolenomerite. The species are widely allopatric with *D. icana* occurring in the southeastern corner of the Blue Ridge Province and *D. medialis* in central and southwestern Georgia. *Dynoria* and its close relative *Furcillaria* occupy a separate evolutionary branch of the Apheloriini, and are distantly related to the "sigmoid" taxa. They are remnants of an early piedmont immigration wave from the Appalachian mountains, and all the species except *D. medialis* seem headed toward extinction.

The milliped family Xystodesmidae is the dominant faunal element in the southeastern United States. Genera like *Apheloria, Sigmoria, Cherokia,* and *Pleuroloma* occur throughout much of the region and have been collected repeatedly since the mid-19th century. Consequently, they were often cited in taxonomic publications and became entangled in nomenclatorial confusion. Clarification has recently been achieved of the last three through tedious, painstaking revisions, in which all past names were reevaluated, all type specimens reexamined, and all valid species and subspecies redescribed and illustrated (Hoffman 1960; Shelley 1980, 1981a). Not all southeastern genera are this widespread, however; some occur in only one or two states or are restricted to a single physiographic province. These taxa have rarely been encountered by field collectors and have therefore received only a few citations. Consequently, their taxonomy enjoys greater stability and can be easily reviewed. One such genus is *Dynoria.*

The first specimen of *Dynoria* was collected in 1910, but it was not described until 1939, when Chamberlin established the genus for the type species, *D. icana.* In 1947 he proposed a second species, *D. parvior,* from the mountains of northern Georgia, but Chamberlin and Hoffman (1958) correctly assigned this binomial to the synonymy of *Cherokia georgiana* (Bollman). Chamberlin (1949) described *D. medialis* from Atlanta, and both *D. icana* and *D. medialis* were listed in the 1958 checklist as components of the American fauna. Hoffman (1979) assigned *Dynoria* to the tribe Apheloriini and reported that it consisted of two species in the southeastern states.

As with most Chamberlinian diagnoses and descriptions, those of *Dynoria* and its two species are inadequate by modern standards, amounting to mere validation statements for the scientific names. The illustrations are rough sketches that do not begin to reveal the important features and complexity of the *Dynoria* gonopod. Consequently, Shelley (1981b) had to deal briefly with *Dynoria* and put forth a short generic definition in order to diagnose adequately the new, related genus *Furcillaria. Dynoria* was defined as the only genus in the tribe Apheloriini lacking the characteristic torsion of the acropodite at ¼ to ⅓ length, which results in a crossing of the prostatic groove from the medial to the lateral surfaces. In *Dynoria,* the groove runs entirely along the medial side of the acropodite stem and is visible solely from this perspective until it passes onto the apical solenomerite. The groove is therefore obscured in lateral aspect, except for the terminal part on the solenomerite. These statements by Shelley (1981b) are the only definitive remarks ever made on *Dynoria,* and are expanded here into a formal generic diagnosis with parallel accounts of the two species. Relatively few preserved specimens of *Dynoria* are available in museum and private collections, and their repositories are indicated by the following acronyms in the species accounts:

AMNH—American Museum of Natural History, New York, New York.

CC—Biology Department, Columbus College, Columbus, Georgia.

FSCA—Florida State Collection of Arthropods, Gainesville, Florida.

NCSM—North Carolina State Museum of Natural History, Raleigh, North Carolina. The invertebrate catalog numbers of material in this collection are indicated in parentheses.

RLH—Private collection of Richard L. Hoffman, Radford, Virginia.

RVC—Private collection of Ralph V. Chamberlin, now being accessioned by the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Taxonomic Characters

The taxonomic characters of *Dynoria* are found exclusively on the gonopods, and allow for easy recognition of the genus and distinction of the species. Color pattern has no taxonomic value because sympatric species of *Cleptoria* and other genera also exhibit the red paranota and metatergal stripes of *Dynoria.* Likewise in *Dynoria,* the length and configuration of the process of the fourth sternum are not sufficiently different from their conditions in other genera to allow for authentic determinations.

The most important diagnostic character of the gonopods of *Dynoria* is the aforementioned absence of torsion in the acropodite. No other xystodesmid genus in the eastern United States, in any of the four tribes, displays this trait.

At the species level, the taxonomically useful characters are located distally on the acropodite, at the division into tibial process and solenomerite branch. Differences in the length and configuration of the solenomerite branch are important along with the presence or absence of further division into a solenomerite proper and a parasolenomerite. In *D. medialis* the solenomerite branch is not subdivided and curves across the stem of the acropodite medial to the tibial process. A parasolenomerite is present in *D. icana,* and the solenomerite is directed subanteriad, away from the stem of the acropodite. Thus in *D. icana,* the tibial process is completely visible in medial view, whereas in *D. medialis* it is largely obscured by the solenomerite.

Dynoria Chamberlin

Dynoria Chamberlin, 1939:7.—Chamberlin and Hoffman, 1958:31.—Hoffman, 1979:159.

Type-species.—Dynoria icana Chamberlin, 1939, by original designation.

Description.—A genus of large, robust xystodesmids with the following characteristics:

Body composed of head and 20 segments in both sexes; size varying from 10–11.5 mm wide and 41–49 mm long; W/L ratio similarly varying from around 22–25%. Body essentially parallel sided in midbody region, tapering at both ends.

Color in life the typical apheloriine pattern of red paranota and red metatergal stripes on black background.

Head of normal appearance, smooth, polished. Epicranial suture shallow, indistinct, terminating in interantennal region, not apically bifid; interantennal isthmus relatively wide; genae not margined laterally, with shallow central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Antennae moderately slender, varying in length, becoming progressively more hirsute distally, with 4 conical sensory cones on ultimate article; no other sensory structures apparent. Facial setae greatly reduced, only clypeal and labral present.

Terga smooth, polished, becoming slightly coriaceous on anterior half. Collum variably broad, ends extending slightly beyond those of following tergite. Paranota relatively flat or moderately depressed, interrupting slope of dorsum in males but continuing slope in females, caudolateral corners rounded on anteriormost segments, becoming blunt in midbody region and progressively more acute posteriorly. Peritremata distinct, strongly elevated above paranotal surface; ozopores located at about midlength, opening subdorsad. Prozonites smaller than metazonites; strictures distinct, smooth.

Caudal segments normal for family.

Sides of metazonites irregular, with varying shallow, curved impressions. Strictures sharp, distinct. Pregonopodal sterna of males modified as follows: that of segment 4 with variable, apically divided process, shorter than or subequal to lengths of adjacent coxae; sternum of segment 5 with two small knoblike processes between 4th legs and two elevated, flattened areas between 5th legs; sternum of segment 6 with shallow convex recession between 7th legs. Postgonopodal sterna generally flattened, with varying shallow grooves and depressions, strongly bilobed on segment 8. Gonapophyses on 2nd leg pair of males short, only slightly elevated above coxal surfaces, with round, apical knobs. Pregonopodal legs densely hirsute; postgonopodal legs becoming progressively less hirsute caudally. Coxae with low tubercles in caudal half of body; prefemoral spines moderately long and sharply pointed; tarsal claws bisinuate. Hypoproct broadly rounded; paraprocts with margins strongly thickened.

Gonopodal aperture round to ovoid, with slight anterolateral indentations, front flush with metazonal surface, sides elevated. Gonopods in situ lying either entirely within aperture or slightly overlapping posterior margin; acropodites either lying beside each other and overhanging opposite coxa, or with tips overlapping. Coxae moderately large in size, without apophyses, connected by membrane only, no sternal remnant. Prefemur moderately large, without prefemoral process. Acropodites moderately thick and heavy, extending directly ventrad from prefemur, without torsion or twisting, divided at ⅔–¾ length into lateral tibial process and another more medial branch carrying prostatic groove, with or without further division. Tibial process usually short, straight, and subacute apically, usually subequal in length to solenomerite branch. Solenomerite branch either undivided and curving gently mediad to tibial process or divided basally into short, straight, blunt solenomerite and more caudal, sharply acute parasolenomerite. Latter lying close to and running parallel to solenomerite, extending across distal extremity of acropodite to tibial process, forming pocket on distomedial face of acropodite. Prostatic groove arising in pit in base of prefemur, running entirely along medial side of stem of acropodite to base of solenomerite, continuing on anterior or lateral sides of latter to terminal opening.

Cyphopodal aperture broad, encircling 2nd legs, sides elevated above metazonal surface. Cyphopods in situ located lateral to 2nd legs, variously oriented in aperture. Receptacle small, situated ventrad or dorsad to valves, surface finely granulate. Valves relatively large, equal or unequal in size, surface finely granulate. Operculum large or small, located under free end of valves.

Distribution.—Southeastern extremity of the Blue Ridge Province in North Carolina and Georgia, extending slightly into the Piedmont Plateau of western South Carolina and well into the Piedmont and Coastal Plain of central and southwestern Georgia. *Dynoria* has basically a north-south, longitudinal distribution, and the two species are allopatric with some 60 miles between them (Fig. 10).

Species.—Two. Due to the intensity with which the range of *Dynoria* and neighboring areas have been collected, I am confident that no additional species exist.

Remarks.—Both species of *Dynoria* have the typical apheloriine recession in the sternum of the 6th segment. This cavity is common in genera with curved acropodites that extend forward over the anterior edge of the aperture, and provides space for the acropodites when the body segments are compressed. However, the acropodites in *Dynoria* lie either within the aperture or overlap slightly the caudal margin. Hence, the depression is nonfunctional in this genus.

Dynoria icana Chamberlin

Figs. 1–5

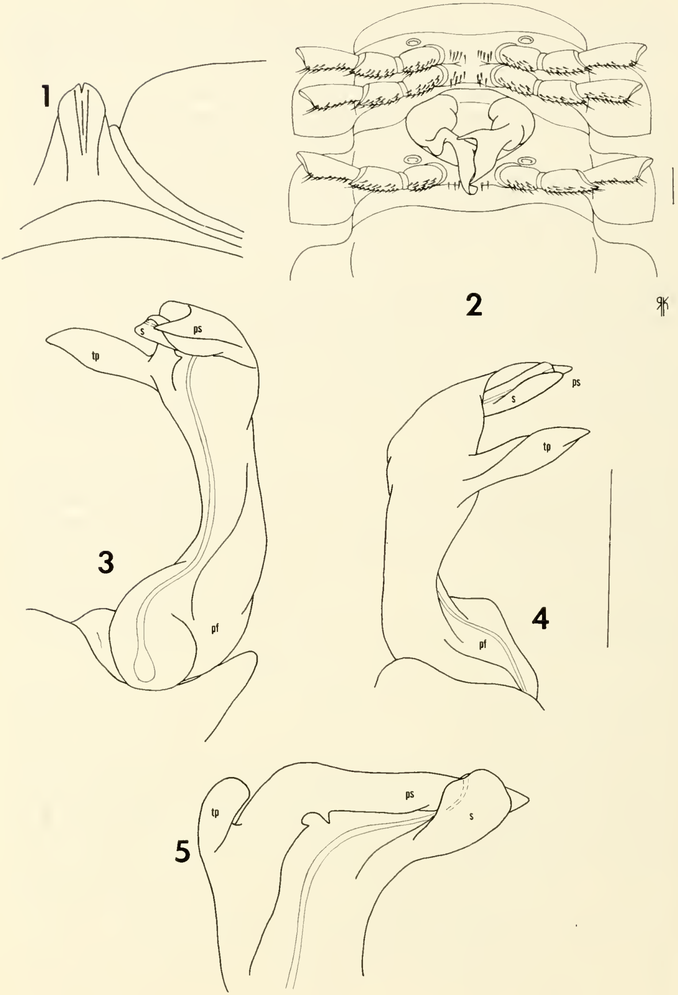
Dynoria icana Chamberlin, 1939:7, pl. 2, figs. 13–14.—Chamberlin and Hoffman, 1958:32.

Type specimens.—Male holotype and female allotype (RVC) collected by R. V. Chamberlin, 31 Jul 1910, from Tallulah Falls, Habersham County, Georgia.

Diagnosis.—Gonopods in situ with tips of acropodites overlapping each other and caudal margin of aperture; solenomerite branch divided into solenomerite proper and parasolenomerite; tibial process fully visible in medial view.

Holotype.—Body badly fragmented and unmeasurable; measurements taken from Rabun County specimen: Length 49.1 mm, maximum width 11.2 mm, W/L ratio 22.8%, depth/width ratio 60/7%, segmental widths as follows:

collum	7.8 mm	10th–14th	11.2
2nd	9.1	15th	10.6
3rd	9.6	16th	9.7
4th	10.1	17th	7.9
5th	10.6	18th	5.9
6th–9th	11.0		



Figs. 1–5. *Dynoria icana.* 1, Process of 4th sternum of holotype, caudal view; 2, Gonopods in situ, ventral view of male from Macon Co., NC; 3, Telopodite of left gonopod of holotype, medial view; 4, The same, lateral view; 5, Distal half of acropodite of male from Rabun Co., GA, dorsal view. pf,

Color in life not indicated. The four specimens that I collected were black with red paranota and red stripes along the caudal margins of the metaterga. There was also a red stripe along the anterior margin of the collum.

Head capsule smooth, polished; width across genal apices 5.1 mm; interantennal isthmus 1.9 mm. Epicranial suture shallow. Antennae extending caudad to middle of third metatergite; relative lengths of antennomeres 2 > 3 > 5 = 6 > 4 > 1 > 7, 2–6 clavate. Genae not margined laterally, with shallow central impression, ends broadly rounded and extending beyond adjacent cranial margins. Facial setae as follows: epicranial, interantennal, frontal, and genal not detected and presumed absent; clypeal about 10-10, labral about 14-14.

Terga smooth, polished, with only slight wrinkling on anterior part of paranota. Collum moderate in size, ends extending slightly beyond those of following tergite. Paranota relatively flat, interrupting slope of dorsum; caudolateral corners rounded through segment 6, becoming blunt and progressively more pointed posteriorly. Peritremata distinct, clearly elevated above paranotal surface; ozopores situated at about midlength, opening subdorsad.

Sides of metazonites with varying shallow grooves and impressions. Strictures distinct. Sternum of segment 4 with moderate apically divided process between 3rd legs, subequal in length to widths of adjacent coxae (Fig. 1); sternum of segment 5 with moderately long knobs between 4th legs and elevated flattened areas between 5th legs; 6th sternum with shallow convex recession between 7th legs. Postgonopodal sterna flat, plate-like, with shallow, transverse and longitudinal grooves on segments 8–10, disappearing thereafter. Coxae with low, blunt teeth on segments 8–10, becoming more sharply pointed posteriorly and continuing to segment 17.

Gonopodal aperture broadly ovoid, 3.4 mm wide and 2.1 mm long at midpoint, indented anterolaterally, sides flush with metazonal surface. Gonopods in situ (Fig. 2, not this specimen), with acropodites projecting ventromediad from aperture, apices overlapping and overhanging caudal margin of aperture. Gonopod structure as follows (Figs. 3–5): Acropodite projecting directly ventrad from prefemur, not twisted or curved. Tibial process with smooth, continuous margins, apically subacuminate, directed subanteriad, length subequal to solenomerite branch. Latter divided into solenomerite proper and parasolenomerite on caudal side. Solenomerite apically blunt with slight depression in midline, directed subanteriad, with small, rounded basal lobe. Parasolenomerite apically acute, closely appressed to, and apically parallel to, solenomerite; outer margin forming distal extremity of acropodite, extending in sublinear fashion and bending proximal to insertion near base of tibial process; inner margin extending across medial face of acropodite stem to insertion at about ⅔ length, forming pocket on distomedial face of acropodite, margin irregular, with two sharply pointed teeth near midlength. Prostatic groove arising in pit in base of prefemur, running entirely along

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prefemur; ps, parasolenomerite; s, solenomerite; tp, tibial process. Scale line for Fig. 2 = 1.00 mm; line for other figs. = 1.00 mm for 1 and 5, 1.77 mm for 3–4. Setation is omitted from all sternal and dissected gonopod drawings in this paper.

medial side of acropodite, curving onto solenomerite and continuing to apical opening.

Female allotype.—Length 41.1 mm, maximum width 10.1 mm, W/L ratio 24.6%, depth/width ratio 75.2%. Agreeing closely with male in all somatic details; paranota only slightly more depressed. Cyphopods in situ with edge of receptacle and valves visible in aperture, valves directed anterolaterad. Receptacle small, situated ventrad to valves, surface finely granulate, margin finely scalloped. Valves relatively large and unequal, outer one larger, surface finely granulate. Operculum minute, hidden under free end of valves.

Variation.—The tibial process and parasolenomerite of *D. icana* vary in several respects. The former has a sinuous margin in the male from Clayton, Georgia, but otherwise it is straight with a slight lobe on the proximal edge. In most males the tibial process is parallel to, and subequal in length to, the solenomerite; however, in the South Carolina males it is longer and directed more ventrad. The parasolenomerite has a subterminal tooth in the specimen from near the Chatooga River, South Carolina and is directed more dorsad than the solenomerite in both South Carolina males. The number of teeth on the inner margin varies from two to four.

Ecology.—Despite intensive sampling in its range, I have only collected *D. icana* once, under a thick layer of leaves in a slight depression in mixed deciduous woods near Hartwell Reservoir. This was a rather dry, oak-hickory forest, 100 feet or so from the lake, and unlike the damp, moist habitat of most apheloriine species. The site was also unusual in its thick leaf layer, as opposed to the thin layers of maple or dogwood leaves under which most apheloriines occur.

Distribution.—The southeastern extremity of the Blue Ridge Province and adjacent fringe of the Piedmont Plateau in the contiguous corners of North Carolina, South Carolina, and Georgia (Fig. 10). The area lies mostly on the southern and western sides of the Savannah River, but as I noted in 1981, it spreads slightly across headwater rivers into the western fringe of Oconee County, South Carolina. Specimens were examined as follows:

NORTH CAROLINA: *Macon Co.*, 2.5 mi. W Otto, Coweeta Hydrological Station, 6 M, 9 Jul 1958, R. L. Hoffman (RLH).

SOUTH CAROLINA: *Oconee Co.,* 2 mi. N Mountain Rest, Ridge along Chatooga R. off SC hwy. 28, M, 21 Jul 1958, R. L. Hoffman (RLH); and 6.8 mi. S Westminster, along SC hwy. 67 near Hartwell Res., M, 3 F, 9 Jun 1978, R. M. Shelley and W. B. Jones (NCSM A2063).

GEORGIA: *Rabun Co.,* Clayton, M, Jul 1910, W. T. Davis (AMNH). *Habersham Co.,* Tallulah Falls, M, F, 31 Jul 1910, R. V. Chamberlin (RVC) TYPE LOCALITY.

Remarks.—Proper interpretation of the gonopod of *D. icana* is dependent upon understanding the parasolenomerite, but this is usually hampered by debris which accumulates in the pocket on the distomedial face of the acropodite. This must be removed with a fine insect pin to reveal the inner margin of the parasolenomerite. If it is not removed, the cavity can be easily overlooked even in a detailed examination, resulting in misinterpretation of the gonopod structure.

Chamberlin and Hoffman (1958) reported *D. icana* from Saluda, South Carolina, which is far from the actual range of the species and a highly doubtful locality. The male on which this record is based is in the Chamberlin collection, but its gonopods are lost. The vial contains the label, "SC, Saluda, 5 August 1910, R. V. Chamberlin." I found this vial in a jar with others Chamberlin collected at Saluda, North Carolina, on the same date, one of which contained the holotype of *Sigmoria divergens.* Thus it is obvious that Chamberlin was in Saluda, North Carolina, on this date instead of Saluda, South Carolina, and that this specimen is of *Sigmoria divergens* rather than *Dynoria icana.* The Saluda, South Carolina, record is therefore deleted.

Dynoria icana seems a genuinely rare species. With all the collecting that has taken place over the past 50 years in the southern Blue Ridge Mountains, it has only been taken five times, and I only found it once in a dozen or so trips to the range. Population sizes appear to be small, as most samples have only one or two specimens. The species may be declining in numbers toward extinction, and thus a worthy candidate for state and national endangered species lists.

Dynoria medialis Chamberlin
Figs. 6–9

Dynoria medialis Chamberlin, 1949:3, figs. 5–6.—Chamberlin and Hoffman, 1958:32.

Type specimens.—Male holotype (RVC) collected by P. W. Fattig, 12 Jul 1946, from Atlanta, Georgia, without indication of the county or section of Atlanta.

Diagnosis.—Gonopods in situ with acropodites wholly enclosed within aperture, lying transversely beside each other and overhanging opposite coxa; solenomerite branch without parasolenomerite, not divided, curving gently anteriad and obscuring much of tibial process in medial view.

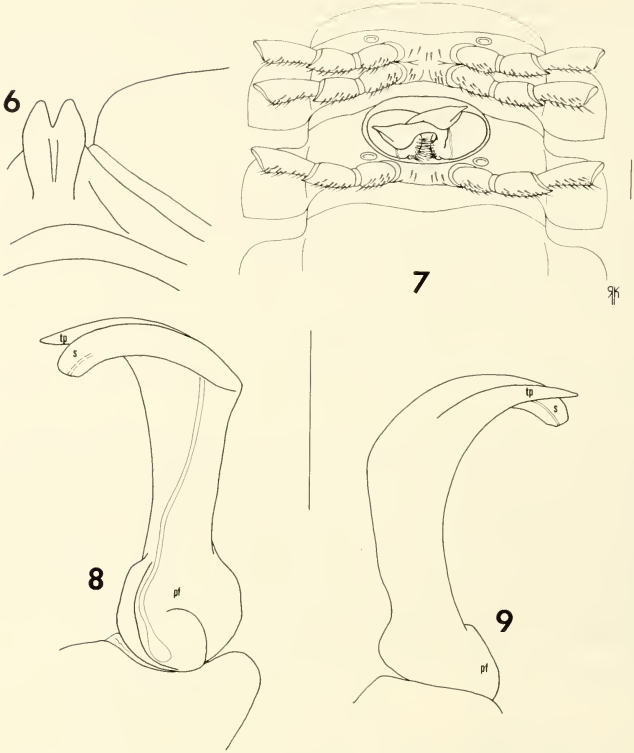
Holotype.—Body badly fragmented and unmeasurable; following segmental measurements taken from topotypical male collected in DeKalb County section of Atlanta in 1960: length 42.2 mm, maximum width 10.6 mm, W/L ratio 25.1%, depth/width ratio 57.5%. Segmental widths as follows:

collum	8.0 mm	10th–13th	10.6
2nd	9.1	14th–15th	10.2
3rd	9.4	16th	9.5
4th	9.8	17th	8.3
5th–9th	10.4	18th	6.3

Color in life not indicated, but all the specimens that I collected had the same markings as *D. icana.*

Somatic features similar to those of *D. icana* with following exceptions: Width across genal apices 5.4 mm; interantennal isthmus 2.7 mm. Antennae long and narrow, extending to middle of fourth tergite. Facial setae as in *D. icana* except labral about 16-16.

Process of 4th sternum apically divided, shorter in length than widths of adjacent coxae (Fig. 6); sternum of segment 5 with small lobes between 4th legs and elevated flattened areas between 5th legs; 6th sternum convexly recessed between 7th legs. Postgonopodal sterna flat, plate-like, with only faint, shallow, central impressions. Coxae with low blunt tubercles beginning on segment 10 and continuing to segment 17.



Figs. 6–9. *Dynoria medialis.* 6, Process of 4th sternum of holotype, caudal view; 7, Gonopods in situ, ventral view of male from Harris Co., GA; 8, Telopodite of left gonopod of holotype, medial view; 9, The same, lateral view. Abbreviations as in Figs. 1–5. Scale line for Figs. 6 and 7 = 1.00 mm, for Figs. 8 and 9, 1.77 mm.

Gonopodal aperture rounded, 3.7 mm wide and 2.3 mm long at midpoint, indented anterolaterally, sides flush with segmental surface. Gonopods in situ (Fig. 7, not this specimen) with acropodites projecting mediad from aperture, extending over coxa of opposite gonopod and lying wholly within aperture. Gonopod structure as follows (Figs. 8–9): Acropodite projecting directly ventrad from prefemur, not twisted or curved. Tibial process with smooth, continuous margins, apically acute, directed subanteriad, largely concealed in medial view by solenomerite. Solenomerite subequal in length to tibial process, curving gently across

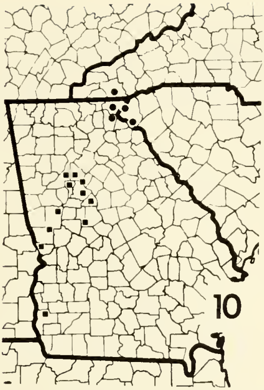


Fig. 10. Distribution of *Dynoria*. dots, *icana*; squares, *medialis*.

stem of acropodite on medial side of tibial process, margins smooth and continuous, tip blunt, directed downward (dorsad) toward coxa. Parasolenomerite absent. Prostatic groove arising in pit in base of prefemur, running entirely along medial side of acropodite to base of solenomerite, continuing onto lateral side of solenomerite to apical opening.

Female topotype.—Length 42.3 mm, maximum width 10.7 mm, W/L ratio 25.3%, depth/width ratio 26.5%. Agreeing closely with male in somatic features, except paranota more strongly depressed, giving appearance of more highly arched body.

Cyphopods in situ with valvular opening visible in aperture, valves directed ventrad. Receptacle small, located on caudal side of valves, surface finely granulate. Valves large, subequal, surface finely granulate. Operculum relatively large, clearly visible under medial end of valves.

Variation.—The only significant gonopodal variation in *D. medialis* involves the relative lengths of the solenomerite and tibial process in the southern part of the range. The former is much longer in the males from Muscogee and Early counties and curves appreciably dorsad apically, so that its overall configuration is of an arc with broad diameter.

Ecology.—All the specimens of *D. medialis* that I collected were found in moist spots under thin layers of leaves on relatively hard substrates.

Distribution.—The Piedmont Plateau and Coastal Plain of central and southwestern Georgia between the Chattahoochee and Ocmulgee rivers, ranging from Atlanta to just north of the common point of Georgia, Alabama, and Florida (Fig. 10). The species is restricted to Georgia and the eastern side of the Chattahoochee River. It has not been encountered in Alabama despite its occurrence in the adjacent tier of counties in southwestern Georgia. Specimens were examined as follows:

Fig. 11. Hypothetical dispersal routes for ancestral stock of *Furcillaria* and *Dynoria*. The dashed line is the approximate boundary of the southern Appalachian (Blue Ridge) Mountains.

GEORGIA: ?*Fulton Co.,* Atlanta, M, 12 Jul 1946, P. W. Fattig (RVC) and M, 2 Apr 1948, P. W. Fattig (RVC) TYPE LOCALITY. *DeKalb Co.,* Atlanta, M, F, Oct 1960, E. Davidson (FSCA). *Clayton Co.,* 0.4 mi. S Conley, M, 4 Dec 1960, L. Hubricht (RLH). *Rockdale Co.,* Panola Mountain State Park, M, 2 F, 30 Jul 1977, R. M. Shelley (NCSM A1611). *Henry Co.,* W of Ola, M, 4 Dec 1960, L. Hubricht (RLH). *Butts Co.,* Indian Springs State Park, M, F, 20 Nov 1977, R. M. Shelley (NCSM A1790). *Monroe Co.,* 1.5 mi. N Culloden, M, 4 May 1961, L. Hubricht (RLH). *Meriwether Co.,* 0.8 mi. N Avalon, M, 11 Mar 1961, L. Hubricht (RLH). *Harris Co.,* Franklin D. Roosevelt State Park, 3 M, F, 29 Jul 1977, R. M. Shelley (NCSM A1609). *Muscogee Co.,* Columbus, Columbus College Campus, M, 24 Jul 1974, collection unknown (CC). *Early Co.,* Kolomoki Mounds State Park, 2 M, 19 Nov 1977, R. M. Shelley (NCSM A1784), and 5 M, F, 1 May 1983, R. M. Shelley and P. B. Nader (NCSM A4022).

Remarks.—The range of *D. medialis* is much greater than that of *D. icana,* and it is also much more abundant in its range. The ease with which I have found it suggests that *D. medialis* would be encountered in most suitable habitats between Atlanta and a line connecting Macon and Columbus. South of this level, however, it becomes rare, and the Early County record is about 70 miles from Columbus, the closest locality. I have searched unsuccessfully in the intervening counties for *D. medialis,* and the Early County population may be disjunct from the main population in central Georgia.

Relationships and Evolution

With the common features of a lateral tibial process and a medial solenomerite, *Dynoria* and *Furcillaria* comprise a separate evolutionary branch in the Apheloriini. Hoffman (1963) suggested that the lowland genera *Dynoria, Lyrranea,* *Cleptoria,* and *Stelgipus* might constitute a separate tribe and listed potential characters of the tribe, but it is now evident that such a taxon is unjustified because of synapomorphies with more typical "sigmoid" apheloriine genera. These synapomorphies include the process on the 4th sternum, the depression in the 6th sternum, and, for *Furcillaria* and *Cleptoria,* the flanges on the medial faces of the acropodites. As mentioned in the generic account the sternal depression is nonfunctional in *Dynoria,* but its presence links the genus to those in the Apheloriini with curved or rounded acropodites, which project anteriad from the aperture and insert into the depression when the body segments are compressed. The processes of the 4th sterna in both *Dynoria* and *Furcillaria* are similar to those of species of *Sigmoria, Brevigonus,* and other genera (Shelley 1981a, c), and another indicator of phylogenetic affinity. Finally, the flange on the peak zone of the acropodite in *Furcillaria* is in a similar position to, and apparently homologous to, those of most montane species of *Sigmoria.*

On the basis of these observations, I propose the evolutionary scheme depicted in Fig. 11. Ancestral "sigmoid" stock moved into the western Piedmont of South Carolina from the adjacent Blue Ridge Mountains, and a form lacking torsion split from the main population. The latter pushed eastward into South Carolina, and populations became progressively more isolated from each other as younger and more successful apheloriine competitors spread into the area. All that remains of this early penetration are the three species of *Furcillaria* (Shelley 1981b). The form without torsion, the proto-*Dynoria* stock, underwent a second dichotomy in the Savannah River Valley, with one descendant moving up the valley and reentering the mountains. The other spread farther into Piedmont Georgia, eventually reaching the Coastal Plain. Thus, I think that the presence of *D. icana* in the southern Blue Ridge is due to a reinvasion from the Piedmont, and that it did not originate there or migrate there from another section of the mountains.

The nature of the original ancestral stock cannot be surmised. No known Appalachian species of *Sigmoria* possesses an apically divided acropodite or even a vestigial tibial process, so *Furcillaria* and *Dynoria* are therefore the sole survivors of both an early line of descent in the Apheloriini and an early Piedmont immigration wave. The area in Georgia inhabited by *D. medialis* contains few other tribal representatives, and it therefore encounteres little competitive resistance. *Cleptoria rileyi* (Bollman) and *Lyrranea persica* Hoffman are the only sympatric or nearly sympatric piedmont species, and an undescribed form of *Hubroria* is sympatric and syntopic at Kolomoki Mounds in the Coastal Plain of southwestern Georgia. However, population sizes of *D. icana* are small, and it is rarely encountered. The three species of *Furcillaria* occupy narrow, relictual ranges (Shelley 1981b: fig. 17) and probably experience strong competition from several sympatric apheloriine species. Habitat destruction within their ranges could accelerate the natural decline and bring them to extinction in a few decades.

Acknowledgments

I thank Richard L. Hoffman for the loan of specimens in his collection and access to the types of *D. icana* and *D. medialis* in the Chamberlin collection. Materials in the collections of the AMNH, FSCA, and Columbus College were kindly loaned by Norman I. Platnick, Howard V. Weems, Jr., and George E. Stanton, respectively. Specimens from Franklin D. Roosevelt, Indian Springs, Kolomoki Mounds, and Panola Mountain state parks, Georgia, were taken with permission of the parks and Historic Sites Division, Georgia Department of Natural Resources. Figures 2 and 6 were prepared by Renaldo G. Kuhler, NCSM scientific illustrator. This study was supported in part by National Science Foundation grants numbers DEB 7702596 and DEB 8200556.

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ANNOTATED LIST OF THE FISHES OF NEVADA

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Abstract.—160 native and introduced fishes referable to 108 species, 56 genera, and 19 families are recorded for Nevada. The increasing proportion of introduced fishes continues to burden the native ichthyofauna.

The first list of all fishes known from Nevada by La Rivers and Trelease (1952) eventually culminated in La Rivers' Fishes and Fisheries of Nevada, published in 1962. Over the past twenty years, a number of changes have occurred in the fish fauna of the state. These include additions through "official" actions as well as by "unofficial" means. Some taxa have become extinct and many have become much less abundant (Deacon 1979, Deacon *et al.* 1979). Numerous changes have also occurred in our understanding of probable taxonomic relationships of the fishes. The increased number of subspecies recognized since the 1962 list reflects a better understanding of distribution and geographic variation of the ichthyofauna.

Our purpose is to produce a checklist that includes all taxa known from the state within historical times. The list includes all fishes native to Nevada and those that have been introduced into the state, whether or not they have become established. Our checklist reflects current understanding of the fauna and highlights those areas where additional work is needed.

Including subspecies, we record 160 fishes in the present fauna of Nevada referable to 108 species, 56 genera, and 19 families. We recognize 67 subspecies referable to 15 species. The Cyprinidae is by far the most diverse fish family in Nevada and is represented by 39 subspecies, 31 species, and 18 genera.

Introduced fishes (those not native to the state) continue ever-increasingly to contribute to the Nevada fauna. Sixty-three species (58%) have been introduced and 45 (42%) are native. However, if subspecies are included, 69 fishes (43%) have been introduced and 91 (58%) are native. Only six of the 19 fish families are native to the state. La Rivers and Trelease (1952) reported 33 introduced fishes including subspecies and fishes unsuccessfully introduced into Nevada (but excluding the royal silver trout and emerald trout, which were actually introduced rainbow trout), and La Rivers (1962) reported 40. We record the addition of 29 introduced fishes since the 1962 list.

At least seven of the native fishes of Nevada are extinct throughout their range. Another four native fishes appear to have been extirpated from Nevada but are still extant outside the state.

The natural drainage systems of Nevada are divided as follows: Great Basin (including Lahontan, Bonneville and other endorheic drainage basins); Colorado River (including White, Moapa and Virgin rivers, Meadow Valley Wash and Las Vegas Creek); Snake River; and Amargosa River (including Ash Meadows). Forty-six native fishes, including three also found in the Snake River drainage, occur in the Great Basin. Within the Great Basin system the Lahontan drainage, with

12 native fishes, has the most diverse ichthyofauna. Twenty-nine native fishes occur in the Colorado River system, 13 in the Snake River system and six in the Amargosa River system.

In our list, families are ordered phylogenetically, and genera, species and subspecies are listed alphabetically within families. For Cyprinodontiform fishes, we follow the recent classification of Parenti (1981). When available, we follow the scientific and common names recommended by the American Fisheries Society (Robins *et al.* 1980), except *Lepidomeda mollispinis,* for which we prefer the common name Virgin River spinedace. We adopt poolfish as the common name for members of the genus *Empetrichthys.* The use of poolfish seems appropriate following placement of *Empetrichthys* in the Goodeidae (Parenti 1981) and agrees with the common names utilized by La Rivers (1962).

Native and Introduced Fishes of Nevada
(**BOLDFACE** = native; italic = introduced)

Osteoglossidae—Osteoglossids

1. *Osteoglossum bicirrhosum* (Vandelli). Arawana. Unsuccessfully introduced into Forest Spring in Ash Meadows, Nye County, during an illegal fish farming operation (Soltz and Naiman 1978).

Anguillidae—Freshwater Eels

1. *Anguilla* sp. Eel. An unidentified species was introduced into Lake Mead (Minckley 1973). Individuals are occasionally taken by sport fisherman, most recently on 25 September 1982.

Clupeidae—Herrings and Shads

1. *Alosa sapidissima* (Wilson). American shad. Unsuccessfully introduced into the Colorado River (Miller and Alcorn 1946).
2. *Dorosoma petenense* (Gunther). Threadfin shad. Introduced and abundant in reservoirs of the Colorado River.

Salmonidae—Trout, Salmon and Whitefish

1. *Coregonus clupeaformis* (Mitchill). Lake whitefish. Unsuccessfully introduced into Lake Tahoe (Miller and Alcorn 1946).
2. *Oncorhynchus keta* (Walbaum). Chum salmon. Unsuccessfully introduced into several Lahontan Basin waters (Miller and Alcorn 1946).
3. *Oncorhynchus kisutch* (Walbaum). Coho salmon. Introduced into the Colorado River as a gamefish but stocking has been discontinued.
4. *Oncorhynchus nerka* (Walbaum). Kokanee salmon. Introduced and established in Lake Tahoe (Cordone *et al.* 1971; Fraser and Pollitt 1951; Miller and Alcorn 1946). Also introduced into Wild Horse Reservoir, Elko County, and Lake Mohave.
5. **ONCORHYNCHUS TSHAWYTSCHA** (Walbaum). Chinook salmon. Native to north Pacific coastal waters including certain headwater tributaries of

the Snake River in northeastern Nevada (Miller and Miller 1948). Extinct in Nevada.

6. **PROSOPIUM WILLIAMSONI** (Girard). Mountain whitefish. Native to Lake Tahoe and certain streams of the Lahontan Basin (La Rivers 1962) as well as tributaries of the Snake River in northeastern Nevada (Miller and Miller 1948).
7. *Salmo aguabonita* Jordan. Golden trout. Introduced into high-elevation lakes in the Ruby Mountains, Elko County, but no longer found in those waters.
8. **SALMO CLARKI** Richardson. Cutthroat trout.
    - 8a. *Salmo clarki bouvieri* Bendire. Yellowstone cutthroat trout. Introduced and established in various waters in northern Nevada (Behnke 1979; Miller and Alcorn 1946).
    - 8b. **SALMO CLARKI HENSHAWI** Gill and Jordan. Lahontan cutthroat trout. Native to Pyramid, Tahoe and Walker lakes as well as the Truckee, Walker, Carson and Quinn rivers and their tributaries in the Lahontan Basin, and Summit Lake in Summit Basin. Transplanted into other waters in northern Nevada (La Rivers 1962) and into lakes Mead and Mohave.
    - 8c. **SALMO CLARKI** ssp. Alvord cutthroat trout. An undescribed subspecies endemic to streams in the Alvord Basin of southeastern Oregon and northwestern Nevada (Williams and Bond 1983). Extinct.
    - 8d. **SALMO CLARKI** ssp. Humboldt cutthroat trout. An undescribed subspecies native to headwater tributaries of the Humboldt River in Elko County and headwater tributaries of the Reese River in Nye County (Behnke 1979; Coffin 1981). This subspecies is closely related to *Salmo clarki henshawi* and is considered by some authorities to be synonymous with that subspecies.
    - 8e. *Salmo clarki stomias* Cope. Greenback cutthroat trout. Introduced into the Humboldt River near Elko, Elko County, but never established (Miller and Alcorn 1946).
    - 8f. **SALMO CLARKI UTAH** Suckley. Bonneville cutthroat trout. Native to streams of the Bonneville Basin of eastern Nevada and northwestern Utah (Behnke 1979) and introduced into certain northern Nevada waters (Miller and Alcorn 1946).
9. *Salmo gairdneri* Richardson. Rainbow trout. Widely introduced and established in Nevada lakes and streams.
10. *Salmo salar* Linnaeus. Atlantic salmon. Introduced and at one time abundant in Lake Tahoe (Miller andAlcorn 1946), but probably no longer present.
11. **SALMO** sp. Redband trout. Native to certain basins in southern Oregon and northeastern California as well as certain tributaries of the Snake River, including small streams in northeastern Nevada (Coffin 1975).
12. *Salmo trutta* Linnaeus. Brown trout. Widely introduced and established in Nevada lakes and streams.
13. **SALVELINUS CONFLUENTUS** (Suckley). Bull trout. Native in Nevada to tributaries of the Snake River in Elko County (Cavender 1978).
14. *Salvelinus fontinalis* (Mitchill). Brook trout. Introduced and established in certain streams in northern Nevada.
15. *Salvelinus namaycush* (Walbaum). Lake trout. Introduced into Truckee Riv-

er, Walker Lake and Lake Tahoe (Miller and Alcorn 1946), but apparently established only in the latter locality.

16. *Thymallus arcticus* (Pallas). Arctic grayling. Introduced into certain high-elevation lakes in northern Nevada (Miller and Alcorn 1946), most recently into Steele Lake, Elko County.

Esocidae—Pikes

1. *Esox lucius* Linnaeus. Northern pike. Introduced into certain Nevada waters and established in Comins and Basset lakes, White Pine County and JD Reservoir, Eureka County.

Cyprinidae—Carps and Minnows

1. **ACROCHEILUS ALUTACEUS** Agassiz and Pickering. Chiselmouth. A native species of the Columbia River system whose distribution includes Salmon Falls Creek, Elko County (Miller and Miller 1948).
2. *Carassius auratus* (Linnaeus). Goldfish. Widely introduced into Nevada waters but established in relatively few localities.
3. *Ctenopharyngodon idella* (Valenciennes). Grass carp. Introduced but not established in Virginia Lake, Washoe County, and in golf course ponds in Las Vegas, Clark County.
4. *Cyprinus carpio* Linnaeus. Common carp. Widely introduced into Nevada waters and abundant in the Colorado River.
5. **EREMICHTHYS ACROS** Hubbs and Miller. Desert dace. Restricted to thermal springs and their outflows in Soldier Meadows, Humboldt County (Nyquist 1963).
6. **GILA ALVORDENSIS** Hubbs and Miller. Alvord chub. Endemic to the Alvord Basin of northwestern Nevada and southeastern Oregon (Williams and Bond 1983).
7. **GILA ATRARIA** (Girard). Utah chub. Native to streams of the Bonneville Basin of eastern Nevada, and Utah, as well as the upper Snake River of southern Idaho and western Wyoming. Introduced elsewhere in northeastern Nevada (Hubbs *et al.* 1974).
8. **GILA BICOLOR** (Girard). Tui chub.
    - 8a. **GILA BICOLOR EUCHILA** Hubbs and Miller. Fish Creek Springs tui chub. Endemic to Fish Creek Springs and Fish Creek in Eureka County (Hubbs and Miller 1972).
    - 8b. **GILA BICOLOR EURYSOMA** Williams and Bond. Sheldon tui chub. Native to streams in the Guano Basin of northwestern Nevada and southeastern Oregon (Williams and Bond 1981).
    - 8c. **GILA BICOLOR ISOLATA** Hubbs and Miller. Independence Valley tui chub. Endemic to Warm Springs in Independence Valley, Elko County (Hubbs *et al.* 1974). Now extinct.
    - 8d. *Gila bicolor mohavensis* (Snyder). Mohave tui chub. Unsuccessfully introduced into an artificial pool at Paradise Spa south of Las Vegas, Clark County (Hoover and St. Amant 1983).
    - 8e. **GILA BICOLOR NEWARKENSIS** Hubbs and Miller. Newark Valley

tui chub. Native to springs in Newark Valley, White Pine County (Hubbs *et al.* 1974).

8f. **GILA BICOLOR OBESA** (Girard). Lahontan creek tui chub. Native to streams and lakes of the Lahontan and Diamond Basins (Hubbs *et al.* 1974).

8g. **GILA BICOLOR PECTINIFER** (Snyder). Lahontan lake tui chub. Native to lacustrine remnants of pluvial Lake Lahontan (Hubbs *et al.* 1974; Snyder 1917).

8h. **GILA BICOLOR** ssp. Kate Spring tui chub. An undescribed subspecies endemic to Kate Spring in Railroad Valley, Nye County. The complex of tui chub subspecies in Railroad Basin remains an enigma pending detailed investigations. We follow the field notes of C. L. Hubbs in recognizing six distinct subspecies. This differs from his original published appraisal (Hubbs and Miller 1948a), where he recognized eight subspecies, but is in close agreement with his later work (Hubbs *et al.* 1974).

8i. **GILA BICOLOR** ssp. Butterfield Spring tui chub. An undescribed subspecies restricted to Butterfield Spring in Railroad Valley, Nye County.

8j. **GILA BICOLOR** ssp. Blue Eagle Spring tui chub. An undescribed subspecies restricted to Blue Eagle Spring in Railroad Valley, Nye County.

8k. **GILA BICOLOR** ssp. Bull Creek tui chub. An undescribed subspecies endemic to Bull Creek in northern Railroad Valley, Nye County.

8l. **GILA BICOLOR** ssp. Green Springs tui chub. An undescribed subspecies endemic to Green Springs near the northern extent of Railroad Valley, White Pine County.

8m. **GILA BICOLOR** ssp. Railroad tui chub. An undescribed subspecies native to Duckwater Creek in Railroad Valley, springs in Little Fish Lake Valley and Twin Springs in Hot Creek Valley (Hubbs *et al.* 1974; Williams and Williams 1981).

8n. **GILA BICOLOR** ssp. Big Smoky Valley tui chub. An undescribed subspecies native to the springs along the west side of pluvial Lake Toiyabe in Big Smoky Valley, Nye County (Hubbs and Miller 1948a).

8o. **GILA BICOLOR** ssp. Charnock Springs tui chub. An undescribed subspecies endemic to Charnock Springs along the east side of pluvial Lake Toiyabe in Big Smoky Valley, Nye County (Hubbs and Miller 1948a).

8p. **GILA BICOLOR** ssp. Dixie Valley tui chub. An undescribed subspecies endemic to springs in Dixie Valley, Churchill County (Hubbs and Miller 1948a).

8q. **GILA BICOLOR** ssp. Fish Lake tui chub. An undescribed subspecies endemic to waters of Fish Lake Valley, Esmeralda County (Hubbs and Miller 1948a).

9. **GILA COPEI** (Jordan and Gilbert). Leatherside chub. Apparently native to Goose Creek, Snake River drainage, in Elko County (Hopkirk and Behnke 1966) and introduced into the Colorado River as a baitfish but no longer present (Miller 1952).

10. **GILA CYPHA** Miller. Humpback chub. Native to the Colorado River Basin as far south as just below the present site of Hoover Dam (Miller 1955). Extinct in Nevada.

11. **GILA ELEGANS** Baird and Girard. Bonytail. Native to the Colorado River Basin, but now very rare in Lake Mohave and perhaps extinct in the upper Colorado River.
12. **GILA ROBUSTA** Baird and Girard. Roundtail chub.
    - 12a. **GILA ROBUSTA JORDANI** Tanner. Pahranagat roundtail chub. Native to the outflows of Crystal, Hiko and Ash springs in Pahranagat Valley, Lincoln County, but now confined to a small portion of the outflow of Ash Springs (Hardy 1980, 1982; Tanner 1950).
    - 12b. **GILA ROBUSTA ROBUSTA** Baird and Girard. Roundtail chub. Native to the Colorado River Basin, and probably extinct in Nevada.
    - 12c. **GILA ROBUSTA SEMINUDA** Cope and Yarrow. Virgin River roundtail chub. Native to the Virgin River of Utah, Arizona and Nevada (Cross 1978).
    - 12d. **GILA ROBUSTA** ssp. Moapa roundtail chub. An undescribed subspecies confined to the Moapa River in Clark County.
13. **LEPIDOMEDA ALBIVALLIS** Miller and Hubbs. White River spinedace. Endemic to cool springs in the upper White River drainage of White Pine County (Miller and Hubbs 1960). Now very rare following extirpation of Preston Big Spring population because of habitat modification.
14. **LEPIDOMEDA ALTIVELIS** Miller and Hubbs. Pahranagat spinedace. Native to Ash Springs and Upper Pahranagat Lake, Lincoln County (Miller and Hubbs 1960). Extinct.
15. **LEPIDOMEDA MOLLISPINIS** Miller and Hubbs. Virgin River spinedace.
    - 15a. **LEPIDOMEDA MOLLISPINIS MOLLISPINIS** Miller and Hubbs. Virgin River spinedace. Native to the Virgin River system of Utah, Arizona and Nevada (Miller and Hubbs 1960; Rinne 1971).
    - 15b. **LEPIDOMEDA MOLLISPINIS PRATENSIS** Miller and Hubbs. Big Spring spinedace. Native to Big Spring and nearby Meadow Valley Wash in Condor Canyon, Lincoln County, but has been extirpated from the former locality.
16. **MOAPA CORIACEA** Hubbs and Miller. Moapa dace. Endemic to the thermal-spring sources and nearby headwaters of the Moapa River, Clark County (Hubbs and Miller 1948b).
17. *Notemigonus crysoleucus* (Mitchell). Golden shiner. Introduced as baitfish into the Colorado River (Miller 1952) and Lake Tahoe. Also introduced and established in the Amargosa River north of Beatty, Nye County.
18. *Notropis lutrensis* (Baird and Girard). Red shiner. Widely introduced into the lower Colorado River system (Hubbs 1954) and now abundant in downstream portions of the Virgin and Moapa rivers (Cross 1975, 1976).
19. *Notropis venustus* (Girard). Blacktail shiner. Introduced into but not established in the downstream portions of the Virgin River (Branson 1968).
20. *Orthodon microlepidotus* (Ayres). Sacramento blackfish. Introduced into the Truckee Meadows area near Reno and possibly still extant in irrigation ditches east of Sparks, Washoe County (La Rivers 1962). Also introduced and established in Lahontan Reservoir, Lyon and Churchill counties.
21. *Pimephales promelas* Rafinesque. Fathead minnow. Introduced into the lower Colorado River and occasionally collected from the Moapa River, Clark County.
22. **PLAGOPTERUS ARGENTISSIMUS** Cope. Woundfin. Native to the Vir-

gin River of Utah, Arizona and Nevada (Deacon 1979). One individual has been taken from the Moapa River, a pre-impoundment tributary of the Virgin River (Deacon and Bradley 1972).

23. **PTYCHOCHEILUS LUCIUS** Girard. Colorado squawfish. Native to the Colorado River Basin, but now extinct in Nevada.
24. **PTYCHOCHEILUS OREGONENSIS** (Richardson). Northern squawfish. Native to the Columbia River drainage including the Jarbridge, Bruneau and Owyhee rivers as well as Salmon Falls Creek (Miller and Miller 1948).
25. **RELICTUS SOLITARIUS** Hubbs and Miller. Relict dace. Native to waters in the valleys of pluvial lakes Franklin, Gale, Waring, Steptoe and Spring in northeastern Nevada (Hubbs *et al.* 1974; Vigg 1982).
26. **RHINICHTHYS CATARACTAE** (Valenciennes). Longnose dace. Native to the Columbia River system where it occurs in Goose Creek, Elko County (Hopkirk and Behnke 1966).
27. **RHINICHTHYS OSCULUS** (Girard). Speckled dace.
    - 27a. **RHINICHTHYS OSCULUS CARRINGTONI** (Cope). Snake River speckled dace. Native to the Snake River drainage including streams of northeastern Nevada.
    - 27b. **RHINICHTHYS OSCULUS LARIVERSI** Lugaski. Big Smoky Valley speckled dace. Native to waters of Big Smoky Valley, Nye County (Hubbs *et al.* 1974; Lugaski 1972).
    - 27c. **RHINICHTHYS OSCULUS LETHOPORUS** Hubbs and Miller. Independence Valley speckled dace. Endemic to Warm Springs in Independence Valley, Elko County (Hubbs *et al.* 1974).
    - 27d. **RHINCHTHYS OSCULUS MOAPAE** Williams. Moapa River speckled dace. Restricted to the Moapa River, Clark County (Williams 1978).
    - 27e. **RHINICHTHYS OSCULUS NEVADENSIS** Gilbert. Ash Meadows speckled dace. Native to Rogers, Longstreet, Fairbanks, Crystal, Forest, Tubbs, Point-of-Rocks, Bradford, Big and Jack Rabbit Springs and their outflow creeks in Ash Meadows, Nye County, but extant only in latter three springs.
    - 27f. **RHINICHTHYS OSCULUS OLIGOPORUS** Hubbs and Miller. Clover Valley speckled dace. Native to two springs in Clover Valley, Elko County (Hubbs *et al.* 1974).
    - 27g. **RHINICHTHYS OSCULUS RELIQUUS** Hubbs and Miller. Grass Valley speckled dace. Endemic to a single spring-fed creek in Grass Valley, Lander County (Hubbs *et al.* 1974). Extinct.
    - 27h. **RHINICHTHYS OSCULUS ROBUSTUS** (Rutter). Lahontan speckled dace. Native to waters of the Lahontan Basin.
    - 27i. **RHINICHTHYS OSCULUS** ssp. Preston speckled dace. An undescribed subspecies native to springs in the upper White River drainage, White Pine County.
    - 27j. **RHINICHTHYS OSCULUS** ssp. Meadow Valley speckled dace. An undescribed subspecies native to Meadow Valley Wash, Lincoln County.
    - 27k. **RHINICHTHYS OSCULUS** ssp. Diamond Valley speckled dace. An undescribed subspecies native to waters of Diamond Valley, Eureka County.

- 27l. **RHINICHTHYS OSCULUS** ssp. Monitor Valley speckled dace. An undescribed subspecies native to waters of Monitor Valley, Nye County.
- 27m. **RHINICHTHYS OSCULUS** ssp. Amargosa River speckled dace. An undescribed subspecies native to the upper Amargosa River drainage near Beatty and Springdale, Nye County.
- 27n. **RHINICHTHYS OSCULUS VELIFER** Gilbert. Pahranagat speckled dace. Native to spring remnants of the pluvial White River in Pahranagat Valley, Lincoln County.
- 27o. **RHINICHTHYS OSCULUS YARROWI** (Jordan and Evermann). Colorado River speckled dace. Native to streams of the Colorado River drainage including the Virgin River in Nevada.

28. **RHINICHTHYS** sp. Las Vegas dace. An undescribed species restricted to Las Vegas Creek, Clark County. Extinct.
29. **RICHARDSONIUS BALTEATUS** (Richardson). Redside shiner.
    - 29a. **RICHARDSONIUS BALTEATUS HYDROPHLOX** (Cope). Columbia redside shiner. Native to the middle and upper Columbia River and pluvial Lake Bonneville systems including streams of northeastern Nevada (Miller and Miller 1948).
30. **RICHARDSONIUS EGREGIUS** (Girard). Lahontan redside. Native to rivers, lakes and their tributaries in the Lahontan Basin and introduced into Summit Lake, Humboldt County.
31. *Tinca tinca* (Linnaeus). Tench. Apparently unsuccessfully introduced near Virginia City, Storey County (Miller and Alcorn 1946).

Catostomidae— Suckers

1. **CATOSTOMUS ARDENS** Jordan and Gilbert. Utah sucker. Native to streams of the Bonneville Basin of eastern Nevada and northwestern Utah and the upper Snake River of southeastern Idaho and western Wyoming. Introduced into the lower Colorado River, apparently as a baitfish (Miller 1952), where it does not survive.
2. **CATOSTOMUS CLARKI** Baird and Girard. Desert sucker.
    - 2a. **CATOSTOMUS CLARKI INTERMEDIUS** (Tanner). White River desert sucker. Native to remnant waters of the pluvial White River system near Preston and Lund, White Pine County, and Pahranagat Valley, Lincoln County. Extinct in Pahranagat Valley and very rare in upper White River Valley except in Lund Town Spring.
    - 2b. **CATOSTOMUS CLARKI** ssp. Meadow Valley desert sucker. An undescribed subspecies from Meadow Valley Wash, Lincoln county.
    - 2c. **CATOSTOMUS CLARKI UTAHENSIS** (Tanner). Virgin River desert sucker. Native to the Virgin River of Utah, Arizona and Nevada (Smith 1966; Tanner 1932, 1936). Also introduced as a baitfish in lower Colorado River (Miller 1952).
3. **CATOSTOMUS COLUMBIANUS** (Eigenmann and Eigenmann). Bridgelip sucker. Native to the Columbia River drainage including tributaries of the Snake River in Elko County (Miller and Miller 1948).
4. **CATOSTOMUS LATIPINNIS** Baird and Girard. Flannelmouth sucker. Native to the Colorado River system, including the Virgin River. Probably now absent in the mainstream Colorado River in Nevada but still common in the Virgin River (Cross 1975).

5. **CATOSTOMUS MACROCHEILUS** Girard. Largescale sucker. Native to the Columbia River drainage including streams tributary to the Snake River, Elko County (Miller and Miller 1948).
6. **CATOSTOMUS PLATYRHYNCHUS** (Cope). Mountain sucker.
    - 6a. **CATOSTOMUS PLATYRHYNCHUS LAHONTAN** (Rutter). Lahontan mountain sucker. Native to streams in the Lahontan Basin.
    - 6b. **CATOSTOMUS PLATYRHYNCHUS PLATYRHYNCHUS** (Cope). Bonneville mountain sucker. Native to streams of the Bonneville Basin of eastern Nevada and northwestern Utah.
7. **CATOSTOMUS** sp. Wall Canyon sucker. An undescribed species endemic to Wall Canyon, Surprise Valley, Washoe County.
8. **CATOSTOMUS TAHOENSIS** Gill and Jordan. Tahoe sucker. Native to lakes, rivers and their tributaries in the Lahontan Basin
9. **CHASMISTES CUJUS** Cope. Cui-ui. Endemic to Pyramid Lake and its principal tributary, the Truckee River.
10. **XYRAUCHEN TEXANUS** (Abbott). Razorback sucker. Native to the Colorado River Basin where it presently is abundant only in Lake Mohave (Minckley 1983).

Ictaluridae—Bullhead Catfish

1. *Ictalurus catus* (Linnaeus). White catfish. Introduced and established in Indian Lakes and Stillwater Marsh, Churchill County (La Rivers 1962; Miller and Alcorn 1946), Lahontan Reservoir, Lyon and Churchill counties, and Humboldt River, Lander County.
2. *Ictalurus melas* (Rafinescque). Black bullhead.
    - 2a. *Ictalurus melas catulus* (Girard). Southern black bullhead. Introduced into Las Vegas Creek, Clark County (Miller and Alcorn 1946). Black bullhead, presumably *I. m. catulus,* are also present in the Moapa River (Deacon and Bradley 1972) and Lake Mead (Minckley 1973).
    - 2b. *Ictalurus melas melas* (Rafinesque). Northern black bullhead. Introduced and established in the Carson River and canals near Fallon, Churchill County, Washoe Lake, Washoe County, as well as the lower Walker River and Humboldt River (Miller and Alcorn 1946).
3. *Ictalurus natalis* (Lesueur). Yellow bullhead. Introduced and established in the Colorado River.
4. *Ictalurus nebulosus* (Lesueur). Brown bullhead. Introduced and established in several Nevada waters (Miller and Alcorn 1946), notably Squaw Valley Reservoir, Washoe County.
5. *Ictalurus punctatus* (Rafinesque). Channel catfish. Widely introduced and established in Nevada waters.

Clariidae—Labyrinth Catfish

1. *Clarias batrachus* (Linnaeus). Walking catfish. Unsuccessfully introduced into Rogers Spring near Lake Mead, Clark County (Courtenay and Deacon 1983).

Loricariidae—Armored Catfish

1. *Hypostomus plecostomus.* Suckermouth catfish. Introduced and established in Indian Springs, Clark County (Courtenay and Deacon 1982).

Fundulidae—Topminnows

1. *Fundulus zebrinus* Jordan and Gilbert. Plains killifish. Introduced along the Colorado River and seemingly established in certain small streams tributary to Lake Mead.
2. *Lucania parva* (Baird). Rainwater killifish. Introduced into springs and ponds in the Blue Lake area near the Utah border, Elko County.

Goodeidae—Goodeids

1. *Ameca splendens* Miller and Fitzsimons. Butterfly goodeid. Introduced into Rogers Spring near Lake Mead, Clark County (Courtenay and Deacon 1983).
2. **CRENICHTHYS BAILEYI** (Gilbert). White River springfish.
   - 2a. **CRENICHTHYS BAILEYI ALBIVALLIS** Williams and Wilde. Preston White River springfish. Endemic to spring remnants of the uppermost White River drainage near Preston and Lund, White Pine County (Williams and Wilde 1981).
   - 2b. **CRENICHTHYS BAILEYI BAILEYI** (Gilbert). White River springfish. Restricted to Ash Springs in Pahranagat Valley, Lincoln County (Gilbert 1893; Hubbs and Miller 1941).
   - 2c. **CRENICHTHYS BAILEYI GRANDIS** Williams and Wilde. Hiko White River springfish. Native to Hiko and Crystal springs in Pahranagat Valley, Nevada, but now extant in only the latter spring (Williams and Wilde 1981).
   - 2d. **CRENICHTHYS BAILEYI MOAPAE** Williams and Wilde. Moapa White River springfish. Native to headwater springs of the Moapa River, Clark County (Williams and Wilde 1981).
   - 2e. **CRENICHTHYS BAILEYI THERMOPHILUS** Williams and Wilde. Moorman White River springfish. Native to Moorman, Hot Creek and Moon River springs in the pluvial White River drainage, Nye County (Williams and Wilde 1981).
3. **CRENICHTHYS NEVADAE** Hubbs. Railroad Valley springfish. Native to seven thermal springs in Railroad Valley, Nye County. Introduced into Chimney Hot Springs, Nye County, and into springs at Sodaville, Mineral County (Hubbs 1932; Williams and Williams 1981).
4. **EMPETRICHTHYS LATOS** Miller. Pahrump poolfish.
   - 4a. **EMPETRICHTHYS LATOS CONCAVUS** Miller. Raycraft Ranch poolfish. Endemic to a single spring on Raycraft Ranch in Pahrump Valley, Nye County (Miller 1948). Extinct.
   - 4b. **EMPETRICHTHYS LATOS LATOS** Miller. Pahrump poolfish. Endemic to a single spring on Manse Ranch in Pahrump Valley, Nye County (Miller 1948). Now extirpated at Manse Ranch but introduced populations persist at Corn Creek Springs Pond on the Desert National Wildlife Refuge, Clark County, and at Shoshone Ponds, White Pine County.
   - 4c. **EMPETRICHTHYS LATOS PAHRUMP** Miller. Pahrump Ranch poolfish. Endemic to two springs on Pahrump Ranch in Pahrump Valley, Nye County (Miller 1948). Extinct.
5. **EMPETRICHTHYS MERRIAMI** Gilbert. Ash Meadows poolfish. Endemic to larger, lower-elevation springs in Ash Meadows, Nye County (Miller 1948). Extinct.

Cyprinodontidae—Pupfish

1. **CYPRINODON DIABOLIS** Wales. Devils Hole pupfish. Endemic to Devil's Hole in Ash Meadows, Nye County (Baugh and Deacon, 1983a, b; James 1969; Wales 1930). Introduced into artificial refugia in Ash Meadows and along the Colorado River below Hoover Dam, Clark County (Williams 1977).
2. **CYPRINODON NEVADENSIS** Eigenmann and Eigenmann. Amargosa pupfish.
    - 2a. *Cyprinodon nevadensis amargosae* Miller. Amargosa pupfish. Unsuccessfully introduced into a spring on Pahrump Ranch in Pahrump Valley, Nye County (Miller 1968).
    - 2b. **CYPRINODON NEVADENSIS MIONECTES** Miller. Ash Meadows Amargosa pupfish. Endemic to larger, lower-elevation springs in Ash Meadows, Nye County (Miller 1948).
    - 2c. **CYPRINODON NEVADENSIS PECTORALIS** Miller. Warm Springs Amargosa pupfish. Endemic to smaller, mid-elevation springs in Ash Meadows, Nye County (Miller 1948).

Poeciliidae—Livebearers

1. *Gambusia affinis* (Baird and Girard). Mosquitofish. Widely introduced and established in Nevada waters.
2. *Poecilia latipinna* (Lesueur). Sailfin molly. Introduced and established in Big Jack Rabbit, Point-of-Rocks, Bradford and other springs in Ash Meadows, Nye County, Ash Springs in Lincoln County (Hubbs and Deacon 1964), and in Blue Point and Rogers springs near Lake Mead, Clark County (Deacon *et al.* 1964; Courtenay and Deacon 1982).
3. *Poecilia mexicana* Steindachner. Shortfin molly. Introduced and established in Rogers and Blue Point springs near Lake Mead, Clark County, Hiko, Ash and Crystal springs and their outflows in Pahranagat Valley, Lincoln County, and in the Moapa River (Cross 1976; Deacon and Bradley 1972; Hubbs and Deacon 1964).
4. *Poecilia reticulata* Peters. Guppy. Introduced into certain Nevada waters and established in Big Warm Spring, Nye County (Williams and Williams 1981), Indian Springs, Clark County (Courtenay and Deacon 1982), Blue Point Spring, Clark County, Lund Town Spring, and Preston Town Spring, White Pine County (Deacon *et al.* 1964), and Thousand Creek Spring and Dufurrena Campground Pond in Humboldt County (Williams 1980).
5. *Xiphophorus helleri* Heckel. Green swordtail. Introduced into Indian Springs, Clark County (Courtenay and Deacon 1982).
6. *Xiphophorus maculatus* (Günther). Southern platyfish. Introduced into Blue Point Springs near Lake Mead and as a hybrid (with *X. helleri*) into Indian Springs, Clark County (Courtenay and Deacon 1982).

Percichthyidae—Temperate Bass

1. *Morone chrysops* (Rafinesque). White bass. Introduced and established in Lahontan Reservoir and throughout the Truckee-Carson Irrigation District system in Lahontan Valley. Also introduced into Rye Patch Reservoir, Pershing County, and Washoe Lake, Washoe County.

2. *Morone saxatilis* (Walbaum). Striped bass. Introduced and established in Lake Mead, Clark County, and recently found just downstream in Lake Mohave.

Centrarchidae—Sunfish

1. *Archoplites interruptus* (Girard). Sacramento perch. Widely introduced into northern Nevada lakes (La Rivers 1962) and established in Pyramid Lake, Washoe County (Vigg and Kucera 1981) as well as in Grass Springs, Steptoe Valley, White Pine County.
2. *Lepomis cyanellus* Rafinesque. Green sunfish. Widely introduced and established in Nevada waters.
3. *Lepomis gibbosus* (Linnaeus). Pumpkinseed. Introduced and established in the Dufurrena Ponds, Humboldt County.
4. *Lepomis macrochirus* Rafinesque. Bluegill. Widely introduced and established in Nevada waters.
5. *Lepomis microlophus* (Gunther). Redear sunfish. Introduced and established in the lower Colorado River (Minckley 1979, 1983).
6. *Micropterus dolomieui* Lacepede. Smallmouth bass. Introduced and established in the Humboldt River (La Rivers 1962).
7. *Micropterus punctulatus* (Rafinesque). Spotted bass. Introduced into Eagle Valley Reservoir, Lincoln County.
8. *Micropterus salmoides* (Lacepede). Largemouth bass.
    - 8a. *Micropterus salmoides floridanus* (Lesueur). Florida largemouth bass. Introduced into reservoirs on the Pahranagat National Wildlife Refuge and Echo Canyon Reservoir, Lincoln County.
    - 8b. *Micropterus salmoides salmoides* (Lacepede). Largemouth bass. Widely introduced and established in Nevada waters.
9. *Pomoxis annularis* Rafinesque. White crappie. Introduced and established in northern Nevada waters.
10. *Pomoxis nigromaculatus* (Lesueur). Black crappie. Introduced into Nevada waters and abundant in reservoirs of the Colorado River.

Percidae—Perch

1. *Perca flavescens* (Mitchill). Yellow perch. Introduced as a gamefish and established in Walker Lake, Mineral County, Rye Patch Reservoir, Pershing County and Lahontan Reservoir, Lyon and Churchill counties.
2. *Stizostedion vitreum* (Mitchill). Walleye.
    - 2a. *Stizostedion vitreum vitreum* (Mitchill). Walleye. Introduced and established as a gamefish into the Colorado River, Rye Patch Reservoir, Pershing County, Chimney Dam Reservoir, Humboldt County, and Lahontan Reservoir, Lyon and Churchill counties.

Cichlidae—Cichlids

1. *Cichlasoma cyanoguttatum* (Baird and Girard). Rio Grande cichlid. Introduced into Rogers Spring near Lake Mead, Clark County, but no longer present (Courtenay and Deacon 1983).
2. *Cichlasoma nigrofasciatum* (Günther). Convict cichlid. Introduced and es-

tablished in Rogers Spring, Clark County, Ash and Crystal springs, Lincoln County (Courtenay and Deacon 1982; Hubbs and Deacon 1964).

3. *Cichlasoma severum* (Heckel). Banded cichlid. Unsuccessfully introduced into Rogers Spring near Lake Mead, Clark County (Courtenay and Deacon 1982; Hubbs and Deacon 1964).
4. *Melanochromis auratus* (Boulenger). Golden mbuna. Introduced but not established in Rogers Spring near Lake Mead, Clark County (W. R. Courtenay, pers. comm.).
5. *Melanochromis johanni* (Eccles). Unnamed mbuna. Introduced but not established in Rogers Spring near Lake Mead, Clark County (W. R. Courtenay, pers. comm.).
6. *Pseudotropheus zebra* (Boulenger). Zebra mbuna. Introduced into Rogers Spring near Lake Mead, Clark County (Courtenay and Deacon 1982, 1983).
7. *Tilapia mariae* (Boulenger). Spotted tilapia. Introduced and abundant in Rogers Spring near Lake Mead, Clark County (Courtenay and Deacon 1982, 1983).
8. *Tilapia zilli* (Gervais). Redbelly tilapia. Introduced but no longer present in ponds in Cottonwood Park, Pahrump Valley, Nye County (Courtenay and Deacon 1982).

Cottidae—Sculpins

1. **COTTUS BAIRDI** (Girard). Mottled sculpin.
    1a. **COTTUS BAIRDI SEMISCABER** (Cope). Mottled sculpin. Native to the Bonneville Basin of eastern Nevada and northwestern Utah as well as the upper Snake River of southestern Idaho and western Wyoming.
2. **COTTUS BELDINGI** Eigenmann and Eigenmann. Paiute sculpin. Native to the Lahontan and Bonneville basins as well as the Columbia River drainage (La Rivers 1962).

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MAMMALS FROM CAMIGUIN ISLAND, PHILIPPINES

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Abstract.—Fifteen species of mammals are known to occur on Camiguin Island, a small oceanic island that lies near the north coast of Mindanao in the southern Philippines. Ten of the species are bats, one is a native Philippine rodent, and four are suspected of having been introduced (one insectivore, two rodents, and one carnivore). The depauperate nature of the non-volant land mammal fauna seems to be due to the lack of a Pleistocene land-bridge connection, although dispersal across a narrow salt-water gap by at least one rodent is implied.

The island of Camiguin is a small (265 km^2, 1713 m elev.), active volcanic cone that lies 8 km north of Mindanao in the Mindanao Sea (centered at 9°10′N, 124°43′E). In spite of Camaguin's proximity to Mindanao, the water between the two has a minimum depth of 385 m; thus it is unlikely that Camiguin was part of the Mindanao land mass during the Pleistocene. Because of these circumstances, Camiguin is potentially significant as an indicator of the importance of over-water dispersal by land mammals in the Philippines. However, the only previous records of mammals from the island are those of *Paradoxurus* by Gray (1843) and *Harpyionycteris whiteheadi* by Peterson and Fenton (1970). Additionally, the specimens reported here are important because the mammalian fauna of the southern Philippines is poorly known, especially on the small islands.

Three field teams from Mindanao State University collected mammals on Camiguin over a period of three years. The first, led by D. P. Empesso and R. B. Gonzales, collected from 17 to 31 May 1967; specimens are in the Royal Ontario Museum, Toronto (ROM). The second two teams, led by D. S. Rabor, worked on Camiguin from 11 to 28 June 1968, and 13 to 29 June 1969; specimens are in the Delaware Museum of Natural History (DMNH). Collecting was carried out by trapping, netting, and shooting. The purpose of this paper is to describe these collections, which include 215 specimens representing 15 species of mammals.

Methods

I took all cranial and forearm measurements with dial calipers graduated to 0.05 millimeter (mm); measurements listed are means (± one standard deviation for samples with $n > 3$). Limits of measurements are defined by DeBlase and Martin (1974). I measured forearms of all bats on dried skins. Distributional records are summarized for those species not covered by Heaney and Rabor (1982). Specimens examined from other islands in the Philippines are in the United States National Museum of Natural History (USNM).

Mammal specimens were obtained at ten localities; reference is made in species accounts only to the name of the Barrio or geographic feature. Mt. Timpong is more generally known as Mt. Mambajao; the names, spelling, and elevations given here are those used on the specimen labels. Specimens from the first seven localities are in the DMNH; those from the last three localities are in the ROM.

1. Catarman Mt., 2500–4500 ft, Catarman Municipality.
2. Gidag-on, 500–1500 ft, Catarman Municipality.
3. Kasang-sangan, 1000–2000 ft, Catarman Municipality.
4. Lasak-lasak, 4000–5200 ft, Mt. Timpong, Mahinog Municipality.
5. Matugnao, Mt. Timpong, Mahinog Municipality.
6. Puntod, 800 ft, Mahinog Municipality.
7. Mt. Timpong Peak, 5700 ft, Mahinog Muncipality.
8. Mahidlaw, 2500–3500 ft, Mt. Mambajao, Catarman Muncipality.
9. Sangsangan, 1400–3300 ft, Mt. Mambajao, Catarman Muncipality.
10. Tag-ibo Cave, 400 ft, Catarman Municipality.

Accounts of Species

Order Insectivora

Suncus murinus occultidens. A single subadult specimen of the house shrew was taken on Mt. Timpong Peak. Although the cranium had not completed growth, measurements of the fully-erupted permanent dentition are typical of this widespread commensal species (Heaney *et al.* 1981; Taylor 1934). Measurements: I^1 to M^3, 11.9; P^4 to M^3, 6.4; M^2 to M^2 (labial), 8.4; palatal width at M^3, 3.1.

Order Chiroptera

Cynopterus brachyotis luzoniensis. This geographically widespread species is apparently common at most elevations on the island. These bats averaged slightly smaller than a series from Dinagat and Siargao islands (Table 1; Heaney and Rabor 1982). Specimens examined: Lasak-lasak, 3; Kasang-sangan, 12; Mahidlaw, 2; Mt. Timpong Peak, 6; Puntod, 10; Sangsangan, 14.

Harpyionycteris whiteheadi whiteheadi. This species has been reported previously from Camiguin, as well as from Mindanao, Mindoro, and Negros (Peterson and Fenton 1970). Specimens examined: Kasang-sangan, 1; Lasak-lasak, 1; Mahidlaw, 1. The Mahidlaw specimen was reported by Peterson and Fenton (1970) as being from Langoangon, a misreading of the specimen label.

Macroglossus minimus lagochilus. This widespread nectarivorous species was apparently common on Camiguin. The specimens are slightly larger than those from Mindanao or Negros (Table 1; Heaney and Rabor 1982). Specimens examined: Kasang-sangan, 12; Matugnao, 5; Puntod, 2; Sangsangan, 8.

Ptenochirus jagori. Specimens of this species are intermediate in size between samples from Dinagat and Luzon (Table 1; Heaney and Rabor 1982). The previous record of this species from Camiguin reported by Heaney and Rabor refers to another island of the same name that lies off of northern Luzon (Andersen 1912). Specimens examined: Kasang-sangan, 6; Matugnao, 6; Sangsangan, 9.

Pteropus hypomelanus. Specimens of this series are similar in cranial morphology to those from Panay and Dinagat, but differ in color. The mantle of the Camiguin specimens is a sandy, golden-yellow color and extends in a continuous band onto the throat and chest; dark fur on the venter of the head is confined to the chin. The pale yellow fur extends slightly further laterally and posteriorly on

Table 1.—Mean measurements (± standard deviation) of adult bats from Camiguin Island, Philippines.

	Sex	n	Condylobasal length	Zygomatic breadth	Interorbital breadth	C^1 to last M	Molariform toothrow	Forearm
Cynopterus brachyotis	♂	9	27.2 ± 0.64	18.1 ± 0.62	5.9 ± 0.33	9.2 ± 0.26	6.5 ± 0.25	61.5
Cynopterus brachyotis	♀	16	26.5 ± 0.56	17.9 ± 0.47	5.7 ± 0.28	8.9 ± 0.29	6.2 ± 0.21	61.5 ± 1.7
Harpyionycteris whiteheadi	♂	1	41.5	25.1	6.7	16.4	12.5	87.5
Harpyionycteris whiteheadi	♀	1	40.5	24.3	6.9	15.7	11.8	—
Macroglossus minimus	♂	7	24.9 ± 0.73	15.2 ± 0.93	4.9 ± 0.33	8.7 ± 0.43	5.4 ± 0.22	40.9 ± 0.9
Macroglossus minimus	♀	4	24.9 ± 0.50	13.6	4.7 ± 0.22	8.6 ± 0.53	5.6 ± 0.62	41.5 ± 2.3
Ptenochirus jagori	♂	7	34.5 ± 0.56	24.0 ± 0.58	7.1 ± 0.35	12.2 ± 0.30	8.6 ± 0.35	78.6 ± 2.3
Ptenochirus jagori	♀	5	34.6 ± 0.53	23.8 ± 0.70	7.3 ± 0.27	12.3 ± 0.24	8.8 ± 0.26	79.6
Pteropus hypomelanus	♂	2	61.3	35.2	8.8	23.4	16.4	141
Pteropus hypomelanus	♀	2	61.0	34.8	9.1	23.6	16.1	138
Pteropus tablasi	♂	4	49.2 ± 1.39	27.9 ± 0.47	7.3 ± 0.61	18.0 ± 0.39	12.6 ± 0.10	106 ± 2.2
Pteropus tablasi	♀	3	48.6	27.5	6.9	17.5	12.2	105
Emballonura alecto	♀	2	13.8	8.7	2.8	5.5	4.0	44.2
Rhinolophus arcuatus	♂	6	19.8 ± 0.43	10.1 ± 0.24	1.8 ± 0.19	7.8 ± 0.17	5.6 ± 0.06	43.1
Rhinolophus subrufus	♂	1	23.2	12.1	2.1	9.3	6.8	51.2

the venter, and has a sharper edge with the dark lateral fur, than on bats from Dinagat or Panay. The mantle and ventral fur on Camiguin specimens varies from pale yellow to sandy brown to golden on different specimens. Specimens examined: Gidag-on, 2; Matugnao, 2; Lasak-lasak, 1; Sangsangan, 3.

Pteropus tablasi. This small, golden-mantled flying fox was apparently common on Camiguin. Allocation of these bats to *P. tablasi* is tentative, pending revision of the species-group by D. J. Klingener (pers. comm.); there are no differences apparent between specimens from Camiguin and those taken at Lake Balinsasayao, Negros Island (Heaney et al. 1981). Specimens examined: Kasang-sangan, 19; Matugnao, 2; Puntod, 1; Sangsangan, 20.

Emballonura alecto alecto. Bats in this series average slightly larger than others from the Philippines (Heaney and Rabor 1982), but sample sizes are generally small, and no other differences are evident. Specimens examined: Sangsangan, 2; Tag-ibo Cave, 2.

Rhinolophus arcuatus exiguus. A series of six males is indistinguishable from a series from Montalban Caves, Rizal Province, Luzon (USNM). Previous records of this subspecies are from Guimaras, Mindanao (Taylor 1934), and Negros (Sanborn 1952); the nominate subspecies has been recorded on Luzon and Mindoro (Taylor 1934). I base the subspecies designation solely on locality. Specimens examined: Matugnao, 6.

Rhinolophus subrufus subrufus. The single specimen is indistinguishable from a series from Clark Air Base, Pampanga Province, Luzon (USNM). Other records of the subspecies are from Luzon, Mindanao (Hollister 1913), Mindoro (Lawrence 1939), and Tablas (Matschie 1898); *R. s. bunkeri* is known only from southerm Mindanao (Lawrence 1939). Specimens examined: Matugnao, 1.

Pipistrellus sp. A single skin without skull appears similar to *P. javanicus,* but its specific identity must be regarded as uncertain. Specimen examined: Matugnao, 1.

Order Rodentia

Rattus everetti. Specimens from Camiguin appear very similar to a series from Mt. Katanglad, Mindanao (DMNH; Heaney and Rabor 1982). Only a single fully grown adult with damaged skull is present (Table 2). Specimens examined: Kasang-sangan, 4; Lasak-lasak, 1; Matugnao, 2.

Rattus exulans. Specimens of this commensal rat are similar to series from Dinagat and Mindanao (Table 2; Heaney and Rabor 1982); only a single adult is present. Specimens examined: Lasak-lasak, 1; Matugnao, 7.

Rattus rattus mindanensis. This common commensal rat was apparently abundant on Camiguin. Specimens from Camiguin average slightly smaller than a series from Mindanao, but are similar to several from Dinagat (Table 2; Heaney and Rabor 1982). Specimens examined: Catarman Mt., 2; Gidag-on, 6; Kasang-sangan, 3; Lasak-lasak, 6; Matugnao, 22.

An additional species of murid may be present on Camiguin, as indicated by a case involving mis-matched skulls. The skin of a juvenile *R. rattus* (DMNH

Table 2.—Mean measurements (± standard deviation) of adult rodents from Camiguin Island, Philippines.

	Sex	n	Condylobasal length	Zygomatic breadth	Mastoid breadth	Maxillary toothrow length	Diastema length	Total length	Tail length
Rattus everetti	♀	1	—	—	—	9.8	14.9	456	268
Rattus exulans	♂	1	31.8	—	13.9	5.6	8.8	277	144
Rattus rattus	♂	6	40.9 ± 1.31	20.8 ± 1.01	16.6 ± 0.70	7.2 ± 0.18	11.5 ± 0.67	349 ± 11.8	181 ± 11.5
Rattus rattus	♀	6	40.8 ± 0.77	21.0	16.5 ± 0.49	6.9 ± 0.32	11.2 ± 0.41	364 ± 13.3	191 ± 11.8

4124) is mistakenly matched with the skull of a juvenile *Bullimus bagobus.* A specimen with the skin of a juvenile *R. everetti* (DMNH 4174) has a skull of a juvenile *R. rattus.* No *Bullimus bagobus* skin is present. It is possible that the mix-up occurred at the museum during the cleaning process or on Camiguin.

Order Carnivora

Paradoxurus hermaphroditus philippinensis. Gray (1843) listed specimens of *Paradoxurus* from Camiguin under the name *P. zeylanicus.* Thomas (1909) referred these specimens to *P. minax,* which Hollister (1913) regarded as very similar to *P. philippinensis.* Recent authors (e.g., Davis 1962) consider all Philippine members of this genus to be *P. hermaphroditus.*

Discussion

The known mammalian fauna of Camiguin is made up of three groups. The first group is composed of the bats, four of which are widely distributed in Southeast Asia (*Cynopterus brachyotis, Macroglossus minimus, Pteropus hypomelanus,* and *Emballonura alecto*), four of which are widespread in the Philippines (*Harpyionycteris whiteheadi, Ptenochirus jagori, Rhinolophus arcuatus,* and *R. subrufus*), and one of which is confined to the southern Philippines (*Pteropus tablasi*). The second group is composed of commensal, introduced species (*Suncus murinus, Rattus exulans,* and *Rattus rattus*); *Paradoxurus hermaphroditus* is thought to have been introduced to some islands in Southeast Asia (Groves 1976), and may belong in this group. Finally, the endemic non-volant land mammal fauna is represented by *Rattus everetti,* and possibly by *Bullimus bagobus.*

Although the collecting may not have obtained specimens of all species present on the island, it was sufficient to support two major conclusions. First, it is apparent that Camiguin has a depauperate non-volant land mammal fauna relative to islands that were connected to Mindanao. For example, Dinagat, a shallow-water land bridge island, has 17 known non-volant land mammals compared to Camiguin's five (including commensals), although the two islands are similar in size (671 km^2 vs. 265 km^2, respectively). Camiguin is thus similar to islands in the Negros-Panay faunal region, which also support depauperate land mammal faunas and are thought to have lacked Pleistocene land bridge connections to Mindanao or other large islands (Heaney and Rabor 1982). Second, in spite of Camiguin's apparent lack of a land bridge connection to Mindanao during the Pleistocene, as suggested by a distance of 6.5 km in which the water depth is greater than 180 m, a large number of bats have crossed over to Camiguin, as has at least one rodent. Of these species, only one (*Pteropus hypomelanus*) shows evidence of morphological differentiation.

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97(1), 1984, p. 126

CAUDRIELLA, A NEW NAME FOR *MARGARITELLA* CAUDRI, 1974 (FORAMINIFERIDA), *NON* MEEK AND HAYDEN, 1860 (MOLLUSCA)

D. Haman and R. W. Huddleston

Caudri (1974:307) introduced the new generic name *Margaritella*, with *M. ospinae* as type-species, for larger Foraminifera obtained from the uppermost level of the Punta Mosquito Formation of Middle Eocene age on Margarita Island, Venezuela. This generic name is preoccupied twice, by *Margaritella* Meek and Hayden, 1860 (Jurassic and Cretaceous trochid molluscs of Nebraska), and the gastropod genus *Margaritella* Thiele, in Troschel (1891:259), later corrected (Thiele, in Troschel 1893:406) with the replacement name *Margarella*.

Caudriella is proposed as a replacement name, under Art. 53 (ICZN) for *Margaritella* Caudri, 1974. The new name *Caudriella* is constructed in honor of C. M. Bramine Caudri in recognition of his micropaleontological studies.

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(DH) Chevron Oil Field Research Company, P.O. Box 446, La Habra, California 90631; (RWH) Scientific Research Systems, 11044 McGirk, El Monte, California 91731.

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OSTRACODA FROM THE WEST COAST OF CENTRAL AMERICA (MYODOCOPINA: CYPRIDINACEA)

Louis S. Kornicker

Abstract.—*Rutiderma pax,* new species, is described and illustrated from specimens collected off the west coast of El Salvador. An A-1 female of *Zeugophilomedes fonsecensis* (Hartmann, 1959) from El Salvador is described. The range in the Pacific of the genus *Harbansus* Kornicker, 1978, is extended to El Salvador.

While preparing a paper on the Rutidermatidae of Southern California (Kornicker and Myers 1981), I borrowed for comparative purposes from the Hamburg Zoological Museum and Zoological Institute, Germany, a vial of specimens from El Salvador that had been referred to *Rutiderma rostratum* Juday, 1907, by Hartmann (1959:198). We concluded in our paper that the specimens, although having a carapace similar to that of *R. rostratum,* are not that species; neither are they *R. hartmanni* Poulsen, 1965, to which they had been referred by Poulsen (1965: 32) (Kornicker and Myers 1981:4). The species is described as *Rutiderma pax,* new species, herein.

The vial with *Rutiderma pax* also contained two additional species: one A-1 female of *Zeugophilomedes fonsecensis* (Hartmann, 1959) and one imperfect ovigerous female of an unidentified species of *Harbansus.* Because the morphology of many appendages of *Z. fonsecensis* has not been described previously, the A-1 female is described herein. The occurrence of *Harbansus* off El Salvador is noted because previously the genus had not been reported in the Pacific off Central America (Kornicker 1978:49).

All specimens have been returned to Dr. Gerd Hartmann, Hamburg Zoological Museum and Zoological Institute, Hamburg, Germany.

Rutiderma pax, new species
Figs. 1–3a

Rutiderma rostrata.—Hartmann, 1959:198.—Kornicker and Myers, 1981:4 (only specimens of Hartmann).

Rutiderma hartmanni Poulsen, 1965:32 (part; includes only *R. rostrata* of Hartmann in synonymy).

Etymology.—From the Latin *pax,* meaning "peace," used as a noun in apposition.

Holotype.—Ovigerous female, specimen labeled number 3, on slide and in alcohol; part of lot number 27314, Zoologisches Institut und Zoologisches Museum der Universität, Hamburg, West Germany.

Type-locality.—Off Mejanguera Island, Gulf of Fonseca, El Salvador, sublittoral, depth 12 m (Hartmann 1959:195, 196).

Paratypes.—All from same sample as holotype (lot number 27314): Specimen number 1 and 2, disarticulated left and right valves; specimen number 4, 1 ovigerous female; 14 specimens (adult females and juveniles of both sexes).

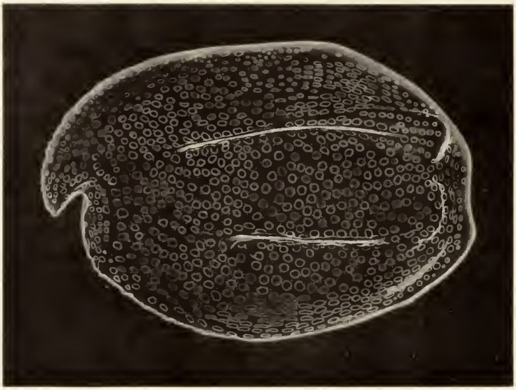

Fig. 1. *Rutiderma pax*, adult female, holotype, complete specimen, length 1.00 mm.

Distribution.—Collected only at type-locality.

Description of adult female (Figs. 1–3a).—Carapace more-or-less ovoid in lateral view with overhanging rostrum (Figs. 1, 2a); caudal process narrow, projecting posteriorly only slightly (Figs. 1, 2b, c).

Ornamentation: Two faint ribs present, one dorsal and one ventral to central adductor muscle attachments (Fig. 1); 2 low swellings present in posterior part of valve (Fig. 1); valve surface with abundant small oval fossae; anterior end of rostrum with minute scallops (Fig. 1).

Infold: Infold of rostrum with 7 bristles forming row parallel to anterior margin (Fig. 2a); 2 short bristles present at inner edge of incisur; anteroventral infold and anterior end of infold of ventral margin with total of about 5–6 bristles forming row parallel to anterior margin (bristle near incisur with wide space between it and following bristles); posteroventral infold including caudal process with 13–14 bristles (about 7 of these on caudal infold) (Fig. 2b, c); infolds of caudal process of left and right valves similar (Fig. 2b, c).

Selvage: Wide lamella prolongation fringed along anterior and ventral margins except along posterior end of latter; prolongation narrower and without fringe along edge of caudal process and posterior margin of valve; selvage divided at inner end of incisur. (Selvage not divided at edge of caudal process as on *R. rostratum* (see Kornicker and Myers 1981:fig. 2*b*).)

Size: Specimen no. 3, length 1.00 mm, height 0.71 mm; specimen no. 1, left valve, length 1.00 mm, height 0.70 mm; specimen no. 2, right valve, length 0.95 mm, height 0.66 mm; specimen no. 4, length 1.00 mm, height 0.70 mm; ovigerous female, length 0.97 mm, height 0.64 mm. (Disarticulated valves labelled specimens 1 and 2 did not have appendages so assumption that they are adult females may be false.)

First antenna: Similar to that of *R. rostratum* illustrated by Kornicker and Myers (1981:fig. 2*d*).

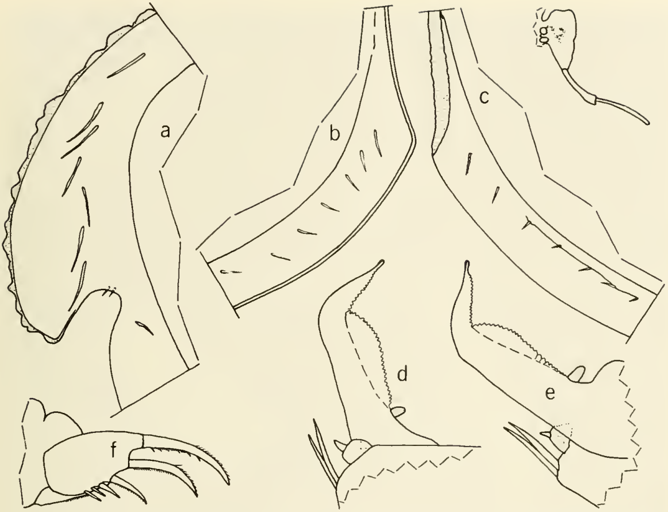

Fig. 2. *Rutiderma pax,* adult female, holotype: a, Rostrum of right valve, inside view; b, Caudal process of right valve, inside view; c, Caudal process of left valve, inside view; d, Stout terminal claw of 2nd endopodial joint of right mandible, medial view; e, same, left mandible, lateral view; f, medial eye and organ of Bellonci.

Second antenna: Protopodite bare. Endopodite similar to that of *R. rostratum* illustrated by Kornicker and Myers (1981:fig. 2*c*). Exopodite similar to that of *R. rostratum* described by Kornicker and Myers (1981:6).

Mandible: Similar to that of *R. rostratum* illustrated by Kornicker and Myers (1981:fig. 2*e*), except for produced tip of stout terminal claw of 2nd endopodial joint being about ½ length of that of *R. rostratum* (Figs. 2d, e, 3a).

Maxilla: Similar to that of *R. rostratum* illustrated by Kornicker and Myers (1981:fig. 2*f*).

Fifth limb: Epipodial appendage with 37 bristles. Except for having only 1 bristle on inner lobe of 3rd exopodial joint on single limb examined, limb similar to that of *R. rostratum* described and illustrated by Kornicker and Myers (1981: 6, fig. 2*h–j*).

Sixth limb: 2 bristles (shorter of these hirsute, other bare) in place of epipodial bristle on single limb examined. Except for having 2 instead of 3 bristles on 4th endite, endites similar to that of *R. rostratum* described and illustrated by Kornicker and Myers (1981:7, fig. 2*k*). End joint with 3 anterior bristles on projection having depth about ½ that of limb of *R. rostratum* illustrated by Kornicker and Myers (1981:fig. 2*k*), limb otherwise similar.

Seventh limb: Each limb with 3 or 4 proximal bristles (1 or 2 on each side)

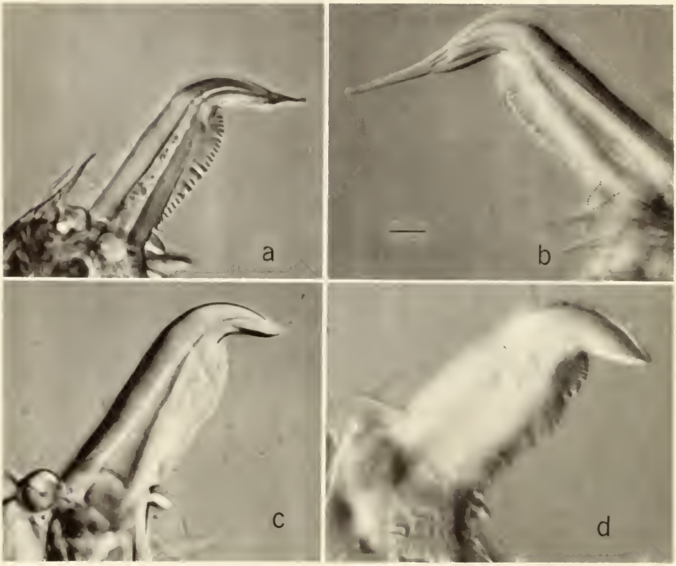

Fig. 3. Stout terminal claw of 2nd endopodial joint of mandible of adult female, medial views: a, *Rutiderma pax*, holotype, right limb; b, *Rutiderma rostratum*, USNM 158222, left limb; c, *Rutiderma licinum*, USNM 154187, right limb; d, *Rutiderma rostratum*, USNM 110918, right limb. Photographs taken by Dr. Robert P. Higgins using Nomarski interference contrast. Length of scale bar 10 μm.

and 5 or 6 distal bristles (2 or 3 on each side); each bristle with up to 6 bells and marginal spines; terminus with opposing combs.

Furca (Fig. 2f): Each lamella with 4 stout claws followed by 2 weak secondary claws. On some specimens 4th claw could be interpreted to be large secondary claw.

Beilonci organ (Fig. 2g): Elongate, broadening near middle and with broadly rounded tip and suture near middle.

Eyes: Medial eye with brown pigment, tapering anteriorly (Fig. 2g). Lateral eyes absent.

Y-sclerite: Typical for genus.

Number of eggs: Specimen no. 3 and the unnumbered female each with 1 large egg in marsupium.

Comparisons.—Three species similar to *R. pax* in having carapaces with poorly defined lateral ribs and in not having a prominent backward projecting caudal process are *R. rostratum* Juday, 1907, *R. licinum* Kornicker, 1983a, and a species identified as *R. rostratum* Juday by McKenzie (1965), but which is probably a new species (USNM 110918). The three species can be distinguished from *R. pax,* as well as from each other, by the morphology of the tip of the stout terminal claw of the second endopodial joint of the female mandible (Fig. 3).

Zeugophilomedes Kornicker, 1983

Type-species.— *Philomedes multichelata* Kornicker, 1958.

Remarks.—Although main claws other than claws 1 and 2 on the furcae of members of this genus are fused to the lamella, a low lip extending the length of the inner side of the lamella at the base of the fused main claws has led to illustrations that could be misinterpreted as indicating sutures at the base of the fused claws (Kornicker 1958:fig. 50E; 1967b:fig. 3f, g; Hartmann 1959:fig. 29: 2, 4).

The three species of *Zeugophilomedes* from the eastern Pacific and western Atlantic, *Z. oblongus* (Juday, 1907:145); *Z. fonsecensis* (Hartmann, 1959:197); *Z. multichelatus* (Kornicker, 1958:230; 1967b:2) have an unusual forked end joint on the 6th limb suggesting that they are more closely related to each other than to the two species from the Indian Ocean and Red Sea, *Z. arostratus* (Kornicker, 1967a:2; 1967c:14) and *Z. polae* (Graf, 1931:37; Kornicker, 1967c:2) on which the end joint is not forked. The 6th limb of *Z. fonsecensis* is described for the first time herein. The forked nature of the 6th limb of *Z. oblongus* was observed during the present study on a female (USNM 139159) from Monterey Bay, California.

Zeugophilomedes fonsecensis (Hartmann, 1959)
Fig. 4

Philomedes fonsecensis Hartmann, 1959:197, pl. 29:1–5, pl. 33:34.
Euphilomedes fonsecensis.—Poulsen, 1962: 363 [key].
Zeugophilomedes fonsecensis.—Kornicker, 1983b:478.

Holotype.—Not extant.

Type-locality.—Gulf of Fonseca, El Salvador (Hartmann 1959: 197).

Material.—1 A-1 female, El Salvador, sublittoral, depth 12 mm.

Remarks.—Dr. Hartmann (1959:197) described and illustrated an adult female and a juvenile male. A single specimen (A-1 female) received in a collection borrowed from Dr. Hartmann provided the opportunity to study the species and to describe the A-1 female.

Description.—Carapace similar in shape to adult female illustrated by Hartmann (1959:pl. 33:34). Minute rounded lateral process at inner end of incisur. Central adductor muscle attachments similar to those of *Z. multichelatus* illustrated by Kornicker (1967b:fig. 4*e*). Bristles of infold similar to those illustrated for *Z. multichelatus* by Kornicker (1967b:fig. 4*f, g*).

Size: Length 0.79 mm, height 0.49 mm.

First antenna (only right limb examined): 1st joint bare. 2nd joint with ventral and medial spines and 3 bristles (1 ventral, 1 dorsal, 1 lateral). 3rd joint short with ventral spines, 1 ventral bristle and 2 dorsal bristles (1 long, 1 short). 4th joint elongate with ventral spines and 3 bristles (2 ventral, 1 dorsal). 5th joint elongate; sensory bristle with 2 short proximal filaments and 3 distal filaments (2 short, 1 long). 6th joint minute, fused to 5th joint, with spinous medial bristle near dorsal margin (bristle longer than 4th joint). 7th joint: a-bristle about same

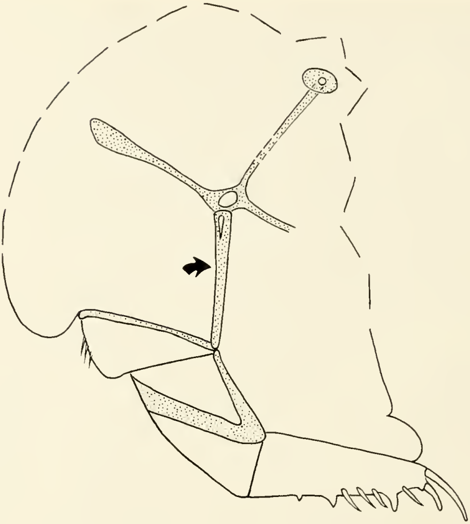

Fig. 4. *Zeugophilomedes fonsecensis*, specimen 3, A-1 female, posterior of body from right side showing right lamella of furca, right Y-sclerite (arrow), and additional sclerites (stippled).

length as bristle of 6th joint, with numerous long hairs near middle; b-bristle about ⅔ length of sensory bristle of 5th joint, with short filament near tip; c-bristle slightly shorter than sensory bristle of 5th joint, with 2 short proximal filaments and 3 distal filaments (2 short, 1 long). 8th joint: d- and e-bristles subequal (d-bristle slightly longer and stouter than e-bristle and slightly longer than c-bristle), bare, with blunt tips; f-bristle slightly shorter than c-bristle but longer than b-bristle, with 2 short proximal filaments and 3 distal filaments (2 short, 1 long). Tips of filaments and stems of b-, c-, f-, g-bristles as well as sensory bristle of 5th joint with 1 or 2 minute processes.

Second antenna: Protopodite bare. Endopodite similar to that of *Z. multichelatus* (see Kornicker 1967b:fig. 5*d*). Exopodite: 1st joint with minute, medial, terminal bristle; bristles of joints 2–8 short, with closely spaced ventral spines but without natatory hairs; 9th joint with 4 bristles (ventral bristle about same length as joints 2–9, with ventral spines; dorsal bristles short, bare).

Mandible: Coxale endite bifurcate, spinous. Basale: dorsal margin with stout midbristle with long spines near middle, and 2 long terminal bristles; about 10 short bristles on or near ventral margin (see Kornicker 1967b:fig. 5*i*). Exopodite reaching past middle of dorsal margin of 1st endopodial joint, with spinous tip and 2 subterminal bristles (shorter of these about ½ length of other). 1st endopodial joint with 4 ventral bristles (1 short, others long). 2nd endopodial joint: ventral margin with bristles forming 2 distal groups (proximal group with 2 ringed bristles; dorsal group with 2 pectinate unringed bristles and 1 ringed bristle); dorsal margin with 2 ringed bristles proximal to middle and 5 near middle; medial side near midbristles with indistinct broad but short bristle resembling triaenid bristle. End joint with 2 long claws, 1 minute dorsal claw, and 3 ringed bristles. Basale and 2nd endopodial joint with spines forming rows.

Maxilla: Precoxale and coxale with dorsal fringe of long hairs. Coxale with short dorsal bristle. Basale with 2 long terminal bristles (1 ventral, 1 dorsal), both with long spines near middle; 1 short, lateral, proximal bristle present near base of endites. 1st endopodial joint with 1 alpha-bristle with long spines near middle, and 2 beta-bristles (longer of these about same length as alpha-bristle and with short marginal spines). 2nd endopodial joint with about 8 claws and bristles. Exopodite with 3 bristles (2 long, 1 short). 3 endites present, each with 4 or more bristles.

Fifth limb: Similar to that of *Z. multichelatus* described and illustrated by Kornicker (1967b:8, fig. 6*d–f*). Exopodite: a stout bristle present on posterior side of 2nd joint proximal to pair of bristles shown by Kornicker (1967b:fig. 6*e*); 1 small bristle present at outer distal corner of 2nd joint; inner lobe of 3rd joint with 3 bristles; outer lobe with 2 bristles; 4th and 5th joints fused, with total of 6 bristles.

Sixth limb: Similar to that of *Z. multichelatus* described and illustrated by Kornicker (1967b:9, fig. 6*g*). Endite I missing; endite II with 1 short proximal medial bristle and 3 spinous end bristles; endite III with 7 spinous terminal bristles; bristles of endite IV inadvertently not counted. End joint bilobate as on *Z. multichelatus* (Kornicker 1967b:fig. 6*g*); 5 bristles along distal margin of anterior lobe, 3 stout hirsute bristles followed by 1 small bristle on posterior lobe (small bristle could represent epipodite).

Seventh limb: Each limb with 1 proximal bristle with 2 distal bells, and 5 terminal bristles (3 on peg side, 2 on comb side), each bristle with 1–2 terminal bells; all bristles strongly tapering (juvenile character), some with marginal spines. Terminus consisting of 1 pointed peg and 1 elongate peg, both opposite central fanlike comb having smaller fan on each side (Kornicker 1967b:fig. 6*i*).

Furca (Fig. 4): Each lamella with 2 stout anterior claws with sutures separating them from lamella, followed by 1 secondary claw, 1 primary claw fused to lamella, 3 secondary claws, 1 primary claw fused to lamella, then a space and 1 small primary claw fused to lamella. Claw 1 with about 16 teeth along lateral side and about 10 teeth along medial side (proximal medial teeth much larger than others); claw 2 with slender teeth forming medial and lateral row; secondary claws with slender teeth along posterior edge; teeth not observed on 3rd primary claw; last and next-to-last primary claws with teeth forming row extending obliquely onto lateral side of lamella; a few minute spines present along anterior edge of lamella; medial hairs not observed at base of claws or on lamella following claws.

Y-sclerite (Fig. 4): Linear, typical for genus.

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A NEW SUBSPECIES OF THE PIT VIPER, *AGKISTRODON BILINEATUS* (REPTILIA: VIPERIDAE) FROM CENTRAL AMERICA

Roger Conant

Abstract.—A new subspecies of the cantil, *Agkistrodon bilineatus howardgloydi,* is reported from Costa Rica, Honduras, and Nicaragua. This snake is known locally as the castellana, and is distinguished from other subspecies of *A. bilineatus* by several pattern characteristics of the head and body and by a low number of ventral scales.

During the preparation of a monograph (Gloyd and Conant) on the pit vipers, subfamily Crotalinae, of the genus *Agkistrodon* (sensu lato), I assembled virtually all the known museum specimens of *A. bilineatus* from Central America. By comparison of these with numerous examples of the several subspecies indigenous to Middle America, the following facts emerged: (1) *A. b. russeolus* Gloyd occurs in disjunct subhumid areas of northern Belize, as suggested by Hoevers and Henderson (1974), Henderson and Hoevers (1975), and Henderson (1978); (2) the range of the nominate subspecies, *A. b. bilineatus* Günther, extends southeastward from southern Sonora, Mexico, through the Pacific coastal plain and versants of the adjacent mountains, and terminates in El Salvador; and (3) a distinct form, a specimen of which Cruz, et al. (1979), and Wilson and Meyer (1982) were unable to assign to any of the described taxa, occurs in Costa Rica, Honduras, and Nicaragua. This last form merits taxonomic recognition.

Agkistrodon bilineatus howardgloydi, new subspecies
Spanish name: Castellana
Fig. 1

Holotype.—American Museum of Natural History (AMNH 125525), total length 746 mm, male, collected by Louis W. Porras and John C. Rindfleish, 8 Aug 1982, in tropical dry forest (=tropical deciduous forest) 0.8 km north of Mirador el Cañon del Tigre, Parque Nacional Santa Rosa, Provincia Guanacaste, Costa Rica.

Paratypes.—COSTA RICA, Provincia Guanacaste, Colonia Jobo de la Cruz, Bahía Salinas (AMNH 125526–125527); Hacienda Bejuco, 5 km east of Bahía Naranjo, Golfo de Papagayo, 25 km northwest of Liberia (Universidad de Costa Rica, UCR 3051 and UCR 3336); near the Río Cuajiniquil (near the Río Salada), Parque Nacional Santa Rosa (UCR 8062).

HONDURAS, Departamento Valle, Isla de Zacate Grande (Universidad Autónoma de Honduras, UNAH 5516).

NICARAGUA, Departamento Granada, vicinity of Granada (AMNH 108600–108601); Departamento Masaya, near Masaya (Cornell University, CU 10020).

Diagnosis.—This subspecies may be distinguished from the three others (*bili-*

Fig. 1. *Agkistrodon bilineatus howardgloydi,* Holotype: Right side of head showing distinctive facial markings. (From a color transparency by Louis W. Porras.)

neatus Günther, *russeolus* Gloyd, and *A. b. taylori* Burger and Robertson) by the following combination of characters: lower light facial stripe divided in two parts that approach each other and usually meet at an obtuse angle at the common juncture of the 2nd and 3rd supralabials; lower light stripe subtended by a narrow dark line; lower parts of supralabials pale, unmarked, and same color as infralabials and ground color of chin and throat; upper light facial stripe narrow, often disrupted or even absent posterior to the supraocular in adults; chin and throat pale and sharply set off from dark venter at level of 1st to 6th ventral; medial third or fourth of venter (on posterior ¾ of body) unpatterned or slightly so in comparison with its outer portion; young bright red or reddish. In all other races of *bilineatus* the lower light facial stripe normally is single and continuous, and the young are gray, brown, or reddish-brown; *howardgloydi* shares the narrow upper light facial stripe and the unpatterned belly center with *russeolus,* but differs in having a lower average number of ventrals (see dichotomous key below).

Description of holotype.—Crown with 9 symmetrical plates, paired internasals, prefrontals, supraoculars, and parietals, and a single frontal; parietals slightly truncate posteriorly. Rostral slightly higher than wide, apex not rising above canthus. Nasals 2, the anterior (at its upper edge) about 1½ times width of posterior nasal; nostril chiefly in prenasal. Preoculars 2, the upper separated from the postnasal by a quadrangular loreal, wider at its base; loreal on left split obliquely (in a somewhat vertical direction) into 2 subequal scales; lower preocular forming upper posterior border of facial pit; a small postfoveal enters orbit, another borders pit inferiorly. Sum of post- and suboculars 3 on left side, 4 on right. Orbit surrounded by 7 scales on left, 8 on right (including postfoveals). Supralabials 8, the upper portion of 2nd forming anterior border of pit. Infralabials 11. Temporals in somewhat irregular rows, 1st one of lower row conspicuously larger than all others; 1st and 2nd rows of temporals without keels. First pair of infralabials extending posteriorly in long, narrow points that are in contact with each other posterior to tip of mental. One enlarged pair of chin shields, each about twice as long as wide. Median gulars in 2 pairs; lateral gulars in 2 to 5 oblique rows.

Dorsal scales with paired apical pits; all with keels except those of lowermost row anteriorly. Scale rows 25-23-21-19; order and places of reduction, in accordance with the Dowling (1951) recount system:

$$25\ \frac{5+6\,(15)}{-6\,(14)}\ 23\ \frac{4+5\,(85)}{4+5\,(78)}\ 21\ \frac{-5\,(111)}{4+5\,(113)}\ 19\ \ (129)$$

Ventrals 129; anal plate single; hemipenes not everted. Subcaudals 61, the 30th and the distal 28 divided; terminal spine sharp, extending downward but curved at end to point away from tail tip.

Total length (measured when snake was relaxed after euthanization) 746 mm; length of tail 149 mm, 20 percent of total length.

General coloration (in life soon after capture) varying shades of brown, the darker ones purplish in tone. Crown and sides of head dark purplish brown. A broad dark purplish-brown cheek stripe bordered by bold narrow light lines (facial stripes) above and below. Upper light line cream-colored (slightly yellowish anteriorly), beginning at anterior tip of internasal and extending along the canthus on edges of internasal, prefrontal, supraocular, and uppermost postocular, and then diagonally posteriorly on second row of temporals and downward to the neck; upper light line slightly intermittent, distinctly narrower than lower light line, and subtended in part by a thin line of dark brown pigment. Lower light line white, divided into two parts, which narrowly make contact at an obtuse angle at posterior edge of 2nd supralabial. Anterior part of lower light stripe meets the upper light stripe at outer edge of internasal and then extends obliquely downward across the anterior nasal, lower edge of postnasal, upper tip of 1st supralabial, and continues at a slightly different angle across 2nd supralabial. Posterior portion of lower light line begins on 3rd supralabial and continues in a more or less straight line to last (8th) supralabial where it turns sharply downward at a right angle across 10th infralabial, anterior edge of 11th infralabial, and the adjacent gulars; it then continues posteriorly as a series of white spots almost to join the downward extension of the upper light line. The lower light stripe is narrowly subtended by a thin dark brown line. Lower edges of supralabials, all of infralabials, and ground color of throat bright (slightly brownish) orange, which color extends irregularly onto first five ventrals and terminates almost abruptly at level of 6th ventral. A series of small white, mostly dark-bordered, streaks and spots on chin and throat. Rostral and mental each marked medially by a broad vertical white bar narrowly bordered by brown against a ground color that almost matches chin color.

Dorsal ground color, which appears in pale areas between crossbands and down sides of body, is medium brown. The 11–12 purplish-brown crossbands are darker at their edges and incompletely bordered by white spots which are larger and more conspicuous on lower sides of body. The dark brownish-gray ventro-lateral blotches are broadly connected with the crossbands and merge below with the dark grayish stippling of the venter. Last several crossbands with pairs of faint dark markings near their centers at level of scale rows 2 to 5, some accompanied by flecks of white. Venter dark and marked with numerous bold white spots and curved lines anteriorly and also along the sides posteriorly. Longitudinal central 4th of venter distinctly paler (light pinkish) than outer portions of belly on posterior ¾ of body, thus imparting appearance of a pale midventral stripe. Eight dark crossbands on tail that become pale where distal half of tail is medium pale gray. Anal plate dark gray; orange pigment on parts of first 16 subcaudals; remainder of underside of tail dark gray; terminal spine black except for a narrow vertical pale gray stripe on left side.

Immediately after euthanization the coloration of the tongue was orange-pink, tips pale yellowish; the pupil of the eye was black, the upper half of the iris matched the coloration of the upper light facial stripe, and the lower half was slightly paler than the dark cheek stripe.

The holotype was held in captivity for six months before I received it alive, and by that time there had been changes in coloration. It had shed its skin, and its general appearance was reddish-brown; the purplish tones had disappeared. Also, probably from rubbing its snout against some object, possibly the cloth sack used in shipping, the upper portion of the anterior surface of the rostral had been abraded. The upper portion of the vertical white bar, which had been slightly forked at its apex, according to a series of excellent color photographs taken soon after the snake was captured, had thus been eliminated. Most veteran reptile keepers have experienced cases in which specimens in their care became paler after ecdysis. Louis W. Porras (pers. comm.), however, noted subtle changes in the snake's coloration from day to day and under varying light conditions (metachrosis?) during the several weeks it was in his possession. The colors of the preserved snake, after three months in alcohol, more closely resembled those seen soon after its capture than they did after shedding.

Variation among paratypes.—In these nine specimens, five males and four females, the diagnostic characters of coloration and pattern are all consistently present with minor exceptions, and most of the latter are attributable to the darkening of large adult males in which some details are obscured.

The two separate components of the lower light facial stripe usually resemble those of the holotype in that they barely touch at the juncture of the 2nd and 3rd supralabials; exceptions occur in AMNH 125526 and UCR 3051, where the two light lines fail to meet but are in close proximity, and in UCR 3336 and UCR 8062, where there is a distinct gap because the anterior component terminates slightly beyond the middle of the 2nd supralabial. Also, on the right side of the head in UCR 8062 the posterior component is intermittent on supralabials 6 and 7. The lower portions of the supralabials are pale, unmarked, and match the coloration of the underside of the head in all specimens except two large males, viz.: in AMNH 108601 considerable dark stippling is present, and in CU 10020, an exceptionally dark snake, the lower edges of the supralabials are almost uniformly black.

In large specimens the upper light facial stripe tends to be narrow and may be only faintly indicated posterior to the eye; this may, in part, be an artifact of preservation. For example, in AMNH 125526 (female) and AMNH 125527 (male) the upper light stripe terminates at the middle of the supraocular and is virtually non-existent, respectively, in the two preserved specimens; both of these snakes were photographed in life, however, at which time the upper (yellow) light stripe, although quite narrow, was clearly evident from snout to supraocular, but intermittent and only faintly indicated posterior to the eye. In a large male (AMNH 108601), however, the upper light stripe, although intermittent, is well-defined throughout its length and, through a series of light spots at the rear of the head, is connected with the posterior extension of the lower light stripe. In the very dark male (CU 10020) the upper light line is represented, posterior to the eye and on the neck, by an intermittent series of small pale streaks. A more or less continuous connection between the upper and lower light stripes is discernible in two young specimens (UCR 3051 and UCR 3336), but in the other juvenile (AMNH 108600) the upper stripe is almost totally absent, possibly because of fading following preservation.

The pale coloration of the underside of the head terminates rather abruptly and is replaced by the dark coloration of the venter at levels varying from the 1st to 5th ventral scutes. In the two large males there is dark stippling (in AMNH 108601) and a profusion of dark gray (in CU 10020) on the chin and throat. The medial ⅓ or ¼ of the venter (on the posterior ¾ of the body) is unpatterned in all specimens or virtually so; the coloration varies from pale orange, lightly stippled with brown (in life in AMNH 125526), to black (in CU 10020). The medial portion of the venter may or may not be paler than the sides of the belly; the essential fact is that it is not patterned or only slightly so.

The pale ground color between the dark dorsal crossbands normally descends to, or almost to, the ventrals, but dark stippling is usually present on the lowermost 2 to 5 scale rows. In some large specimens the dark stippling blends with the coloration of the adjacent crossbands, and the dorsal portion of the ground color, when viewed from above, appears as a series of more or less diamond-shaped pale areas. This is particularly noticeable in the two large dark males and the female (UNAH 5516) from Honduras.

Total lengths and sexes among the paratypes are as follows: Males (CU 10020 = 960 mm), (AMNH 108601 = 945 mm), (UCR 8062 = 830 mm), (AMNH 125527 = 730 mm), and (UCR 3336 = 319 mm); females (AMNH 125526 = 820+ mm), (UNAH 5516 = 715+ mm), (UCR 3051 = 495 mm), and (AMNH 108600 = 335 mm). Tail ratios (tail length/total length) among specimens with complete tails are 17–21 percent in males and 18–20 percent in females; mean 19 percent in both sexes.

Remarks.—Proof that the young of *howardgloydi* may be bright red was provided by photographs taken in the field in the Parque Nacional Santa Rosa by Daniel H. Janzen. Two of the smaller specimens (UCR 3051 and UCR 3336), although faded since their preservation, were obviously strongly reddish in life. Jaime Villa (1962 and personal communication) reported that juveniles from Nicaragua are reddish or brick red.

The lower light facial stripe is divided into two components as an occasional anomaly in *russeolus* (5 occurrences among the 42 possiblities in the 21 available specimens), and such a separation is present in the (male) holotype of that taxon (University of Kansas, KU 70905). The holotype is unlike *howardgloydi*, however, in the following key characteristics: the lower light facial stripe is subtended by uniformly dark pigment that extends to the commissure; the chin and throat are uniformly dark (except for several narrow white streaks and spots) and the dark coloration blends imperceptibly with the dark pigmentation of the venter; the upper light facial stripe, although narrow, is distinct and continuous (in most specimens of *howardgloydi* of comparable length the upper light stripe is intermittent, vague, or even absent posterior to the supraocular); ventrals 137 (129–135 in male *howardgloydi*).

These comments on the holotype of *russeolus*, in conjunction with other data accumulated during studies I have made for the monograph (Gloyd and Conant), indicate that *howardgloydi* is much more closely related to the geographically distant *russeolus* (of northern Yucatan and northern Belize) than it is to the nominate subspecies, *bilineatus*, which is known to occur at least as far southeastward as central El Salvador.

Key to the Subspecies of *Agkistrodon bilineatus*

1. Lower light facial stripe extending downward to the commissure; subcaudal counts low (45 to 56 in males; 40 to 47 in females); marked sexual dimorphism in adults . . . . *taylori*
(Northeastern Mexico—Nuevo León, San Luis Potosí, and Tamaulipas)

– Lower light facial stripe bordered inferiorly by dark pigment; subcaudal counts high (56 to 71 in males; 46 to 67 in females); little or no sexual dimorphism 2

2. Adults almost plain black or dark brown, juveniles with brown or reddish-brown crossbands; facial stripes relatively wide, prominent, and continuous; venter dark but sprinkled with whitish markings throughout its width . . . . *bilineatus*
(Southern Sonora in northwestern Mexico to El Salvador, Central America)

– Adults patterned with crossbands that are often reddish; upper facial stripe narrow, often interrupted or greatly reduced posterior to the supraocular; medial ⅓ or ¼ of venter virtually unpatterned on posterior three-fourths or more of body, sometimes appearing as a pale midventral stripe, especially in young specimens 3

3. Lower facial stripe normally continuous and subtended by dark pigment extending to the commissure (except in very young specimens); ground color of chin and throat brown or blackish and blending with dark venter; ventrals in males 131–141 (mean 136.0), females 132–139 (mean 136.2) . . . . *russeolus*
(Northern Yucatan, Mexico, and subhumid areas of northern Belize)

– Lower facial stripe divided in two parts that narrowly meet at an obtuse angle at or near suture between 2nd and 3rd supralabials; lower light stripe subtended by a narrow dark line; lower parts of supralabials pàle and matching ground color of pale chin and throat; pale coloration of under side of head terminating abruptly, being replaced by dark coloration of venter; ventrals in males 129–135 (mean 131.5), females 128–134 (mean 130.5) . . . . *howardgloydi*, new subspecies
(Dry Pacific lowland areas of Honduras, Nicaragua, and Costa Rica)

Etymology.—This subspecies is named for the late Howard K. Gloyd, my close friend, colleague, and expert on pit vipers, especially the rattlesnakes. Gloyd worked for decades on the genus *Agkistrodon* (sensu lato), and he had predicted that a new race of *A. bilineatus* would eventually be described from lower Central America.

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Permits, including those for import from the Miami office of the U.S. Fish and Wildlife Service, have been deposited in the Department of Herpetology of the American Museum of Natural History, in New York.

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TWO NEW SPECIES OF TUBIFICIDAE (OLIGOCHAETA) FROM THE NORTHERN TERRITORY OF AUSTRALIA

Ralph O. Brinkhurst

Abstract.—*Antipodrilus magelensis,* new species, differs from the two other *Antipodrilus* species with bifid setae in that the penes have thickened internal basement membranes which look like penis sheaths in whole mounted specimens. *Rhyacodrilus billabongus,* new species, has bifid setae and muscular atria without prostates, as does *R. fultoni,* but the penial setae and atria differ from those of the latter. This species is discussed in relation to two recently described monotypic marine littoral genera (*Vadicola, Ainudrilus*) which have no external prostates on the atria.

Magela Creek, Northern Territory, Australia, is a branch of the East Alligator River about 250 km east of Darwin. A series of studies of this system has been made prior to the start of uranium mining in the Ranger deposit, which lies within the watershed. The macroinvertebrate fauna was described by Marchant (1982) but the Oligochaeta have been unidentified until now. Material sent to me by P. M. Outridge from this system consisted of specimens collected in four billabongs (Nankeen, Mudginberri, Georgetown, and Bowerbird) at various dates in 1981–1982. The locations of the billabongs are indicated in Marchant (1982) and are shown on Australian Topographic 1:100,000 series maps 5473 (East Alligator), 5572 (Howship) and 5472 (Cahill). Three genera of the family Naididae and two genera of the family Tubificidae were identified, the tubificid genera being represented by two species new to science.

Methods and Materials

All of the material was preserved in alcohol. Specimens were either mounted unstained in polyvinyl lactophenol (Gurr) or were stained in borax carmine, dehydrated, and mounted in Canada balsam whole or after dissection in the final mounting medium.

Antipodrilus magelensis, new species
Figs. 1, 2

Holotype.—USNM 80692, a slide-mounted, dissected specimen.

Type-locality.—Mudginberri Billabong, Magela Creek, Northern Territory, Australia, mixed sand and silt, 4 May 1981.

Paratypes.—USNM 80693–97, 80700, 2 dissected specimens on 2 slides, 6 whole mounted specimens on 3 slides, 19 specimens in fluid. Brinkhurst collection, 15 mature and 39 immature specimens, whole mounted or dissected, on 28 slides. Paratypes from Mudginberri, Georgetown and Bowerbird billabongs, only immature specimens from Nankeen Billabong.

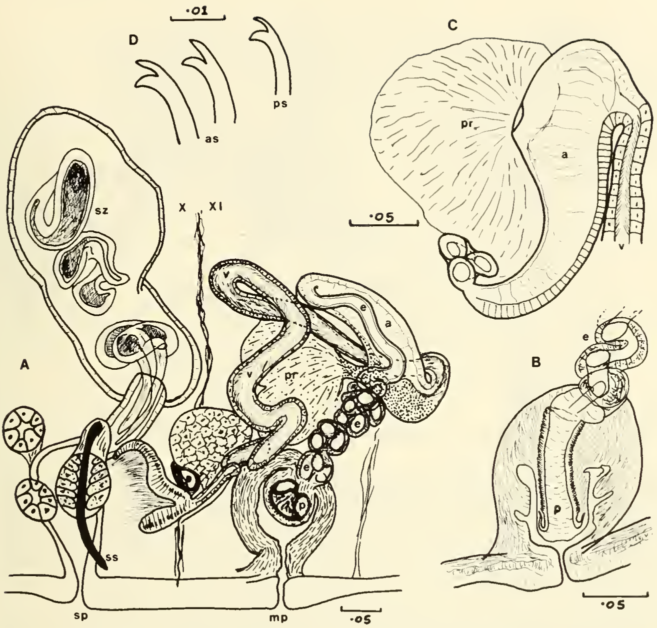

Fig. 1. *Antipodrilus magelensis,* reproductive system and setae: A, Lateral view of dissected holotype, segments X/XI, anterior to left; B, Detail of penis; C, Detail of atrium, vas deferens and prostate gland unions; D, Anterior and posterior somatic setae. a—atrium, as—anterior seta, e—ejaculatory duct, mp—male pore, p—penis, pr—prostate gland, ps—posterior seta, sp—spermathecal pore, ss—spermathecal seta, sz—spermatozeugmata, v—vas deferens. Scales in mm.

Etymology.—Worm from Magela Creek.

Description.—Length 0.9 mm, breadth at widest 0.3 mm, 40 segments in single intact specimen. Setae of preclitellar segments 4–6 per bundle with setal teeth equal in length and breadth. Setae diminish in number in postclitellar segments to 2 per bundle, the upper teeth becoming shorter and thinner than the lower. The ventral setae of X are replaced by modified spermathecal setae in glandular sacs in mature specimens (Figs. 1, 2); the sacs appear to bear 2 small glandular bodies. The spermathecal setae and pores may lie close together near the midline of X or may lie in the normal setal line. The spermathecae have distinct ducts and elongate, voluminous ampullae filled with elongate spermatozeugmata in mated specimens. The vasa deferentia are about 3 times the length of the atria; they open into the atria subapically and on the opposite side to the prostate glands. The short atria terminate in strongly coiled ejaculatory ducts that must be longer

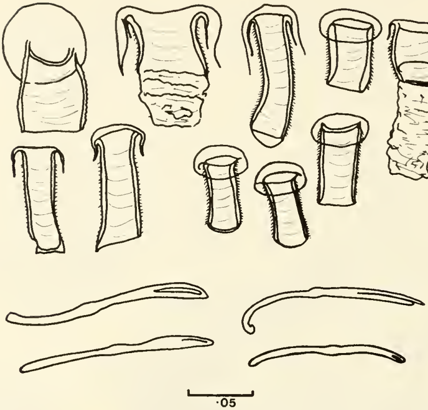

Fig. 2. *A. magelensis,* apparent penis sheaths (above) and spermathecal setae (below). Scale in mm.

than the atria, though their length is impossible to determine due to the strong coiling. The penes are large and muscular, and are set in muscular sacs. The basement membranes of the penial muscle cells form thick clear layers within the penes that resemble cuticular penis sheaths in whole-mounted specimens mounted in polyvinyl lactophenol. These false penis-sheaths vary in length and width, presumably depending on the state of contraction of the penes (Fig. 2).

Remarks.—Indistinct versions of the false penis sheaths can be seen in one other *Antipodrilus* species (*A. timmsi,* see Brinkhurst 1971:fig. 2C, pe) but have not been observed in the others. *Antipodrilus timmsi* Brinkhurst has hair and pectinate setae in dorsal bundles, and while this alone would not exclude the possibility of identifying the new material as part of that species, other factors such as the long vas deferens, uncoiled ejaculatory duct and short spermatozeugmata of *A. timmsi* indicate a clear separation of the two. In *A. plectilus* Brinkhurst and Fulton there are more anterior setae than in *A. magelensis,* and the setae also have shorter upper teeth; the ejaculatory ducts are short and uncoiled in *A. plectilus.* As the name suggests, there are even more setae in *A. multiseta* Brinkhurst and Fulton, and the ejaculatory ducts, while quite elongate, were not seen to be coiled (Brinkhurst and Fulton 1979). *Antipodrilus davidis* (Benham) has hair and pectinate setae and short, uncoiled, ejaculatory ducts.

Habitat.—Wide range of substrates from fine mud with high organic content to gravel, in billabongs (pools in or near a dry creek bed).

Distribution.—Known only from Magela Creek to date.

Rhyacodrilus billabongus, new species

Fig. 3

Holotype.—USNM 80698, a dissected specimen.

Type-locality.—Bowerbird Billabong, Magela Creek, Northern Territory, Aus-

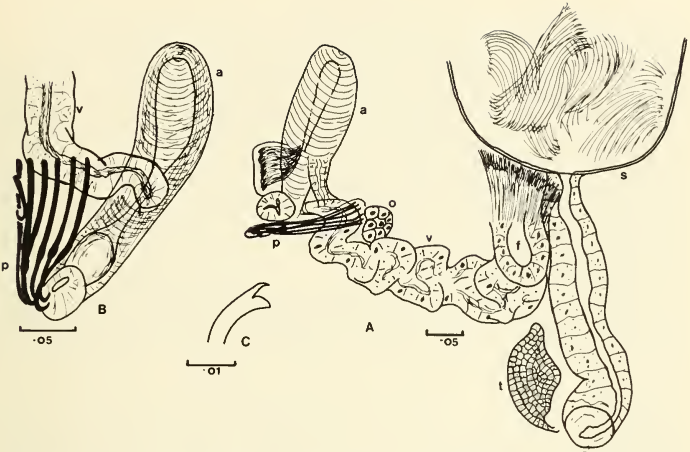

Fig. 3. *Rhyacodrilus billabongus*, reproductive system and setae: A, Lateral view of dissected holotype, segment X/XI, anterior to right; B, Detail of vas deferens, atrium and penial setae; C, Anterior somatic seta. a—atrium, f—male funnel, o—ovary, p—penial setae, s—spermatheca, t—testis, v—vas deferens. Scales in mm.

tralia, a long, narrow, deep lagoon which feeds a perennially-flowing creek; in the dry season a fast-flowing riffle some 10 cm deep, heavily covered with macrophytes, over a substrate of sand, gravel, and rock; in the wet season a torrent up to 20 m deep (type date: 21 Aug 1981).

Paratypes.—USNM 80699, a whole mounted specimen; Brinkhurst collection, a dissected specimen, both from the type-locality.

Etymology.—Worm from a billabong.

Description.—No dimensions available as worms fragmented; anterior end of undissected specimen c. 0.5 mm wide after flattening. Setae of preclitellar segments 4–6 per bundle, with teeth equally long but the upper teeth thinner than the lower, and sometimes slightly bent distally (Fig. 3), number of setae reduced to 3 in immediate postclitellar segments, no posterior end available for inspection. Ventral setae of XI are modified as penial setae, 6 in each bundle, strongly recurved distally with a distal nodulus (Fig. 3p). Spermathecal pores lie anteriorly on X, in the ventral setal line; spermathecal ducts are long and narrow, sharply set-off from the globular ampullae (Fig. 3). Sperm is in loose masses in the spermathecae. The vasa deferentia are wide and glandular, and appear to be about twice the length of the muscular, upright atria. There are no external prostate cells on the atria. While the male terminalia cannot be clearly seen, there are no signs of penes; the superficial male pores are small circular openings on the body-wall (Fig. 3). The vasa deferentia enter the atria just above their bases. There appears to be a bundle of sperm associated with the base of one atrium in the holotype (Fig. 3), but as this was seen on a dissected specimen it may be displaced from a spermatheca. Coelomocytes are large and abundant.

Remarks.—Most *Rhyacodrilus* species have prostate glands on the atria. *Rhyacodrilus* (*Taupodrilus*) *simplex* (Benham) does not, and may revert to its status as the type-species of the genus *Taupodrilus* once the much needed revision of these genera is undertaken. *Rhyacodrilus fultoni* Brinkhurst lacks the dorsal hair and pectinate setae of *R. simplex,* and also lacks prostate glands. However, it has 10–13 setae per bundle anteriorly instead of the small number in the new material, and the penial setae are both more numerous and straighter than in *R. billabongus.* The atria in *R. fultoni* are almost spherical and open into a second pair of spherical chambers; the vasa deferentia do not appear to be wide and glandular as they are in the new material (Brinkhurst 1982).

While the distinction between *R. billabongus* and other *Rhyacodrilus* species is clear, there is a residual taxonomic problem at the generic level. There are two monotypic marine littoral rhyacodriline genera that should be mentioned here. The genus *Vadicola* was erected by Baker (1982) for a species with bifid somatic setae, glandular vasa deferentia and atria without prostate glands. The vasa deferentia join the atria just below their ental ends, or apically if the short atria are considered to be bent over entally. The atria terminate in muscular ducts termed ejaculatory ducts by Baker, and these are separated from the atria by inwardly directed internal projections that may suggest a total eversion of the lower parts of the system during copulation. In *Ainudrilus* the setae are also limited to simple bifids in the somatic bundles, but Finogenova (1982) interprets the male ducts differently from Baker (1982). In *Ainudrilus* there is a ciliated tubular part of the male duct running from the funnel to an upright muscular structure, and these appear to be quite similar to the structures described in *Vadicola.* However, where Baker referred to glandular vasa deferentia and naked atria, Finogenova sees the ciliated glandular duct-like section as atrial and the upright muscular structure as constituting a penis sac. *Vadicola* is known from intertidal habitats along the whole Pacific coast of British Columbia, including the Queen Charlotte Islands, and *Ainudrilus* is also intertidal, from the Pacific coast of the Soviet Union (Urup Islands). The basis of the interpretation by Finogenova must be that prostate cells arise by the penetration of the muscular walls of the atria by developing prostatic cells derived from the atrial linings, whereas the vasa deferentia grow back towards the atria from the male funnels during ontogeny. However, many species of the family Naididae have prostate cells on the vasa deferentia, and Baker (1982) suggests that the vasa deferentia of *Vadicola* have taken over the prostatic function from the atrial cells. The ciliation of the tubular and glandular ducts termed atria by Finogenova suggests that they are possibly vasa deferentia and, as Baker suggested, that glandular vas deferens cells differ from prostatic cells, the histology of the secretory cells of these two genera will have to be carefully compared.[1] Both of these genera are quite distinct from *R. billabongus* in atrial form and the position of the union of the vasa deferentia and atria, and so I prefer to leave the new material assigned to the predominantly freshwater genus *Rhyacodrilus,* perhaps to be ultimately allocated to *Taupodrilus.*

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[1] Note added in proof: C. Erseus (pers. comm.) has been able to compare material of both *Ainudrilus* and *Vadicola* and suggests that these taxa are at least congeneric.

Other Taxa

Six other species were present in the collection. The commonest species was *Aulodrilus pigueti* Kow., with 31 specimens at Georgetown, 11 at Mudginberri but only 1 at Nankeen. *Aulodrilus pluriseta* was present at the first two of these billabongs (7 and 2 specimens respectively). No other tubificids were found. Twelve specimens of the naidid *Allonais inaequalis* (Stephenson) were found at Bowerbird Billabong, the specimens conforming to the description in Brinkhurst (1971). Three specimens of *Branchiodrilus hortensis* (Stephenson) were tentatively identified, 1 from Nankeen and 2 from Georgetown Billabong. Gills were present throughout most of the rather fragmented specimens, but the hair setae were enclosed in the gills, whereas there are supposed to be some free hair setae posteriorly in this species. A total of 3 *Dero* specimens was found, but these could not be identified to species. This species list is typical of many tropical and subtropical habitats (apart from the restriction of *Antipodrilus* to the Antipodes), but the absence of *Limnodrilus* and *Branchiura* (Tubificidae) is unusual, especially as both genera are well-represented in disturbed and marginal habitats.

Acknowledgments

I am indebted to Peter Outridge for access to the collection and for the information about the habitats involved, and to R. D. Kathman for critical review of the manuscript.

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FOUR NEW SPECIES OF SPIONIDAE (POLYCHAETA) FROM NEW ZEALAND, WITH COMMENTS ON A SYNTYPE OF *SPIO AEQUALIS* EHLERS FROM CHATHAM ISLAND

James A. Blake

Abstract.—Four new species of Spionidae are described from New Zealand. *Microspio maori* is a widespread intertidal species occurring on both of the main islands. *Microspio elegantula* occurs intertidally in Wellington Harbor. *Spio readi* occurs in the intertidal zone of Wellington Harbor and from 50–105 m off the Otago Peninsula of South Island. *Carazziella proberti* closely resembles two Australian species and occurs off Otago in 122 m. *Spio aequalis* Ehlers is known only from its original find on Chatham Island. The syntype bears unusually large posterior branchiae.

Recent ecological studies of benthic habitats in offshore areas, shallow water embayments and estuarine systems of both North and South Islands of New Zealand have catalogued numerous species of polychaetes, many of which are new to science.

The present paper describes four new species of Spionidae of the genera *Microspio, Spio,* and *Carazziella.* No species of *Microspio* and *Spio* have previously been reported from New Zealand, although several are known from Australia (Blake and Kudenov 1978). *Spio aequalis* Ehlers was originally described from Chatham Island (Ehlers 1904). In order to compare *S. aequalis* with the new collections, a syntype was obtained from the British Museum and the description is supplemented.

The most important works for identifying Spionidae of the Southern Ocean are Day (1967), Rainer (1973), Read (1975), Blake and Kudenov (1978) and Blake (1983). The genera treated in the present study follow the scheme of Blake and Kudenov (1978) and readers are referred to that work for generic diagnoses, keys and discussion of species complexes.

Type-material is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and the National Museum of New Zealand, Wellington (NMNZ).

Microspio maori, new species
Fig. 1

Material examined.—NEW ZEALAND, North Island, intertidal, coll. G. B. Read: Coromandel Peninsula, Tairua Harbor, 26 Jul 1978, muddy sand, 7 paratypes (NMNZ); Pakawau Flats, Golden Bay, 11 Dec 1976, coarse sand, 30+ paratypes (NMNZ); Waikanae River Estuary, Wellington Province, 8 Oct 1978, holotype and 11 paratypes (USNM 80491–2); Pauatahanui Inlet, near Wellington, 10 Nov 1976, sand flats, 15 paratypes (NMNZ); Hutt River Estuary, Wellington, 15 Feb 1977, fine sand, 70 paratypes (USNM 80493); Ohiwa Harbor, Bay of

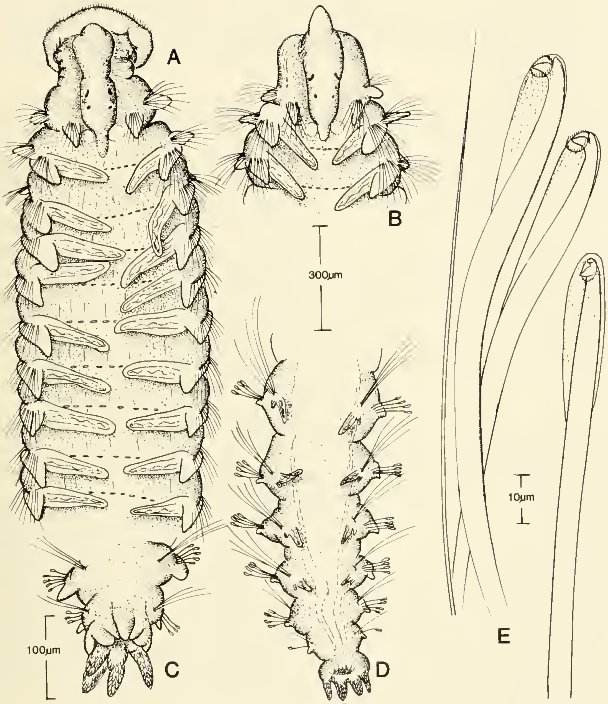

Fig. 1. *Microspio maori* (paratype, USNM 80492): A–B, Anterior ends, dorsal view, palps omitted; C–D, Posterior ends, dorsal view; E, 3 hooded hooks and accompanying capillary seta from middle neuropodium.

Plenty, 1979, intertidal sand, coll. N. Z. Ministry, Agric. & Fish., Fish. Management Division, Sta. 126, 2 juveniles (NMNZ).—NEW ZEALAND, South Island, intertidal, coll. G.B. Read: Wairau River Estuary, near Blenheim, 17 Dec 1976, fine sand, 30 specimens (NMNZ); Avon-Heathcote Estuary, Christchurch, 4 Dec 1976, fine sand, 10 specimens (USNM 80494); Waikouaiti River Estuary, Otago Peninsula, 5 Dec 1976, shelly sand, 15 specimens (NMNZ).

Description.—A long, slender species; holotype largest, 17.0 mm long and 0.5 mm wide for 75 setigers; other specimens generally smaller. Color in alcohol: light tan, with irregularly arranged black spots on posterior setigers and pygidium.

Prostomium narrow, slightly expanded anteriorly, tapering to entire tip, sometimes appearing conical (Fig. 1A, B); narrowing posteriorly to short caruncle, terminating indistinctly in middle of setiger 2; no occipital tentacle; with 2 pairs of eyes, anterior pair cup-shaped, posterior pair oval-shaped. Peristomium well developed, slightly inflated, partly fused to setiger 1 (Fig. 1A); proboscis saclike, with heavily ciliated anterior border; palps moderately long, extending posteriorly for 9–10 setigers.

Setiger 1 biramous, well developed, with triangular notopodial postsetal lamellae and elliptical neuropodial postsetal lamellae. Branchiae from setiger 2, basally fused to notopodial lamellae, anteriorly long, straplike, extending to middorsal line (Fig. 1A), becoming shorter and narrower posteriorly (Fig. 1D); branchiae with ciliated bands on inner margins, continuing dorsally across each setiger. Anterior notopodia with lamellae large, triangular, becoming shorter and narrower, with bacillary glands in posterior setigers, but still basally fused to branchiae. Neuropodia with lamellae elliptical in anterior setigers and reduced to short glandular extensions of enlarged neuropodial lobes in posterior setigers.

Anterior parapodia with capillary noto- and neurosetae, arranged in 2 rows, setae of anterior row shorter, with fine granulations on shaft and clear narrow sheaths; setae of posterior rows longer, non-granulated. Posterior notopodia with few (5–6) very long capillary setae, with narrow sheaths. From setiger 17–19, neuropodia with hooded hooks gradually replacing both rows of capillaries, 2–3 at first with 11–12 capillaries, increasing to 9–12 hooks with 5–6 capillaries in middle setigers, with about 9 hooks and 2–3 capillaries, usually in inferiormost position in posterior setigers; hooks bidentate, with slightly recurved shaft and clear, large hood, with opening finely serrated (Fig.1E).

Pygidium with 4 equal cirri, 2 ventral and 2 ventrolateral (Fig. 1 C–D). Pygidial ciri, and noto- and neuropodial postsetal lamellae of posterior setigers with prominent bacillary glands.

Remarks.—*Microspio maori* differs from related species in having a conical-shaped prostomium, appearing almost pointed in some specimens. Related species have either a smoothly rounded prostomium or one which is distinctly incised on the anterior margin. *Microspio maori* is also unusual in the replacement pattern of the capillaries by hooded hooks. In most species the hooks replace the posterior row of capillaries, leaving the anterior row intact throughout the body. In *M. maori* the hooks entirely replace both capillary rows with a single row of hooded hooks. Accompanying capillaries are much thinner and usually limited to the lower part of the ramus. The occurrence of prominent bacillary glands in the parapodial lamellae and pygidial cirri is typical for species of *Microspio* and in this respect, *M. maori* conforms well with its congeners. The form and arrangement of the pygidial cirri, however, differs from that usually seen in species of *Spio* and *Microspio*. In *M. maori*, the 4 anal cirri are equal in size and located in the ventral half of the pygidial segment leaving a bare open ring above the anal opening. In other species, the 4 cirri are equally spaced around the anus.

Ecological notes.—*Microspio maori* is present in densities ranging from 2600–6300 per m^2 ($\bar{x}$ = 4100 per m^2) on intertidal sand flats of the Pauatahanui Inlet near Wellington. The sediments are moderately well sorted fine to very fine sands (M_z 2.9–3.3 phi) having a silt-clay content of 2–6%. Salinities range from 10–33‰. At Pauatahanui, the species is associated with a large maldanid, *Axiothella serrata* Kudenov and Read (1977), while in Wellington Harbor in organically rich, very fine sands, the most common associates are *Boccardia* spp.

Etymology.—The epithet is selected in honor of the native Maori people of New Zealand.

Distribution.—North and South Islands of New Zealand, in intertidal sandy substrata of estuaries.

Microspio elegantula, new species
Fig. 2

Material examined.—NEW ZEALAND, North Island, Wellington Harbor, Evans Bay, SW of marina, intertidal, sand and gravel, 25 Feb 1981, coll. G. B. Read, holotype (USNM 80490).

Description.—A moderate-sized species, holotype 8 mm long and 0.8 mm wide for 52 setigerous segments. Color in life: pale yellow-green, with yellow palps having prominent dark reddish brown pigment spots and numerous small, inconspicuous spots bordering ciliated groove; additional large, conspicuous brown pigment patch located mid-dorsally on prostomium and with smaller interramal spots on setigers 1–18; some white pigment present on posterior and lateral margins of peristomium. Color in alcohol: light tan, with reddish brown pigment as above; white pigment not apparent.

Prostomium broad anteriorly, with curved, slightly incised margin (Fig. 2A), gradually tapering posteriorly to narrow caruncle merging indistinctly with middle of setiger 2; 2 pairs of eyes, with anterior pair cup-shaped, widely spaced; posterior pair oval, narrower, without occipital tentacle; nuchal organs not apparent. Peristomium well developed, not especially inflated (Fig. 2A); palps long, extending posteriorly for at least 12 setigers when preserved.

Setiger 1 biramous, with well-developed, conical noto- and neuropodial postsetal lamellae and setal fascicles. Notopodial lamellae from setiger 2, broader, thin, fused to basal part of branchiae; middle and posterior lamellae narrower, somewhat elliptical, free from basal part of branchiae, with numerous bacillary glands. Neuropodial lamellae thin, somewhat square-shaped (Fig. 2C).

Notosetae all capillaries, arranged in 2 rows, with setae of anterior row shorter, with granulated sheaths and smooth shafts; setae of setigers 1–3 with unusually large, conspicuous granules, imparting golden appearance to sheath (Fig. 2D); setae from anterior row of subsequent setigers with fine granules (Fig. 2E); setae of posterior row longer, with clear sheaths and smooth shafts (Fig. 2F). Neurosetae of setigers 1–10 similar to notosetae in structure and arrangement except for especially enlarged granules in anterior row; hooded hooks first present in posterior row, increasing to 6–7 over following setigers and replacing all capillaries in posterior row; anterior row of capillaries remaining intact through middle setigers, then becoming thinner and non-granulated in posterior setigers and finally lost entirely in far posterior setigers, hooks numbering 3–5 (Fig. 2C); hooks with long main fang surmounted by pair of long apical teeth and second pair of smaller teeth (Fig. 2G–H); without inferior sabre setae.

Branchiae from setiger 2, continuing to near posterior end, with numerous glands, especially prominent in middle and posterior setigers (Fig. 2A, C); single row of ciliated patches extending dorsally across each segment from bases of branchiae (Fig. 2A). Pygidium with 2 broad, ventrolateral lobes (Fig. 2B).

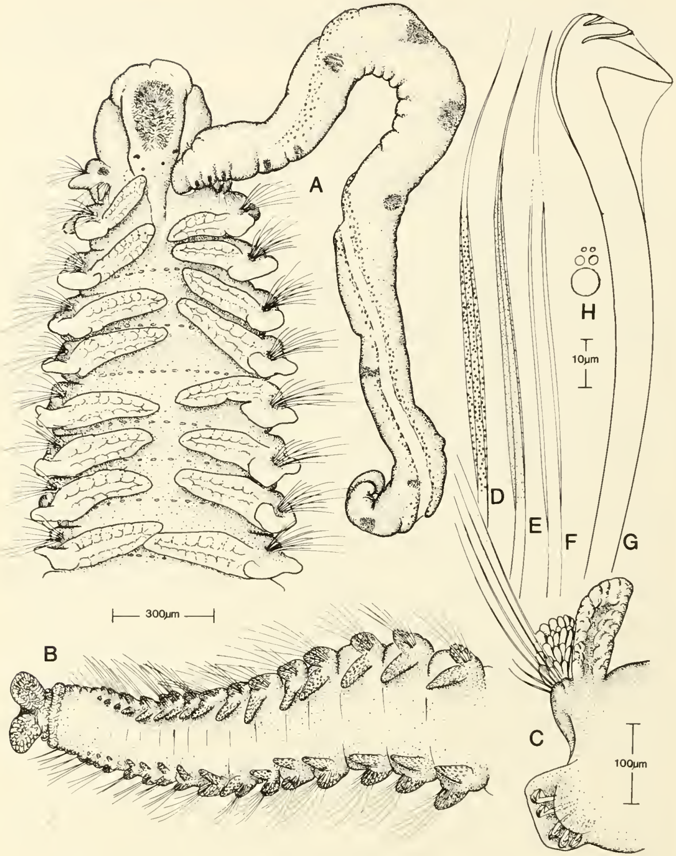

Fig. 2. *Microspio elegantula* (holotype, USNM 80490): A, Anterior end, dorsal view, left palp omitted; B, Posterior end, dorsal view; C, Left setiger 35 in anterior view; D, Notoseta from setiger 2; E, Notoseta from anterior row of middle setiger; F, Notoseta from posterior row of middle setiger; G, Hooded hook, lateral view, H, Diagram of hooded hook showing tooth arrangement.

Remarks.—*Microspio elegantula* superficially resembles *Microspio pigmentata* (Reish), originally described from southern California as *Spiophanes pigmentata* (Reish, 1959), in having a prominent middorsal pigment spot on the prostomium. The holotype of *S. pigmentata* has been examined. The hooded hooks have a main fang surmounted by a large unpaired apical tooth and a pair of small teeth, the anterior margin of the prostomium is entire, posterior notopodia include numerous needlelike capillaries providing a distinct spinous appearance to the posterior end, and the pygidium has four anal cirri. *Microspio elegantula,* in contrast, has the main fang of the hooded hooks surmounted by two pairs of apical teeth, the prostomium is weakly incised on the anterior margin, the posterior notopodia include only long capillaries, instead of numerous needlelike spines, and the pygidium is formed of two broad lobes.

Distribution.—Known only from Wellington Harbor, intertidal in sand.

Spio readi, new species

Fig. 3

Material examined.—NEW ZEALAND, North Island, Wellington Harbor, Evans Bay, SW of Marina, intertidal in fine sand, 22 Aug 1974, coll. G. B. Read, holotype and paratype (USNM 80488–9).—NEW ZEALAND, South Island, off Otago Peninsula, coll. Portobello Marine Laboratory 1974 and 1975: R/V *Munida* Sta. Mu 74–179, 45°50.2′S, 170°48.4′E, 55 m, 1 specimen (NMNZ); Sta. Mu-74-197, 45°48.2′S, 170°49.6′E, 50 m, 1 specimen (NMNZ); Sta. Mu-75-71, 45°50′S, 170°55.5′E, 105 m, 1 specimen (NMNZ).

Description.—A moderate-sized species; holotype complete, 13.5 mm long and 1.0 mm wide for 54 setigerous segments. Color in alcohol: light tan, with large paired patches of reddish brown pigment located dorsally on peristomium and some anterior setigers, with additional dark reddish brown pigment on peristomium and as fine lines on some anterior setigers.

Prostomium narrow, entire on anterior margin, continuing posteriorly as indistinct caruncle to setiger 3, without occipital tentacle; 2 pairs of eyes, anterior pair cup-shaped, more widely spaced than posterior oval pair; transverse ciliated crest on setiger 3, with 2 large curved nuchal organs lateral to caruncle and transverse crest (Fig. 3A).

Setiger 1 well developed, with long straplike branchiae basally fused to notopodial postsetal lamellae. Branchiae long, ciliated on inner surface, meeting middorsally, continuing to posterior end, becoming short and stubby. Each segment with double row of cilia across dorsum between bases of branchiae (Fig. 3A). Notopodial postsetal lamellae elongate, with smooth rounded margin. Neuropodial postsetal lamellae elliptical.

Notosetae all capillaries, arranged in 2 rows, setae of anterior rows shorter, with finely granulated shafts and clear sheaths (Fig. 3C), setae of posterior rows longer, with non-granulated shafts and clear sheaths (Fig. 3D); superiormost capillaries of posterior rows longest. Neurosetae of setigers 1–10 similar to notosetae in arrangement and appearance; 9–10 bidentate hooded hooks replacing posterior row of capillaries from setiger 11, leaving anterior row of capillaries intact and adding third row of very fine, hairlike capillaries alternating with hooded hooks; 3–4 inferior sabre setae present in ventralmost location in setal fascicle; hooks reduced to 4–5 per fascicle in posterior setigers, hooks with main fang forming nearly right angle with shaft and apical tooth applied closely to main fang, with hood slightly inflated (Fig. 3E); sabre setae nongranulated, without sheath, with fine bristles from middle of seta to curved tip (Fig. 3F).

Pygidium with 4 broad, flattened anal cirri, ventral and ventrolateral, with broad dorsal gap; cirri with fine bacillary glands; anus terminal.

Remarks.—*Spio readi* is closely related to *S. filicornis* (O. F. Müller) reported

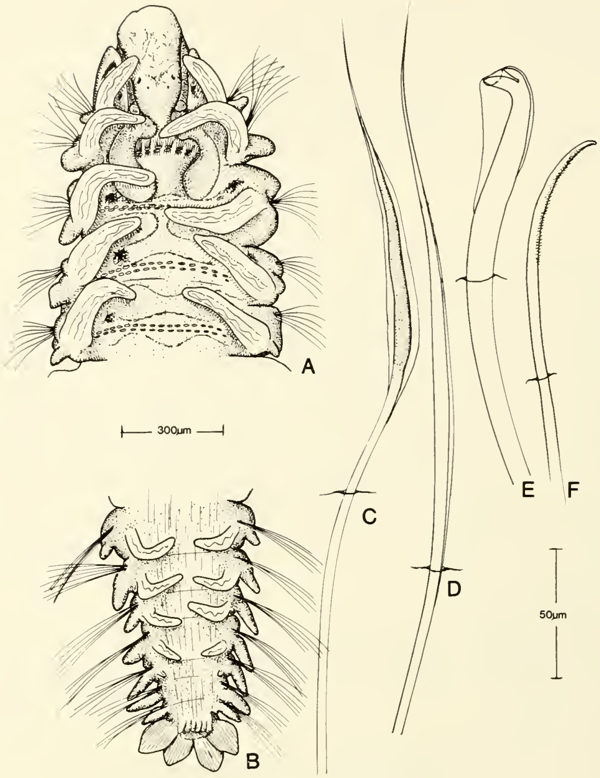

Fig. 3. *Spio readi* (holotype, USNM, 80488): A, Anterior end, dorsal view, palps omitted; B, Posterior end, dorsal view; C, Notoseta from anterior row; D, Notoseta from posterior row; E, Hooded hook; F, Sabre seta.

from worldwide localities in having an entire prostomium and bidentate hooded hooks. *Spio readi* differs from *S. filicornis* in having 4 ventrally located anal cirri instead of dorsal and ventral. According to N. J. Maciolek (Pers. comm., *S. filicornis* has 6 ventral glands on each segment, lacking in *S. readi.*

Etymology.—This species is named for Dr. Geoffrey Read, University of Wellington.

Distribution.—North and South Island of New Zealand, intertidal to 105 m.

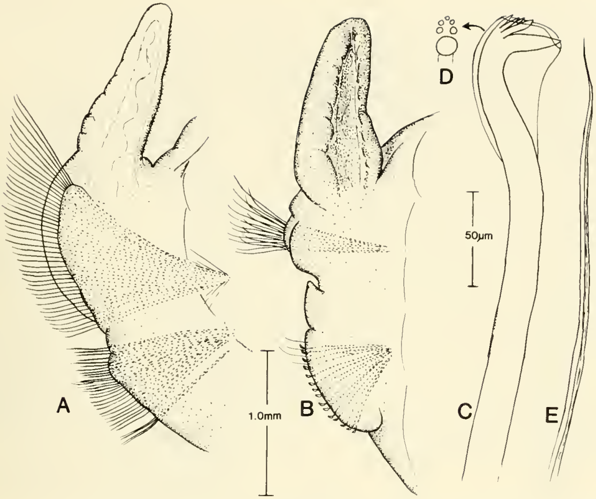

Fig. 4. *Spio aequalis* (syntype, BMNH ZB 1908.5.9.6): A, Right parapodium from setiger 12, anterior view; B, Same from setiger 150, anterior view; C, Hooded hook, lateral view; D, Frontal diagram of same, showing tooth arrangement; E, Neuropodial capillary from posterior setiger.

Spio aequalis Ehlers, 1904
Fig. 4

Spio aequalis Ehlers, 1904:40–42, pl. 5, figs. 18–21, pl. 6, figs. 1–4.

Material examined.—CHATHAM ISLAND, coll. Herr Schauinsland, 1896–97, syntype (BMNH ZB 1908.5.9.6).

Description.—A large species; syntype almost complete, coiled, measuring approximately 5 mm wide and 55 mm long for about 155 setigerous segments. Color in alcohol: gray. Tissue of syntype soft, tending to crumble, with considerable distortion of original prostomial features (see Remarks).

Anterior parapodia prominent, well developed; notopodial lamellae basally fused to branchiae, smoothly rounded, with dorsally directed presetal lobe (Fig. 4A); posterior notopodia reduced to rounded lobes (Fig. 4B). Anterior noto- and neuropodia broadly elliptical, becoming low setal tori posteriorly.

Anterior parapodia with numerous noto- and neurosetae in form of granulated capillaries arranged in 5 distinct rows, reduced to 2–3 rows after about setiger 15. Multidentate neuropodial hooded hooks from setiger 22, replacing posterior row of capillaries for about first 50 setigers, anterior row reduced to few superior, thin, nongranulated capillaries accompanying hooks (Fig. 4E); hooks numbering up to 15 per row in middle and posterior setigers; each with long main fang surmounted by 5 apical teeth arranged in 2 pairs surmounted by single apical tooth (Fig. 4C–D); distinct inferior sabre setae lacking, although ventralmost neuropodial capillaries sometimes separated into small group.

Branchiae long, straplike in anterior setigers, becoming short, thick, squat, and distinctly set off from parapodia in posterior setigers. Pygidium unknown.

Remarks.—As depicted by Ehlers (1904, pl. 5, figs. 19–20), the prostomium flares anteriorly into two diverging lobes, between which is a small medial protrusion. The syntype is poorly preserved and the prostomium is narrow, conical anteriorly, continuing posteriorly to the margin of setiger 1. There is no evidence of eyes or occipital tentacle. There appears to be a weakly-developed peristomial wing present at the level of the palp scars.

Despite the poor condition of the syntype, there should be no trouble distinguishing *S. aequalis* in future collections. The species differs from all other described species of *Spio* in the numerous capillaries arranged in five rows in the anterior parapodia, combined with presence of multidentate hooded hooks and the short, thickened posterior branchiae. *Spio setosa* Verrill, 1873, from the east coast of North America has the capillaries arranged into three to four rows, bidentate hooded hooks and thin, straplike branchiae. *Spio singularis* Blake and Kudenov, 1978, from Queensland is similar to *S. aequalis* in having multidentate hooded hooks but the capillaries are arranged in only two rows.

Distribution.—Chatham Island.

Carazziella proberti, new species
Fig. 5

Material examined.—NEW ZEALAND, South Island, off Otago Peninsula, coll. Portobello Marine Laboratory, R/V *Munida* Sta. 75-72, 45°53.5′S, 170°59′E, 122 m, holotype (USNM 80495) and 2 paratypes (USNM 80496; NMNZ).

Description.—A moderate-sized species up to 5.5 mm long and 0.6 mm wide for 42 setigers. Color in alcohol: light brown.

Prostomium entire, rounded on anterior margin, widest at level of eyes, narrowing to blunt caruncle terminating in middle of setiger 2, followed by nuchal ridge to posterior margin of setiger 2 (Fig. 5A); without occipital tentacle; 2 pairs of eyes present, anterior pair cup-shaped, more widely spaced than oval-shaped posterior pair; lateral brown pigment spots located between eyes. Peristomium inflated, extending anteriorly beyond prostomium; palps moderately long, extending posteriorly for about 8–9 setigers.

Setiger 1 fused with peristomium, biramous, with unusually long notopodial postsetal lamellae, extending posteriorly to end of setiger 2 and bearing short fascicles of capillaries (Fig. 5A); neuropodia with conical postsetal lamellae and with large fascicles of capillaries arranged in 2 rows. Capillary noto- and neurosetae of setigers 2–4, and neurosetae of setigers 6–7 and notosetae of setiger 6 arranged in 2 rows; setae of anterior row shorter, with granulated shafts and clear, unilimbate sheaths (Fig. 5G), setae of posterior row longer, without granulations. Notosetae of far posterior setigers long, thin providing spinous appearance to posterior end (Fig. 5H). Neuropodia with bidentate hooded hooks from setiger 8, arranged in single row in anterior and middle setigers, with 5–6 hooks and 4 lower granulated capillaries; hooks with wide angle between main fang and shaft and reduced angle between apical tooth and main fang (Fig. 5F). Modified setiger 5 larger than

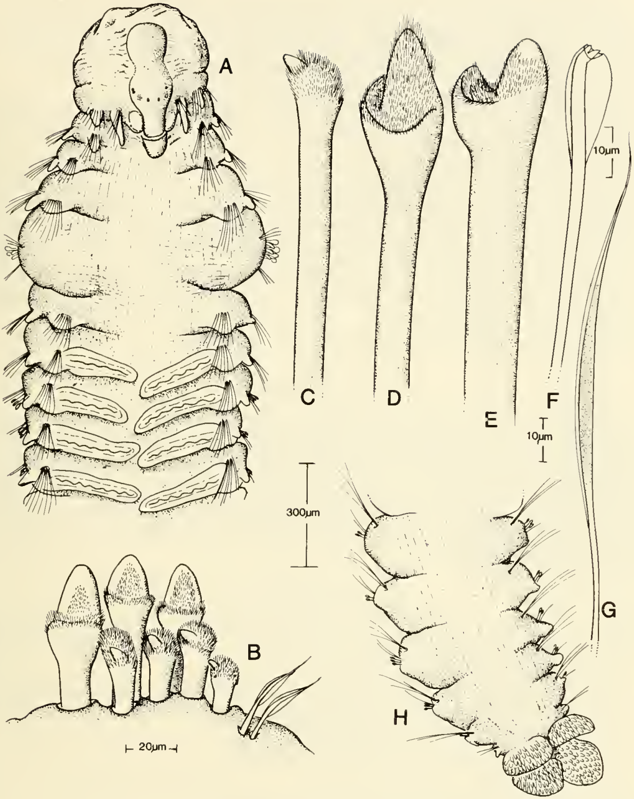

Fig. 5. *Carazziella proberti* (holotype, USNM 80495): A, Anterior end, dorsal view, palps omitted; B, Setae of setiger 5, Dorsal capillaries to right of major spines; C, Bristle-topped falcate spine from setiger 5; D–E, Bristle-topped non-falcate spines from same; F, Hooded hook, lateral view; G, Neuroseta from anterior row of anterior setiger; H, Posterior end in dorsal view.

preceeding and succeeding setigers, with few (0–3) dorsal short bilimbate capillaries (Fig. 5B), double curved row of 2 types of bristle-topped major spines and ventral fascicle of 7–8 long, granulated capillaries; major spines of 2 types: dorsal spines, falcate, with tooth emerging from dense cloak of bristles (Fig. 5C); ventral spines larger, with bristled tooth enclosed on one side by thick bristled shelf, with intermediate densely bristled concavity (Fig. D–E); bristles shorter when worn.

Dorsal postsetal lamellae on setiger 2 conical, becoming broad and platelike on setigers 3–4 and 6 (Fig. 5A); branchiae from setiger 7, fused with dorsal postsetal lamellae, continuing for 10–11 setigers and absent from posterior two-thirds of body. Branchiae elongated, extending to dorsal midline (Fig. 5A). Pygidium formed of 4 broad lobes, with numerous bacillary glands (Fig. 5H).

Remarks.—*Carazziella proberti* is the twelfth species to be described for the genus and appears to be most closely related to *C. phillipensis* Blake and Kudenov, 1978, from Victoria, Australia in having notosetae and long notopodial postsetal lamellae on setiger 1. *Carazziella phillipensis,* however, has an incised instead of an entire prostomium, narrow instead of broad pygidial lobes and the enlarged major spines of setiger 5 have a different form. (See Blake and Kudenov (1978) for the descriptions of *C. phillipensis* and the closely related *C. victoriensis* Blake and Kudenov. See Blake (1979) for a discussion of other species of *Carazziella*).

Etymology.—This species is named for Dr. Keith Probert of the New Zealand Oceanographic Institute.

Distribution.—South Island, New Zealand, 122 m.

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ENANTIOSIS CAVERNICOLA, A NEW GENUS AND SPECIES OF DEMERSAL COPEPOD (CALANOIDA: EPACTERISCIDAE) FROM SAN SALVADOR ISLAND, BAHAMAS

Douglas J. Barr

Abstract.— *Enantiosis cavernicola,* is described from Lighthouse Cave, San Salvador Island, Bahamas. The main diagnostic characters are the specialized mouthparts, primitive swimming legs, and structure of the male fifth legs. Distribution of the family Epacteriscidae is discussed.

Demersal calanoid copepods occupy restricted habitats on or near the bottom, and their investigation often requires special collection methods. Esterly (1911), for example, collected *Ridgewayia marki* from a cave on Agar's Island, Bermuda, using a net fastened to a pole. More recent workers have employed diver-held nets (Bowman and González 1961), Ockelmann detritus sledges (Fosshagen 1968a, b, 1970a, b, 1972, 1973), and suction devices (Humes and Smith 1974). Nine genera of demersal calanoids have been described from shallow-water habitats in the western tropical North Atlantic. The new genus described below was collected with a hand-held net from a marine cave on San Salvador Island, Bahamas.

San Salvador Island (24°N, 74°W) is located on the eastern edge of the Bahama Platform, about 550 km east of Miami, Florida. Lighthouse Cave, near Dixon Hill Lighthouse on the northeastern end of the island, 800 m inland, has water-filled passages up to 2 m in depth. There is a tidal fluctuation of up to 60 cm in the cave, and the salinity of the water is approximately 35‰. Biological expeditions to Lighthouse Cave since the mid-1970's have resulted in the description of two isopods, *Bahalana geracei* Carpenter, 1981 and *Neostenetroides stocki* Carpenter and Magniez, 1982; three sponges (Van Soest and Sass 1981); and a terrestrial pseudoscorpion, *Paraliochthonius carpenteri* (Muchmore, in press).

Plankton collections from the cave in January–February 1981 and May–June 1982 included three genera of demersal calanoids: *Ridgewayia, Stephos,* and a new genus belonging to the family Epacteriscidae. This family presently contains only a single species, *Epacteriscus rapax* Fosshagen, 1973, described from Florida and Colombia.

Family Epacteriscidae Fosshagen, 1973 (emended)

Prosome with all 5 pedigers free. Urosome 3-segmented in female, 4-segmented in male. Female genital segment produced ventrally, openings close together. First antenna of female 24–25-segmented, right antenna geniculate in male. Rostrum broad, bilobed, bearing filaments. Mouthparts with reduced numbers of setae. Mandibular endopod vestigial or absent; gnathobasis may bear ventral serrate process. Second maxilla and maxilliped with strong spinous endopodal setae. All swimming legs except male fifth pair primitive, with 3-segmented rami. Male fifth legs only slightly modified (*Epacteriscus*) or transformed into complex grasping organ (*Enantiosis*).

Enantiosis, new genus

Diagnosis.—Both female and male left antenna 25-segmented, reaching end of prosome; male right antenna geniculate, 22-segmented. Each lobe of rostrum angular, bearing single filament.

Labrum broadly truncate, distomedial margin of oral surface bearing 6 strong teeth. Labium bifid, each lobe cuspidate medially. Mandibular gnathobasis with bicuspid molars; palp with weakly segmented exopod, endopod vestigial. First maxilla with well developed lobes but reduced number of setae. Female fifth legs not reduced. Male fifth legs prehensile, all rami 3-segmented.

Type-species.—*Enantiosis cavernicola.*

Etymology.—From *Enantiosis* (G.), meaning contradiction, referring to the advanced male fifth legs, as opposed to the primitive fifth pair in other members of the Epacteriscidae. Gender feminine.

Enantiosis cavernicola, new species

Material.—Male holotype 1.20 mm (USNM 195388), and female allotype 1.37 mm (USNM 195389) collected 5 June 1982 from Lighthouse Cave, San Salvador Island, Bahamas. 6 female and 2 male paratypes (USNM 195390) collected on same date from same locality.

Description.—Female (Fig. 1a, b): average length 1.37 mm, range 1.29–1.46 mm, length/width ratio 2.73. Prosome oval in dorsal view, rounded posteriorly. Anal segment slightly longer than preceding segment, posterior margin dentate dorsally. Caudal ramus with 1 dorsal, 1 lateral, and 4 apical setae. Second-from-innermost seta longest, longer on left side than corresponding right seta. Left innermost seta hirsute at base, corresponding right seta bare at base. Of the apical setae, only left innermost without breaking plane near base.

First antenna (Fig. 1e) reaching genital segment, setae and esthetes concentrated proximally. Segments 3, 7, 12, 14, and 24 each with especially long seta.

Second antenna (Fig. 2a) with basipods 1 and 2 weakly separated, bearing 1 and 2 setae, respectively. Exopod 7-segmented, carrying 2 proximal, 5 medial and 3 terminal setae. Endopod 2-segmented, segment 1 with 2 medial setae, segment 2 with 3 medial and 6 terminal setae.

Labrum (Fig. 1f) broadly truncate. Distomedial margin of oral surface bearing 6 strong teeth, 2 outer teeth larger than 4 equal central teeth; distolateral corners each with row of stout bristles. Remainder of oral surface beset with various patches of hairs oriented in different directions. Posterior half of aboral surface with single row of long, slender spines extending just beyond distal margin.

Labium (Fig. 1g) deeply cleft; medial margins of labial lobes cuspidate, distal tooth largest, denticulate along posterior edge. Lamina labialis trilobed, central lobe angular, lateral lobes truncate. Lamina labialis flanked on both sides by 6 prominent spines (serrula sexdentata). Remainder of oral surface with reduced number of hairs.

Mandibular endopod (Fig. 1h) bearing 2 short setae. Exopod composed of 3

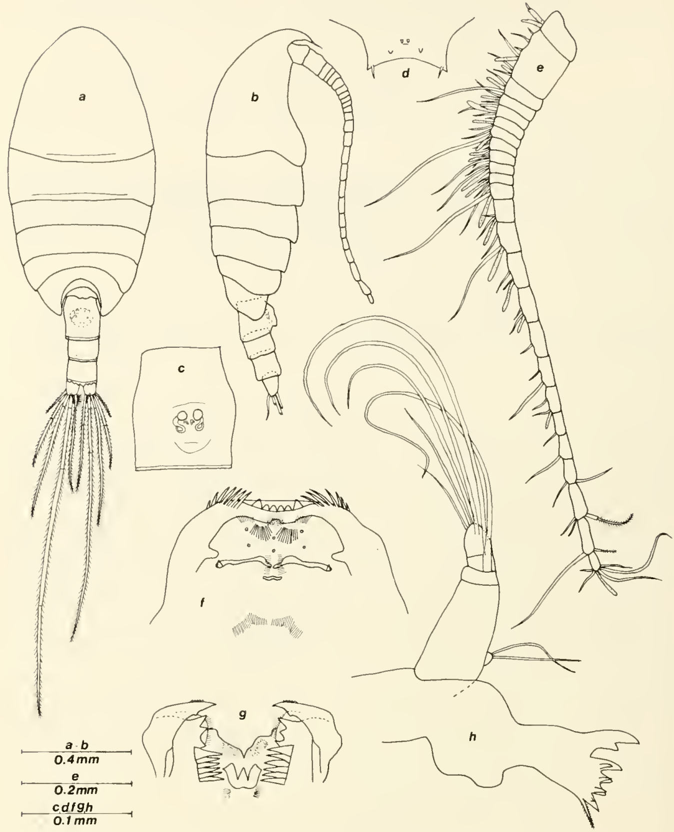

Fig. 1. *Enantiosis cavernicola,* female: a, Habitus, dorsal; b, Habitus, lateral; c, Genital segment, ventral; d, Rostrum; e, First antenna; f, Labrum; g, Labium; h, Mandible.

poorly defined segments, carrying 3 medial and 3 terminal setae. Gnathobasis with 5 bicuspid teeth, ventral tooth largest, set off from remaining teeth by deep incision.

Basipod of first maxilla (Fig. 2b) with 1 outer and 2 inner lobes. Outer lobe with 6 long setae. First inner lobe bears 13 spinous setae; second inner lobe small, with 2 unequal setae. Basipod 2 with small distal seta and proximal endite bearing

Fig. 2. *Enantiosis cavernicola,* female: a, Second antenna; b, First maxilla; c, Second maxilla; d, Maxilliped; e, Leg 1; f, Leg 2; g, Leg 3; h, Leg 4; i, Leg 5.

1 seta. Endopod 1-segmented, carrying 1 proximal, 1 medial and 4 terminal setae. Exopod 1-segmented, with 4 outer and 3 terminal setae.

Basipod 1 of second maxilla (Fig. 2c) with 4 endites bearing 4, 3, 3, and 3 setae, respectively. Basipod 2 with group of 4 medial setae and distal endite carrying 1 slender and 3 spinous setae. Endopod reduced, unsegmented, bearing 7 long spinous setae.

First basipod of maxilliped (Fig. 2d) with 1 proximal seta and 3 groups of 2, 4, and 3 setae, respectively. Basipod 2 with 3 medial setae, central one bulbous and hirsute at base. Endopod 4-segmented, carrying 4, 4, 3, and 7 setae, respectively.

All 5 swimming legs essentially unmodified. Exopod segment 3 of first leg (Fig. 2e) with 2 outer spines; long terminal spine unflanged, flexible, only slightly thicker than 4 inner setae. Legs 2–4 (Fig. 2f–h) with distomedial corner of endopod segments 1 and 2 acutely pointed.

Fifth leg (Fig. 2i) smaller than fourth, with 1 less seta on each of the following segments: basipod 1, exopod segments 1 and 3, and endopod segments 2–3. Medial seta on exopod segment 1 replaced by small angular process.

Male (Fig. 3a): average length 1.20 mm, range 1.15–1.23 mm, length/width ratio 2.54. Prosome as in female. Posterodorsal margin of urosome segment 1 with 4 small teeth. Anal segment dentate posterodorsally as in female.

Right first antenna (Fig. 3b) 22-segmented, geniculate between segments 18 and 19. Segment 18 excavate distally, bearing 1 seta. Segment 19 excavate proximally, with 2 small setae and 1 esthete.

Other cephalic appendages, rostrum and legs 1–4 as in female.

Fifth legs (Fig. 3c) asymmetrical, highly modified. All rami 3-segmented. Right basipod 1 (Fig. 3d) with 2 short rows of posterior surface spinules. Right basipod 2 with long, slender, recurved inner process and dense pubescence medial to base of endopod. Right endopod with 1 inner seta on segments 1 and 2; segment 3 with 6 setae jointed near midlength. Right exopod lacking setae; segments 1 and 2 each with 1 small outer spine; segment 3 prehensile, falcate, swollen base bearing 1 medial recurved spine. Left basipod 1 (Fig. 3d) with small irregular cluster of posterior surface spinules. Left basipod 2 unmodified. Left endopod segment 1 (Fig. 3e) produced laterally into thumb-like process; segment 2 produced distally into spiniform process, outer margin with 2 brushes of long hairs, margin incised at base of proximal brush; segment 3 broad, bearing 6 setae jointed near midlength. Left exopod segment 1 (Fig. 3f) bearing 1 long, unflanged spine reaching length of segment 2, with pair of short setae and angular spine at its base. Segment 2 ovate, with proximal anterior protuberance, outer distal margin with small angular process and styliform, unflanged spine. Left exopod segment 3 a complex membranous structure, dissected into several finger-like processes. Outer margin with proximal styliform process and 2 lateral processes: first process inserted posteriorly, slender; second process attached anteriorly, spatulate. Medial margin with bulge at midlength and short, digitiform, posterior process. Distal margin of left exopod segment 3 with 5 processes from medial to outer margin: first process spatulate, curving medially; second process styliform, recurved into triangle at base; third process styliform, sinous; fourth process with lobe near midlength and acute apex; fifth, outermost process, styliform.

Etymology.—The specific name, *cavernicola,* is a composite of *caverna* (L.) meaning cave and *cola* (L.) meaning dweller.

Discussion.—*Enantiosis cavernicola* is considered to be a bottom-dwelling copepod because of the robust spines on the exopods of the swimming legs and morphology of the male fifth legs. Though several families of demersal calanoids have morphological features in common, their phylogenetic relationships remain

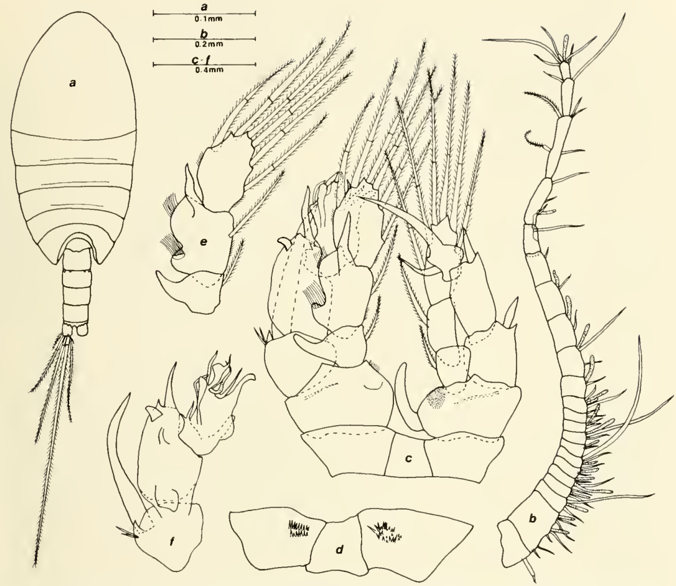

Fig. 3. *Enantiosis cavernicola,* male: a, Habitus, dorsal; b, Right first antenna; c, Fifth legs, anterior; d, First basipods, fifth legs, posterior; e, Left fifth endopod; f, Left fifth exopod.

unclear. *Enantiosis,* based on the structure of the male fifth legs, seems most closely allied to the Ridgewayiidae. The left exopod resembles *Ridgewayia,* bearing a long spine on segment one and a membranous third segment. The male fifth endopods are trimerous in *Enantiosis, Epacteriscus,* and *Exumella* (Ridgewayiidae), while those of *Ridgewayia* are unsegmented. The Epacteriscidae, however, lack the typical modification of the female fifth legs seen in the Ridgewayiidae, suggesting that these families are not closely related.

Morphology of the mouthparts of *Enantiosis* indicates a predaceous lifestyle similar to *Epacteriscus rapax.* The vestigial mandibular endopod, deeply incised mandibular gnathobasis with pointed cusps, reduced number of setae on the first maxillae, and spinous setae of the second maxillae and maxillipeds, all suggest that *E. cavernicola* is not a filter-feeding copepod. The absence of a serrate mandibular process, however, implies that *E. cavernicola* may be less voracious than *E. rapax.*

In addition to the type-locality, an *Enantiosis* species has been collected from several caves among the Bermuda Islands (Fosshagen, pers. comm.). The family Epacteriscidae, however, apparently has a circumtropical distribution. An undescribed *Epacteriscus* and four females of *Enantiosis* were recently collected during a study of reef-associated zooplankton at Quezon, Philippines (Walter *et* *al.* 1982). These animals were collected with emergence traps secured in shallow water among corals, a habitat similar to that of *Epacteriscus rapax* in the tropical Atlantic. The Philippine specimens of *Enantiosis* are slightly larger (1.50–1.59 mm) than those from the Bahamas and their first antennae do not reach beyond the third pediger. Because these females are otherwise indistinguishable from the Bahamian specimens, their description has been deferred until the male of the species can be examined.

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ECHINASTER GRAMINICOLA, A NEW SPECIES OF SPINULOSID SEA STAR (ECHINODERMATA: ASTEROIDEA) FROM THE WEST COAST OF FLORIDA

David B. Campbell and Richard L. Turner

Abstract.—A new species of the sea-star genus *Echinaster* is described from shallow-water seagrass and oyster beds of the west coast of Florida. The new species and *E. spinulosus* Verrill are sibling species, morphologically distinguished only by spination and differences in the secondary skeleton. The two species also differ in coloration and in many physiological, reproductive, and ecological characteristics.

On the west coast of Florida, there are two shallow-water forms of *Echinaster* which conform to Downey's (1973) description of *E. modestus* Perrier, 1881. Prior to Downey's monograph of sea stars of the Caribbean Sea and Gulf of Mexico, authors called both forms *E. echinophorus* or *E. spinulosus* (see Ferguson 1975a). Until recently (Campbell and Turner 1979), the morphological differences between the two forms were unknown (Ferguson 1976). Our recent examination of the type specimens of *E. modestus* has shown that neither form belongs to this species (Turner and Campbell 1981).

Turner and Lawrence (1979) used the terms "light" and "dark" to describe the two forms based on reliable differences in color of the integument of live animals. These morphs have also been called "Type I" and "Type II," respectively, by Atwood (1973a) and subsequent workers. In addition to coloration, the two forms differ in larval development (Atwood 1973a) and environmental tolerances (Watts *et al.* 1982), other life-history parameters (Scheibling 1982; Scheibling and Lawrence 1982), fatty-acid profiles (Ferguson 1976), physical and chemical properties of their eggs (Turner and Lawrence 1979), habitat (Campbell 1978), and diet (Scheibling 1982). Ferguson (1976), Turner and Lawrence (1979), and Watts *et al.* (1982) suggested that the two forms might be different species. We have positively identified the light form (Type I) as *Echinaster spinulosus* Verrill, 1869, by comparison with Verrill's type-specimens at the Peabody Museum. The dark form (Type II) is herein described as a new species, types of which are deposited in: U.S. National Museum of Natural History, Smithsonian Institution (USNM); Museum of Comparative Zoology, Harvard University (MCZ); Peabody Museum of Natural History, Yale University (YPM); Marine Research Laboratory, Florida Department of Natural Resources (DNR FSBC); British Museum (Natural History) (BMNH).

Family Echinasteridae Verrill, 1867
Echinaster Müller and Troschel, 1840
Echinaster graminicola, new species
Figs. 1–3

Diagnosis.—Small. Rays 5, tapered. Madreporite circular, with convoluted gyri; peripheral spinules often present, few; gyral spinules usually absent or few. Serial ossicles of rays: carinals (sometimes separated by intercalary ossicles), adradials, 1 row of dorsolaterals, superomarginals, long row of intermarginals, inferomarginals, adambulacrals; all series except proximal superomarginals with distal imbrication; patches of glassy tubercles well developed; spines small, conical, subacute, and generally 0–1 per ossicle except for adambulacrals (2–4, of which only 1 is a furrow spine). Actinolaterals absent. Each mouth plate with 1 preoral spine and 1–2 furrow spines; 2 furrow spines rarely on more than 5 mouth plates.

Material.—HOLOTYPE (USNM E28934): dry specimen (R = 20.9 mm, r = 6.4 mm), Sarasota Bay, Bradenton Beach, Florida, USA, 14 Jul 1981 (<1 m, oyster bed, 27°28.2′N, 82°42.1′W). PARATYPES: (USNM E28966), 16 dry specimens (R = 10.1 mm, r = 3.2 mm to R = 28.9 mm, r = 7.3 mm), same collection data as holotype; (USNM E28935), 8 specimens in ethanol (R = 12.2 mm, r = 4.2 mm to R = 17.0 mm, r = 5.4 mm), same location as holotype, 13 Jun 1977; (USNM E28936), 3 dry specimens (R = 16.5 mm, r = 4.9 mm to R = 21.0 mm, r = 5.5 mm), Sunshine Skyway Causeway, St. Petersburg, Florida, USA, 21 Jan 1978 (1 m, seagrass bed, 27°39.0′N, 82°40.5′W); (MCZ 4669), 12 specimens in ethanol (R = 14.8 mm, r = 4.5 mm to R = 24.9 mm, r = 7.3 mm), same collection data as USNM E28935; (YPM 10574), 13 specimens in ethanol (R = 14.2 mm, r = 5.2 mm to R = 20.4 mm, r = 5.8 mm), same collection data as USNM E28935; (DNR FSBC I 29872), 39 dry specimens (R = 6.8 mm, r = 2.3 mm to R = 22.4 mm, r = 5.4 mm), South Pass-a-Grille Channel, Cabbage Key, Tierra Verde, Florida, USA, 9 & 19 Apr 1975 (intertidal oyster bar, 27°40.3′N, 82°43.8′W); (BMNH 1982.11.26.1–10), 12 specimens in ethanol (R = 15.8 mm, r = 4.8 mm to R = 18.9 mm, r = 5.7 mm), same collection data as USNM E28935. Non-type material: (USNM E28967), 1 specimen in ethanol (R = 17.3 mm, r = 5.2 mm), St. Joseph Bay, Port St. Joe, Florida, USA, 31 Oct 1980 (seagrass bed, 29°47.9′N, 85°18.1′W) [originally, 6 specimens were examined].

Morphology.—Except where specifically mentioned, the following description is based on representative specimens from the type series. The body size is small, the largest specimen in the type-series having R = 28.9 mm. The 5 rays taper uniformly to somewhat rounded tips, with no inflation near the bases (Fig. 1A, B). The ratio of ray length (R = 20.9 mm) to disc radius (r = 6.4 mm) is 3.27 in the holotype. The body is covered by a thick skin, which obscures the small spines and the rest of the skeleton, even in dry specimens.

The 10 ossicles of the primary circlet, including the madreporite, are distinct. In the trivium, each is connected to an adjacent member by an intercalary ossicle. Primary radials overlie the intercalary ossicles. Each primary radial connects distally and abradially with the first members of the paired adradial series of a ray. The primary interradials generally underlie the intercalary ossicles; but the madreporite has 2–4 basal projections (Fig. 1C) which directly underlie adjoining primary radials of the bivium, intercalary ossicles being absent. Each primary radial bears 1 spine in the holotype and 0–1 spine in the paratypes. Each primary interradial bears 0–1 spine in the holotype and 0–2 in the paratypes. The outer face of the madreporite is circular, flat, and slightly raised above the body wall. Madreporic gyri and sulci rarely have a radiating pattern; they usually form a meandering pattern with some gyri isolated from the periphery (Fig. 1C). Peripheral madreporic spinules are present and few (9 in the holotype, 2–16 in the paratypes); a few gyral spinules are sometimes present (3 in the holotype, 0–10

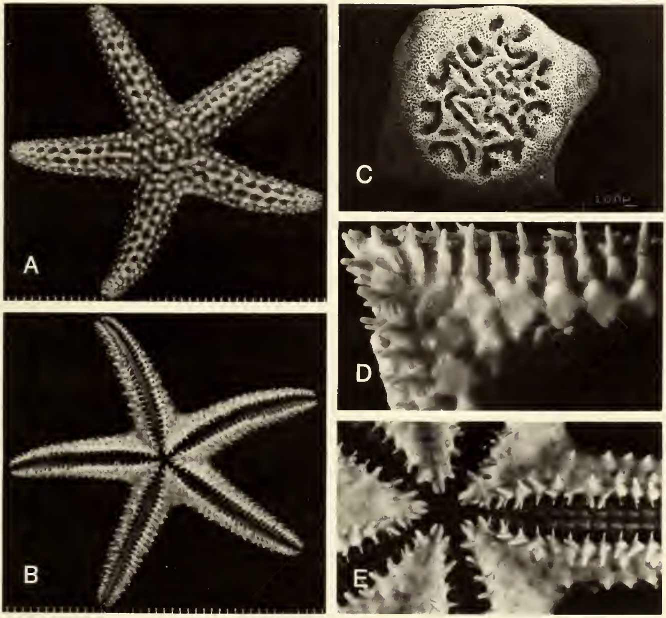


Fig. 1. *Echinaster graminicola.* A, Holotype, abactinal view; B, Holotype, actinal view; C, Madreporite, treated with alkali and prepared for scanning electron microscopy, specimen from type locality; D, Paratype (DNR FSBC I 29872), actinal view of a jaw and associated adambulacral and inferomarginal ossicles (with glassy tubercles), treated with alkali; E, Holotype, actinal view of disc and proximal part of a ray, showing oral and adambulacral spination.

in the paratypes). Spination of the madreporite seems to vary among populations. Within the primary circlet are numerous periproctal plates, connected to form a reticulate complex; each plate sometimes bears a spine. The anus is surrounded by several spinules (5 in the holotype, 3–8 in paratypes), which are not attached to periproctal plates.

The series of primary and secondary ossicles of the outer wall of the rays are the carinals, adradials, dorsolaterals, superomarginals, intermarginals, inferomarginals, and adambulacrals (Fig. 2). Actinolaterals are absent. All ossicles except the dorsolaterals, intermarginals, and adambulacrals bear a central patch of glassy tubercles (Fig. 1D). Each ossicle of a series overlaps the next distal ossicle (distal imbrication), except as noted below. Papulae occur between all series. Papular areas are approximately equal in size to the surrounding ossicles in the proximal half of the ray. Papulae are most abundant (2–10) between the carinals and adradials. The carinals are triangular and bear 0–1 spine distally. Ossicles of the

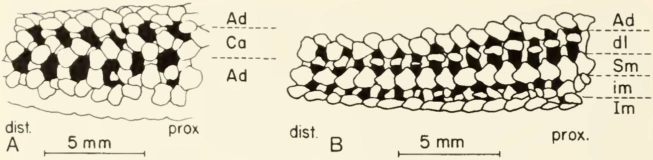


Fig. 2. *Echinaster graminicola.* Skeletal morphology of (A) abactinal and (B) lateral surfaces of the ray. Abbreviations: Ad, adradial ossicles; Ca, carinal ossicles; dist., distal end; dl, dorsolateral ossicles; Im, inferomarginal ossicles; im, intermarginal ossicles; prox., proximal end; Sm, superomarginal ossicles.

carinal row alternate left and right of the midline of the ray. Each carinal has one apex directed proximally, one distally, and one laterally. Intercalary plates often appear between successive carinals (Fig. 2A). The adradial ossicles are quadrilateral. They alternate left and right of the midline of the series, with one contacting a carinal ossicle and the next contacting a dorsolateral. Adradials bear 0–1 spine on the distal edge. Accessory ossicles connect the adradial and carinal ossicles. Adradials are connected to the superomarginals by 1, rarely 2, transversely oriented, cylindrical, dorsolateral ossicle. Each dorsolateral underlies an adradial at one end and a superomarginal at the other. The dorsolateral series sometimes includes a row of longitudinally oriented ossicles which overlie successive transverse ossicles (Fig. 2B). Proximal members of the dorsolateral series may bear 0–1 central spine. The series extends at least half the length of the ray.

The superomarginal ossicles are quadrilateral and bear 0–1 spine near the distal apex. No spines are found on the most proximal superomarginals. The ossicles form a linear, rather than alternating, row. The pattern of imbrication changes as the series progresses along the ray (Fig. 2B); ossicles near the disc have proximal imbrication; ossicles nearer the ray tip have distal imbrication; the point of change in pattern varies widely. An accessory plate (a transverse intermarginal ossicle) overlaps the adoral margin of each superomarginal. Near the ray tip, where dorsolateral and intermarginal ossicles are absent, the superomarginals overlap the adradials and underlies the inferomarginals. The intermarginal series, like the dorsolateral series, is composed of a row of cylindrical, transversely oriented ossicles (Fig. 2B). The intermarginals and dorsolaterals are similar in organization, spination, and length, with the two following exceptions: the aboral end of a transverse intermarginal overlies a superomarginal; the intermarginals form a crowded complex of flattened ossicles in the interradius. The inferomarginal ossicles are quadrilateral, and each bears 1, sometimes 0, spine distally. The most proximal inferomarginals bear no spines. The adoral apex of an inferomarginal overlaps 1–2 adambulacral ossicles. The inferomarginal series of adjacent rays meet behind the mouth plates, where there is usually a single inferomarginal ossicle in common (Fig. 1D).

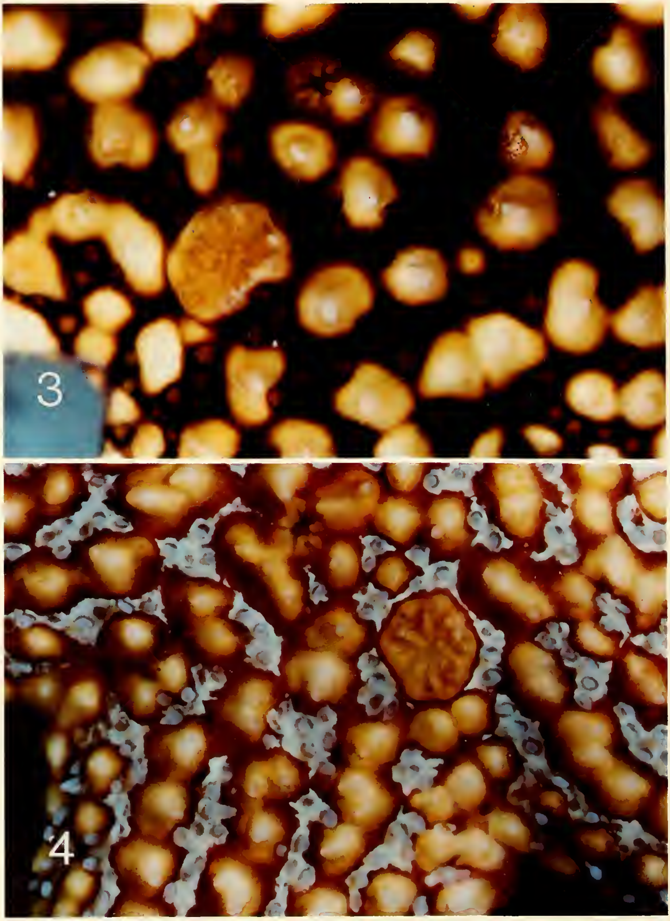
Adambulacrals have 1 furrow spine, 1 (sometimes 2) spine within the groove, and occasionally a subambulacral spine (Fig. 1E). When cleaned of skin, the furrow spine has a slightly flattened base; the column of the spine is cylindrical and narrower; the tip is enlarged, cylindrical, and provided all round with fine teeth;

the spine has a slight curvature toward the groove. Lying high within the ambulacral groove, there is a thin, small, compressed spine which curves toward the furrow spine. There is often an extra spine of intermediate size lying in the groove just above and slightly proximal to the furrow spine; it is more similar morphologically to the furrow spine; in some specimens, there appear to be 2 furrow spines, due to the projection of the extra spine out of the ambulacral groove. Subambulacral spines are single; they occur on few adambulacrals of specimens from Bradenton Beach and are more frequent in specimens from Cabbage Key and non-type material from St. Joseph Bay. Specimens usually have 2–3 spines per adambulacral; 4 spines is rare. Adjacent furrow spines are webbed together, as are a furrow spine and the 1 or 2 smaller spines which occur in the ambulacral groove.

Superambulacrals are present. Each connects an ambulacral and an inferomarginal. The circumoral ossicle and the distalmost ambulacrals do not have superambulacrals. The mouth plates bear 3–5 spines (Fig. 1E): 1 large preoral spine and 1–2 furrow spines, which are all webbed together; 1–2 small spines which occur within the groove; and, rarely, 1 suboral spine. Specimens with only 1 furrow spine on all mouth plates have been observed; specimens with 2 furrow spines on more that 5 mouth plates are rare.

Color.—Color terminology used here is based on Kelly and Judd (1955). The integument covering the ossicles ranges from deep orange yellow (ISCC-NBS number 69) to vivid orange yellow (no. 66), and the papular areas are blackish red (no. 21). The darker integument forms a continuous network surrounding islands of lighter integument (Fig. 3). This pattern gives the sea star a generally dark coloration with numerous light-colored knobs. The actinal surface is pale yellow (no. 89), with lines of dark brown (no. 59) where the few actinal papulae occur. Podia are vivid orange (no. 48). The distinctive coloration is lost upon preservation.

Ecological, reproductive, and physiological studies.—Possibly the first record of *E. graminicola* is that of Heilprin (1887), who found "*Echinaster* sp.?" in seagrass beds near Anclote Keys, Florida on 19 February 1886 during his cruise on the schooner "*Rambler.*" Unfortunately, specimens were apparently not deposited in collections of the Wagner Free Institute of Science (J. Graham, pers. comm.). Definite records of *E. graminicola* in the literature begin with Ferguson's (1966) pharmacological study of tonal changes in pyloric caeca. Ferguson (1967) recognized early in his work that unresolved taxonomic problems with the genus required specification of the source of his material, and his practice of including cautionary footnotes fortunately was adopted by other investigators in the Tampa Bay area. *Echinaster graminicola* was the subject of Ferguson's (1967, 1968, 1970, 1975a, 1980a, b, 1982) several papers on the uptake and translocation of amino acids and other dissolved organic matter by sea stars. Ferguson (1974, 1975a, b, 1976) also studied the annual reproductive cycle and the changes in chemical composition of body components associated with the cycle. Atwood (1973a) described embryogenesis, larvigenesis, and early post-metamorphic growth. Turner (1977) described the use of yolk during development, and Turner and Lawrence (1979) characterized the shape, volume, and biochemical composition of the egg. Watts *et al.* (1982, 1983) described the effects of salinity and temperature combinations on morphogenesis and growth. More general studies of the life history



Figs. 3–4. 3, *Echinaster graminicola.* Abactinal view of part of disc of live animal from type-locality. 4, *Echinaster spinulosus.* Abactinal view of part of disc of live animal from Mullet Key, St. Petersburg, Florida (2m, sandy bottom).

and population ecology of *E. graminicola* were done by Scheibling (1982) and Scheibling and Lawrence (1982). Atwood and Simon (1973) localized and histochemically analyzed neurosecretory granules in various organs. Atwood (1973b) presented evidence that the granules were gonad stimulating substance (GSS) by histological examination of radial nerves before, during, and after spawning; Atwood (1973c) assayed for the presence of GSS in several organs. Further work in reproductive endocrinology was done by Turner (1976). Campbell's (1978) study of ossicle and skeletal morphology led to the discovery by Turner and Campbell (1981) that the species was not *E. modestus*. It is possible that *E.* (*Othilia*) *modestus* used by Blake (1978, 1980) for comparative studies of ossicle and skeletal morphology were *E. graminicola,* but we have not examined his specimens.

Based on the studies mentioned above, the following profile of *E. graminicola* emerges. Animals have an annual reproductive cycle, spawning in April and May apparently under influence of the same hormonal system found in other asteroids. The egg is an orange, oblate spheroid measuring 0.84–0.88 mm in diameter and about 0.260 ml in volume. The egg has a lipid-to-protein ratio close to 1:1 and has a very high density of organic matter. The egg is adherent to seagrass blades and other substrata and hatches within 2 days into a demersal lecithotrophic larva. Larvae are quite tolerant of changes in temperature, less tolerant of changes in salinity. The mouth opens at 14 days post-fertilization after the loss of 20–25% of the original egg organic weight. Juveniles require about 2 yr to reach sexual maturity, at a size of R = 11–12 mm. During this period of growth, they remain in seagrass (*Thalassia testudinum, Syringodium filiforme, Halodule wrightii*) and oyster beds at shallow depths, feeding on epibiota and facultatively absorbing dissolved organic matter released by the sessile organisms that form the substratum.

Type-locality.—Sarasota Bay, Bradenton Beach, Anna Maria Key, Florida, USA (27°28.2′N, 82°42.1′W), <1 m depth, along bulkhead, on oysters and pilings.

Distribution.—*Echinaster graminicola* has been collected extensively in the Tampa Bay area: from oyster beds, bulkheads, and pilings in Sarasota Bay; from *T. testudinum* beds along the Sunshine Skyway Causeway; from *T. testudinum* beds, oyster beds, pier pilings, and cement bulkheads around Mullet, Madelaine, and Cabbage keys. The species has been found at Seahorse Key, Cedar Keys, Florida in *S. filiforme* beds. Specimens from *T. testudinum* beds in St. Joseph Bay, Florida have been identified by us as *E. graminicola.* The maximum depth at which the species has been collected is 2 m.

Relationships.—Among the several species of western Atlantic *Echinaster, E. graminicola* is most similar to *E. spinulosus,* with which it has been repeatedly confused. The discussion below and accompanying Table 1 are given to emphasize the differences between the two species.

Live specimens of *E. graminicola* and *E. spinulosus* can be readily distinguished by color (Figs. 3, 4). The integument covering ossicles of the aboral surface of *E. spinulosus* is deep reddish orange (ISCC-NBS number 36) to deep orange yellow (no. 69), and the papular areas are bluish white (no. 189). The papular areas are numerous but small, and the animal overall looks "orange." On the adoral surface, the sea star is pale yellow (no. 89), and no areas of bluish white integument occur.

Preserved specimens of the two species are distinguished by few differences in spination and morphology. Some of the differences listed in Table 1 might reflect a neotenic condition in *Echinaster graminicola,* but the differences are not always related to body size of specimens we examined. *Echinaster graminicola* is generally less spiny than *E. spinulosus,* but it is difficult to identify individual specimens. Even the adambulacral armature of one species is easily derivable from the other: in *E. graminicola,* the 3 spines are in a slightly curved vertical row; in *E. spinulosus,* the "middle" spine is close enough to the distal furrow spine in position and morphology to be considered a second furrow spine. Oral armature, on the other hand, seems to be a reliable character for identification of individual specimens.

Many differences other than adult morphology of the two species have been found by other authors (Table 1). The species differ especially in reproduction, development, biochemistry, physiology, microhabitat, and general size. Scheibling (1982) and Watts *et al.* (1982) give evidence of a genetic basis for some of these differences.

Echinaster graminicola and *E. spinulosus* are easily distinguished from the rarer and deeper-water *E. modestus,* which has an actinolateral series, more complex organization of dorsolaterals, predominance of proximal imbrication, shorter and more compact series of intermarginals, poorly developed patches of glassy tubercles, and spinier adambulacrals and mouth plates (Turner and Campbell 1981). They are similarly distinct from specimens on which Downey (1973) and Tortonese and Downey (1977) based their taxonomic treatment of *Verrillaster* Downey, 1973. On the other hand, *E. graminicola* and *E. spinulosus* are allied to *E. sentus,* which also lacks actinolaterals and has well-developed patches of glassy tubercles.

Etymology.—graminicola, from the Latin *gramen,* grass, and *colo,* to dwell; referring to the frequent occurrence of this species in seagrass beds, used as a noun in apposition.

Discussion.—Echinaster graminicola and *E. spinulosus* are sibling species (sensu Kohn and Orians 1962; Mayr 1969). They are sympatric and morphologically similar, with a high degree of niche specialization. They have been recognized as distinct forms for at least 16 years (Ferguson 1967) on the basis of ecological and other non-morphological data. The two species were hybridized by Scheibling (1982) and Watts *et al.* (1982) but are isolated by different spawning times and microhabitats. Only recently (Campbell 1978; Campbell and Turner 1979) was a morphological basis for their distinction as species found.

The sea star family Echinasteridae Verrill, 1867 is a problematical group that includes *Echinaster, Henricia,* and other genera which have undergone repeated taxonomic revision (Fisher 1919; Rasmussen 1965; Tortonese and Downey 1977). Grainger (1966) wrote that species of *Henricia* are "chronic sources of trouble to students of the group;" and Downey (1973) described the genus *Echinaster* as "the most confusing one [among the Asteroidea] occurring in the tropical and subtropical Atlantic." One reason for the taxonomic problems is the high degree of intraspecific morphological variability. The presence of non-morphological variability within and among other western Atlantic populations of *Echinaster* (Tuttle and Lindahl 1980), in addition to the present case, suggests to us that problems in the Echinasteridae might be due to the existence of numerous sibling species.

Table 1.—Contrasting characteristics of *Echinaster graminicola* and *E. spinulosus*. References: 1, this report and authors' unpublished observations; 2, Atwood (1973a); 3, Turner and Lawrence (1979); 4, Scheibling and Lawrence (1982); 5, Watts *et al.* (1982); 6, Scheibling (1982).

Character	*Echinaster graminicola*	*Echinaster spinulosus*	Ref.
Color			
Papular areas	Blackish red	Bluish white	1
General pattern	Dark red with numerous yellow knobs	Orange	1
Meristics and morphology			
Aboral disc spines	Tapered, subacute	Cylindrical, obtuse	1
Mouth plate spines	2–3	3–4	1
Ray spines	0–1	1–2	1
Furrow spines	1	2	1
Intercalary carinals	Usually present	Usually absent	1
Madreporic gyri	Meandering	Radiating	1
Gyral spines	0–10	3–34*	1
Peripheral spines	2–16	12–37*	1
Egg			
Color	Orange	Brown	2, 3
Shape	Oblate spheroid	Prolate spheroid	3
Diameter	.84–.88 mm	1.0–1.3 mm	2
Volume	.258 ml	.199 ml	3
Lipid : protein ratio	1:1	5:2	3
Organic density	595 μg/ml	439 μg/ml	3
Buoyancy upon spawning	Sinks	Floats	2, 3
Reproduction and growth			
Spawning	April–May	Late May–June	4
Larva	Demersal	Pelagic	2
Larval temperature tolerance	Greater	Less	5
Growth rate 1st yr	10 mm/yr	22 mm/yr	6
Maturity	Later age, smaller size	Earlier age, larger size	4
Reproductive effort	Higher	Lower	4
Fecundity	1 ×	3–5 ×	4
Reproductive output	Lower	Higher	4
Caloric investment/egg	1.7 ×	1 ×	4
General size	Smaller	Larger	1, 6
Ecology			
Habitat	Shallow; seagrass and oyster beds, pilings, bulkheads	Deep; bare sand, pilings, bulkheads	1, 6
Diet**	Sessile epifauna	Sessile, sedentary epifauna; scavenging	1, 6

* Based only on 5 cotypes, YPM 1771.

** Dietary differences are probably greater, based on analysis of fatty-acid composition of adults (Ferguson 1976).

Blake (1973) found that the morphology of individual ossicles of the primary skeleton was sufficiently consistent intraspecifically to be useful in taxonomic studies of four Recent asteroid families. The detailed examination of individual primary ossicles was, however, of limited value in the present case (Campbell

1978). In closely related species of *Echinaster,* evolution has probably occurred faster in the morphology of the secondary skeleton (Schuchert 1915) than in the morphology of primary ossicles; and the subtle differences might not be discovered until *Echinaster* populations are better known ecologically.

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Note added in proof:
Echinaster graminicolus, nomen nudum, has inadvertently appeared in Ferguson (1984).

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A NEW SPECIES OF *OREOHELIX* (GASTROPODA: PULMONATA: OREOHELICIDAE) FROM THE SEVEN DEVILS MOUNTAINS, IDAHO

H. Lee Fairbanks

Abstract.—*Oreohelix hammeri,* a new species of pulmonate land snail, is described from the Seven Devils Mountains of western Idaho. Comparisons are made with six taxa each having some characteristics in common with *O. hammeri.* A range extension for *Oreohelix elrodi* (Pilsbry) is noted.

Species of the land snail genus *Oreohelix* may be found throughout the Rocky Mountains of the western United States, from Arizona to Montana and Idaho. One area of the Rockies that has been visited frequently by malacologists is the southwestern portion of Idaho County, Idaho. Nine species and subspecies of *Oreohelix* have been described from this area (Pilsbry 1939; Solem 1975). This particular part of Idaho County is deeply cut by the Salmon River and its tributaries, forming many large and small canyons. These canyons create many and varied habitats which may have been the stimulus for the high levels of speciation observed here.

In July 1982, William P. Hammer, a longtime friend and an ardent outdoorsman, went on a backpacking trip into the Seven Devils Mountains of southwestern Idaho County. This paper describes a new species of *Oreohelix* collected by Mr. Hammer during that trip.

Oreohelix hammeri, new species
Figs. 1A–C

Description of holotype.—Shell heliciform, strongly depressed, whorls convex above and below, sutures somewhat impressed, body whorl strongly keeled, descending slightly at aperture, ashy horn color with no banding; widely umbilicate with umbilicus contained approximately three times in diameter. Embryonic shell of approximately 2¼ whorls, the first whorl with fine spiral lines over faint radial ridges, the remainder of embryonic whorls having progressively stronger radial ridges. Postembryonic whorls with spiral lines more or less continuous to aperture, radial ridges more prominent, irregularly spaced; sculpture on dorsal surface similar to ventral surface. Aperture ovate; parietal callus thin.

Measurements of holotype: Diameter—20.2 mm; height—8.4 mm; umbilicus diameter—6.6 mm; whorls—5¼; embryonic whorls—2¼.

Genitalia of holotype (Figs. 2A, 3A–B): Atrium short. Penis of relatively constant diameter, pustulose portion more than one-half total length of penis, penial verge large, verge opening submedial. Epiphallus with many ridges angled toward verge opening. Penial rectractor muscle inserted on penis and epiphallus. Vagina expanded slightly at proximal end, proximal half pustulose. Free oviduct short, tapering slightly proximally. Beginning of spermathecal duct expanded, tapering

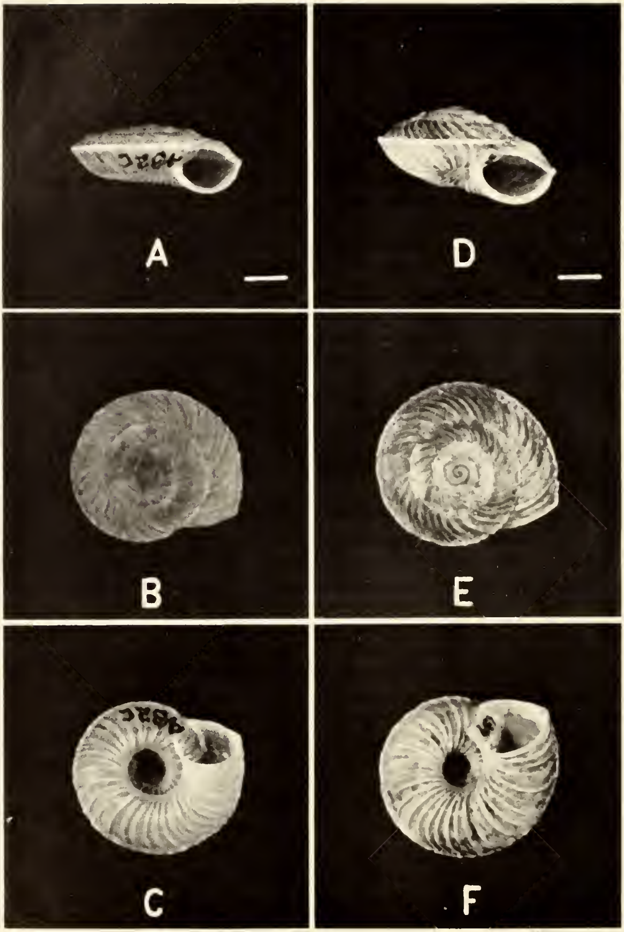

Fig. 1. Shells. Left column, *Oreohelix hammeri* (holotype): A, Side view; B, Top view; C, Bottom view. Right column, *Oreohelix elrodi* (topotype): D, Side view; E, Top view; F, Bottom view. Scale bars equal 5 mm.

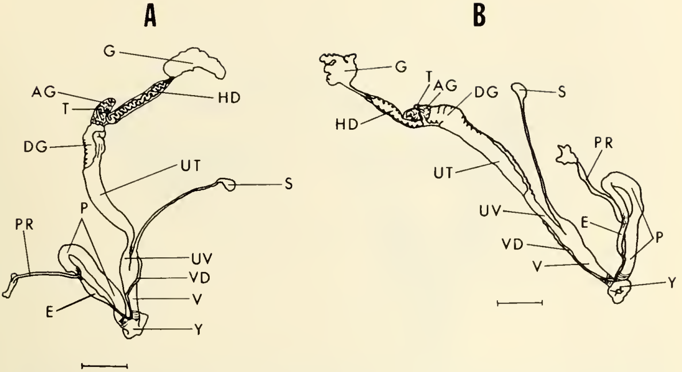

Fig. 2. Genitalia: A, *Oreohelix hammeri,* holotype. B, *Oreohelix elrodi.* Scale bars equal 5 mm, AG, albumin gland; DG, prostate gland; E, epiphallus; G, ovotestis; HD, hermaphroditic duct; P, penis; PR, penial retractor muscle; S, spermatheca; T, talon; UT, uterus; UV, free oviduct; V, vagina; VD, vas deferens; Y, atrium.

rapidly to slender duct; spermatheca ovoid. Uterus typical, without embryos. Prostate gland, albumin gland, and talon typical. Hermaphroditic duct long, tightly coiled. Ovotestis composed of 6 multilobular clumps, clumps angled slightly to columellar axis.

Measurements of holotype genitalia: Penis—15.5 mm, pustulose part—10.5 mm, ridged part—5.0 mm; epiphallus—5.0 mm; vagina—6.0 mm; free oviduct—4.0 mm; hermaphroditic duct (coiled part)—7.5 mm.

Pallial region of holotype (Fig. 4); Mantle gland well developed; vessels from mantle collar passing over mantle gland connecting with pulmonary vein. Kidney and heart typical; closed portion of ureter less than one-half length of kidney, reflexed ureteric sulcus bordered by low renal ridges. Hindgut very wide, intestinal loop along proximal edge of kidney.

Type-locality.—Loose rock of a knife-edge rock outcrop on the southeastern slope of Mt. Sampson, Seven Devils Mountains, ca. 5500 feet, Idaho County, Idaho, NE¼ sec 22 T23N R1W. No other known localities.

Disposition of type-material.—Holotype, USNM 809997, paratypes USNM 809998; H. Lee Fairbanks 432. USNM = United States National Museum of Natural History.

Diagnosis.—A species characterized by a shell that is of moderate size, with keeled periphery, has strong irregularly spaced radial ridges, and is strongly depressed.

Differential diagnosis.—*Oreohelix hammeri* is an allopatric species of the genus that is distinctive in terms of shell characteristics, genital characteristics, and ecological requirements. Six species or subspecies of *Oreohelix* appear somewhat similar to *O. hammeri*; however, each has distinct differences from this new species.

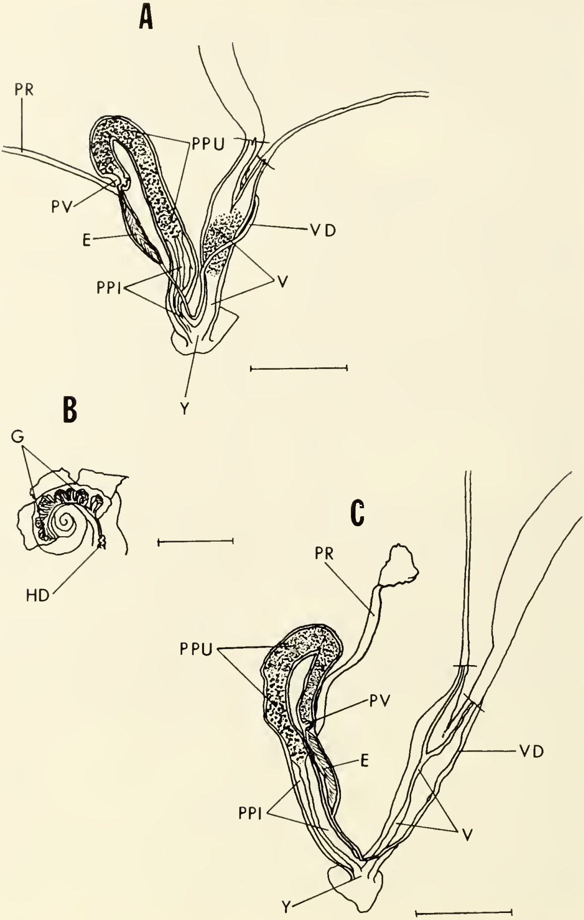

Fig. 3. A, terminal genitalia: *Oreohelix hammeri,* holotype, B, ovotestis: *Oreohelix hammeri.* paratype. C, terminal genitalia: *Oreohelix elrodi*. Scale bars equal 5 mm. E, epiphallus; G, ovitestis; HG, hermaphroditic duct; PPI, penial pilasters; PPU, penial pustules; PR, penial retractor muscle; PV, penial verge; V, vagina; VD, vas deferens; Y, atrium.

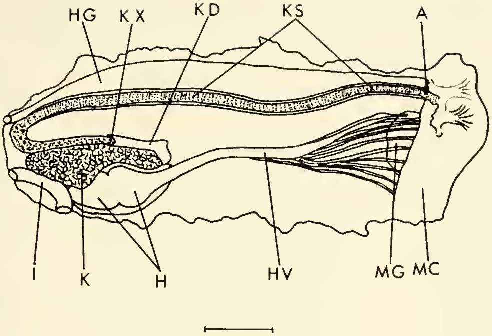

Fig. 4. Holotype, *Oreohelix hammeri,* pallial region. Scale bar equals 5 mm. A, anus; H, heart; HG, hindgut; HV, pulmonary vein; I, intestine; K. kidney; KD, closed portion of ureter; KS, ureteric sulcus; KX, opening of KD; MC, mantle collar; MG, mantle gland.

Oreohelix metcalfei radiata Pilsbry and Ferriss, found in the Black Range of Grant County, New Mexico, has a shell similar to that of *O. hammeri,* but the latter species has a shell that is more depressed, more umbilicate, and has stronger sculpturing (Pilsbry 1939:508; Fig. 1A–C). Most significant is the fact that the penis of *O. metcalfei radiata* has a ridged portion that is more than one-half the total length of the penis (Pilsbry 1939:512), whereas the penis of *O. hammeri* has a ridged portion that is less than one-half the total length of the penis (Table 2; Fig. 3A).

Oreohelix intersum (Hemphill), *O. waltoni* Solem, *O. idahoensis* (Newcomb), and *O. i. baileyi* Bartsch are found in Idaho County, Idaho. The shells of these four taxa are much smaller, less keeled, and much less depressed that the shell of *O. hammeri* (Solem 1975; Pilsbry 1939; 457–459; Fig. 1A–C). The reproductive system of *O. waltoni* has a loosely coiled hermaphroditic duct, a medial verge opening, and lacks a pustulose region in the vagina (Solem 1975). In *O. hammeri* the hermaphroditic duct is tightly coiled, the verge opening is submedial, and the vagina has a pustulose region (Figs. 2A; 3A). The reproductive systems of *Oreohelix idahoensis* and *O. i. baileyi* have loosely coiled hermaphroditic ducts and lateral verge openings (Solem 1975). Also, in these taxa the epiphallus (relative to the penis) is longer than that of *O. hammeri* (Solem 1975; Pilsbry 1939:459; Fig. 3A). In addition, the four taxa above are found in relatively mesic conditions, i.e., relatively near a river or stream (Solem 1975; Pilsbry 1939). *Oreohelix hammeri* is found in a xeric habitat.

Oreohelix elrodi (Pilsbry) is found in the Mission Mountains and Swan Mountains of Lake County, Montana. The shell of *O. elrodi* resembles that of *O. hammeri* more closely than the taxa noted above (Fig. 1). However, *O. elrodi* has a shell that is larger, is much less depressed, is less umbilicate, and has a greater number of whorls than *O. hammeri* (Table 1). The reproductive system of *Oreo-*

Table 1.—Shell comparisons of *Oreohelix hammeri* and *O. elrodi*. Numbers are means and standard deviations with the range in parentheses. Measurements, in millimeters, were obtained with vernier caliper.

	O. hammeri	*O. elrodi* (Mission Mts.)	*O. elrodi* (Swan Mts.)
Number	63	22	45
Diameter (D)	18.24 ± 1.97 (13.9–22.7)	22.46 ± 1.92 (19.5–25.8)	21.15 ± 1.93 (17.4–26.0)
Height (H)	7.07 ± 1.11 (5.0–9.6)	10.96 ± 0.86 (9.6–12.8)	10.19 ± 1.16 (8.4–13.1)
H/D ratio	.3874 ± 0.041 (.2888–.4725)	.4895 ± 0.034 (.4326–.5545)	.4829 ± 0.049 (.3995–.5970)
Whorls	4.62 ± 0.27 (4.0–5.33)	5.29 ± 0.19 (5.0–5.75)	5.17 ± 0.19 (5.0–5.75)
Umbilicus dia. (U)	5.31 ± 0.83 (3.7–6.9)	5.28 ± 0.74 (4.1–6.8)	4.96 ± 0.74 (3.3–6.8)
D/U ratio	3.47 ± 0.26 (3.06–4.03)	4.30 ± 0.42 (3.65–5.23)	4.31 ± 0.42 (3.71–5.94)

helix elrodi (Figs. 2B, 3C) has a shorter epiphallus (relative to the penis), a longer free oviduct (relative to the vagina), and a shorter hermaphroditic duct than that of *O. hammeri* (Table 2). In addition, *O. elrodi* has a smaller verge than *O. hammeri* (Fig. 3A, C). Also, *O. elrodi* is found in a relatively mesic habitat whereas *O. hammeri* is found in a xeric habitat. Finally, according to Pilsbry (1939:461) *O. elrodi* lacks ". . . side cusps or cutting points . . ." on the central and lateral teeth; the radular tooth formula is 27.1.27. In *Oreohelix hammeri* the central tooth is tricuspid, the lateral teeth are bicuspid, and the tooth formula is 24.1.24 with approximately 10 lateral teeth and 14 marginal teeth. The transition from laterals to marginals occurs between tooth numbers 9 and 14.

Etymology.—*Oreohelix hammeri* is named in recognition of William P. Hammer, Ronan, Montana, a valued friend, colleague, and student of western land snails.

Discussion

Solem (1975) reviewed the criteria that should be used to determine species in the genus *Oreohelix*, particularly when comparing allopatric populations. Those criteria include ecological parameters, shell differences, and reproductive system differences.

In the differential diagnosis, the above criteria were used in comparisons between six taxa and *Oreohelix hammeri*. Each of these taxa had some characteristics in common with *O. hammeri*, but in each case there were significant ecological, shell, and reproductive system differences.

Shell comparisons between *Oreohelix hammeri* and *O. elrodi* (Table 1) included specimens of *O. elrodi* collected above Lion Creek in the Swan Range, Lake County, Montana. This locality is approximately 20 miles east of the type-locality and is the first report of *O. elrodi* outside of the Mission Mountains. Voucher specimens have been sent to the USNM.

Table 2.—Reproductive system comparisons of *Oreohelix hammeri* and *O. elrodi*. Numbers are means and standard deviations with the range in parentheses. Measurements, in millimeters, were obtained with ocular micrometer.

	O. hammeri	*O. elrodi*
Number	4	3
Penis–total length	14.7 ± 1.55 (12.5–16.0)	18.8 ± 0.26 (18.5–19.0)
Pustulose part	9.9 ± 0.80 (8.8–10.5)	12.4 ± 0.79 (11.5–13.0)
Ridged part	4.8 ± 0.72 (3.8–5.5)	6.4 ± 0.53 (6.0–7.0)
Epiphallus	4.3 ± 0.70 (3.5–5.0)	4.7 ± 0.58 (4.0–5.0)
Retractor muscle	7.7 ± 1.55 (6.5–10.0)	8.3 ± 0.76 (7.5–9.0)
Vagina	6.3 ± 0.77 (5.5–7.3)	7.8 ± 0.29 (7.5–8.0)
Free oviduct	4.3 ± 0.39 (4.0–4.8)	5.8 ± 1.04 (5.0–7.0)
Spermathecal duct	15.2 ± 2.27 (13.5–18.5)	16.6 ± 0.40 (16.2–17.0)
Hermaphroditic duct (coiled portion)[2]	6.3 ± 1.44 (5.0–7.5)/	6.4 ± 0.21 (6.2–6.5)

[2] Only 2 specimens measured for *O. elrodi*.

Two additional sets of data should be noted. First, although the shell of the holotype of *Oreohelix hammeri* has no bands, many of the paratypes have a single dark band on the ventral surface approximately in the center of the whorl and a single dark band on the dorsal surface near the periphery of the whorl. Second, two of four dissected specimens of *O. hammeri* had embryos in the uterus (6 in one specimen, 9 in the other). The mean diameter of the embryonic shell was 4.0 mm ± 0.29 mm (3.5 mm–4.5 mm); the mean whorl number was 2.18 mm ± 0.20 mm (2.0 mm–2.5 mm).

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NEW RECORDS OF SNAPPING SHRIMPS (FAMILY ALPHEIDAE) FROM CALIFORNIA

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Abstract.—Thirteen species of snapping shrimps are known from California: *Automate dolichognatha, Alpheopsis equidactylus, Synalpheus lockingtoni, Betaeus ensenadensis, B. longidactylus, B. gracilis, B. harfordi, B. setosus, B. macginitieae, B. harrimani, Alpheus clamator, A. bellimanus,* and *A. californiensis. Automate dolichognatha* is reported from California for the first time. Northern range extensions are provided for *S. lockingtoni, B. ensenadensis,* and *A. clamator.* The range of *Alpheopsis equidactylus* is extended to the south. A key to the species is provided. Only four of the snapping shrimps range further north than Monterey Bay, California.

Snapping shrimps (family Alpheidae) are common in warm marine waters. Thirteen species, however, range into the cooler waters of the Californian Province, south of Point Conception, California; ten of them have been recorded as far north as Monterey Bay; four extend north of San Francisco Bay; and two have their northern limits in British Columbia or Alaska. Discussions of the species have been provided by Schmitt (1921), Hart (1964), Word and Charwat (1976), Butler (1980), and Wicksten (1981).

Range extension of *Automate dolichognatha* and *Betaeus ensenadensis* were found among material collected during environmental impact surveys. The specimens were provided by Dale Straughan and Dorothy Soule, respectively. Range extensions of *Alpheopsis equidactylus* and *Alpheus clamator* were discovered among material in the holdings of the Allan Hancock Foundation (AHF), University of Southern California. The specimen of *Synalpheus lockingtoni* was studied in the collections of the California Academy of Sciences (CAS).

Extensions of Range

Automate dolichognatha De Man

Automate dolichognatha De Man, 1887:529–532, pl. 22, fig. 5.—Wicksten, 1981: 1104–1105.

Previous records.—Pantropical; in the eastern Pacific north to Clarion Island, off Mexico (Wicksten 1981).

Material.—One specimen. 2.9 mi, 292° true from Church Rock, Santa Catalina Island (33°18′55″N, 118°22′46″W), 20 m, in box core, 10 Mar 1973, *Velero IV* sta 18666, AHF.

Alpheopsis equidactylus (Lockington)

Alpheus equidactylus Lockington, 1877:7, 35.
Crangon equidactylus.—Schmitt, 1921:76–77, fig. 53.
Alpheopsis equidactylus.—Word and Charwat, 1976:38.

Previous records.—Monterey to Santa Barbara (Schmitt 1921); Palos Verdes, 60 m (Word and Charwat 1976).

Material.—One specimen. 11 mi NW of buoy, Cortez Bank (32°32′30″N, 119°18′10″W–32°32′30″N, 119°17′50″W), 83–85 m, 11 Jun 1941, *Velero III* sta 1347-41, AHF.

Alpheus clamator Holmes

Alpheus clamator Holmes, 1900:182, pl. 2, figs. 38–40.—Holthuis, 1952:49.—Word and Charwat, 1976:45.
Alpheus dentipes.—Schmitt, 1921:74–75, fig. 50.
Not *Alpheus dentipes* Guérin, 1832 (eastern Atlantic species).

Previous records.—San Bartholome Bay, Lower California, Mexico to Farallon Islands, California (Schmitt 1921).

Material.—2 specimens. Horseshoe Cave, Sonoma County (38°19′N, 123°05′W), shore, 27 May 1967, R. J. Menzies AHF sta 1674-49.

Betaeus ensenadensis Glassell

Betaeus ensenadensis Glassell, 1938:416–419, pl. 28.—Hart, 1964:445–447, figs. 23–25, 28, 35, 36, 43–45.—Word and Charwat, 1976:48.

Previous records.—El Estero de Punta Banda, Baja California, Mexico; Mission Bay, False Bay, California (Hart 1964).

Material.—One specimen. Los Angeles Harbor, 10 m, 10 Apr 1978, R. V. *Van Tuna,* L. A. Harbor Project sta A 14, AHF.—One specimen. Long Beach Harbor, 3–4 m, 16 Oct 1978, R. V. *Golden West,* Harbors Environmental Projects sta D10, AHF. Both at about 33°40′N, 118°15′W.

Synalpheus lockingtoni Coutière

Synalpheus lockingtoni Coutière, 1909:21–23, fig. 1.—Schmitt, 1921:77–78, fig. 54.—Word and Charwat, 1976:64.—Standing, 1981:778.

Previous records.—Port Escondido, Port Mulege, and other points in the Gulf of California; Santa Monica Bay, Venice Beach, San Diego Bay, Palos Verdes, Elkhorn Slough (Word and Charwat 1976; Standing 1981).

Material.—One specimen. On wharf piles, Santa Cruz, (36°58′N, 122°04′W), 18 Sep 1960, John P. Strohbeen, CAS.

Remarks.—Rathbun (1910) and Standing (1981) reported *S. lockingtoni* from Santa Elena Bay, Ecuador. The record originally came from Nobili (1897). However, Nobili mentioned that his specimen (as *Synalpheus laeviusculus* [Lockington]) had a short rostrum, not exceeding the orbital spines. Probably, the record of *S. lockingtoni* from Ecuador is based on a misidentification.

Ranges of Snapping Shrimps in California

The ranges of snapping shrimps known from California are given in Table 1. An additional species, *Alpheus barbara* Lockington, 1878, was reported from Santa Barbara (Schmitt 1921). This species has not been seen since its description in 1878.

Table 1.—Ranges of species of snapping shrimps.

Species reaching their northern limits in southern California:

Automate dolichognatha: circumtropical, to Santa Catalina Island, California.
Alpheus californiensis: Magdalena Bay, Baja California, Mexico to San Pedro, California (Schmitt 1921)
Betaeus ensenadensis: Estero de Punta Banda, Baja California, Mexico to Los Angeles Harbor, California.

Species reaching their northern limits in Monterey Bay:

Alpheopsis equidactylus: Cortez Bank, California to Monterey.
Alpheus bellimanus: Islas Secas, Panama to Monterey Bay (Wicksten 1983).
Betaeus gracilis: Laguna Beach to Monterey Bay (Hart 1964).
Betaeus macginitieae: Santa Catalina Island to Monterey (Hart 1964).
Betaeus longidactylus: Tepoca Bay, Gulf of California to Elkhorn Slough (Hart 1964).
Synalpheus lockingtoni: Gulf of California to Santa Cruz.

Species reaching their northern limits in northern California:

Betaeus harfordi: Magdalena Bay, Baja California, Mexico to Fort Bragg, California (Hart 1964).
Alpheus clamator: San Bartolome Bay, Baja California, Mexico to Horseshoe Cove, Sonoma County, California.

Species ranging north to British Columbia or Alaska:

Betaeus harrimani: Newport Harbor, California to Sitka, Alaska (Hart 1964).
Betaeus setosus: Morro Bay, California to Hecate Strait, British Columbia (Hart 1964).

Shrimps of the family Alpheidae are most diverse in tropical waters. Perhaps this is why only four species range further north than Monterey Bay, a protected area which may have warmer waters than areas to the immediate north along the coast.

Key to the Species of Snapping Shrimps in California

1. Triangular movable plate articulated at posterolateral angle of sixth abdominal somite lateral to base of uropod 2
– No triangular movable plate articulated at posterolateral angle of sixth abdominal somite lateral to base of uropod 9
2. Rostrum prominent, orbital hoods armed with spines. (Subtidal only) .... *Alpheopsis equidactylus* (Lockington)
– Rostrum absent, front without spines. (Intertidal–subtidal) . . *Betaeus* spp. 3
3. Dactyls of walking legs slender and simple 4
– Dactyls of walking legs stout and bifid 6
4. Chelae of first legs with fingers longer than palm. Large male with gaping fingers of chelipeds .... *Betaeus longidactylus* Lockington
– Chelae of first legs with fingers not longer than palm. Large male with heavier, stouter chelae, but without gaping fingers 5
5. Blade of antennal scale broad distally. Fixed finger of first cheliped decreasing in width evenly to sharp curved tip . *Betaeus harrimani* Rathbun
– Blade of antennal scale narrow distally. Fixed finger of first cheliped truncate before sharp curved tip .... *Betaeus ensenadensis* Glassell

6. Front curved, not emarginate. Commensal with sea urchins (*Strongylocentrotus* spp.) .... *Betaeus macginitieae* Hart
– Front emarginate. Commensal with abalone, or free-living 7
7. Emargination of front shallow. Telson with posterolateral spines small or missing. Commensal with abalones (*Haliotis* spp.) .... *Betaeus harfordi* (Kingsley)
– Emargination of front deep. Telson with posterolateral spines well developed 8
8. Peduncle of first antenna less than 0.5 carapace length. Merus of cheliped with lower inner ridge with long bristles, upper ridge ending in sharp tooth; chela with fingers subequal to palm; chela 3 times as long as wide .... *Betaeus gracilis* Hart
– Peduncle of first antenna subequal to carapace length. Merus of cheliped with lower inner ridge usually tuberculate, upper ridge with tuft of hair; chela with fingers longer than palm; chela twice as long as wide .... *Betaeus setosus* Hart
9. Eyes fully exposed dorsally. (Burrowing in soft bottoms) .... *Automate dolichognatha* De Man
– Eyes covered by carapace. (Burrowing in soft bottoms or not) 10
10. Pereopods without epipods. Dactyls of pereopods 3–5 bifid .... *Synalpheus lockingtoni* Coutière
– Pereopods with epipods. Dactyls of pereopods 3–5 with simple tips .. .. *Alpheus* spp. 11
11. Dactyl of major chela closing horizontally. Merus of third pereopod with prominent inferior spine .... *Alpheus clamator* Holmes
– Dactyl of major chela closing vertically. Merus of third pereopod without prominent inferior spine 12
12. Orbital hoods with spines. Minor chela with prominent spine posterior to movable finger, movable finger flattened (lamellate) .... *Alpheus bellimanus* Lockington
– Orbital hoods without spines. Minor chela without prominent spine posterior to movable finger, movable finger not flattened .... *Alpheus californiensis* Holmes

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CRENATOSQUILLA, A NEW GENUS OF STOMATOPOD CRUSTACEAN FROM THE EAST PACIFIC

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Abstract.—*Crenatosquilla,* a new genus, is proposed for *Squilla oculinova* Glassell, 1942, until now assigned to *Meiosquilla.* This new genus differs from *Meiosquilla* in shape of eyes and antennal scales, and in ornamentation of the antennal and antennular peduncles.

While examining eyes of different stomatopods as part of a cooperative project with Helga Schiff, University of Torino, Italy, on eye shape and function in members of this group, we examined the eyes in *Meiosquilla oculinova* (Glassell) to see how they compared with those of *Squilla mantis* (Linnaeus, 1758), another squillid. This examination demonstrated that the eye in *M. oculinova* differs from any of the eyes heretofore studied in the Stomatopoda. An account of the eye shape and facets will be published elsewhere (Schiff and Manning, in preparation).

Eye shape is an important generic character in stomatopods (see Manning 1968: fig. 5, for figures of eyes of different squillid genera), and the unique eyes of Glassell's species, in combination with its uniquely ornamented antennal and antennular peduncles and its uniquely shaped antennal scales, suggest that it should be placed in a genus separate from *Meiosquilla.*

Crenatosquilla, new genus

Definition.—Body smooth, compact, size small, total length of adults less than 50 mm. Eye large, cornea bilobed, broader than stalk, anterior margin of cornea scalloped, deeply indented; ocular scales separate. Antennular and antennal peduncles ornamented with hooked spines or processes. Antennal scale cordiform, tapering distally. Carapace smooth, narrowed anteriorly, anterolateral angles unarmed; carinae reduced, median and intermediates absent, at most reflected marginals and posterior part of each lateral carina present; cervical groove indistinct; posterior median margin evenly concave, posterolateral margins broadly rounded. Exposed thoracic somites with intermediate carinae, submedians absent; lateral process of fifth thoracic somite an inconspicuous diagonal or flattened lobe, a ventral spine present on each side; lateral processes of next 2 somites evenly rounded, not bilobed; ventral keel of eighth somite low. Mandibular palp absent; 4 epipods present on maxillipeds 1–4. Dactylus of raptorial claw with 4 teeth, outer margin evenly convex; propodus with outer part of opposable margin evenly pectinate, with 3 proximal movable teeth, middle smallest; dorsal ridge of carpus indistinct; ischiomeral articulation terminal. Endopods of walking legs slender, elongate. Abdomen with anterior 5 somites lacking submedian carinae; intermediates, laterals, and marginals present, usually unarmed anterior to fifth somite; sixth abdominal somite with armed submedian, intermediate, and lateral carinae. Telson broad, median and long submedian carinae present dorsally; 3 pairs of marginal teeth present, submedians with movable apices; prelateral lobes absent;

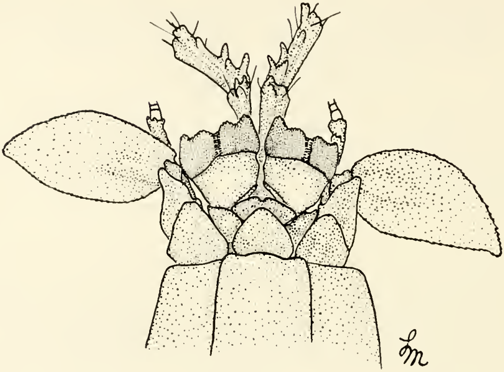

Fig. 1. *Crenatosquilla oculinova* (Glassell), female, total length 27 mm: front.

postanal keel low. Basal prolongation of uropod with inner spine the longer, inner margin lined with denticles or short teeth; rounded lobe present on outer margin of inner spine.

Type-species.—*Squilla oculinova* Glassell, 1942, by present designation and monotypy.

Etymology.—The generic name is formed from the Latin, "crena," a rounded projection, in combination with the generic name *Squilla.* The gender is feminine.

Remarks.—Three of the features of *Crenatosquilla* distinguish it not only from the species of *Meiosquilla,* which it resembles in basic facies, but also from all other stomatopods: the anteriorly scalloped eyes, the lobed projections on the antennular and antennal peduncles, and the strongly cordiform antennal scales. In addition to these morphological features, *Crenatosquilla oculinova* may well differ from species of *Meiosquilla* in habitat preferences. Reaka and Manning (1980) reported that *C. oculinova* was found in coarse habitats of rubble and rock in Coast Rica (where some other specimens of *Meiosquilla* species also were found), but at least some *Meiosquilla,* like most species of squillids, frequent level bottom habitats in sand or mud.

Acknowledgments

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SYSTEMATICS OF THE OPHIDIASTERID SEA STARS *COPIDASTER LYMANI* A. H. CLARK, AND *HACELIA SUPERBA* H. L. CLARK (ECHINODERMATA: ASTEROIDEA) WITH A KEY TO SPECIES OF OPHIDIASTERIDAE FROM THE WESTERN ATLANTIC

John E. Miller

Abstract.—*Copidaster lymani* A. H. Clark, 1948, is reported and redescribed from new material collected at Carrie Bow Cay (Belize), Portobelo (Panama), and Ascension Island. These are the first western Atlantic records of *C. lymani* since description of the holotype from Florida. Revisions by earlier authors, in which *Copidaster* is synonymized with the genera *Leiaster* or *Ophidiaster,* are rejected, and *Ophidiaster schismochilus* H. L. Clark, 1922, is referred to the genus *Copidaster.* A redescription of *Hacelia superba* H. L. Clark is presented. Previous accounts of this species from the western Atlantic have been limited to the type-locality, Barbados; new locality records from North and South Carolina, the east coast of Florida and the northern Gulf of Mexico are reported herein. Relationships between *H. capensis* Mortensen, 1925, from South Africa and *H. superba* are discussed. A key to the species of Ophidiasteridae from the western Atlantic is included.

In the tropical western Atlantic, Caribbean, and Gulf of Mexico, the asteroid family Ophidiasteridae is represented by 13 nominal species (Downey, unpublished; this study). For four species, *Copidaster lymani* A. H. Clark, 1948, *C. schismochilus* (H. L. Clark, 1922) new combination, *Hacelia superba* H. L. Clark, 1921, and *Ophidiaster bayeri* A. H. Clark, 1948, no new material has been reported from the western Atlantic since description of the holotypes.

At Carrie Bow Cay, Belize, Central America, four specimens of an unusual ophidiasterid sea star were found in shallow tide pools beneath heaps of coral rubble. They proved to be *Copidaster lymani,* a species previously known only from the type-specimen collected off Key Largo, Florida, and from material described by Nataf and Cherbonnier (1975) from the west coast of Africa. Subsequent examination of unidentified or misidentified material housed at the Smithsonian Institution revealed numerous additional specimens from Carrie Bow Cay and Ascension Island.

The generic position of *C. lymani* has been a matter for debate since Clark's (1948) description of this species. Downey (1973) referred *C. lymani* to the genus *Leiaster,* while Nataf and Cherbonnier (1975) preferred to drop the name *Copidaster* in favor of *Ophidiaster.* In the present study, important morphological characters of *Copidaster, Leiaster* and *Ophidiaster* are compared and the need to retain the generic name *Copidaster* is demonstrated. Additionally, *C. lymani* and *C. schismochilus* are shown to be congeneric.

During diving operations aboard Research Submersible *Johnson-Sea-Link* I, several specimens of another ophidiasterid, *Hacelia superba,* were collected from a submerged oolithic reef off Sebastian, Florida. Although *H. superba* has been reported from the eastern Atlantic, off St. Helena (Mortensen 1933) and Angola (Nataf and Cherbonnier 1975, questionable record), its recorded distribution in the western Atlantic has been limited to Barbados, the type-locality. Catalogued material of *H. superba* at the Smithsonian Institution confirmed additional records from off the coasts of North and South Carolina and in the northwestern Gulf of Mexico. New information on distribution, variation, coloration, and habitat of *H. superba* is presented here. *Hacelia superba* and the South African species *H. capensis* Mortensen, may be conspecific; their similarities are discussed.

Voucher specimens have been deposited at the British Museum (Natural History) [BM(NH)], the Indian River Coastal Zone Museum, Harbor Branch Foundation, Inc. [IRCZM], the Museum of Comparative Zoology, Harvard University [MCZ] and the National Museum of Natural History, Smithsonian Institution [USNM].

Family Ophidiasteridae Verrill, 1867
Copidaster lymani A. H. Clark, 1948
Figs. 1, 2, 3A

Copidaster lymani A. H. Clark, 1948:55, figs. 1, 2.—1954:376 [listed].—Downey, 1979:80 [key].

Leiaster lymani.—Downey, 1973:62 [discussed].

Ophidiaster lymani.—Nataf and Cherbonnier, 1975:818, pl. I, fig. A, pl. II, figs. A, B, C, E, F.

Material examined.—Holotype (R = 85 mm, r = 9 mm, R/r = 9.4), USNM E7177, Key Largo, Florida, outer reefs, F. Lyman, Sep 1947.—1 specimen (R = 98 mm, r = 10 mm, R/r = 9.8), Paris Museum EC AS 1380, *Calypso,* Sta 50, Guinee, 1°24′04″S, 5°36′45″E, 7–10 m, 13 Jun 1956.—2 specimens (R = 100 mm, r = 10 mm, R/r = 10.0; R = 72 mm, r = 10 mm, R/r = 7.2), Paris Museum EC AS 1378, *Calypso,* Sta 103, Guinee, off Annobon Island, calcareous algae bottom, 4 Jul 1956.—1 specimen (R = 85 mm, r = 9 mm, R/r = 9.4), Paris Museum EC AS 1384, *Calypso,* Sta 42, Cape Verde, rock bottom, 15–30 m, 20 Nov 1959.—1 specimen (R = 21 mm, r = 4 mm, R/r = 5.3), USNM E19272, R/V *Pillsbury,* Sta P-926, West Indies, 73 m, 14 Jul 1969.—5 specimens (R = 57 mm, r = 7 mm, R/r = 8.1; R = 50 mm, r = 7 mm, R/r = 7.1; R = 46 mm, r = 5 mm, R/r = 9.2; R = 45 mm, r = 6 mm, R/r = 7.5; R = 42 mm, r = 5 mm, R/r = 8.4), USNM E18680, Carrie Bow Cay, Belize, 16°48′N, 88°05′W, east side of cay in rubble field, intertidal, F. H. C. Hotchkiss (CBC-178), 3 May 1974.—1 specimen (R = 46 mm, r = 6 mm, R/r = 7.7), USNM E28829, Carrie Bow Cay, Belize, 16°48′N, 88°05′W, inner edge of reef crest, intertidal, F. H. C. Hotchkiss (CBC-154), 4 May 1974.—1 specimen (R = 57 mm, r = 6 mm, R/r = 9.5), USNM E18679, Carrie Bow Cay, Belize, 16°48′N, 88°05′W, east side of cay, rubble field, intertidal, F. H. C. Hotchkiss (CBC-17), 5 May 1974.—1 specimen (R = 37 mm, r = 5 mm, R/r = 7.4), USNM E18689, Carrie Bow Cay, Belize, 16°48′N,88°05′W, east side of cay, rubble field, intertidal, F. H. C. Hotchkiss, 6 May 1974.—1 specimen (R = 45 mm, r = 6 mm, R/r = 7.5) USNM E18678, Carrie Bow Cay, Belize, east side of cay, rubble field, intertidal, F. H. C. Hotchkiss (CBC-97), 7

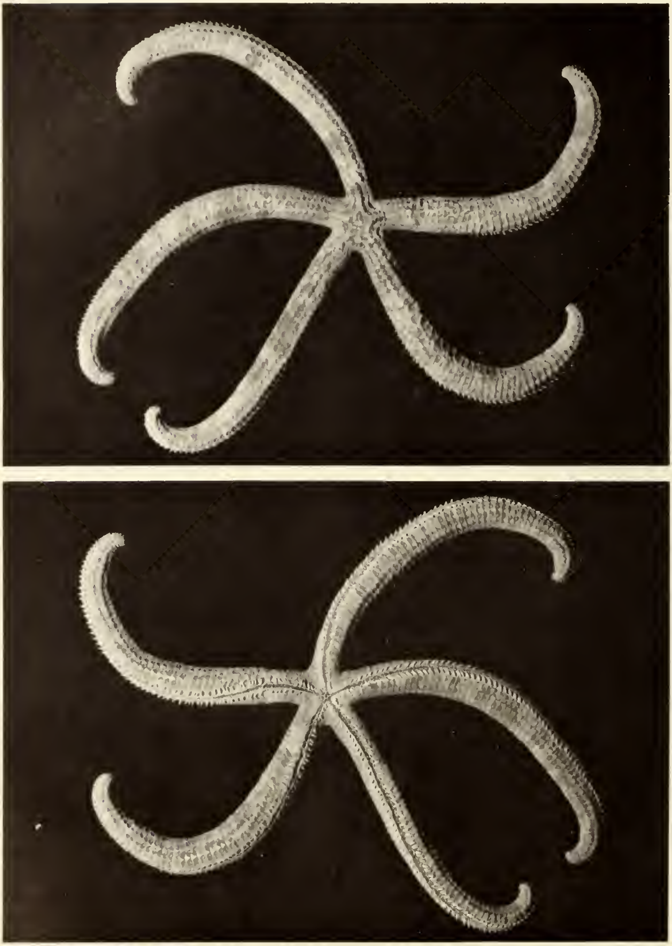

Fig. 1. *Copidaster lymani,* USNM E28831, R/r = 155 mm/13 mm. Upper, abactinal view; lower, actinal view.

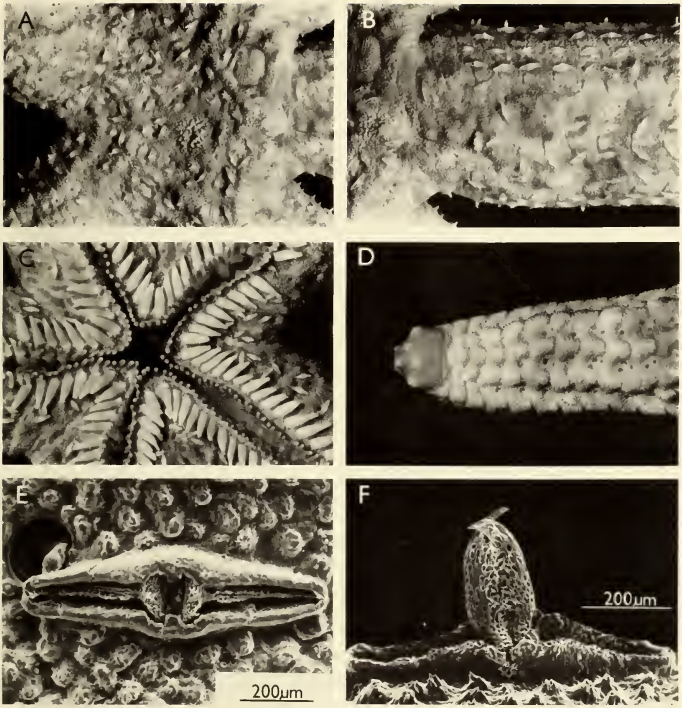

Fig. 2. *Copidaster lymani*, IRCZM 73:247. A, B (R/r = 55 mm/6 mm); A, Disk; B, Basal part of ray; C, D (R/r = 45 mm/5 mm); C, Mouth and basal part of rays; D, Distal tip of ray showing ocular plate; E, F, SEM micrographs of pedicellariae; E, Open valves laying in aveolus; F, Lateral view, valves closed, skin partly removed with bleach.

May 1974.—1 specimen (R = 45 mm, r = 5 mm, R/r = 9.0), USNM E29504, Iron Castle Point, Portobelo, Panama, under coral rubble, 1.5–3.0 m, G. Hendler, 8 Sep 1974.—1 specimen (R = 44 mm, r = 5 mm, R/r = 8.8), USNM E29505, Iron Castle Point, Protobelo, Panama, under rock, 0–1.5 m, G. Hendler, 27 Oct 1974.—2 specimens (R = 160 mm, r = 13 mm, R/r = 12.3; R = 155 mm, r = 13 mm, R/r = 11.9), USNM E28831, Ascension Island, offshore from Comfortless Cove, sandy and coarse sand, 33.5 m, B. S. McDowell, Apr 1981.—1 specimen (R = 125 mm, r = 10 mm, R/r = 12.5), USNM E28830, Ascension Island, 18 m off pierhead at Georgetown, common on rock and sand bottom, M. McDowell, May 1981.—1 specimen (R = 130 mm, r = 10 mm, R/r = 13.0) USNM E24787,

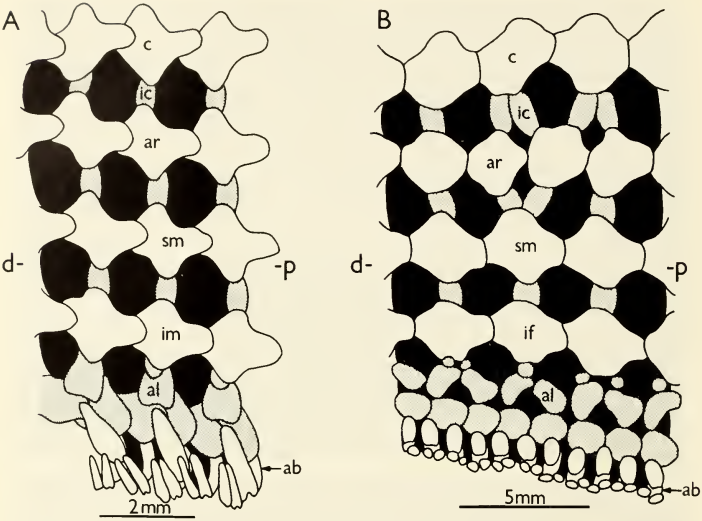

Fig. 3. Planar views of skeletal plates near mid-portion of ray. A, *Copidaster lymani,* IRCZM 73: 247, R/r = 55 mm/6 mm; B, *Hacelia superba,* IRCZM 73:227, R/r = 68 mm/14 mm. Abbreviations: d, distal; p, proximal; c, carinal; ic, internal connecting ossicle; ar, adradial; sm, superomarginal; im, inferomarginal; al, actinolateral; ab, adambulacral.

Ascension Island, 18 m off pierhead at Georgetown, under rocks, M. McDowell, Aug 1981.—4 specimens (R = 55 mm, r = 6 mm, R/r = 9.2; R = 50 mm, r = 5 mm, R/r = 10.0; R = 45 mm, r = 5 mm, R/r = 9.0; R = 42 mm, r = 5 mm, R/r = 8.4), IRCZM 73:247, Carrie Bow Cay, Belize, 16°48′N, 88°05′W, tide pools among storm rubble of reef crest, intertidal, J. E. Miller, 23 Mar 1981.—2 specimens (R = 39 mm, r = 5.5 mm, R/r = 7.1; R = 41 mm, r = 5 mm, R/r = 8.2), MCZ 4672, Carrie Bow Cay, Belize, 16°48′N, 88°05′W, among storm rubble of reef crest, 0–1 m, G. Hendler, B. Littman, 11 Jan 1983.—3 specimens (R = 47 mm, r = 5 mm, R/r = 9.4; R = 45 mm, r = 6 mm, R/r = 7.5; R = 39 mm, r = 5 mm, R/r = 7.8), BM(NH) 1983.8.18.2–4, Carrie Bow Cay, Belize, 16°48′N, 88°05′W, reef crest and shallow spur and groove zone, 0–5 m, G. Hendler, B. Littman, 12 Jan 1983.—2 specimens (R = 58 mm, r = 5 mm, R/r = 11.6; R = 46 mm, r = 5 mm, R/r = 9.2), IRCZM 73:248, Carrie Bow Cay, Belize, 16°48′N, 88°05′W, among storm rubble of reef crest, 0–1 m, G. Hendler, B. Littmann, 20 Jan 1983.—1 specimen (R = 43 mm, r = 5 mm, R/r = 8.6), USNM E29502, Carrie Bow Cay, Belize, 16°48.1′N, 88°04.8′W, reef crest, under rubble, 0–2 m, G. Hendler, 23 Mar 1983.—2 specimens (R = 38 mm, r = 5 mm, R/r = 7.6; R = 35 mm, r = 5 mm, R/r = 7.0), USNM E29503, Carrie Bow Cay, Belize, 16°48.1′N, 88°04.8′W, reef crest, under rubble, 0–2 m, G. Hendler, 5 Apr 1983.

Diagnosis.—Skeleton concealed by thin, squamulose skin; scales or granules present in skin covering actinal interradial area; longitudinal series of abactinal plates connected by single internal plates; width of adambulacral plates alternating broad and narrow; proximal adambulacrals connected to inferomarginals by 3 series of actinolateral plates; 8 series of papular areas; excavate pedicellariae numerous.

Description.—Disk flat, small (R/r = 7.2–13.0); rays, 5, long, cylindrical, often unequal in length. Rays constricted at their bases, inflated medially, gently tapering to a blunt tip. Oculars conspicuous, swollen, subcircular, carrying 6–12 large tubercles. Actinal surface of oculars with prominent groove. One (occasionally 2 or more) short, conical spine arises from either side of groove, frequently meeting over middle of groove. Single, large, circular to oval madreporite with smooth, fine gyri. Anus near center of disk, surrounded by 20–40 enlarged granules.

Entire skeleton concealed by thin skin, embedded with numerous, imbricating scales actinally and abactinally. Scales noticeably larger on summits of primary abactinal plates, conspicuously marking regular transverse and longitudinal series. Viewed laterally, a transverse series of plates consists of carinal, adradial, superomarginal, inferomaginal, actinolateral (3 rows proximally), adambulacral ossicles. Primary abactinals quadrilobate; distal plates overlap proximal plates. In larger specimens, adradial plates often reniform beyond basal portion of ray; quadrilobate shape reappearing near distal tip. In smaller specimens, adradial series usually consisting of double row of plates near medial or distal portion of ray. Beneath and between adjacent longitudinal rows of primary abactinals lie a series of internal ossicles. Adambulacral ossicles alternately broad and narrow. Larger adambulacrals connected to inferomarginals by series of 3 (2 in smaller specimens) actinolateral plates. Proximal adambulacral plates carry one large, flattened subambulacral spine. Further out on ray, subambulacral spines shorter, more cylindrical and confined to wider adambulacral plates only. Marginal face of each adambulacral plate bears two subequal, cylindrical furrow spines. Each half jaw bears a single, cylindrical, bluntly rounded preoral spine, 4 similar though shorter, marginal spines and one large, flattened suboral spine.

Eight longitudinal rows of papular areas with 7–15 papulae per area (large specimens R ≥ 150 mm with up to 30). Largest papular areas found on inflated abactinal portion of rays.

Excavate pedicellariae numerous on all surfaces, especially disk, basal part of rays and actinal-interradial area. Conspicuous presence of pedicellariae gives specimens a spinous appearance when examined with naked eye. Pedicellaria consists of 2 sickle-shape valves lying in narrow, elongate alveolus, 600–800 μm in length. Distal tips of valves tapering to acute terminal tooth, crossing when valves close.

In life, abactinal surface pigmented reddish tan or orange, with darker red mottling or irregular banding. Distal portion of rays usually uniformly red. Oculars red or orange. Actinal surface orange; subambulacral spines and furrow spines white proximally and distally, orange medially. Tube feet transparent orange, distinctly tipped with white suckers. Lighter specimens with pink to tan ground color and orange mottling. Very dark specimens almost uniformly blood red. Pedicellariae and madreporite white, conspicuously contrasted by darker surrounding skin. Color fades rapidly in ethanol.

Type.—National Museum of Natural History, Smithsonian Institution, USNM E7177.

Type-locality.—Key Largo, Florida, outer reefs, depth not recorded.

Distribution.—In the western Atlantic, presently known from Carrie Bow Cay (Belize), Protobelo (Panama) and the type-locality, intertidal to 5 m. Also verified from Ascension Island, down to 33.5 m (present study). Reported from the west coast of Africa off Cape Verde, Guinea and Annobon Island, 10–30 m, (Nataf and Cherbonnier 1975).

Habitat.—The majority of specimens from Carrie Bow Cay was collected intertidally (0–1 m), among thick layers of coral rubble on the reef crest and the leeward base of the crest. A few specimens were found beneath rubble in the shallow (3–5 m) spur and groove zone of the reef. At Portobelo, specimens were taken in shallow water beneath rock and rubble. Specimens from Ascension Island were found on rock and sand bottoms. At Annobon Island (Gulf of Guinea), two specimens were taken from a calcareous algal bottom (Nataf and Cherbonnier 1975).

Discussion.—At present, considerable confusion exists over the generic status of *Copidaster.* Noting obvious similarities between *Copidaster* and *Leiaster* (skin concealing skeleton, alternately broad and narrow adambulacral plates, presence of excavate pedicellariae), Downey (1973:62) stated that *Copidaster* should be considered as a synonym of *Leiaster.* Later, Nataf and Cherbonnier (1975) placed *Copidaster lymani* in the genus *Ophidiaster* because they failed to distinguish the alternately broad and narrow adambulacral plates in their specimens from West Africa. I have examined their specimens, and they indeed possess adambulacral plates alternating in width. Table 1 lists several important taxonomic characters in the genera *Copidaster, Leiaster* and *Ophidiaster.* Through comparison of these characters, it can be noted that the distinctions between the genera are clear. The presence of a thin but conspicuous skin, and alternately broad and narrow adambulacral plates in *Copidaster* serves to separate that genus from *Ophidiaster,* which lacks a conspicuous skin and has adambulacral plates of equal width. Furthermore, *Leiaster,* with two rows of actinolaterals proximally and a thick, fibrous skin lacking granules, is distinct from *Copidaster,* with three rows of actinolaterals proximally and a thin, squamulose skin. Clearly, *Copidaster,* as envisioned by A. H. Clark (1948), merits full generic rank.

Ophidiaster schismochilus H. L. Clark can be referred to the genus *Copidaster,* Although *Copidaster schismochilus* is presently known only from the type-specimen taken off Bermuda, the affinities between *C. schismochilus* and *C. lymani* are unmistakable, and *C. schismochilus* is therefore regarded herein as a new combination. It is possible that *C. schismochilus* and *C. lymani* are conspecific and that the differences noted are due to geographic and bathymetric variation. Some of the eastern Atlantic specimens of *C. lymani* superficially look like *C. schismochilus.* Lacking additional comparative material of *C. schismochilus,* a synonomy of the two species would seem unwise. If future material does suggest that *C. schismochilus* and *C. lymani* are conspecific, then *C. schismochilus* would have priority. Similarities between these species can be found in Table 1; important differences are noted in the Ophidiasteridae key (p. 206).

Remarks.—In reference to the pedicellariae of *C. lymani,* A. H. Clark (1948) states that in life the lateral borders of the alveoli can be brought together completely, concealing the valves of the pedicellariae. In examining Clark's type and all the new material examined herein, I have failed to find a single example of a

Table 1.—Comparative morphological characters of *Ophidiaster*, *Copidaster* and *Leiaster*.

Species examined	Skeletal covering	Number of pedicellariae	Jaw shape of pedicellariae	Arrangement of subambulacral spines beyond proximal 1/3 of ray	Number of longitudinal rows of actinolaterals proximally	Width of adjacent adambulacral plates
Ophidiaster *alexandri* Verrill *bayeri* A. H. Clark *bullisi* (Downey) *guildingi* Gray *ophidianus* (Lamarck) *reyssi* Sibuet	Fine layer of granules or scales, skin not evident	Variable, absent to numerous	Sugar-tongs, (sickle-shaped in *O. bullisi*)	Variable	2–5	Equal
Copidaster *lymani* A. H. Clark *schismochilus* H. L. Clark	Thin skin containing numerous scales and granules	Numerous	Sickle-shaped	Present on alternating adambulacral plates	3	Alternating broad and narrow
Leiaster *analogus* Fisher *callipeplus* Fisher *coriaceus* Peters *leachi* (Gray) *teres* (Verrill)	Thick, fibrous skin lacking visible scales and granules	Variable, absent to numerous	Sickle-shaped	Present on alternating adambulacral plates	2	Alternating broad and narrow

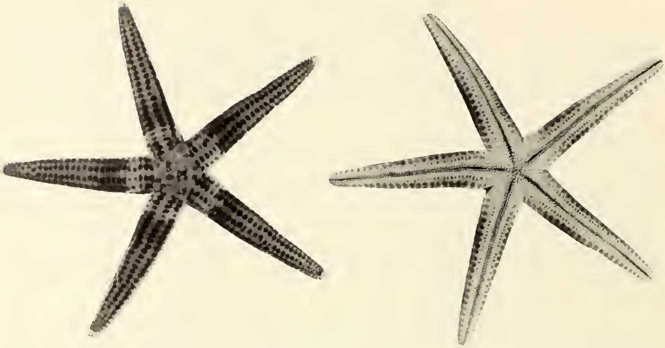

Fig. 4. *Hacelia superba,* IRCZM 73:227, R/r = 82 mm/15 mm, left, abactinal view; right, actinal view.

closed alveolus. This finding has been confirmed by G. Hendler (pers. comm.) who has observed live material at Carrie Bow Cay, Belize. Even direct mechanical stimulation of the pedicellariae failed to elicit a response in which the jaws of a pedicellaria were concealed by the alveolus.

At Carrie Bow Cay, *C. lymani* often occurs with *Ophidiaster guildingi* Gray which it frequently resembles in size, color and morphology. In the field, *C. lymani* can readily be distinguished from *O. guildingi* by the presence of conspicuous pedicellariae and a slimy skin in the former.

Hacelia superba H. L. Clark, 1921
Fig. 3B, 4, 5

Hacelia superba H. L. Clark, 1921:87, pl. 32, figs. 1, 2.—Mortensen, 1933:426, figs. 8, 9.—Downey, 1970:81 [key].—1973:61 [discussed].—A. M. Clark, 1974: 436 [discussed].

? *Ophidiaster superbus.*—Nataf and Cherbonnier, 1975:820, pl. III, figs. A, B.

[Non *Hacelia floridae.*—A. H. Clark, 1954; 376, (footnote b)]

Material examined.—Holotype (R = 73 mm, r = 14 mm, R/r = 5.2), MCZ 764, Barbados, *Hassler* Expedition, 183 m.—1 specimen (R = 45 mm, r = 7 mm, R/r = 6.4), Paris Museum EC AS 662, J. Meuleubergh coll., Angola, between Luanda and Novo Redondo, Jan 1966.—1 specimen (R = 26 mm, r = 6 mm, R/r = 4.3), IRCZM 73:022, R/V *Gosnold* Cruise 262, Sta 785, 27°50.0′N, 79°58.3′W to 27°51.0′N, 79°57.5′W, box dredge, 70–90 m, L. Becker, L. Scotto, 13 Aug 1975.—1 specimen (R = 60 mm, r = 13 mm, R/r = 4.6), USNM E18202, Texas A&M Cruise 78-69 III, Dive No. 115, Geyer Bank, northern Gulf of Mexico, 923–122 m, T. Bright, 10 Dec 1978.—1 specimen (R = 60 mm, r = 11 mm, R/r = 5.5), USNM E19196, Texas A&M *Black Seal* Cruise 79, Dive No. 5, West Flower Gardens, Gulf of Mexico, T. Bright, 23 Sep 1979.—1 specimen (R = 73 mm, r =

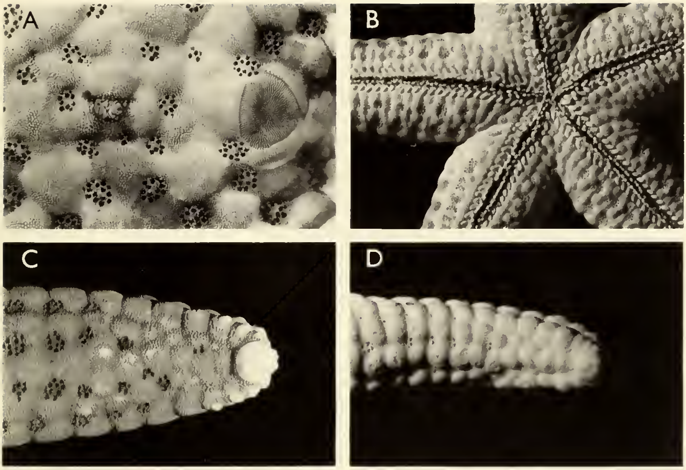

Fig. 5. *Hacelia superba,* A, B, MCZ 4670, R/r = 53 mm/11 mm; A, Disk; B, Mouth and basal part of rays; C, MCZ 4670, R/r = 58 mm/11 mm, distal tip of ray, adult specimen; D, IRCZM 73:022, R/r = 26 mm/6 mm, distal tip of ray, juvenile specimen, note central bare areas on distal carinal plates.

15 mm, R/r = 4.9), USNM E26486, R/V *Eastward* Sta 505, SE of Cape Lookout, North Carolina, 33°48′18″N, 77°34′06″W, 100 m, Wm. Kirby-Smith.—1 specimen (R = 47 mm, r = 12 mm, R/r = 3.9), USNM E26487, R/V *Eastward,* South Carolina Marine Resource Research Institute, SE of Cape Lookout, North Carolina, 33°48′18″N, 76°34′06″W, 100 m, Wm. Kirby-Smith, 14 May 1981.—1 specimen (R = 43 mm, r = 10 mm, R/r = 4.3) USNM E26488, R/V *Eastward,* SE of Cape Lookout, North Carolina, 33°48′42″N, 76°34′30″W, 99 m, Wm. Kirby-Smith, 14 May 1981.—3 specimens (R = 82 mm, r = 15 mm, R/r = 5.5; R = 70 mm, r = 13 mm, R/r = 5.4; R = 68 mm, r = 14 mm, R/r = 4.9), IRCZM 73:227, R/V *Johnson* Cruise J-147, *JSL*-I Dive No. 1266, off Sebastian, Florida, 27°46.2′N,79°58.4′W, coral rubble, 68 m, G. Hendler, 22 Sep 1982.—1 specimen (R = 45 mm, r = 9 mm, R/r = 5.0), BM(NH) 1983.8.18.1, R/V *Johnson* Cruise J-147, *JSL*-I Dive No. 1267, off Sebastian, Florida, 27°46.2′N, 79°58.4′W, coral rubble, 65 m, J. E. Miller, 23 Sep 1982.—2 specimens (R = 58 mm, r = 11 mm, R/r = 5.3; R = 53 mm, r = 11 mm, R/r = 4.8), MCZ 4670, R/V *Johnson* Cruise J-153, *JSL*-I Dive No. 1323, off Sebastian, Florida, 27°46.1′N, 79°58.5′W, coral rubble, 65 m, J. E. Miller, 14 Mar 1983.

Diagnosis.—Actinal surface of rays distinctly flattened; distalmost marginal plates with central bare area; adambulacrals connected to inferomarginals by series of 3 actinolateral plates; 10 rows of large, conspicuous papular areas (8 in specimens with R < 55 mm), with up to 60 papulae per area.

Description.—Disk small, flat; 5 moderately long rays, tapering gently throughout their length, distal tips curved dorsally. Rays distinctly flattened actinally, somewhat triangular in cross section. Oculars prominent, swollen, circular, each carrying 4–5 distinct tubercles often worn smooth in larger specimens. Well-defined circular, square or triangular madreporite with fine, straight to undulating gyri, situated near margin of disk. Anus in contact with central plate, concealed by 10–15 enlarged scales, many with a distinct concavity.

Actinal and abactinal surfaces uniformly covered with dense layer of granules, commonly spherical, becoming polygonal to form mosaic platform on summits of abactinal plates on disk and proximal portion of rays. Distalmost 2–4 (up to 8) marginal plates swollen, with central bare area. Skeletal plates prominent, arranged in regular transverse and longitudinal series. Viewed laterally, transverse series consists of carinal, adradial, superomarginal, inferomarginal, actinolateral (3 rows proximally), adambulacral ossicles. Abactinal and marginal plates quadrilobate, proximal margin overlapping distal margin of adjoining plate. Longitudinal series from carinal to inferomarginal connected by internal ossicles. Three rows of actinolaterals between inferomarginals and adambulacrals. Lowest row with circular to square plates, extending total length of ray. Middle row with reniform plates, extending ⅔ length of ray; these plates angled at 45° to lower row, thus forming arch for passage of papulae. Upper row with subcircular plates, extending ½ length of ray. Each adambulacral plate carries 1 (2 often on proximalmost and distalmost plates) subambulacral spine and 2 furrow spines. Proximally, subambulacral spines short, swollen, truncate. More distally, spines conical, becoming granuliform near distal tip of ray. Furrow spines subequal, laterally compressed, triangular to oval in cross section. Each half jaw bears a single, heavy preoral spine, 3–4 truncate marginal spines and a large inflated, bluntly rounded suboral spine.

Ten rows of papular areas, 2 below inferomarginals. Lowest papular row on each side of ray often lacking or visible as isolated papulae in specimens with $R < 55$ mm. In larger individuals, lowest papular row ending ½ to ⅔ along length of ray. Abactinal and marginal papular areas large, lying in deep depressions formed by elevated surrounding skeletal plates. Number of papulae per area varies considerably with size: $R > 80$ mm, 40–60 papulae per area; $R = 45–60$ mm, 15–1 papulae per area; $R = 26$ mm, 5–7 papulae per area. Papular areas on actinal face with fewer papulae. Individual papulae surrounded by 6–8 elongate granules.

Pedicellariae usually absent; when present, on actinal surface overlying actinolaterals in proximal part of ray. Valves spatulate, situated in deep, elongate alveoli, lying just below surface of surrounding granulation.

In life, disk and proximal part of rays pink to orange, remainder of rays dark red. Some specimens distinctly banded with reddish brown and pink. Madreporite dark orange. Actinal surface white to light tan with red or orange papular areas. Tube feet white. Color fades rapidly in ethanol. Dried, formalin-fixed specimens generally retain natural pigmentation.

Type.—Museum of Comparative Zoology, Harvard University, MCZ 764.

Type locality.—Barbados, *Hassler* Expedition, 183 m.

Distribution.—In the western Atlantic, presently known off North and South Carolina, the east coast of Florida, NW Gulf of Mexico and Barbados, 65–183

m. In the eastern Atlantic, reported from St. Helena (Mortensen 1933) and Angola (Nataf and Cherbonnier 1975, questionable record, see remarks), 40–100 m.

Habitat.—Specimens collected with the *Johnson-Sea-Link* submersible were taken from a deep-water, pinnacle reef found in 85 m off the east central coast of Florida, 27°46.2′N, 79°58.5′W. Covering the east, west and northern slopes of the reef was a thick layer or rubble, remains of the branching scleractinian coral *Oculina varicosa* Lesueur. Scattered about the southern slope were large intact mounds of dead *Oculina.* The reef supported a diverse fauna of fish and invertebrates, especially crustaceans, echinoderms, cnidarians and mollusks. *Hacelia,* although a relatively common component of this fauna, appeared to occur only at 65–70 m on the southern slope of the pinnacle. No specimens were observed near the crest (58 m) or the base (84 m) of the pinnacle nor on any other slope. Additional information on structure and faunal composition of the reef is given in Hendler and Miller (in press).

Discussion.—As in the holotype of *H. superba,* all but one specimen examined have carinal and adradial plates completely covered with granulation and several (up to 8) marginal plates with a central bare area. In the exceptional specimen, R/r = 26 mm/6 mm (smallest specimen examined), 2 distal carinal plates, as well as several marginal plates, have central bare areas (see Fig. 5D). This arrangement is reminiscent of *H. capensis,* from off Natal, originally described as a variety of *H. superba* by Mortensen (1925). Mortensen distinguished his variety of *H. superba* from the western Atlantic *H. superba* on the basis of central bare areas on several radial and lateral plates. The size of the holotype was not stated by Mortensen (1925), but Clark (1974, 1976) reported on a second specimen of *H. capensis* from Natal, R/r = 15 mm/3 mm in which several carinal plates had central bare areas. It is likely that the presence or absence of bare areas on distal carinal or adradial plates is simply a growth character related to age. As *H. superba* has been confirmed from the eastern Atlantic (Mortensen 1933), perhaps *H. capensis* represents nothing more than the young of *H. superba.* Even Mortensen (1933:427) in his description of several specimens of *H. superba* from St. Helena states, "Here and there a single one of the dorsal plates at the end of arm may show a small naked spot." Ironically, Mortensen felt that this finding added further evidence for the validity of his variety *capensis* (here Mortensen inadvertently substituted the name "africana" for "capensis" p. 427).

Considering the numerous pedicellariae found on the small specimen of *H. capensis* examined by Clark (1974), the presence or absence of pedicellariae appears to be an unreliable character in both *H. capensis* and *H. superba.* Mortensen (1925) made no mention of pedicellariae on his type of *H. capensis,* and with the exception of one specimen taken in the northern Gulf of Mexico, none of the western Atlantic specimens of *H. superba* described herein nor the St. Helena specimens described by Mortensen (1933) possess pedicellariae.

Although *H. superba* from the western Atlantic and St. Helena may be conspecific with *H. capensis* from South Africa, combining the species would seem a hasty approach with so little comparative material of *H. capensis* available.

Remarks.—In his species list of the echinoderms from the Gulf of Mexico, Clark (1954:376) included *Ophidiaster alexandri* Verrill, *O. pinguis* H. L. Clark and *Hacelia superba* H. L. Clark as synonyms of *Hacelia floridae* = [*Tamaria* *floridae* (Perrier, 1881)]. Downey (1973:61) reversed Clark's assignment after examining the types of these species and finding them to represent valid species. Further investigation by Downey (in preparation) has shown that the holotype of *D. pinguis* represents a large specimen of *O. alexandri*. During the course of this study, I also had an opportunity to examine the types of *O. alexandri, O. pinguis, H. superba* and *T. floridae,* and I concur with Downey's findings.

A small specimen (R/r = 47 mm/7 mm) of ?*H. superba* from Angola was described by Nataf and Cherbonnier (1975) as possessing 8 rows of papular areas. My examination of this animal has revealed at least three isolated papulae occurring actinally below the row of papular areas adjacent to the inferomarginal series of plates. This condition is what one would expect in a specimen of this size and confirms the genus *Hacelia*. Whether or not this individual is a valid specimen of *H. superba* remains uncertain. The specimen is in poor condition (two rays incomplete, much of the granulation rubbed off, many ambulacral spines broken), but the broad-based rays steadily tapering to a fine tip and the distinctly unequal furrow spines are both characters reminiscent of *H. attenuata* (Gray). In any case, their reassignment (based on a single specimen) of *H. superba* to the genus *Ophidiaster,* a genus in which all species have eight rows of papular areas was unjustified.

Key to the species of Ophidiasteridae from the western Atlantic, Caribbean and Gulf of Mexico
(modified in part from Downey, 1970, 1973)

1\. Primary plates arranged in regular transverse and longitudinal series ... 2
– Primary plates not arranged in regular transverse and longitudinal series ... 11
2\. Papular areas at base of rays in 10 longitudinal series (8 in specimens with R < 55); actinal surface of rays distinctly flattened ... *Hacelia superba* H. L. Clark
– Papular areas at base of rays in 4–8 longitudinal series; actinal surface of rays not distinctly flattened ... 3
3\. Papular areas present on actinal surface below inferomarginals ... 4
– Papular areas absent from actinal surface below inferomarginals ... 9
4\. Skeletal plates covered by distinct skin containing numerous scales or granules; adambulacral plates alternately broad and narrow ... 5
– Skeletal plates covered by fine layer of naked granules, skin not evident; adambulacral plates equal in width ... 6
5\. Carinal series of plates connected to adradial series by 2–3 dorsolateral plates in proximal half of ray; skin covering actinal interradial area lacking scales or granules ... *Copidaster schismochilus* (H. L. Clark), new combination
– Carinal series connected to adradial series by single internal plate in proximal half of ray; skin covering actinal interradial area containing scales or granules ... *Copidaster lymani* H. L. Clark
6\. Pedicellariae present ... 7
– Pedicellariae absent ... 8

7\. Valves of pedicellariae sickle-shaped, most numerous on abactinal surface .... *Ophidiaster bullisi*[1] (Downey)
– Valves of pedicellariae sugar-tong shaped, most numerous on actinal surface .... *Ophidiaster alexandri* Verrill
8\. Adambulacral series armed with single row of subambulacral spines .... *Ophidiaster guildingi* Gray
– Adambulacral series armed with double row of subambulacral spines .... *Ophidiaster bayeri* A. H. Clark
9\. Rays short (R/r < 3.0), subpetaloid .... *Tamaria passiflora* Downey
– Rays long (R/r > 3.5), tapering 10
10\. Papular areas with average of 3–4 papulae; oculars small, inconspicuous .... *Tamaria floridae* (Perrier)
– Papular areas with average of 7–8 papulae; oculars large, conspicuous .... *Tamaria halperni* Downey
11\. Rays triangular in cross section; papulae isolated, scattered .... *Narcissia trigonaria* Sladen
– Rays circular in cross section, papulae grouped 12
12\. Large, swollen plates scattered randomly on rays and disk; madreporite single .... *Linckia nodosa* Perrier
– Large, swollen plates absent, frequently 2 madreporites present .... *Linckia guildingi* Gray

Acknowledgments

I wish to express my gratitude to Dr. David L. Pawson, National Museum of Natural History (NMNH), for the use of his research facilities during several visits to the Smithsonian Institution and for subsidizing my trip to Carrie Bow Cay, through a grant from the Smithsonian Marine Station at Link Port (SMSLP). The successful completion of this study would have been impossible without the help of Miss Maureen Downey, NMNH, who initiated specimen loans, offered her time for consultation and allowed me reference to a manuscript in preparation. I thank Dr. G. Hendler, Smithsonian Oceanographic Sorting Center, for collecting, photographing and observing live material at Carrie Bow Cay. Loans of specimens from other institutions were made possible through Miss Ailsa M. Clark, British Museum (Natural History), Dr. Robert M. Wollacott and Miss Mary Sue Brancato, Museum of Comparative Zoology, Harvard University and Dr. Alain Guille, Muséum National d'Histoire Naturelle, Paris. Special thanks are extended to the crews of R/V *Johnson* and Research Submersible *Johnson-Sea-Link* for their efforts on my behalf. Mr. Tom A. Smoyer, Harbor Branch Foundation, Inc. (HBF) and Miss Julie Piraino, SMSLP, provided assistance with photography. Several

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[1] In describing the genus *Drachmaster,* type-species *D. bullisi,* Downey (1970) characterized *Drachmaster* by the presence of internal connecting ossicles which were believed to be absent from other genera in the family Ophidiasteridae. Her further examination has shown that many ophidiasterid genera possess internal connecting ossicles. Accordingly Downey (in preparation) has referred *Drachmaster* to synonymy with *Ophidiaster* and her new combination *O. bullisi* is accepted herein.

constructive comments by Miss Downey, Dr. Pawson and Dr. Richard L. Turner, Florida Institute of Technology, improved the manuscript. The manuscript was typed and edited by Mrs. Adrienne Gesimondo, HBF. This paper represents contribution No. 353 from Harbor Branch Foundation, Inc. and contribution No. 132 from Investigations of Marine Shallow-Water Ecosystems Program (IMSWE), Reef and Mangrove Study—Belize, Smithsonian Institution, partly supported by the Exxon Corporation. I am grateful to Dr. Klaus Rützler, Coordinator of IMSWE, for his cooperation and support.

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FRESHWATER TRICLADS (TURBELLARIA) OF NORTH AMERICA. XV. TWO NEW SUBTERRANEAN SPECIES FROM THE APPALACHIAN REGION

Roman Kenk

Abstract.—*Phagocata procera* n. sp. from a cave in Jackson County, North Carolina, and *Sphalloplana hypogea* n. sp. from outlets of tile drains in Isle of Wight County, Virginia, are described. They differ from related species chiefly by the anatomy of their reproductive systems.

Several active speleologists have taken the trouble of sending me living specimens of triclads or planarians collected in their explorations of subterranean habitats. This is of particular importance in the case of triclads, as it is very difficult to preserve these worms properly in the field and impossible to preserve the often characteristic shape of the quietly gliding animals. I wish to thank Dr. Cato O. Holler, Jr. of the North Carolina Cave Survey, Old Fort, North Carolina, and Dr. John R. Holsinger of Old Dominion University, Norfolk, Virginia, for their thoughtful collaboration in the study of these little known animals. Thanks are due also to Dr. John C. Harshbarger, in whose laboratory the photographs were prepared, and to Dr. Marian H. Pettibone who kindly reviewed the manuscript.

The planarians were preserved with a hot solution of mercuric chloride ($HgCl_2$) and the sections stained with Ehrlich's acid hematoxylin and Eosin-Phloxine B.

The type-material is deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Family Planariidae

Genus *Phagocata* Leidy, 1847

Phagocata procera, new species

Type-material.—Holotype, set of sagittal sections on six slides, USNM 81294; five paratypes, sagittal and transverse sections on 23 slides, USNM 81295-81299.

External features (Fig. 1A).—This is an exceedingly slender species, mature specimens measuring up to 17 mm in length and about 1 mm in width. The species is unpigmented (white) and blind. The anterior end is truncate, with a rather straight frontal margin and a pair of pointed auricular projections extending anterolaterally. Behind the anterior end the body widens gradually and soon reaches its maximum width which is maintained for the greater part of the body length. Behind the copulatory apparatus, the body narrows and terminates in a bluntly pointed posterior end.

The pharynx, measuring about ⅙ of the body length, is inserted slightly behind the middle of the body. The copulatory apparatus is visible in living specimens as a transparent elongated area situated at about the middle of the postpharyngeal region. The intestinal area begins a certain distance from the anterior end. The branches of the intestine could be demonstrated by feeding the worms a mixture

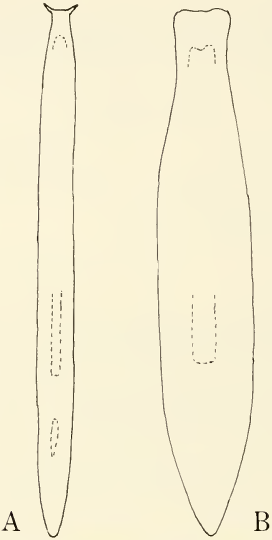

Fig. 1. Outline drawings of living planarians, indicating locations of pharynx and anterior intestinal border, ×6. A, *Phagocata procera*; B, *Sphalloplana hypogea*.

of liver tissue and carbon powder. The anterior intestinal trunk bears 17–22 pairs of lateral branches and each of the posterior trunks 25–29 rather short lateral diverticula.

Anatomy.—The anterior end has no special adhesive organ. The marginal adhesive zone is normally developed and seems to surround the anterior end without interruption.

In the reproductive system, the ovaries are located behind or below the fourth pair of the anterior intestinal branches. The testes (Fig. 2) are ventral, arranged on either side of the midline in a narrow longitudinal zone beginning posterior to the ovaries and ending at the level of the pharyngeal root. In transverse sections only one or two testes are seen in each zone.

The copulatory apparatus (Fig. 3) is situated a certain distance behind the pharyngeal pouch. The genital opening or gonopore (*gp*) leads into the atrial cavities: posteriorly the common atrium (*ac*) and anteriorly the male atrium (*am*). The penis has a rather small bulb (*bp*) and a large, finger-shaped papilla (*pp*). The penial lumen is rather wide in the bulb, forming the seminal vesicle (*vs*), narrows toward the papilla as an ejaculatory duct (*de*), and widens again near its outlet on the dorsal side of the papilla. A rather large, rounded protuberance projects into the seminal vesicle from the dorsal side. The lining of the lumen in the bulb and the basal part of the papilla consists of a rather tall glandular epithelium,

Fig. 2. *Phagocata procera,* sagittal section of prepharyngeal region, × 190. *in,* intestinal branch; *te,* testis; *vd,* vas deferens.

while in the distal part of the lumen (*de*) the epithelum is cuboidal. Many gland ducts with a granular, slightly bluish secretion penetrate the bulb from the surrounding mesenchyme and open into the penis lumen through the tall epithelium. The sperm ducts or vasa deferentia (*vd*), after forming the enlarged spermiductal vesicles, ascend at the level of the penis bulb, enter the bulb dorsolaterally or laterally, and open into the anterior end of the penial lumen separately, but close together.

The common oviduct (*odc*) enters the atrial cavity from the dorsal side at the boundary between the male and common atria. The copulatory bursa (*b*) shows no peculiarities. Its outlet, the bursal stalk or duct (*bd*) runs as a narrow canal along the dorsal side of the penis, then gradually widens, becomes more convoluted, and acquires a very thick muscle coat of intermingled circular and longitudinal fibers. This portion of the duct may properly be called a vagina (*va*).

The copulatory complex has no infranucleate epithelia.

Distribution and ecology.—Phagocata procera was collected by Dr. Cato O. Holler, Jr. and his son in two pools from a seep in Cat Den Cave, near the community of Tuckaseigee in Jackson County, North Carolina, on 8 August 1982. Seven specimens were sent to me alive, but all proved to be immature. They were placed in a culture dish, kept at 14°C, and fed beef liver once a week until they matured after several months.

Taxonomic position.—Phagocata procera belongs to a group of Appalachian

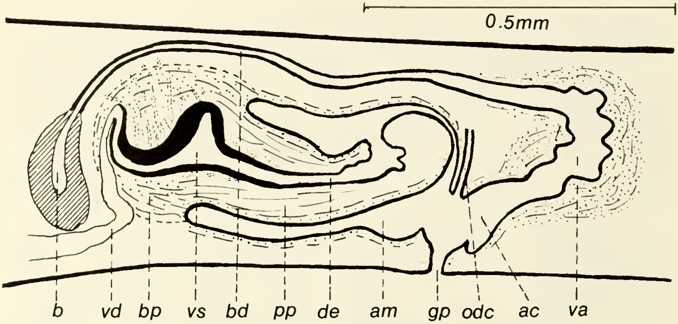

Fig. 3. *Phagocata procera*, semidiagrammatic view of copulatory apparatus in sagittal section. *ac*, common atrium; *am*, male atrium; *b*, copulatory bursa; *bd*, bursal duct; *bp*, penis bulb; *de*, ejaculatory duct; *gp*, gonopore; *odc*, common oviduct; *pp*, penis papilla; *va*, vagina; *vd*, vas deferens; *vs*, seminal vesicle.

species characterized by prepharyngeal testes, lack of pigmentation, partial or total reduction of the eyes, and a tendency to subterranean occurrence (*P. bursaperforata* Darlington, 1959; *P. angusta* Kenk, 1977b; *P. holleri* Kenk, 1979a; *P. carolinensis* Kenk, 1979b; and several still undescribed species). This group bears a great similarity to several European species frequently assigned to the genus *Atrioplanaria*. Whether or not there is a phyletic relationship between these two groups, will have to be considered from additional evidence such as possibly by a karyological or a biochemical relationship. *Phagocata procera* differs from all the related members by the dorsal opening of the penis lumen on the penial papilla and by the extraordinary development of the highly muscular vagina. It is also the most slender species of the genus as far as we know.

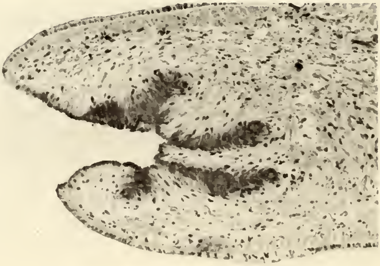

Fig. 4. *Sphalloplana hypogea*, adhesive organ in sagittal section, ×109.

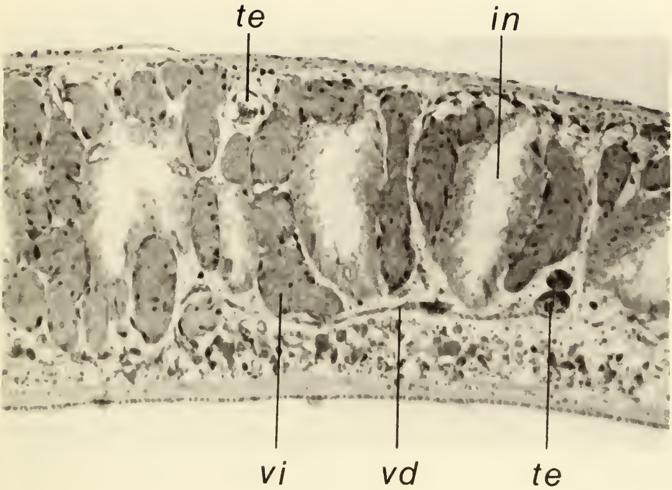

Fig. 5. *Sphalloplana hypogea,* sagittal section of prepharyngeal region, × 108. *in,* intestinal branch; *te,* testis; *vd,* vas deferens; *vi,* vitellarium.

The specific name, *procera* (Latin, slender), refers to the general shape of the species.

Family Kenkiidae
Genus *Sphalloplana* Beauchamp, 1931
Subgenus *Speophila* Hyman, 1937
Sphalloplana (*Speophila*) *hypogea,* new species

Type-material.—Holotype, set of sagittal sections on eight slides, USNM 81300; paratype, set of sagittal sections on thirteen slides, USNM 81301.

External features (Fig. 1B).—Of the seven available specimens, two were sexually mature. The largest specimen measured 17 mm in length and 3 mm in width. The anterior end is truncate, with a slight incurving in the mid-portion of the frontal margin and with rounded, only slightly protruding lateral edges, lacking distinct auricular extensions. The anterior border of the intestinal area shows a slight indentation, as is characteristic of the species of the genus that have a well-developed adhesive organ. The root of the pharynx is situated at about the middle of the body and its length amounts to ⅐ to ⅛ the length of the body.

Anatomy.—The lateral margins of the body have a thickened epithelium underlaid by densely-packed rhabdite glands, as is typical for the family Kenkiidae. The adhesive gland (Fig. 4) is well developed and consists of a deeply invaginated depression that branches into several distinct pockets, rather than a folded pit

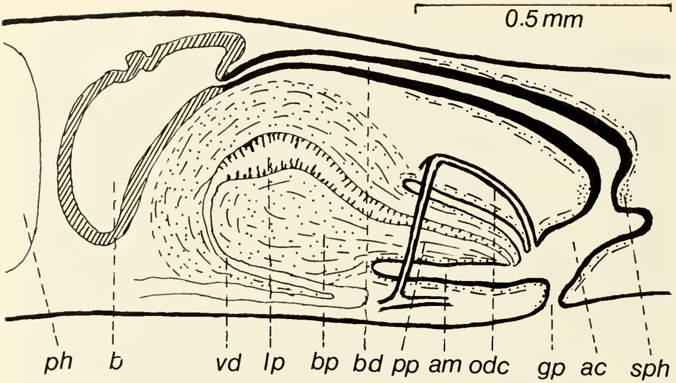

Fig. 6. *Sphalloplana hypogea,* semidiagrammatic view of copulatory apparatus in sagittal section. *ac,* common atrium; *am,* male atrium; *b,* copulatory bursa; *bd,* bursal duct; *bp,* penis bulb; *gp,* gonopore; *lp,* penis lumen; *odc,* common oviduct; *ph,* pharyngeal pouch; *pp,* penis papilla; *sph,* sphincter; *vd,* vas deferens.

that is usually seen in the subgenus *Speophila* (cf. Mitchell 1968). The internal pharyngeal musculature consists of two separate layers, an internal layer of circular fibers surrounded by a layer of longitudinal muscles.

The two ovaries are situated on the medial sides of the ventral nerve cords at the level behind the fourth lateral branches of the anterior intestinal trunk. There are no parovaria developed. The oviducts or ovovitelline ducts proceed along the upper side of the nerve cords. The testes (Fig. 5, *te*) are very small and not numerous, scattered in the dorsal, ventral, and intermediate portions of the mesenchyme. They do not form a compact zone as is usually the case, but appear on either side of the midline individually between the intestinal branches and the amply developed vitellaria (*vi*) in the region between the ovaries and the pharyngeal root. The ventral testes may be atached directly to the anterior sperm ducts or vasa deferentia (*vd*) that run somewhat medially along the oviducts, while the dorsal ones connect with the sperm ducts by vertical efferent ductules. In the region of the pharynx the sperm ducts enlarge to form the spermiductal vesicles (or false seminal vesicles).

The copulatory apparatus (Fig. 6) occupies the anterior half of the postpharyngeal region. The gonopore (*gp*) leads into a small common atrium (*ac*) that connects dorsally with the bursal duct (*bd*) and anteriorly with the male atrium (*am*). The penis is rather large, with a rounded, highly muscular bulb (*bp*) and a conical or finger-shaped papilla (*pp*). The penis lumen (*lp*) is elongate, starting in the bulb as a rather wide cavity and proceeding toward the papilla, gradually narrowing, and finally opening at the tip of the papilla. The lining of the lumen consists of an epithelium that projects numerous villus-like extensions into the cavity. The widened lumen in the bulb apparently corresponds to a seminal vesicle and the narrowed duct in the papilla to an ejaculatory duct, although there is no histological difference between the linings of these two parts.

The two vasa deferentia (*vd*), after forming a small posterior loop, enter the penis bulb ventrolaterally, proceed in a curve upward and toward the midline, and open into the anterior end of the penis lumen separately, but close together.

At the level of the male atrium, each oviduct sends a branch of variable length (160 to 550 μm) posteriorly toward the vitellaria of the tail end of the body, while the principal oviduct ascends dorsally and unites with the duct of the opposite side. The common oviduct (*odc*) curves ventrally and opens at the junction of the male and common atria. The ascending oviducts and the common oviduct receive the outlets of numerous eosinophilic glands, the shell glands.

The copulatory bursa (*b*) is rather large and is situated immediately posterior to the pharyngeal pouch (*ph*). Its outlet, the bursal duct (*bd*). gradually widens posteriorly and acquires a thicker muscle coat consisting of intermingled circular and longitudinal fibers. Just before it joins the common atrium, it is surrounded by a strong sphincter (*sph*).

None of the epithelia of the copulatory apparatus are infranucleate.

Distribution and ecology.—Sphalloplana hypogea was collected by Dr. John R. Holsinger in two drain-tile outlets on the farm of Robert Taylor in Isle of Wight County (3.5 miles north of Chuckatuck, Nansemond County), Virginia, on 27 March and 24 April 1983. The tiles, about five feet beneath ground, drain a large pasture field. It appears, therefore, that the natural habitat of the species is groundwater. A total of seven specimens were sent to me alive, two of which proved to be sexually mature.

Taxonomic position.—The well-developed adhesive organ places the species in the subgenus *Speophila*. The most outstanding specific characters, apart from the configuration of the copulatory complex, are the modification of the adhesive organ, the arrangement of the testes, and the presence of a sphincter on the bursal duct. Compared to the other American species of the subgenus (see Kenk 1977a), the principal differences are the following: *S. virginiana* has ventral testes; *S. holsingeri* has the ejaculatory duct opening on the dorsal surface of the penis papilla; *S. pricei* and *S. hubrichti,* possibly the nearest relatives, have the penial lumen divided into two histologically different sections; *S. weingartneri* differs chiefly by having the penis bulb very large and the penis papilla greatly reduced; *S. buchanani* and *S. chandleri* have the testes confined to the dorsal side; and *S. mohri* is a polypharyngeal species. They all lack the sphincter on the bursal duct.

The specific name *hypogea* (from the Greek *hypogeios,* subterranean) refers to the occurrence of the species in groundwater.

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A NEW COMMENSAL OSTRACOD OF THE GENUS *MICROSYSSITRIA* FROM SOUTH AFRICA (OSTRACODA: ENTOCYTHERIDAE: MICROSYSSITRIINAE)

C. W. Hart, Jr. and Janice Clark

Abstract.—A new species of entocytherid ostracod, *Microsyssitria nhlabane,* is described from the wood-boring isopod *Sphaeroma terebrans* collected from Lake Nhlabane, South Africa. The new species is compared with the closely related *M. indica* from India, and the diagnosis of the subfamily Microsyssitriinae is emended.

In 1967, Hart, Nair, and Hart described *Microsyssitria indica,* the first entocytherid ostracod known to be commensal on the wood-boring isopod *Sphaeroma terebrans* Bate, 1866. The isopod hosts were collected from two estuarine locations in Kerala State, India, and their commensal ostracods were placed in a new genus and a new subfamily, the Microsyssitriinae. Recently, a second species was found associated with *S. terebrans* collected by P. E. Reavell from submerged logs in Lake Nhlabane, north of Richard's Bay, South Africa. The isopods were identified by Dr. Brian Kensley, who noted the presence of the commensal ostracods and gave them to us for identification.

This new species, described below, is sufficiently different from *M. indica* to necessitate emendations to the diagnosis of the subfamily.

Microsyssitriinae

Diagnosis (emended).—A subfamily of the family Entocytheridae. Antennule with 5 podomeres. Dorsal antennal claw spiculiform, with or without setae on flexor face. Mandibular protopodite with distal row of 5 multicuspid teeth. Peniferum terminating in 1 or 2 movable claws. Penis straight, vertically oriented, and situated in distal portion of peniferum. Commensal on wood-borng isopods in Indian and South African waters.

Type-genus.—*Microsyssitria* Hart, Nair, and Hart, 1967.

Microsyssitria nhlabane, new species
Figs. 1–10

Male.—Shell (Fig. 1) subelliptical in outline with eyespot situated approximately ⅕ shell length from anterior end. Shell margin of adult specimens with very slight concavity posterodorsally (Fig. 1). Antennal gland conspicuous, situated posterior to eyespot. Measurements of 3 adult males range from 330 to 350 μm in length (average, 340 μm); from 200 to 220 μm in height (average, 210 μm).

Antennule (Fig. 2) composed of 5 podomeres, antipenultimate subequal in length to basal. Antipenultimate podomere with 2 setae at midlength extending almost to base of ultimate podomere, and 4 apical setae extending past distal extremity of ultimate podomere. Penultimate podomere devoid of setae. Ultimate

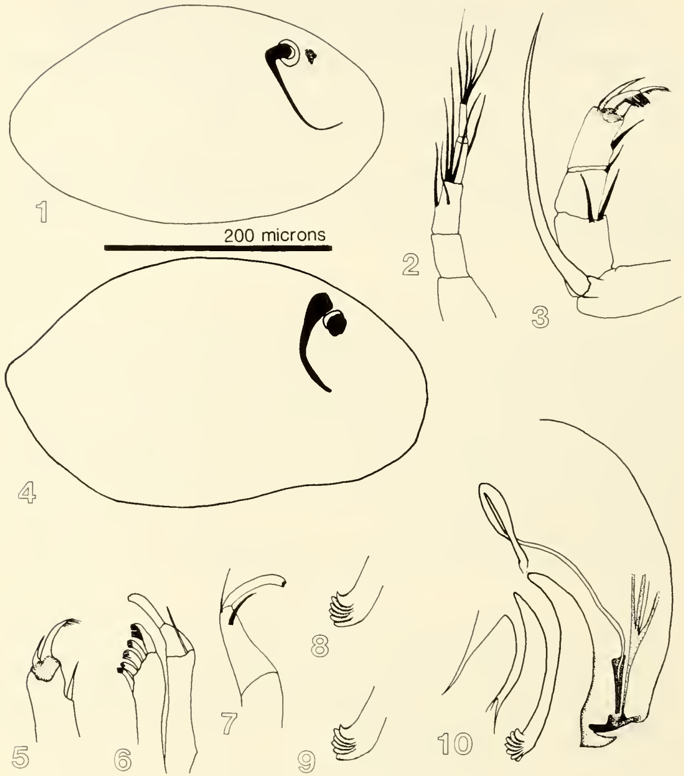

Fig. 1–10. *Microsyssitrinae nhlabane,* 1, Adult male (showing position of eyespot and antennal gland, posterior to it); 2, Antennule; 3, Antenna of male; 4, Adult female (showing position of eyespot and antennal gland, posterior to it); 5, Terminal portion of antenna of adult female; 6, Mandible of male; 7, Maxilla of male; 8–9, Terminal portions of clasping apparatus showing dentition variations; 10, Copulatory apparatus. Scale refers to Figs. 1 and 4.

podomere bearing 5 apical setae subequal in length to combined ultimate and penultimate podomeres.

Antenna (Fig. 3) consisting of 4 podomeres (see Discussion, below). Basal podomere devoid of setae, and with exopodite, or "flagellum," extending from its distolateral extensor margin beyond terminal claws. Second, or antipenultimate, podomere bearing 2 setae of subequal length on its distal flexor margin, both setae reaching approximately to base of ultimate podomere. Penultimate podomere, distinguishable from ultimate podomere by suture visible only in adult specimens,

Table 1.—Comparisons of certain adult features of *M. nhlabane* with those of *M. indica.*

	M. indica	*M. nhlabane*
Size (male, length)		
Range	380–420 μm	330–350 μm
Average	395 μm	340 μm
Size (female, length)		
Range	360–420 μm	370–380 μm
Average	391 μm	373 μm
Peniferum	2 terminal claws	1 terminal claw
Clasping apparatus	Reaching distinctly beyond ventral end of peniferum	Reaching little, if any, beyond ventral end of peniferum
Dorsal antennal claw	With setae	Without setae

bearing single seta on distal flexor margin. Ultimate podomere with 1 short seta at midlength of flexor margin, and 3 terminal claws. Dorsal claw subspiculiform, slightly curved, without setae; mesial claw short, thick, and bearing row of setae along distal ½ of length; ventral claw almost twice length of mesial claw, curved, and bearing row of setae along distal ½ of length.

Protopodite of mandible (Fig. 6) with distal row of 5 teeth. Cusps present but indistinct. Podomeres of mandibular palp not clearly defined. Single seta present adjacent to base of rounded spatulate terminal spine of palp. Latter concave on ventral surface.

Maxilla (Fig. 7) with 2 setae and unsegmented palp. Setae extending to midlength of palp, the latter terminating in row of indistinct cusps. Protopodite, or masticatory lobes, apparently absent.

Copulatory complex (Figs. 8, 9, 10) with ventral portion of peniferum terminating in single movable claw opposing recurved blade-like anterior protuberance; claw apparently controlled by muscle originating in midlength of peniferum. Penis straight, well developed, and terminating proximal to movable claw. Mid-portion of peniferum tapering distally. Clasping apparatus ending slightly distal to terminal portion of peniferum, curved slightly throughout length, and terminating in 6 or 7 denticles. Dorsal and ventral fingers present; ventral finger almost reaching ventral extremity of peniferum, terminating in 2 or 3 spinous processes; dorsal finger tapering, simple.

Female.—Shell of presumably adult female (Fig. 4) slightly larger than that of male; well defined concavities posterodorsally and anteroventrally. Antennal gland conspicuous, situated posterior to eyespot. Measurements of three female specimens range from 370 to 380 μm in length (average, 373 μm); 230 to 240 μm in height (average, 230 μm).

Discussion.—With regard to segmentation of the antenna, some ostracodologists prefer to think of the antenna as having 5 podomeres—the ultimate podomere being the somewhat amorphous-appearing area serving as the base of the terminal claws. For purposes of our description, we consider the anntenna to have only 4 podomeres, the basal attachments of the terminal claws being merely the distal end of the 4th podomere.

The uncertainty expressed above concerning whether or not the female specimens represent adults lies in the fact that all previously reported adult female entocytherids possess 3 terminal antennal claws, whereas specimens of *M. nhlabane,* that with respect to size appear to be adults, possess but 2 (Fig. 5).

Relationships.—This ostracod has its closest affinities with *Microsyssitria indica,* differing from it primarily in size, the length of the clasping apparatus, the number of peniferal claws, and the setation of the dorsal antennal claw (see Table 1).

Type-locality.—Lake Nhlabane, north of Richard's Bay, South Africa (32°16'E, 28°36'S). The species is at present known only as a commensal of *Sphaeroma terebrans* collected from submerged logs at the type-locality.

Etymology.—Named for the type-locality, Lake Nhlabane, and used as a noun in apposition.

Disposition of types.—The holotypic male, USNM 195110, allotypic female, USNM 195111, and a series of paratypes, USNM 195112 are deposited in the National Museum of Natural History, Smithsonian Institution.

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BOMOLOCHUS PAUCUS, A NEW SPECIES OF COPEPOD PARASITIC ON SCIAENID FISHES FROM SOUTHERN CALIFORNIA

Roger F. Cressey and Masahiro Dojiri

Abstract.—A new species of bomolochid copepod, *Bomolochus paucus*, from California sciaenid fishes differs from all other *Bomolochus* species by the combination of bearing 5 setae on the last exopod segment of leg 4, spinules on the ventral surface of the last abdominal segment only, and the endopod of leg 4 only slightly longer than the exopod.

As part of a general survey of copepods parasitic on fishes occurring at the Orange County sewer outfall, California, one of us (MD) examined 237 white croaker *Genyonemus lineatus* (Ayres) and 97 queenfish *Seriphus politus* Ayres. A new species of parasitic copepod (Bomolochidae) was collected from these sciaenid fishes, and is described below.

A low incidence and intensity of infestation is indicated as only 1 queenfish and 8 white croakers were infested.

Type specimens have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

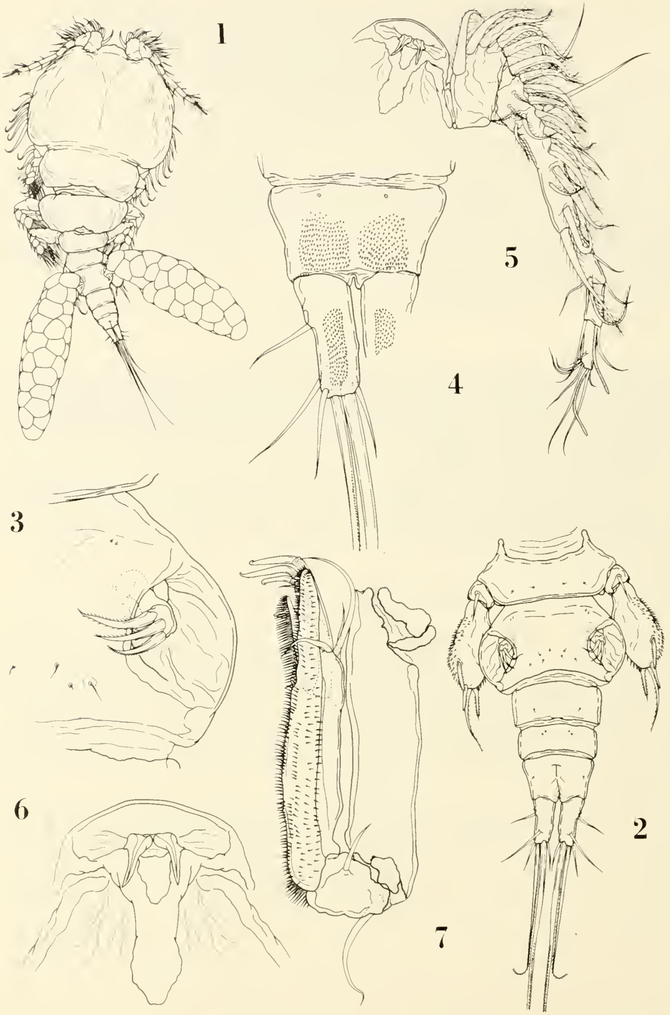
Bomolochus paucus, new species

Figs. 1–21

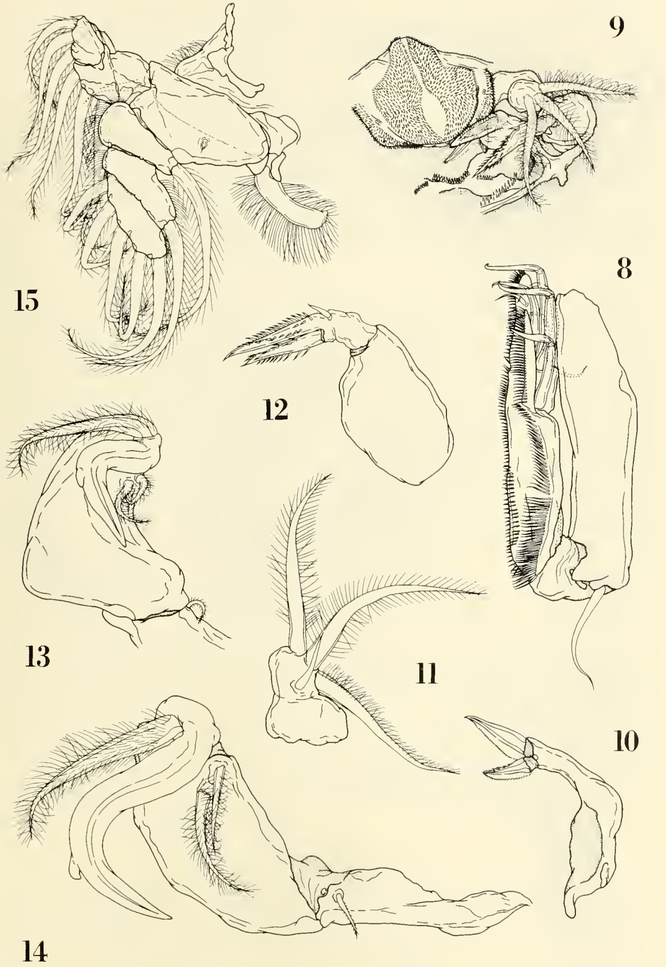
Material examined.—From the white croaker *Genyonemus lineatus* (Ayres): Holotype female (USNM 210491) from station T0 (33°37′N, 117°59′W), 7 Apr 1976. Four paratype females (USNM 210492) from station T0 and T3 (33°34′N, 117°58′W), 7 Apr 1976. Additional specimens consisting of 1 female cephalothorax and 1 immature female from station T0; 1 immature male from station T3; and 1 nonovigerous female from the queenfish, *Seriphus politus* Ayres from station T0.

Description.—Female: Body form as in Fig. 1. Total length 1.11 mm (0.99–1.21 mm), greatest width 0.59 mm, (0.55–0.64 mm). Cephalothorax wider than long (479 × 611 μm) comprising about 40% of total body length. Thoracic segments bearing legs 2–5 free, first 2 segments nearly equal in width (anteriormost slightly wider). Genital segment (Fig. 2) wider than long (124 × 175 μm), 3 setae of leg 6 short, not extending to margins of segment (see Figs. 2–3). Abdomen 3—segmented, (Fig. 2) segments measure 55 × 115 μm, 41 × 104 μm, 53 × 94 μm (l × w) respectively. Ventral surface of abdomen and caudal rami with spinules (see Fig. 4). Caudal rami longer than wide (55 × 26 μm) bearing 2 major setae and 4 minor setae, both major setae with spinules along inner margin, longest seta 432 μm long.

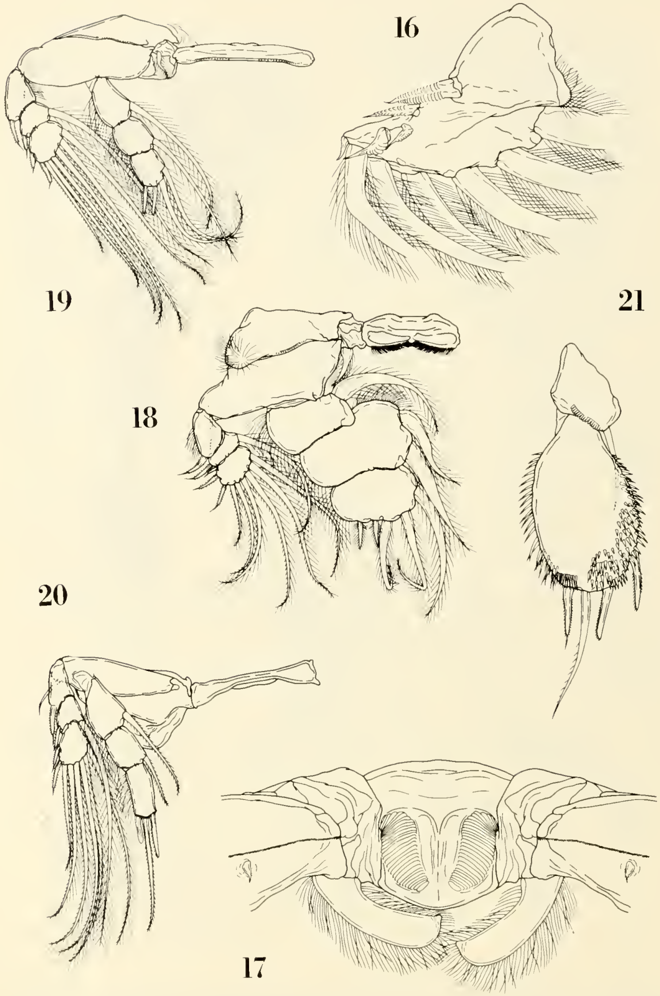
First antenna (Fig. 5) 5-segmented ventrally (second segment appears 3-seg-



Figs. 1–7. *Bomolochus paucus,* new species, female: 1, Dorsal; 2, Thoracic segment bearing leg 5, genital complex, abdomen, caudal rami, dorsal; 3, Genital area, dorsal; 4, Last abdominal segment and caudal rami, ventral; 5, First antenna, ventral; 6, Rostral area, ventral; 7, Second antenna, inner.



Figs. 8–15. *Bomolochus paucus,* new species, female: 8, Second antenna, outer; 9, Oral area, ventral; 10, Mandible, antero-inner; 11, First maxilla, postero-outer; 12, Second maxilla, anteroventral; 13, Maxilliped, ventral; 14, Maxilliped, ventral; 15, Leg 1, ventral.



Figs. 16–21. *Bomolochus paucus,* new species, female: 16, Leg 1 exopod, dorsal; 17, Leg 1 interpodal plate, ventral; 18, Leg 2, ventral; 19, Leg 3, ventral; 20, Leg 4, ventral; 21, Leg 5, ventral.

mented dorsally), fourth seta of first segment somewhat recurved in manner of congeners, setal formula 5, 23 (or 15, 4, 4), 4, 2 + 1 aesthete, and 7 + 1 aesthete. Rostral area between bases of first antenna with ventral hooks (Fig. 6). Second antenna (Figs. 7–8) with last segment bearing indiscrete rows of sparsely spaced spinules, 4 terminal articulated spines bent at nearly right angles, and 4 setae. Labrum (Fig. 9) with patches of spinules as in figure. Mandible (Fig. 10) with 2 short terminal blades; longer blade serrated along posterior margin, shorter blade with serrations on anterior margin and finer serrations along posterior margin. First maxilla (Fig. 11) with 3 stout plumose setae, nearly equal in length, and short naked seta. Second maxilla (Fig. 12) with 2 terminal spinose processes and short naked subterminal seta. Maxilliped (Figs. 13–14) with heavily sclerotized recurved claw bearing a short, blunt accessory process; claw bent at nearly right angle.

Legs 1–4 biramous. Leg 1 (Fig. 15) typical of genus; exopod segments bearing modified spines at outer corners of segments as in Fig. 16, interpodal plate (Fig. 17) with padlike surface; inner coxopodal seta spatulate. Leg 2 (Fig. 18) coxopod with cluster of long hairs at distal outer corner; exopod relatively small; endopod segments much wider than long, midsegment bearing 2 inner setae. Leg 3 (Fig. 19) rami about equal in size, midendopod segment with 1 seta. Leg 4 (Fig. 20) similar to leg 3, endopod only slightly longer than exopod, last endopod segment bearing blunt spine at outer corner, terminal spinulose seta, and inner bladelike spine. Leg 5 (Fig. 21) basal segment with posterior row of spatulate spinules and outer seta; second segment with patches of heavy spinules as in figure, 1 outer subterminal spine, terminal seta flanked by 2 shorter spines, innermost with terminal flagellum; 3 spines of about equal length. Leg 6 (see Fig. 3) represented by 3 setae at area of egg sac attachment.

Etymology.—The specific name *paucus* is Latin for "few," alluding to the extremely low incidence and intensity of infestation.

Discussion.—The new species can be distinguished from all known species of *Bomolochus* except *B. soleae* Claus, *B. multiceros* Pillai, and *B. unicirrus* Brian by the presence of 5 setae on the last exopod segment of leg 4 of the female (all other species have 4). It can be distinguished from *B. multiceros* and *B. unicirrus* as these 2 species possess an elongated endopod of leg 4 of the female (nearly twice length of exopod). It can be easily separated from *B. soleae* as the ventral surfaces of all 3 abdominal segments of *B. soleae* bear patches of spinules (pers. obs.). This condition is uncommon in bomolochids (spinules, when present, usually only on last segment).

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A NEW SCALE-WORM COMMENSAL WITH DEEP-SEA MUSSELS ON THE GALAPAGOS HYDROTHERMAL VENT (POLYCHAETA: POLYNOIDAE)

Marian H. Pettibone

Abstract.—Some polynoid polychaetes, found living commensally in mantle cavities of deep-sea mussels on the Galapagos Rift vent area, are described as a new genus and new species, *Branchipolynoe symmytilida,* and referred to the new subfamily Branchipolynoinae. They are unusual in having well-developed arborescent branchiae. A series of young, juveniles, and adults allows observation of their growth stages.

Among unusual animals discovered in submarine hydrothermal vents on the Galapagos Rift and collected by the submersible *Alvin* is a polynoid scale-worm found living commensally in mantle cavities of the giant deep-sea vent mussels. This association was noted earlier by Grassle *et al.* (1979:7) and Turner (1981: 5). According to this group, the abundant mussels found in the vicinity of active vents were hosts for the polynoid polychaetes. At some vents, almost all the mussels contained a polynoid symbiont in the mantle cavity, whereas at other vents they were rarely found; usually a large and small specimen were found together. Mussels with the polynoid commensals were collected on three vent areas: the Mussel Bed, named for the abundant mytilid bivalves, the Garden of Eden, named for its numerous and interesting forms, and the Rose Garden, named for the dense beds of red-tipped vestimentiferan worms living in white tubes (*Riftia pachyptila* Jones). The polynoids were observed leaving their hosts when the mussels were disturbed by the *Alvin* manipulator (Ballard and Grassle 1979: 600). On videotape, the blood-red polynoids can be seen leaving their hosts, swimming freely, scurrying about and hiding among the clusters of mussels. According to Dr. Vida C. Kenk (in litt.), who is describing the mussels, about one-third of the preserved specimens she examined contained a polynoid in the mantle cavity, usually in the posterior region. Gills of the mussels containing the polynoids were often thickened and uneven, possibly due to disturbance by the worms.

For the present study, specimens available were collected during 14 dives of the *Alvin* in 1979 (January–February, November–December) to about 2500 meters depth (2447–2495). Most of the polynoids were removed from the mussels by Isabelle Williams of the Woods Hole Oceanography Institution (WHOI). In addition, soft parts of five mussels with the polynoid commensals still in place in the mantle cavities were made available. Additional specimens of the same species, including many small ones, were separated from partially sorted mussel washings, washings from a clam box with mussels, rubble residue, and vestimentiferan washings from the Galapagos area.

Types and additional specimens are deposited in collections of the Department of Invertebrate Zoology, Smithsonian Institution (USNM).

Branchipolynoinae, new subfamily

Branchipolynoe, new genus

Type-species.—*Branchipolynoe symmytilida,* new species.

Gender.—feminine.

Diagnosis.—Body short, flattened, spindle-shaped, segments 21, first achaetous. Elytra and elytrophores, 10 pairs on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 and 19. Dorsal cirri on non-elytra-bearing segments with short cirrophores and short styles. Dorsal tubercles on cirrigerous segments indistinct. Branchiae well developed, arborescent, on all parapodia from segment 2. Prostomium bilobed, subtriangular anterior lobes bearing minute frontal filaments; with short median antenna and pair of short palps; without lateral antennae and eyes. First or tentacular segment fused to prostomium, visible dorsally as short ring, achaetous; stout tentaculophores lateral to prostomium with 2 pairs of short tentacular cirri; without facial tubercle. Second or buccal segment with first pair of elytra and short ventral buccal cirri. Parapodia subbiramous. Notopodia small, with few short acicular notosetae. Neuropodia short, truncate, without projecting acicular lobes; with very numerous neurosetae including upper stout, slightly hooked ones separated by partition from very numerous slender ones. Ventral cirri short. Pygidium with pair of short anal cirri. Pharynx with 5 pairs of papillae and 2 pairs of jaws. Enlarged ventral papillae on segments 11 and 12. Commensal with mussels on deep-sea thermal vents.

Etymology.—*Branchia,* gills, plus *polynoe,* polynoid worm, (from genus *Polynoe*); referring to the characteristic gills on the polynoid worm.

Branchipolynoe symmytilida, new species
Figs. 1–8

Material.—East central Pacific, from dives of the *Alvin* on 3 vent areas along the Galapagos Rift in 1979, associated with deep-sea mussels:

MUSSEL BED, 00°47.89′N, 86°09.21′W: Dive 879-1, 20 Jan, 2495 m, paratype (USNM 80627). Dive 880-24, and mussel washings, 21 Jan, 2493 m, 3 paratypes (USNM 80628, 80629) and 2 specimens from mussel washings (USNM 81255). Dive 887-12, 12 Feb, 2488 m, paratype (USNM 80630) and young specimen from mussel washings (USNM 81256). Dive 895, 20 Feb, 2482 m, 2 young from washings and clam box washings (USNM 81257). Dive 991-58, 59, 8 Dec, 2490 m, 2 paratypes (USNM 80634) and 5 young from mussel washings (991-121, USNM 81258).

GARDEN OF EDEN, 00°47.69′N, 86°07.74′W: Dive 883-L3, 24 Jan, 2492 m, paratype (USNM 80624). Dive 884-2, 6, 11, 25 Jan, 2482 m, 3 paratypes (USNM 80625, 80626) and 6 young from clam bucket with mussels and rubble residue (USNM 81263).

ROSE GARDEN, 00°48.25′N, 86°13.86′W: Dive 890-28, 32, 15 Feb, 2447 m, 2 paratypes (USNM 80622). Dive 892-5, 17 Feb, 2454 m, paratype (USNM 80623). Dive 894-14, 17, 19, 20, 21, 23, 31, 19 Feb, 2457 m, 7 paratypes (USNM 80631). Dive 896-1, 7, 16, 21 Feb, 2460 m, 3 paratypes (USNM 80632) and 2 young from Instant Ocean washings (896-22, USNM 81260). Dive 983, 30 Nov, 2457 m, holotype (983-73, USNM 80615); paratype (983-81, USNM 80616);

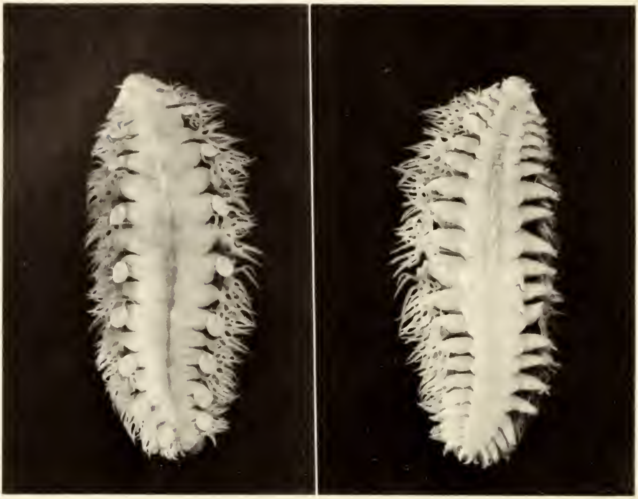

Fig. 1. *Branchipolynoe symmytilida,* holotype, USNM 80615 (983-73): Dorsal view, left; ventral view, right. 2×.

paratype (983-34A, USNM 80620); 2 paratypes (983-34B, C, USNM 80621); 12 paratypes (983-16, 18, 30, 52, 53, 64, 66, 74, 80, 86, 90, 109, USNM 80633); 2 paratypes (983-85, USNM 80617); 2 paratypes (983-87, USNM 80618); 3 paratypes (983-102, USNM 80619); 1 specimen from washings (983-112, USNM 81261). Dive 984-32, 1 Dec, 2451 m, 6 young from mussel washings (USNM 81259). Dive 990-41, 7 Dec, 2451 m, 4 young from vestimentiferan washings (USNM 81262).

Measurements.—Holotype (USNM 80615, 983-73) 37 mm long, 18 mm wide, including branchiae, with 21 segments. Largest paratype (USNM 80627, 879-1) 42 mm long, 18 mm wide, 21 segments.

Description.—The body is short, spindle-shaped, slightly tapered anteriorly and posteriorly, flattened ventrally and strongly arched dorsally (Fig. 1). Fully-developed worms have 21 segments, the first achaetous, with 10 pairs of elytra on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 and 19. The elytra are small, oval, and leave the greater part of the dorsum uncovered (Figs. 1, 2A). They are attached to low elytrophores, the first pair in the central part of the elytron, the following ones eccentrically, near their anterior borders (Fig. 2C–E). The elytra are rather thick, opaque and lack tubercles and papillae. The dorsal cirri on the non-elytra-bearing segments have short cylindrical cirrophores and short tapered styles with slender tips. They are attached posterior to the small notopodia and extend to about the

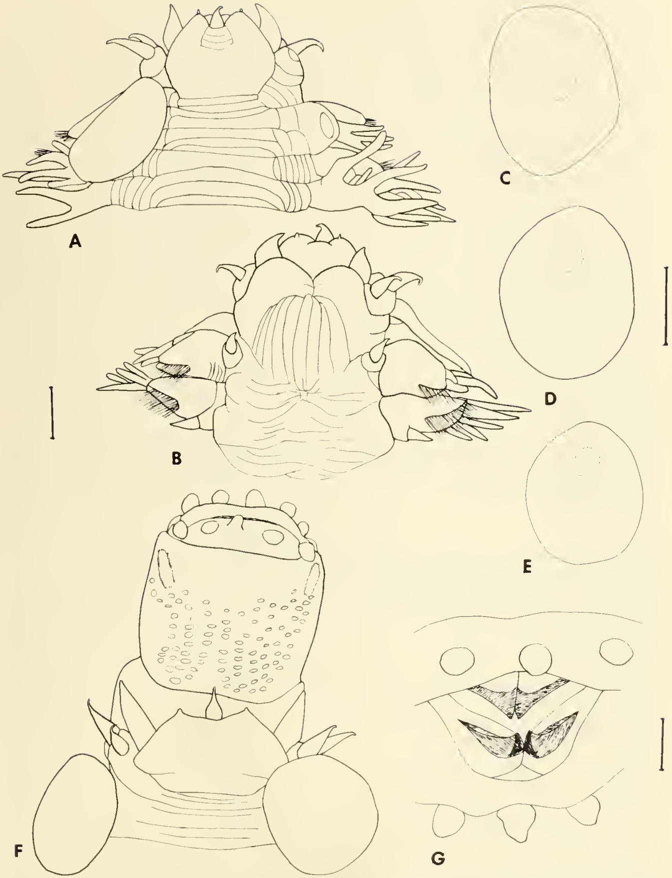

Fig. 2. *Branchipolynoe symmytilida*, A–E, holotype, USNM 80615 (983-73); F–G, paratype, USNM 80616 (983-81): A, Dorsal view of anterior end, style of right dorsal tentacular cirrus and right elytron on segment 2 broken off; B, Ventral view of anterior end; C, Right first elytron from segment 2; D, Right sixth elytron from segment 11; E, Right tenth elytron from segment 19; F, Dorsal view of anterior end, pharynx extended; G, Frontal view of pharynx slit open, showing jaws and medial papillae. Scales = 1.0 mm for A, B, F; 1.0 mm for C–E; 0.5 mm for G.

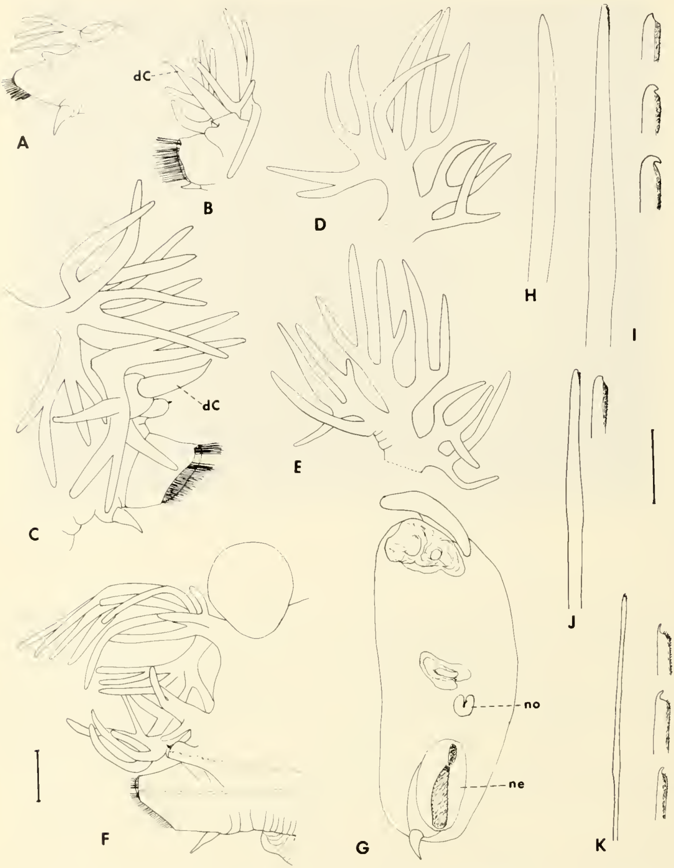

Fig. 3. *Branchipolynoe symmytilida.* A–F, H–K, holotype, USNM 80615 (983-73); G, paratype, USNM 80627 (879-1): A, Right elytragerous parapodium from segment 2, anterior view, elytron removed; B, Right cirrigerous parapodium from segment 3, anterior view; C, Right cirrigerous parapodium from segment 8, posterior view; D, Lower branchia from same; E, Upper branchia from same; F, Right elytragerous parapodium from segment 13, anterior view, acicula and neuropodial acicular lobe dotted; G, Diagrammatic end view of same, only bases of branchiae shown; H, Notoseta; I, Neuroseta from upper group with detail of three tips enlarged; J, Upper stout neuroseta from lower group, with tip enlarged; K, Slender neuroseta from lower group with detail of three tips enlarged. Scales = 1.0 mm for A–G; 0.1 mm for H–K. dC, dorsal cirrus; ne, neuropodium; no, notopodium.

tips of the setae (Fig. 3B, C). Dorsal tubercles on the cirrigerous segments are indistinct. Branchiae are well developed, arborescent, with long filaments. They emerge from the body in 2 main short trunks, a lower smaller group dorsoposterior to the notopodia and an upper large one more medial and near the elytrophores and dorsal tubercles (Fig. 3C–G). The branchiae begin on segment 2 as a single small group lateral to the elytrophore (Fig. 3A); they become larger, with more numerous branches and occur on all the following segments.

The prostomium is relatively small and bilobed, with subtriangular anterior lobes bearing minute frontal filaments. The median antenna has the ceratophore fused to the prostomium and is rather indistinct; the short subulate style in the anterior notch extends only slightly beyond the prostomium; the lateral-ventral palps are short, thick, and tapered, and extend slightly beyond the prostomium; lateral antennae and eyes are lacking (Fig. 2A, B, F). The first or tentacular segment is fused to the prostomium; the tentaculophores lateral to the prostomium are short and bulbous, each with a pair of tentacular cirri; the dorsal ones are about the length of the palps, the ventral ones slightly shorter; setae and facial tubercle are lacking. The tentacular segment is visible dorsally as a short ring and contributes ventrally to the lateral and posterior lips of the ventral mouth (Fig. 2B).

The thick muscular pharynx was extended on 2 specimens. There are 5 pairs of dorsal and ventral soft, delicate, sac-like papillae around the opening; subdistally on each side there is a dorsal and ventral raised diagonal area; more proximally a rather indistinct papillate area is followed by a smooth proximal area near the prostomium (Fig. 2F). The 2 pairs of jaws are rather small, light amber-colored, and lack denticulated bases (Fig. 2G).

The parapodia of segment 2 are subbiramous and bear the first pair of elytra. The ventral or buccal cirri are attached basally on the neuropodia, lateral to the ventral mouth (Fig. 2B). The buccal cirri are short, similar in length to the following ventral cirri (not extra long, as usually found in the Polynoidae). A single branchia with 3 branches is attached to the lateral side of the elytrophore; the notopodium is short, digitiform and lacks notosetae (Fig. 3A).

The following parapodia are subbiramous, short, thick and hidden from view dorsally by the well-developed branchiae (Fig. 3B–G). The notopodia are much shorter than the neuropodia; they are nodular to digitiform, curled dorsally, forming a slit on the upper side that encloses a few (1–3) scarcely projecting, dark amber-colored, stout, smooth and slightly tapered notosetae (Fig. 3H). The larger and stouter neuropodium, enclosing the inner conical acicular lobe, ends distally in a smaller upper truncate part and a larger obliquely truncate lower part; the distal tip of the acicular lobe forms an internal partition separating the neurosetae into upper and lower groups (Fig. 3F, G). The tips of the neurosetae scarcely project beyond the neuropodium. The upper (supra-acicular) neurosetae (about 11–13) are light amber-colored, stout, wider basally and gradually taper to blunt, slightly hooked tips; they are essentially smooth except for some indistinct distal serrations (Fig. 3I). The lower (subacicular) and larger group of neurosetae are very numerous; a small upper group (about 8) are similar to the supra-acicular neurosetae but about half as stout (Fig. 3J); the numerous remaining neurosetae are very slender and colorless, with slender notched, hooked tips and minute distal serrations (Fig. 3K). The ventral cirri, attached to the middle of the neuropodia, are short, not reaching the tips of the neuropodia (Fig. 3C, F).

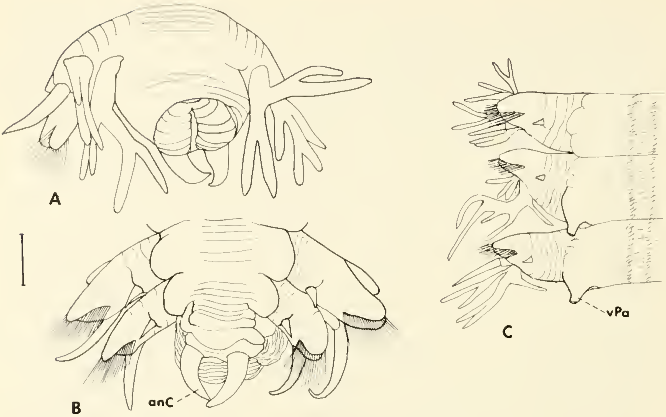

Fig. 4. *Branchipolynoe symmytilida,* A, paratype, USNM 80616 (983-81); B, C, holotype, USNM 80615 (983-73): A, Dorsal view of posterior end showing segment 21 and pygidium, with anus open; B, Ventral view of posterior end showing segments 20, 21 and pygidium, with protruding anal bulge; C, Ventral view of right side of segments 10 to 12. Scale = 1.0 mm for A–C. anC, anal cirrus; vPa, ventral papilla.

The pygidium, with the terminal anus, is rather large and bulbous. It is enclosed in the parapodia, longer dorsal cirri, and branchiae of the last segment; the ventral anal cirri are stout, short and curved medially (Fig. 4A, B). When the anus is open, ridged vascular areas are visible, sometimes appearing as a protruding anal bulge (Fig. 4B).

Distinct segmental or nephridial papillae are not present, except for 2 pairs of large ventral papillae on segments 11 and 12 that project posteriorly (Figs. 1, 4C).

Etymology.—Neo-Latin adjective from *sym*-"with," plus *mytilida*-"mytilid mussel," in reference to association with mytilids.

Developmental Variations

1. Adult with extra small elytra and upper neurosetae larger, darker and fewer in number (Fig. 5A–F).—The adult paratype (USNM 80630) from Dive 887-12 is 31 mm long, 14 mm wide, with 21 segments and enlarged ventral papillae on segments 11 and 12. The 10 pairs of elytra are very small, much smaller than on the figured holotype (Fig. 5A). The branchiae have more numerous branches (Fig. 5C). The upper group of neurosetae are fewer in number (1–2) and much stouter and darker amber-colored (Fig. 5A, B, D). The upper neurosetae of the lower group are also fewer in number (1–2) stout, wider subdistally, with slightly hooked tips (Fig. 5E) and are similar in shape to those of younger specimens (see below).

2. Juvenile with 20 segments and 9 pairs of elytra (Fig. 6A–K).—The paratype (USNM 80620) from Dive 983-34A is 12 mm long, 5 mm wide, with 20 segments,

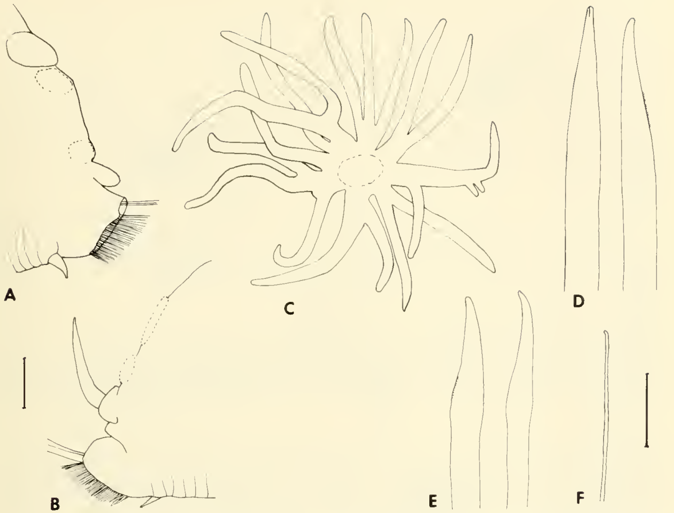

Fig. 5. *Branchipolynoe symmytilida*, paratype, USNM 80630 (887-12): A, Right elytragerous parapodium, posterior view; two groups of branchiae cut off (bases dotted); B, Right cirrigerous parapodium, anterior view; two groups of branchiae cut off (bases dotted); C, Upper branchia from same; D, Two neurosetae from upper group; E, Two neurosetae from upper part of lower group; F, Slender neuroseta from lower group. Scales = 1.0 mm for A–C; 0.1 mm for D–F.

the last one very small; elytra are lacking on segment 19. The 9 pairs of elytra are larger in proportion to the size of the body and cover more of the dorsum (Fig. 6A, B). They are somewhat more delicate and show faint "veining" (Fig. 6D, E). The branchiae occur in the usual 2 groups but have fewer branches (Fig. 6F–H). The notopodia appear to be larger in proportion to the neuropodia, with up to 3 stout notosetae (Fig. 6F, I). The neuropodia are rounded distally, bearing only 2 upper stout neurosetae with slightly hooked tips (Fig. 6J) and numerous lower slender neurosetae (Fig. 6K). Enlarged ventral papillae occur only on segment 12.

3. Juvenile with 18 segments and 9 pairs of elytra (Fig. 7A–E).—The paratype (USNM 80626) from Dive 884–6 is 5 mm long, 3 mm wide, with 18 segments and 9 pairs of elytra. The upper 2 neurosetae are stout and strongly hooked (Fig. 7A, B, D), the lower ones slender, hooked and distally serrated (Fig. 7E). There are no enlarged ventral papillae.

4. Young with 14 segments and 7 pairs of elytra (Fig. 8A–F).—A small paratype (USNM 80628) collected from mussel washings on Dive 880 has 14 segments, the last one very small; it is 2.5 mm long, 1.5 mm wide, including setae, with 7

Fig. 6. *Branchipolynoe symmytilida,* juvenile paratype, USNM 80620 (983-34A): A, Dorsal view of anterior end, first right elytron removed; B, Dorsal view of posterior end; C, Right first elytron from segment 2; D, Right fifth elytron from segment 9; E, Right ninth elytron from segment 17; F, Right elytragerous parapodium from segment 9, anterior view, elytron removed; G, Right cirrigerous parapodium from segment 8, posterior view, branchiae cut off; H, Upper and lower branchiae from same; I, Three notosetae; J, Two upper neurosetae; K, Lower neuroseta, with detail of tip. Scales = 1.0 mm for A, B; 0.5 mm for C–E; 0.5 mm for F–H; 0.1 mm for I–K.

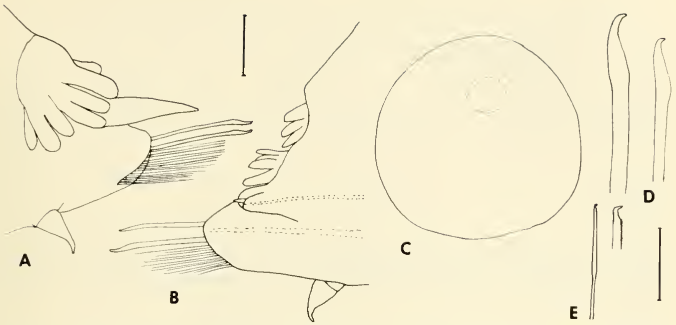

Fig. 7. *Branchipolynoe symmytilida,* juvenile paratype, USNM 80626 (884-6): A, Right cirrigerous parapodium, posterior view; B, Right elytragerous parapodium, anterior view, acicula dotted; C, Elytron; D, Upper and middle neurosetae; E, Lower neuroseta with detail of tip. Scales = 0.2 mm for A–C; 0.1 mm for D, E.

pairs of elytra. Branchiae are just beginning to be developed (Fig. 8C). The neurosetae are few in number: 3 upper and middle stouter ones with hooked tips (Fig. 8E) and 5 lower more slender ones (Fig. 8F).

Association of Commensal Polynoids with Deep-Sea Mussels

Forty-seven polynoids were removed from the mantle cavities of 41 mussels, one per mussel except for two that harbored two polynoids and two that each contained three polynoids (Table 1). Thirty-two mussels were collected in the area referred to as Rose Garden, 4 in the Garden of Eden and 5 in the Mussel Bed. Two additional polynoids were collected in mussel washings from the Mussel Bed. The shell lengths of the mussels ranged from 33.8 to 152.0 mm (measured by I. P. Williams, WHOI). The polynoids ranged in length from 2 mm (young, in mussel with shell length of 80 mm) to 42 mm (adult, in mussel with shell length of 135 mm). There was no consistent correlation between lengths of the polynoids and the mussels. Thus, the largest mussel with a shell length of 152 mm contained a polynoid of only 12 mm in length.

Of the 49 available polynoids associated with the deep-sea mussles, 30 are considered to be adults, having the full number of 21 segments, 10 pairs of elytra on segments 2, 4, 5, 7, 9, 11, 13, 15, 17 and 19, and two pairs of large ventral papillae on segments 11 and 12 (Figs. 1–5). They vary in length from 10 to 42 mm and in width from 5.5 to 19.0 mm. All but one of them were removed from mussels with shell lengths of 44.9 to 152.0 mm. The other polynoid, an adult of 24.0 mm in length and 8.5 mm in width, was collected in mussel washings from Dive 880.

The remaining 19 polynoids are considered to be juveniles or young. Twelve polynoids in this group, so-called juveniles (Fig. 6), have 20 segments, 9 pairs of

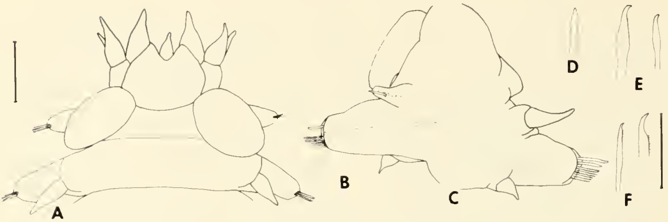

Fig. 8. *Branchipolynoe symmytilida*, young paratype, USNM 80828 (880-mussel washings): A, Dorsal view of anterior end; B, Right elytragerous parapodium, anterior view, acicula dotted; C, Right cirrigerous parapodium, posterior view; D, Notoseta; E, Upper and middle neurosetae; F, Lower neuroseta with detail of tip. Scales = 0.2 mm for A–C; 0.1 mm for D–F.

elytra, and a pair of large ventral papillae on segment 12 only, with three exceptions: one (890-28) has ventral papillae on both segments 11 and 12; one (983-90) has 21 segments but with the last 2 very small, and lacks ventral papillae; and one (983-102A) has 21 segments, the last 2 very small. They vary in length from 9 to 17 mm and in width from 4.5 to 8.0 mm. They were removed from mussels with shell lengths of 33.8 to 133.2 mm. Four younger juveniles (Fig. 7) have 18 segments, 9 pairs of elytra; ventral papillae are lacking. Lengths vary from 5.0 to 5.5 mm and widths from 2.5 to 3.0 mm. They were found in mussels with the shell lengths of 50.9 to 96.0 mm. The three youngest polynoids (Fig. 8) have 12 to 14 segments, 6 to 7 pairs of elytra and also lack ventral papillae. Lengths are 2 to 3 mm and widths 1.2 to 1.5 mm. Two of them (983-102) were found in a mussel with a shell length of 80.0 mm, the other (880), in mussel washings.

Among a collection of unsorted polynoids from the Galapagos Rift, also collected in 1979 and sent to me later, some additional specimens of the commensal *B. symmytilida* were found. These included 3 adults collected in mussel washings from the Mussel Bed and washings from the Rose Garden area, as well as 26 young specimens: 6 from a clam bucket with mussels and rubble residue in the Garden of Eden, 8 from mussel washings in the Mussel Bed, and 12 from Instant Ocean, mussel and vestimentiferan washings in the Rose Garden. They included the smallest specimens examined, consisting of 10 to 14 segments, 1 to 2 mm in length and 0.7 to 1.5 mm in width. It was possible to separate the minute young of *B. symmytilida* from the young of the other polynoids found in the same collections by their characteristic short antenna, palps, tentacular and dorsal cirri, as well as by their neuropodia with relatively few stout hooked neurosetae (Fig. 8).

For the four mussels found harboring more than one polynoid commensal, one (983-87) contained an adult and young, one (983-34) an adult and 2 juveniles, one (983-102) a juvenile and 2 young, and one (983-85) 2 young (Table 1).

Most of the commensal polynoids were removed from the deep-sea mussels at WHOI by I. P. Williams, with the vent area, *Alvin* dive and mussel number, and

Table 1.—Data on four deep-sea mussels harboring more than one polynoid commensal.

Alvin dive-mussel no.	Mussel shell length (mm)	Polynoid commensal *Branchipolynoe symmytilida*					
		No. segments	No. elytral prs.	Length (mm)	Width (mm)	Ventral papillae on segments	USNM cat. no.
983-87	96.0	A 21	10	24	12	11 & 12	80618
		Y 18	9	5.5	3	None	
983-34	133.2	A 21	10	33	14	11 & 12	80621
		J 20	9	10.5	4.5	12	(B) (C)
		J 20	9	12	5	12	80620 (A)
983-102	80.0	J 21*	9	13.5	6.5	12	80619
		Y 14*	7	3	1.5	None	
		Y 12	6	2	1.2	None	
983-85	50.9	Y 18	9	5	2.5	None	80617
		Y 18	9	5	2.5	None	

A, Adult; J, Juvenile; Y, Young.
* Last 2 segments very small and incomplete.
Alvin dive 983 in Rose Garden area.

shell length indicated. Soft parts of five mussels with the commensal polynoids still present in the mantle cavities of the host were sent to me. The data are summarized in Table 2. Three of the commensals are considered to be adults, having the full number of 21 segments and 10 pairs of elytra, and as well as 2 pairs of ventral papillae on segments 11 and 12. The other two are juveniles, with only 9 pairs of elytra and 20 segments (or 21, with the last two very small) and a single pair of ventral papillae on segment 23 (not on 11) or lacking altogether. The commensal polynoids were found occupying the anterior and ventral parts of the mantle cavity, anterior to the byssus threads. In one case, the polynoid was wrapped around the foot of the mussel.

A number of studies have been carried out dealing with the unnamed deep-sea mytilid mussels from the Galapagos Rift. Rau and Hedges (1979:649) suggested a chemosynthetic food source for the mussels and other filter feeders in the proximity of the vents. Lutz, Jablonski, Rhoads, and Turner (1980:127) presented evidence which strongly suggests that the mytilid host for the polynoid possesses a demersal planktotrophic larval stage with relatively long planktonic existence and that the unusual biological and physico-chemical conditions (such as high microbial densities, elevated water temperature and hydrogen sulfide concentrations) might very well provide a stimulus to larval settlement and concentration of relatively sedentary organisms in and around these geographically isolated deep-sea hydrothermal vents. Rhoads, Lutz, Cerrato and Revelas (1982) studied the mytilid mussels at the hydrothermal vents in connection with growth and predation activity. The largest mussel collected, with a shell length of 184 mm, was estimated to be 19 ± 7 years old, based on results of transplant mark and recapture experiments. Mussels less than 20 mm in length showed damage from predation by the vent crab *Bythograea thermydron* Williams. They concluded that the

Table 2.—Data on five commensal polynoids removed from five deep-sea mussels.

	Deep-sea mussel		Polynoid commensal *Branchipolynoe symmytilida*					
Alvin dive-mussel no.	Shell length (mm)	Soft parts length × height (mm)	No. segments	No. elytral prs.	Length (mm)	Width (mm)	Ventral papillae on segments	USNM cat. no.
983-18	116.6	72 × 48	A 21	10	38	14	11 & 12	80633
991-59	67.0	42 × 30	A 21	10	16	7	11 & 12	80634
983-16	48.5	30 × 17	A 21	10	12	6	11 & 12	80633
983-74	62.6	36 × 22	J 20	9	16	8	12	80633
983-90	67.0	40 × 21	J 21*	9	14	6	None	80633

A, Adult; J, Juvenile.

* Last 2 segments very small and incomplete.

Alvin dive 983 in Rose Garden area; Dive 991 in Mussel Bed.

mytilids have a high growth rate, with a relatively long life span, and continue to grow throughout life, fed by dense chemosynthetic microbes associated with the vents.

Remarks.—Based on the structure of the prostomium and tentacular segment, *Branchipolynoe* could have been placed in the subfamily Macellicephalinae Hartmann-Schröder, as revised by Pettibone (1976, 1979) and Levenstein (1982) or in Lepidonotopodinae Pettibone (1983), having the prostomium bilobed with short frontal filaments on the anterior lobes, a median antenna with the ceratophore in the anterior notch, without lateral antennae, and with paired palps and two pairs of tentacular cirri lateral to the prostomium. *Branchipolynoe* differs from all the genera in the above two subfamilies in having well-developed arborescent branchiae, very small notopodia with only a few short, stout notosetae, truncate neuropodia without projecting acicular lobes and neurosetae of different type and distribution.

The presence of well-developed arborescent branchiae is an unusual feature in the Polynoidae. Branchiae in the form of simple digitiform extensions or pustules are known in some species, such as *Chaetacanthus* and *Euphione.* The great development of arborescent branchiae in *Branchipolynoe* may be another example of an adaptation to an environment that can be low in dissolved oxygen, as pointed out by Williams (1980:465) for the vent crab *Bythograea thermydron,* which has capacious branchial areas with large afferent and efferent branchial openings. Another example is the elaborate vascularization of the obturacular plume of the vestimentiferan *Riftia pachytila* (Jones 1981:1309).

Branchipolynoe symmytilida shows a number of features connected with its commensalism, such as small elytra that leave a large part of the dorsum uncovered, and smooth elytra lacking tubercles. The short stubby head appendages and dorsal and anal cirri suggest an adaptation for living in the large mantle cavities of the mytilid host, a fine place to escape from predators, such as crabs, shrimps, and fishes.

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REDESCRIPTION OF *ARCTURELLA LINEATA* (STEBBING) FROM SOUTH AFRICA (CRUSTACEA: ISOPODA: ARCTURIDAE)

Brian Kensley and Marilyn Schotte

Abstract.—*Arcturella lineata,* a poorly known arcturid isopod from South Africa, is redescribed and fully figured, from fresh material. The confusion arising from vaguely defined generic diagnoses in the Arcturidae is demonstrated, as there appears to be little real difference between *Arcturella* and *Astacilla.*

Arcturella lineata was described by Stebbing (1873) based on material from Algoa Bay, South Africa, and has since been recorded on five separate occasions. The species, however, has never been fully described, and the only figures available are those of a whole female in dorsal view (Stebbing 1873, pl. 3, fig. 3; Kensley 1978, fig. 7D). Fresh material, collected alive along with the host gorgonacean, provided the opportunity for full description and figures to be given, and the generic position to be reexamined.

Arcturella lineata Stebbing
Figures 1, 2

Arcturus lineatus Stebbing, 1873:97, pl. 3 (fig. 3); 1875:187.
Arcturus (?) *lineatus.*—Barnard, 1914:207.
Arcturella lineata.—Barnard, 1920:392; 1940:509.—Day, Field, and Penrith, 1970: 49.—Kensley, 1978:21, fig. 7D.

Material examined.—In addition to Barnard's material in the South African Museum collections, the following fresh material was examined: South African Museum, 2 ♂, TL 8.0–9.0 mm, 5 ovig. ♀, TL 7.0–8.0 mm, 1 ♀, TL 6 mm, 74 juveniles; Cape Point Nature Reserve, False Bay, South Africa, 34°20′S, 18°30′E, 10 m, on *Lophogorgia flammea,* collected by Mr. W. R. Liltved, 29 May 1983.

Description.—Ovigerous Female: Body about 4.5 times longer than greatest width at pereonite 4; not usually geniculate. Integument with scattered very small rounded granules. Head with large well pigmented dorsolateral eyes; anterior margin deeply concave, with tiny rostral point; anterolateral lobes of head rounded, with short distolateral spine; dorsum convex; ventrolateral margins barely developed, mouthparts and pereopod 1 visible in lateral view. Pereonite 1 fused with head, line of fusion marked by shallow groove; coxal plate with 3 points, separated from ventrolateral margin of head by narrow slit; low middorsal tubercle present. Pereonite 2 shorter than pereonite 3, coxal plate rounded. Pereonite 4 almost as wide proximally as middorsal length, tapering posteriorly, somewhat dorsoventrally flattened, with strong rounded middorsal tubercle in proximal half, and smaller tubercle near posterior margin. Pereonites 5–7 decreasing in length and width posteriorly, coxal plates rounded; pereonite 7 with low rounded middorsal lobe. Marsupium formed by 3 pairs of oostegites on pereonites 2–4, oostegite 4 largest; marsupium containing 30 eggs. Pleon consisting of 2 weakly

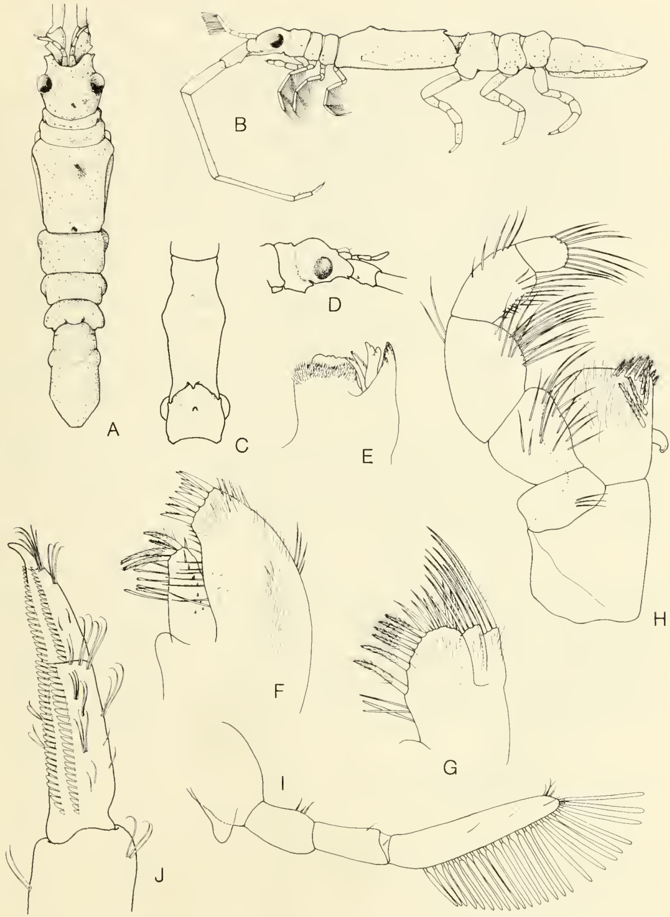

Fig. 1. *Arcturella lineata:* A, Ovigerous female in dorsal view; B, Male in lateral view; C. Pereonites 4 and 5 of male in dorsal view; D, Head of female in lateral view; E, Mandible; F, Maxilla 1; G, Maxilla 2; H, Maxilliped; I. Antenna 1; J, Flagellum of antenna 2.

indicated fused pleonites plus pleotelson; second fused pleonite with weak posterolateral 'shoulder,' seen in dorsal view; pleotelson dorsally evenly convex, pentagonal in outline, apex truncate in dorsal view.

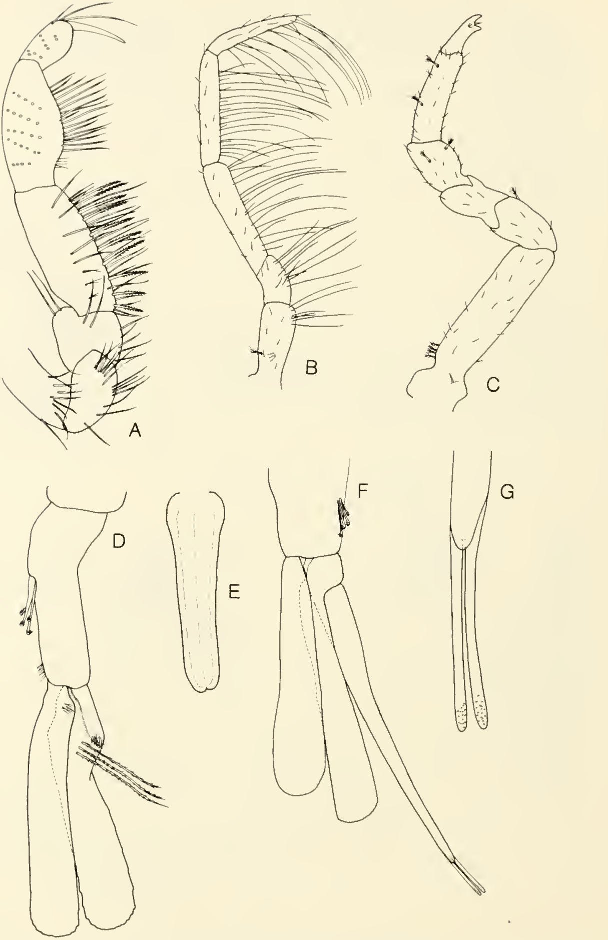

Fig. 2. *Arcturella lineata:* A, Pereopod 1, some setae omitted; B, Pereopod 4; C, Pereopod 7; D, Male pleopod 1; E, Penis; F, Male pleopod 2; G, Apex of copulatory stylet enlarged.

Antenna 1 with basal peduncle segment having ventrodistal rounded lobe-flange; segment 2 about half width and ⅔ length of segment 1; segment 3 slightly narrower and subequal in length to segment 2; flagellum consisting of very short partly obscured dorsal segment plus elongate distal article bearing 24 ventral aesthetascs.

Antenna 2, basal peduncular segments ⅔ length of segment 2, latter with lateral tooth; segment 3 twice length of but narrower than segment 2; segments 4 and 5 narrow, cylindrical, each almost twice length of segment 3; flagellum of 2 articles, basal article 1.6 times length of distal article, each with 2 ventrolateral rows of flattened scale-spines; distal article tipped with short claw.

Mandible lacking palp; sclerotized incisor of 4 cusps; lacinia stout, with several distal cusps; 2 fringed spines in spine-row; molar stout, distally truncate and sclerotized, with serrate margins.

Maxilla 1, inner ramus half width of outer, with 1 short and 3 elongate fringed setae distally; outer ramus with 9 distal simple and serrate spines.

Maxilla 2, inner ramus broadly rounded, with numerous fringed spines on mediodistal margin; inner lobe of outer ramus bearing 5 elongate sparsely fringed and distally serrate spines; outer lobe with 4 elongate fringed and serrate spines.

Maxillipedal endite with single coupling hook, 10 or 11 fringed spines on mediodistal margin; 5-segmented palp with numerous setae on mesial margins; segment 3 longest and broadest.

Pereopod 1, all segments bearing setae on inner and medial surfaces; carpus longest segment, armed with 10 fringed spines in addition to setae on medial margin; propodus and dactylus densely setose; dactylus with stout apical claw.

Pereopods 2–4 similar, becoming longer posteriorly; dactyli lacking; propodi, carpi, meri, ischia, and bases armed with elongate setae on posterior margins.

Pereopods 5–7 similar, stout, prehensile; dactylus biunguiculate, 2 corneous claws subequal.

Uropods with outer ramus triangular, fringed with setules; inner ramus half length and half basal width of outer ramus, apically with 3 elongate fringed spines.

Male: Body elongate-cylindrical, 7 times longer than greatest width at pereonite 4. Head, antennae, and mouthparts as in female. Pereonite 4 twice longer than wide, with slight dorsoventral flattening, widening just anterior to midlength, with low rounded middorsal tubercle in anterior half, hook-like middorsal spine on posterior margin. Pereonite 5 with subacute middorsal tubercle near anterior margin. Remaining pereonites and pleon as in female. Penis reaching to base of rami of pleopod 1, apically bilobed.

Pleopod 1, basis with 4 coupling hooks; rami subequal in length, longer than basis, with elongate plumose setae on distal rounded margins; exopod with proximal notch and 3 elongate fringed setae.

Pleopod 2, basis with 4 coupling hooks on medial margin; exopod shorter than endopod; latter with copulatory stylet articulating near base; copulatory stylet tapering, slender, reaching well beyond rami, distally having 2 slender processes sheathed basally by rounded lobe; processes with several scale-spines distally.

Color.—All the specimens were a bright wine-red, matching very closely the color of the host gorgonacean *Lophogorgia flammea.* The color derives from evenly and densely arranged integumental chromatophores. The animals were observed alive for a short time, and while a few specimens had a geniculate appearance (clinging to the host by the posterior three pairs of pereopods, the body flexed between pereonites 4 and 5) most, including ovigerous females, crawled about in a non-geniculate position.

Remarks.—Apart from allowing a redescription of a poorly known species, the fresh material from False Bay also stimulated a reexamination of the generic position.

Monod (1925) cast doubt on the validity of the generic placement of some species of *Arcturella.* He was of the opinion that, in spite of the relatively short length of pereonite 4 in several species, some *Arcturella* species should be placed in *Astacilla.* Only those species having a well calcified and dorsoventrally flattened pereonite 4 should be placed in *Arcturella.*

The type-species of *Arcturella, A. dilatata* (Sars, 1882, and originally described as an *Astascilla*) agrees with many of the features used to define *Astacilla* (sensu Lew Ton, pers. comm.). These include the presence of a strong dactylar claw on pereopod 1, lack of dactyli on pereopods 2–4, a notch in the exopod of the male pleopod 1, and an apically trifid copulatory stylet on the male pleopod 2 endopod.

Clearly, present separation of *Astacilla* and *Arcturella* is ill-defined. Until the already commenced generic revision of the Arcturidae is completed (Poore and Kensley, in prep.), it would be of little benefit to place the present species in *Astacilla.* Nevertheless, redescription of the present species serves a cautionary note for future generic placements within the Arcturidae.

Acknowledgments

We thank Mr. W. Liltved of the South African Museum, for collecting and drawing the first author's attention to specimens of *A. lineata*; Dr. F. Bayer of the Smithsonian Institution for identifying the host gorgonacean; and Dr. T. E. Bowman for reviewing the manuscript.

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A NEW *GASTROCOPTA* (MOLLUSCA: PULMONATA: PUPILLIDAE) FROM BAJA CALIFORNIA SUR, MEXICO

Barry Roth and Carl C. Christensen

Abstract.—*Gastrocopta* (*Immersidens*) *allyni,* a new species of minute pulmonate land snail found at numerous localities in southern Baja California Sur, Mexico, is described. The species is distinctive in having a free, continuous peristome, strong apertural dentition, and platelike apertural barriers along the inner and outer lips.

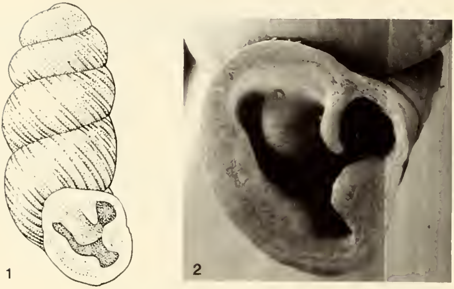
The California Academy of Sciences-Belvedere Scientific Fund expedition to the Cape Region of Baja California Sur in December 1958 and January 1959 collected an undescribed minute snail of the genus *Gastrocopta* at five stations. Additional specimens were taken when the same parties returned to the Cape Region in November 1959. The species was recognized as new by the late Allyn G. Smith in the course of a faunistic study of land mollusks of Baja California. Field work by the junior author and Walter B. Miller over the years 1970–1975 secured the species at a number of additional localities, and there is now ample material available to permit its description as new and to characterize its geographic range. The species is distinctive in its strong apertural dentition, detached peristome, and the presence of platelike apertural barriers parallelling the peristome on the inner and outer lips. Designation of the latter structures as barriers follows the usage established by Solem (1972).

Institutional and private collections in which specimens of the new species are deposited are abbreviated as follows: Academy of Natural Sciences, Philadelphia (ANSP); Bernice P. Bishop Museum (BPBM); California Academy of Sciences (CAS); Field Museum of Natural History (FMNH); U.S. National Museum of Natural History (USNM); Department of General Biology, University of Arizona (UA); collection of Carl C. Christensen, Honolulu, Hawaii (CCC); collection of Walter B. Miller, Tucson, Arizona (WBM).

Gastrocopta (*Immersidens*) *allyni,* new species
Figs. 1, 2

Diagnosis.—Small, cylindrical *Gastrocopta* (*Immersidens*) of 4.5–5.0 whorls; dextral, body whorl sulcate, with conspicuous crest; base narrow, umbilicate; peristome continuous, free, inner and outer lips with platelike barriers parallelling peristome; large parietal lamella fusing with angular lamella deep inside aperture; columellar lamella not reaching peristome.

Description.—Shell small for the genus, dextral, cylindrical, of 4.5–5.0 whorls; apex blunt; sutures strongly impressed. Profile of first 2.5–3.0 whorls evenly convex; of fourth whorl, slightly attenuated in front and flattened at periphery. Last whorl tumid below suture, compressed and attenuated toward base; with shallowly impressed spiral sulcus commencing on back of whorl, opposite aperture, and



Figs. 1, 2. *Gastrocopta* (*Immersidens*) *allyni,* n. sp. 1, paratype CAS 032997, X32; 2, paratype CAS 032994, detail of aperture, X75.

extending as far as the crest behind outer lip. Base narrow, with large, oblique umbilical slit bordered by low, tumid, round-topped ridge. Last ¼ whorl almost straight in basal view; crest conspicuous, particularly on lower quadrant of whorl, protruding as far as outturned outer lip. Aperture oval to subquadrate; peristome well expanded, continuous, free; with elongate, platelike barrier on middle of outer lip, another extending from middle of inner lip to basal margin, these barriers sometimes connected by additional callus thickening. Angular lamella strong, projecting beyond plane of aperture, curving to right internally, often almost meeting outer lip tooth. Parietal lamella large, more deeply immersed than angular lamella, sigmoid, flexed to right internally, where it fuses with angular, forming a *lambda*-shaped figure. Columellar lamella deeply immersed, scarcely visible in frontal view, arising ½ whorl back, free end horizontal, remainder strongly flexed downward along columella. Palatal folds two, at about same level inside outer lip, flange formed by fusion of angular and parietal lamellae extending into gap between them; inner fold longer, extending almost to back of body whorl. Basal fold oblique to aperture, subtending columellar lamella, roughly trapezoidal in shape, with small knoblike expansion at peripheral end. Sculpture: first 1.5–2.0 whorls smooth, succeeding whorls with fine, raised, retractive riblets extending from suture to suture, parallel to lines of growth. Ribbing equally strong on base and continuing into umbilicus, although sometimes interrupted (by wear?) over circum-umbilical ridge. Color pale brown.

Length 1.5–1.9 mm; diameter 0.6–0.8 mm; length/diameter ratio 2.0–2.6.

Type-locality.—MEXICO: Baja California Sur: Arroyo ca. 15 mi [24 km] S of La Paz, in drift, A. G. Smith coll., 2 Nov 1959.

Type material.—Holotype, CAS 032993; length 1.7 mm, diameter 0.7 mm, 4.75 whorls. Figured paratypes, CAS 032994, CAS 032997; two additional paratypes, CAS 032995, from same locality as holotype. Additional paratypes (one each) are deposited in ANSP, BPBM, FMNH, and USNM.

Additional localities.—MEXICO: Baja California Sur: 0.4 mi [0.6 km] N of Km 105 along Transpeninsular Highway N of La Paz, C. C. Christensen, W. B. Miller coll., 6 Dec 1974 (BPBM *ex* CCC 3354). Arroyo de Los Pozos, 12.9 mi [20.6

km] E of La Paz, on road to Las Cruces, A. G. Smith coll., 4 Jan 1959 (CAS 032989). Sierra Cacachila, 9.8 mi [15.7 km] E of La Paz-Cabo San Lucas highway, elev. 1400 ft [420 m], C. C. Christensen, J. A. Christensen coll., 18 Dec 1975 (BPBM *ex* CCC 3858). Km 5000.2 [?] S of San Antonio, in leafmold, A. G. Smith coll., Jan 1959 (CAS 032991). 1 km SE of San Bartolo, elev. ca. 800 ft [240 m], W. B. Miller coll., 28 Dec 1970 (UA 5803; WBM 6496). 5.3 mi [8.5 km] NW of Todos Santos along road to La Pastora, A. G. Smith coll., 13 Jan 1959 (CAS 032992). Along road to La Burrera, 7.0 mi [11.2 km] from Cabo San Lucas-Todos Santos road, elev. 1000 ft [300 m], C. C. Christensen, J. A. Christensen coll., 20 Dec 1975 (BPBM *ex* CCC 3550). Bahía San Pedrito, 3.9 mi [6.2 km] SE of Todos Santos, A. G. Smith, A. E. Leviton coll., 14 Jan 1959 (CAS 032988). Along road from Cabo San Lucas to Todos Santos, 2.2 mi [3.5 km] N of El Saucito, in granite outcrops W of road, elev. 1500 ft [450 m], C. C. Christensen, J. A. Christensen coll., 22 Dec 1973 (BPBM *ex* CCC 3102); C. C. Christensen coll., 9 Aug 1974 (BPBM *ex* CCC 3228). Along road from Cabo San Lucas to Todos Santos, 2.1 mi [3.4 km] N of El Saucito, elev. 1500 ft [450 m], C. C. Christensen, J. A. Christensen coll., 22 Dec 1975 (BPBM *ex* CCC 3610). 0.2 mi [0.3 km] SSE of San José del Cabo on road to La Playa, in stream drift. A. G. Smith, A. E. Leviton coll., 7 Jan 1959 (CAS 032990).

These localities are plotted on the map (Fig. 3).

Discussion.—The array of apertural folds and lamellae in *Gastrocopta* (*Immersidens*) *allyni* is basically that typical of the subgenus *Immersidens* Pilsbry and Vanatta, 1900, but with certain peculiarities of its own. Apertural armature is more strongly developed in this species than in any other member of the subgenus. Internal fusion of the parietal and angular lamellae in a *lambda* or "reversed y" configuration is diagnostic of *Immersidens.* In *G. allyni* the angular lamella projects beyond the plane of the aperture, its free edge frequently almost reaches the upper end of the tooth on the outer lip (Fig. 2), and the parietal lamella is so large that it nearly fills the center of the aperture. The development of thickening barriers around the peristome (so extensive that the basal and palatal folds are concealed and the columellar lamella scarcely visible in front view) is unique in the subgenus. The barriers are not obviously homologous with any of the usual apertural teeth found in *Gastrocopta* (compare Pilsbry 1948, fig. 469).

In size and placement of parietal and angular lamellae, *Gastrocopta* (*Immersidens*) *ashmuni* (Sterki, 1898) and *G.* (*I.*) *cochisensis* (Pilsbry and Ferriss, 1910) are similar to *G. allyni.* However, *G. cochisensis* lacks a crest and the columellar lamella is short, not descending as strongly as in *G. allyni.* In *G. ashmuni* the columellar lamella runs forward in a straight vertical extension upon the parietal wall (Pilsbry 1948, fig. 484). In all three species, the palatal folds are at approximately the same level inside the outer lip, although the lower fold of *G. ashmuni* is remote and more deeply entering.

In *Gastrocopta* (*Immersidens*) *dalliana* (Sterki, 1898), another species of the arid southwestern United States and northwest Mexico, the angular and parietal lamellae are close together and run parallel for most of their length; *G. dalliana* lacks a prominent crest.

In *Gastrocopta* (*Immersidens*) *rixfordi* (Hanna, 1923), from Baja California Sur, the peristome is adnate, not free; the aperture is less oblique than in *G. allyni* and sometimes bowed inward at the top. The angular and parietal lamellae are closer

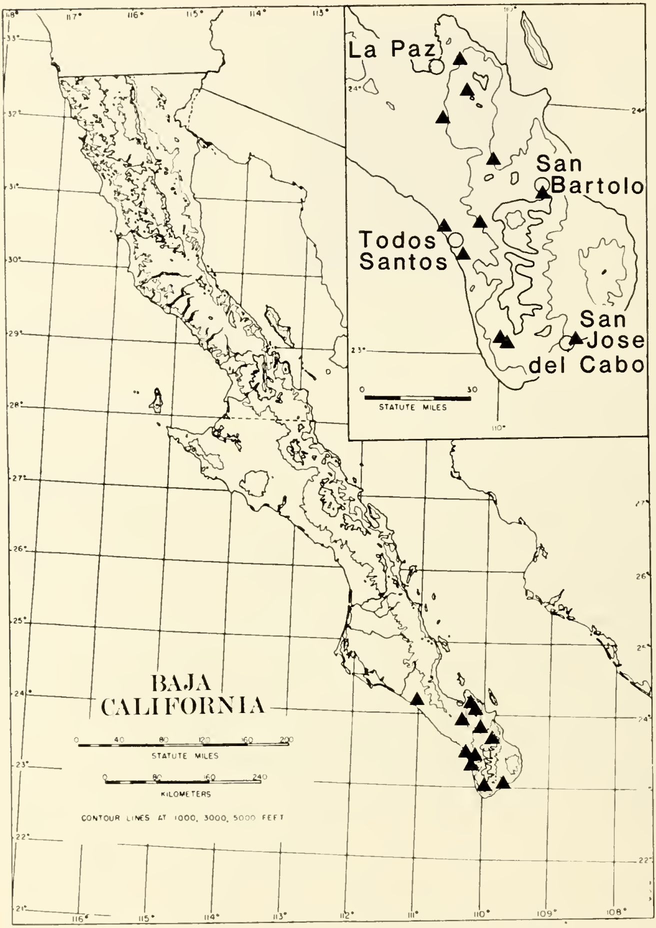


Fig. 3. Map of Baja California (inset: Cape Region); triangles indicate localities for *Gastrocopta* (*Immersidens*) *allyni.* Contour lines at 1000, 3000, and 5000 ft.

together (although this feature is variable), the angular reaching the plane of the peristome. The palatals are staggered, the lower one entering deeply—not at practically the same level as in *G. allyni. Gastrocopta rixfordi* resembles *G. dalliana* and was reported under the name *G. dalliana dalliana* from Baja California by Bequaert and Miller (1973). In *G. dalliana* the aperture is smaller, the columellar lamella emerges farther on the inner lip, and the angular and parietal lamellae are smaller and closer together than in *G. rixfordi.* Nonetheless, these are differences of degree, and the two taxa are undeniably similar. Although originally assigned by Hanna (1923) to the subgenus *Albinula* Sterki, 1892, *G. rixfordi* has the apertural dentition of *Immersidens. Gastrocopta allyni* and *G. rixfordi* are sympatric at San Bartolo (Smith, Miller, Christensen, and Roth, in preparation).

Gastrocopta (*Immersidens*) *prototypus* (Pilsbry, 1899), described from the Mexican state of Michoacan and subsequently recognized in Arizona in the form of *G. oligobasodon* (Pilsbry and Ferriss, 1910) (Bequaert and Miller, 1973), differs in having the dentition smaller throughout, the angular and parietal lamellae fusing near the outer tip of the latter (cf. Pilsbry 1948, fig. 487B), and the columellar lamella entirely horizontal.

Gastrocopta (*Albinula*) *holzingeri* (Sterki, 1889), which Pilsbry (1948) keyed with *Immersidens* because of its bifid angulo-parietal tooth, shows otherwise the characters of the subgenus *Albinula.* The columellar lamella is thin, high, and reaches well forward in the aperture.

The subgenus *Immersidens* is a Neotropical group, with three species precinctive in the Nearctic Southwestern Molluscan Province (Bequaert and Miller 1973), one (*G. prototypus*) with a disjunct distribution in the Southwestern Province and southern Mexico-Guatemala, and an undetermined number of species in Brazil and Argentina (Pilsbry 1916–1918). The similarities of *G. allyni* seem to lie with *G. ashmuni* and *G. cochisensis* of the Southwestern Province; we regard the strong dentition of these three species and the broad *lambda* configuration of the angular and parietal lamellae as synapomorphic. The further exaggeration of the angulo-parietal dentition and the thickening around the base of the peristome are autapomorphies of *G. allyni.*

The Cape Region of Baja California is known as a center of land mollusk endemism, particularly in the bulimulid genus *Rabdotus,* which has undergone a significant adaptive radiation there (Christensen 1979). The oreohelicid genus *Radiocentrum* includes one precinctive species in the Cape Region, another also present somewhat farther north in Baja California Sur, and several species in the Southwestern Province—a pattern much like that shown here for *Immersidens.*

While this pattern, in which a few localized species are scattered over a large geographic area, suggests relictual origins, the autapomorphies of *G. allyni* indicate a certain amount of independent evolution as well. It is significant that *Radiocentrum discus* Christensen and Miller, 1976, of the Cape Region has the most highly specialized shell form known in that genus. Perhaps the most important finding, from the standpoint of biogeographic generalizations, is that a group of minute mollusks like this species of *Gastrocopta* and its sister-group taxa of the Southwestern Province evidences an apparent history like that of the much larger—and presumably less easily dispersed—*Radiocentrum.*

Resumen

Se describe una nueva especie de caracol terrestre diminuto, *Gastrocopta* (*Immersidens*) *allyni,* escogida en localidades numerosas en Baja California Sur, Méx-

ico. La especie se distingue por el perístomo libre y continuo, la abertura con dentición fuerte, y las barreras laminares a lo largo de los labros interno y externo.

Acknowledgments

We are indebted to Allyn Smith and Walter B. Miller for an enduring collaboration on the study of Baja California mollusks, during which this species was diagnosed as new. The late Joseph C. Bequaert (who independently recognized *G. allyni* as undescribed) encouraged CCC in the investigation of minute mollusks. Stanley C. Williams kindly provided a base map and, along with Ken Letch, made available the SEM facilities of San Francisco State University.

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A REVISION OF THE SHORE FLY GENUS *HOMALOMETOPUS* BECKER (DIPTERA: EPHYDRIDAE)

Wayne N. Mathis

Abstract.—Species of the genus *Homalometopus* (type-species: *H. albiditinctus* Becker) are revised and now comprise six species of which four are new: *H. castaneus* (Israel), *H. corfuensis* (Greece), *H. ibericus* (Spain), *H. lukinatcha* (Senegal). One species, *H. platycephalus* (Becker, new combination, Tunisia, previously a synonym of *H. albiditinctus*), is resurrected from synonymy. *Homalometopus* is an Old World genus with a primarily circum-Mediterranean distribution but with extensions along the coast of West Africa (Senegal) and along the Red Sea (Gulf of Aqaba). The genus is halophilous, occurring mostly in coastal areas but also inland, where saline conditions exist.

While conducting field work in Israel for a faunal study of the Ephydridae of the Middle East (Fauna Palestina Series), two species of the genus *Homalometopus* Becker were collected. Becker (1926) treated only one species in the most recent revision of the genus, and I became interested in discovering if that species were represented by any of the specimens from Israel. The present study developed from that research.

Homalometopus, with *H. albiditinctus* Becker as type-species, was described early in this century (Becker 1903) from specimens collected at Port Said, Egypt. Since then, the genus has received meager attention. In 1907 Becker described a related genus and species from specimens collected in Tunisia, which he appropriately named *Tunisia platycephala.* Later, however, Becker (1926) considered that species to be conspecific with *H. albiditinctus.* Several years afterward, Collin (1949) published an excellent diagnosis for *Homalometopus* and also pointed out inaccuracies in the illustrations and text of Becker (1926). Collin's only lapse was his statement that no prescutellar bristles, except the dorsocentrals, are present. The lapse resulted from not having access to species of the genus other than *H. albidinctus,* the only species of *Homalometopus* lacking these bristles. After Collin, no further taxonomic work has appeared on the genus.

Beyond taxonomic works, there are a few publications providing new distributional data for the genus. In each case, however, the authors failed to recognize that they were dealing with mostly undescribed species, which were misidentified as *H. albiditinctus.* Czerny and Strobl (1909) reported *H. albiditinctus* (=*H. ibericus,* new species) from the Mediterranean coast of Spain; Soika (1956), in a study of animal populations of the Sahara, published a distributional map of *H. albiditinctus* (=four species), outlining its circum-Mediterranean distribution; and Canzoneri (1981) reported the occurrence of *H. albiditinctus* (=*H. lukinatcha,* new species) from Senegal.

The descriptive terminology used here follows that published in the recent *Manual of Nearctic Diptera, Vol. 1* (McAlpine 1981) with one exception. I have followed Sabrosky (in press) in using "microtomentum" rather than pruinescence or pollinosity for the dustlike vestiture over much of the cuticular surface. The dustlike appearance is the result of cuticular microtrichia at various densities, not a waxy substance as on a plum (pruinescence), or dust (pollinosity). The scutellar ratio used in the descriptions is defined as the scutellar length/scutellar width as measured between the two basal scutellar creases. All ratios are averages of three specimens. In quoting information on labels, I have cited data as they appear, with clarifying or interpretive remarks in brackets. A double set of quotation marks is used to distinguish data occurring on one label from those on another.

Acronyms used in the text, to indicate depositories of specimens, are as follows: BMNH, British Museum (Natural History), London, England; DCSA, Dipterorum Collectionis Strobl, Admont; DEI, former Deutsches Entomologisches Institut, collections in the Institut für Pflanzenschutzforschung, Zweigstelle Eberswalde, Abteilung Taxonomie der Insekten, Eberswalde, DDR; HU, Humboldt Universität, Berlin, DDR; MCV, Museo civico di Storia Naturale de Venezia, Italy; NMW, Naturhistorisches Museum, Wien, Austria; TAU, Tel Aviv University, Tel Aviv, Israel; USNM, former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Homalometopus Becker

Homalometopus Becker, 1903:175 [type-species: *Homalometopus albiditinctus* Becker, by monotypy].—Becker, 1905:205 [palaearctic catalog].—1926:95–96 [revision].

Tunisia Becker, 1907:399 [type-species: *Tunisia platycephala* Becker, by monotypy].—Becker, 1926:95 [synonymy].

Homalometopon [sic].—Collin, 1949:215 [generic diagnosis, discussion].

Diagnosis.—Small to moderately small shore flies, length 1.55 to 2.60 mm.

Head: Wider than high; mesofrons prominent as a rectangular, well-sclerotized plate, lateral margins parallel sided, anterior margin broadly rounded, sparsely but evenly setose, setae dark and conspicuous, with 1 slightly larger seta inserted laterally, about ⅓ distance back from anterior margin, mostly microtomentose but less so posteriorly, especially around ocelli; ocellar bristles lacking; 3 fronto-orbital setae, anterior 2 proclinate, posterior seta with lateroclinate to reclinate orientation; ocelli arranged to form an equilateral or isosceles triangle and with distance between posterior pair slightly larger; arista with ciliate fringe above and below; face most prominent between antennae, appearing swollen, otherwise face evenly arched transversely, with 2–4 conspicuous facial setae laterally in row nearly parallel to facial suture; eye broadly oval, setulose; gena high, over half eye height; clypeus generally exposed as a broad band; prementum normally developed, small, not unusually projected.

Thorax: Entirely microtomentose, mostly gray but frequently with some brownish coloration dorsally. Chaetotaxy, generally weakly developed, as follows: acrostichal setulae in 2–4 rows, frequently 1 prescutellar acrostichal bristle well developed; only 1 posterolateral dorsocentral bristle, dorsocentral setulae slightly larger than acrostichal setulae; 1 prominent presuteral seta; 1 postalar seta; 2 scutellar bristles, scutellum sparsely setulose dorsally; 1 postpronotal seta, although sometimes lacking; 2 notopleural setae, both inserted at about same level;

1 anepisternal seta. Legs with femora and tibiae similar in coloration and vestiture to pleural area, first 4 tarsomeres pale, yellowish, apical one dark. Wing with veins pale and membrane lightly milky white; costal vein ratio approximately 0.25; M vein ratio approximately 0.40; alula well developed.

Abdomen: Microtomentose, mostly grayish; terga 2–4 about equal in size, narrow; 5th tergum of male longer or as long as wide, lateral margin slightly angled inwardly, posterior angle broadly rounded; 5th tergum of female about as long as combined length of 3rd and 4th terga but lateral margins angled sharply inward forming acutely-pointed posterior angle. Male terminalia as follows: epandrium, in posterior view, shaped like inverted U, with arms short, not extended ventrally below level of cerci; cerci oblong, 2–3 times longer than wide; surstylus long and relatively narrow, shape and length varying with species; aedeagus a simple sclerotized tube with apical membranous portion folding back on sclerotized portion; aedeagal apodeme, in lateral view, triangular to lunate; hypandrium a broad, lightly sclerotized plate attached basally to aedeagal apodeme and base of surstyli. Female abdomen and terminalia as follows: segments 1–5 with terga well developed, wide and long, slightly narrowed ventrally; segments 6–7 with terga and sterna formed into narrow, fairly elongate tube; 8th segment and epiproct apparently lacking; hypoproct cordiform distally, pointed proximally, basal lobes setose; cerci broad, lobes rounded, setose; a narrow, sclerotized band between cerci and hypoproct. Female ventral receptacle with operculum comparatively much larger than extended process, helmet-shaped with ventral extension, asymmetrical in lateral view, symmetrical in frontal view, dorsum much wider, opercular opening ventrolateral; extended process apparently lacking cervex, corpus reduced to 2 footlike, basal processes.

Distribution.—Old World. Circum-Mediterranean (Egypt, Libya, Spain, Italy, Greece, Israel), Red Sea (Gulf of Aqaba), and west coast of Africa (Senegal).

Natural History.—Species of *Homalometopus* are halophilous, occurring on beaches of marine or inland saline areas. The immature stages are unknown. Adults are collected infrequently, although they may be abundant locally if the habitat is sampled properly. The cryptic coloration of adults makes them difficult to observe on a sandy background of similar coloration.

Discussion.—The genus *Homalometopus* belongs in the tribe Atissini, subfamily Psilopinae, where it is closely related to *Glenanthe* Haliday, and *Paraglenanthe* Wirth. As in the latter two genera, the arista is brushlike with ciliate fringe of about equal length above and below.

Homalometopus is distinct from other genera of Atissini, and its monophyly is established by the following characters.

1. Mesofrons distinct from remainder of frons as a conpicuous, well-sclerotized, rectangular plate that is bluntly rounded anteriorly, and sparsely setose.
2. Mesofrons with 1 seta that is slightly longer than the others and is inserted laterally, about ⅓ the distance back from the anterior margin.
3. Ocellar setae lacking.
4. Fronto-orbital setae 3, anterior 2 setae proclinate, posterior seta lateroclinate to reclinate in orientation.
5. Katepisternal bristle either lacking or much reduced and pale.
6. Basotarsomeres uniformly long, their length subequal to combined length of other tarsomeres.

7. Great similarity of structure of male terminalia (see generic description and figures).

Key to Species of *Homalometopus* Becker
(Primarily for males)

1. Prescutellar acrostichal bristles lacking or not evident, all acrostichal setae short and subequal in length (Egypt, Israel, Libya) .. *H. albiditinctus* Becker
– Prescutellar acrostichal bristles conspicuous, distinctly longer than other acrostichal setae 2
2. Mesonotum and posterior portion of frons a golden brown color (Israel) .... *H. castaneus,* new species
– Mesonotum and posterior portion of frons mostly grayish, if brownish coloration evident, it is very pale 3
3. Surstylus, in posterior view, longer than combined width across basal portions of surstyli 4
– Surstylus, in posterior view, shorter than combined width across basal portions of surstyli 5
4. Surstylus, in lateral view (Fig. 13), with taper of anterior and posterior margins about even, anteroapical portion angulate, posteroapical portion rounded; apex spatulate (Greece) .... *H. corfuensis,* new species
– Surstylus, in lateral view (Fig. 15), with posterior margin straight, anterior margin parallel with posterior margin except for abrupt taper at apical ¼ to narrower apex (Spain) .... *H. ibericus,* new species
5. Surstylus, in lateral view, with slightly recurved, subfalcate apex (Senegal, Spain) .... *H. lukinatcha,* new species
– Surstylus, in lateral view, with posterior margin nearly straight, not recurved, anterior margin with a prominent swelling at midlength (Tunisia) .... *H. platycephalus* (Becker)

Homalometopus albiditinctus Becker
Figs. 1–8

Homalometopus albiditinctus Becker, 1903:175.—Becker, 1905:205 [palaearctic catalog]; 1926:96 [in part, revision, figures of head].—Soika, 1956:113 [distribution map, list, Touggourt: Bahr Mahdjoub and Temacine].—Steyskal, 1968: 113 [list, Egypt: Salum, Dekheila, Maryut, Halaib, Hurghada, Amria, figures of head].

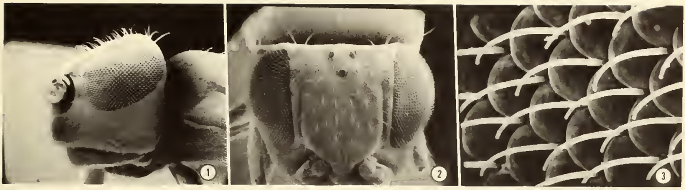
Homalometopon [sic] *albiditinctus.*—Collin, 1949:215 [discussion, Libya: Khamissa, Siwa].

Diagnosis.—Small to moderately small shore flies, length 1.65 to 2.20 mm.

Head (Figs. 1–5): Frons mostly gray to very slightly brownish grey.

Thorax (Fig. 6): Mesonotum mostly gray, some specimens with some brownish coloration. Prescutellar acrostichal bristles lacking. Scutellum short, posterior margin bluntly rounded; scutellar ratio 0.75.

Abdomen: Male terminalia (Figs. 7–8) as follows: epandrium with arms of inverted U more or less parallel; surstylus long and slender, over 5 times longer than wide, margins nearly parallel–sided in both posterior and lateral views, only base enlarged, apex evenly rounded.



Figs. 1–3. *Homalometopus albiditinctus.* 1, Head, lateral view; 2, Head, dorsal view; 3, Setulae of eye.

Type material.—Lectotype female, herein designated, is labelled "[Egypt] Port. Said. 45022. IV [handwritten]" "albiditinc-tus. Beck. [handwritten]" "Typus [red]" "LECTOTYPE [red print] ♀ Homalometopus albiditinctus Becker By W. N. Mathis [name handwritten, black subborder]." Paralectotype female, herein designated, bears the same label data as the lectotype. The lectotype is mounted on a minuten nadel in a foam rectangle, is in good condition, and is housed in the Museum für Naturkunde, Humboldt Universität, Berlin, DDR.

Other specimens examined.—LIBYA. Khamissa, 29 Jun 1935, J. Omer-Cooper (2 ♂, 6 ♀; BMNH). Sitra, 14 Jun 1935, J. Omer-Cooper (1 ♂; BMNH). EGYPT. Solloum, 11 Aug 1926, Kasim and Tewfik (4 ♂, 3 ♀; USNM). Sinai: Ofira, 22 Mar 1981, A. Freidberg (5 ♂; TAU); Quseima, 24 May 1981, W. N. Mathis (5 ♂, 7 ♀; USNM). ISRAEL. Sinai: Ras Burka, 23 Mar 1980, A. Freidberg and W. N. Mathis (1 ♀; USNM); Solar Lake, 14 km S Eilat, 23 May 1980, W. N. Mathis and A. Freidberg (32 ♂, 22 ♀; USNM). Kalia, 20 Mar 1980, W. N. Mathis and A. Freidberg (3 ♂, USNM). Ne'ot Ha'Kikar, 21 Mar 1980, A. Freidberg and W. N. Mathis (2 ♂, 5 ♀; USNM).

Distribution.—Eastern Mediterranean (Egypt, Israel, Libya) and Red Sea (Gulf of Aqaba: Ofira [Egypt], Ras Burka [Israel]). Many of the localities noted above are inland saline areas, such as along the Dead Sea (Kalia and Ne'ot Ha'Kikar). This is the most widespread species of the genus.

Remarks.—This species is the most easily recognized of the genus. Both sexes are most readily distinguished from congeners by the lack of a distinct pair of prescutellar acrostichal bristles. The shape of the various structures of the male terminalia are also diagnostic as illustrated and described.

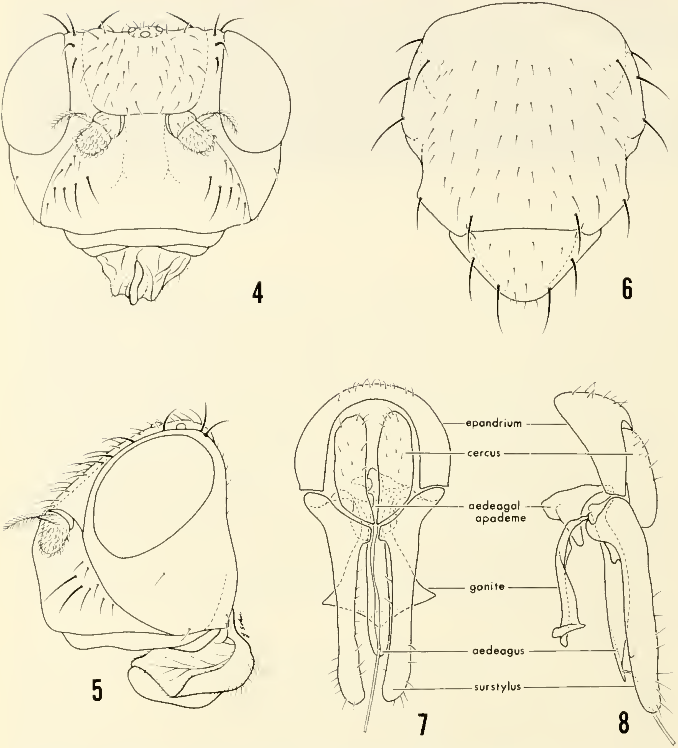
Homalometopus castaneus, new species
Figs. 9–11

Diagnosis.—Small to moderately small shore flies, length 1.90 to 2.60 mm.

Head: Frons with posterior portion and area of vertex surrounding ocelli brownish, contrasted with grayish anterior portion of frons.

Thorax (Fig. 9): Prescutellar acrostichal setae well developed, subequal in length to posterior dorsocentral setae. Mesonotum mostly brownish to golden brown. Scutellum long and with apex more acutely angulate; scutellar ratio 0.85.

Abdomen: Male terminalia (Figs. 10–11) as follows: epandrium with arms of inverted U slightly flared. Surstylus moderately long, tapered, in posterior view,

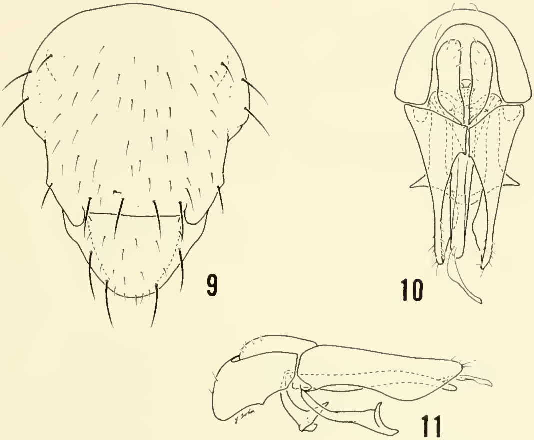


Figs. 4–8. *Homalometopus albiditinctus.* 4, Head, anterior view; 5, Head, lateral view; 6, Thorax, dorsal view; 7, Male genitalia, posterior view; 8, Male genitalia, lateral view.

to a narrow process; in lateral view, with anterior margin very slightly flared outward to form subapical enlargement, thereafter tapered inward to acutely rounded apex.

Type material.—Holotype male is labelled "ISRAEL. Akhziv, 20 Aug 1982, A. Freidberg." Allotype female and 51 paratypes (20 ♂, 31 ♀; TAU, USNM) bear the same label data as the holotype. Other paratypes as follows: ISRAEL. Rosh Haniqra, 2–3 Jun 1981–1982, A. Freidberg (2 ♂, 3 ♀; TAU, USNM). The holotype is mounted on a minuten nadel in a polyporus block, is in excellent condition, and is housed in the insect collection of Tel-Aviv University, Israel.

Distribution.—Levantian (Israel).



Figs. 9–11. *Homalometopus castaneus.* 9, Thorax, dorsal view; 10, Male genitalia, posterior view; 11, Male genitalia, lateral view.

Remarks.—This species is distinguished from *H. albiditinctus* by the presence of prescutellar acrostichal bristles. From the other congeners, it can be distinguished only by reference to structures of the male terminalia (see species description and figures).

Homalometopus corfuensis, new species
Figs. 12–13

Diagnosis.—Small to moderately small shore flies, length 1.85 to 2.15 mm.

Head: Frons more or less uniformly colored, mostly gray to very lightly tannish gray anteriorly.

Thorax: Prescutellar acrostichal setae well developed, subequal in length to posterior dorsocentral setae. Mesonotum mostly gray, some specimens with some brownish coloration. Scutellum short and bluntly rounded; scutellar ratio 0.75.

Abdomen: Male terminalia (Figs. 12–13) as follows: epandrium with arms of inverted U distinctly flared outward; surstylus moderately long and slender, tapered gradually, in posterior view, to an acutely rounded apex; in lateral view, with anterior margin tapered inward from base to just before middle, thereafter slightly flared outward to bluntly rounded apex.

Type material.—The holotype male is labelled "ISOLA CORFU' Sotioriotisa (Konkodali) Salicornieto, terr. nudo 22-VIII-57 A. G. Soika" "HOLOTYPE Homalometopus corfuensis Mathis [handwritten, red]." The holotype is glued to a paper point, is in good condition, and is housed in the Museo civico di Storia Naturale, Venezia (Venice, Italy). The allotype female and 16 other paratypes (13

♂, 1 ♀, 2?; BMNH, MCV, USNM) bear the same locality label data as the holotype. Other paratypes are as follows: GREECE. Thrace: Porto Lago, 1 Jun 1961, A. G. Soika (3 ♂, 25 ♀, MCV, USNM).

Distribution.—This species is known from Greece (Island of Corfu and Thrace [Porto Lago]).

Remarks.—This species is easily distinguished from *H. albiditinctus* by the presence of a pair of well-developed prescutellar acrostichal setae. From other congeners, however, it differs only in structural details of the male terminalia (see figures and description).

Homalometopus ibericus, new species
Figs. 14–17

Homalometopus albiditinctus non Becker, Soika, 1956:113–114 [misidentification].

Diagnosis.—Small to moderately small shore flies, length 1.95 to 2.35 mm.

Head: Frons mostly gray to slightly brownish gray in color.

Thorax: Prescutellar acrostichal setae well developed, subequal in length to posterior dorsocentral setae. Mesonotum mostly gray, some specimens with some brownish coloration. Scutellum long and moderately rounded apically; scutellar ratio 0.85.

Abdomen: Male terminalia (Figs. 14–17) as follows: epandrium with arms of inverted U slightly flared outward; surstylus moderately long, slender, basal ½ tapered gradually, apical ½ more or less parallel sided, apex bluntly rounded, subspatulate; surstylus, in lateral view, with basal ¾ somewhat parallel sided, thereafter abruptly narrowed to parallel-sided apex.

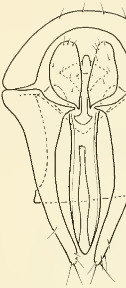
Type material.—The holotype male is labelled "SPAGNA ALICANTE saline barene 21-VII[Jul]-[19]54 A. Giordani Soika" "HOLOTYPE Homalometopus ibericus Mathis [handwritten, red]." The holotype is glued to a paper point, is in good condition, and is housed in the Museo civico di Storia Naturale, Venezia (Venice, Italy). The allotype female and 31 paratypes (17 ♂, 17 ♀; MCV, USNM) bear the same locality label data as the holotype. Other paratypes are as follows: SPAIN. Murcia: Mar Menor, San Javier (Ooued che muore in apiaggia terr. nudo), 24 Jul 1954, A. G. Soika (1 ♂, 8 ♀, MCV, USNM).

Other specimens examined.—SPAIN. Murcia: Cartagena (Capo de Palos), 22 Jul 1954, A. G. Soika (3 ♂, 2 ♀; MCV, USNM).

Distribution.—This species is known from the Mediterranean coast of Spain (provinces of Alicante and Murcia).

Remarks.—This species is easily distinguished from *H. albiditinctus* by the presence of a pair of well-developed prescutellar acrostichal setae. From other congeners, however, it can only be distinguished by characters of the male terminalia (see figures and description).

Slight variation is apparent in the shape of the surstylus of this species. In lateral view, the surstylus of the paratype males has an abrupt taper at the apical ¾, followed by a narrow, parallel-sided, apical process (Fig. 15). In males from Cartagena, the taper at the apical ¾ is not as abrupt, and the apical process is slightly tapered, not parallel sided (Fig. 17). The latter series could represent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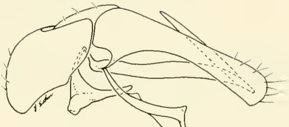
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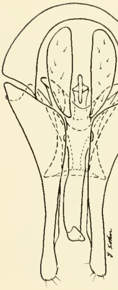
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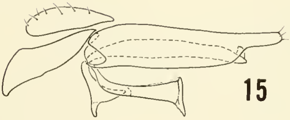
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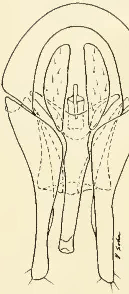
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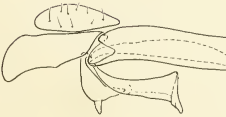
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Figs. 12–17. Male genitalia. 12, *Homalometopus corfuensis,* posterior view; 13, *H. corfuensis,* lateral view; 14, *H. ibericus* (paratopotype); 15, *H. ibericus* (paratopotype); 16, *H. ibericus* (Spain: Cartagena); 17, *H. ibericus* (Spain: Cartagena).

another species, although without more specimens and data I consider this series to be conspecific with the type series.

Homalometopus lukinatcha, new species
Figs. 18–19

Homalometopus albiditinctus, non Becker, Czerny and Strobl, 1909:270 [misidentification list, Spain. Cadiz Province: Algeciras].—Canzoneri, 1981:214 [misidentification list, Senegal: Kaolac].

Diagnosis.—Small to moderately small shore flies, length 1.55 to 2.35 mm.

Head: Frons mostly gray to slightly brownish gray in color.

Thorax: Prescutellar acrostichal setae well developed, subequal in length to posterior dorsocentral setae. Mesonotum mostly gray, some specimens with some brownish coloration. Scutellum long and moderately rounded apically; scutellar ratio 0.85.

Abdomen: Male terminalia (Figs. 18–19) as follows: epandrium with arms of inverted U slightly flared outward; surstylus moderately short, triangular, tapered gradually, in posterior view, to an acutely rounded apex; surstylus in lateral view, with anterior and posterior margins slightly sinuate, margin more or less straight on basal ⅔, thereafter tapered to posterior margin, forming an acutely rounded apex, posterior margin shallowly falcate.

Type material.—The holotype male is labelled "SENEGAL Kaolac fiume salm. Saolum 27-VI-[19]73 A. G[iordani] Soika" "HOLOTYPE Homalometopus lukinatcha Mathis [handwritten, red]." The holotype is mounted on a minuten nadel in a polyporus block, is in excellent condition, and is housed in the Museo civico di Storia Naturale, Venezia (Venice, Italy). The allotype female and 47 paratypes (18 ♂, 29 ♀; MCV, USNM) bear the same locality label data as the holotype. Other paratype are as follows: SPAIN. Cadiz: Algeciras, L. Czerny (1 ♂; NMW).

Distribution.—This species is known from the Mediterranean coast of Spain (Cadiz Province) and the coast of west Africa.

Remarks.—This species is easily distinguished from *H. albiditinctus* by the presence of a pair of well-developed prescutellar acrostichal setae. From its other congeners, however, reference only to characters of the male terminalia will distinguish them (see figures and description).

In the NMW there is a female from the San Fernando Mountains (Spain) that is probably conspecific, but without a male specimen, the determination is tentative.

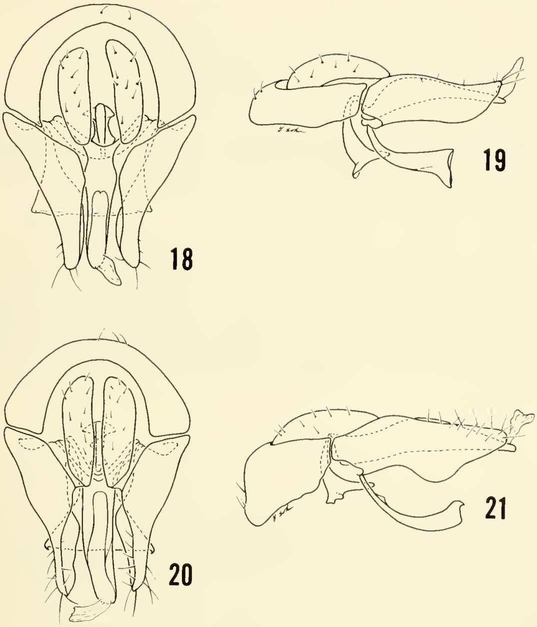
The species epithet is a noun in apposition.

Homalometopus platycephalus (Becker), new combination
Figs. 20–21

Tunisia platycephala Becker, 1907:400 [Tunisia: Tunis (May)].—Becker, 1926: 96 [in part, misidentification, synonymy with *H. albiditinctus*].

Diagnosis.—Moderately small shore flies, length 2.20 to 2.27 mm.

Head: Frons mostly a uniform gray to slightly brownish gray.



Figs. 18–21. Male genitalia. 18, *Homalometopus lukinatcha*, posterior view; 19, *H. lukinatcha*, lateral view; 20, *H. platycephalus*, posterior view; 21, *H. platycephalus*, lateral view.

Thorax: Prescutellar acrostichal setae well developed, subequal in length to posterior dorsocentral setae. Mesonotum mostly gray, some specimens with some brownish coloration. Scutellum long, moderately rounded apically; scutellar ratio 0.86.

Abdomen: Male terminalia (Figs. 20–21) as follows: epandrium with arms of inverted U distinctly flared outward; surstylus moderately long, triangular, tapered gradually, in posterior view, to acutely rounded apex; in lateral view, with anterior margin enlarged near middle, thereafter tapered to form a rounded apex, posterior margin with basal ⅓ flared outward, thereafter straight.

Type material.—Lectotype male, herein designated, is labelled "[Tunisia: Tunis] La Marsa 52938. [handwritten]" "Typus [red]" "LECTOTYPE Tunisia platycephala Becker By W. N. Mathis [handwritten, red]." The lectotype is mounted on a minuten nadel in a foam rectangle (there is also a second but bare minuten nadel in the foam block), is in good condition, and is housed in the Museum für Naturkunde, Humboldt Universität, Berlin, DDR. I have also examined two male and two female paralectotypes (HU, USNM) that have identical label data as the lectotype.

Distribution.—This species is known from the type series only.

Remarks.—Until this study, *H. platycelphalus* was considered to be a junior synonym of *H. albiditinctus,* although previously Becker (1907) had given separate generic and species status to this species. Later, Becker (1926) synonymized *Tunisia* with *Homalometopus* and considered their type species to be conspecific. The distinctiveness of *H. platycephalus* is quite evident based particularly on the male terminalia (see diagnosis and figures) of the type series.

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REVISION OF THE MILLIPED GENUS *CHEIROPUS* (POLYDESMIDA: XYSTODESMIDAE)

Rowland M. Shelley

Abstract.—The xystodesmid milliped genus *Cheiropus* is the southernmost genus in the tribe Apheloriini and is located primarily in the Coastal Plain physiographic province. The nominal genera *Stelgipus* and *Lyrranea* are subjective synonyms of *Cheiropus*, which consists of four allopatric species: *plancus* Loomis, *agrestis* (Loomis), *persicus* (Hoffman), and *serratus*, new species. A separate solenomerite in various positions on the lateral side of the acropodite stem diagnoses the genus, and the position of the solenomerite and the distal configuration of the acropodite are important specific characters. *Cheiropus* appears closely related to the Appalachian genus *Prionogonus* and represents ancestral stock that penetrated the lowland provinces of South Carolina, Georgia, and Florida. Cladal variation in the degree of serration, the breadth of the acropodal expansion, and the curvature of the acropodite reflects ancestral variation that has been retained independent of phylogeny.

The center of diversity and abundance of the xystodesmid milliped tribe Apheloriini is the southern Blue Ridge Province, occupied by seven genera and over 35 species. At both taxonomic levels, numbers decline to the east and south, so that only five genera and six species occur in the Coastal Plain of the Carolinas, and only three genera and four species inhabit coastal Georgia. Two of these nominal Georgian genera, *Cheiropus* and *Stelgipus*, are monotypic; so is *Lyrranea*, which occurs in the central Fall Zone region near Macon. I have long been intrigued by the prospect of three monotypic lowland genera in such close proximity, and I was prompted to review their concepts by discovering a new species in southeastern Georgia. This new species appeared to belong to *Stelgipus*, but since none of the taxa had been adequately diagnosed, I had to consider all of them in describing the new form. Eventually I concluded that only one genus was justified, and *Cheiropus* has priority, since it was published three pages before *Stelgipus* by Loomis (1944). The chief diagnostic character of *Cheiropus* is a lateral solenomerite that is distinct from the acropodite proper; specific differences obtain in the shape of the solenomerite, its position on the acropodite, and the distal configuration of the latter. *Cheiropus* is endemic to the southeastern Atlantic lowlands, and it is the genus farthest removed from the center of tribal abundance. However, it seems related to the Appalachian taxa through affinity to *Prionogonus*.

The history of *Cheiropus* begins with Loomis (1944), and with *Cheiropus*, *Stelgipus*, and their single species. Chamberlin and Hoffman (1958) recognized the former genus and *C. plancus* Loomis, but they synonymized *Stelgipus* with *Fontaria* thus publishing *F. agrestis* (Loomis), as recommended by Hoffman (1952). Hoffman (1963) proposed *Lyrranea* for a species from Peach County, Georgia, which he named *L. persica*. In 1979 Hoffman revived *Stelgipus*, which he included with *Cheiropus* and *Lyrranea* as components of the Apheloriini, and I (1979) revived Loomis' original combination, *S. agrestis,* for a form from Jacksonville, Florida. This record, however, was a misidentification of the new species, which is here named *serratus.*

In the present contribution I present a modern diagnosis of *Cheiropus,* a description and redescription of the four species, and discussions on ecology, distribution, and relationships. A key and detailed gonopodal illustrations are presented to facilitate identifications. I have been fortunate in having access to the small amount of preserved study material, whose repositories are indicated in the species accounts by the following acronyms:

AMNH—American Museum of Natural History, New York, New York.

FSCA—Florida State Collection of Arthropods, Gainesville, Florida.

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

NCSM—North Carolina State Museum of Natural History, Raleigh, North Carolina. The invertebrate catalog numbers of specimens in this collection are indicated in parentheses after appropriate locality citations.

RLH—Private collection of Richard L. Hoffman, Radford, Virginia.

WAS—Private collection of William A. Shear, Hampden-Sydney, Virginia.

ZMC—Zoologisk Museum, Copenhagen, Denmark.

Taxonomic Characters

The taxonomic characters of *Cheiropus* are found exclusively on the gonopods. Color pattern is of no value in making determinations because sympatric or nearly sympatric species of other apheloriine genera demonstrate the striped pattern with colors similar to those displayed by *Cheiropus.* Likewise, differences in the lengths and configurations of the processes of the fourth sterna in species of *Cheiropus* and sympatric taxa are insufficient to allow for valid determinations.

The chief diagnostic character of *Cheiropus,* the segregation of the solenomerite from the stem of the acropodite on the gonopods, is clearly visible in *persicus* and *plancus,* but it is masked by the expanded distal extremity of the acropodite in *agrestis* and *serratus.* Thus to distinguish *Cheiropus,* one has only to look for a separate solenomerite or an apically expanded acropodite.

At the species level the taxonomically useful characters involve the position of the solenomerite, the configuration of the acropodite, and the condition of its distal margin. *Cheiropus persicus* is distinguished by the relatively narrow acropodite that tapers to an acuminate tip and by the nearly basal origin of the solenomerite. The other three species have distally expanded acropodites, and the solenomerite is located on the under (concave) surface of the expansion in *F. agrestis* and *serratus* and laterally at its base in *plancus.* The expansion in western populations of *plancus* lacks marginal teeth, being smoothly rounded with one or two blunt terminations, but in eastern forms there are from one to five sharp dentations. The expansion in *agrestis* and *serratus* is truncate and variably jagged. These two species differ in the configuration of the solenomerite (slender and falcate in *serratus*; a thick, heavy boss in *agrestis*) and the marginal condition of the acropodite (with a single row of up to 12 distinct teeth in *agrestis*; with two or more rows of numerous small teeth and serrations in *serratus*).

Cheiropus Loomis

Cheiropus Loomis, 1944:170–171.—Chamberlin and Hoffman, 1958:25.—Hoffman, 1979:159.
Stelgipus Loomis, 1944:173.—Hoffman, 1979:159.
Fontaria: Chamberlin and Hoffman, 1958:33.
Lyrranea Hoffman, 1963:114–115; 1979:159.

Type species.—Of *Cheiropus, C. plancus* Loomis, 1944, by original designation; of *Stelgipus, S. agrestis* Loomis, 1944, by original designation; of *Lyrranea, L. persica* Hoffman, 1963, by original designation.

Description.—A genus of moderate to large xystodesmids with the following characteristics:

Body composed of head and 20 segments in both sexes; size varying from 8.0–10.5 mm wide and 32–40 mm long; W/L ratio similarly varying from around 23–27%. Body essentially parallel-sided in midbody region, tapering at both ends.

Color in life: paranota red, pink, or orange; metaterga black with red, pink, or orange stripes along caudal margins connecting paranotal spots; collum with concolorous stripe along anterior margin.

Head of normal appearance, smooth, polished. Epicranial suture shallow, distinct, terminating in interantennal region; interantennal isthmus moderately wide; genae not margined laterally, with shallow central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Antennae moderately slender, varying in length, becoming progressively more hirsute distally, with 4 conical sensory cones on ultimate article; no other sensory structures apparent. Facial setae reduced; epicranial and interantennal absent; frontal, genal, clypeal, and labral present.

Terga generally smooth, polished, becoming slightly coriaceous anteriorly. Collum variably broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, generally continuing slope of dorsum, caudolateral corners rounded on anteriormost segments, becoming blunt in midbody region and progressively more acute posteriorly. Peritremata distinct, strongly elevated above paranotal surface; ozopores located just caudal to midlength, opening dorsolaterad. Prozonites smaller than metazonites; strictures distinct, smooth.

Caudal segments normal for family.

Sides of metazonites smooth or irregular, with varying shallow, curved impressions. Strictures sharp, distinct. Pregonopodal sterna of males modified as follows: that of segment 4 with low, apically divided process between 3rd legs, much shorter than widths of adjacent coxae; that of segment 5 with two small projections between 4th legs, much shorter than widths of adjacent coxae, and unmodified or with low, flattened areas between 5th legs; that of segment 6 convexly recessed between 7th legs to accommodate apices of acropodites when body segments compressed. Postgonopodal sterna generally with broad, subtriangular lobes on segments 8–9, becoming flattened with shallow transverse and longitudinal grooves or depressions caudally. Gonapophyses on 2nd leg pair of males distinctly elevated above coxal surfaces, with round, apical knobs. Pregonopodal legs densely hirsute; postgonopodal legs becoming progressively less hirsute caudally. Coxae with variable, low tubercles beginning on pregonopodal or postgonopodal legs; prefemoral spines moderately long and sharply pointed; tarsal claws bisinuate. Hypoproct broadly rounded; paraprocts with margins strongly thickened.

Gonopodal aperture ovoid to elliptical, with slight or strong anteriolateral indentations, front flush with metazonal surface, sides and caudal edge elevated. Gonopods in situ with acropodites projecting ventrad from aperture, extending either anteriad in subparallel arrangement to beyond anterior margin of aperture, or anteriomediad, crossing in midline, and located wholly within aperture. Coxae moderate to large, without apophyses, connected by membrane only, no sternal remnant. Prefemora moderate to large, without prefemoral process, though occasionally with vestige. Acropodites moderately thick and heavy, well sclerotized, extending sublinearly from prefemur in most species, curving broadly anteriad through a single vertical plane in *agrestis*; either tapering smoothly to acuminate tip or with a cupulate, apically truncate, distal expansion at ⅔ length, apical margin of expansion variable, smooth or with a few or many sharply acute teeth and serrations on one or more rows, undersurface of expansion also variable, smooth, striated, or with numerous minute teeth, becoming larger and denser near apical margin. Solenomerite variable, a long to moderate process arising from stem of acropodite near base or at origin of distal expansion, or a short falcate projection or thickened boss located on undersurface of expansion. Prostatic groove arising in pit on medial side of prefemur, crossing to lateral side at variable distances along acropodite stem, opening apically on solenomerite.

Cyphopodal aperture broad, encircling 2nd legs, sides slightly elevated above metazonal surface. Cyphopods in situ located lateral to 2nd legs, usually with valves and corner of receptacle visible in aperture. Receptacle small to moderate in size, variously positioned with respect to valves, surface rugulose to granulate, without lobes. Valves moderate and subequal in size, surfaces finely granulate. Operculum minute, hidden under free end of valves.

Distribution.—Outer Coastal Plain of South Carolina to mid-peninsular Florida, ranging inland to the Fall Zone and central Piedmont Plateau of Georgia. The Cooper-Santee River may be the northern range limit in South Carolina, but there is no tangible southern boundary, as *plancus* extends beyond the Withlacoochee River. Likewise, there is no definite western limit; *agrestis* occurs well into piedmont Georgia and might be found along the base of the Blue Ridge escarpment. *Cheiropus* is chiefly a Coastal Plain genus, one of the few occurring on the coastal islands of Georgia and southeastern South Carolina.

Species.—Four.

Remarks.—To Loomis, the position of the solenomerite with respect to the distal acropodal expansion in *plancus* suggested a cupped hand with its palm outward opposed by the thumb, and hence he based the generic name on the Greek word for hand.

Because of the gonopodal variability of *Cheiropus*, I decided against using the terminology devised for *Sigmoria* and adopted for *Prionogonus* (Shelley 1981, 1982), although *Cheiropus* appears to share a common ancestor with the latter (see relationships section). The gonopods of *persicus*, for example, are highly modified and the zones of "sigmoid" acropodites are not apparent, so this terminology would be meaningless. The acropodites of the other three species terminate at the distal extremity of the "peak," but the solenomerite, which represents the repositioned "distal zone," is neither distal nor stationary in *Cheiropus* and thus cannot be characterized by this terminology. Consequently, new language is required for the species of *Cheiropus,* and their accounts cannot be compared directly with those of the "sigmoid" species.

Key to Species of *Cheiropus* (Based on Adult Males)

1. Acropodite broadened distally into cupulate expansion or cap; solenomerite either beneath and partly or completely obscured by cap, or located laterally at its base 2
– Acropodite relatively narrow, widest basally, tapering smoothly to acuminate tip; solenomerite about half the length of acropodite, arising near base of, and running subparallel to, acropodite; Fall Zone of central Georgia .... *persicus* (Hoffman)
2. Solenomerite distinctly visible on lateral side of acropodite at base of expansion; except for eastern populations, margin of expansion not strongly serrated; Thomas Co., Georgia, to Hernando Co., Florida .... *plancus* Loomis
– Solenomerite located beneath cap and partly or completely obscured; margin of expansion strongly serrated 3
3. Acropodite in form of continuous, broadly curved arc, extending in medial view beyond level of prefemur; margin of expansion with a single row of up to 12 teeth; solenomerite a thickened, sclerotized boss; Charleston Co., South Carolina, to Clarke and Burke cos., Georgia .... *agrestis* (Loomis)
– Acropodite in form of inverted L, stem relatively straight, bent sharply anteriad at level of cap, overhanging prefemur in medial view; margin of expansion highly serrate, with two or more rows of variable teeth; solenomerite a thin, falcate projection tucked under teeth, distal to boss; Liberty Co., Georgia, to Duval Co., Florida .... *serratus,* new species

Cheiropus plancus Loomis
Figs. 1–7

Cheiropus plancus Loomis, 1944:171–172, Fig. 3.—Chamberlin and Hoffman, 1958:26.

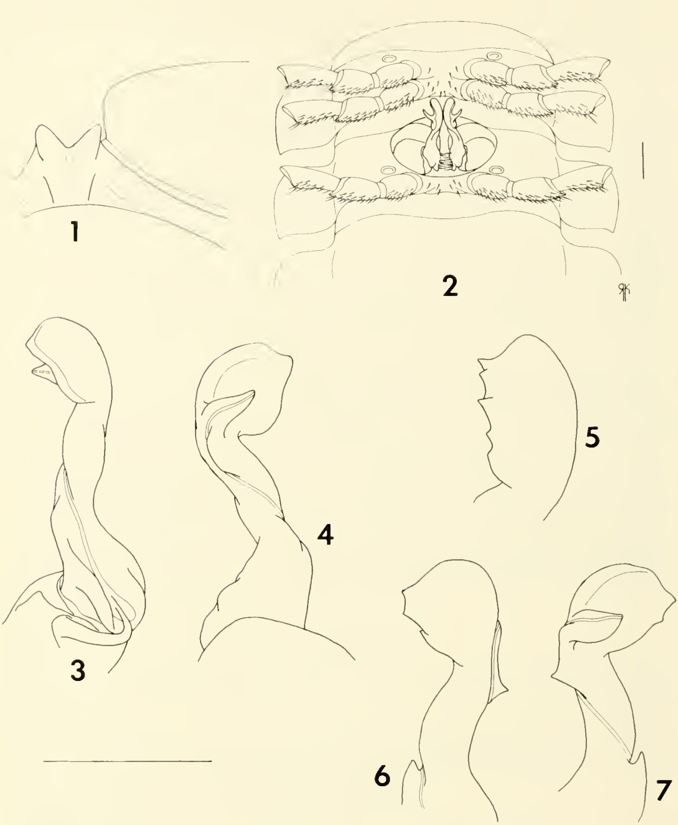
Type specimens.—Male holotype (MCZ) collected by V. E. Shelford, 27 Jul 1942, from Thomasville, Thomas Co., Georgia. Male paratype (MCZ) taken by same collector, 24 Jul 1942, from Gainesville, Alachua Co., Florida.

Diagnosis.—Solenomerite a short, blunt projection arising at base of distal expansion of acropodite; margin of latter usually smooth with one or two blunt terminations, occasionally sharply pointed teeth; stem of acropodite twisted at midlength.

Holotype.—Length 39.2 mm, maximum width 9.8 mm, W/L ratio 25.0%; depth/width ratio 56.1%. Segmental widths as follows:

collum	5.8 mm	8th–14th	9.8
2nd	7.4	15th	9.5
3rd	8.3	16th	9.1
4th–5th	9.1	17th	8.3
6th–7th	9.5	18th	5.7

Color in life unknown; the pigments reported by Loomis (1944) are obviously the faded colors of preservation.



Figs. 1–7. *Cheiropus plancus.* 1, Process of 4th sternum of holotype, caudal view; 2, Gonopods in situ, ventral view of near topotypical male from Thomas Co., Georgia; 3, Left gonopod of holotype, medial view; 4, The same, lateral view; 5, Acropodite expansion of paratype, submedial view; 6, Telopodite of left gonopod of male from Alachua Co., Florida, medial view; 7, The same, lateral view. Scale line for Fig. 2 = 1.00 mm; line for other Figs. = 1.00 mm for 1, 6–7; 1.33 mm for 3–4; and 0.80 mm for 5. Setation is omitted from all sternal and dissected gonopod drawings in this paper.

Head capsule smooth, polished, width across genal apices 4.1 mm, interantennal isthmus 1.5 mm. Epicranial suture thin but distinct, terminating in interantennal region, bifid. Antennae reaching back nearly to caudal margin of 4th tergite, becoming progressively more hirsute distally; relative lengths of antennomeres

2>3>6>4=5>1>7. Genae not margined laterally, with distinct medial impression, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Facial setae as follows: epicranial and interantennal absent; frontal 1-1, genal 4-4, clypeal about 11-11, labral about 28-28.

Terga smooth, polished, becoming slightly coriaceous on paranota. Collum broad, ends slightly beyond those of following tergite. Paranota moderately depressed, angled slightly ventrad and continuing slope of dorsum; anterior corners rounded, caudolateral corners rounded through segments 4, becoming blunt and progressively more pointed posteriorly. Peritremata thick and conspicuous, sharply set off from paranotal surface. Ozopores located in slight swellings near middle of peritremata, opening dorsad.

Sides of metazonites relatively smooth. Strictures sharp, distinct. Sternum of segment 4 with two small, blunt, widely spaced and diverging lobes, much shorter than adjacent coxal widths (Fig. 1); of segment 5, with two minute, widely separated tubercles between 4th legs, unmodified between 5th legs; of segment 6, convexly recessed between 7th legs to accommodate apices of telopodites. Postgonopodal sterna with two broad, subtriangular lobes along caudal edges on segments 7–8 and two blunt tubercles subtending posterior coxae on remaining segments; with shallow, central impressions and shallow, transverse grooves between leg pairs. Pregonopodal legs densely hirsute, postgonopodal legs becoming progressively less hirsute caudally. Small coxal tubercle present on legs of segments 9–17; prefemoral spines beginning on segment 6, becoming progressively longer and sharper caudally; tarsal claws bisinuately curved. Hypoproct broadly rounded; paraprocts with margins strongly thickened.

Gonopodal aperture elliptical, 2.4 mm wide and 1.3 mm long at midpoint, without indentations, caudolateral edges raised above metazonal surface. Gonopods in situ (Fig. 2, not this specimen) with telopodites projecting anteriad from aperture, either lying beside each other in parallel fashion or crossing distally, extending forward just beyond anterior margin of aperture. Gonopod structure as follows (Figs. 3–4): Acropodite extending ventrad from prefemur, widening at about ⅔ length into broad, rounded, cupulate distal swelling or expansion, shielding and obscuring base of solenomerite in medial view; acropodite stem proximal to bend strongly twisted, with low, rounded shoulder laterally at base of solenomerite; expansion with wide, central impression on lateral side, margin smoothly curved proximad, indented slightly at midlength and extending into single, blunt termination. Solenomerite short and blunt, subtriangular, about half as long as expansion, arising from lateral side of acropodite stem at base of expansion, base obscured by latter in medial view, tip directed toward distalmost point of swelling. Prostatic groove arising in pit in base of prefemur, crossing to lateral side at torsion in midlength of acropodite stem, running behind lateral shoulder onto solenomerite, opening apically.

Male paratype.—The male paratype from Gainesville, Alachua County, Florida, designated by Loomis (1944) was taken some 125 miles SE of the type locality. It differs most notably from the holotype in the irregular margin of the expansion, which is lined with five sharply pointed teeth (Fig. 5). Other characteristics of the Alachua County population are discussed under variation.

Female topotype.—Length 38.8 mm, maximum width 10.2 mm, W/L ratio

26.2%, depth/width ratio 65.7%. Somatic features agreeing essentially with holotype, except paranota more strongly depressed, giving appearance of more highly arched body.

Cyphopods in situ with opening of valves and corner of receptacle visible in aperture. Receptacle relatively small, cupped around caudolateral surface of valves, surface finely granulate.

Variation.—Western populations in Jefferson County, Florida, and the vicinity of Tallahassee agree closely with the holotype. Eastern males from Bradford to Hernando counties differ, however, in that the margin of the expansion possesses from one to five sharp teeth. Some have a vestigial prefemoral process (Figs. 6–7), and a basal spine on the shoulder of the acropodite. The shoulder is larger in these males and is slightly visible in medial view, along with the prostatic groove, which passes behind it before entering the solenomerite.

Ecology.—*Cheiropus plancus* is available during the hot summer months. Most specimens were collected from June–August, and I have not encountered it in October or November at Devil's Millhopper State Park, where it is common in the summer. According to Loomis (1944), the holotype came from climax magnolia-beech woods, and numerous specimens have been collected from damp slopes along Hogtown Creek in Gainesville. The sinkhole at Devil's Millhopper is surrounded by hardwoods, and *plancus* occurs under leaves in moist spots. At Ichetucknee Springs it was found on damp moss in cracks on a concrete retaining wall a few feet above the river. The material from Brooksville was discovered under thin leaf layers on hard, moist substrate in an area dominated by sweet gum trees and overgrown with kudzu. I have never found *plancus* under live oaks and believe it occurs solely in litter of broad-leaved species. Tracts of these are rare in Florida, but *plancus* may be expected in the few that do exist west of the St. John's River.

Distribution.—Southern Georgia to west-central, peninsular Florida, from Thomasville to Brooksville. The area lies east of the Ochlockonee River and extends across the Suwannee and Withlacoochee rivers. The easternmost known locality is some 35 miles west of the St. John's River. Specimens were examined as follows:

GEORGIA: *Thomas Co.,* Thomasville, M, 27 Jul 1942, V. E. Shelford (MCZ), and Millpond Plantation, Thomasville, M, 16 Jul 1973, F. A. Coyle (WAS), and 3M, 3F, 25 Jun 1978, H. W. Levi (MCZ) TYPE LOCALITY; S of Boston, Bar-M-Ranch, M, 2F, Apr 1968, and 2M, 15 Jul 1973, W. Sedgwick (WAS), and M, 25 Jun 1978, H. W. Levi (MCZ).

FLORIDA: *Leon Co.,* Tallahassee, 2M, 30 Jun 1952, H. H. Humm (FSCA); and Tall Timbers Research Station, M, 25 Oct 1972, D. L. Harris (FSCA); M, 8 Apr 1968, A. M. Chickering (MCZ); M, F, 17 Jul 1972, W. W. Whitcomb (FSCA); and 2M, 2F, 30 Jul 1973 (FSCA). *Jefferson Co.,* Monticello, Big Bend Horticultural Lab, M, date and collector unknown (FSCA). *Hamilton Co.,* Stephen Foster St. Pk., 10M, 4F, 15 Jun 1959, A. Williams (FSCA). *Columbia Co.,* Ichetucknee Springs, 4F, 22 Jun 1977, J. E. Cooper (NCSM A1599). *Bradford Co.,* 3 mi. NNE Brooker, M, F, 9 Aug 1959, L. Hubricht (RLH). *Alachua Co.,* Gainesville, M, 24 Jul 1942, V. E. Shelford (MCZ), along Hogtown Cr. in Gainesville, 11M, 7F, 23 Jun 1959, H. V. Weems and W. J. Platt (FSCA), and many other males and females collected in May, June, July, and August (FSCA); Devil's Mill Hopper

St. Pk., 2M, F, 5 Jun 1959, N. B. Causey (FSCA), other males and females in summers of various years (FSCA), and 2M, F, 9 Jun 1983, R. M. Shelley and J. L. Staton (NCSM A4149). *Hernando Co.*, Brooksville, corner of Bailey and Lamar Sts., 7M, 4F, 13 Jun 1983, R. M. Shelley (NCSM A4159).

Remarks.—In life the proterga of *plancus* are black, and the metaterga are black with orange stripes along the caudal edges. The stripes become wider on the caudal halves of the paranota, and the peritremata are also orange; however, the anterior halves of the paranota are black. There is also an orange stripe along the anterior margin of the collum, which connects laterally with the caudal stripe.

Cheiropus plancus is the southernmost representative of the tribe Apheloriini. The only xystodesmids known from farther south in Florida are *Dicellarius okefenokensis* (Chamberlin) and *Pleuroloma cala* (Chamberlin), of the tribes Pachydesmini and Rhysodesmini, respectively. Until 1983, Gainesville was the southernmost known locality, but the discovery of a population in Brooksville, Hernando County, represents a range extension of around 85 miles and establishes its presence in the western side of the northern half of the peninsula.

Cheiropus persicus (Hoffman), new combination
Figs. 8–11

Lyrranea persica Hoffman, 1963:115–119, Figs. 1–4.

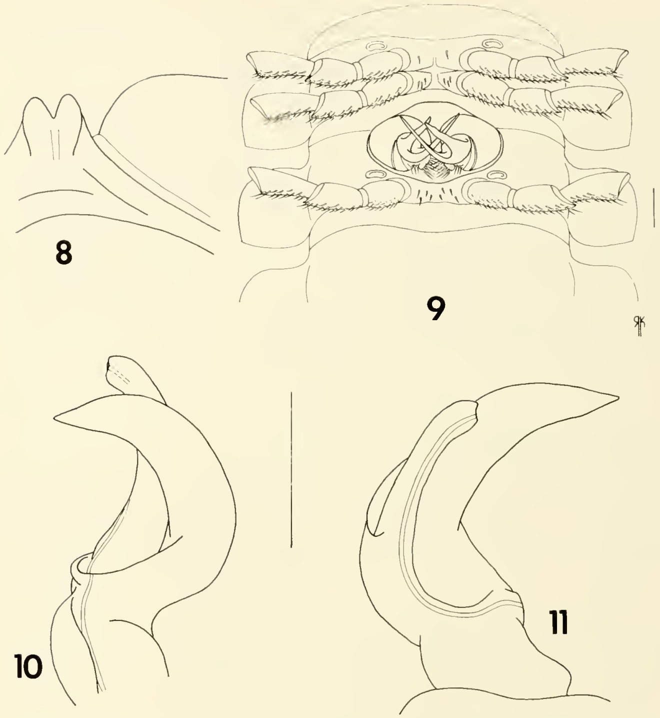
Type specimen.—Male holotype (USNM) collected by L. Hubricht, 24 Apr 1960, from 3 mi. W Fort Valley, Peach Co., Georgia.

Diagnosis.—Solenomerite relatively long, arising near base of, and extending subparallel to, acropodite; latter without expansion, tapering smoothly to acuminate tip.

Description.—I did not examine the holotype of this species, which was thorougly described and illustrated by Hoffman (1963). However, the gonopods must be redescribed for comparison with the other species of *Cheiropus.* The in situ drawing of the gonopods (Fig. 9) differs from that of Hoffman (1963, Fig. 1) in being from the ventral aspect instead of the anterior. This view is more useful to collectors attempting to identify xystodesmids in the field and is the standard one I present in papers. I also show in Fig. 8 the process of the 4th sternum, which Hoffman verbally characterized. The following is a composite description of the gonopods of all males available to me, encompassing all aspects of variation.

Gonopodal aperture subovoid, about 3.5 mm wide and 1.8 mm long at midpoint, indented anteriolaterad, sides elevated above metazonal surface. Gonopods in situ (Fig. 9) with telopodites projecting ventrad from aperture, extending over opposite side of aperture and crossing in midline, either lying entirely over aperture or tips extending just beyond anterior margin. Gonopod structure as follows (Figs. 10–11): Solenomerite diverging laterally from acropodite at about ⅓ length, extending subparallel to acropodite for about ¾ of length of latter, directed ventrad, slightly curved and wider distad, apically blunt. Acropodite with concavity subtending solenomerite, curved broadly anteriad and extending beyond level of prefemur, margin smooth, sides narrowing smoothly to acuminate tip. Prostatic groove arising in pit in prefemur, running along anterior edge of concavity onto solenomerite, opening apically in center of latter.

Description of female.—Length 36.3 mm, maximum width 8.9 mm, W/L ratio



Figs. 8–11. *Cheiropus persicus.* 8, Process of 4th sternum of male from Houston Co., Georgia, caudal view; 9, Gonopods in situ, ventral view of male from Houston Co.; 10, Telopodite of left gonopod of male from Houston Co., medial view; 11, The same, lateral view. Scale line for Fig. 9 = 1.00 mm; line for other Figs. = 1.00 mm for each.

24.5%, depth/width ratio 71.9%. Agreeing closely with males in somatic features, except paranota more strongly depressed, creating appearance of more highly arched body.

Cyphopods in situ with opening of valves and corner of receptacle visible in aperture. Receptacle relatively small, subtriangular, located medial to valves, surface finely granulate.

Ecology.—*Cheiropus persicus* occurs in typical piedmont apheloriine habitat, under thin layers of leaves (usually dogwood or maples) on relatively hard substrates near water sources.

Distribution.—Known only from four counties in the Fall Zone region of west-central Georgia, but doubtlessly occupies a larger area in the Fall Zone and adjacent parts of the Piedmont Plateau and Coastal Plain. Specimens were examined as follows: all were collected by the author or an assistant:

GEORGIA: *Peach Co.,* 2 mi. W Fort Valley, along Georgia hwy. 96, 2F near topotypes, 12 Apr 1978 (NCSM A1839). *Houston Co.,* 4 mi. NW Perry, along US hwy. 341 at Bay Cr., 5M, 16 Sep 1979 (NCSM A2880); and 4 mi. SW Perry, along US hwy. 341 at Flat Cr., M, 16 Sep 1979 (NCSM A2878). *Crawford Co.,* 4 mi. E Roberts, along Georgia hwy. 42, 2.6 mi. E US hwy. 80, M, 16 Sep 1979 (NCSM A2883). *Taylor Co.,* along Georgia hwy. 96 just E of Reynolds, F, 12 Apr 1978 (NCSM A1839).

Remarks.—In life *persicus* displays the red striped color pattern of many apheloriine xystodesmids. The metaterga are black with wide red stripes along the caudal edges connecting red paranota. There is a concolorous red stripe along the anterior margin of the collum.

The highly modified acropodites of *persicus* lack cupulate distal expansions and are thus distinct from those of its congeners. Some may therefore question the congeneric status of *persicus,* but as discussed elsewhere in this paper, the basal origin of the solenomerite from the acropodite culminates the trend in these lowland forms to more proximal derivation. Thus, absence of the expansion, like the basal origin of the solenomerite, are best regarded as autapomorphic traits of *persicus* rather than as criteria for a distinct generic taxon. Were *Lyrranea* to be retained for *persicus, Stelgipus* would have to stand for *agrestis* and *serratus,* since their solenomerites are in different positions from that of *plancus.* Since the species are linked by common, inferred, ancestral species, only one genus is justified, which is defined as having a variably positioned solenomerite. It is also worth noting that the acropodal curvature of *persicus* is similar to that of the geographically proximal population of *agrestis* (compare Figs. 10 and 13).

Cheiropus agrestis (Loomis), new combination

Figs. 12–16

Stelgipus agrestis Loomis, 1944:173–174, Fig. 5.
Fontaria agrestis:—Chamberlin and Hoffman, 1958:33–34.

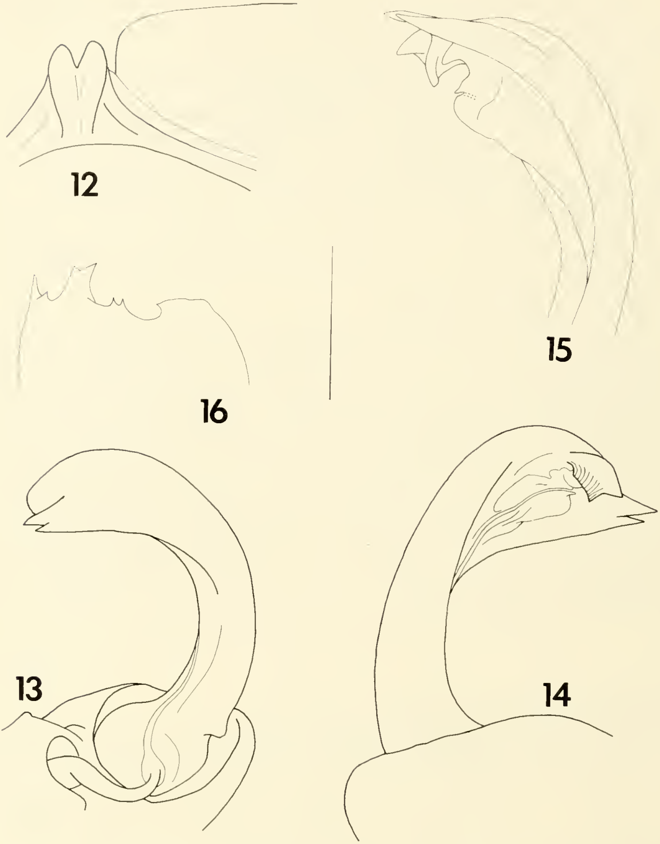
Type-specimen.—Male holotype (MCZ) collected by H. F. Loomis, Jun 1943, from Waynesboro, Burke Co., Georgia.

Diagnosis.—Acropodite in form of continuous, broadly curved arc, extending in medial view well beyond level of prefemur, with distal expansion and moderately serrate apical margin consisting of a single row of up to 12 teeth; solenomerite a thick, heavy boss located on undersurface of expansion.

Holotype.—Length 37.4 mm, maximum width 9.4 mm, W/L ratio 24.9%; depth/width ratio 63.4%. Segmental widths as follows; segments 2–7 are damaged and cannot be measured.

collum	7.6 mm	13th–15th	9.4
8th	8.8	16th	9.1
9th–10th	9.0	17th	8.0
11th–12th	9.2	18th	6.1

Color in life unknown; Loomis (1944) reported that it was bleached when found.



Figs. 12–16. *Cheiropus agrestis.* 12, Process of 4th sternum of holotype, caudal view; 13, Left gonopod of holotype, medial view; 14, The same, lateral view; 15, Distal half of acropodite of same, submedial view; 16, Distal extremity of expansion of same, subventral view. Scale line = 1.00 mm for Figs. 12–15, 1.33 mm for 16.

Somatic features similar to those of *plancus,* with following exceptions:

Width across genal apices 4.7 mm, interantennal isthmus 1.8 mm. Antennae reaching back only to caudal margin of 2nd tergite, relative lengths of antennomeres 2>3=5>6>4>1>7. Facial setae as in *plancus* except genal 3-3, clypeal about 16-16, labral about 22-22, merging with clypeal series and continuing for short distance along genal margins.

Sides of metazonites with several shallow, grooved impressions. Sternum of segment 4 with small, apically divided process between 3rd legs, much shorter than widths of adjacent coxae (Fig. 12); of segment 5, produced into two paramedial knobs between 4th legs, shorter than adjacent coxal widths, and two broad elevated areas between 5th legs; of segment 6, convexly recessed between 7th legs to accommodate apices of telopodites. Postgonopodal sterna with caudal margins produced into broad, subtriangular lobes on segments 7–9 and short, blunt teeth subtending adjacent coxae on remaining segments; center of sterna slightly depressed, with transverse groove between leg pairs. Coxae without projections; prefemoral spines beginning on segment 5.

Gonopodal aperture subelliptical, about 3.8 mm wide and 2.4 mm long at midpoint, strongly indented anteriolaterally, sides flush with metazonal surface. Gonopods in situ not observed but probably similar to condition in *serratus* or with apices overlapping. Gonopod structure as follows (Figs. 13–16): coxa massive, surrounding base of prefemur. Acropodite short but massive, heavily sclerotized, curving strongly but smoothly at midlength and extending in arc well beyond level of prefemur; portion distal to bend greatly widened into umbrellar-shaped expansion shielding and protecting solenomerite, inner surface deeply concave and highly irregular with numerous scattered striae and minute teeth, striae and teeth clustered distally near solenomerite; apical margin of expansion with two lobes, two sharply pointed, irregularly subdivided spines on medial lobe, lateral lobe with two small inner teeth, becoming smooth and straight laterally and overhanging short, vertical, striated lamina; latter extending nearly to level of solenomerite and continuing as thin, irregularly toothed lamella to base of solenomerite. Solenomerite a short, thickened, heavily sclerotized boss or callus located distally on lateral part of acropodite beneath lateral marginal lobe, visible only in lateral view, masked by medial marginal lobe in medial view; solenomerite apically broad, with numerous minute teeth and one longer, curved tooth at opening of groove. Prostatic groove arising in pit in base of prefemur, crossing to lateral side of acropodite stem basally, continuing onto solenomerite to apical opening.

Variation.—The acropodite expansion is broader in the Clarke County male and curves dorsad medially so that its overall configuration resembles an umbrella. In the South Carolina male the expansion is reduced and flattened, and does not curve dorsad medially thus resembling the condition in *serratus*. The acropodite is also more serrated in the latter individual.

Distribution.—Piedmont Plateau and Coastal Plain of northern Georgia and southern South Carolina. *Cheiropus agrestis* is one of the few apheloriine millipeds occurring in both physiographic provinces and one of only two traversing the Savannah River, the other being an undescribed species of *Hubroria*. Specimens were examined as follows:

SOUTH CAROLINA: *Charleston Co.,* Wadmalaw Island, Rockland Plantation, M, 28 Jun, year unknown, O. F. Cook (RLH).

GEORGIA: *Clarke Co.,* Bogart, M, 2 Jul 1973, R. M. Duffield (RLH). *Burke Co.,* Waynesboro, M, Jun 1943, H. F. Loomis (MCZ) TYPE LOCALITY; and 5 mi. SE Waynesboro, M, 22 May 1960, L. Hubricht (RLH).

Remarks.—Males of *agrestis* are the largest in the genus and are equivalent in size to those of *Cleptoria rileyi* (Bollman) and *C. abbotti* Hoffman. No females have been discovered, so the cyphopodal condition is unknown.

Cheiropus agrestis has been encountered only four times, with a single male being taken each time. I have searched for it repeatedly but unsuccessfully, even on Wadmalaw Island and at Waynesboro. Never having collected a specimen myself, I cannot report the living color or preferred habitat. No useful notes were in the sample vials, but the preserved specimens exhibit a striped pattern that suggests the red paranota and metatergal stripe coloration of other apheloriine species. The South Carolina male resembles *serratus* in the acropodite expansion and its occurrence in the outer Coastal Plain. However, it has the solenomerite boss of *agrestis,* and I include it with this species because of the importance of the solenomerite in the taxonomy of this genus. Additional material between Burke County, Georgia, and Charleston County, South Carolina, would help clarify this matter.

Cheiropus serratus, new species

Figs. 17–22

Type-specimens.—Male holotype (NCSM A3589) and three male and four female paratypes collected by R. M. Shelley and R. W. Jones, 2 Oct 1980, from Crooked River State Park, Camden Co., Georgia. Male paratype collected by R. M. Shelley at same locality, 3 Jul 1977. Male and female paratypes deposited in FSCA.

Diagnosis.—Acropodite in form of inverted L, stem relatively straight, bent sharply anteriad at ⅔ length and overhanging prefemur in medial view, with distal expansion and highly serrate, jagged apical margin consisting of two or more rows of variable teeth; solenomerite thin and falcate, located on undersurface of expansion beneath overhanging rows of teeth.

Holotype.—Length 35.8 mm, maximum width 8.3 mm, W/L ratio 23.2%, depth/width ratio 62.7%. Segmental widths as follows:

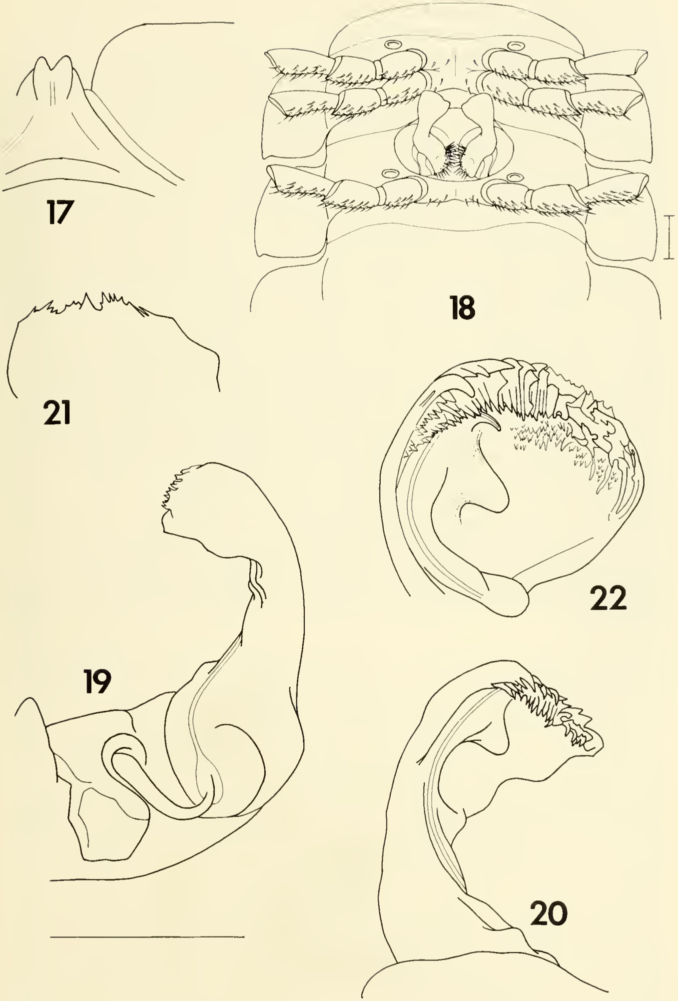
collum 5.2 mm
2nd 6.8
3rd 7.3
4th 7.8
5th 8.1
6th–14th 8.3
15th 8.0
16th 7.6
17th 6.4
18th 4.6

Color in life: paranota pink-orange, metaterga black with narrow, pink-orange stripes along caudal margins connecting paranotal spots; collum with stripes along both anterior and caudal edges.

Somatic features similar to those of *plancus,* with following exceptions:

Width across genal apices 3.6 mm, interantennal isthmus 1.3 mm. Facial setae as in *plancus* except genal 2-2, clypeal about 10-10, and labral about 15-15.

Sides of metazonites with several curved, shallow impressions. Sternum of segment 4 with two minute lobes between 3rd legs, much shorter than widths of adjacent coxae (Fig. 17); that of segment 5 with two low paramedial knobs between 4th legs, shorter than width of adjacent coxae, and two low elevated areas between 5th legs; that of segment 6 with deep, convex recession between 7th legs to accommodate apices of acropodites. Postgonopodal sterna flat and unmodified, with narrow transverse grooves between leg pairs and wide, shallow, longitudinal



Figs. 17–22. *Cheiropus serratus.* 17, Process of 4th sternum of holotype, caudal view; 18, Gonopods in situ, ventral view of paratype; 19, Left gonopod of holotype, medial view; 20, The same, lateral view; 21, Distal extremity of expansion of same, subventral view; 22, Undersurface of expansion of male from Duval Co., Florida, subdorsal view. Scale line for Fig. 18 = 1.00 mm; line for other Figs. = 1.00 mm for 17 and 20–22, and 1.33 mm for 19.

depressions along midline. Coxae with low blunt tubercles on segments 9–17; preformal spines beginning on segment 5.

Gonopodal aperture subovoid, 2.8 mm wide and 1.4 mm long at midpoint, indented anteriolaterally, sides raised above metazonal surface. Gonopods in situ (Fig. 18, of paratype) with telopodites projecting ventrad from aperture, bending anteriad and extending in subparallel arrangement just beyond anterior margin of aperture, not overlapping. Gonopod structure as follows (Figs. 19–22): Prefemur with elevated flattened area along anterior surface at usual position of prefemoral process. Acropodite short, heavily sclerotized, bending sharply at about ⅔ length and overhanging prefemur, with folds on medial side at level of bend; widened into broad expansion distal to bend, medial and lateral margins smoothly rounded and continuous, apical margin straight, without lobes but extremely jagged, with two or more rows of sharply pointed teeth, serrations, and ridges, most teeth directed toward undersurface of expansion or stem of acropodite; undersurface deeply concave, smooth basally, with fine serrations merging into rows of sharp teeth near distal margin, with a broad, apically rounded lobe near midlength on lateral side of midline. Solenomerite a narrow, falcate projection located distal to large, rounded boss on undersurface of expansion, tucked under and shielded by overhanging rows of teeth on apical margin of expansion, obscured in both medial and lateral view, visible only in subdorsal perspective looking directly under apical teeth. Prostatic groove arising in pit in base of prefemur, crossing to lateral side on acropodite stem, continuing on undersurface of expansion to base of solenomerite, opening terminally on latter.

Male paratypes.—Except for minor differences in jaggedness on the distal margin of the expansion, the male paratypes agree closely with the holotype.

Female paratype.—Length 32.1 mm, maximum width 8.8 mm, W/L ratio 27.4%, depth/width ratio 63.6%. Agreeing especially with males in somatic features, except paranota more strongly depressed, creating appearance of more highly arched body.

Cyphopods in situ with corner of receptacle and valves visible in aperture, valves directed caudolaterad. Receptacle moderate in size, cupped around caudomedial side of valves, surface moderately rugulose.

Variation.—The only significant gonopodal variation in *serratus* involves the degree of serration on the apical margin of the acropodal expansion and the distal extremity of its undersurface. There is a trend to increased serration from north to south, but the individual teeth become shorter. Thus in the Florida male the marginal teeth are the shortest, and the solenomerite is therefore more visible (Fig. 22). In all males the longer marginal teeth are always on the lateral side, above and overhanging the solenomerite. The teeth are fewer and shorter on the medial side away from the solenomerite, and southern males have more than one lamella on this side with ridges and teeth directed with the marginal axis instead of perpendicular to it. Beneath the marginal overhang the serrations become progressively longer distally and are sometimes clustered laterally along the distal part of the prostatic groove, thus obscuring it from view. The best view of the solenomerite and prostatic groove is the subdorsal one, obtained by "standing the gonopod on its head" with the coxa and apodeme directed up. This view also shows the serrations on the undersurface of the expansion, which lie in rows of increasing size distally, in an arrangement similar to shark's teeth.

Ecology.—The type specimens were found under thin layers of leaves on sandy-humus soil in a hardwood forest in the undeveloped section of Crooked River State Park beyond the vacation cabins. Live oak and magnolia dominate this locality, but *serratus* was absent from the litter of these species. The male from McIntosh County (NCSM A3591) was discovered under leaves in a small depression on a mowed lawn outside Fort King George Historical Site. At the type locality in July 1977 I collected one male of *serratus* and several males and females of an undescribed species of *Hubroria,* the first time I have ever found syntopic apheloriine species. However, in October 1980 *serratus* was abundant and the species of *Hubroria* was absent. Perhaps the life histories of these species are adjusted so as to minimize ecological competition, with *serratus* emerging in midsummer and becoming dominant by late summer and early fall, and the species of *Hubroria* dominant in spring. This situation contrasts markedly with that of montane species of *Sigmoria,* where only one occurs at a given site even within overlapping ranges, thus avoiding competition (Shelley 1981).

Distribution.—The coastal islands and Coastal Zone of southeastern Georgia and northeastern Florida. The precise locality of the Jacksonville male is unknown, but the Georgia specimens were collected east of highways I-95 and US 17, less than five air miles inland. The St. John's River is a plausible southern range boundary. Specimens were examined as follows:

GEORGIA: *Liberty Co.,* Sunbury State Hist. Site, 2M, 2F, 20 Jun 1983, R. M. Shelley (NCSM A4161). *McIntosh Co.,* Sapelo Island, M, F, 8 May and 27 Jun 1971, E. Rasmussen (ZMC); 1.3 mi. E Darien, nr. Ft. King George Hist. Site, several males and females, 15 Nov 1959, L. Hubricht (RLH) and M, 1 Oct 1980, R. M. Shelley and R. W. Jones (NCSM A3591); and Darien, 2M, F, 11 Sep 1959, L. Hubricht (RLH). *Glynn Co.,* St. Simons Island, M, 12 Sep 1959, L. Hubricht (RLH). *Camden Co.,* Crooked River St. Pk., M, 3 Jul 1977, R. M. Shelley (NCSM A1604) and 4M, 4F, 2 Oct 1980, R. M. Shelley and R. W. Jones (NCSM A3589) TYPE LOCALITY.

FLORIDA: *Duval Co.,* Jacksonville, M, 13 Feb 1921, collector unknown (AMNH).

Remarks.—*Cheiropus serratus* is the smallest species in the genus and considerably smaller than *C. agrestis,* its closest relative. It has a spotty occurrence because of the rarity of suitable habitat, but it can be locally abundant under proper conditions. The MCZ has a female apheloriine from Cumberland Island, Georgia, collected by O. Bangs in March–April 1896, which, based on time of collection, is probably the undescribed species of *Hubroria.* However, *serratus* should be expected on this national seashore later in the year.

Ecology

Few ecological generalizations hold for all four species of *Cheiropus. Cheiropus persicus,* and probably also piedmont populations of *agrestis,* occur in typical piedmont climax-subclimax hardwood tracts, but this environment is rare in the coastal areas occupied by the other three species. *Cheiropus plancus* and *serratus* therefore occur in a variety of predominantly hardwood sites, which are the best spots available in the generally unfavorable coastal environments. The same is probably also true for coastal populations of *agrestis.*

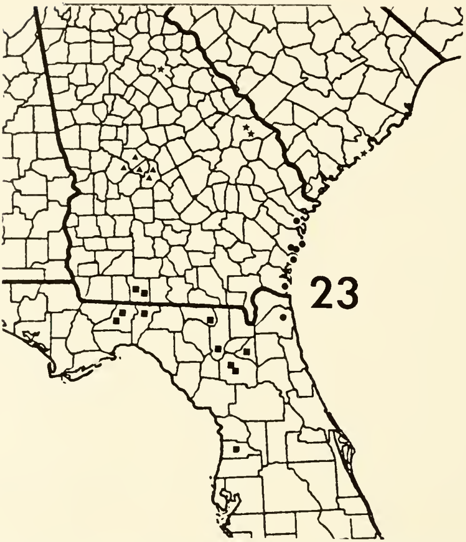


Fig. 23. Distribution of *Cheiropus.* dots, *serratus*; squares, *plancus*; triangles, *persicus*; stars, *agrestis.*

The species also occur at different times of the year. *Cheiropus plancus* is prevalent in midsummer but absent in autumn when *serratus* is available. On the other hand, *persicus* has been encountered in both spring and fall, but as its area has not been sampled in summer I do not know if it is available throughout the warm seasons of the year.

Distribution

The distribution of *Cheiropus* extends in the north-south direction from the Coastal Plain of southeastern South Carolina to west-central peninsular Florida, and east-west from the Atlantic Ocean to the central Piedmont Plateau of northern Georgia (Fig. 23). It is the most southern and most coastal apheloriine genus, and its type species is the southernmost in the tribe. Only *Dicellarius* and *Pleuroloma* occur farther south, each represented by one species in peninsular Florida, but the centers of abundance for these taxa lie outside the Atlantic Coastal Plain.

The four species of *Cheiropus* are entirely allopatric. Except for *persicus,* all span large rivers, and except for *agrestis,* all are limited to a single physiographic province. The known range of *serratus* is unusual for an apheloriine millipedin being linear and extremely narrow, resembling in this regard that of *Furcillaria aequalis* Shelley (Shelley 1981b). The two southernmost taxa, *plancus* and *serratus,*

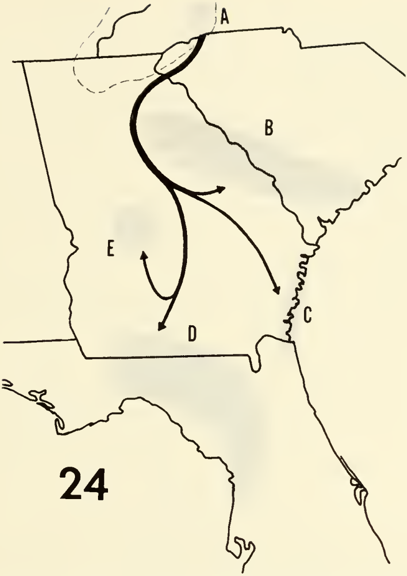


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Fig. 24. Relationships in *Cheiropus* and *Prionogonus*. A, *Prionogonus*; B, *agrestis*; C, *serratus*; D, *plancus*; E, *persicus*. The dashed line is the approximately boundary of the southern Appalachian (Blue Ridge) Mountains.

are partly sympatric with the undescribed species of *Hubroria,* and in central Georgia, the range of *persicus* is near those of *Dynoria medialis* Chamberlin and *Cleptoria rileyi* (Bollman) (Shelley in press; Hoffman 1967). *Cheiropus agrestis* spans the ranges of several species of *Crotania, Brevigonus,* and *Cleptoria* in both South Carolina and Georgia (Shelley 1977, 1981c; Hoffman 1967).

The distributions within the ranges differ. *Cheiropus persicus* occurs continuously in its known area, but the other three species have patchy distributions reflecting the spotty occurrence of suitable lowland and coastal habitat. Thus, sizeable hiatuses, spanning a number of counties, exist between sample sites of *agrestis,* and smaller ones occur within the ranges of *plancus* and *serratus.*

Relationships

The generic affinities of *Cheiropus* are not easily inferred, because there are no obvious similarities with other genera. Of the geographically proximal taxa, *Huboria* is closely related to *Sigmoria* (Shelley 1981a), and the gonopods of *Cleptoria, Croatania,* and *Brevigonus* conform to different patterns from that of *Cheiropus. Dynoria* and *Furcillaria* have separate but non-homologous solenomerites because they are on the medial sides of the acropodites rather than on the lateral as in *Cheiropus.* Thus, the affinities of *Cheiropus* are not with another lowland genus and must be sought elsewhere.

In 1982 I stated that the separate solenomerite beneath the peak and the absence of the distal zone and apical curve in *Prionogonus,* in the eastern Blue Ridge Mountains of North Carolina, suggested the condition in *Cheiropus,* and it should also be noted that the solenomerite in *P. haerens* and *P. divaricatus* Shelley, as in all four species of *Cheiropus,* is on the lateral part of the flared acropodite peak and most clearly visible from this perspective. There is a superficial similarity in medial view between gonopods of *P. haerens* and *plancus* (compare Fig. 3 of this paper with Fig. 3 of Shelley 1982), and I think that *Cheiropus* is most closely related to *Prionogonus.* The occasional appearance in *plancus* of a spur on the lateral shoulder at the base of the solenomerite (Figs. 6–7) may be additional evidence of this affinity. Thus, I think that *Cheiropus* shares a common ancestor with *Prionogonus,* through which it is linked to the "sigmoid" taxa that constitute the bulk of the Apheloriini.

I consider the configuration of the acropodite and the position of the solenomerite in *Prionogonus* to be plesiomorphic, and their conditions in *Cheiropus* to be apomorphic. The sigmoid curvature displayed by the vast majority of apheloriine taxa is retained in *Prionogonus,* and only in the short, straight acropodites of the four species of *Cheiropus* is this curvature lost. This condition may therefore be considered derived with respect to the former. The distal acropodite expansion in *plancus, agrestis,* and *serratus* is homologous to the flared acropodite peak in *Prionogonus,* but it has become thicker, more heavily sclerotized, and developed secondary marginal modifications. The distally narrow, tapering acropodite of *persicus* is an apomorphic specialization in contrast to the plesiomorphic state in the other species and *Prionogonus.*

Most apheloriine species lack a solenomerite, and the prostatic groove opens terminally at the tip of the acropodite. Comparatively few species possess a divided acropodite or a separate projection from the stem of the latter that carries the groove and hence is termed a solenomerite. The presence of a solenomerite is thus considered apomorphic with respect to its absence. The most plesiomorphic position possible for a solenomerite in this tribe is terminally on the acropodite as in *Prionogonus,* since the groove opens terminally in the majority of species. More proximal locations are thus apomorphic with respect to more distal ones. Hence, *persicus* exhibits the most apomorphic solenomerite, since it arises basally just distal to the prefemur. The position in *plancus* is apomorphic with respect to that in *agrestis* and *serratus,* which in turn is apomorphic with respect to that in *Prionogonus.* Consequently, there is a southward cline from distal to more proximal solenomerites that is interrupted by *persicus* in central Georgia. *Cheiropus,* then, represents apheloriine stock that dispersed in a southeastward direction from a probable source area in the eastern Blue Ridge Mountains and escarpment where *Prionogonus* occurs today. *Prionogonus* probably originated there since it appears to share a common ancestor with the sympatric species, *Sigmoria stibarophalla* Shelley (Shelley 1982). Its limited range suggests that *Prionogonus* represents a relict population that remained in the area when the proto-*Cheiropus* stock dispersed. The sequence of events in the evolution of *Cheiropus* probably involved an early dichotomy in northern Georgia into one form with the solenomerite on the undersurface of the distal expansion (the ancestor of *agrestis* and *serratus*) and a more southern form with the solenomerite shifted basally (the ancestor of *plancus* and *persicus*). These ideas on relationships are depicted in Fig. 24.

Superimposed on this analysis of *Cheiropus* is geographic variation that crosses cladistic lines. For example, a trend toward increased serration in the eastern part of the generic range is manifested by more and sharper acropodal teeth in the populations of *plancus* that are most proximal to *serratus*. Likewise, the acropodal expansion in *agrestis* is reduced, flattened, and more serrate in the Charleston County male, which occurs at about the same longitude as *serratus*. The acropodite in this individual also resembles that of *serratus* in being more upright and linear than the broadly curved forms in Georgia whose general configurations resemble that of *persicus*. These features appear to conflict with the phylogeny of *Cheiropus*, but they are geographically logical if an ancestral stock with clines in such characters undergoes vicariance partitioning in several places. The resultant clades would resemble each other in their most proximal populations, and in non-vagile organisms like millipeds that tend to be localized, the similarity would persist indefinitely. Thus, the four species of *Cheiropus* exhibit residual ancestral variation that is independent of phylogeny, and the same can be expected in other diplopod taxa. This phenomenon may be especially valuable in interpreting mosaic patterns of species in complex genera like *Sigmoria*.

Acknowledgments

The types of *Cheiropus plancus* and *Stelgipus agrestis* were examined through the courtesy of Herbert W. Levi, MCZ, who also loaned non-type material and donated two Kodachrome slides of *C. plancus* from which the living color was determined. Material in the FSCA and AMNH was loaned by Howard V. Weems, Jr., and Norman I. Platnick, respectively. My colleagues Richard L. Hoffman and William A. Shear kindly donated specimens from their private collections. The samples from Crooked River State Park, Georgia, were taken with permission of the Parks, Recreation, and Historic Sites Division, of the Georgia Department of Natural Resources. I thank Donald R. Whitehead, for his astute, invaluable review, and Renaldo G. Kuhler, NCSM scientific illustrator, for preparing Figs. 2, 9, 14–16, and 19–22. This project was supported in part by NSF Grants DEB 7702596 and 8200556.

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REVISION OF *DEMONAX* KINBERG, *HYPSICOMUS* GRUBE, AND *NOTAULAX* TAUBER, WITH A REVIEW OF *MEGALOMMA* JOHANSSON FROM FLORIDA (POLYCHAETA: SABELLIDAE)

Thomas H. Perkins

Abstract.—A study to clarify the systematics of some Sabellinae was conducted. The systematic importance of setae, uncini and the branchial crown of the subfamily are discussed. *Demonax* Kinberg, *Parasabella* Bush, and *Distylidia* Hartman are synonyms. *Demonax lacunosus,* n. sp., is described from Florida, and *D. microphthalmus* (Verrill), *D. rugosus* (Moore), *D. pallidus* (Moore), and *D. japonicus* (Moore) are new combinations; a key for 9 American *Demonax* species is provided. *Hypsicomus* Grube is redefined based on examination of the type-species, *Sabella stichophthalmos* Grube, which is redescribed. Other species previously included in *Hypsicomus,* except *Anamobaea orstedii* Krøyer and *Hypsicomus caecus* Iroso, are transferred to *Notaulax* Tauber with type-species *N. rectangulata* Levinsen. *Notaulax bahamensis,* n. sp., and *N. paucoculata,* n. sp., are described from the Bahamas. *Sabella brevicollaris* Grube, *S. torquata* Grube, and *Protulides elegans* Webster are synonyms of *Notaulax nudicollis* (Krøyer). *Parasabella sulfurea* Treadwell, *Sabella alba* Treadwell, and *Hypsicomus purpureus* Treadwell are synonyms of *Notaulax occidentalis* (Baird), new combination. *Notaulax californica* (Treadwell) and *N. midoculi* (Hoagland), new combinations, are redescribed. Twelve additional taxa in *Notaulax,* some of which are indeterminable or are synonyms, are listed; a key for 10 *Notaulax* species is provided. *Megalomma bioculatum* (Ehlers) and *M. lobiferum* (Ehlers) are redescribed; *M. pigmentum* Reish is newly reported from western Atlantic waters and additionally described; and *M. heterops,* n. sp., is described from Florida.

This paper is the fourth of a series of systematic papers on polychaetes (Perkins 1979, 1980, 1981) based for the most part on specimens collected between September 1971 and July 1973 in an environmental baseline study of marine biota near the Florida Power and Light Company nuclear generating plant at Hutchinson Island, St. Lucie County, Florida. Polychaetes proved to be a dominant and diverse group. However, there were many systematic problems with animals collected during the study, and a long-term project evolved in an attempt to solve some of them. The filter feeding subfamily Sabellinae, although not as important on soft bottom habitats as on hard bottom ones, nevertheless required an extensive systematic study. Numerous other specimens from Florida, the Caribbean Sea, and worldwide localities were examined to clarify generic and specific problems, resulting in the need to revise three genera and describe several new species.

The Hutchinson Island study area and methods and materials were described by Gallagher and Hollinger (1977). Sediments were described by Gallagher (1977), and other aspects of the physical and chemical environment were reported by

Worth and Hollinger (1977). Brief descriptions of sampling stations and methods were also given by Perkins (1979).

In addition to specimens deposited in the Invertebrate Collection of the Florida Department of Natural Resources Marine Research Laboratories (FSBC I), specimens were borrowed from or deposited in the following museums: American Museum of Natural History (AMNH), through H. S. Feinberg; Academy of Natural Sciences, Philadelphia (ANSP), through Tran-ngoc Loi; British Columbia Provincial Museum, Victoria, B.C., Canada (BCPM), through P. Lambert; British Museum (Natural History) (BMNH), through A. I. Muir; Indian River Coastal Zone Museum, Fort Pierce, Florida (IRCZM), through J. E. Miller; Museum of Comparative Zoology, Harvard University (MCZ), through H. W. Levi; Naturhistoriska Riksmuseet, Stockholm (NRS), through R. Oleröd; Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Florida (UMML), through G. L. Voss; U.S. National Museum of Natural History, Smithsonian Institution (USNM), through K. Fauchald and M. H. Pettibone, including some specimens collected by the U.S. Fish Commission (USFC); Peabody Museum of Natural History, Yale University (YPM), through W. D. Hartman; Zoologisches Museum für Naturkunde der Humboldt-Universitat zu Berlin (ZMB), through G. Hartwich; Zoologisk Museum, Copenhagen (ZMC), through M. E. Petersen; and Zoologisches Institut und Zoologisches Museum, Hamburg (ZMH), through G. Hartmann-Schröder. Additional specimens were donated by T. Cuba, University of South Florida, St. Petersburg; R. G. Ernest, Applied Biology, Inc., Jensen Beach, Florida; T. S. Hopkins, Dauphin Island Sea Lab, Dauphin Island, Alabama; Joan Uebelacker, Dauphin Island Sea Lab and Barry Vittor & Associates, Mobile, Alabama; and R. W. Virnstein and J. K. Reed, Harbor Branch Foundation, Inc., Fort Pierce, Florida. Some specimens donated by J. K. Reed were collected by *Johnson-Sea-Link* submersibles I and II (JSL); the dive number follows the submersible designation in the material examined.

M. E. Petersen (ZMC), M. H. Pettibone (USNM), K. Fauchald (USNM) and P. Knight-Jones, University College of Swansea, Wales, U.K., provided information and copies of papers not available to me. E. W. Truby, Florida Department of Natural Resources, sectioned setae and helped with photography. W. G. Lyons, R. O. Reese, R. H. McMichael, Jr., M. J. Durako, and K. Fauchald critically read the manuscript and suggested important changes. Many individuals from the Florida Department of Natural Resources Bureau of Marine Research and from Applied Biology, Inc., participated in the Hutchinson Island study, for which Florida Power and Light Co., provided partial funding.

Abbreviations used on figures to indicate parts of the branchial crown and anterior end are as follows:

dl	dorsal lip
vl	ventral lip
ra	radiolar appendage
pa	pinnular appendage
vs	ventral sac
pl	parallel lamella
al	aricular lamella
ppl	prostomial-peristomial lamella

pm	palmate membrane region
bl	basal lamina
fr	radiolar flange
fb	basal flange

Sabellinae Rioja, 1923

Figs. 1, 2

Setae and uncini.—The various shapes of setae and uncini have often been misinterpreted using light microscopy, and the importance of some characters has been overlooked by some authors, including myself. The following is an explanation of some forms of setae and uncini and their systematic importance, especially at the generic level.

Avicular hooks, shaped somewhat like a swan or a "Z," have a large, pointed main tooth, fang or beak surmounted by a crest with a large number of small teeth. Below the crest, hooks are bent at greater than 90°, forming a moderately long neck and rounded breast, then bent in the opposite direction from the beak at about 90°, forming the handle or manubrium. Small teeth of the crest are often not resolvable with light microscopy unless the hook has been crushed. More than moderate intraspecific differences in avicular hooks are correlated with animal size, and only pronounced differences in them are important. They usually have short handles when not accompanied by companion setae, as in *Branchiomma* Kölliker, 1858. When accompanied by companion setae, handles may be moderately long to long, as in *Demonax* Kinberg, 1867, and *Megalomma* Johansson, 1927, or very long, as in *Potamethus* Chamberlin, 1919.

Companion setae (Fauchald 1977a:135, 156), found in tori in an adjacent row anterior to thoracic avicular hooks of most genera, are formed of an embedded shaft aligned in the same direction as handles of avicular hooks. The core apparently ends abruptly at the end of the shaft just outside the body. The tip of a companion seta, which is bent at about a right angle more or less anteriorly or obliquely away from the avicular hooks, appears to be a continuation of the thin outer covering of the shaft and is usually teardrop shaped, pennonate, with the proximal part broader than the shaft. The tip somewhat resembles the blade or hooded region of a *broadly hooded seta,* described below, but is without the central core. In lateral view, emergent parts of companion setae are usually shaped somewhat like a foot with a rounded heel and pointed tip (Fig. 28I).

Companion setae of *Demonax* (Figs. 5X; 8A, B) have similar shafts (they may have an indistinct breast), but cores are expanded as broad and avicular tips. They may have a crest of small teeth, visible using a light microscope, above a beak-like tip. A hyaline mucro extends from the center of the outer surface of the beak or from the penultimate tooth. Except for the mucro, these are similar in form to thoracic hooks of *Chone* Krøyer, 1856 (Fabriciinae).

Setae, in contrast to uncini, are found only on the collar segment, notopodia of the thorax, and neuropodia of the abdomen, and thus it is not necessary to designate them as notosetae and neurosetae. They take various forms, from paleae in the lower group of thoracic setae of some genera, as in *Notaulax* Tauber, 1879, *Potamilla* Malmgren, 1866, and *Pseudopotamilla* Bush, 1905, to slender capillary setae in the abdomen of *Notaulax* and *Hypsicomus* Grube, 1870. However, except for the possible exception of capillary setae, most of the emergent parts of setae of most, if not all, genera are hooded (K. Fauchald, pers. comm.). They are formed of a central core of fused rods surrounded for the most part by a region of irregular, lacunar spaces and an outer shell (Fig. 1A–E). The outer shell appears to be formed of loosely fused rods or plates (Knight-Jones 1981: figs. 46, 47, 51). Lacunar spaces are found on lateral, anterior, and posterior sides. Upper thoracic setae are slightly bent medially, and lower thoracic setae are usually more strongly bent medially in the direction opposite from the lacunate spaces. Tips of rods forming the outer shell may appear as spines on the surface. Embedded parts are similar in cross section to setae described by Orrhage (1971) in being formed of hollow rods. These rods appear to extend into the middle part of the central core of the emergent parts, where the hollow parts of the rods appear to be more filled in. These have been described as limbate setae by most authorities.

Paleate setae are very stout forms of the setae described above. Emergent parts are short, thick, somewhat inflexible, spoon-shaped, and strongly curved in cross section, with concave surfaces of thoracic ones facing medially (Knight-Jones 1981: figs. 48, 49). This type of seta is usually found in the lower thoracic group, but occurs on the abdomen of some genera. Paleate setae are usually mucronate but may not be so on the thorax of some *Notaulax* species; the central core appears to be very broad. Paleae on the thorax of *Notaulax* species are arranged in oblique rows; they are arranged in transverse rows on *Potamilla, Pseudopotamilla,* and most other genera.

Setae in the upper thoracic group, usually found in an arc above the notopodial papilla or lobe of most genera, are almost circular in cross section and slender; a transverse line, in reference to the body of the worm through a cross section of a seta, bisects the central core (Fig. 1A). Such setae in *Notaulax* are stout, spine-like, and longitudinally oval in cross section (Fig. 1D). Setae similar to upper thoracic setae almost always occur on the collar segment, and similar setae may be found in the abdomen. These setae are defined as *narrowly hooded setae* because of this shape and the arrangement of lacunate spaces.

Lower parts of notopodia of genera with transversely arranged groups of setae, of which paleae are a special form, usually have setae in which a line, longitudinal to the body of the worm, drawn through the greatest diameter of a cross section, does not bisect the longitudinally oval central core (Fig. 1C). Termed *broadly hooded setae,* these may be slender on some species but are broader than adjacent upper setae; when short and broad, they may approach the paleate condition noted above. This type of seta is found on *Demonax* and *Megalomma,* for example. Setae of the abdomen of the latter and some other genera may be intermediate between broadly and narrowly hooded setae.

Lower thoracic setae of *Sabella* Linné, 1767 (Fig. 1B), and *Branchiomma,* which in most cases are arranged in longitudinal or oblique groups, are stout, spine-like, and appear to be narrowly hooded in lateral view. They appear similar in form to upper thoracic setae found in those genera but are usually much stouter and transversely oval in cross section. However, in these setae, a transverse line drawn through the greatest diameter of a cross section bisects the transversely oval, central core. The exact orientation of the long axis of a cross section of these setae probably varies by as much as 45° from the transverse. These are defined as *spine-like setae.*

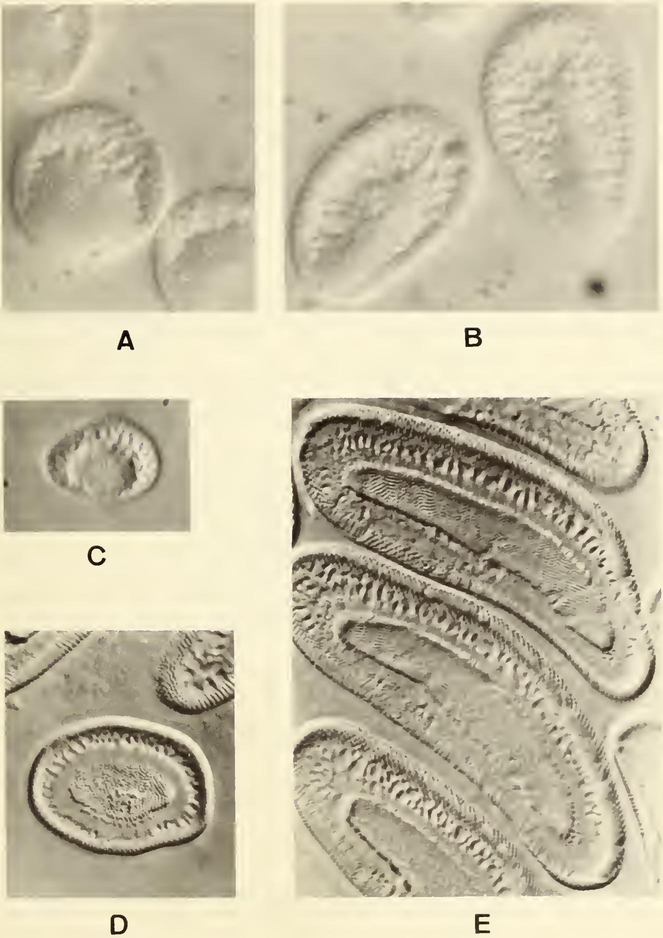

Fig. 1. A, Cross section of upper thoracic seta of *Sabella variegata* from Tampa Bay, Florida; B, Cross section of lower thoracic setae of same; C, Cross section of lower thoracic seta of *Demonax microphthalmus*; D, Cross section of upper thoracic seta of *Notaulax nudicollis*; E, Cross section of lower thoracic setae (paleae) of same (A, B, FSBC I 27682; C, FSBCI 14534; D, E, FSBC I 24006; not scaled).

Setae were embedded in Spurr's epoxy resin (Spurr 1969) used for transmission electron microscopy, cross sectioned with an ultramicrotome, dried on a microscope slide, and covered with a cover slip. Photographs were taken using Zeiss Nomarski interference-contrast optics.

The branchial crown.—The branchial crown is as important in the classification of Sabellidae as are the opercula in Serpulidae and Spirorbidae. Its structure is emphasized here in addition to the arrangement and types of setae and uncini and other characters, especially in generic diagnoses. Anatomy, histology, and functions of the crown have been described in detail for *Sabella pavonina* Savigny, 1820, in a classical paper by Nicol (1931). Homologues of the parts of the crown of *Sabella penicillus* non Linné (=*S. pavonina*) and several other species have been discussed by Orrhage (1980). The fine structure of the junction between the branchial crown and body of *Sabella penicillus* non Linné (=*S. pavonina*) has been described by Kryvi (1975) and by Kennedy and Kryvi (1980), and fine structure of its endoskeletal cartilage has been described by Kryvi (1977).

The crown is composed of a fused, horsecollar-like base supported by a cartilaginous skeleton which is continuous dorsally but not ventrally. The base supports paired branchial lobes and the dorsal and ventral lips. Dorsal and ventral lips are inside the usually circularly arranged group of radioles. Branchial lobes can simply be spread apart to observe the dorsal and ventral lips in some cases; however, if sufficient specimens are available, it is better to remove one of the branchial lobes with associated lips and spread it out. This can be done by pressing a blunt dissecting needle on one side of the ventral margin at the junction of the branchial crown and body, described briefly below.

The endoskeleton of the base of the crown consists of a pair of short to long lateral bars or horns and a dorsal transverse bar. The transverse bar apparently functions as a fulcrum allowing opening and closing of the branchial crown. Lateral horns, from which develop skeletons of the radioles, are joined to longitudinal muscles of the body by interdigitating connective tissue of the cartilagenous matrix of the skeleton and the epimysium of the muscles. The connective tissue is held together by muscle cells with paramyosin filaments (Kryvi 1977). On *S. pavonina,* this junction was shown to function as an abscission zone by Kennedy and Kryvi (1980) and, although possibly not having identical function, was morphologically similar on several other sabellid species examined by them.

Dorsal lips (Figs. 1A, B, 7C, 15F), which function at least in some species to remove wastes, are for the most part arranged vertically. In some genera, e.g., *Megalomma,* they appear to be almost completely separated, while in others, e.g., *Sabella,* each half is joined to the other medially above the mouth (ventromedially) by a thin lamella (Orrhage 1980: fig. 1d; Fig. 2A). They may have two types of appendages (Orrhage 1980), those formed by a modified radiole which have lamellae on their upper and lower sides for part of their length, and those on the upper side joined to the upper lamella which are modified pinnules of the first dorsal radioles. The former are called *radiolar appendages* (Figs. 2A, 7C), and the latter are termed *pinnular appendages* (Figs. 2B, 7C) rather than simply "appendages of the dorsal lips" as defined by Orrhage (1980). Upper lamellae are fused with the base of the first dorsal radiole, with or without pinnule appendages (Figs. 2A, 7C, 23B, 43A). An example of a species having dorsal lips with only radiolar appendages is *Sabella pavonina* (Fig. 2A); a species with only pinnular

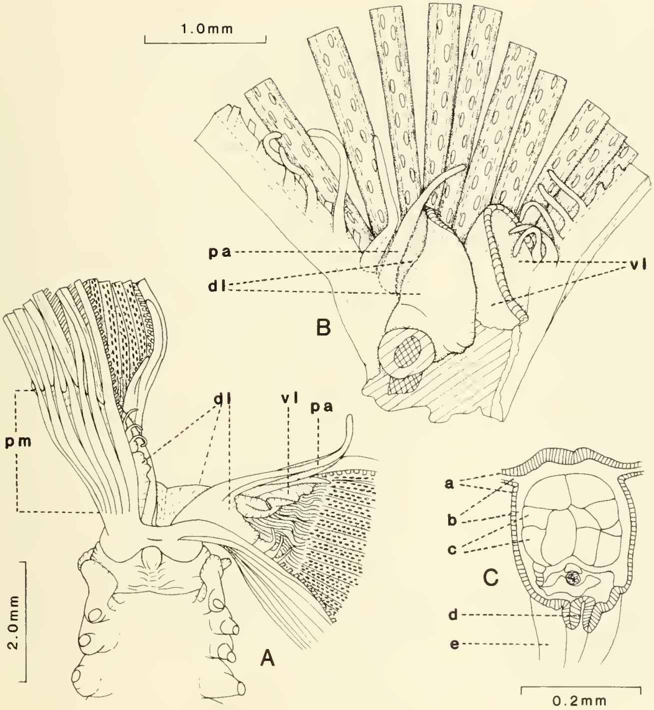

Fig. 2. A, Anterior end of body and proximal part of branchial crown of *Sabella pavonina* (River Roach, Essex, England; BMNH ZH 1865.6 22.2) B, Proximal part of left half of branchial crown of *Potamilla torelli* (Bay of Fundy; USNM 44756); C, Cross section of radiole in region of palmate membrane of *Sabella variegata* (Tortugas, Florida USNM 23567; a, columnar epithelium; b, cartilaginous sheath of skeleton; c, cartilaginous skeletal cells; d, basal groove; e, pinnule).

appendages is *Potamila torelli* Malmgren, 1866 (Fig. 2B); and species with both pinnular appendages and radiolar appendages are *Demonax microphthalmus* (Verrill) (Fig. 7C) and *Megalomma heterops,* n. sp. (Fig. 43A). Ventral lips are paired structures on most Sabellinae but may be fused to some extent ventral to the mouth (Nicol 1931; also on *Laonome* Malmgren, 1866, see P. Knight-Jones, pers. comm.). On most Sabellinae, they begin on the dorsal end of paired lamellae which extend between ventral lappets of the collar and the beginning of the branchial lobes. Termed *parallel lamellae,* these lamellae may form vesiculate lobes which are termed *ventral sacs* on *Sabella* and some *Megalomma* species (e.g., *Megalomma bioculatum,* Fig. 38A, B; *M. pigmentum,* Fig. 41A–C), or they may be short and straight, as on *Demonax* and other *Megalomma* species (*Demonax microphthalmus,* Fig. 7B). Free margins of ventral lips extend dorsally about to the dorsal lips, then turn ventrally and end on branchial lobes near the origins of ventralmost radioles; fused margins of ventral lips join proximal parts of radioles for about the lower half of branchial lobes (*Demonax pallidus,* Fig. 15F; *Sabella pavonina.*—Fauvel 1927:299, fig. 102a).

Branchial lobes usually originate on a short, fused, thick base. The radioles become separated from the skeleton of the branchial crown at this point. Broad flanges may occur on dorsal and ventral margins of bases of branchial lobes, as on *Notaulax* and *Pseudopotamilla,* or be absent, as on *Sabella, Demonax,* and *Megalomma.* When long, bases have been termed a *basal lamina* or *basal sheet* (*Notaulax nudicollis,* Fig. 27A, B). Radioles may be completely separated above the usually short base or longer basal lamina, or joined for part of their length by a palmate membrane. A *palmate membrane* (Figs. 2A, 27B) consists of an extension between the radioles of the outer part of the sheath of the radiolar skeleton covered on both sides by columnar epithelium (*Sabella variegata* Krøyer, 1856; Fig. 2C; *Sabella penicillus* of Orrhage, 1980:125, fig. 4).

The stem of a radiole consists of a skeleton comprised of vacuolate cartilaginous cells surrounded by an extracellular cartilaginous sheath containing some anastomosing cells. Each skeletal cell is surrounded by a thick-walled, chondroid matrix. The sheath of the skeleton is covered by columnar epithelum. The stem or rachis houses paired nerves, a coelomic space, blood sinus (Fig. 28Ba–c), and associated muscular and sensory structures, and on the interior surface produces alternating rows of ciliated pinnules on each side of a ciliated basal groove (Fig. 2C). The latter two structures function to collect and move food to the mouth. Radioles may have lateral rows of cilia (Fig. 6A–C) or be flanged on outer lateral corners. Flanges, usually found distally on radioles, are composed of a lateral extension of the sheath and possibly also skeletal cells and associated columnar epithelium (Fig. 28B–D). Satisfactory cross sections of radioles can usually be made on a microscope slide with a razor blade.

Demonax Kinberg, 1867

Demonax Kinberg, 1867:354; 1910:72.—Johansson, 1925:26, 27; 1927:136.—Berkeley and Berkeley, 1952:115.—Uschakov, 1955:412.—Hartman, 1959:541.—Fauchald, 1977a:138.

Parasabella Bush, 1905:191, 199, 200.

Distylidia Hartman, 1961:129 [in part].—Fauchald, 1977a:138.—Banse, 1979:870.

Sabella (*Demonax*).—Banse, 1979:877, 878.—Hobson and Banse, 1981:106, 107 [in part; not *Distylia volutacornis* var. *pacifica* Berkeley and Berkeley, 1954].

Type-species.—*Demonax krusensterni* Kinberg, 1867; subsequent designation by Bush (1905:191).

Kinberg (1867) originally included five species in *Demonax.* One species incorrectly reported by Kinberg as *Demonax tilosaulus* (not *Sabella tilosaula* Schmarda, 1861) is a *Chone* species according to Hartman (1959:514); the others, questionably including the type-species, are included in this paper under *D. leucaspis* Kinberg. Designation of *D. krusensterni* as the type-species by Bush (1905) was unfortunate since figures of the other three included species were published posthumously in the second part of Kinberg's paper on the polychaetes of the Eugenie Expedition (Kinberg 1910), and the holotype of *D. krusensterni* is in poor condition (Johansson 1925; this paper). This was probably the reason *D. krusensterni* was omitted from Kinberg's (1910) paper. Johansson (1925) reexamined Kinberg's *Demonax* types and commented that *D. leucaspis, D. incertus, D. cooki,* and questionably *D. krusensterni* were all examples of a single species. Later (1927), he included them in all synonymy under *D. leucaspis,* with a questionable synonymy for *D. krusensterni.* Hartman (1959), following Johansson (1927), designated *D. leucaspis* as the type-species, a mistake in violation of Article 69 of the International Code of Zoological Nomenclature (1964), and others (Fauchald 1977a; Banse 1979) followed Hartman.

Diagnosis.—Radioles in semicircles or partial spirals arising from spiralling of cartilaginous bases of branchial lobes, in single row on cartilaginous bases or formed into 2 or 3 rows with inner semicircles or partial spirals apparently caused by bases of outer radioles "growing over" inner ones and forcing them toward middle of branchial crown, thus obscuring them from outside view; usually with longitudinal bands of cilia on outer lateral corners; without flanges or stylodes; with cartilaginous skeleton oval or reniform in cross section and formed of irregularly arranged cells; without palmate membrane; with or without simple eyespots. Dorsal lips with radiolar appendage functioning as midrib, with lamellae above and below joined to proximal part of midrib and 1–3 pinnular appendages (modified pinnules of first dorsal radiole) fused with upper lamella; ventral lips paired, well-developed, beginning ventrally between ventral lappets of collar, with margin extending dorsally to near dorsal lips, curving ventrally and joining bases of branchial lobes near first ventral radioles; ventral sacs absent. Collar bilobed, beginning dorsally on collar segment above setae, widely separated dorsally, entire laterally, ending ventrally in triangular or rounded lappets. Eight or fewer thoracic setigers. Collar setae of single type, in 2 short rows or elongate oval group, similar to upper setae of other thoracic setigers, often of unequal lengths; upper thoracic setae in arc above notopodial lobes, slender, with narrow hood; lower thoracic setae long and slender to short and nearly paleate, with hooded region broader in longitudinal plane of body than in transverse plane, in 2 or more transversely arranged rows or transversely arranged groups, often of unequal lengths. Thoracic tori with numerous avicular hooks and companion setae; avicular hooks with moderately long to long handles; companion setae slightly avicular, with tip enlarged into bulbous, well-defined, avicular head, with narrow, thin blade or mucro extending from narrow center of head or from penultimate tooth. Abdominal setae of single type, hooded, in 2 transverse rows or transverse elongate-oval group; abdominal avicular hooks similar to those of thorax but with shorter handles.

Remarks.—Previous concepts of the genus have emphasized the nearly paleate setae in lower parts of notopodia (Johansson 1927) or the nearly paleate setae and partially spiraled branchial lobes on *D. leucaspis* (Fauchald 1977a). These setae (Fig. 16A–D) can be considered to be short forms of broadly hooded setae. However, it is not entirely possible to designate points of separation in the continuum between nearly paleate setae, slightly more elongate hooded setae such as those that appear on *D. microphthalmus* (Fig. 7D–H), and longer, more slender, slightly hooded setae such as those of *D. rugosus* (Fig. 10D–K). The same is true between partially spiraled and semicircular arrangements of radioles, which are definitely spiraled on type-specimens of all the included species described by Kinberg (1867). Radioles are slightly spiraled, probably from contraction, on a few large specimens of *D. microphthalmus* (Verrill) but not on others. They are partially spiraled on large but not small specimens of *D. rugosus* (Moore). Radioles are apparently added at the ventral margins of branchial lobes after the semicircle is completed. The same condition may be found on some *Sabella* species (Bush 1905:193). Other characters are common among all members of the genus except the development of more than one semicircle or partial spiral of radioles on large but not small specimens of *D. rugosus* (Moore) and *D. medius* (Bush). The development of additional rows of radioles, as in the case of the partially spiraled radiolar base on some species in the genus, is considered to be an ontogenetic character and not of generic importance. The most important character common to all members of the genus is the shape of companion setae; companion setae of species of most other genera of Sabellinae have thin, transparent, teardrop-shaped or pennonate blades at right angles to the shafts.

Sabella aulaconota Marenzeller (1884:210, pl. 2, fig. 8; = *Demonax aulaconotus*) from Japan was reported as an older synonym of *Parasabella media* Bush, 1905, by Johansson (1927; as *Sabella aulaconota*), who in the same paper reported *P. media* as a distinct species in *Demonax*. Monro (1933) referred *Sabella aulaconota* to *D. leucaspis* Kinberg. The species was reported as *Demonax aulaconota* by Hartman (1959) and by Imajima and Hartman (1964). I have not examined specimens of this species and can add nothing to the description. It may be similar to *D. medius* (Bush) but apparently has much longer lower thoracic setae. The description is insufficient for me to include it in the key.

A type-specimen of *Sabella japonica* Moore (Moore and Bush 1904:157–159, pl. 11, figs. 1, 2, pl. 12, figs. 39, 40) was examined and is also a *Demonax*; it is included in the key. *Demonax japonicus* and *D. lacunosus,* n. sp., are unique in the genus in having tori of the thorax well separated from ventral shields. Phyllis Knight-Jones (1983) discussed European and some other species of *Demonax.*

Distylia volutacornis var. *pacifica* Berkeley and Berkeley, 1954, referred to *Sabella* (*Demonax*) by Banse (1979), is not a species of *Demonax* and may not be a species of *Sabella* Linné, 1767. Thoracic setae are similar to those of *Sabella,* but the collar begins near the middorsal groove and forms distinct dorsolateral pouches. The type-specimen may be presently indeterminable to genus, since all tissue is lost from the branchial lobes, and only the cartilaginous skeleton remains.

In contrast to *Demonax* Kinberg, species of *Sabella* Linné, 1767, with type-species *Serpula penicillus* Linné, 1758, have palmate membranes between radioles occupying about 1/10 of their lengths; blade-like or spine-like lower thoracic setae organized into oval, longitudinal groups; companion setae with thin, teardrop-shaped or pennonate blades at right angles to shafts; and abdominal setae organized into spiral groups. Specimens reported as *Bispira volutacornis* from California by Berkeley and Berkeley (1961:662) (not *Amphitrite volutacornis* Montagu, 1804), and reported as ?*Sabella* sp. by Banse (1979:880) are a typical oculate *Sabella* species.

Potamilla Malmgren, 1866, with type-species *Sabella neglecta* Sars, 1850, has dorsal lips of the branchial crown without radiolar appendages, companion setae similar to those of *Sabella* species, and may also have a short palmate membrane between radioles.

Pseudopotamilla Bush, 1905, with type-species *Amphitrite reniformis* Bruguière (1789:57; synonyms: "die nierenförmige *Amphitrite*" Müller, 1771:194; and *Amphitrite reniformis* Gmelin, 1791:3110, attributed to Linné 1788, in Hartmann 1959), has broad flanges on the upper and lower margins of the cartilaginous bases of the branchial lobes, companion setae like those of *Sabella* species but with thicker blades, and composite eyes occurring singly along some of the radioles. Except for being larger, species of *Eudistyla* Bush, 1905, differ from *Pseudopotamilla* Bush only in having branchial lobes with partially spiraled cartilaginous bases and in having numerous radioles organized into two or three rows. Radioles are organized in two or three rows on large specimens of *D. rugosus* (Moore) and *D. medius* (Bush), but are organized in single rows in other species of *Demonax*. It is likely that some small specimens from the northeast Pacific Ocean referred to *Pseudopotamilla* are conspecific with large specimens referred to *Eudistyla*. *Schizobranchia* Bush, 1905, differs from *Pseudopotamilla* in having dichotomously branched radioles.

Key to American Species of *Demonax*

1. Radioles in partial spiraled arrangement at least on large specimens . . . 2
– Radioles in semicircular arrangement on all sizes 3
2. Radioles forming 2 or more rows on large specimens; lower thoracic setae long, slender (Fig. 10D–K) . . . . *D. rugosus* (Moore)
– Radioles in single row; lower thoracic setae short, broad (Fig. 5B–V) . . . . *D. leucaspis* Kinberg
3. Companion setae with stout handles (Fig. 17G–I) . *D. jamaicensis* (Augener)
– Companion setae with slender handles (Fig. 8A, B) 4
4. Radioles of large specimens in 2 rows, numbering up to about 40, with up to 27 in outer row; thoracic avicular hooks with long handles (Fig. 13O, P) . . . . *D. medius* (Bush)
– Radioles in single rows of 20 or less; thoracic avicular hooks with handles of moderate length (Fig. 7J, K) 5
5. Ventral shield of collar segment broader than long; thoracic tori extending from notopodia to ventral shields 6
– Ventral shield of collar segment about as long or longer than broad; thoracic tori well separated from ventral shields 8
6. Ventral shield of collar segment about twice broader than long . . . . *D. microphthalmus* (Verrill)
– Ventral shield of collar segment about 3 times broader than long 7
7. Lower thoracic notosetae with hooded parts (including tips) 3–4 times longer than broad (Fig. 16A–D); radioles with "diffuse eyespots" or uncolored, without cross-bands of reddish-brown . . . . *D. pallidus* (Moore)
– Lower thoracic notosetae with hooded parts (including tips) 4–5 times longer than broad (Fig. 20B, C); radioles without "diffuse eyespots," with about 7 dark, reddish-brown cross-bands . . . . *Demonax* sp.
8. Ventral shield of collar segment longer than broad, with grooves forming "V" with apex anterior; 15 pairs of radioles . . . . *D. japonicus* (Moore)

– Ventral shield of collar segment about as long as broad, plain; up to 10 pairs of radioles .... *D. lacunosus*, n. sp.

Demonax leucaspis Kinberg, 1867
Figs. 3–5

?*Demonax krusensterni* Kinberg, 1867:354.—Bush, 1905:191.—Johansson, 1925: 22, 24, fig. 8, no. 1–6.

Demonax leucaspis Kinberg, 1867:354; 1910:72, pl. 27, fig. 8.—Johansson, 1925: 24, fig. 8, no. 7–11; 1927:136, text-fig. 14, no. 4, 6, 7.—?Monro, 1933:1075, 1076, text-fig. 22 [in part, not *Parasabella media* Bush, *P. maculata* Bush, *P. pallida* Moore and *Sabella aulaconota* Marenzeller].—Hartman, 1966:235, 236 [diagnosis partly incorrect; no additional specimens].

Demonax incertus Kinberg, 1867:354; 1910:73, pl. 28, fig. 1.—Johansson, 1925: 22, 24, fig. 8, no. 1–6.

Demonax cooki Kinberg, 1867:355; 1910:73, pl. 28, fig. 2.—Bush, 1905:186.—Johansson, 1925:26, fig. 9, no. 5–8.—Hartman, 1959:541.

Material examined.—PERU: Holotype of *D. leucaspis,* San Lorenzo Is., near Callao, intertidal [*summa aqua* = highest water], Eugenie Expedition, 1851–1853 (NRS 575).—CHILE: Holotype of *D. incertus,* Valparaiso, under seaweed on sand and stone, 4–6 m, Eugenie Expedition, 1851–1853 (NRS 580).—HAWAII: Holotype of *D. krusensterni,* Honolulu, Oahu, under dead coral on beach [*summa aqua*], Eugenie Expedition, 1851–1853 [damaged specimen; NRS 577]. Two syntypes of *D. cooki,* Honolulu, Oahu, under dead coral on beach [*summa aqua*], Eugenie Expedition (NRS 579).

Description.—Tube unknown. Lateral sides and pinnules of branchial lobes cross-banded on type of *D. incertus* (Johansson 1925), highly colored on syntypes of *D. cooki* (color partially retained); all other types now with branchial crown uncolored (but epithelium lost and only skeleton remaining on type of *D. krusensterni*). Total length 9–27 mm, width 2–4 mm, 50–65 setigers. Branchial crown ⅓–⅕ body length, 21 plus single vestigial pairs of radioles on types of *D. leucaspis* and *D. incertus,* 10–17 on syntypes of *D. cooki,* 27 on type of *D. krusensterni*; all spiraled about 1½ semicircles (Fig. 3A); radioles with smooth tips about 0.4 mm long and gradually lengthening pinnules (Fig. 4A) on type of *D. leucaspis,* similar on some radioles of type of *D. incertus* and syntypes of *D. cooki*; radiolar skeletons in cross section (Fig. 4C, E, G–I) with numerous cells, with thick sheath surrounded by moderately thick columnar epithelum; basal pinnular skeletal cells flattened, wider than long (except on syntype of *D. cooki* which has some long ones), others gradually decreasing in width and increasing in length distally (Fig. 4B, D, F). Dorsal lips short, triangular, with radiolar appendage joined by lamella to single upper filament (pinnular appendage), fused with branchial lobes at base of first dorsal radiole. Collar extending for about half length of fused base of branchial crown but perhaps shorter on type of *D. leucaspis* (Kinberg, 1910: pl. 27, fig. 8, pl. 28, figs. 1, 2), beginning about half distance from collar setae to dorsal groove, concave ventrolaterally, ending in short, rounded lappets at ventral incision, damaged on type of *D. krusensterni.* Thorax with 8 setigers, with slight depression on anterior dorsal part; notopodial lobes short, conical. Ventral shields of setiger 1 (collar segment) short, 3½–5 times broader than long (Fig. 3B–E), only slightly

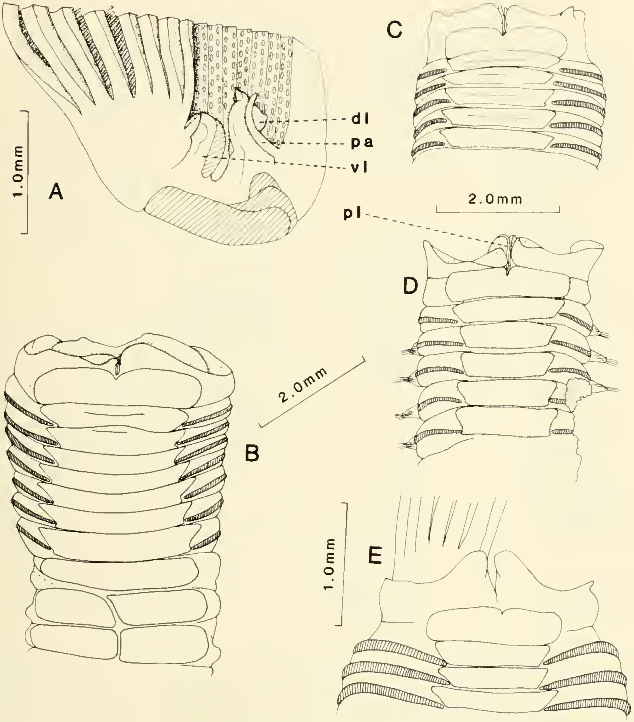

Fig. 3. *Demonax leucaspis*: A, Proximal part of detached branchial crown of holotype of *D. leucaspis* right half, medial view; B, Anterior end of body of holotype of *D. krusensterni*, ventral view; C, Same, of *D. leucaspis*; D, Same, *D. incertus*; E, Anterior end of body and lower part of half of branchial crown, syntype of *D. cooki*.

longer than those following, rectangular, with rounded corners but incised anteromedially; ventral shields of other thoracic setigers trapezoidal, broader anteriorly; not as broad on types of *D. cooki* as on others. Collar segment with 2 short rows of slender, narrowly hooded setae; other thoracic segments with curved, upper, longitudinal row of slender, narrowly hooded setae (Fig. 5A) above 2 or more transverse rows of short, broadly hooded setae; lower thoracic setae of anterior row shorter, broader than on posterior row, with hooded part about 3 times broader than shaft and, including tips, 5 times as long as broad; posterior row of setae slightly longer and more slender, with hooded part about twice broader than shaft and, including tips, 6 times longer than broad on type *D. leucaspis*;

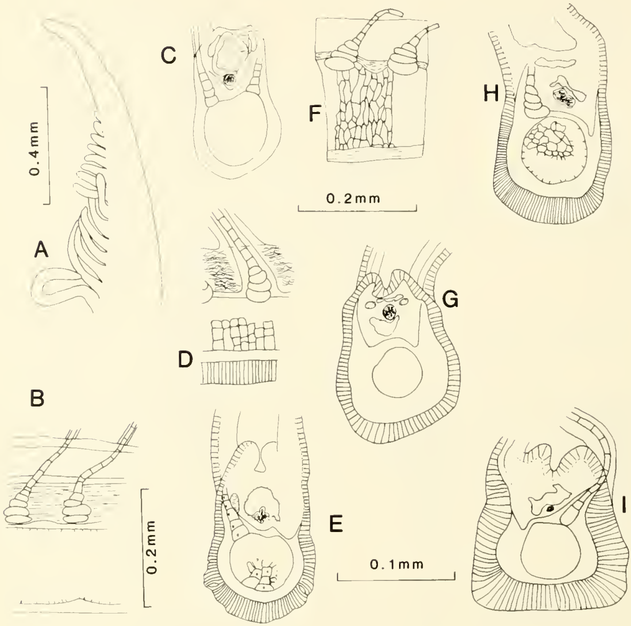

Fig. 4. *Demonax leucaspis*: A, Tip of fourth dorsal radiole, holotype of *D. leucaspis*; B, Internal structure of radiole, holotype of *D. krusensterni*, sagittal view, skeletal cells and columnar epithelium missing; C, Cross section of radiole of same; D, Internal structure of radiole, *D. incertus*, sagittal view; E, Cross section of same; F. Internal structure of radiole, *D. leucaspis*, sagittal view, columnar epithelium omitted; G, Cross section of same, skeletal cells lost; H, Same, skeletal cells damaged; I, Cross section of radiole, *D. cooki*, skeletal cells lost.

broader, shorter and all similar on type of *D. incertus* and syntypes of *D. cooki*; all similar and intermediate between anterior and posterior ones of *D. leucaspis* on type of *D. krusensterni* (Fig. 5B–V). Thoracic avicular hooks with moderately long handles (Fig. 5W) and companion setae (Fig. 5X), in long tori from notopodia to ventral shields; companion setae with slender shaft, with broadly winged, avicular head, with long, slender, hyaline mucro extending from middle of outer part of tip and beak. Abdominal avicular hooks similar to those of thorax but with shorter handles; abdominal setae hooded, in 2 transverse rows.

Remarks.—Kinberg's figure of *D. cooki* (Kinberg, 1910: pl. 28, fig. 2) is incorrect in showing the collar extending past the fused base of the branchial crown; in fact, collars of syntypes of *D. cooki* are similar to those of other specimens (Fig. 3E). Also, the long basal pinnular skeletal cells found in radioles of *D. cooki* (Fig. 4I) are, in my opinion, a juvenile character.

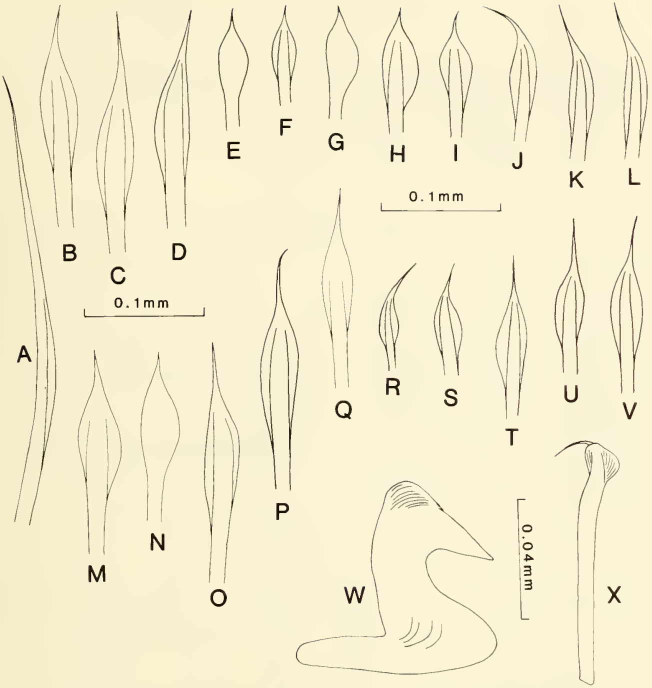

Fig. 5. *Demonax leucaspis*: A, Upper thoracic seta, *D. krusensterni*; B–D, Lower thoracic setae, *D. krusensterni* (B, upper; C, middle; D, lower); E–L, Lower thoracic setae, *D. incertus* (E, Upper, anterior row; F, Same; G. middle, anterior row; H, Lower, anterior row; I, Upper, posterior row; J, Same, K, Middle, posterior row; L, Posterior row); M–Q, Lower thoracic setae, *D. leucaspis* (M, Upper, anterior row; N, Same; O, Upper, posterior row; P, Same; Q, Lower); R–V, Lower thoracic setae, *D. cooki* (R, Upper, anterior row; S, Same; T, Lower anterior row; U, Upper, posterior row; V, Lower, posterior row); W, Thoracic avicular hook, *D. cooki*; X, Companion seta of same.

Although this species is widespread (tropical Hawaii, warm temperate western South America and questionably tropical western Central America) there are only minor differences among the types examined. There are slight variations of shape of lower thoracic notosetae between anterior and posterior rows, number of radioles, length of branchial crown compared with body length, width of thoracic ventral shields compared with body width, and coloration of branchial crown. However, without more and better preserved specimens from the three type-localities, I cannot determine that any of these differences are important, and thus concur with Johansson (1925, 1927) that the types represent but a single species.

Demonax microphthalmus (Verrill, 1873), new combination
Figs. 6–8

Sabella microphthalma Verrill, 1873:618.—Johansson, 1927:128.—Hartman, 1942a:80; 1945:47; 1951:117.—Taylor, 1961:253; 1971:720–722.—Wells and Gray, 1964:74.—Smith 1964:57, 76 [key], pl. 9, figs. 53, 54.—Kerby, 1972:16–22, figs. 1–7 [complete synonymy; not specimen from Puerto Rico].—Day, 1973: 127.—Hall and Saloman, 1975:19.

Parasabella microphthalma.—Bush, 1905:200.

Material examined.—MASSACHUSETTS: Vineyard Sound and vicinity, USFC, 1871, 9 syntypes (USNM 13079).—NORTH CAROLINA: Cape Hatteras, N. Jetty, coll., H. W. Wells, 6 Aug 1960, 5 specimens (USNM 65902). Cape Lookout, intertidal; woven into tube of cerianthid, coll. Fox, 6 Apr 1974, 7 specimens (USNM 53986). Same, in cemented material of *Petaloproctus socialis* Andrews, coll. H. Wilson, Nov–Dec 1974, 6 specimens (USNM 53985). Bogue Sound, E. of Atlantic Beach bridge, sand, shells, 2.5 m, coll., M. E. Petersen and class, 10 May 1972, 3 specimens (ZMC).—FLORIDA: Off Cape Canaveral, 28°35.9′N, 80°18.6′W, 26 m, on *Argopecten gibbus,* R/V *Hernan Cortez,* coll., D. Barber *et al.*, 6 Mar 1974, 5 specimens (FSBC I 23784). Indian River Coastal Zone Study, sta 130D, Haulover Canal, Brevard County, E. side of river on N. shore of NE spoil bank, 10 m offshore, 2 Dec 1975, 18 specimens (IRCZM 50:585). Same, sta 63A, Banana River, Eau Gallie, Brevard County, E. of marker no. 1, N. of harbor cut, 10 m offshore, 30 Jul 1974, 1 specimen (IRCZM 50:587). Same, sta 73C, Brevard County, just N. of Sebastian Inlet on NE side of river, 100 m offshore, 10 Oct 1974, 3 specimens (IRCZM 50:586). Same, sta 81C, 15 Nov 1974, 1 specimen (IRCZM). Same, sta 81D, 15 Nov 1974, 2 specimens (IRCZM). Same, sta 105A, 27 Mar 1975, 2 specimens (FSBC I 23786). Same, sta 173B, Fort Pierce, St. Lucie County, W. side of river, 100 m N. of N. jetty of Link Port Canal, 13 m offshore, 20 Apr 1976, 2 specimens (IRCZM 50:584). Same, sta 136B, 8 Dec 1975, 2 specimens (FSBC I 23787). Canaveral Pool, Indian River, Brevard County, coll., R. Ernest *et al.*, Dec 1978, 10 specimens (FSBC I 23785). Hutchinson Island, sta II, 27°21.6′N, 80°13.2′W, 11 m, coarse calcareous sand, 2 specimens (FSBC I 23788, 23789). Same, sta IV, 27°20.7′N, 80°12.8′W, 11 m, coarse calcareous sand, 2 specimens (USNM 54723; FSBC I 23790). Same, sta V, 27°22.9′N, 80°13.9′W, 11 m, coarse calcareous sand, 2 specimens (USNM 54724; FSBC I 23791). About 27 km ENE of Ft. Pierce Inlet, 27°33.2′N, 80°03.2′W, 33 m, sand and shell, R/V *Johnson,* coll., R. W. Virnstein, 1977, 20 juvenile specimens (IRCZM 50:850). Same, R/V *Gosnold,* coll., R. W. Virnstein, 1977, 2 juvenile specimens (IRCZM 50:851). Off St. Lucie Inlet, 27°11.2′N, 80°01′W, 41.8 m, on coral *Oculina varicosa* Lesueur, JSL II 144, coll., F. Stanton, 26 Oct 1976, 1 specimen (IRCZM 50:853). National Marine Fisheries Service, Tampa Bay area study, coll., J. Taylor and C. Saloman, 1963–1964, Terra Ceia Bay, 27°32′04″N, 82°35′47″W, 1 m, algae, *Halodule* and *Syringodium* cover, 1 specimen (FSBC I 13444). Same, Old Tampa Bay, 27°53′43″N, 82°36′34″W, 2 m, sand, algae and *Syringodium* cover, 1 specimen (FSBC I 10430). Same, 27°54′53″N, 82°38′44″W, 1 m, sand, algae and *Halodule* cover, 1 specimen (FSBC I 13223). Same, Boca Ciega Bay, 27°43′27″N, 82°43′24″W, 2 m, sand, 1 specimen (FSBC I 12535). Same, 27°40′37″N, 82°41′13″W, 1 m, sand, algae, *Syringodium* and *Thalassia* cover, 1 specimen (FSBC I 12603). Same, 27°41′09″N, 82°42′51″W, 1 m, sand,

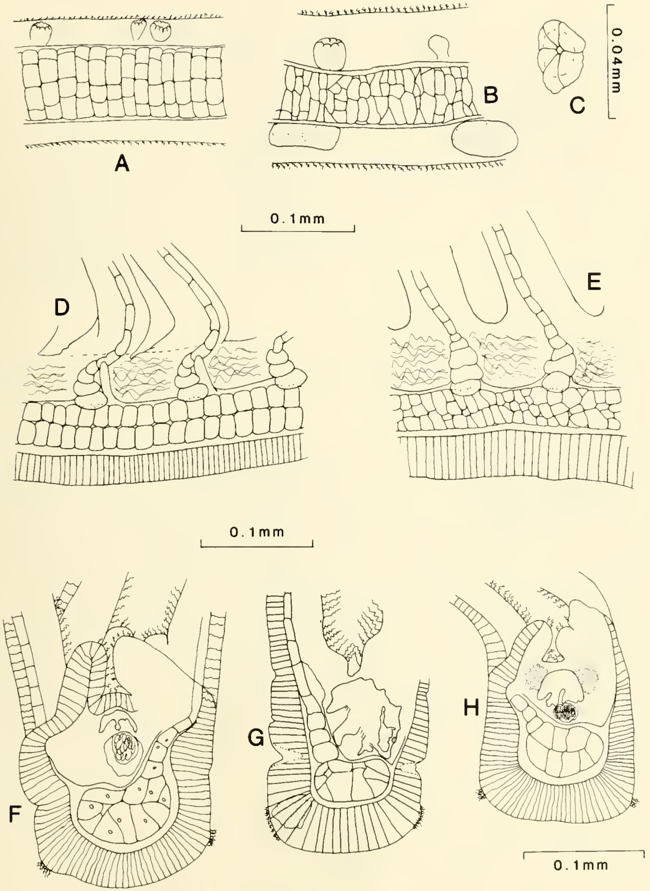

Fig. 6. *Demonax microphthalmus*: A, B, Internal structure of radioles, frontal view; C, Structure of radiolar eyespot, surface view, magnified; D, E, Internal structure of radioles, sagittal (lateral) view; F–H, Cross sections of radioles (A, C, D, FSBC I 17307, FSBC I 23784; B, E, G, USNM 53985; F, syntype; H, FSBC I 23790).

algae and *Thalassia* cover, 4 specimens (FSBC I 12744). Same, 27°38′58″N, 82°41′58″W, 2 m, sand, algae and *Syringodium* cover, 2 specimens (FSBC I 12793). Same, 27°45′18″N, 82°44′53″W, 1 m, sand, algae and *Thalassia* cover, 9 specimens (FSBC I 13293). Same, 27°45′20″N, 82°44′48″W, 1 m, sand, 20

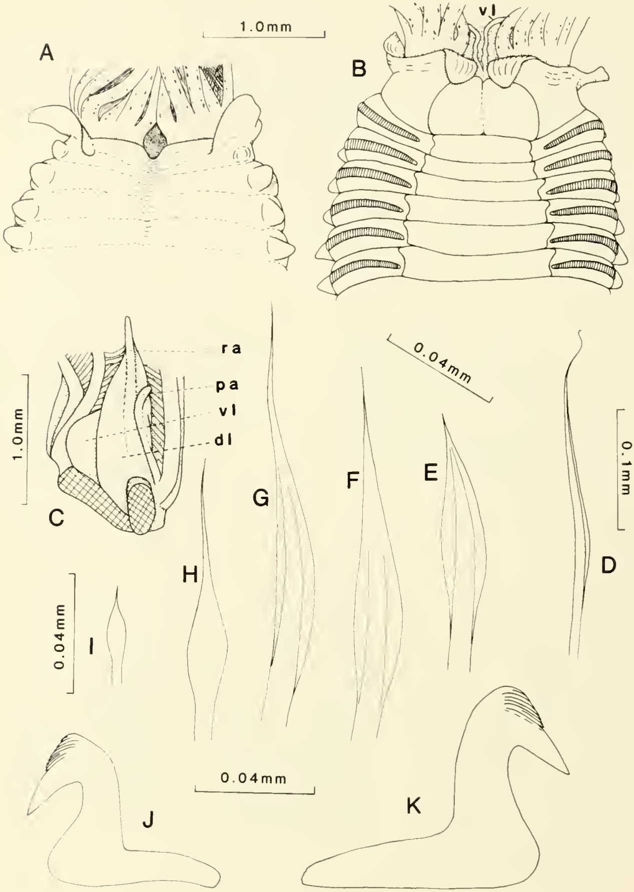

Fig. 7. *Demonax microphthalmus*: A, Anterior end of body and part of branchial crown, dorsal view; B, Same, ventral view; C, Lower part of right half of branchial crown, medial view, showing dorsal lips and ventral lips; D, Upper thoracic seta; E–I, Lower thoracic setae (E, Upper, anterior row; F, Lower, anterior row; G, Upper, posterior row; H, Middle of bundle of juvenile; I, Upper part of bundle of same); J, K, Thoracic avicular hooks (A–G, Syntypes; H, I, FSBC I 14534; J, FSBC I 23789; K, USNM 53985).

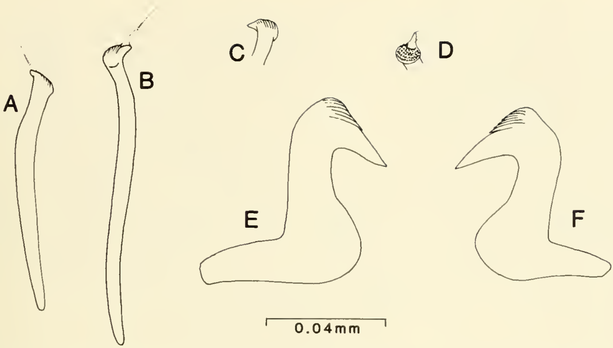

Fig. . 8. *Demonax microphthalmus*: A–D, Companion setae; E, F, Abdominal avicular hooks (A, F, FSBC I 23789; B, E, USNM 53985; C, D, FSBC I 23790).

specimens (FSBC I 13298). Same, 27°46′35″N, 82°45′53″W, 3 m, silty sand, 6 specimens (FSBC I 13304). Same, 27°37′33″N, 82°43′43″W, 2 m, sand, algae and seagrass cover, 19 specimens (FSBC I 13525). Same, 27°48′17″N, 82°45′53″W, 2 m, sand, 17 specimens (FSBC I 14532). Same, 27°48′17″N, 82°45′53″W, 2 m, sand, algae cover, 17 specimens (FSBC I 14534). Same, 27°44′35″N, 82°44′37″W, 1 m, sandy mud, algae and *Thalassia* cover, 12 specimens (FSBC I 14551). Same, 27°44′35″N, 82°44′37″W, 1 m, sand, algae and *Thalassia* cover, 4 specimens (FSBC I 14558). Same, 27°43′52″N, 82°42′23″W, 2 m, sand, 3 specimens (FSBC I 14569). Anclote Anchorage, Tarpon Springs, Pinellas County, 28°12.7′N, 82°46.7′W, 1.5 m, sand, seagrass cover, coll., J. Studt and R. Ernest, 26 Jul 1972, 2 specimens (FSBC I 17307). Seahorse Key, Cedar Keys, Levy County, on shells and pilings, coll., J. Taylor, 1960, 4 specimens (FSBC I 23783). Northeastern Gulf of Mexico, Proj. EGMEX 70, sta 22, 28°04′N, 84°41′W, 76.8 m, dredged, R/V *Hernan Cortez,* coll., J. Williams *et al.*, 9 May 1970, 3 specimens (FSBC I 23781). Same, Proj. EGMEX 70, sta 4, 29°07′N, 85°20′W, 36.5 m, 5 May 1970, 23 specimens (FSBC I 23782). Florida Middle Ground, 28°32′20″N, 84°18′36″W, 23–27 m, on coral, *Madracis detactis* (Lyman), BLM Cruise no. 1, sta 151, 5 Oct 1978, 2 specimens (USNM 61102).—PUERTO RICO: San Juan Harbor, 0–4 m, coll., J. Bruce, 27 May 1975, 1 specimen (USNM 53235).—COLOMBIA; Bahia de la Cartagena, 10°30′N, 75°30′W, less than ½ m, coll., R. Rojas, 1 specimen (USNM 49660).

Description.—Tube mostly rigid, usually orange, covered with cemented sand grains; white, not rigid, sparsely covered with sand grains on Hutchinson Island specimens. Some branchial lobes with 5–6 orange-brown to reddish-brown pigment bands, with pigment also extending onto pinnules; often without pigment bands; radioles with simple eyespots in 2 irregular rows laterally on outer sides; eyespots variable in size, dark orange, red to reddish brown, occasionally absent, diffuse or distinct and in some specimens, composed of distinct cells surrounding clear central areas, often combined to form dashes of varying lengths (Fig. 6A–C). Body without color pattern; pygidium with eyespots; pair of eyespots on prostomium of some small, apparently juvenile, specimens (IRCZM 50:850, 50: 851); maximum body length about 50 mm, width to about 4 mm; branchial crown up to 12 mm long or about ¼ as long as body; maximum of about 80 segments; largest syntype about 18 mm total length, 2.5 mm width, with about 50 segments. Branchial crown with maximum of 17 pairs of radioles, mostly with 10–14, arranged in semicircles, rarely with 2–3 pairs of radioles on ventral sides extending in very slight spiral (FSBC I 13298, 14584). Radiolar basis fused for short length, extending about as far as anterior margin of collar. Radioles with 30–100 pinnules, tips flattened, tapered; basal cell of pinnular skeleton in lateral view mostly not recessed into radiolar skeleton, next 2–3 cells flattened, nearly rectangular (Fig. 6D, E); radioles in cross section (Fig. 6F–H) with rounded outer corners, with ciliated band on or medial to corners; radiolar skeleton with thin sheath; sheath surrounding reniform group of about 8–12 skeletal cells and surrounded by thick columnar epithelium; dorsal lips (Fig. 7C) about ¼ length of radioles; ventral lips about half as long. Collar (Fig. 7A, B) beginning above collar setae, extending to beginning of radioles dorsolaterally, slightly concave laterally, ending ventrally in slightly elongate, often overlapping, rounded-triangular lappets. Thorax of 8, rarely 7 or 9, setigers, usually somewhat fusiform; notopodial lobes conical; tori long, extending from notopodia to ventral shields; ventral shield of collar segment (Fig. 7B) moderately long, about twice as broad as long, usually superficially divided by longitudinal line, incised anteriorly; ventral shields of other thoracic segments gradually broader, trapezoidal, with broader anterior margins, lateral margins concavely curved arond ventral magins of tori. Upper thoracic setae slender, narrowly hooded (Fig. 7D); lower thoracic setae (Fig. 7E–G) in 2 transverse rows, with moderately long, broad hooded region and drawn-out tips; hooded region about twice as broad as shafts and, including tips, 5–10 times longer than broad on adults, differing slightly on juvenile specimens (Fig. 7H, I). Thoracic avicular hooks (Fig. 7J, K) in rows of up to 50 on setiger 2, diminishing posteriorly, larger in upper parts of tori, smaller posteriorly, crest above beak with about 100 fine teeth; companion setae (Fig. 8A–D) with avicular heads, with crests of numerous small teeth, with hyaline mucro extending from entire center line and ending in fine tip. Abdominal avicular hooks (Fig. 8E, F) in short rows of up to about 30.

Remarks.—The presence of *D. microphthalmus* is confirmed from shallow water areas of the east coast of the Americas from Massachusetts to Florida, the Gulf of Mexico, Puerto Rico, and Colombia. Rullier and Amoureux (1979) reported a damaged specimen from Brazil as *D. microphthalmus*. However, little descriptive information was given, and I cannot confirm their record.

Demonax rugosus (Moore, 1904), new combination

Figs. 9, 10

Distylia rugosa Moore, 1904:499–501, pl. 38, figs. 38–41; 1909:289.—Loi, 1980: 143, 144.

Demonax medius.—Berkeley and Berkeley, 1952:115 [not *Parasabella media* Bush, 1905].

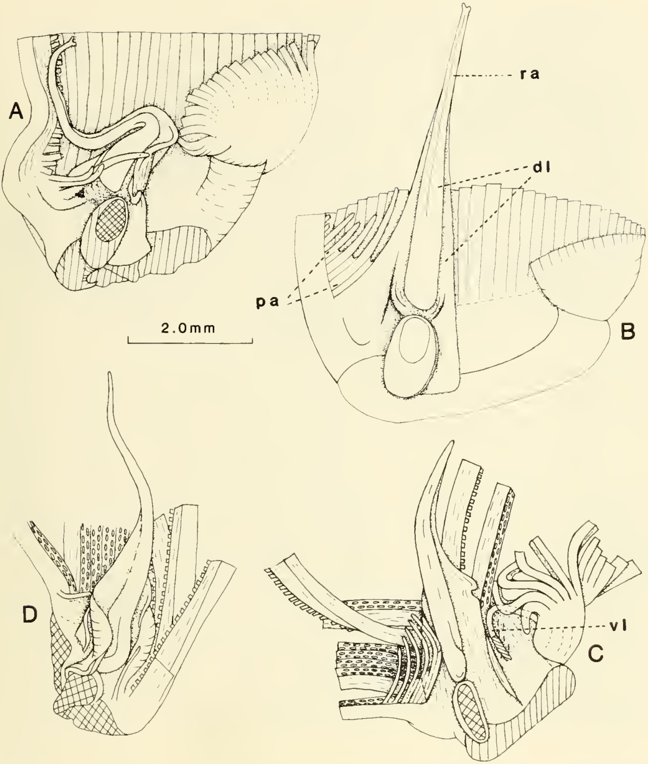

Fig. 9. *Demonax rugosus*: A, Proximal part of left half of branchial crown, medial view; B, Same, diagrammatic; C, Same; D, Same, right half of branchial crown of juvenile (A, B, Paratype, ANSP 2596; C, USNM 41465; D, USNM 41464).

Distylidia rugosa.—Hartman, 1961:129; 1969:667 [in part; figures = *Demonax medius* (Bush)].—Banse, 1979:870.

Sabella (*Demonax*) media.—Banse, 1979:878–880.—Hobson and Banse, 1981: 107. [in part; not *Parasabella media* Bush].

Material examined.—CALIFORNIA: Paratype, San Diego, coll., E. C. Starks, (listed as cotype; ANSP 2596).—WASHINGTON: Off Lake Hancock, Whidby Is., 36–72 m, coll., M. Pettibone, 1 Jul 1938, 1 specimen (USNM 44855). San Juan Channel, 140 m, coll., M. Pettibone, 10 Jul 1940, 1 specimen (USNM 44853).

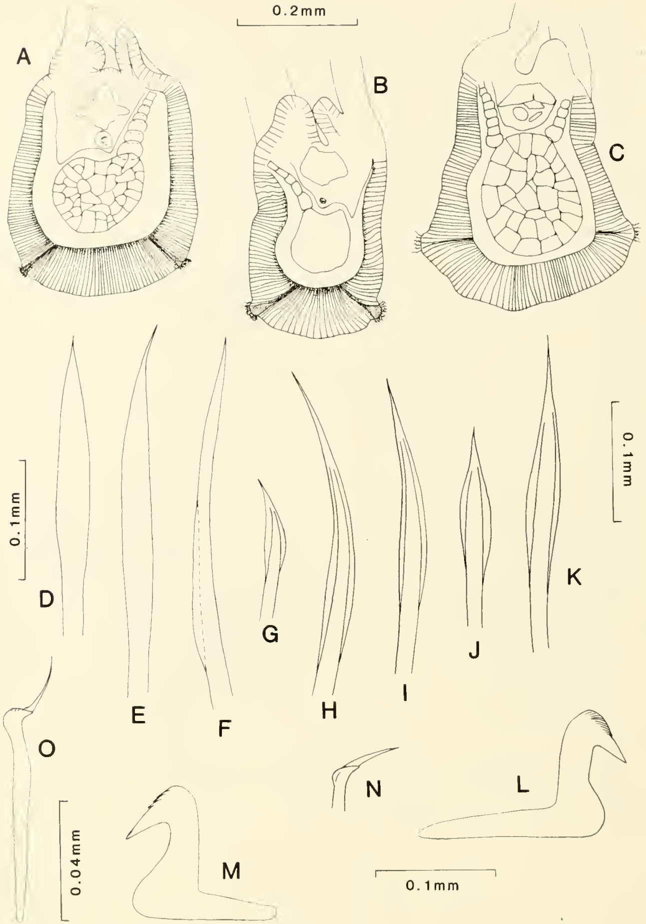

Fig. 10. *Demonax rugosus*: A–C, Cross sections of radioles; D–K, Lower thoracic setae (D, Middle, anterior row; E, Upper, posterior row; F, Same, turned; G, Upper, anterior row; H, I, Posterior row; J, Anterior row; K, Posterior row); L, Thoracic avicular hook, large specimen; M, Same, small specimen; N, Companion seta; O, Same, small specimen (A, D–F, Paratype, ANSP 2596; B, G–I, L, N, USNM 41465; C, J, K, USNM 41464; M, O, USNM 38241).

Same, among *Modiolus,* 12 Jul 1940, 1 specimen (USNM 44856). Friday Harbor, San Juan Is., on cannery pilings, coll., M. Pettibone, 23 Aug 1938, 1 specimen (USNM 44857). Puget Sound, 47°44′31″N, 122°31′53″W, Haul 10, 22 m, Apr 1963, 3 juveniles (station 3 of Banse and Hobson, 1968; USNM 38241).—BRITISH COLUMBIA: (?)Gabriola Pass, 11 Jun 1920, 3 specimens (USNM 41464). Ucluclet, coll., J. Hart, May 1935, 1 specimen (USNM 41465). Reef in Pearse Canal, 54°50.3′ N, 130°28.4′W, less than 23 m, shell, cobble, coll., P. Lambert, 13 Jun 1974, 1 specimen (BCPM 974-224-68).

Description.—Large species with body up to 70 mm long, 8 mm wide, branchial crown to about 20 mm long, body usually depressed, 8 thoracic and about 100 abdominal setigers. Tube similar to that of *D. medius* (Bush); radioles stiff, up to about 60 on each side, in spiraled arrangement of about 1 ¼ semicircles (Fig. 9A–C), in 2–3 irregular rows on each side on larger specimens (including paratype), single row on smaller specimens (USNM 41465). Radiolar skeletons in cross section (Fig. 10A–C) composed of numerous irregular cells surrounded by thick sheath. Dorsal lips (Fig. 9A–D) tapered, with radiolar appendage functioning as midrib, upper lamellae fused at upper margin with up to 3 enlarged pinnules of first dorsal radiole; dorsolateral parts of dorsal lips joined with short length of upper part of base of each branchial lobe and initially angled to ventrum. Collar beginning about ½ distance between collar setae and midline, ending at ventral incision in short, rounded lappets, extending for about ½ length of fused region at base of branchial crown [collar about as long as that of *D. medius* (Bush) but fused base of branchial crown longer]. Ventral shield of collar segment about 3 times wider than long, anteromedially incised, wider than other thoracic ventral shields and about twice as long; other thoracic ventral shields trapezoidal with anterior margins broader than posterior ones; shields gradually increasing in width posteriorly. Posterior dorsum rugose. Lower thoracic notosetae (Fig. 10D–K) very long, longer on posterior parts of bundles than on anterior, hooded region, including tips, 10–12 times longer than wide, 1 ½ times as wide as shafts. Thoracic tori long, extending from setae to ventral shields, with up to about 100 avicular hooks on setiger 2 accompanied by equal number of companion setae. Avicular hooks (Fig. 10L, M) of upper parts of thoracic tori of adults with free part of handles slender, long; companion setae (Fig. 10N, O) similar to those of *D. medius* (Bush).

Remarks.—Hartman (1961:129) designated *Distylia rugosa* Moore as the type-species of her new genus, *Distylidia.* The species differs from the type-species of *Parasabella, P. media* Bush, in having partly spiraled branchial lobes on adults and much longer lower notopodial setae in the thorax. The species differs from the included species of *Demonax* Kinberg, *D. krusensterni, D. leucapsis, D. cooki* and *D. incertus,* in having branchial lobes of adults with 2–3 rows of radioles on each side rather than single rows and also much longer, lower setae in the thorax. I do not consider the above characters to be of generic importance. Thus, *Distylia rugosa* Moore, the type-species of *Distylidia* Hartman, is included in *Demonax* Kinberg.

The posterior dorsa of large specimens of *Demonax medius, D. pallidus* (Moore), and *D. rugosus* are rugose, a feature not clearly characterizing the latter species. Hartman (1961) was apparently mistaken in stating that the rugose folds on the dorsum of *D. rugosus* "most clearly characterized" the genus *Distylidia.*

Demonas medius (Bush, 1905)
Figs. 11–14

Parasabella media Bush, 1905:200, 201, pl. 27, figs. 3–5, pl. 33, figs. 34–36, pl. 34, fig. 3, pl. 36, figs. 13, 14, pl. 37, fig. 30.

Parasabella maculata Bush, 1905:201, pl. 28, figs. 8, 9, pl. 33, figs. 8, 12, 33, pl. 34, fig. 2, pl. 36, figs. 12, 15, 16, 21, 22.

Potamilla californica.—Moore, 1923:243 [not Treadwell, 1906].

Sabella aulaconota.—Johansson, 1927:124, 215 [in part].

Demonax medius.—Johansson, 1927:136.—Hartman, 1969:675, 676, figs. 1–5 [in part; not *Parasabella pallida* Moore and probably not other specimens from southern California].

Sabella media.—Hartman, 1942a:79, 80, figs. 159, 160; 1944:285, pl. 23, fig. 42 [in part; not *Parasabella pallida* Moore].

Distylia rugosa.—Berkeley and Berkeley, 1952:112, figs. 230–232 [not Moore, 1904].

Distylidia rugosa.—Hartman, 1969:667 [in part; figs. 1–5 only, taken from Berkeley and Berkeley, 1952; not *Distylia rugosa* Moore].

Sabella (*Demonax*) *media.*—Banse, 1979:878, fig. 4c, d.—Hobson and Banse, 1981:107 [in part].

Material examined.—ALASKA: Holotype of *P. media* Bush [figured specimen designated as holotype in vial], Kodiac Is., coll., W. R. Ritter, 3 Jul 1899 (YPM 2691); 8 paratypes, same data (YPM 2692, 2693). Holotype of *P. maculata* Bush, Kodiac Is., coll., W. R. Coe, 3 Jul 1899 (YPM 2775). Canoe Bay, off NW corner of Pavlof Bay, Alaska King Crab Investigation, coll., W. L. Schmitt, 23 Sep 1940, 1 specimen (USNM 23536).—BRITISH COLUMBIA: Mudge Is., 28 May 1919, 24 specimens (USNM 40332). Off Pilot Bay, Lomb Bay, Aug 1931, off rock, 2 specimens (USNM 41502). Vancouver Is., west coast, 3 specimens (USNM 41503). Sooke Reef, Vancouver Is., coll., Fernald, 10 Jul 1976, 4+ specimens (BCPM 977-231-1). Mudge Is., 30 Aug 1913, 1 specimen (USNM 41505). Mouth of Winter Inlet, 54°50.3′N, 130°28.2′W, 6–9 m, shell and mud, coll., P. Lambert, 11 Jun 1974, 1 specimen (BCPM 974-222-29).—WASHINGTON: False Bay, San Juan Is., in roots of sea basket grass, coll., M. Pettibone, 14 Aug 1936, 1 juvenile specimen (USNM 44854).—CALIFORNIA: Bodega Bay, coll., L. C. Oglesby, 6 May 1961, 2 specimens (USNM 39619, 39674). Monterey Bay, *Albatross* sta 4496, 18 m, 19 May 1904 [as *Potamilla californica* by Moore], 1 specimen (USNM 17119).

Description.—Tube leathery, thick but moderately flexible, translucent, yellow to reddish brown, often partially covered with fine sediment or detritus. Large species up to 10 cm long. Radioles in semicircular to slightly spiraled arrangement, additional irregular medial row on adults (Fig. 11A–E); up to 27 outer radioles and 10 inner ones on each side. Radiolar skeletons in cross section (Fig. 12A–F) with numerous (20–60) irregularly arranged cells surrounded by thin sheath and moderately thick columnar epithelium, ciliated on rounded outer lateral margins on most specimens [however, cilia not present on type-specimens of *Parasabella media* and on another specimen from Alaska (USNM 23536)]; proximal skeletal cells reduced in number, with thicker walls, slightly increased in number distally,

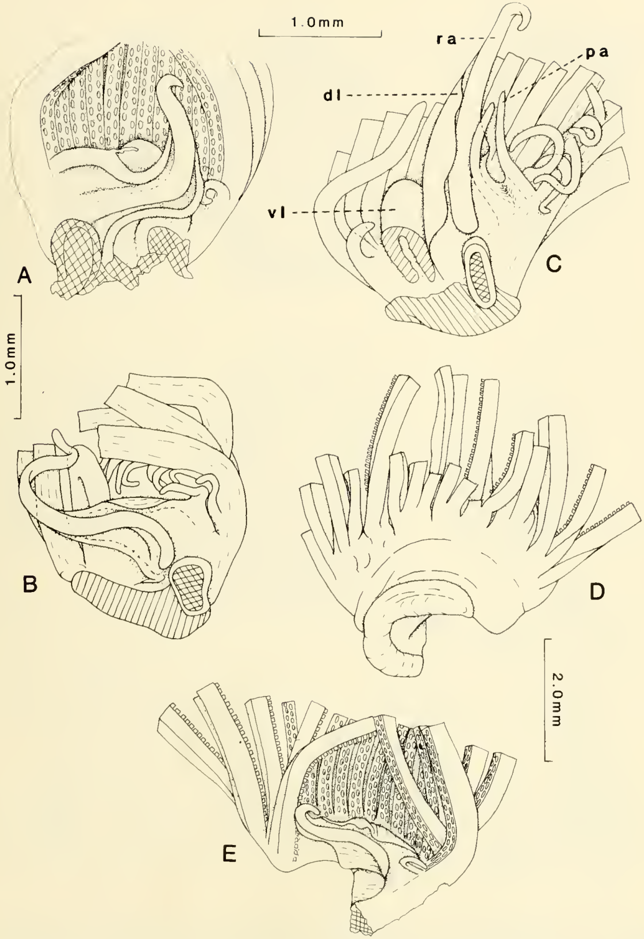

Fig. 11. *Demonax medius,* Proximal parts of branchial crown: A, Left half, medial view, holotype of *Parasabella media*; B, Right half, medial view, paratype of *Parasabella media*; C, Same, holotype of *Parasabella maculata*; D, Right half, outer view; E, Same, medial view (B, YPM 2693; D, E, USNM 41502).

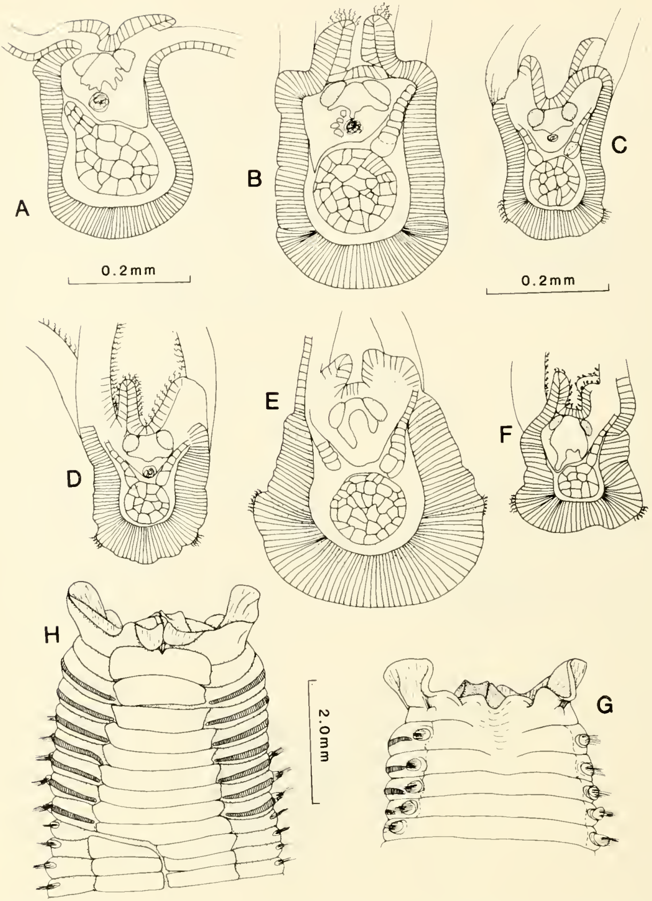

Fig. 12. *Demonax medius*: A–F, Cross sections of radioles (A, Proximal part; B, Middle part; C, Proximal part; D, Middle part; E, From large specimen; F, From small specimen); G, Anterior end of body of holotype of *Parasabella media,* dorsal view; H, Same, ventral view (A, B, YPM 2692; C, D, YPM 2775; E, F, USNM 40322).

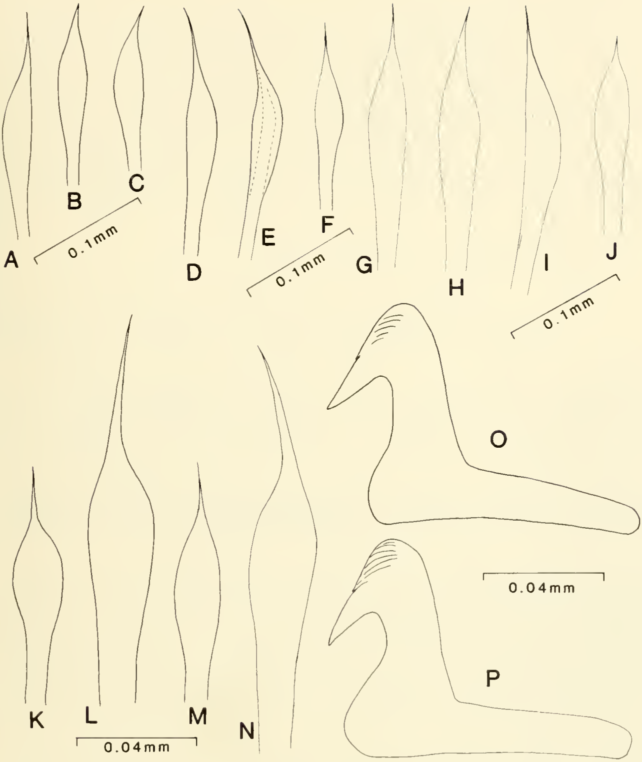

Fig. 13. *Demonax medius*: A–N, Lower thoracic setae (A, Upper, anterior row; B, Lower, anterior row; C, Same; D, Upper, posterior row; E, Same; F, Lower, posterior row; K, Upper, anterior row, small specimen; L, Lower, small specimen; M, Upper, anterior row, juvenile specimen; N, Upper, posterior row, juvenile specimen); O, P, Thoracic avicular hooks (A–F, O, YPM 2691; G, H, USNM 17119; I, J, USNM 41502; K, L, USNM 40332; M, N, USNM 44854; P, YPM 2775).

then reduced in number toward tips; sheaths thicker proximally, basal pinnular skeletal cells slightly flattened, gradually narrower and longer distally. Dorsal lips (Fig. 11A–C, E) fused for most of their basal lengths with upper part of branchial lobes, mostly directed ventrally, then turned anteriorly, broad basally, long, tapered, with radiolar appendage functioning as midrib, joined at margin of upper lamella with 1–2 pinnules (pinnular appendages) of first dorsal radioles, fused pinnules much longer, broader than others, other pinnules diminishing distally.

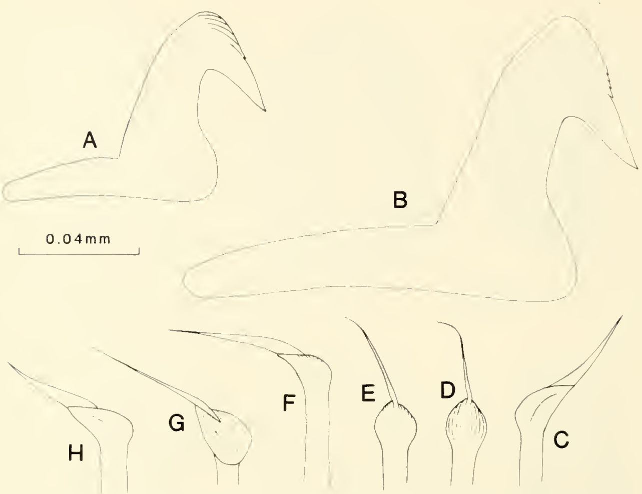

Fig. 14. *Demonax medius*: A, Thoracic avicular hook, small specimen; B, Same, large specimen; C–H, Companion setae (A, USNM 40332; B, G, H, USNM 41502; C–E, YPM 2691; F, YPM 2775).

Usually 8 thoracic setigers (apparent regenerating specimens may have fewer). Collar (Fig. 12G, H) extending past fused bases of branchial crown to beginning of radioles. Ventral shield of collar segment rectangular, greater than 3 times wider than long, incised anteromedially; other thoracic ventral shields trapezoidal with broader anterior margins; shields gradually wider posteriorly. Upper thoracic setae slender, narrowly hooded; lower setae (Fig. 13A–N) broadly hooded, all similar on adults, moderately short, with hooded part including tip about twice broader than shaft and 5–7 times longer than broad. Thoracic tori long, with numerous avicular hooks and companion setae, extending from notopodia to ventral shields; avicular hooks (Figs. 13O, P; 14A, B) of large adults with long handles; companion setae (Fig. 14C–H) with long, slender shafts 1½ length of bases of avicular hooks, with avicular tips, with slender, tapered mucros extending from narrow part of middle of outer margin.

Remarks.—All specimens that I have examined from British Columbia originally identified by Berkeley and Berkeley (1952:112) as *Distylia rugosa* Moore and later changed to *Sabella* (*Demonax*) *media* by Banse (1979:878–880) are *Demonax medius.* Other specimens identified by Berkeley and Berkeley (1952) as *Demonax medius* and changed to *Sabella* (*Demonax*) *media* by Banse, with the possible exception of one lot (USNM 41464), are *D. rugosus* (Moore).

Bush's (1905) figures of lower thoracic setae are incorrect. Those on the types are actually much slenderer (Fig. 13A–N). Bush's figures of lower thoracic setae are, in fact, very similar to those I have provided for *D. pallidus* (Moore) (Fig. 16A–D). However, radioles of *D. pallidus* have skeletons in cross section composed of about ten thick-walled cells (Fig. 15B–E), whereas skeletal cells in cross section are much more numerous in *D. medius* and *D. rugosus*.

Juvenile specimens of the above three species are similar and difficult to separate. All have radioles arranged in semicircles and lower thoracic setae which are not diagnostic. The collars of such specimens, however, appear to be similar to those of adults, with that of *D. rugosus* being short.

Demonax medius is here reported from the eastern Pacific Ocean from Alaska south to Monterey Bay, California.

Demonax pallidus (Moore, 1923), new combination
Figs. 15, 16

Parasabella pallida Moore, 1923:241, 242.—Loi, 1980:144.
Sabella media.—Hartman, 1944:285 [in part, not pl. 23, fig. 42].
Demonax medius.—Hartman, 1969:675, 676 [in part, not figs. 1–5].

Material examined.—CALIFORNIA: Off Santa Cruz Lighthouse, Monterey Bay, fine grey sand and rock, 18 m, Albatross sta 4496, 19 May 1904, holotype (USNM 17360). Scorpion Harbor, Santa Cruz Is., coll., W. G. Hewatt, 1 Jul 1939, 1 specimen (identified as *Demonax leucaspis* by Berkeley and Berkeley; USNM 41463). Los Angeles Harbor, coll., V. L. Human, 1 specimen (USNM 49795).

Description.—Tube unknown. Holotype completely without color markings; body 10 mm long, 1.5 mm wide, branchial crown about 4 mm long, 12–13 pairs of radioles with naked tongue-like tips about 1 mm long (Fig. 15A). Other specimens with faint, light brown color spots on radioles, slightly larger, body up to 13 mm long, 2.7 mm wide, branchial crown up to 7.5 mm long with 14–16 pairs of radioles with proportionately shorter tips. Eight thoracic and about 50 abdominal setigers; largest specimen (USNM 41463) apparently regenerating posteriorly, with about 40 abdominal setigers. Radioles in semicircular arrangement, with long, slender pinnules, with rachis in cross section (Fig. 15B–E) having outer corners rounded. Ciliated band not observed. Skeleton consisting of 8–10 irregularly arranged, thick-walled cells; holotype with columnar epithelium poorly preserved, with small skeleton surrounded by thin sheath and thick columnar epithelium; skeleton of largest specimen relatively larger, surrounded by thick sheath and thinner columnar epithelium. Dorsal lips (Fig. 15F) with single pinnular appendage, with radiolar appendages on largest specimen slightly longer than figured. Collar beginning dorsally about midway between collar setae and middorsal line, straight laterally, slightly elongated ventrally as pair of short, pointed lobes at ventral incision, moderately long and extending past basal fused part of branchial crown to beginning of radioles. Thoracic ventral shields almost identical with those of *Demonax medius* (Bush) (Fig. 12H). Posterior dorsum of large specimen (USNM 41463) rugose as on *D. medius* and *D. rugosus*. Lower thoracic setae (Fig. 16A–D) of adults with very short hooded region and long mucronate tip about half total length of remainder of hooded region, with hooded region, including tip, 3–4 times longer than wide and greater than 2 times wider than shaft; blades broader and shorter in anterior parts of bundles. Thoracic

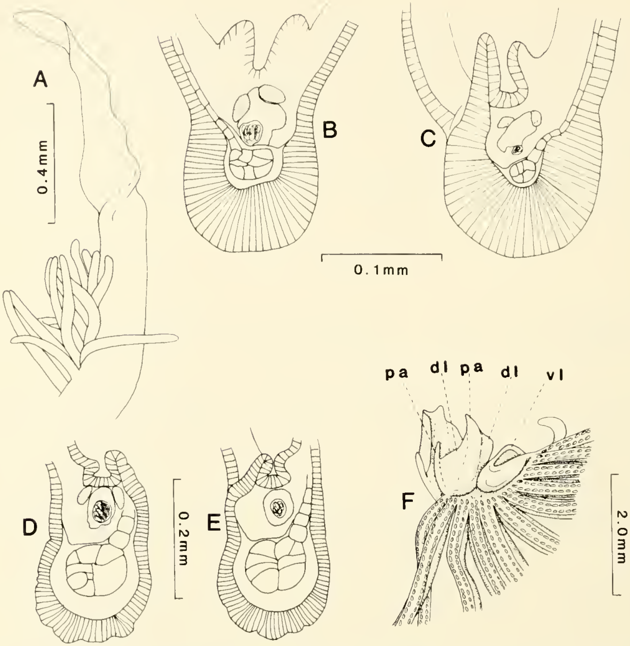

Fig. 15. *Demonax pallidus*: A, Tip of second dorsal radiole; B–E, Cross sections of radioles (B, Proximal; C, Middle; D, E, From middle of proximal half); F, Branchial crown, proximal part, lateral view of dorsal lips, ventral lips, and medial view of radioles (A–C, F, Holotype; D, E, USNM 41463).

avicular hooks (Fig. 16E–H) moderately stout, with handles of moderate length, accompanied by similar number of companion setae (Fig. 16I–L), in long rows from notopodia to ventral shields.

Remarks.—The holotype of *Parasabella pallida* is a subadult specimen as indicated by developing radioles on lower parts of the branchial crown. Lower thoracic setae of small specimens of *Demonax* often have relatively longer points than those on adults of the same species. However, the width of the hooded area compared with that of the shaft is reasonably constant in all specimens irrespective of size. I found only a single lower thoracic seta on the holotype, and it had a broken tip. The seta is similar to those of the posterior part of the bundle of setiger 7 of an adult specimen (USNM 41464). Other lower thoracic setae of the adult are much broader. Further, Moore (1923) stated that notosetae of *D. pallidus* were similar to those incorrectly described for *D. medius* by Bush (1905), also indicating that they had broad blades compared with widths of shafts. As indicated in my description, lower thoracic setae of *D. medius* have a much slenderer blade

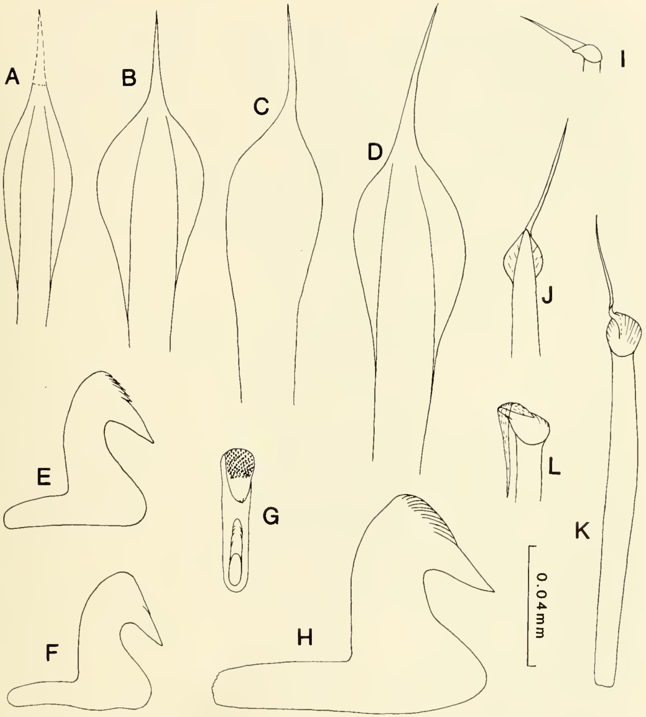

Fig. 16. *Demonax pallidus*: A–D, Lower thoracic setae (B, Upper, anterior row; C, Upper, posterior row; D, Lower, posterior row); E–H, Thoracic avicular hooks (E, F, H, lateral view; G, face view); I–L, Companion setae (A, E–G, I, Holotype; B–D, H, J–L, Large specimen, USNM 41463).

than originally described. Finally, radioles of the holotype and other specimens of *D. pallidus* have a skeleton of 10 or fewer cells in cross section also differing from specimens of *D. medius* to which the species had been referred by Hartman (1944). Difference in thickness of columnar epithelium of radioles between the holotype and other specimens is probably the result of poor preservation and the subadult status of the holotype.

Demonax jamaicensis (Augener, 1924)
Fig. 17

Parasabella jamaicensis Augener, 1924:48.
Demonax jamaicensis.—Johansson, 1927:136.
Sabella jamaicensis.—Hartman, 1959:560.

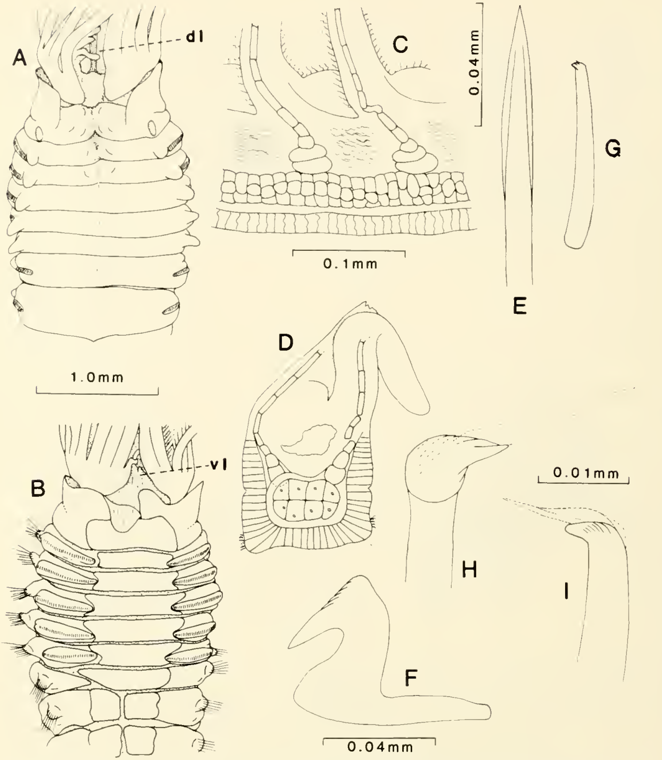

Fig. 17. *Demonax jamaicensis*: A, Anterior end of body and part of branchial crown, dorsal view; B, Same, ventral view; C, Internal structure of radiole, sagittal (lateral) view; D, Cross section of radiole; E, Lower thoracic seta; F, Thoracic avicular hook; G, Thoracic companion seta, mucro missing; H, I, Same, magnified, mucro present (G, Not scaled).

Material examined;—JAMAICA: Holotype, Kingston, (ZMH V-6791).

Description.—Tube rigid, formed of silicate sand grains cemented in yellow translucent matrix, giving overall orange color (mostly covered by sponge). Body ocher-yellow; branchial crown with about 5 crossbands on pinnules and partially on radioles; retained coloration of radioles faint. Branchial crown about 5.5 mm long, body about 13 mm long and 1.5 mm wide at thorax, with 6 thoracic and 25 abdominal setigers [Augener (1924) stated that there were 56 abdominal segments on an animal 13 mm long]; thorax somewhat flattened, with short segments;

abdomen cylindrical, with more elongate segments. Branchial lobes fused proximally for short length, with fused region extending well past collar (Fig. 17A, B). Dorsal and ventral lips of branchial crown not observed. Radioles numbering 10 pairs; ventral pair shorter, ⅓ length of others on left lobe, vestigial on right lobe (Fig. 17B); in sagittal view (Fig. 17C), pinnular skeleton of radioles showing 2 large, oval cells proximally, with basal cell not recessed into skeleton; nearly rectangular in cross section (Fig. 17D) with angular outer corners; radiolar skeleton oval, with 2 rows of skeletal cells of 4 cells each; radiolar sheath moderately thick, surrounded by moderately thick columnar epithelium; ciliated bands present on radioles below outer lateral corners. Collar short, widely separated dorsally, beginning slightly anterior and medial to collar setae, concave ventrolaterally, changing to 2 moderately long, rounded lappets at ventral incision (Fig. 17B). Thorax with slight medial furrow on anterior 2–3 segments. Notopodia on conical lobes; tori extending from notopodia to ventral shields. Ventral shield of collar segment rectangular, about twice wider than long and broader than those following; other thoracic ventral shields gradually wider and longer, rectangular to trapezoidal with broader anterior margins; those after setiger 3 with lateral sides concavely curved around lower parts of tori. Collar setae numbering about 17, slender, in 2 short rows or elongate-oval group; other thoracic segments with upper arc of narrowly hooded setae and 2 lower transverse rows of shorter setae with hooded area only very slightly broader than shaft (Fig. 17E); about 18 lower setae on setiger 2, fewer on more posterior thoracic segments. Thoracic avicular hooks (Fig. 17F) with slender, long handles, numbering about 42 on setiger 2, 38 on setiger 4. Companion setae (Fig. 17G–I) with shaft very stout basally, very slightly bent, gradually tapered from base to tip, head not much broader than shaft, mucro extending from middle of entire length of beak and ending in long, pointed tip. Abdominal tori with about 20 avicular hooks similar to those of thorax but with much shorter handles; abdominal setae about 19 in each bundle, hooded, similar to upper thoracic setae, arranged in 2 transverse rows.

Remarks.—The species is known only from the original report of Augener (1924). The holotype may have been regenerating the anterior end as indicated by the reduced number of thoracic segments; it does not appear to be a juvenile. I did not examine the dorsal and ventral lips; the specimen was returned to the Zoologisches Museum, Hamburg, before the necessity to do so became apparent to me. However, *Parasabella jamaicensis* appears to be a *Demonax*, closely related to *D. microphthalmus* (Verrill).

Demonax lacunosus, new species
Figs. 18–20

Material examined.—FLORIDA: Hutchinson Island, sta V, 27°22.9′N, 80°13.9′W, 11 m, coarse calcareous sand, coll., Gallagher, Jul 1973, holotype (USNM 54725), 3 paratypes (USNM 60897; FSBC I 23792).

Description.—Tubes lost. Branchial crown of large specimen (Fig. 18A; USNM 60897) with yellowish brown pigment spots on outer, lateral margins of radioles and extending onto pinnules, spiraling anteriorly from dorsal to ventral sides in about 7 bands; distal pigment spots more prominent and appearing in more irregular arrangement; smaller specimens, including holotype, with indistinct pig-

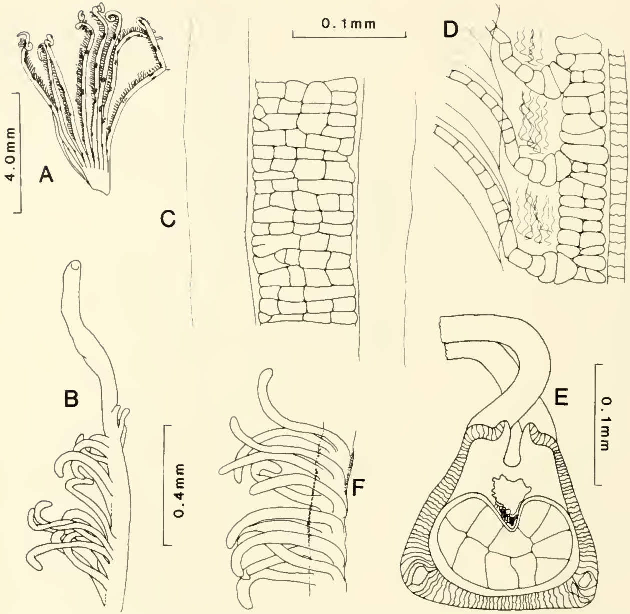

Fig. 18. *Demonax lacunosus,* large paratype (USNM 60879): A, Detached branchial crown, view from left side; B, Tip of radiole; C, Internal structure of radiole, frontal view; D, Same, sagittal (lateral) view; E, Cross section of radiole; F, Middle of radiole.

ment spots proximally, prominent ones distally; eyespots absent. Pygidium with paired, red eyespots. Large specimen (damaged, apparently regenerating posterior end) with body 10 mm long, 1.4 mm wide; branchial crown 7 mm long; 8 thoracic and 27 abdominal setigers. Holotype of 8 thoracic setigers (7 on right side), 33 abdominal setigers; body 3.1 mm long, branchial crown 2.5 mm long. Large specimen with 10 pairs of radioles and additional, vestigial pair ventrally; smaller specimens with 6–7 pairs of radioles; branchial lobes fused proximally for short length; radioles with short, tongue-shaped distal ends without pinnules (Fig. 18B). Radioles in frontal view (Fig. 18C) with broad skeleton of cartilaginous cells organized in irregular transverse rows of 3–5 cells; broad columnar epithelium laterally; elongate, oval pigment spots on outer lateral margins, more distally on borders away from dorsal midline; empty spaces usually visible in columnar epithelium near lateral margins. In sagittal view (Fig. 18D), basal pinnular skeletal cells deeply recessed into radiolar skeleton at angle of 90–120°. Radioles in cross section view (Fig. 18E) trapezoidal, much broader on outer margin than at at-

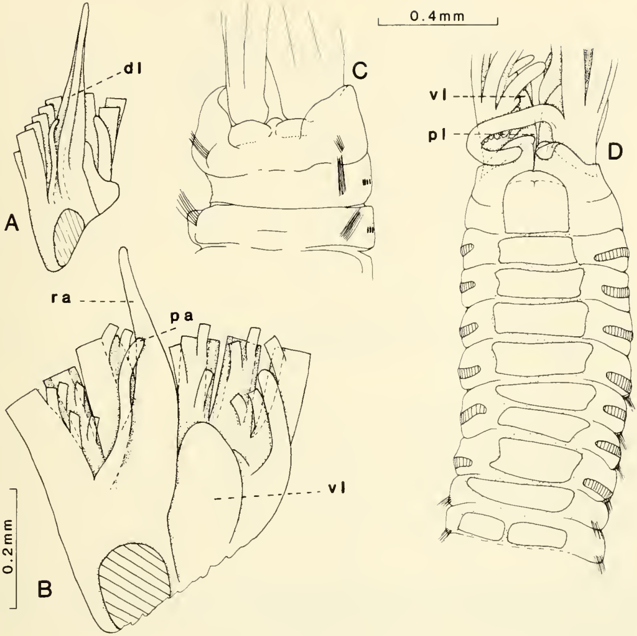

Fig. 19. *Demonax lacunosus*: A, Left side of branchial crown, medial view, most of radioles omitted; B, Same; C, Anterior end of body and part of branchial crown, dorsal view; D, Same, ventral view (A, Large paratype, USNM 60879; B, Small paratype, FSBC I 23792; C, Small paratype; D, Holotype; A, Not scaled).

tachment of pinnules; outer lateral corners almost angular, probably angular in life; skeleton reniform in outline, formed of 8–11 cells, surrounded by thin sheath and moderately thin columnar epithelium; epithelium with cavities in outer lateral corners surrounded by epithelial cells (or with highly vacuolate cells); outer lateral corners with obscure rows of cilia (visible on holotype but not on large specimen). Pinnules short, widely spaced and not more than 3 times longer than thickness of radioles (Fig. 18F). Dorsal lips (Fig. 19A, B) slender, about ¼ length of radioles, elongate-triangular, fused on basal ⅔ of upper margin with modified pinnules of first dorsal radiole (pinnular appendage). Ventral lips extending ⅓ of length of dorsal lips. Collar short (Fig. 19C, D), extending for about half length of fused, cartilaginous base of branchial crown, widely separated dorsally, beginning about half distance from dorsal midline to collar setae, not notched but concave laterally, ending at ventral incision in long, triangular lappets. Dorsum of thorax with small,

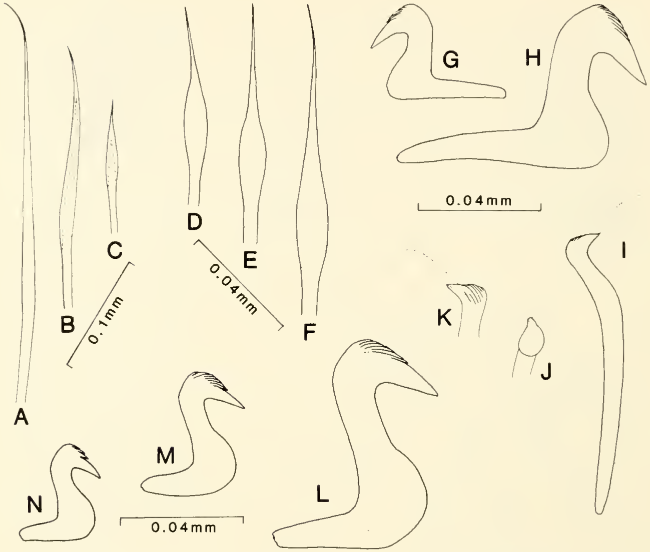

Fig. 20. *Demonax lacunosus*: A, Upper thoracic seta; B–F, Lower thoracic setae (B, Posterior row; C, Anterior row; D, Upper, anterior row; E, Upper, posterior row; F, Lower, posterior row); G, Thoracic avicular hook from lower part of torus, setiger 2; H, Same, from upper part of torus; I–K, Companion setae; L–N, Abdominal avicular hooks (L, From lower part of bundle; M, N, From upper part of bundle) (A–C, G–N, Large paratype, USNM 60879; D–F Holotype).

anterior, medial groove; ventral shield of collar segment about as long as wide, pentagonal with broader posterior margin or rectangular with rounded anterior margin (Fig. 19D); remaining thoracic ventral shields rectangular but slightly concave laterally, greater than twice broader than long on small specimens, longer than broad on large specimen; neuropodial tori of thorax well separated from ventral shields. Collar segment with 2 short rows of narrowly hooded setae, hooded parts on those of upper row longer by ratio of 10:7 and similar to upper setae of setigers 2–8; setae of setigers 2–8 (Fig. 20A–F) with arc of long, very slender setae above notopodial lobe, elongate-oval group or 2 transverse rows of shorter, slender, more broadly hooded setae below; latter type with hooded parts including tips 9–13 times longer than wide, slightly less than twice broader than shafts, shorter by ½ on anterior row than on posterior row on large specimen, slightly less so on smaller specimens. Thoracic tori with about 36 pairs of avicular hooks and companion setae on setiger 2 of large specimen, diminishing in number posteriorly; avicular hooks (Fig. 20G, H) slender, with handles of moderate length; companion setae (Fig. 20I–K) with slender shafts, denticulate, avicular heads

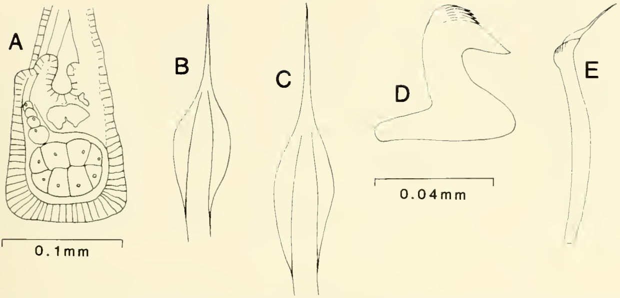

Fig. 21. *Demonax* sp.: A, Cross section of radiole; B, C, Lower thoracic setae (B, Lower, anterior row; C, Middle, posterior row); D, Thoracic avicular hook; E, Companion seta.

slightly broader than widest part of shaft, and long, tapered hyaline mucro extending from complete length and most of width of beaked part. Abdominal setae slender, hooded, in 2 transverse rows or elongate-oval group. Abdominal avicular hooks similar to those of thorax but with much shorter handles and relatively longer necks (Fig. 20L–N), with about 23 hooks in tori of first abdominal setiger of large specimen, diminishing in number posteriorly and in size from lower to upper parts of tori.

Remarks.—*Demonax lacunosus* is a small species and differs from most other members of the genus in the following characters: 1) the branchial crown is more than half as long as the body; 2) radioles are nearly trapezoidal in cross section, with a large skeleton, thin sheath, and moderately thin columnar epithelium with spaces in the outer lateral corners; 3) dorsal lips are very slender; 4) the two rows of collar setae are of distinctly unequal lengths; 5) the ventral shield of the collar segment is about as long or longer than wide; and 6) thoracic tori do not extend to the ventral shields. *Demonax lacunosus* differs from *D. japonicus,* to which it appears to be closely related, in having up to 10 rather than 15 pairs of radioles.

Etymology.—The specific name is derived from the Latin and refers to the spaces in the outer lateral corners of the radioles.

Demonax sp.
Fig. 21

Material examined.—BAHAMA ISLANDS: Lucaya, near Freeport, Grand Bahama Is., on jetty, about 1.5 m, coll., W. Jaap and Sylvia Earle, 7 Apr 1974, 1 specimen (FSBC I 24195).

Description.—Tube absent. Body 8 mm long, about 1 mm wide across thorax; 7 thoracic and 23 abdominal segments plus 1 mm long, regenerating posterior end. Branchial crown with about 7 reddish-brown cross bands, without eyespots, with 9 pairs of radioles in semicircular arrangement; radioles in cross section (Fig. 21A) with somewhat rounded outer lateral corners, with moderately large, oval skeleton of 8–10 cells, without prominent ciliated bands; dorsal lips similar to those of *D. microphthalmus.* Collar well separated dorsally, moderately long, straight laterally, ending at ventral incision in triangular lappets. Ventral shield of collar segment short, about 3 times broader than long, slightly longer than those following, incised anteromedially; other thoracic ventral shields narrower, trapezoidal, with broader margin anterior; shields gradually narrower posteriorly. Setae and uncini (Fig. 21B–E) similar to those of *D. microphthalmus* but lower thoracic setae with hooded parts about 2½ times broader than shafts and, including tips, 4–5 times longer than broad.

Remarks.—As indicated in the key, this small, subadult specimen closely resembles *D. pallidus* (Moore). It does not appear to be a juvenile of *D. microphthalmus,* a species widely distributed on the east coast of the Americas from Massachusettts to Colombia. Juvenile specimens of *D. microphthalmus* have lower thoracic notosetae with long, drawn-out points, but with hooded parts only about twice as wide as shafts (Fig. 7H, I), and the ventral shield of the collar segment of juvenile *D. microphthalmus* is much longer.

Hypsicomus Grube, 1870

Hypsicomus Grube, 1870:348.

Type-species.—Sabella stichophthalmos Grube, 1863; subsequent designation by Bush (1905:191).

Grube (1870) originally included the following four species in *Hypsicomus: Sabella stichophthalmos; S. alticollis* Grube, 1868; *S. brevicollaris* Grube, 1858; and *S. simplex* Grube, 1870. *Sabella stichophthalmos* does not conform to the original diagnosis that Grube gave for the genus, because collar setae are arranged not in a long row but in a short one, the collar is not a low ring but four-lobed, and the basal lamina is not unusually high. Nevertheless, the species was correctly designated as the type-species of *Hypsicomus* in accordance with Article 69 of the International Code of Zoological Nomenclature (1964). Augener's later (1924) designation of *Sabella phaeotaenia* Schmarda, 1861, as the type-species, which was not one of the species included in *Hypsicomus* by Grube (1870) but which was followed by Hartman (1959) and several others, must yield to the earlier designation by Bush. I have seen Grube's original descriptions of *S. simplex, S. alticollis,* and *S. brevicollaris,* Schmarda's original description of *S. phaeotaenia,* and examined a specimen of *S. brevicollaris* identified by Grube; in my opinion, all are species of *Notaulax* Tauber, below.

Diagnosis.—Radioles in semicircular to slightly spiraled arrangement, joined proximally by palmate membrane for ¼ to ⅓ of their length, without stylodes, with punctate, lensed ocelli on lateral margins distal to palmate membrane, with flanges on outer lateral corners near tips, and with medial flanges on upper pair in region of palmate membrane; branchial crown without flanges proximally on upper and lower parts of fused, cartilaginous base. Dorsal lips beginning ventrally near ventral margin of branchial lobes, long, slender, with radiolar appendage functioning as midrib joined dorsally to base of first dorsal radiole by lamella, without pinnular appendages. Ventral lips reduced; ventral sacs present. Prostomium long. Two pairs of accessory lamellae on prostomium-collar segment, including pair of auriculate lamellae on dorsum of prostomium originating dorsolaterally, curved medially, and pair of collar-like lamellae beginning on anteromedial margin of prostomium, extending straight laterally, ending ventrally under ventral lappets of collar, or slightly more anterior, below or partially covering ventral sacs. Collar with dorsal origins widely separated, incised laterally and ventrally. Collar setae in short bundles or 2 short rows, slender, narrowly hooded, similar to upper setae of other thoracic segments. Setae of other thoracic segments consisting of upper arc of slender, hooded setae above 2 transverse rows or transverse, elongate group of paleate setae. Thoracic avicular hooks with handles of moderate length; companion setae with broad, thin, pennonate blades at right angles to shafts. Abdominal setae, including mucronate paleae and slender capillaries, in short, transverse rows; avicular hooks similar to those of thorax but with shorter handles.

Remarks.—*Hypsicomus stichophthalmos* was reported as *Sabella* (*Potamilla*) *stichophthalmos* from Madeira by Langerhans (1884) and later referred to *Potamilla* Malmgren by Fauvel (1927). About the only important character in common between *H. stichophthalmos* and *Potamilla neglecta* (Sars, 1850), the type-species of *Potamilla,* is the presence of paleae on the lower parts of thoracic notopodia. Among other characters, *Potamilla* has dorsal lips without radiolar appendages and hooded setae of one type but of greatly different lengths in the abdomen, whereas *Hypsicomus* has dorsal lips with radiolar appendages and two types of setae in the abdomen, slender capillaries and mucronate paleae.

Anamobaea Krøyer, 1856, an older name with type-species *A. orstedii* Krøyer, is similar to *Hypsicomus* in having similar setae and uncini, branchial crown, and collar. However, the two pairs of accessory lamellae on the prostomium-collar segment region of *Hypsicomus* are not present on *A. orstedii,* the only known species in the genus, and the latter has branchial lobes with broad flanges proximally on the upper and lower margins in the region of a long basal lamina, both of which are absent on *Hypsicomus.*

Potamethus Chamberlin, 1919, with type-species *Potamis spathiferus* Ehlers, 1887, is similar to *Hypsicomus* in having two types of setae on abdominal segments, a long prostomium-collar segment region and similar setae on thoracic setigers. However, both a definite palmate membrane and lensed ocelli are absent from the branchial crown of *Potamethus,* and thoracic neuropodia of *Potamethus* have avicular hooks and companion setae with very long handles. *Potamethus dubius* (Eliason, 1951) has accessory lamellae on the ventrum of the prostomium-collar segment region which appear to be similar to the lateroventral accessory lamellae of *H. stichophthalmos.*

Hypsicomus stichophthalmos (Grube, 1863)

Figs. 22, 23

Sabella stichophthalmos Grube, 1863:62, 63, pl. 6, fig. 3.—Wiktor, 1980:281 [report of syntype].

?*Sabella stichophthalmos.*—Marion and Bobretzky 1875:92, 93, pl. 11, figs. 23a–g.

Sabella (*Hypsicomus*) *stichophthalmos.*—Grube, 1870:348.

?*Sabella* (*Potamilla*) *stichophthalmos.*—Langerhans, 1884:267.

?*Hypsicomus caecus* Iroso, 1921:70, 71.

Potamilla stichophthalmos.—Fauval, 1927:311, 312 [in part; fig. 106k; not *P. stichophthalmos* of Fauvel, 1914a:315, 316, pl. 31, figs. 30–35].

Material examined.—YUGOSLAVIA: Crivizza, Lussin [Losinj] Is., Adriatic Sea, 8 syntypes (ZMB 372, ZMB Q 5240).

Description.—Tube (Fig. 22A) with smooth, thick covering of grey silt, free part fragile, embedded part horny, reddish-orange. Body 36 mm long, 2 mm wide (Grube 1863), up to 190 segments; branchial crown 11 mm long. Branchial lobes with 13–16 pairs of radioles united by palmate membrane (Fig. 22A) for ⅕–¼ their length, with moderately long, fused region proximally; radioles with outer lateral corners rectangular proximally, flanged near tips; tips long, cylindrical; skeleton in cross section of 4 cells surrounded by thick sheath and columnar epithelium (Fig. 23A); ciliated bands absent. Dorsal lips (Fig. 23B) ¼ length of radioles, long, slender, with upper lamella "Z" shaped, ventral lips reduced or absent (looked for but not observed). Prostomium anteriorly pointed on dorsal side; auricular lamellae on dorsum of prostomium bent medially; lateroventral prostomial-peristomial lamellae under collar slightly prolonged ventrally, forming triangular lappets. Ventral collar lamellae (Fig. 22C, D) extending to beginning of branchial crown, with rounded tips; dorsolateral lamellae extending less than half as far, beginning dorsally above collar setae, extending anteriorly to posterior margins of auricular lamellae of prostomium with dorsal margins about twice longer than ventral ones (Fig. 22A, B). Nine to 13 thoracic setigers. Ventral shield of collar segment (Fig. 22C, D) rectangular posteriorly, broadened and rounded anteriorly, deeply incised anteromedially, often divided by transverse furrow; ventral shields of other thoracic segments rectangular. Collar setae slender (Fig. 23C), with blades about twice longer on medial than on lateral row, otherwise similar. Upper setae of other thoracic setigers (Fig. 23D) similar to long ones of collar segment; lower paleate setae arranged in 2 transverse rows (Fig. 23E–G), some with slender mucronate tips. Thoracic avicular hooks in moderately long rows not extending to ventral shields (Fig. 23H), with broad handles of moderate length; companion setae (Fig. 23I–K) with long, thin, slender, pennonate blades extending from entire surface of head, ending in symmetrical tips. Abdominal avicular hooks (Fig. 23L) with handles shorter than those of thorax; setae consisting of slender capillaries and mucronate paleae with asymmetrical tips in 2 short, transverse rows (Fig. 23M).

Remarks.—*Hypsicomus stichophthalmos* may have been confused with one or more other species from the time of its original description. A syntype lot (ZMB Q 5240) contains eight specimens of *H. stichophthalmos* and one specimen of another species which appears to be related to *Pseudopotamilla* Bush. The latter specimen has avicular hooks of thoracic setigers with extremely long rather than moderately long to long handles, and punctate, lensed ocelli scattered along the sides of radioles rather than circular, composite eyes on the outer surface as on *P. reniformis,* the type-species of *Pseudopotamilla.*

Fauvel's (1927) description of *Potamilla stichophthalmos* contains the original figure of Grube and also figures of another species from the Cape Verde Islands which he mistakenly reported under the same name. Bellan (1964) also may have included two species in his account of *Potamilla stichophthalmos* from the Mediterranean, because he described two types of tubes.

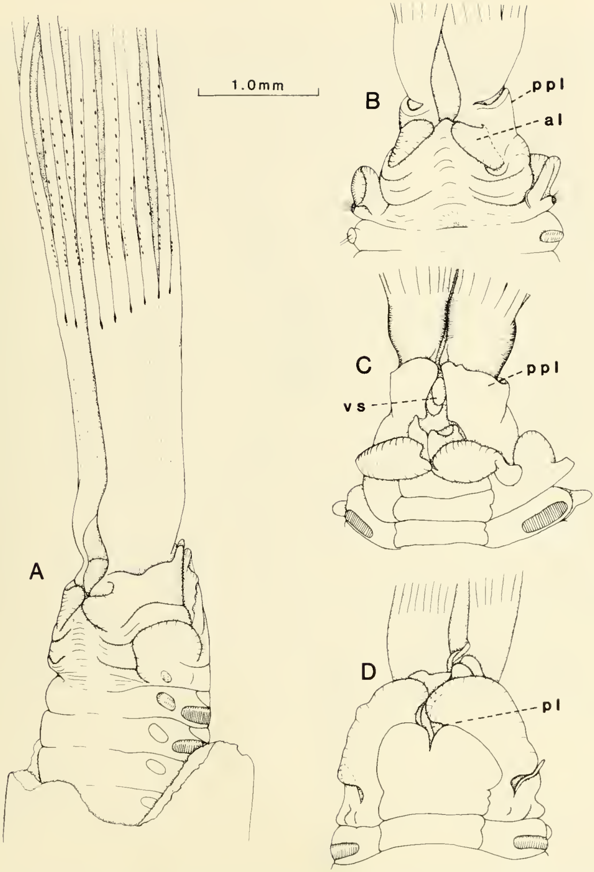

Fig. 22. *Hypsicomus stichophthalmos*, syntypes (ZMB Q 5240): A, Tube, anterior end of body and about half of branchial crown, dorsolateral view; B–D, Anterior end of body and part of branchial crown (B, Dorsal view; C, Ventral view, ventral lappets of collar folded back; D, Ventral view, ventral lappets of collar extended).

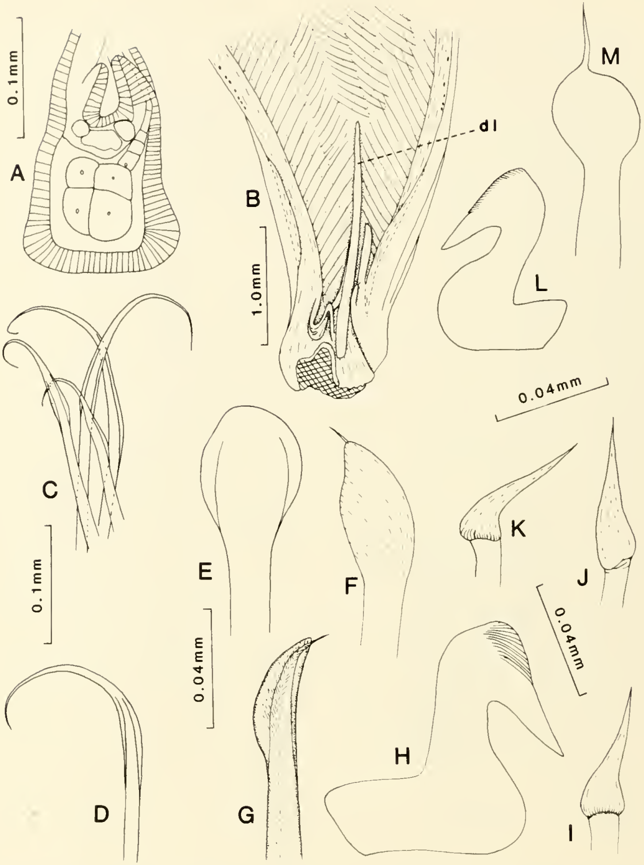

Fig. 23. *Hypsicomus stichophthalmos,* syntypes (ZMB Q 5240): A, Cross section from proximal half of radiole; B, Left half of branchial crown, proximal part, medial view, left side is dorsal; C, Collar setae; D, Upper thoracic seta; E–G, Lower thoracic setae (E, Medial view, concave side; F, Outer, lateral side, turned; G, Sagittal view); H, Thoracic avicular hook; I–K, Companion setae; L, Abdominal avicular hook; M, Abdominal paleate seta.

Hypsicomus stichophthalmos is known from the Adriatic Sea and possibly from Gulf of Marseille and Madeira; I cannot confirm from their descriptions that the records of Marion and Bobretzky (1875) and Langerhans (1884), respectively, actually were *H. stichophthalmos.*

Notaulax Tauber, 1879

Hypsicomus Grube, 1870:348 [in part; not *Sabella stichophthalmos* Grube].—Marenzeller, 1884:211 [in part].—Johansson, 1927:137 [in part].—Fauvel, 1927: 312.—Hartman, 1959:546, 547 [in part]; 1965a:77.—Hartmann-Schröder, 1971: 502.—Fauchald, 1977a:139 [in part].

Notaulax Tauber, 1879:136.—Levinsen, 1883:185, 187, 188.

Protulides Webster, 1884:325.

Eurato Saint-Joseph, 1894:219, 220.

Hypsicomatopsis Augener, 1924:49.

Type-species.—*Notaulax* n. sp. Tauber, 1879; = *N. rectangulata* Levinsen, 1883; by monotypy.

Diagnosis.—Radioles in semicircles, joined by palmate membrane for up to about ⅓ total length (Figs. 27A, 33A), with punctate, lensed ocelli scattered along radioles on lateral margins distal to palmate membrane, or organized into various groups; without stylodes; with flanges on outer lateral corners at least distally (Fig. 28B–D); skeleton in cross section consisting of 4, rarely 5, cells. Dorsal lips (Fig. 27C) long, slender, with radiolar appendage forming midrib, joined by short lamella with base of first dorsal radiole, without pinnular appendages. Ventral lips rather small, beginning ventrally below collar, folded and joining branchial lobes near origin of first ventral radiole; ventral sacs absent. Branchial lobes with long, smooth, basal lamina overlying prostomium proximal to origins of radioles; basal lamina with broad, overlapping flanges on both dorsal and ventral margins, extending to origins of radioles. Collar entire to 4-lobed. Eight or more thoracic setigers. Ventral shield of collar segment short, nearly rectangular, usually with golden-brown bar on anterior margin; other thoracic ventral shields longer, with anterior margins usually broader than posterior ones, concavely curved laterally around tori; posterior thoracic ventral shields often dark brown; abdominal ventral shields rectangular, usually dark brown. Collar setae short, spine-like, in long, longitudinal to oblique, often sinuate rows. Other thoracic setae including stout, spine-like setae in arc above 2 oblique rows of stout paleae; paleae often with minute mucros; avicular hooks with broad handles of moderate length; companion setae with broad, thin, teardrop-shaped blades at right angle to shafts. Abdominal hooks with handles shorter than those of thorax, in short tori; setae in short transverse rows consisting of paleae and capillary setae; paleae with long mucros.

Remarks.—Species in this genus form a very homogeneous group. *Sabella stichophthalmos* Grube, 1863, and *Anamobaea orstedii,* Krøyer, 1856, included in *Hypsicomus* by Johansson (1927) and Hartman (1959), are not members of *Notaulax* because they have collar setae in a bunch or short oval group. *Sabella stichophthalmos* is included in this report as the type-species of *Hypsicomus; Hypsicomus caecus* Iroso, 1921, from the Bay of Naples, described in a very brief account without figures, may be synonymous with *H. stichphthalmos* or possibly may be the species similar to *Pseudopotamilla* noted in the syntype lot of that species (ZMB Q 5240).

Nominal species of *Notaulax* which are not included here in systematic accounts either as distinct species or their synonyms are listed in Table 1.

Many of these species have been referred to *Notaulax phaeotaenia* by various authors, including Johansson (1927) and Hartman (1959). Descriptive informa-

Table 1.—Names, original citations, type-localities, and other citations of *Notaulax* species not included in species accounts.

Name	Original citation	Type-locality	Other citations
Sabella phaeotaenia Schmarda	1861:35, pl. 22, fig. 188	Ceylon	*Hypsicomus phaeotaenia.*—Augener, 1914: 113–115 [in part, report of types]
Sabella tilosaula Schmarda	1861:34, pl. 23, fig. 191	Chile	
Sabella alticollis Grube	1868:638, 639, pl. 7, fig. 6	Red Sea	*Hypsicomus phaeotaenia.*—Marenzeller, 1884:212, pl. 3, fig. 3 [not *S. phaeotaenia* Schmarda]
Sabella simplex Grube	1870:348, 349	Port du Roi Georges, Mediterranean Sea	
Sabella fuscotaeniata Grube	1874:328, 329	Ceylon	*Hypsicomus phaeotaenia.*—Hoagland, 1920: 626 [not *S. phaeotaenia* Schmarda]
Sabella pyrrhogaster Grube	1878:250, 251, pl. 15, fig. 1	Bohol, Philippine Islands	
Sabella velata Haswell	1884:671, 672, pl. 34, fig. 8	Port Jackson, Australia	*Hypsicomus phaeotaenia.*—Augener, 1914: 113–115 [in part, not *S. phaeotaenia* Schmarda]
Hypsicomus circumspiciens Ehlers	1887:271–277, pl. 55, figs. 5–13, pl. 56, figs. 1–3	Carysfort Reef, Florida	
Hypsicomus lyra Moore	Moore and Bush, 1904:161–164, pl. 11, figs. 7–13, pl. 12, fig. 42	Suruga Bay, Japan	
Hypsicomus marenzelleri Gravier	1906a:34–36	Red Sea	Gravier, 1906b: pl. 6, figs. 247–251; 1908:78–81, text-figs. 418–423.
Hypsicomus pigmentatus Gravier	1906a:36, 37	Red Sea	Gravier, 1906b: pl. 6, figs. 252–254; 1908:81–84, text-figs. 424–431
Hypsicomus capensis Day	1961:537, fig. 13.f–m	Agulhas Bank, South Africa	Day, 1967:761, fig. 37.2.a–h
Hypsicomus longithoracalis Hartmann-Schröder	1980:79, 80, figs. 124–129	Port Samson, Australia	

tion indicates that they certainly comprise several species. Descriptions of many are brief, and material of some has been lost. However, an attempt has been made to include as many of these species as possible in the key to species, below, in order to facilitate and encourage further research.

Sabella tilosaula Schmarda and *S. simplex* Grube are not included in the key because of insufficient descriptive information. *Sabella velata* Haswell is not included in the key because descriptions of it and *S. alticollis* Grube indicate that they differ principally in color pattern, and, in the absence of other characters, such a difference is not usually considered to be important. *Sabella phaeotaenia* Schmarda is not included in the key. It appears to be similar to *S. alticollis.* But radiolar ocelli have not been reported for *S. phaeotaenia.* It is likely that ocelli are present, but if so, their arrangement is unknown; it is possible that they had faded by the time Augener (1914) reexamined the types. *Sabella pyrrhogaster* Grube is included in the key with some reservations, because I suspect that the description is incorrect. Grube (1878) stated specifically that ocelli were absent. His description indicates that branchial lobes were damaged on the largest specimen, and it is likely that radiolar ocelli were sloughed off with epidermal tissue or faded. Grube (1878) also reported that only paleae were present in thoracic notopodia of *S. pyrrhogaster* and did not note companion setae. He did not report companion setae on any of the *Notaulax* species he described, but I am not certain what importance should be attributed to the absence of the upper group of thoracic setae; I suspect that such setae are present. Saint-Joseph (1894) included *S. pyrrhogaster* and some other species for which only one type of thoracic notosetae had been reported in his new genus *Eurato,* and Bush (1905) designated it as the type-species of the genus.

Characters of specific importance are the arrangement and position of radiolar ocelli, the shape of the collar, the number of thoracic setigers, the cross sectional structure of the radioles, and pronounced differences in the setae or uncini.

Collars of some species change during development from a 4-lobed structure on juveniles to a 1- or 2-lobed structure on adults. Dorsally, the anterior margin may be completely entire and free from the collar segment, incised medially and immediately merged with the anterior margin of the collar segment forming a dorsal notch, or gradually divergent from the margin well lateral to the midline. The margin of the collar of adults may be ventrally incised, entire, or incised both laterally and ventrally. Only major differences in setation are important. Further, in juveniles of most species, the position and organization of the ocelli are not diagnostic. Therefore, several specimens should be examined before a specific determination is made.

Minute mucros were sometimes observed on the concave side of thoracic notopodial paleae on species for which they have not been previously reported. These were apparently not developed or were broken on other paleae of those species. They may be absent on thoracic paleae of some species.

Key to Some Species of *Notaulax*

1. Collar 4-lobed 2
– Collar 1- or 2-lobed 3
2. Thorax with 8 setigers; radiolar ocelli in single rows of about 10 .... *N. capensis* (Day)

– Thorax with 13 setigers; radiolar ocelli in single rows of up to 50 .... *N. circumspiciens* (Ehlers)

3\. Collar margin deeply incised dorsally, separated from collar segment, or joined with collar segment immediately or well lateral to midline 4

– Collar margin entire dorsally, always separated from collar segment .. 13

4\. Collar margin of adults entire ventrally [may be incised on juvenile specimens] 5

– Collar margin of adults incised ventrally 7

5\. Radiolar ocelli in single rows .... *N. rectangulata* Levinsen

– Radiolar ocelli in oval groups 6

6\. Collar segment about as long as wide, longer than next 3 segments, with rows of collar setae less than ½ segmental length; radioles completely flanged except for small part of ocellar region ...... *N. bahamensis,* n. sp.

– Collar segment wider than long, about as long as next 2 segments, with rows of collar setae more than ½ segmental length; radioles not flanged between palmate membrane and distal part of region of ocelli. .... *N. nudicollis* (Krøyer)

7\. Anterior margin of collar joining with collar segment only at midline, or margin deeply incised dorsomedially 8

– Anterior margin of collar joining collar segment well lateral to midline 11

8\. Thoracid paleae very dissimilar in anterior and posterior rows; those in posterior row having mucros as long as bladed parts ..... *N. lyra* (Moore)

– Thoracic paleae more or less similar in anterior and posterior rows; mucros, if present, much shorter than blades 9

9\. Radioles with few ocelli, in small groups corresponding to perhaps 4 pinnules in length (Fig. 33F) .... *N. paucoculata,* n. sp.

– Radiolar ocelli much more numerous, in larger groups corresponding to more than 8 pinnules in length 10

10\. Dorsal margin of collar incised medially only; groups of ocelli corresponding to 9 pinnules in length, mostly arranged in single rows with a few pairs proximally (Fig. 37A) .... *Notaulax* sp.

– Dorsal margin of collar incised medially and dorsolaterally; groups of ocelli corresponding to about 15 pinnules in length, arranged in compact group proximally, singly or in pairs distally ...... *N. pigmentata* (Gravier)

11\. Ocelli numerous, irregularly arranged in long, single rows .... *N. occidentalis* (Baird)

– Ocelli few, arranged in small groups or short single rows 12

12\. Dorsolateral and ventromedial regions of collar margin exceeding base of branchial crown; thoracic companion setae with long, slender blades. .... *N. midoculi* (Hoagland)

– Neither dorsal nor ventral regions of collar margin extending to base of branchial crown; companion setae with very broad, short blades (Fig. 31F–H) .... *N. californica* (Treadwell)

13\. Collar margin entire both dorsally and ventrally 14

– Collar margin entire dorsally, incised ventrally 15

14\. Radiolar ocelli absent; ventral margin of collar produced forward as moderately long, obtuse, triangular lobe .... *N. pyrrhogaster* (Grube)

– Radiolar ocelli arranged in compact group on each side; groups corresponding to about 7 pinnules in length, in 2 rows, with less than 15 ocelli in each row; ventral margin of collar only slightly produced forward . . . . *N. alticollis* (Grube)

15. Radiolar ocelli in series of about 30 on each side, extending from just above palmate membrane to near tips . . . . *N. fuscotaeniata* (Grube)

– Radiolar ocelli numbering about 20, in compact group corresponding to about 4 pinnules in length . . . . *N. marenzelleri* (Gravier)

Notaulax rectangulata Levinsen, 1883

Fig. 24

Notaulax, n. sp. Tauber, 1879:136.

Notaulax rectangulatus Levinsen, 1883:185, 188, pl. 2, figs. 1–3, 8 m, n; 1893: 353.

Hypsicomus rectangulatus.—Johansson, 1927:141.

Hypsicomus sp.—Hartmann-Schröder, 1971:502.

Material examined.—DENMARK: Holotype, Lille Baelt (ZMC).

Description.—Tube coreaceous, covered with black mud (Tauber, 1879). Branchial crown with 12 pairs of radioles; radioles flanged near tips, with single, short row of ocelli (Fig. 24A) at region ⅔ distance from palmate membrane to tip; ocelli oriented lateroproximally on proximal end, gradually changing to laterodistal orientation at distal end, covering angle of about 140°; collar (Fig. 24B) a single lobe beginning dorsally at midline, curving anterolaterally, then extending in almost straight, transverse line around body to opposite side [whether free or fused at anterior dorsal margin with collar segment unresolved, but apparently similar to that of *N. nudicollis,* described below]. Collar setae not extending to anterior margin of collar [as originally figured by Levinsen (1883:pl. 2, fig. 2)], in oblique rows sharply bent laterally near posterior end, forming right angle. Eight thoracic setigers.

Remarks.—The only known specimen of the species differs from *N. nudicollis* (Krøyer), described below, primarily in the location and arrangement of radiolar ocelli.

Notaulax rectangulata is also similar to the specimen which Augener (1918) reported as *Hypsicomus torquatus* (not Grube) from West Africa [=*Notaulax* sp.]. The latter is a small specimen on which the slightly incised ventral margin of the collar may be a result of its being immature. The two specimens differ, however, in the orientation of the radiolar ocelli.

The strong curvature on the posterior part of the rows of collar setae of the type-specimen may have been caused by contraction during preservation and may not be important.

Notaulax nudicollis (Krøyer, 1856)

Figs. 25–28

Sabella nudicollis Krøyer, 1856:30, 31.—Levinsen, 1883:188 [footnote; referral to *Notaulax*].

?*Sabella brevicollaris* Grube, 1858:112.

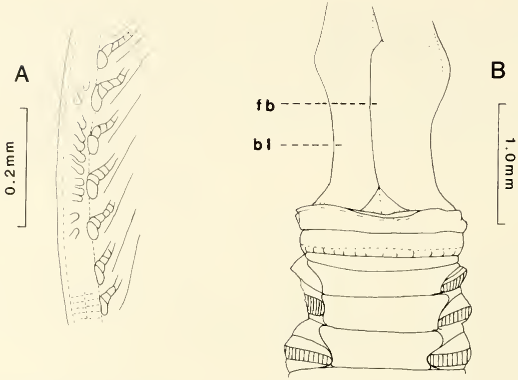

Fig. 24. *Notaulax rectangulata*: A, Region of ocelli of radiole; B, Anterior end of body and part of branchial crown, ventral view.

Sabella torquata Grube, 1877:549, 550 [in part; syntype comprised of loose branchial crown and body with ventrally entire collar].

Protulides elegans Webster, 1884:325, 326, pl. 11, figs. 63–74.—Andrews, 1891: 299.—Treadwell, 1901:209; 1939:300 [in part].—Bush, 1905:184.

Hypsicomus torquatus.—Augener, 1918:572–576, text-fig. 101 [in part; report of type specimens of *Sabella torquata*]; 1924:49; 1927:75; 1934:113.—?Fauvel, 1939:23.—Hartman, 1945:47, 48.—Wells and Gray, 1964:74.

Hypsicomus elegans.—Hartman, 1951:115, 116.—Taylor, 1961:244, 245, pl. 9, fig. 3.—?Wills and Bright, 1974:299, fig. 9.—?Rullier and Amoureux, 1979: 190, 191.

Hypsicomus phaeotaenia.—Day, 1973:125 [not *Sabella phaeotaenia* Schmarda, 1861].

Material examined.—VIRGIN ISLANDS: St. Thomas, holotype of *S. nudicollis,* collected 18 Sep 1845 (ZMC). Same locality, 2 specimens without branchial lobes (ZMC). NORTH CAROLINA: In coquina rock dredged off Ocracoke Is., 9–12 m, coll., H. W. Wells, 20 Jun 1959, 6+ specimens (USNM 65901). Beaufort, coll., Andrews, 1885 (USNM 4913). Off Beaufort, 10 m, on coral, coll., L. R. McCloskey, 1 specimen (USNM 51233). Bogue Sound, 2.3 m, in empty shells, coll., M. E. Petersen, 6 Aug 1962, 21 specimens (ZMC). Same, E. of Atlantic Beach bridge, 2.5 m, sand, shells, coll., M. E. Petersen and Class, 10 May 1972, 3 specimens (ZMC). Bogue Sound, shallow depth, in large shells, coll., S. L. Gardiner, 28 Jul 1973, 3 specimens (USNM 53972). Same, Oct 1971, 2 specimens (USNM 53971). Onslow Bay, 34°20′N, 76°54′N, 24 m, on coral and rock, coll., E. Powell, 4 Nov 1974, 1 specimen (USNM 53973).—FLORIDA: Off Cape Canaveral, 28°32.5′N, 80°10.3′W, 40 m, R/V *Hernan Cortez,* coll., D. Barber, 2 Apr

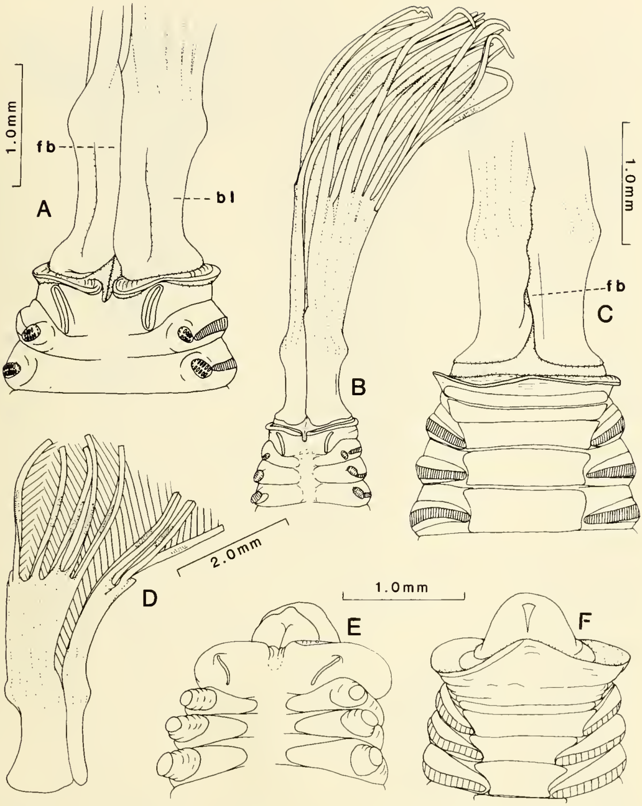

Fig. 25. *Notaulax nudicollis*: A, Anterior part of body and part of branchial crown, holotype of *S. nudicollis*; B, Anterior end, dorsal view of same; C, Anterior part of body and part of branchial crown, ventral view of same; D, Proximal part of detached branchial crown of syntype of *S. torquata*, dorsolateral view; E, Anterior end of body, dorsal view of same; F, Same, ventral view.

1973, 1 specimen (FSBC I 17411). Hutchinson Is., beach seine sta, surf zone, 27°21.4′N, 80°14.5′W, 1 specimen (FSBC I 24016). Same, sta II, 27°21.6′N, 80°13.2′W, 11 m, coarse calcareous sand, on shells, 1 specimen (FSBC I 24010). Same, sta IV, 27°20.7′N, 80°12.8′W, 11 m, coarse calcareous sand, on shells, 7 specimens (USNM 54717; FSBC I 24011–24014). Same, sta V, 27°22.9′N,

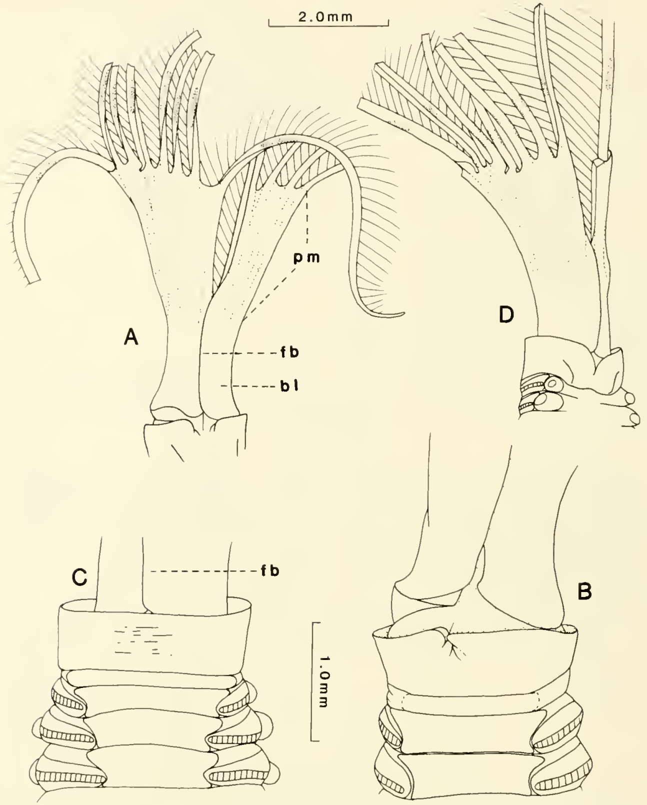

Fig. 26. *Notaulax nudicollis,* anterior ends of thorax and parts of branchial crown: A, Specimen from Brazil identified by Grube as *S. brevicollaris,* dorsal view; B, Same, ventral view; C, Specimen from western Mexico, ventral view; D, Same, dorsolateral view (A, B, ZMB Q 5207; C, D, USNM 41528).

80°13.9′W, 11 m, coarse calcareous sand, on shells, 5 specimens (USNM 54718; FSBC I 24015). Off SE coast, on coral, *Oculina varicosa* Lesueur, 27°10.8′N, 80°00.8′W, 44 m, JSL II 187, coll., L. Edmiston, 19 Apr 1977, 3 specimens (IRCZM 50:856). Same, JSL II 161, coll., F. Stanton, 3 Feb 1977, 1 specimen (IRCZM 50:857). Same, 27°11.4′N, 80°00.9′W, 42 m, JSL II 49, coll., M. Flake,

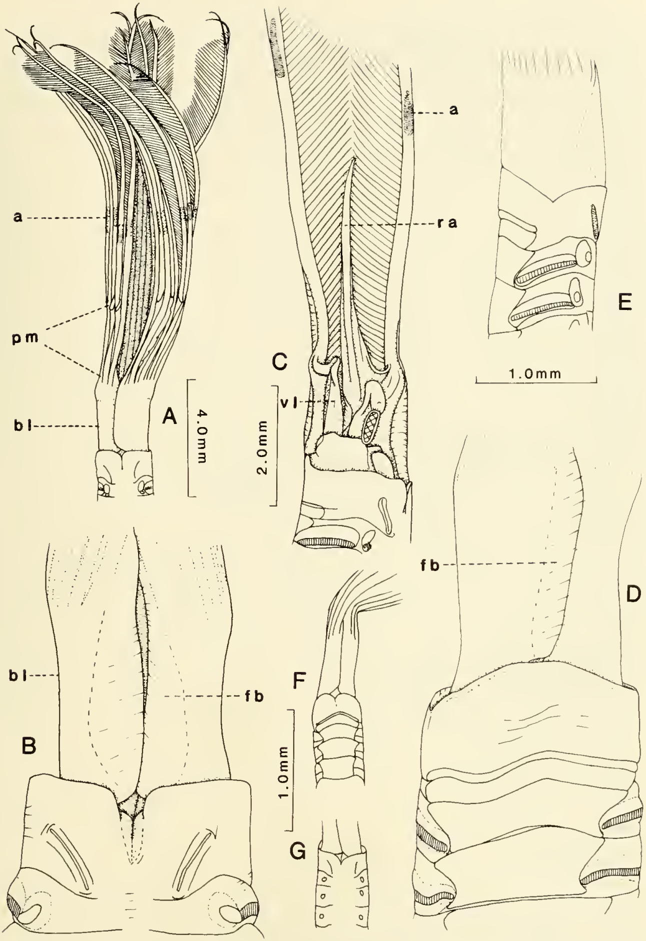

Fig. 27. *Notaulax nudicollis,* Florida specimens: A, Anterior end, dorsal view; B, Anterior end of body and part of branchial crown, dorsal view; C, Same, showing medial view of right half of branchial crown; D, Same, ventral view; E, Same, lateral view of small specimen; F, Same, ventral view of small specimen; G, Same, dorsal view of small specimen (A, FSBC I 24004; B–G, FSBC I 24002; a, region of ocelli).

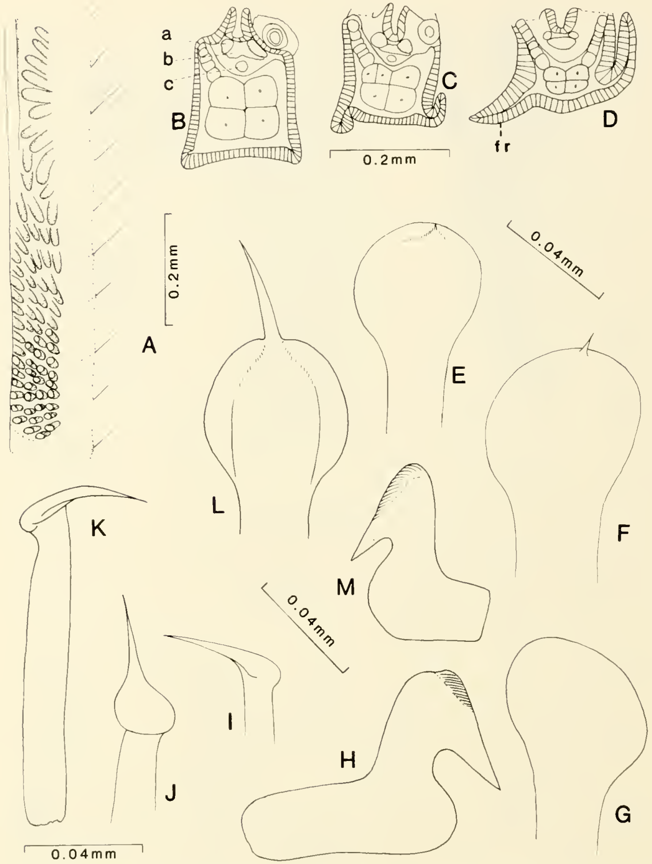

Fig. 28. *Notaulax nudicollis,* Florida specimens: A, Region of ocelli on radiole; B, Cross section of radiole from between palmate membrane and region of ocelli (a, nerve; b, coelomic space; c, blood sinus); C, Same, from distal to ocelli; D, Same, from near tip; E–G, Lower thoracic setae (E, From posterior row; F, Same, with mucro; G, From anterior row); H, Thoracic avicular hook; I–K, Companion setae; L, Abdominal paleate seta; M, Abdominal avicular hook (A–D, FSBC I 24004; E–M, FSBC I 24002).

18 May 1976, 3 specimens (IRCZM 50:798). Same, 27°29.6′N, 80°17.3′W, 5.5 m, SCUBA, coll., L. Edmiston, 28 Jun 1973, 3 specimens (FSBC I 24008). Same, coll., J. Reed, 28 Apr 1977, 1 specimen (IRCZM 50:860). Same, 27°32.8′N, 79°58.8′W, 81 m, JSL I 438, coll., L. Edmiston, 23 Aug 1977, 4 specimens (FSBC I 24009; IRCZM 50:859). Same, 80 m, JSL II 163, coll., F. Stanton, 7 Feb 1977, 2 specimens (IRCZM 50:858). Florida Keys, Monroe County, 1.5 mi N. of Bay Keys, Stock Is., 24°40′02″N, 81°45′20″W, 4 m, coll., W. Jaap *et al.*, 14 Mar 1973, 1 specimen (FSBC I 24005). Safe Harbor, Stock Is., 2.5 m, coll., R. Chesher, 17 Jul 1970, 2+ specimens (USNM 57933). Big Pine Key, 1–2 m, from rock wall of canal, coll., Maynahan, 14 Aug 1973, 1 specimen (USNM 52042). Straits of Florida, 23°36.7′N, 81°06.5′W to 24°36.6′N, 81°05.8′W, 42 m, R/V *Gerda* sta 1033, 26 Feb 1969, 6 specimens (UMML). Gulf of Mexico, Hourglass sta J., 20 nmi off Sanibel Is., 26°24′N , 82°28′W, 18 m, in coral, *Solenastrea,* R/V *Hernan Cortez,* coll., B. Presley, 12 Nov 1965, 18 specimens (FSBC I 24006). Same, 11 May 1966, 11 specimens (BMNH ZB 1980:240–250). Same, Hourglass sta A, 3 nmi off Egmont Key, 27°35′N, 82°50′W, 6 m, sand and shell, R/V *Hernan Cortez,* coll., B. Presley, 2 Jul 1966, 5 specimens (FSBC I 24007). Same, Hourglass sta B, 18 nmi off Egmont Key, 27°37′N, 83°07′W, 18 m, sponge, algae and coral, coll., B. Presley, 11 Sep 1967, 1 specimen (FSBC I 24004). Same, Hourglass sta C, 36 nmi offshore, 27°37′N, 83°28′W, 37 m, in coral, *Solenastrea,* 31 Aug 1966, 31 specimens (FSBC I 24002). Seashore Key, Cedar Keys, Levy County, coll., J. Young, 23 Nov 1957, 1 specimen (USNM 65901). Same, coll., T. Hopkins, Sep 1960, 1 specimen (USNM 65905). Northeastern Gulf of Mexico, Florida Middle Ground, BLM Cr. 01, sta 151, 28°32′02″N, 84°18′36″W, 25–27 m, decalcified from coral, *Madracis decactis* (Lyman), coll., T. Hopkins *et al.*, 5 Oct 1978, 10 specimens (USNM 62084). Proj. EGMEX 70, sta 4, 29°07′N, 85°20′W, 36 m, R/V *Hernan Cortez,* coll., J. Williams *et al.,* 5 May 1970, 1 specimen (FSBC I 24003).—PUERTO RICO: Guanica Bay, USFC str. *Fish Hawk,* 29 Jan 1899, 9 specimens (USNM 16245). Mayaguez Harbor, on corals, USFC str. *Fish Hawk,* 1898–99, 3 specimens (USNM 16217). Ensenada Honda, Culebra Is., USFC str. *Fish Hawk,* 10 Feb 1899, 1 specimen (USNM). Off Vieques Is., USFC str. *Fish Hawk* (157) 6085, 6 Feb 1899, 1 specimen (USNM 16219). Guayanilla Bay, coll., V. Vicente and J. Rivera, 28 Feb 1977, 1 specimen (USNM 54985). Same, 15 Apr 1976, 1 specimen (USNM 54984).—BRAZIL: Santa Catherina Is. (Destero), coll., Müller, 1 specimen identified as *Sabella brevicollaris* by Grube (ZMB Q 5207).—WESTERN MEXICO: Zihuatanejo, coll., Klawe, 6 Sep 1958, 1 specimen (identified by Berkeley and Berkeley as *Hypsicomus phaeotaenia*; USNM 41528).—WEST AFRICA: *Gazelle* Expedition, 2 syntypes of *Sabella torquata* Grube (2 bodies and 1 branchial crown; ZMB 846) [body with ventrally incised collar = *Notaulax* sp., below].

Description.—Tube horny, translucent, not covered with sediment, mostly embedded in carbonate rocks; tip thick, reddish brown, embedded part thin, golden brown. Body up to 75 mm long, 3 mm wide on specimens fixed in tubes, with thorax up to 6 mm long. Branchial crown to 20 mm long, with 4–5 brown to purple crossbands, 9–14 pairs of radioles; radiolar ocelli in tight, elongate-oval group of 30–70 on each side, diminishing in number distally; groups of ocelli on adults separated from palmate membrane by about length of membrane and thus found in second color band above membrane on Florida specimens (Fig. 27A, C); separated from palmate membrane by shorter length on type of *Sabella torquata* and on specimens from Brazil and western Mexico (Figs. 25B, D, 26A, D); ocelli in short single row on juvenile specimens; radioles with flanges on outer lateral corners beginning at distal part of region of ocelli and extending to tips (Fig. 28A–D), in cross section view with skeleton of 4 cells; basal lamina up to 0.15 length of branchial crown of adults; dorsal lips (Fig. 27B) extending slightly farther than palmate membrane. Thorax of 8 setigers. Collar of single lobe on adults (Figs. 25A–C, E, F, 26C, D, 27A–D) 2- or 4-lobed on juveiles (Fig. 27E–G), beginning slightly lateral to dorsal midline, joined dorsomedially beneath collar to lamellae which turn anteriorly and join prostomium, extending laterally in almost straight line, usually convex ventrally (rarely ventrally incised from damage, notably on specimens fixed out of tubes) but straight ventrally on specimen from western Mexico (Fig. 26C), incised ventrally, possibly from damage on specimen from Brazil (Fig. 25B). Ventral shield of collar segment (Figs. 25C, F, 26B, C, 27C–F) usually nearly rectangular, sometimes curved, about as broad as anterior margin but only ½ as long as shield of setiger 2, usually with golden brown bar across anterior margin. Ventral shields of other thoracic setigers trapezoidal, with anterior margin broader than posterior, lateral sides concavely curved around tori. Pygidial eyespots present. Collar setae in straight to slightly curved, oblique rows (Figs. 25A, B, E, 26A, D, 27A–C, E, G); thoracic paleae (Fig. 28E–G) slightly asymmetrical in anterior and posterior rows, often with minute mucros. Thoracic avicular hooks up to about 60 in each torus (Fig. 28H), with moderately broad heads; companion setae (Fig. 28J, K) with broad teardrop-shaped blades at right angle to shafts. Abdominal avicular hooks with handles shorter than those of thorax (Fig. 28M); abdominal palaea with short mucros on anterior segments (Fig. 28L), much longer mucros posteriorly, mucros not recessed into tips of setae.

Remarks.—Minor differences among specimens from the Caribbean Sea and adjacent areas and those from West Africa, Brazil, and western Mexico are attributed to geographic separation but are not considered to be sufficient to indicate speciation. Radioles of the larger syntype of *Sabella torquata* have groups of up to 40 ocelli which are separated from the palmate membrane by about half its length. The same is true on the specimen from western Mexico which has groups of up to about 30 ocelli. The smaller syntype of *Sabella torquata,* from which branchial lobes are missing, has a ventrally incised collar and may be conspecific with *Notaulax* sp., below.

The specimen from Brazil, identified by Grube as *Sabella brevicollaris,* has a collar which has widely spaced dorsal origins and is incised ventrally. However, the specimen is somewhat flaccid, and these differences may be caused by improper preservation and thus may not be important. Ocelli of this specimen are similar in position and number to those of the specimen from western Mexico. Grube's (1858) original description of *S. brevicollaris,* based on specimens from St. Croix, Virgin Islands, did not mention radiolar ocelli but otherwise suggests to me that it is the same as *N. nudicollis.*

Notaulax nudicollis is known from West Africa, the western Atlantic region from North Carolina and the Gulf of Mexico to Brazil, and the tropical eastern Pacific region. The species was reported from Bermuda by Bush (1905:184), but I have not examined specimens from there.

Notaulax occidentalis (Baird, 1865), new combination
Figs. 29, 30

Sabella occidentalis Baird, 1865:159, pl. 5, figs. 7, 8.
Protulides elegans.—Treadwell, 1901:209; 1939:300 [in part; not description; not Webster, 1884].
Sabella alba Treadwell, 1917:266, 267, pl. 3, figs. 10–15; 1939:294, fig. 108.
Parasabella sulfurea Treadwell, 1917:267, pl. 3, figs. 16–23; not 1924:18.—Mullin, 1923:51, 52, pl. 7, figs. 7–11.
Hypsicomus purpureus Treadwell, 1924:20, 21, pl. 2, figs. 30–33.
Hypsicomus circumspiciens.—?Johansson, 1927:139–141.—Hartman, 1942b:133 [holotype of *Hypsicomus purpureus*] [not Ehlers, 1887].
Hypsicomus torquatus.—Hartman, 1956:270 [not *Sabella torquata* Grube, 1877].
?*Hypsicomus elegans.*—Marsden, 1960:1012, 1013 [in part; not *Protulides elegans* Webster, 1884].
?*Hypsicomus phaeotaenia.*—Fauchald, 1977b:62 [damaged specimens; in part; not *Sabella phaeotaenia* Schmarda, 1861].

Material examined.—ST. VINCENT: Syntype of *Sabella occidentalis,* (BMNH ZH 1839:12:27:147).—ANTIGUA: Holotype of *Hypsicomus purpureus,* Pillars of Hercules, Barbados-Antigua Expedition, Univ. Iowa, 1918 (USNM 20325).—FLORIDA: Holotype of *Parasabella sulfurea,* Dry Tortugas, VI-VII-1915 (AMNH 974). Holotype of *Sabella alba,* Dry Tortugas, VI-VII-1914 (AMNH 977). PANAMA (ATLANTIC): Galeta Reef, coll., A. Reimer, 5 Oct 1970, 2 specimens (USNM 73020). Same, 1 Nov 1971, 1 specimen (USNM 66400).—BELIZE: Carrie Bow Cay, 12.5 nmi at 140° from Stann Creek Town, barrier reef, 8 m, coll., W. Jaap, 21–24 Oct 1973, 1 specimen (FSBC I 24017).—PUERTO RICO: Reef at Ponce, USFC str. *Fish Hawk,* 1898–99, 2 specimens (USNM 16218). Caballo Blanco Reef, USFC str. *Fish Hawk,* 1898–99, 4 specimens (USNM 16215). Ensenada Honda. Culebra Is., USFC str. *Fish Hawk,* 10 Feb 1899, 3 specimens (USNM 16216).—BAHAMA ISLANDS: Hydro-Lab, 1.2 nmi at 180° off Bell Channel, Lucaya, near Freeport, Grand Bahama Is., 15 m, in coral, coll., B. A. Vittor and T. S. Hopkins, 28 Jan 1974, 1 specimen (USNM 62083).—?NORTH CAROLINA: Onslow Bay, 34°20′N, 76°54′W, on rock and coral, 24 m, coll., E. Powell, Nov 1974, 1 damaged specimen (USNM 53974).

Description.—Tube dark brown, tough, horny, usually in coral rock (*Sabella alba* and *Parasabella sulfurea* Treadwell, 1917); worms found inhabiting mud tubes in tide pool (*Parasabella sulfurea.*—Mullin, 1923); body usually without color pattern; collar segment occasionally light brown. Branchial crown almost uncolored to highly colored, basal lamina purple to purple brown, region of palmate membrane darker, 4–9 crossbands of purple to brown pigment distal to palmate membrane, pigment extending onto pinules. Body up to 50 mm long; width up to about 5 mm. Branchial crown up to 18 mm long, with 15–17 pairs of radioles; palmate membrane about ¼ total length of branchial crown, with basal lamina about ⅔ length of palmate membrane (Fig. 29A, B). Radioles with 4 skeletal cells in cross section, flanges (Fig. 29D, E) beginning at about middle of free parts, gradually wider distally; tips without pinnules, flattened, long, tongue-shaped; ocelli in single, usually scattered rows of 10–30, beginning just above

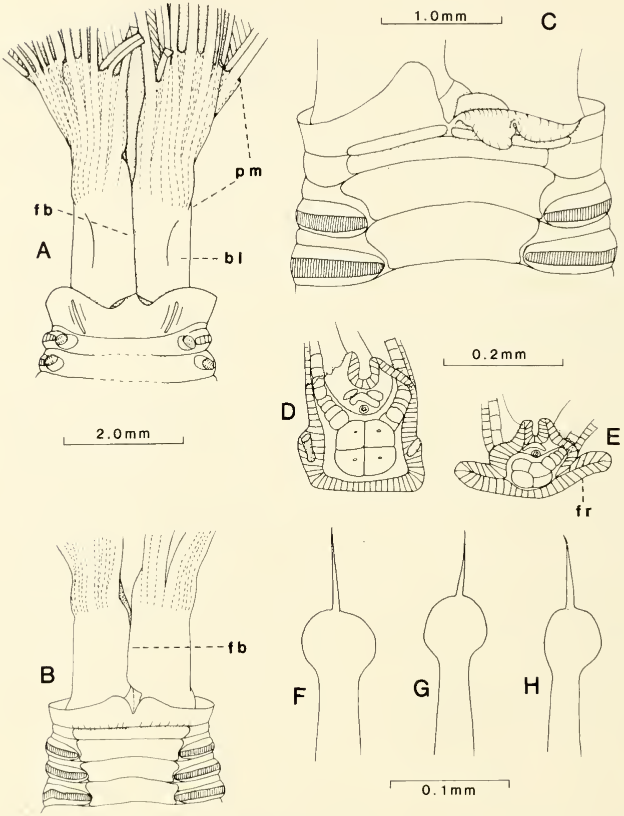

Fig. 29. *Notaulax occidentalis*: A, Anterior end of body and part of branchial crown, dorsal view; B, Same, ventral view; C, Same; D, Cross section of radiole from region of ocelli; E, Same, from near lip; F–H, Abdominal paleate setae from anterior setiger (A, B, F, Syntype of *S. occidentalis*; C–E, G, H, FSBC I 24017).

palmate membrane and extending for up to slightly more than ½ free length (Baird 1865:pl. 5, fig. 8), rows usually longer and eyes more numerous dorsally than ventrally. Dorsal lips and internal organization of branchial crown similar to that of *N. nudicollis* (Fig. 27C). Thorax of 8 setigers; collar bilobed (Fig. 29A–C), beginning dorsally at anterior margin of the collar segment lateral to midline, gradually diverging from margin of collar segment, thereafter flared anteriorly

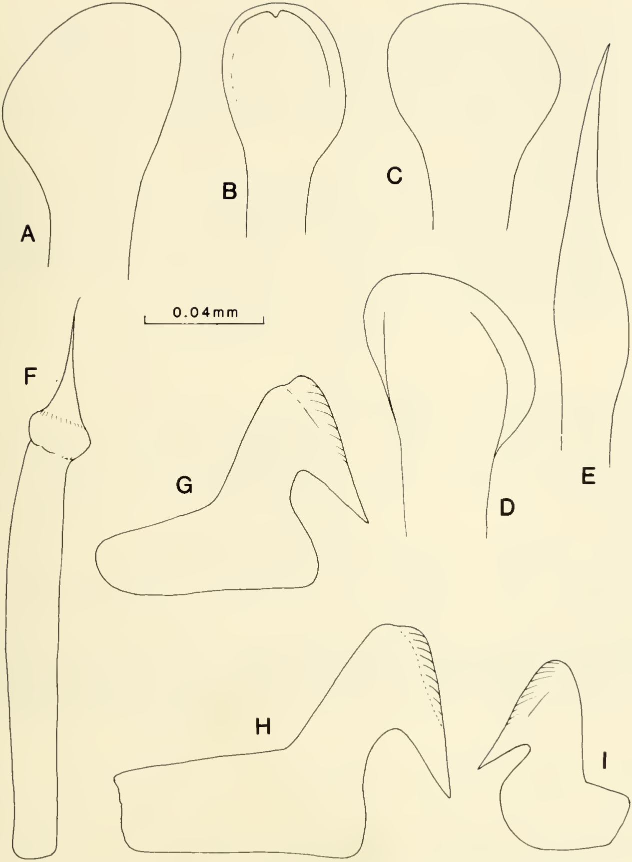

Fig. 30. *Notaulax occidentalis*: A–D, Lower thoracic setae (A, From anterior row; B, From posterior row; C, Same; D, From anterior row); E, Upper thoracic seta; F, Companion seta; G, H, Thoracic avicular hooks; I, Abdominal hook (A, B, E–G, I, FSBC I 24017; C, D, Holotype of *Sabella alba*; H, Holotype of *Parasabella sulfurea*).

around collar setae, slightly concave laterally, incised ventrally, forming 2 short, triangular to rounded lappets. Ventral shield of collar segment rectangular, about as broad as shield of setiger 2 and about ½ as long, often with golden brown bar across anterior margin. Other thoracic ventral shields trapezoidal, with broader anterior margin and lateral margins curved around tori. Collar setae in straight to slightly curved, slightly oblique rows. Thoracic paleae somewhat asymmetrical in anterior and posterior rows on syntype of *S. occidentalis* from St. Vincent and specimens from Belize and North Carolina, very slightly so on types of *S. alba, P. sulfurea,* and *H. purpureus* (Fig. 30A–D). Abdominal paleae with mucros longer than bladed area on anterior segments (Fig. 29F–H), much longer posteriorly. Other thoracic and abdominal setae and uncini as figured (Fig. 30E–I). Pygidial eyespots present.

Remarks.—Specimens reported as *Hypsicomus circumspiciens* [not Ehlers, 1887] by Johansson (1927) from Barthelmy and St. Thomas are questionably the same as *N. occidentalis.* Ocelli of the specimens occupied almost 4/5 of the free length of the radioles, and thus differ from those I have examined. I am not sure that this difference is important. *Notaulax circumspiciens* (Ehlers) has 13 thoracic setigers, thus differing from specimens reported by Johansson.

Notaulax californica (Treadwell, 1906), new combination
Fig. 31

Potamilla californica Treadwell, 1906:1178.
Hypsicomus sp.—Hartman, 1942b:133 [holotype of *P. californica*].
Hypsicomus californicus.—Hartman, 1956:258, 262, 270; 1969:701, 702 [holotype of *P. californica*].
?*Hypsicomus lyra.*—Hartman, 1969:703, 704, figs. 1–6 [not Moore *in* Moore and Bush, 1904].

Material examined.—CALIFORNIA: Holotype, from vicinity of Monterey Bay, 101–83 m, USFC str. *Albatross* sta 4551, 1904 (USNM 5222).

Description.—Tube absent; body without color pattern, incomplete posteriorly; thorax 2.5 mm long, 1.0 mm wide; branchial crown 7 mm long, with 9 pairs of radioles united by palmate membrane about 1.5 mm above 1.1 mm long basal lamina; radioles with groups of 3–5 lensed ocelli on few ventral radioles, separated from palmate membrane by about membrane length (Fig. 31A); radiolar skeleton of 4 cells in cross section, flanges beginning distal to ocelli and gradually increasing in width distally (Fig. 31B, C). Eight thoracic setigers; collar short, not extending to beginning of branchial crown, bilobed (Fig. 31D, E), beginning on dorsal side lateral to midline slightly back from margin of collar segment, gradually curved around collar setae, concave but entire laterally, incised ventrally. Ventral shield of collar segment rectangular, with brown bar on anterior margin; other thoracic ventral shields trapezoidal, with broader anterior margins, lateral margins concavely curved around tori, about as broad as shield of collar segment and twice as long. Blades of thoracic companion setae broad, with short tips (Fig. 31F–H); thoracic hooks with moderately long, broad handles.

Remarks.—*Notaulax californica* does not appear to be the same as *N. lyra* (Moore, 1904) from Japan, as suggested by Hartman (1969). The latter species has very asymmetrical thoracic paleae; those of the posterior row have mucros as long as the paleate region. *Notaulax lyra* also has thoracic avicular hooks with long tapered handles rather than moderately long, broad ones, and a collar which is apparently similar on the dorsal side to that of *N. nudicollis.* Specimens reported by Hartman (1969) from California as *Hypsicomus lyra* may be neither that species

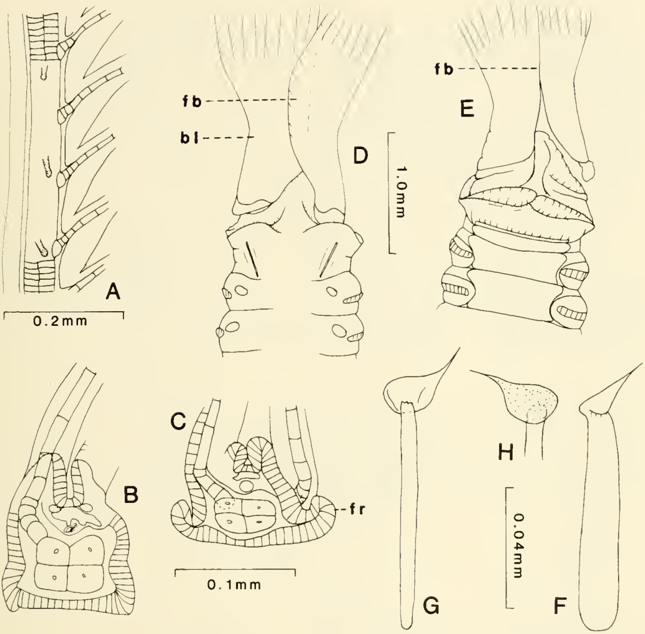

Fig. 31. *Notaulax californica*: A, Region of ocelli on ventral radiole, lateral view showing ocelli and internal structure; B, Cross section of radiole distal from palmate membrane; C, Same, from near tip; D, Anterior part of body and part of branchial crown, dorsal view; E, Same, ventral view; F–H, Companion setae, various views.

nor *N. californica*; Hartman did not illustrate nor note the unique thoracic paleae of *N. lyra*.

One of Hartman's figures of setae of *H. lyra* (1969:703, fig. 6) was redrawn from Moore and Bush (1904:pl. 11, fig. 6) and is a companion seta of *Potamilla acuminata* Moore, 1904.

Notaulax midoculi (Hoagland, 1919), new combination
Fig. 32

Parasabella midoculi Hoagland, 1919:579, pl. 31, figs. 10–14, pl. 32, figs. 1, 2.
Parasabella sulfurea.—Treadwell, 1924:18 [not Treadwell, 1917].
Hypsicomus midoculi.—Johansson, 1927:141.

Material examined.—FLORIDA: Loggerhead Key [probably Dry Tortugas],

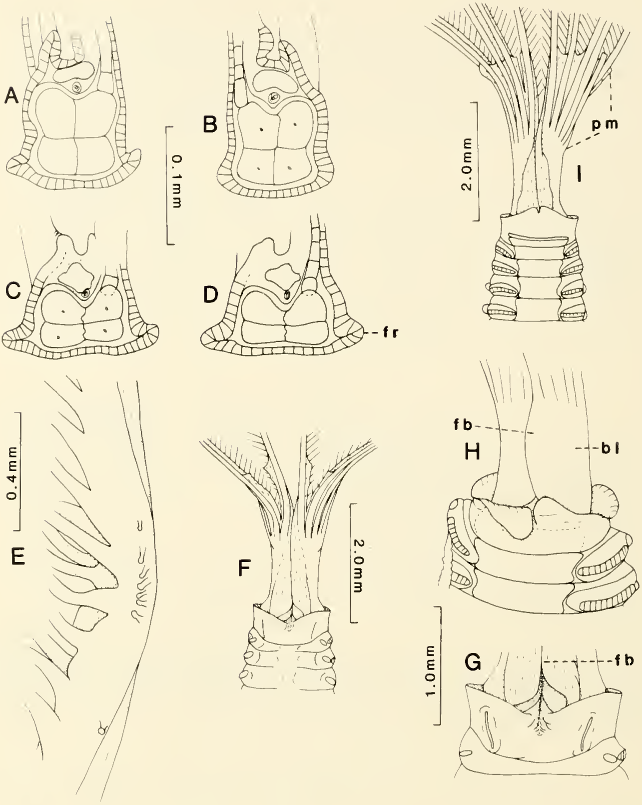

Fig. 32. *Notaulax midoculi*: A–D, cross sections of radiole (A, From immediately distal to end of palmate membrane; B, From immediately distal to region of ocelli; C, D, From between region of ocelli and tip); E, Region of ocelli of radiole; F–I, Anterior end of body and part of branchial crown (F, G, Dorsal view; H, I, Ventral view) (A–E, H, Holotype; F, G, I, USNM 20304).

coll., Treadwell, 1919, holotype (AMNH 1186).—BARBADOS: Bathsheba, Barbados-Antigua Expedition, Univ. Iowa, 1918, 1 specimen (USNM 20304).

Description.—Tube unknown; color pattern absent except for small band near midregion of branchial crown. Body of holotype 40 mm long, 1.5 mm wide across thorax. Branchial crown 5 mm long on holotype, 9 mm long on other specimen; 9–10 pairs of radioles united above basal lamina by palmate membrane for 1/6 of their length; length of basal lamina similar to that of palmate membrane; radiolar skeleton of 4 cells in cross section; radioles only slightly flanged near tips (Fig. 32A–D), with about 6 lensed ocelli on each side in pigment band at midregion of branchial crown (Fig. 32E; also Hoagland, 1919:pl. 31, fig. 11). Eight thoracic setigers. Collar with margins extending past beginning of branchial crown (basal lamina) dorsolaterally and ventrally, bilobed, beginning dorsally lateral to midline and back from margin of collar segment on holotype (Hoagland, 1919:pl. 31, fig. 10), near anterior margin of collar segment on specimen from Barbados (Fig. 32F, G), slightly concave laterally on holotype, straight on specimen from Barbados, ending ventrally in moderately long, rounded lappets on holotype (Fig. 32H) and in shorter lappets on specimen from Barbados (Fig. 32I). Ventral shield of collar segment with very indistinct lateral and anterior margins on holotype (Fig. 32H), similar to those of other species on specimen from Barbados (Fig. 32I). Ventral shields of other thoracic setigers trapezoidal, anterior margins broader, lateral margins concavely curved around ventral margins of tori. Pygidial eyespots present. Setae and uncini similar to those of *N. nudicollis*; no minute mucros visible on thoracic paleae.

Remarks.—On the holotype of *Parasabella midoculi*, both the length and width of branchial lobes appear to be small compared with body size, and the ventral shield of the collar segment is indistinct. This indicates to me that the anterior end of the holotype had recently regenerated and that the collar and branchial lobes of the specimen from Barbados may be more typical of the species. The latter specimen is broken but complete, and the abdomen is full of eggs, indicating that it is mature.

Notaulax paucoculata, new species
Figs. 33, 34

Material examined.—BAHAMA ISLANDS: Hydro-Lab, 1.2 nmi at 180° off Bell Channel, Lucaya, near Freeport, Grand Bahama Is., 26°33′N, 78°34′W, 41 m, coll., Sylvia Earle and Ann Hurley, 8 Jul 1974, holotype (USNM 62077). Same, 9 Jul 1974, paratype (USNM 62079). Same, 12–30 m, coll., Morgan Wells *et al.*, 3–15 Apr 1974, paratype (USNM 62078).

Description.—No tubes present. Branchial lobes cross-banded with purple-brown pigment, with broad, proximal band on lower half of palmate membrane region, with broad middle band just distal to palmate membrane and narrow, distal band at distal ⅔ of free region of radioles (Fig. 33A); body uncolored except for light brown ventral shields beginning at about middle of thorax and extending onto abdomen. Body of complete paratype 25 mm long, thorax 3.3 mm long and 1.8 mm wide; branchial crown about 10 mm long on complete paratype, 11 mm long on holotype. Radioles 10–12 pairs, united proximally above basal sheet for 2/5 of their length (Fig. 33A–C), broadly flanged above palmate membrane for entire length; radiolar skeleton in cross section of 4 cells (Fig. 33D, E); ocelli in small group of 4–5 (Fig. 33A, F) on lateral borders below flanges at distal end of middle color band, separated from palmate membrane by about ⅓ its length; basal lamina slightly less than half length of palmate membrane. Eight thoracic setigers; collar long, exceeding origin of branchial crown (Fig. 33A–C), deeply incised dorsomedially back to anterior ends of rows of collar setae but with dorsal margin completely separated from collar segment or prostomium even at deep incision,

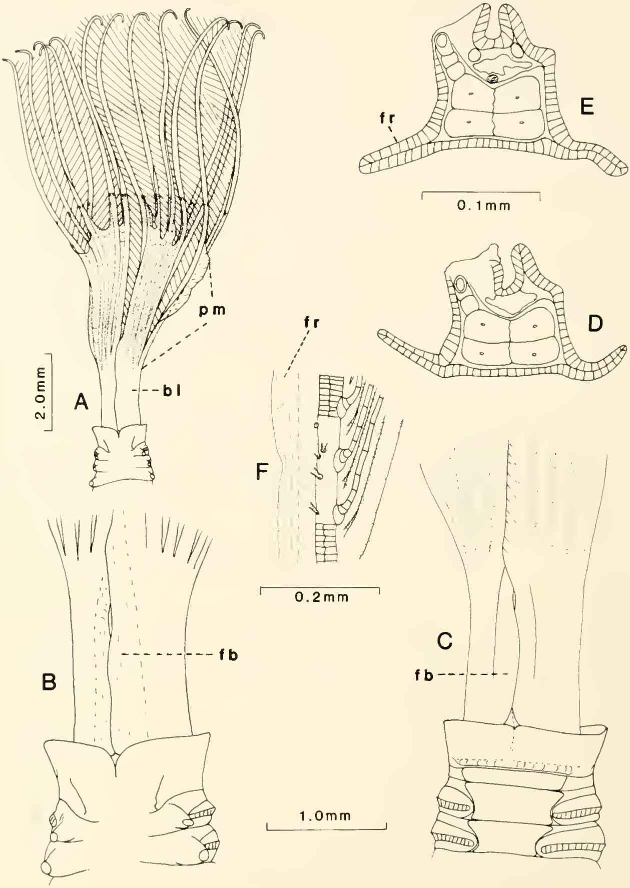

Fig. 33. *Notaulax paucoculata*: A, Anterior end, dorsal view; B, Anterior end of body and part of branchial crown, dorsal view; C, Same, ventral view; D, Cross section of radiole from between palmate membrane and ocelli; E, Same, immediately distal to ocelli; F, Region of ocelli of radiole (A–C, F, Holotype; D, E, Paratype, USNM 62078).

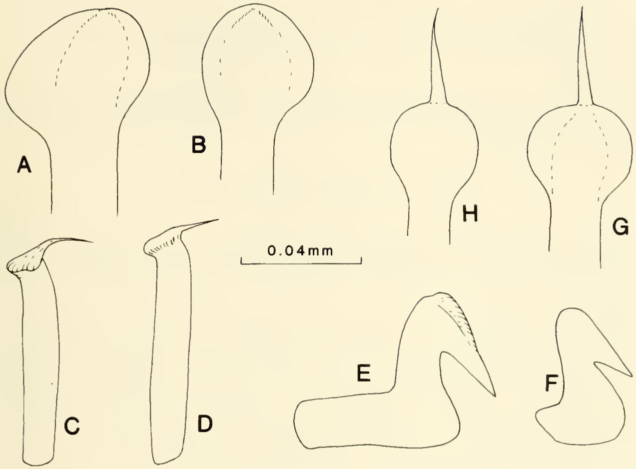

Fig. 34. *Notaulax paucoculata,* paratype (USNM 62078): A, Lower thoracic seta from anterior row; B, Same, from posterior row; C, D, Companion setae; E, Thoracic avicular hook; F, Abdominal avicular hook; G, H, Abdominal paleate setae, first abdominal setiger.

laterally extending in almost straight line to midventrum, with slight midventral incision; ventral shield of collar segment trapezoidal to rectangular, slightly wider than on following segment but less than half as long, with brown bar across anterior margin; other thoracic ventral shields trapezoidal, anterior margins broader, lateral margins curved around tori. Pygidium with eyespots. Collar setae in oblique, curved rows extending from posterior margin of segment about ½ distance to anterior margin of collar. Notosetae of remaining segments including upper arc of short, stout, hooded setae above 2 rows of paleae (Fig. 34A, B); paleae slightly broader in anterior row; no minute mucros observed; thoracic tori with numerous avicular hooks with moderately long handles and crest of minute teeth, and similar number of companion setae (Fig. 34C–E). Abdominal avicular hooks (Fig. 34F) similar to those of thorax but with shorter handles; setae including 2–3 paleae (Fig. 34G, H), those on anterior segments with mucros slightly longer than paleate area, longer posteriorly, mucros not recessed into tips, and similar numbers of long, slender capillaries.

Remarks.—Notaulax paucoculata differs from other species of the genus in the following suite of characters: 1) radioles have few ocelli; 2) the dorsal margin of the collar is deeply incised but not joined at the posterior end of the incision with the peristomium-collar segment; and 3) flanges occur on the complete free length of the radioles. The dorsal region of the collar of *N. paucoculata* superficially resembles that of *N. nudicollis*; however, on the latter species, the collar is joined at the posterior part of the incision with the peristomium-collar segment. Ocelli *N. paucoculata* are similar to those of *N. midoculi*, but radioles and the dorsal region of the collar of the latter species are completely different from those of *N. paucoculata*.

Etymology.—The specific name is derived from the Latin *paucus*, meaning few, and *oculatus*, meaning having eyes, and refers to the small number of ocelli on lateral sides of radioles.

Notaulax bahamensis, new species
Figs. 35, 36

Material examined.—BAHAMA ISLANDS: Hydro-Lab, 1.2 nmi at 180° off Bell Channel, Lucaya, near Freeport, Grand Bahama Is., 26°33′N, 78°34′W, 15 m, on coral, coll., B. A. Vittor and T. S. Hopkins, 28 Jan 1974, holotype (USNM 62082).

Description.—Body without color pattern; branchial lobes with 4 color bands, 2 in region of palmate membrane, 1 immediately distal to palmate membrane, and 1 at about mid-length of free parts of radioles; radioles (Fig. 35A) 12 pairs, united proximally by palmate membrane for about 40% of their length above basal lamina, flanged from palmate membrane to tips except for small part of region of ocelli (Fig. 35B–D); basal lamina half as long as palmate membrane; ocelli numbering up to about 30, in oval groups similar in organization to those of *N. nudicollis* but separated from palmate membrane by only ⅓ of its length. Thorax of 8 setigers; collar of single lobe, margin beginning near dorsal midline well back from anterior margin of collar segment, extending straight anteriorly, abruptly curved, almost straight laterally, with ventral margin convex; collar segment (Fig. 35E, F) much longer than next two setigers, with collar setae on posterior ⅓, with ventral shield subtriangular. Pygidial eyespots present. Thoracic paleae (Fig. 36A, B) strongly asymmetrical in anterior and posterior rows; thoracic avicular hooks (Fig. 36C) with moderately slender necks and broad handles; thoracic companion setae with blades of moderate length (Fig. 36D, E); abdominal paleae (Fig. 36F, G) with base of mucros recessed into tip of setae; abdominal avicular hooks similar to those of thorax but with shorter handles.

Remarks.—*Notaulax bahamensis* appears to be unique in the following characters: 1) the collar segment is longer than the following two segments, has a triangular ventral shield, and has setae only on the posterior ⅓; and 2) bases of mucros on abdominal paleae are recessed into spoon-shaped parts. The species appears to be closely related to *N. nudicollis*, but differs from the latter in having lateral flanges on almost the complete free length of the radioles, and in having thoracic paleae which are strongly asymmetrical in anterior and posterior rows.

Notaulax sp.
Fig. 37

?*Sabella torquata* Grube, 1877:549, 550 [in part].

Hypsicomus pigmentatus.—Fauvel, 1914b:146–148, pl. 8, figs. 252–254 [not Gravier, 1906a].

Hypsicomus torquatus.—Augener, 1918:572–576, text-fig. 101 [in part].

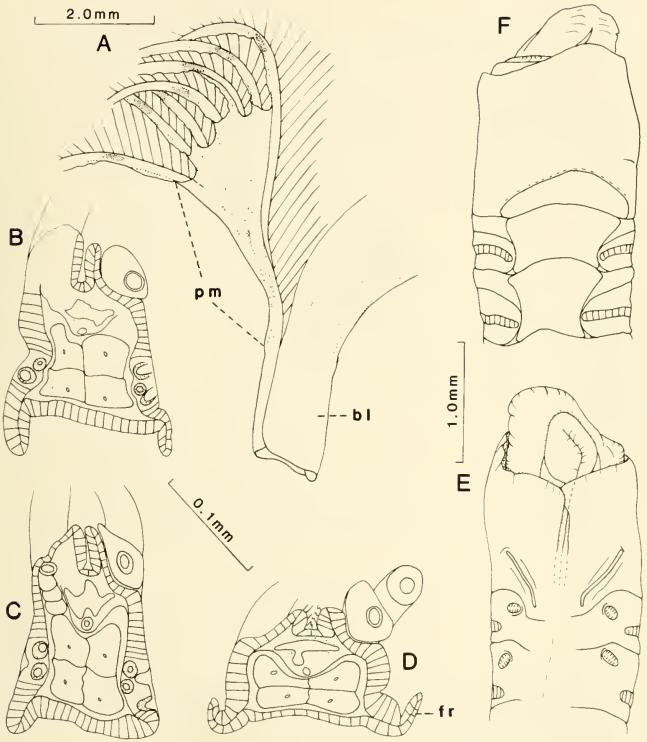

Fig. 35. *Notaulax bahamensis,* holotype: A, Proximal part of detached branchial crown, dorsolateral view; B, Cross section of radiole from middle of region of ocelli; C, Same, from distal part of region of ocelli; D, Same, from about half distance from ocelli to tip; E, Anterior end of body, dorsal view; F, Same, ventral view.

Material examined.—WEST AFRICA: ?*Gazelle* Expedition; syntype of *Sabella torquata* Grube with ventrally incised collar (ZMB 846); specimen misidentified as *Hypsicomus torquatus* (Grube) by Augener, 1918 (ZMH V 8721).

Description.—Body about 22 mm long, branchial crown 9 mm long; thorax 2.5 mm long, 1.7 mm wide, gradually increasing in diameter from collar segment; anterior abdomen slightly wider; 12 pairs of radioles united for about 1/5 of their lengths by palmate membrane, latter about twice longer than basal lamina; radioles flanged distally, each with group of ocelli in single row of 8–15 on each side (Fig.

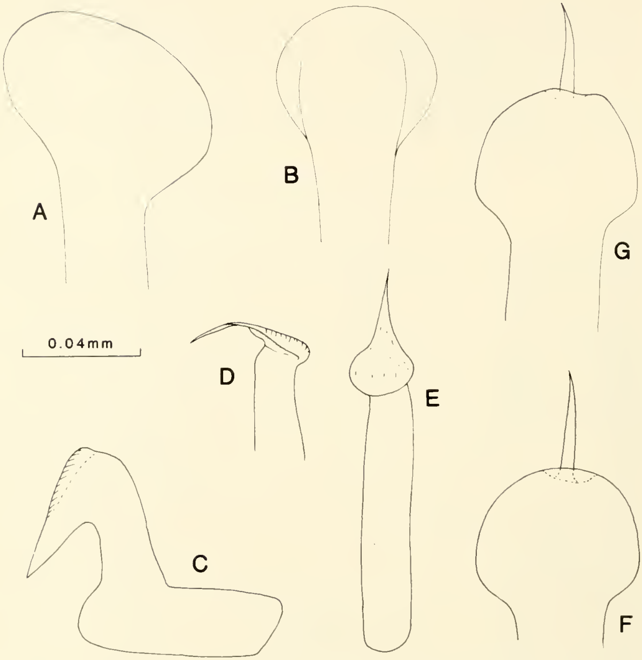

Fig. 36. *Notaulax bahamensis,* holotype: A, Lower thoracic seta, anterior row, setiger 4; B, Same, posterior row; C, Thoracic avicular hook; D, E, Companion setae; F, G, Abdominal paleate seta, second abdominal setiger, opposite views.

37A), separated from palmate membrane by about its length or near midlength of branchial crown; ocelli oriented laterodistally on near end, gradually changing to mediodistal orientation at distal end, covering angle of less than 90°. Thorax with 8 setigers; collar bilobed, similar to that of *N. nudicollis* dorsally, almost straight laterally, slightly incised ventrally (Fig. 37B, C). Ventral shield of collar segment rectangular; other thoracic ventral shields trapezoidal, slightly broader anteriorly, concave laterally. Setae as figured by Augener (1918:574), similar to those of *N. nudicollis.*

Remarks.—The specimen of Augener (1918) may be conspecific with the smaller syntype of *Sabella torquata* Grube, which has a ventrally incised collar. The syntype is missing the branchial crown and, therefore, is probably indeterminable. Augener's specimen is not conspecific with the other syntype of *S. torquata* (Fig. 25D–F), which is a specimen of the west African form of *Notaulax nudicollis.* See also *Remarks* for *N. nudicollis.*

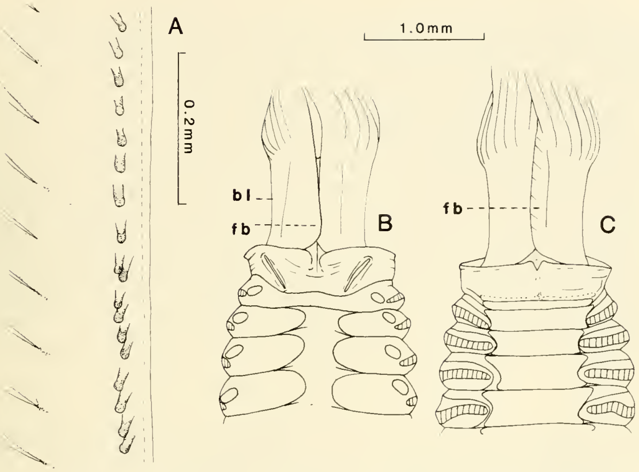

Fig. 37. *Notaulax* sp. (ZMH V-8721): A, Region of ocelli on radiole, lateral view, distal end up; B, Anterior end of body and part of branchial crown, dorsal view; C, Same, ventral view.

Megalomma Johansson, 1927

Branchiomma.—Claparède, 1869:162, 163 [not Kölliker, 1858].
Megalomma Johansson, 1927:130.

Type-species.—*Amphitrite vesiculosa* Montagu, 1815; subsequent designation by Hartman (1959:549).

Diagnosis.—Radioles in semicircular arrangement, without lateral flanges, stylodes or palmate membrane, one or more pairs with composite, subterminal eyes positioned mainly on inner surface, all with broad bands of cilia on outer lateral corners (Fig. 43B); branchial crown without flanges proximally on upper and lower margins of fused base; dorsal lips (palps) with radiolar appendage functioning as midrib with broad lamellae above and below (Figs. 38B, 39B, 43A), with pinnular appendages on upper margin where upper lamellae join first dorsal radioles; ventral lips paired; ventral sacs often present. Collar variable. Collar setae similar to upper thoracic setae, slender, narrowly hooded, in short oval group or 2 rows; upper thoracic setae in arc above notopodial lobe; lower thoracic setae long to short, thus narrowly to broadly hooded, arranged in transverse group or 2 transverse rows; thoracic avicular hooks with moderately long to long handles (Figs. 38H, I, 43H, I); companion setae with moderately thick, spear-shaped or teardrop-shaped (pennonate) blades at right angles to shafts. Abdominal setae of single type, hooded, in 2 transverse rows, sometimes forming elongate-oval group with long axis transverse, both rows bent together forming sharp, blade-like edge; abdominal avicular hooks similar to those of thorax but with shorter handles.

Remarks.—Lower thoracic setae on the type-species are long and slender, with hooded area, including tip, about 10 times longer than broad and only faintly hooded (Fauvel 1927:316, fig. 109h, i), whereas on most other species they are shorter and broadly hooded as on most *Demonax* species (Figs. 41D–F, 43E–G). In fact, on some species they are nearly spatulate.

The collar of some species begins near the dorsal midline on or near the anterior margin of the collar segment, whereas in a few species it begins immediately above the collar setae. In still others, the dorsal origin of the collar may begin somewhere between the above locations, and the dorsal part of the collar may vary during development, with the dorsal origin gradually moving anteriorly and medially as a specimen grows. When the origin of the collar approaches the midline, it may be deeply incised dorsolaterally, or may form deep dorsolateral pockets; similar variation in the shape of the collar occurs on species of *Pseudopotamilla* Bush. Lateral margins of the collar are entire. A key to species is not presented because there are many species of *Megalomma* from Florida waters remaining to be reported or described.

Megalomma bioculatum (Ehlers, 1887)
Fig. 38

Branchiomma bioculatum Ehlers, 1887:260–263, pl. 53, figs. 1–9.—Hartman, 1938:18 [examination of type-specimens; considered as *Megalomma*].
Not *Branchiomma bioculatum.*—Augener, 1918:370–372 [=*Megalomma* sp.].
Megalomma bioculatum.—Johansson, 1927:132.—Hartman, 1965b:234.
Not *Megalomma bioculatum.*—Nonato and Luna, 1970:98, 99, fig. 101 [=*Megalomma* sp.].

Material examined.—STRAITS OF FLORIDA: Hab. 1, W. of Tortugas, 24°37′03″N, 83°36′00″W, 110 fms. (201 m), USCS str. *Blake,* sta 25AG, Dec 1877–Mar 1878; Hab. 2, off Bahia Honda, 24°29′39″N, 81°17′30″W, 91 fms. (166 m), USCS str. *Bibb,* sta 16P, 4 May 1868, 5th dredging, several syntypes (MCZ) [type-locality data from Smith (1889, pp. 963 and 958, respectively); specimens have been dried; in very poor condition; lots possibly mixed]. Off Grassy Key, 24°37.7′N, 80°58.6′W to 24°36.1′N, 80°57.4′W, 139–185 m, 10′ otter trawl, R/V *Gerda,* sta 1035, 26 Feb 1969, 8 specimens (USNM 67956; MCZ; BMNH ZB 1981.23; UMML; FSBC I 27694). Off Big Pine Key, 24°28.4′N, 81°24.3′W to 24°30′N, 81°17.6′W, 135–146 m, 10′ otter trawl, R/V *Gerda,* sta 1028, 25 Feb 1969 (UMML).—MID-ATLANTIC STATES: 39°16.5′N, 72°29.6′W, 136 m, R/V *Pierce,* BLM 04B, sta A3, 22 Aug 1976, 1 small specimen (12 mm total length; USNM 57497).—NEW ENGLAND: 40°31′N, 67°19′W, 143 m, fine sand, R/V *Albatross III,* Cr. 69, coll. 10, 19 Nov 1955, 10 specimens (USNM 57370).—?PUERTO RICO: Palmas Atlas, 90 m, coll., N. Hulings and D. Feray, 1963, 1 very small specimen (5 mm total length; USNM 42792).

Description.—Tube friable, covered with foraminiferan tests on Florida specimens, slightly more rigid and covered with siliceous sand grains on New England specimens (USNM 57370). Body up to 47 mm long, with about 100 segments; branchial crown up to 26 mm long with broad reddish-brown crossband on middle third, with moderately long fused region proximally, and about 15 pairs of radioles; dorsalmost pair of radioles with large subterminal eyes, very short tips distal to

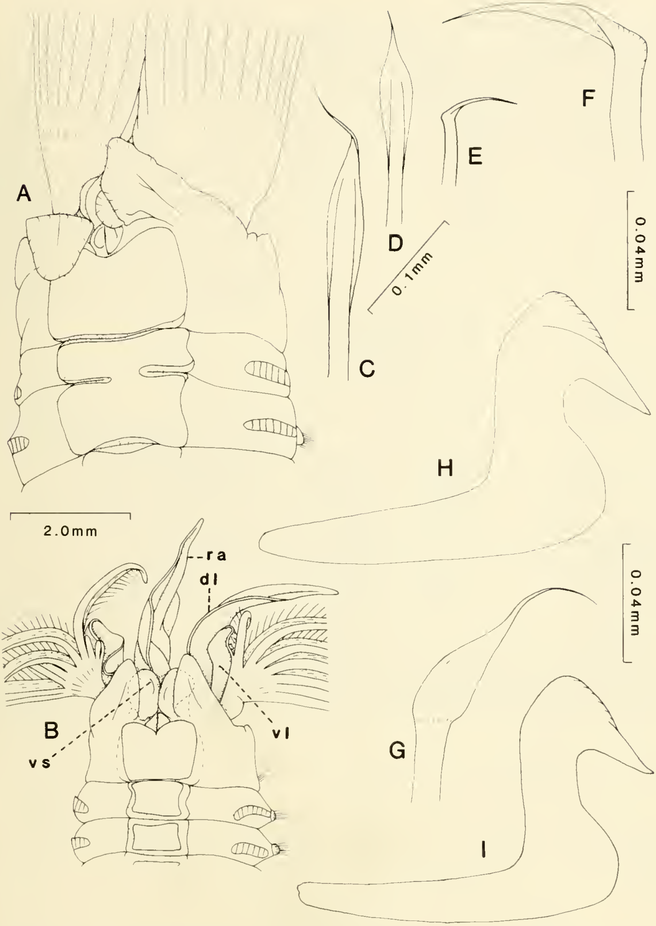

Fig. 38. *Megalomma bioculatum*: A, Anterior end of thorax and part of branchial crown, ventral view, specimen from Straits of Florida; B, Same, specimen from off New England, showing dorsal and ventral lips and ventral sacs; C, D, Lower thoracic setae; E–G, Companion setae; H, Thoracic avicular hook, setiger 3; I, Same, from setiger 7 (A, FSBC I 27694; B, USNM 57370; C–I, Syntypes).

eyes. Dorsal lips moderately long, with short pinnular appendage on margin of upper lamella; ventral sacs well developed; ventral lips moderately high (Fig. 38B). Thorax with 8 setigers; collar bilobed, beginning dorsally near posterior margin of segment just above collar setae and exposing most of collar segment dorsally, extending anteriorly then curving ventrally, straight laterally, ending ventrally in moderately long, triangular lappets; lappets extending to about beginning of radioles midventrally; pair of small, triangular lobes ventromedially between anterior margin of ventral shield and beginnings of ventral sacs. Collar ventral shield plain, longer and broader than others, with anterior margin incised or concave (Fig. 38A, B); other thoracic ventral shields slightly concave laterally. Lower thoracic setae slender, with moderately long blades (Fig. 38C, D); thoracic avicular hooks and companion setae (Fig. 38E–G) in moderately long tori well separated from ventral shields; avicular hooks with long handles (Fig. 38H, I). Abdominal tori shorter than those of thorax; avicular hooks with handles shorter than those of thorax; setae in 2 transverse rows.

Remarks.—Ehlers' figure (1887:pl. 53, fig. 9) of a thoracic avicular hook is incorrect; handles on those of type-specimens that I examined are much shorter than illustrated originally (Fig. 38H, I).

Megalomma bioculatum appears to be a lower shelf-upper slope species. All shallow water specimens identified as *M. bioculatum* that I have examined have proved to be *M. pigmentum* Reish or other species. I suspect that all of the numerous specimens reported as *M. bioculatum* from shallow waters of the Caribbean area belong to other species as well [see Perkins and Savage (1975) and also account of *M. pigmentum,* below]. *Megalomma pigmentum* Reish, which also has only one pair of eyes, has bilobed ventral lappets of the collar, and the ventral shield of the collar segment is divided into two parts by a transverse groove. Further, the small eyes of *M. heterops* n. sp., described below, may be easily overlooked, especially on small specimens, and specimens of that species may be misidentified as *M. bioculatum.*

The reports of *Branchiomma bioculatum* [=*Megalomma*] from shallow water of tropical West Africa by Augener (1918) and *M. bioculatum* from Brazil by Nonato and Luna (1970) are incorrect. The collar described by Augener for his specimens resembles that of *M. heterops* n. sp., as does the collar on specimens reported by Nonato and Luna (1970). However, both West African and Brazilian specimens apparently have only one pair of eyes and are here considered to be undetermined species of *Megalomma.*

The species is known from the Straits of Florida, the Atlantic Ocean off New Jersey and New England, and possibly from Puerto Rico in depths of 90 to about 200 m.

Megalomma lobiferum (Ehlers, 1887)

Figs. 39, 40

Branchiomma lobiferum Ehlers, 1887:254–259, pl. 53, figs. 10–15.—Augener, 1924:52 [list].—Hoagland, 1919:577.—Treadwell, 1924:18; 1939:291, 292, fig. 105.—Hartman, 1938:18 [examination of type-specimen; as *Megalomma*].—Fauvel, 1953:17.—Bellan, 1963:313.

Megalomma lobiferum.—Johansson, 1927:132.—Hartman, 1951:115.—Dauer, 1973:193.

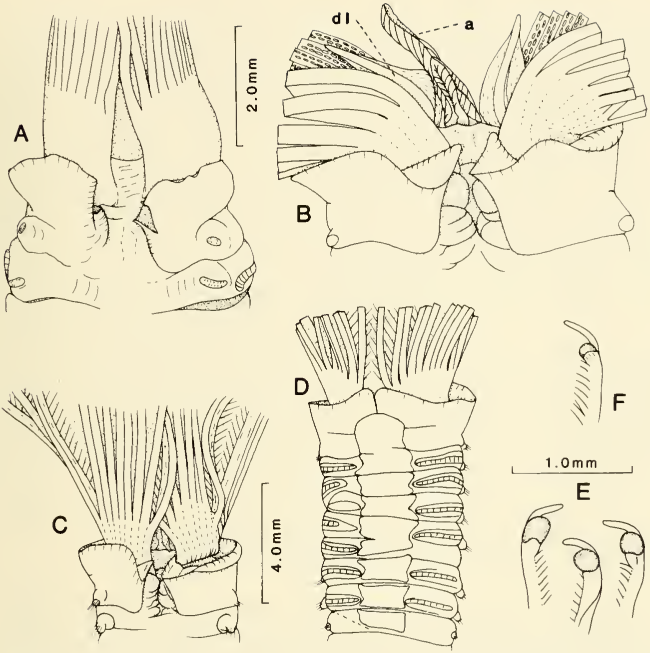

Fig. 39. *Megalomma lobiferum*: A–C, Anterior ends of body and parts of branchial crown, dorsal views (a, caruncle); D, Same, ventral view; E, Eye of first dorsal radiole, various views; F, Eye on another dorsal radiole. (A, E, F, Holotype; B–D, Specimen from Stock Is., near type-locality, MCZ).

Megalomma vesiculosum.—Fauchald, 1977b:62 [in part; not *Amphitrite vesiculosa* Montagu].

Material examined.—FLORIDA: Key West, 2–4 m, holotype (MCZ). Stock Is., near Key West, about 0.5 km SE of entrance to Safe Harbor, 24°33.3′N, 81°43.8′W, 1.5 m, with *Thalassia,* coll., J. Thomas, 29 Jul 1977, 1 specimen (MCZ). Hutchinson Is., sta V, 27°22.9′N, 80°13.9′W, 11 m, coarse calcareous sand, coll., Gallagher *et al.,* 10 Jun 1976, 1 specimen (FSBC I 27695). Off Pepper State Park, St. Lucie County, 27°29.6′N, 80°17.3′W, 5.2 m, on coral, *Oculina varicosa* Lesueur, coll., J. K. Reed and L. Edmiston, SCUBA, 28 Apr 1977, 1 specimen (IRCZM 50:836). St. Petersburg Beach, on sponge washed ashore, coll., C. H. Saloman, 29 Jan 1966, 1 specimen (USNM 67975).—PUERTO RICO: Bahia de San Juan, dredged, coll., E. Ortiz-Corpi, 31 May 1974, 1 specimen (USNM 52061).—PANAMA (ATLANTIC): Galeta Reef, coll., Reimer, 6 specimens (USNM 73019).

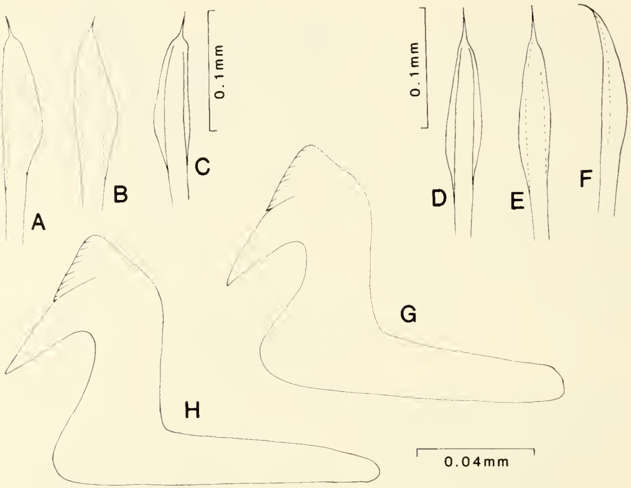

Fig. 40. *Megalomma lobiferum*: A–F, Lower thoracic setae (A, Lower, anterior row; B, Same; C, Middle, posterior row; D, Lower, posterior row; E, Same; F, Same, turned); G, H, Thoracic avicular hooks (A–F, Holotype; G, H, Specimen from Stock Is., near type-locality, (MCZ).

Description.—Tube moderately thick, rigid, almost smooth, covered with thin layer of mud or detritus, with small pieces of sand and shell cemented in yellow, translucent matrix on one specimen (IRCZM 50:836). Body up to 43 mm long, 5.5 mm wide; 8 thoracic and up to 90 abdominal segments. Branchial crown maximally 16 mm long, 18–21 pairs of radioles on larger specimens, 8 left and 9 right radioles on small specimen from Hutchinson Island, crossbanded with yellow-orange pigment extending onto pinnules on IRCZM specimen. Composite eyes on all radioles, moderately large on dorsalmost pair, abruptly smaller, about half as large on second dorsal pair (Fig. 39E, F), very gradually decreasing laterally and ventrally, those on ventralmost pair about equal in diameter to width of tips of radioles; all eyes similar, well defined, spherical, with distinct ommatidia. Branchial crown with moderately long fused region (Fig. 39A–D); dorsal lips moderately long, with margin of upper lamella fused proximally with base of short pinnule of dorsalmost radiole; ventral lips short, rounded; ventral sacs absent on continuation of ventral lips between branchial lobes and collar. Caruncle on anterior margin of shelf region between dorsal lips of branchial lobes and above mouth (Fig. 39B a). Collar bilobed (Fig. 39A–D), with margin beginning dorsally on anterior margin of collar segment about half distance from midline to lateral side, turned medially to near midline, then slightly posteriorly and laterally, forming deep pockets extending to posterior margin of segment, straight on lateral sides, ending ventrally in short, rounded lappets; ventral shield of collar segment

(Fig. 39D) up to twice broader than long, convex laterally, straight to convex anteriorly; other ventral shields of thorax usually concavely rounded laterally around tori. Collar setae moderately long, narrowly hooded; other thoracic segments with arc of slender, narrowly hooded setae above 2 rows of short, lower thoracic setae with hooded regions plus mucronate tips 4–6 times longer than broad (Fig. 40A–F); thoracic avicular hooks with handles ⅓ longer than height (Fig. 40G, H), and companion setae in long tori extending from notopodial lobes to ventral shields.

Remarks.—This species appears to be unique in having a caruncle on the base of the branchial crown between the dorsal lips. This lobe is somewhat longer on the specimen figured than on the type or other specimens examined. Lower thoracic setae, which were not figured by Ehlers, are moderately long, and thoracic avicular hooks have long handles. The latter, with accompanying companion setae, are in long rows extending to ventral shields, whereas on other species of *Megalomma* I have examined, tori are much shorter.

Descriptive information given by most authors in accounts of this species (Hoagland 1919; Augener 1924; Treadwell 1924, 1939; Hartman 1951; Fauvel 1953; Dauer 1973) is insufficient for me to confirm that they actually had *M. lobiferum*; however, considering the account of Bellan (1963) and the specimens reported herein, it is not unreasonable to assume that the species is widely distributed in shallow waters of the Caribbean area. In Florida, the species occurs in shallow water in the Florida Keys and on both the southern Atlantic and Gulf of Mexico coasts.

Megalomma pigmentum Reish, 1963
Fig. 41

Megalomma pigmentum Reish, 1963:430–433, fig. 16.—Hartman, 1969:709, 710, figs. 1–7.

Megalomma bioculatum.—Taylor, 1971:714–716.—Day, 1973:126.—Hall and Saloman, 1975:19 [not *Branchiomma bioculatum* Ehlers, 1887].

Material examined.—WESTERN MEXICO: Bahia de San Quintin, Baja California, sta 43, silty sand, 8 paratypes (USNM).—NORTH CAROLINA: off Beaufort, 34°34′N, 76°25′W, 19 m, fine sand and shell, BST 88R, coll., J. H. Day, 1965, 3 specimens (USNM 51234).—FLORIDA EAST COAST: Hutchinson Is., sta II, 27°21.6′N, 80°13.2′W, 11 m, coarse calcareous sand, 1 specimen (USNM 54719). Same, sta IV, 27°20.7′N, 80°12.8′W, 11 m, coarse calcareous sand, 2 specimens (FSBC I 27702, 27703). Same, sta V, 27°22.9′N, 80°13.9′W, 11 m, coarse calcareous sand, 13 specimens (USNM 54720; FSBC I 27704, 27709). About 27 km ENE of Ft. Pierce Inlet, 27°33.2′N, 80°03.2′W, 33 m, sand and shell, R/V *Johnson,* coll., R. Virnstein, 14 Jul 1977, 27 specimens (IRCZM 50:893; FSBC I 27709).—FLORIDA WEST COAST: National Marine Fisheries Service, Tampa Bay Area Study, coll., J. Taylor and C. Saloman, 1963, sand bottom, Tampa Bay, 6 specimens (USNM 45691). Same, Terra Ceia Bay, 27°34′24″N, 82°33′55″W, 2 m, algae cover, 6 specimens (ZMC). Same, 27°33′17″N, 82°36′05″W, 2 m, algae cover, 2 specimens (FSBC I 13423). Same, 27°31′36″N, 82°36′18″W, 2 m, algae cover, 13 specimens (FSBC I 13460). Same, Lower Tampa Bay, 27°31′43″N, 82°38′43″W, 5 m, algae cover, 1 specimen (FSBC I 12980).

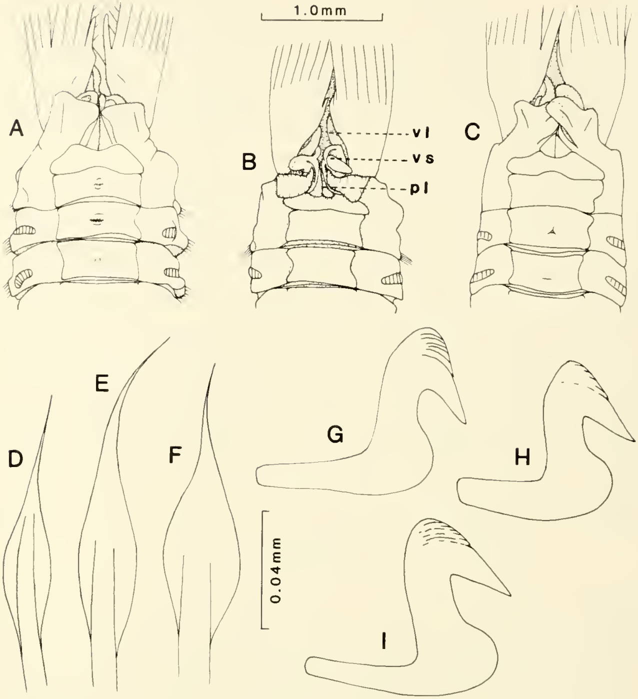

Fig. 41. *Megalomma pigmentum*: A, Anterior end of body and part of branchial crown, ventral view, Tampa Bay, Florida, specimen; B, Same, ventral lappets of collar turned back showing ventral sacs; C, Same, specimen from Venezuela; D–F, Lower thoracic setae (D, Upper seta, anterior row; E, Lower, anterior row; F, Upper, posterior row); G–I, Thoracic avicular hooks (A, B, USNM 45691; C, USNM 57945; D–F, I, FSBC I 12341; G, FSBC I 13395; H, FSBC I 13497).

Same, 27°31′41″N, 82°42′10″W, 3 m, 1 specimen (FSBC I 13145). Same, Boca Ciega Bay, 27°41′58″N, 82°40′18″W, 4 m, 8 specimens (BMNH ZB 1981.214–221). Same, 27°41′13″N, 82°39′51″W, 3 m, 3 specimens (FSBC I 12366). Same, 27°41′37″N, 82°42′01″W, 3 m, 5 specimens (FSBC I 12585). Same, 27°44′09″N, 82°43′55″W, 2 m, 3 specimens (ZMH P-16750). Same, 27°43′27″N, 82°43′24″W, 2 m, 8 specimens (FSBC I 12527). . Same, 27°43′08″N, 82°43′07″W, 3 m, 1 specimen (FSBC I 12547). Same, 27°39′19″N, 82°42′10″W, 4 m, 1 specimen (FSBC I 12787). Same, 27°43′56″N, 82°41′40″W, 2 m, 1 specimen (FSBC I 13481). Same, 27°44′12″N, 82°43′22″W, 3 m, 4 specimens (FSBC I 13497). Same, 27°37′33″N, 82°43′43″W, 2 m, algae, *Halodule* and *Thalassia* cover, 1 specimen

(FSBC I 13510). Same, 27°46′49″N, 82°45′53″W, 5 m, 1 specimen (FSBC I 13323). Same, mouth of Long Bayou, Pinellas County, 27°48′17″N, 82°45′53″W, algae cover, sta PB 1, 1 specimen (IRCZM 50:470).—VENEZUELA: Cumaná, 6–10 m, calcareous sand, coll., R. Edwards, 17 Jan 1971, 7 specimens (USNM 57945).

Description.—Maximum length 46 mm, including 8 mm branchial crown; 8 thoracic and about 60 abdominal setigers. Some Atlantic specimens with up to 3 purple crossbands on branchial crown, including one on fused proximal portion; some specimens with large dark brown spots on dorsum medial to notosetae and on ventrum between tori and ventral shields of first few segments; types from western Mexico more highly colored (Reish 1963). Branchial lobes with up to 15 pairs of radioles; only dorsalmost pair with subdistal eyes, greatly enlarged; tips of oculate radioles exceeding eyes only slightly. Collar beginning dorsally medial to setae near posterior margin of collar segment about half distance to midline, extending diagonally to lateral sides; lateral sides almost straight, ending ventrally in bilobed lappets (Fig. 41A, C). Ventral sacs or vesiculate lobes between collar and branchial lobes well developed, joined ventrally to lamellae originating immediately anterior to ventral shield of collar segment lateral to paired, triangular medial lobes and joined dorsally to ventral lips of branchial crown. Ventral shield of collar segment divided into 2 unequal parts by transverse groove (Fig. 41A–C); other thoracic ventral shields about as wide as posterior part of ventral shield of collar, concave laterally. Lower thoracic setae nearly spatulate (Fig. 41D–F); avicular hooks with moderately long handles (Fig. 41G–I); thoracic tori well separated from ventral shields.

Remarks.—The only difference that I could discover between the type-specimens and those from Atlantic areas is that the type-specimens are more highly colored; I do not consider this difference to be important.

The species is known from southern California (Reish 1963), western Mexico, North Carolina, both Florida coasts, and Venezuela in depths to about 30 m.

Megalomma heterops, new species
Figs. 42, 43

Megalomma lobiferum.—Taylor, 1971:717–719.—Hall and Saloman, 1975:19 [not *Branchiomma lobiferum* Ehlers, 1887].

Material examined.—FLORIDA EAST COAST: Hutchinson Is., sta IV, 27°20.7′N, 80°12.8′W, 11 m, coarse calcareous sand, holotype (coll., R. Gallagher, Sep 1971; USNM 54721), paratype (FSBC I 27696), 1 specimen, (FSBC I 27697). Same, sta II, 27°21.6′N, 80°13.2′W, 11 m, coarse calcareous sand, paratype (FSBC I 27698). Same, sta V, 27°22.9′N, 80°13.9′W, 11 m, coarse calcareous sand, paratype (USNM 54722). Off St. Lucie Inlet, Martin County, on coral, *Oculina varicosa* Lesueur, 27°11.2′N, 80°01.0′W, 42 m R/V *Johnson*, JSL II (submersible) 144A, coll., F. Stanton, 26 Oct 1976, 1 specimen (IRCZM 50:894). Same, 27°10.7′N, 80°01.0′W, 43 m, JSL II 147A, 27 Oct 1976, 1 specimen (IRCZM 50:849). Same, 27°10.8′N, 80°00.8′W, 44 m, JSL II 161B, 3 Feb 1977, paratype (IRCZM 50: 825). Same, 27°32.8′N, 79°58.8′W, 81 m, JSL I 438A, coll., L. Edmiston, 23 Aug 1977, 1 specimen (IRCZM 50:892).—FLORIDA WEST COAST: N. of Tortugas, 25°33′N, 82°55′W, 47 m, sand, Capetown dredge, coll., T. Cuba, 1979, 1 specimen (Univ. South Florida., St. Petersburg). Same, 25°47′N, 82°55′W, 43 m, sand and

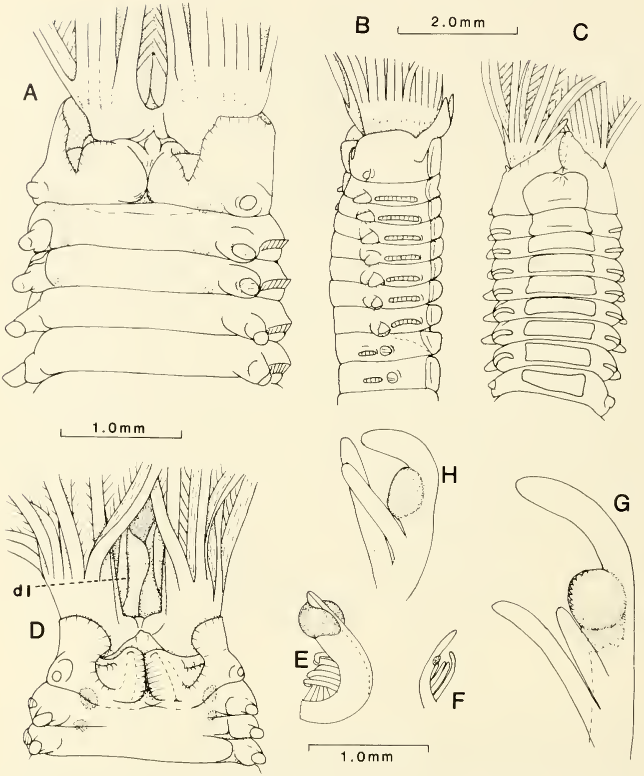

Fig. 42. *Megalomma heterops*: A, Anterior end of body and part of branchial crown, dorsal view; B, Same, lateral view; C, Same, ventral view; D, Same, dorsal view of paratype with dorsomedial parts of collar lamellae not developed; E, Large eye on tip of dorsalmost radiole; F–H, Small eyes on tips of lateral radioles (A–C, E–H, Holotype; D, ZMC; G, H, Not scaled).

shell hash, 1 paratype (FSBC I 27699). Hourglass sta J, 20 nmi W. of Sanibel Is., 26°24′N, 82°28′W, 18 m, algae, living coral, shell and sponge bottom, on coral, *Solenastrea,* dredged, R/V *Hernan Cortez,* coll., B. Presley, 12 Nov 1965, 2 paratypes (BMNH ZB 1981.212–213). Same, 11 May 1966, 5 paratypes (USNM 67953). Same, 5 Jul 1967, paratype (FSBC I 27700). Same, sta C, 26 nmi W. of Egmont Key, Tampa Bay, 27°37′N, 83°28′W, 37 m, sand and *Halodule* bottom, on coral *Solenastrea,* trynet, 31 Aug 1966, 1 specimen (FSBC I 27701). National

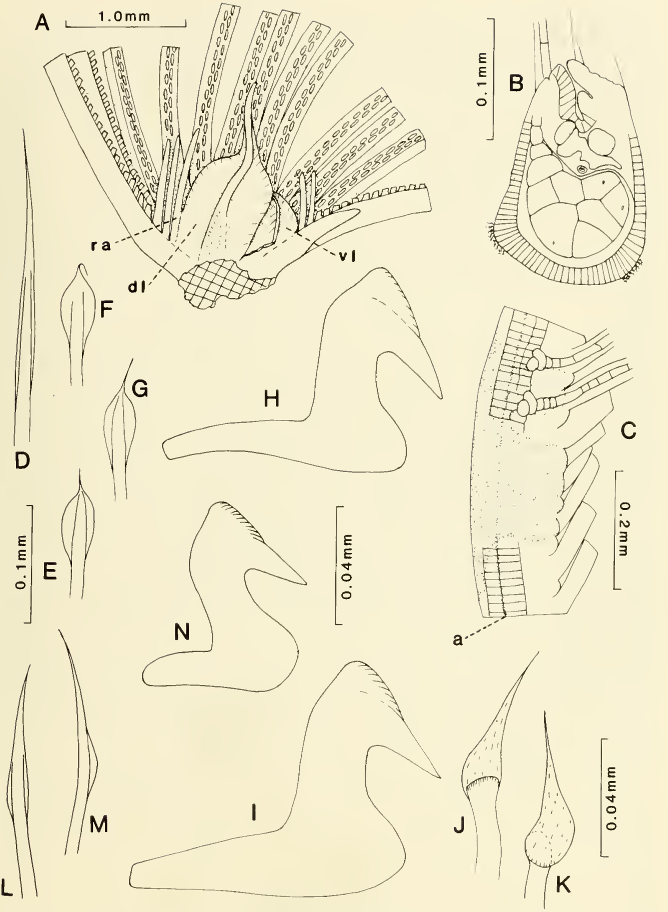

Fig. 43. *Megalomma heterops*: A, Left half of branchial crown, proximal part, medial view; B, Cross section of radiole; C, Part of radiole showing pigment spot, lateral view (a, ciliary row); D, Upper thoracic seta; E–G, Lower thoracic setae (E, Middle, anterior row; F, Upper, posterior row; G, Lower, posterior row); H, I, Thoracic avicular hooks; J, K, Companion setae, opposite views; L, M, Abdominal setae; N, Abdominal avicular hook (A–C, K, FSBC I 27700; D–G, H, J, L–N, Holotype; I, USNM 67953).

Marine Fisheries Service Tampa Bay Area Study, coll., J. Taylor and C. Saloman, 1963–1964, sta PB 1, Boca Ciega Bay, 27°48′17″N, 82°45′53″W, 2 m, sand, algae cover, 2 paratypes (ZMH P-16749). Crystal River, off Florida Power Corporation nuclear power plant, Citrus County, 28°56′24″N, 82°48′30″W, 3 m, 1 paratype (ZMC). Florida Middle Ground, BLM Cr. 01, sta 151, 28°32′02″N, 84°18′36″W, 25–27 m, on coral, *Madracis detactis* (Lyman), coll., T. Hopkins *et al.*, 5 Oct 1978, 3 specimens (USNM 67955). NE Gulf of Mexico, Proj. EGMEX 70, sta 4, 29°07′N, 85°20′W, 36 m, R/V *Hernan Cortez*, coll., J. Williams *et al.*, 5 May 1970, 9 specimens (USNM 67954). Seashorse Key, Cedar Keys, Levy County, on sponge, coll., J. Taylor, 13 May 1960, 2 specimens (USNM 65907). Same, S. shore, coll., J. Taylor, 8 Sep 1960, 1 specimen (USNM 65912). Same, on sponge, coll., T. Hopkins, Sep 1960, 2 specimens (USNM 65910). Whistle buoy area near Alligator Harbor, on sponge, coll., M. Forbes, 2 Jul 1958, 1 paratype (USNM 50480).

Description.—Tube formed of small silicate sand grains in a more or less rigid, translucent matrix, often with large pieces of shell on outside. Body up to 23 mm long, 1.8 mm wide; thorax of 8 setigers; up to 4 mm long; maximum of 70 abdominal setigers; branchial crown up to 8 mm long, with row of elongate pigment spots on fused portion below beginning of radioles (Fig. 42A–D), 4–5 narrow, transverse, purple bands on radioles; bands formed of short pigmented areas on outer and lateral surfaces of radioles, pigment not extending onto pinnules (Fig. 43C), dorsal lips often pigmented on upper surface (Fig. 43A); subterminal eyes also purple but often slightly darker. Body color pattern consisting of paired, purple spots dorsally on anterior margin of collar segment below collar, paired spots on setigers 1–3 medial to notopodia (Fig. 42A, D); some specimens with similar paired spots ventrally on anterior segments and small pigment spots below thoracic and above abdominal tori on posterior thoracic and abdominal segments; pygidium with irregularly arranged eyespots. Radioles 13–16 pairs on specimens with body greater than 15 mm long; radiolar eyes of 2 types, first on dorsalmost pair, greatly enlarged with distinct ommatidia, others much smaller, gradually decreasing ventrally, with smooth surface and ommatidia visible only under high magnification (Fig. 42E–H); dorsalmost radioles greatly enlarged subdistally, with short tips extending past eyes; other radioles not enlarged subdistally, with moderately long, slender tips extending beyond eyes. Proximal cross sections of radioles with 7–8 irregularly arranged skeletal cells surrounded by moderately thick sheath and columnar epithelium (Fig. 43B). Dorsal lips (Figs. 42D; 43A) with moderately long radiolar appendage forming midrib; broad lamellae above and below on proximal ⅔ of midrib, upper lamellae fused proximally with modified pinnule (pinnular appendage) of first dorsal radiole; 2–3 enlarged pinnules adjacent to pinnular appendage, gradually diminishing. Ventral lips beginning between ventral lappets of collar on anterior margin of collar segment, extending anteriorly and dorsally to dorsal lips, turning ventrally and joining branchial lobes proximally at ventral margin (Fig. 43A); ventral sacs absent. Branchial lobes essentially without palmate membrane; cartilaginous (fused) base short, extending well past collar margin dorsally and laterally. Collar bilobed, beginning dorsally on most larger specimens near midline slightly back from margin of collar segment, margin angled backward forming "V," extending well past beginning of branchial lobes medial to collar setae, entire but with slight indentation laterally, ending ventrally in elongate, rounded, triangular lappets extending well past origins of radioles (Fig. 42A–D); dorsomedial parts of collar lamellae not produced on most specimens (Fig. 42D). Ventral shield of collar segment entire, with rounded anterolateral corners and slight anteromedial indentation, twice longer than on other thoracic segments and about as wide. Other thoracic ventral shields rectangular. Notopodia of setigers 2–8 with upper arc of about 5 slender, narrowly hooded setae (Fig. 43D) above two transverse rows of short, subspatulate, broadly hooded setae (Fig. 43E–G), about 10 setae, all similar, in each row. Thoracic tori well separated from ventral shields, gradually shorter posteriorly but of similar distance from shields (Fig. 42B, C), with about 30 pairs of avicular hooks and companion setae anteriorly (Fig. 43H–K); avicular hooks with moderately long, slender handles. Abdominal setae geniculate, hooded (Fig. 43L, M); abdominal avicular hooks in short tori, similar to those of thorax but with shorter handles (Fig. 43N).

Remarks.—*Megalomma heterops* is very similar to the holotype of *M. circumspectum* (*Branchiomma circumspectum* Moore, 1923:239–241, pl. 18, figs. 41, 42). The collar of *M. circumspectum* has dorsomedial parts which extend well past the anterior margin of the collar segment, and dorsolateral parts are only slightly incised, thus forming deep pockets which extend back to the anterior margin of setiger 2. Also, facets on eyes of lateral radioles are visible under a dissecting microscope (e.g., without compound magnification). The collar of *M. heterops* has dorsomedian parts which extend almost to the anterior margin of the collar segment and is deeply incised dorsolaterally, and facets are not visible on lateral radiolar eyes under a dissecting microscope.

There are two additional forms similar to *M. heterops* from North Carolina, Florida and Venezuela (USNM 53976, 53977, 57946; FSBC I 27710; catalogued as *Megalomma* sp. A) and Puerto Rico (USNM 42791, 53233, 53234, FSBC I 27712; catalogued as *Megalomma* sp. C). Both forms have eyes reduced to flat, pigmented regions on the second and very small, rounded regions on the third dorsal pairs of radioles, and all eyes, except possibly those on second and third dorsal pairs of radioles, as observed under low magnification are faceted. The form from North Carolina, Florida, and Venezuela has more slender lower thoracic setae than those of *M. heterops,* whereas such setae on the form from Puerto Rico are similar to those of *M. heterops.* The two forms are not described at this time because of inadequate material.

Etymology.—The specific name is derived from the Greek *heteros,* meaning different, and *ops,* meaning eye, and refers to the small eyes on the tips of most radioles.

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NEW SPECIES OF *PSEUDODIAPTOMUS* FROM THE INDO-PACIFIC, WITH A CLARIFICATION OF *P. AURIVILLI* AND *P. MERTONI* (CRUSTACEA: COPEPODA: CALANOIDA)

T. Chad Walter

Abstract.—*Pseudodiaptomus aurivilli, P. trihamatus,* and *P. bispinosus* were collected from shallow Philippine coastal waters. In addition, other Indo-Pacific species previously misidentified as *P. aurivilli* and *P. mertoni* are assigned separate status as the new species *P. compactus, P. bowmani, P. sewelli,* and *P. baylyi.* These species plus *P. incisus* are herein assigned to the Hyalinus species group, as they all possess a lamellar hyaline membrane on the second exopod of the male left fifth leg, and other common morphological features.

A previous study on the emergence of reef associated zooplankton from Philippine coral reefs (Walter *et al.* 1982) reported the quantitative rates of emergence of zooplankton over 24-hr cycles. This paper and papers in preparation will report on the taxonomic composition of species captured from the Philippines. The results of this study clarify some problems of synonymy in existing species, and ascribe specimens previously identified as *P. aurivilli* and *P. mertoni* to new species *P. compactus, P. bowmani, P. sewelli,* or *P. baylyi.* A fourth species, *P. bispinosus,* is described.

The family Pseudodiaptomidae is composed of two genera: *Pseudodiaptomus* Herrick, 1884, and *Archidiaptomus* Madhupratap and Haridas, 1978; the latter consists of but one species, *A. aroorus.* Sixty species have been assigned to the genus *Pseudodiaptomus* before this study. The addition of five new species brings to 47 those species known from the Indo-Pacific: *P. annandalei* Sewell, 1919; *P. andamanensis* Pillai, 1980; *P. ardjuna* Brehm, 1953; *P. aurivilli* Cleve, 1901; *P. batillipes* Brehm, 1954; *P. beieri* Brehm, 1951; *P. binghami* Sewell, 1912; *P. binghami malayalus* Wellershaus, 1969; *P. brehmi* Keifer, 1938; *P. bulbiferus* (Rose, 1957); *P. bulbosus* (Shen and Tai, 1964); *P. burckhardti* Sewell, 1932; *P. clevei* Scott, 1909; *P. colefaxi* Bayly, 1966; *P. cornutus* Nicholls, 1944; *P. dauglishi* Sewell, 1932; *P. forbesi* (Poppe and Richard, 1890); *P. galleti* (Rose, 1957); *P. heterothrix* Brehm, 1953; *P. hickmani* Sewell, 1912; *P. incisus* Shen and Lee, 1963; *P. inflatus* (Shen and Tai, 1964); *P. inopinus* Burckhardt, 1913; *P. inopinus saccupodus* (Shen and Tai, 1962); *P. jonesi* Pillai, 1970; *P. lobipes* Gurney, 1907; *P. marinus* Sato, 1913; *P. masoni* Sewell, 1932; *P. mertoni* Fruchtl, 1923; *P. nankauriensis* Roy, 1977; *P. nihonkaiensis* Hirakawa, 1983; *P. ornatus* (Rose, 1957); *P. poplesi* (Shen, 1955); *P. poppei* Stingelin, 1900; *P. salinus* (Giesbrecht, 1896); *P. serricaudatus* (T. Scott, 1894); *P. smithi* Wright, 1928; *P. spatulatus* (Shen and Tai, 1964); *P. stuhlmanni* (Poppe and Mrazek, 1895); *P. tollingeri* Sewell, 1919; *P. trihamatus* Wright, 1937; *Pseudodiaptomus* sp. (Nishida, pers. comm.).

Pseudodiaptomids enjoy worldwide distribution in shallow coastal waters and typically remain near or on the bottom during the day and rise into the water column at dusk, and therefore should be searched for in night plankton samples. This diel migration is especially pronounced during new moon or very cloudy conditions. Members of this genus have been found from freshwater lakes and reservoirs to hypersaline conditions. In this study, specimens are strictly marine, collected over coral reef, grass flat, coral rubble, and soft-mud bottom embayments at Padre Burgos, Quezon Province, Luzon (13°53′N, 121°47′E) Philippines.

Abbreviations

A1 = first antenna
P1–P5 = first–fifth swimming legs
Pdg1–5 = pedigers 1–5
Ur = urosome
Pr = prosome
CR = caudal rami
Se = outer spine
St = terminal spine
Re = exopod
Ri = endopod
B1–B2 = basipods 1–2
Ur1–5 = urosome segments 1–5

In general, species determination in pseudodiaptomids relies on the morphology of male P5, with other body characters and female morphology secondary in importance. Males of several species of *Pseudodiaptomus* possess a hyaline membrane on the outer margin of the distal segment of the left Re of P5. Species possessing this character, herein referred to as the "Hyalinus" group, also share the following unique characters which are not repeated in the descriptions of the species: i) Female A1 with 21 segments (compared to the typical 22 segments common to all other pseudodiaptomids), as there are only 4 segments (Fig. 1A) proximal to the partly fused segments which are counted as separate segments. ii) Left and right female A1 and left male A1 lack dorsal barbed seta on antepenultimate segment, though the divided ventral plumose seta is present. iii) Male right A1 with 20 segments (Fig. 1B), left A1 with 22 segments and unlike the female there are 5 segments proximal to partly fused segments. iv) No detectable sexual dimorphism in P1–4 though a lateral row of 11 long spinules on B2 of P1 is present. v) Female Ur1 ventrally possesses 1 pair of spines (the right spine usually longer than the left) and an accompanying pair of posterior setae on each side of genital opening (Fig. 2D). Other common characteristics present but not specific to the Hyalinus group are: i) Terminal esthete of A1 without sexual dimorphism, although these esthetes vary in size and shape among the species. ii) Head and Pdg1 fused. iii) Wings of Pdg5 are large, directed posterolaterally and of similar size in females; small, directed posteriorly and of similar size in males. iv) Ur1 longest segment in females; Ur1–3 with posterodorsal spine rows that increase in size from Ur1 to Ur3. In males, Ur2–4 have posterior spine rows that completely encircle the segments and also increase in size from Ur2 to Ur4.

Females and males of the Hyalinus group possess the following P5 characters. These characters will not be repeated in the descriptions of either male or female P5. Females; P5 symmetrical. B2 with 1 large surface seta and row of fine hairs along outer margin. Re1 with 1 surface seta, row of fine hairs or spinules and plumose Se on lateral margin. Re2 small with fine hairs on proximomedial margin, produced distally into a plumose spiniform process; St plumose on medial margin, more than 2× longer than Re2 process with a plumose auxiliary basal spine almost equal in length to Re2 process; Se short, plumose on medial margin. Males; P5

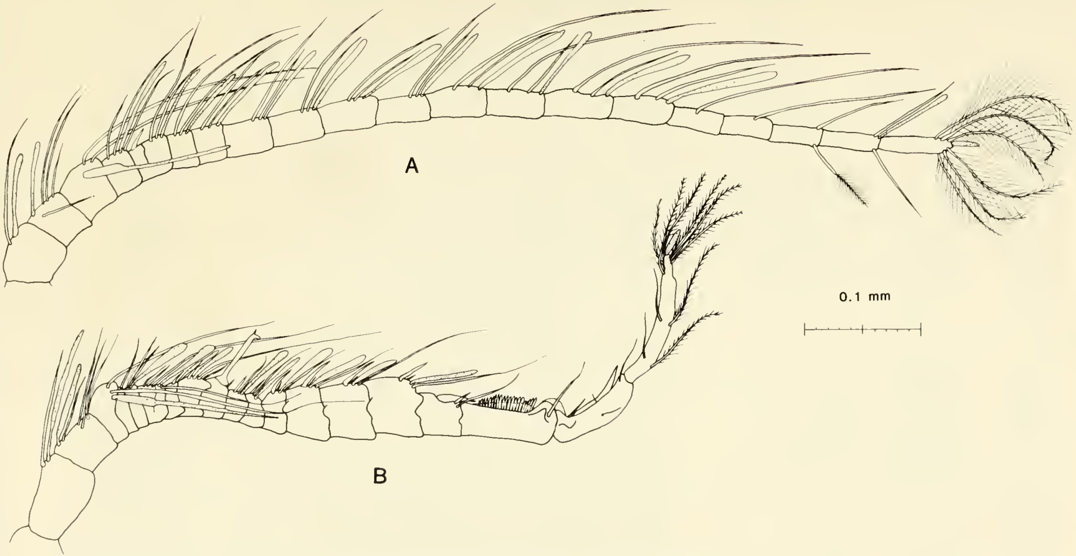


Fig. 1. *Pseudodiaptomus aurivilli* Cleve, USNM 204909: Right A1, medial view: A, Female; B, Male.

Table 1.—Comparison of morphological features between the 2 species-types of the Hyalinus group.

Sex	*aurivilli*-type	*trihamatus*-type
Female		
Genital boss	Very large and swollen	Small or shrunken
Url ventral spines	Somewhat long and robust	Longer and slender, with the right longer
P5	Re1 about 1.2× longer than B2	Re1 about 1.4–1.6× longer than B2
Male		
P5 left Re2	Hyaline membrane convexly curved	Hyaline membrane incised
P5 right Re2	Se small, slender plumose	Se large and stout sometimes possessing medial spines
P5 Ri	Short and compact points	Larger and more elongated digitiform points

non-symmetrical, consisting of right leg with 2 basipods and 3 exopods, left leg with 2 basipods and 2 exopodal segments, and the following features: Posterior view, Right leg: B1 with subapical row of spinules. B2 larger than left B2, with rounded outer lateral margin and 1 large surface seta. Re2 with at least 1 small surface seta. Re3 proximally thickened, with variable basal process and seta; distally produced into spiniform, slightly curved process with plumose medial margin. Left leg: B1 with subapical row of spinules. B2 with 1 large surface seta. Re1 with 1 small surface seta and long plumose Se. Re2 with hyaline process on outer margin. Anterior view, Right leg: B1 with proximal rows of fine hairs and/or spinules. B2 spinule row along lateromedial margin continues onto surface at midlength, a Se of varying shape and a trifid Ri. Re2 ornamented with rows of spinules and hairs. Left leg: B1 with proximal row of fine hairs. B2 with spinule row at midlength.

Members of the Hyalinus group can further be divided into two "species-types" (Table 1) with all species in this group found in the Indo-Pacific region. Their northern range is from the Indian and South China Seas including the Philippines and Indo-Malayan region, south to the northern and eastern coasts of Australia. (* denotes specimens observed and described during present study)

"*aurivilli*-type" = (**P. aurivilli, P. mertoni,* **P. bowmani,* **P. compactus*).

"*trihamatus*-type" = (**P. trihamatus,* **P. sewelli,* **P. bispinosus, P. incisus,* **P. baylyi*).

Length of prosome and urosome were taken dorsally from anterior margin of head to posterior tip of Pdg5, and from anterior margin of Ur1 to distal tip of CR. Since tip of Pdg5 overlaps Ur, specimen total length is less than combined lengths of the Pr and Ur.

Pseudodiaptomus aurivilli Cleve

Figs. 1–2

Pseudodiaptomus aurivilli Cleve, 1901:48–50, pl. 6, figs. 11–22, pl. 7, figs. 1–2.—Thompson and Scott, 1903:248, pl. 2, figs. 24–26.—Scott, 1909:116.—Sewell, 1912:116.—1914:224–226.—Früchtl, 1924:50–52.—Marsh,1933:30–31, pl. 15, figs. 3, 5–7.—Tanaka, 1963:12.

[?] *Pseudodiaptomus aurivilli.*—Krishnaswamy, 1953:118, 122–123, fig. 4.—Björnberg, 1963:100.

[?] *Pseudodiaptomus mertoni* Früchtl.—Sewell, 1932:241, fig. 85b, [=*P.* cf. *aurivilli*].—Brehm, 1934:88, 93, fig. 2.

[non] *Pseudodiaptomus* cf. *P. aurivilli.*—Bayly, 1966:54, 55, figs. 2d–f, 3c–d.

[non] *Pseudodiaptomus aurivilli* Cleve.—Sewell, 1932:240–241, fig. 85a.—Kasturirangan, 1963:36, figs. 31a–d, 32a–c.—Ummerkutty, 1964:48–52, pl. 2, figs. 23–24.—Wellershaus, 1969:254–256, figs. 21–22.—Pillai, 1980:248, fig. 1a–b.

Material.—Philippines: Padre Burgos, Quezon, coral reef, 3 m, 7–10 Jan 1981, 50 males, 50 females; USNM 204909, coll. by Walter and Talaue.

Sex	#	Length (mm)	$\bar{x}$	Pr $\bar{x}$	Ur $\bar{x}$	Pr:Ur
Female	412	1.20–1.30	1.22	0.80	0.49	1.6:1
Male	241	0.94–1.00	0.98	0.68	0.37	1.8:1

Description.—Female Pdg1 posterodorsal margin thickened. Distolateral corners of Pdg2 and 3 with small tufts of fine spinules. Pdg4 and 5 incompletely fused, with pair of fine hairs on each side of urosomal insertion. Usually with 3 pairs of black pigment spots on Pr that gradually fade in ethanol. Ur1 with proximal patch of fine hairs on lateral surfaces; genital boss swollen ventrally, with 1 pair of stout spines (Fig. 2A–D). Ur4 with pair black pigment spots that do not fade in ethanol. CR 7× longer than wide. Ur segments and CR in the proportions 28:13:13:12:34 = 100. A1 as in Fig. 1A. P5 posterior view (Fig. 2C): B1 with slightly pointed distomedial corners. B2 proximomedial corners rounded. Re1 outer medial margin lined with fine spinules. Male Pdg1 with posterodorsal margin thickened. Pdg4 and 5 incompletely fused. Pr with 3 pairs of black pigment spots as in females. Ur1 with distal swelling on right side and patch of very fine hairs at each anterolateral corner (Fig. 2E–G). Ur2 with few proximal hairs and ventral row of small spinules. Ur4 with pair of black pigment spots that do not fade in ethanol. CR 3× longer than wide. Ur segments and CR in the proportions 17:21:17:15:10:20 = 100. A1 as in Fig. 1B.

P5 posterior view (Fig. 2H): Right leg, B1 distal corner bifid, inner process reaching beyond base of Re2, outer process triangular and short. B2 with 2 small surface setae; Se large with recurved apex, medial knob and 1 seta. Re1 very short but produced into a long stout posterolateral process with proximal auxiliary spine. Re2 rectangular with plumose Se. Re3 with 2 setae. Left leg, B1 distomedial corner rounded. B2 with 2 small surface setae. Re2 with 6 setae, semi-circular with hyaline process completing ovoid shape of segment; proximal outer corner with one distally and one medially directed short plumose process. P5 anterior (Fig. 2I): Right leg, B1 with large subapical spinules. Ri forked, outer fork slightly longer and bifid. Re3 with small proximal knob. Left leg, B1 with large subapical spinules. B2 with proximal row of spinules. Re1 with patch of very fine hairs at Se base. Re2 with row of fine hairs at proximal corner.

Remarks.—Cleve's original description of *P. aurivilli* was based on an unknown number of females from the Malay archipelago. As can be seen from the figures, females and males of the Hyalinus group have similar body shapes and P5 structure. Therefore, the designation of Cleve's species from the female only and the similarity among females and males within the genus set the stage for 80 years of taxonomic confusion.

Present females agree with Cleve's female in the following: i) A1 with 21 segments, if one counts partly fused segments separately, which Cleve did not, and an elongate terminal esthete. ii) P5 inner proximomedial corners of B2 rounded and Re1 is shorter than in *trihamatus*-type species. iii) Ur1 without distal marginal swellings dorsally. iv) Ur1 genital boss with two long spines. v) CR 7× longer than wide.

Differences between Cleve's drawings and present females are that the genital boss is more prominent and Pdg4 and 5 are partly fused. Cleve (1901:48) states "*Th*1 and *Th*2 uniting" yet all pseudodiaptomids have the first and second pedigers free; this notwithstanding, I feel that they are the same species. Thompson and Scott (1903) collected specimens of both sexes from the Indian Ocean (Sri Lanka), referred them to *P. aurivilli,* and designated a male for the species. They did not describe either sex and their drawings are uninformative.

Sewell (1912:363) found specimens of *P. aurivilli* and concluded that they "were without exception, females and agreed with Cleve's description." Sewell (1914: 225–226) in support of the above, found numerous examples of both sexes, reported the head and Pdg1 fused with Pdg4 and 5 only partly fused, and that in males "the fifth pair of legs correspond exactly with the description given by Thompson and Scott." Sewell did not illustrate either sex or provide a description of the female. In a later study Sewell (1932) revised his original support of Thompson and Scott's male of *P. aurivilli.* Following Früchtl's (1924) description of *P. mertoni,* Sewell reported his males (1932, fig. 85b) as *P. mertoni.* However, differences between Sewell's figured male and that of Früchtl's include: i) Inner spine of right B1 less than half the length of B2, with absence of shorter triangular process. ii) Left B1 with pointed triangular corner and spiniform process at distomedial margin absent. iii) Se of right B2 short. iv) Re3 with large basal knob. v) Left Re2 hyaline process not drawn. Sewell's 1932 illustration (fig. 85b) does not agree completely with his 1914 statement that the male P5 exactly corresponded to Thompson and Scott's material. Unless additional specimens or original material can be reexamined the status of *P. mertoni* sensu Sewell is vague and my assignment of this species to *P. aurivilli* is tentative. The above discussion, plus my collected material, supports Thompson and Scott's designation of the *P. aurivilli* male, thereby completing the species description.

Pseudodiaptomus mertoni Früchtl

Fig. 3A

Pseudodiaptomus mertoni Früchtl, 1923:455–456, pl. 26, figs. 23–24.—1924:49–53, figs. 31–36.—Brehm, 1934:88, 93, fig. 1a–b.—Bayly, 1966:55, 56, figs. 2g–i, 3e–f.—Greenwood, 1977:66.—1982:58.

[?] *Pseudodiaptomus mertoni.*—Saraswathy, 1967:79.

[?] *Pseudodiaptomus aurivilli.*—Ummerkutty, 1964:48–52, pl. 2, figs. 23–24.

Pseudodiaptomus sp. 3.—Bayly, 1965:327.

[non] *Pseudodiaptomus mertoni.*—Sewell, 1932:241, fig. 85b.—Wellershaus, 1969: 256–258, fig. 23.—Pillai, 1980:246, fig. 1c–d.

Material.—No material was available for study and descriptive purposes. The following remarks are based on information obtained from the literature and comparative species from the Philippines and India.

Remarks.—Früchtl (1924) discussed what he believed to be the correct *P. aurivilli* and *P. mertoni* species pairs from India. He associated what he thought was Thompson and Scott's male of *P. aurivilli* (Fig. 3A) with females of a different undescribed species and designated them as a new species *P. mertoni.* This then left the female of *P. aurivilli* unpaired till Sewell (1932, fig. 85a) re-associated it with a new male (see discussion under *P. sewelli*).

I am of the opinion that Früchtl did not have Thompson and Scott's male of *P. aurivilli* and that his association was incorrect based on the following: i) *P. aurivilli* male with Pdg4 and 5 partly fused, completely fused in Früchtl's male. ii) P5 of Früchtl's male with elongate spiniform process on left B1 (Fig. 3A), right B1 bifid process shorter and left Re2 hyaline membrane different from illustrations of Thompson and Scott (1903) and Sewell (1932). Besides not having the male he thought he had, Früchtl's male and female association was incorrect, as the female lacks a posterodorsal spine row on Ur1 and the ventral surface of Ur1 with dense goatee of felt-like hair (1924:50) ("dichtanliegendem ziegenbartartigem Haarfilz") at genital opening. The lack of two ventral spines and posterodorsal spine row removes it from the Hyalinus group, and it therefore can not be conspecific with the male.

In addition, Früchtl divided these two species by the length of CR setae, which I believe is not an appropriate diagnostic tool for species division in this group. Früchtl's conclusions and species designation of *P. mertoni* were accepted by most later authors, including Sewell (1932).

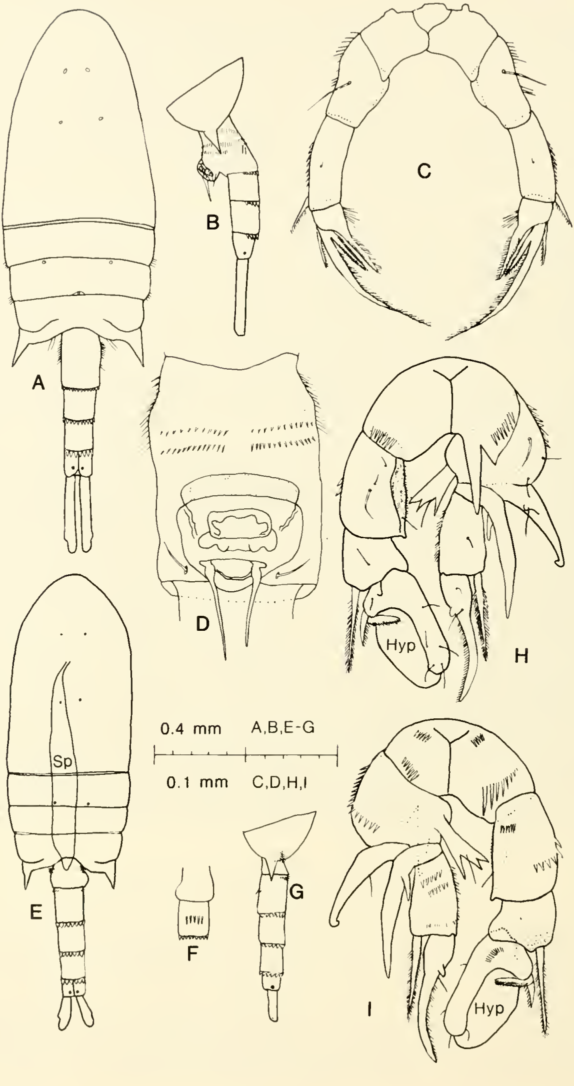
From the above, it is evident that Früchtl's assumption that the male of Thompson and Scott's *P. aurivilli* ought to be associated not with Cleve's female, but with his appropriate female, is invalid. Only his male is representative of the new species *P. mertoni* as it differs from *P. aurivilli,* and as such holds the designation of *P. mertoni,* while the status of the female awaits collection of subsequent material and does not belong to the Hyalinus group.

Australian specimens of *P. mertoni,* both sexes collected by Bayly (1966), agree with Früchtl's *P. mertoni* males with the male-female pairs appearing conspecific, thereby completing the association of sexes. Similar material from Indian waters was referred to *P. aurivilli* by Ummerkutty (1964). I believe Ummerkutty's specimen belongs to *Pseudodiaptomus* cf. *P. mertoni,* as he failed to indicate on male P5 a hyaline membrane on left Re2; right B1 distal spine is longer, and Se of right B2 is shorter than Früchtl's male.

Pseudodiaptomus compactus, new species
Fig. 3B–C

Pseudodiaptomus aurivilli.—Kasturirangan, 1963:36, figs. 31a–d, 32a–c.
Pseudodiaptomus mertoni.—Wellershaus, 1969:256–258, fig. 23.—Pillai, 1980: 246, fig. 1c–d.

Material.—The following is based on the re-examination of Wellershaus's specimen. Kasturirangan's illustration of *P. aurivilli* from the west coast of India appears to be the same species. India: Cochin Backwater, near Cochin outlet,


A
B
C
D
H
Hyp
E
Sp
0.4 mm
A,B,E-G
0.1 mm
C,D,H,I
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Hyp

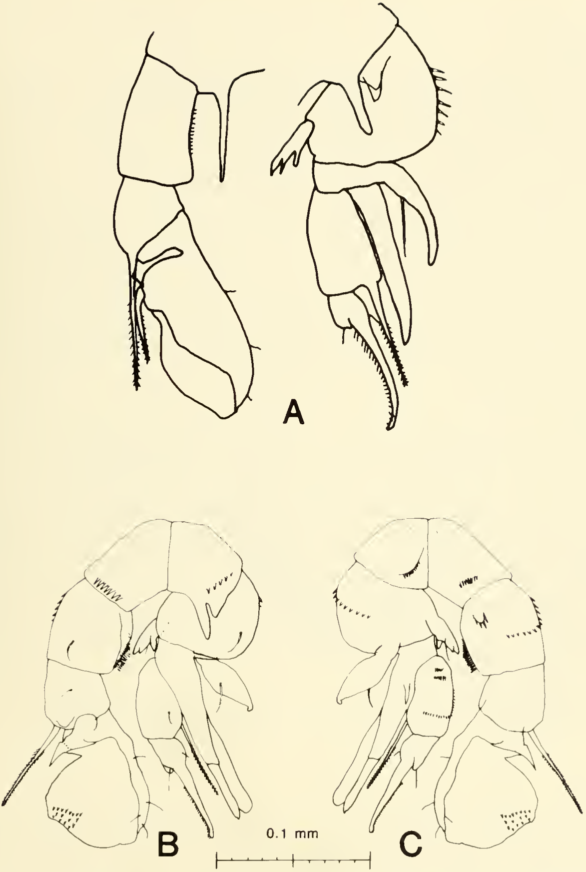


Fig. 3. A, *Pseudodiaptomus mertoni* Früchtl, posterior view of male P5, redrawn from Früchtl (1923). B–C, *Pseudodiaptomus compactus,* new species, holotype, adult male, Zool. Mus. Kiel, Cop. 35: B, P5 posterior view; C, P5 anterior view.

←

Fig. 2. *Pseudodiaptomus aurivilli* Cleve, USNM 204909: A–D, Adult female; A, Dorsal view; B, Lateral view of left side of Ur; C, Posterior view of P5; D, Ventral view of genital segment. E–I, Adult male; E, Dorsal view of specimen; F, Ventral view of Ur1 and 2 showing spinules on Ur2; G, Lateral view of left side of Ur; H, P5 posterior view; I, P5 anterior view. (Hyp = Hyaline membrane; Sp = Spermatophore).

surface, 31 May 1966, Zoological Museum Kiel, 1 male dissected on a slide, Cop. 35, holotype.

Description.—Pdg4 and 5 fused in males; other details not available as specimen was crushed on slide; see Wellershaus (1969) for further description. Female Pdg4 and 5 fused, genital boss very prominent (Kasturirangan 1963, fig. 31a–b).

P5 male, posterior view (Fig. 3B): Right leg, B1 with distomedial corner bifid, inner process longer and bluntly pointed, outer process triangular. Se of B2 short, stout with recurved apex and 1 medial seta. Re1 long (reaching distal end of Re3), divided near distal tip with a straight elongate hyaline plate along posterolateral margin, giving the appearance of a spatulate Se. Re2 with long thin plumose Se. Re3 with 2 setae. Left leg, B1 distomedial corner simple. B2 medial margin lined with small spinules along groove. Re1 with shoulder-like knob at distal corner at base of Se. Re2 narrow with 4 setae along medial edge, proximal ear-shaped protrusion, stout proximolateral spine and large ovoid hyaline process with patch of fine spinules distolaterally. P5 male, anterior (Fig. 3C): Right leg, B1 with fine subapical spinules. Ri compact, longer branch bifid, with 1 seta between the 2 small blunt points. Re1 with pointed basal process. Left leg, B1 with spinule row along distal suture.

Remarks.—Wellershaus's specimen differs from Kasturirangan's in the absence of a hyaline plate on right Re1 and spinules on hyaline process of left Re2. Otherwise, these two descriptions appear the same, with this species differing from *P. mertoni* in: i) Left B1 lacks elongate distal spine. ii) Right B2 with short Se, recurved at apex. iii) Right Re1 elongate, divided near distal end with large auxiliary hyaline plate. iv) Ri more compact with distal two points only slightly separated. v) Left B2 with row of coarse spinules at inner margin. vi) Proximolateral margin of left Re2 with short spine and somewhat circular hyaline process with small spinules along outer margin. These differences warrant a separate species status from *P. mertoni.* Specimens of *P. compactus* from the Cochin Backwater were reported as *P. mertoni,* by Pillai (1980), though his text (p. 248, fig. 1a, b) should read Fig. 1c, d.

Etymology.—The name *compactus* refers to the small compact Ri of the right P5 and blunt closely aligned distal pair of points on the longer branch.

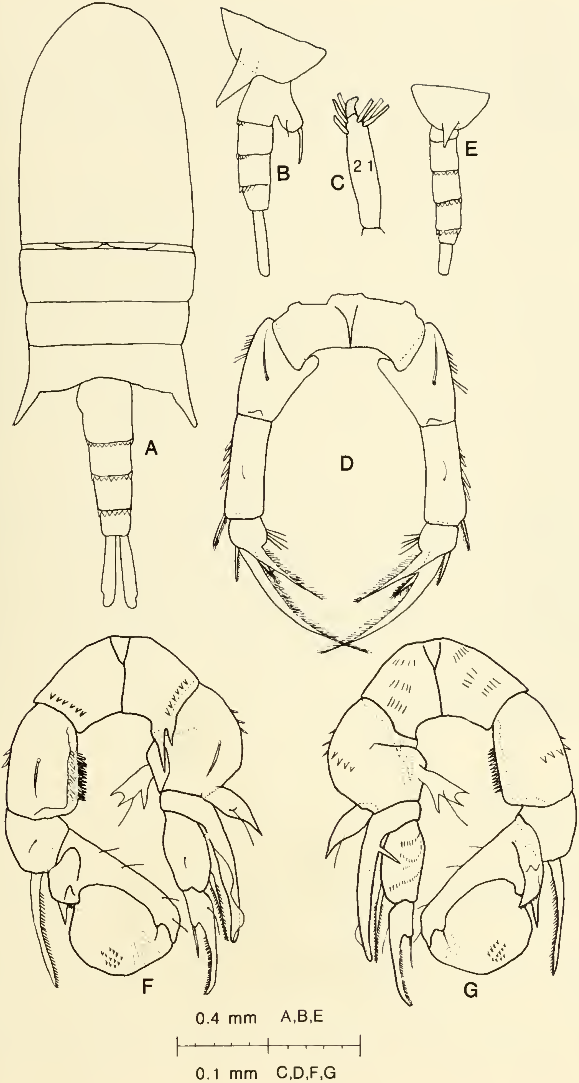
Pseudodiaptomus bowmani, new species
Fig. 4

Material.—India: Cheval Parr, Gulf of Manaar, May and Oct 1955, from the Marine Zoological Society of India, identified by R. B. S. Sewell as *P. aurivilli,* 1 male, 0.98 mm, USNM 102081, holotype: 1 female, 1.24 mm, USNM 204903, allotype.

Description.—Female Pdgl with thickened posterodorsal margin. Pdg4 and 5 fused (Fig. 4A–B). Ur1 without fine hairs, slight swelling at left anterior margin;

⟶

Fig. 4. *Pseudodiaptomus bowmani,* new species, A–D, Adult female allotype, USNM 204903: A, Dorsal view; B, Lateral view of right side of Ur; C, Terminal segment of A1 showing short curved esthete; D, Posterior view of P5. E–G, Adult male holotype, USNM 102081: E, Lateral view of right side Ur; F, P5 posterior view; G, P5 anterior view.


A
B
C
2 1
E
D
F
G
0.4 mm A,B,E
0.1 mm C,D,F,G

genital boss extremely produced ventrally with 1 pair of stout spines. CR 6× longer than wide. Ur segments and CR in the proportions 28:15:15:11:31 = 100. Terminal esthete of A1 short and curved at apex (Fig. 4C). P5 posterior view (Fig. 4D): B1 distomedial corners slightly pointed. B2 with proximomedial corners produced into lobes. Re1 with 4 spinules along outer margin, instead of fine hairs.

Male Pdg4 and 5 fused. Ur without spinules on segments (Fig. 4E). CR 3× longer than wide. Ur segments and CR in the proportions 16:20:17:17:10:20 = 100.

P5 posterior view (Fig. 4F): Right leg, B1 with bifid medial corner; medial process elongate, pointed and twice the lateral. B2 medial margin with plate-like extension; Se short, stout and pointed at apex, with 1 seta. Re1 short produced laterally into large posterior projection with proximal process and medial undulating hyaline membrane extending from midlength to apex. Re2 with plumose Se. Re3 with 2 setae. Left leg, B2 ovoid, inner margin with small spinules along groove. Re1 with long slightly curved plumose Se. Re2 with 5 setae along medial edge, proximal ear-shaped protrusion, proximolateral spine and large circular hyaline process with distolateral cluster of fine hairs and spinules. P5 anterior (Fig. 4G): Right leg, B1 with 3 rows of fine spinules. Ri with longer branch bifid and seta inserted near base of medial proximal branch. Left leg, B1 similar to right in ornamentation. Re2 with small proximolateral spiniform process on lateral margin.

Remarks.—These specimens originally identified as *P. aurivilli* by Sewell (USNM 102081) are closely related to *P. compactus.* However, several distinct differences of male P5 indicate separate species status: i) Right B1 with acutely pointed bifid process. ii) Ri larger, more widely spaced points. iii) Se on right B2 with pointed apex not recurved. iv) Right Re1 shorter (reaching the proximal knob of Re3), distal tip simple with an undulating hyaline process (not straight). v) Re3 and Se of right Re2 shorter. vi) Left B2 groove with coarser spinules at inner margin. vii) Left Re1 Se stouter and slightly curved. viii) Left Re2 hyaline process more circular.

Etymology.—This species is named for Dr. T. E. Bowman for his help and guidance during this study.

Pseudodiaptomus trihamatus Wright
Fig. 5

Pseudodiaptomus trihamatus Wright, 1937:155–157, pl. 1, fig. 1.
Mazellina galleti Rose, 1957:235–240, figs. 1–3, [female only = *P. trihamatus*]

Material.—Philippines: Padre Burgos, Quezon, coral reef, 3 m, 7–10 Jan 1981, 3 males, 7 females; USNM 204907 (1 male) neotype; USNM 204908 pareneotypes, coll. by Walter and Talaue.

Sex	#	Length	$\bar{x}$	Pr $\bar{x}$	Ur $\bar{x}$	Pr:Ur
Female	7	1.18–1.28	1.24	0.85	0.43	2.0:1
Male	3	0.94–1.00	0.96	0.68	0.34	2.0:1

Description.—Female Pdg4 and 5 fused, with 2 pairs of fine hairs along posteromedial margin; besides Pdg5 posterolateral wings there are 2 additional small spines on dorsal surface. Ur1 asymmetrical, fine hairs on anterolateral swellings; right posterodorsal margin with spine row while left margin interrupted, swollen with 2 large spines (Fig. 5A) extending posteriorly from dorsal surface. Ventrally Ur1 with weak genital boss, very long spines (Fig. 5B, C), right spine longer. Ur2 with partial spine row. CR about 6× longer than wide. Ur segments and CR in the proportions 34:16:11:8:31 = 100. Terminal esthete of A1 as in *P. aurivilli* (Fig. 1). P5 posterior view (Fig. 5D): B1 with triangular distomedial corners. B2 with 2 small surface setae, blunt wing-like extensions at proximomedial corners that protrude past segment base, distolateral corners with "shoulder." Re1 proximolateral corner with adjacent shoulder to B2, and interrupted row of fine hairs that become spinules towards distal end.

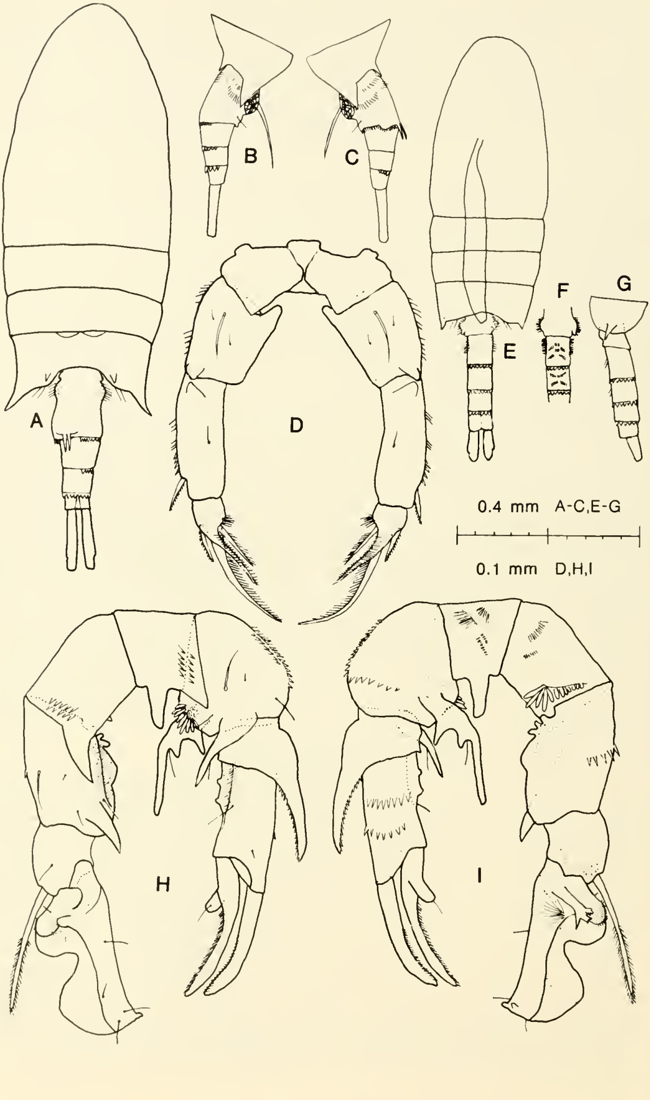
Male Pdg4 and 5 fused, Pdg5 inner margin with 2 pairs of fine hairs as in female (Fig. 5E–G). Ur1 asymmetrical, with swellings on both lateral margins covered with fine hairs. Ur2 with hairs on anterolateral margins. Ur2 and 3 with fine hairs and spinules on ventral surface that in lateral view appear as 2 rows. CR about 3× longer than wide. Ur segments and CR in the proportions 16:20:18:13:13:20 = 100. A1 as in Fig. 1B.

P5 posterior view (Fig. 5H): Right leg, B1 with elongate projection on medial margin, distal corner pointed and 2 rows of subapical spinules. B2 with 2 rows of spinules along lateral margin, 2 small surface setae, palmate cluster of blunt spinules at Ri base, and narrow distomedial curved Se with seta. Re1 large, produced distolaterally into large serrate spine. Re2 proximal inner margin with 2 knobs and patch of fine hairs along groove, 2 surface setae and elongate stout, medially plumose Se (equal in length to Re3). Re3 with ventrally elongate, basal process with seta. Left leg, B1 and B2 each with distomedial corner produced into large, acutely pointed triangular process. B1 with 2 rows of subapical spinules. B2 with 3 small surface setae, irregular projections along proximomedial inner margin. Re2 with proximal "ear-shaped" process, deeply excavated lateral lamellar hyaline membrane, 5 surface setae and small tooth projection at distomedial corner. P5 anterior (Fig. 5I): Right leg, Ri on B2 with 3 digitiform projections with seta between medial and elongate terminal. Re2 with small clump of hairs and hand-like process near proximomedial corner and very fine hairs at proximolateral margin below hyaline indentation.

Remarks.—The original description of *P. trihamatus* was based on 1 fragmented male from Philippine waters (Wright 1937) which I have been unable to locate. Wright did not know where the specimen was collected but assumed it was a freshwater species, which it is not.

The male P5 of *P. trihamatus* is very similar to *P. bispinosus,* but it differs in a number of features: Ri more elongate and digit-like, prominent curved spines on inner distal corners of left B1 and B2, palmate cluster of spines at base of Ri, and Se of right Re2 without auxiliary basal process or spines.

The female of *P. trihamatus* was originally described as a new genus and species, *Mazellina galleti* from Viet Nam (Rose 1957). Rose's diagnosis was based on a few specimens; he made no reference to the genus *Pseudodiaptomus,* though all his specimens exhibit generic characteristics of pseudodiaptomids. Therefore it is suggested that the three species that comprise the genus *Mazellina* (*galleti, ornata,* and *bulbifera*) be referred to *Pseudodiaptomus.* Dr. R. Vaissière of the


A
B
C
D
E
F
G
0.4 mm A-C,E-G
0.1 mm D,H,I
H
I

Musée Océanographique in Monaco informed me that Rose's specimens were left in Algiers and are probably no longer extant.

Rose's description of female and male *P. galleti* indicated the following: i) Head and Pdg1, fused in female, not fused in male. ii) Female A1 and male right A1 with 21 segments (if following group characteristics, all males with 21 segments on right A1 should be paired with females having A1 consisting of 22 segments). iii) Male with modified barbed seta on antepenultimate segment of left A1, while absent on female A1. iv) Female with lateral spinules on B2 of P1, absent in male. These attributes suggest Rose's females and males were not conspecific.

Evidence that the *P. galleti* female and *P. trihamatus* male are conspecific follows: i) Since the male is of the Hyalinus group and similar to *P. bispinosus*, it is expected that the females also be similar. This similarity is manifested in both females possessing swellings on left posterodorsal margin of Ur1 (with an additional pair of spines on present female) and long ventral spines on Ur1. ii) Present female A1 with 21 segments (male with 20 segments), lacks modified barbed seta on antepenultimate segment, and has same type of terminal esthete as in male. iii) Both sexes have identical spinulation patterns on P1–4, with B2 possessing 11 spinules along lateral margin. iv) P5 of female same as in other members of the *trihamatus*-type group.

Pseudodiaptomus sewelli, new species

Fig. 6

Pseudodiaptomus aurivilli.—Sewell, 1932:240–241, fig. 85a.—Wellershaus, 1969: 254–256, figs. 21, 22.—Pillai, 1980:248, figs. 1a, b.

Material.—Sewell's material from Indian waters (Bay of Bengal) is unavailable for study. The following specimens of Wellershaus which agree with Sewell's descriptions were examined.—India: Cochin Backwater, near Cochin outlet, 7.5 m, 29 Apr 1966, 1 male, 0.94 mm, holotype: same locale surface, 4 Dec 1966, 1 female, 1.26 mm, paratype, Zoological Museum Kiel, dissected on slide, Cop. 34.

Description.—The reader is referred to Wellershaus (1969) for a description of female and male general morphology, body measurements and the female P5.

Male P5 posterior view (Fig. 6A): Right leg, B1 with small bifid process at medial margin. Se of B2 short with seta, Ri base set with fine short hairs and spinules. Re1 short, but produced into large distolateral spine, plumose on medial margin, with spiniform basal process. Re2 with 3 knobs along inner medial margin and 2 setae; Se serrate, shorter than Re3, with proximal spiniform projection and similar to Re3. Left leg, Re2 with proximal ear-shaped process, 4 setae, small projection at distomedial corner and hyaline membrane with 2 broad, shallow indentations. P5 anterior (Fig. 6B): Right leg, Ri with proximal 2 points triangular, first widest and largest, 1 fine hair between second and curved terminal point.

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Fig. 5. *Pseudodiaptomus trihamatus* Wright, A–D, Adult female paraneotypes, USNM 204908: A, Dorsal view; B, Lateral view of right side of Ur; C, Lateral view of left Ur; D, Posterior view of P5. E–I, Adult male neotype USNM 204907: E, Dorsal view; F, Ventral view of Ur1–3 showing spinule rows; G, Lateral view of left side of Ur; H, P5 posterior view; I, P5 anterior view.

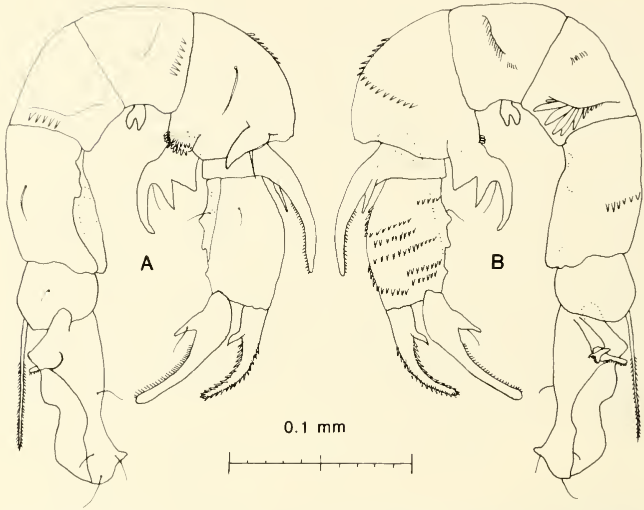

Fig. 6. *Pseudodiaptomus sewelli,* new species, holotype, adult male, Zool. Mus. Kiel, Cop. 34: A, P5 posterior view; B, P5 anterior view.

Left leg, B1 with cluster of large spatulate projections along distal suture line. Re2 with unusual proximal process fringed with short hairs.

Remarks.—This species, collected from Indian waters by Wellershaus (1969) and Pillai (1980), differs from Sewell's drawings of the male P5 in that the right B1 has a small bifid process at distal margin. This notwithstanding, I consider all three reports as the species *P. sewelli.* Pillai's (1980) illustrations belong to fig. 1a, b (not 1c, d as he indicated).

The noteworthy features of the male P5 which separate it from the other species in the *trihamatus*-type group are: i) Ri proximal point large and triangular with recurved distal projection. ii) Se of right Re2 heavily serrate with 1 basal spiniform projection. iii) Hyaline process on left Re2 only slightly indented as compared to *P. bispinosus, P. incisus* or *P. trihamatus.*

Etymology.—*Pseudodiaptomus aurivilli* sensu Sewell does not replace the male of Thompson and Scott's (1903) association and was a new species at that time. Therefore this species is named *P. sewelli* in honor of Dr. R. B. S. Sewell.

Pseudodiaptomus bispinosus, new species
Fig. 7A–I

Material.—Philippines: Padre Burgos, Quezon, coral reef, 3 m, 7–10 Jan 1981, 1 male, 0.98 mm, USNM 204904, holotype; 1 female, 1.24 mm, USNM 204905, allotype: 50 males, 100 females, USNM 204906, paratypes; coll. by Walter and Talaue.

Sex	#	Length	$\bar{x}$	Pr $\bar{x}$	Ur $\bar{x}$	Pr:Ur
Female	276	1.15–1.30	1.24	0.86	0.44	1.9:1
Male	69	0.94–1.00	0.98	0.66	0.34	1.9:1

Description.—Female Pdg1 with thickened posterodorsal margin. Pdg4 and 5 fused with 2 fine hairs on each side of urosomal insertion. Ur1 with fine hairs on anterolateral surface that extend dorsally; posterodorsal left margin with prominent bulge and larger spines than on right side (Fig. 7A–B). Ur1 ventral surface with small proximal knob, small genital boss and 1 pair of long spines with additional pair of small spines at genital opening. Ur2 posterodorsal margin with row of spines including 4 larger spines on left side; ventral surface with row of fine spinules. Ur3 with break in spine row, right half with larger spines. Most females have pair of dark pigment spots in Ur4 that gradually fade with time in ethanol. CR about 6× longer than wide. Ur segments and CR in the proportions 34:14:10:10:32 = 100. Terminal esthete of A1 short (Fig. 7C). P5 posterior view (Fig. 7D): B1 with pointed distomedial corners. B2 proximomedial corners pointed. Re1 elongate (1.5× longer than in *P. aurivilli*).

Male Pr usually with 3 pairs of pigment spots as indicated, which may fade. Pdg4 and 5 fused. Ur1 short and thickly set with fine hairs on lateral surfaces (Fig. 7E–G). Ur2 with proximal patches of fine hairs and 2 ventral rows of fine spinules. Ur3 with ventral row of fine spinules. Ur5 with pair of pigment spots that do not readily fade and present on specimens preserved in ethanol for 2 years. CR 3× longer than wide. Ur segments and CR in the proportions 11:23: 20:16:12:18 = 100. A1 as in Fig. 1B, with terminal esthete same as female.

P5 posterior view (Fig. 7H): Right leg, B1 distomedial corner bifid with 2 large pointed triangular processes, left one with medial suture. B2 with 2 small surface setae, 2 rows of lateral spinules along outer margin, patch of hair at Ri base, and naked elongate Se. Re1 with 1 seta and distolateral corner produced into attenuated large slightly curved projection, medial surface plumose. Re2 elongate, medial margin with pair of proximal knobs, patch of hair and 1 distal papilla, 2 surface setae, and lateral margin with fine hairs; Se serrate and equal in length to Re3, with 2 setae and 2 medial spines, one inserted in front of other. Re3 with large proximal hook-like knob and 2 setae. Left leg, B1 with pointed distal corner, medial protuberence with lengthwise suture line. B2 rectangular with raised posterior surface, 1 large distal and 2 small proximal knobs, patch of hairs at midlength and 1 proximal seta. Re2 large with deeply excavated hyaline process, 5 setae and distomedial corner with small triangular projection. P5 anterior (Fig. 7I): Right leg, B2 with Ri terminating in 3 points of equal length. Re1 with pointed distal spine. Left leg, B1 with cluster of finger-like spines along suture line. Re2 with hand-like process arising from proximal inner corner and row of diverging fine hairs.

Remarks.—This species is most similar to *P. incisus* Shen and Lee, 1963, from China (Fig. 7J–K). Dr. Chen Qing-chao, Academia Sinica, wrote that specimens

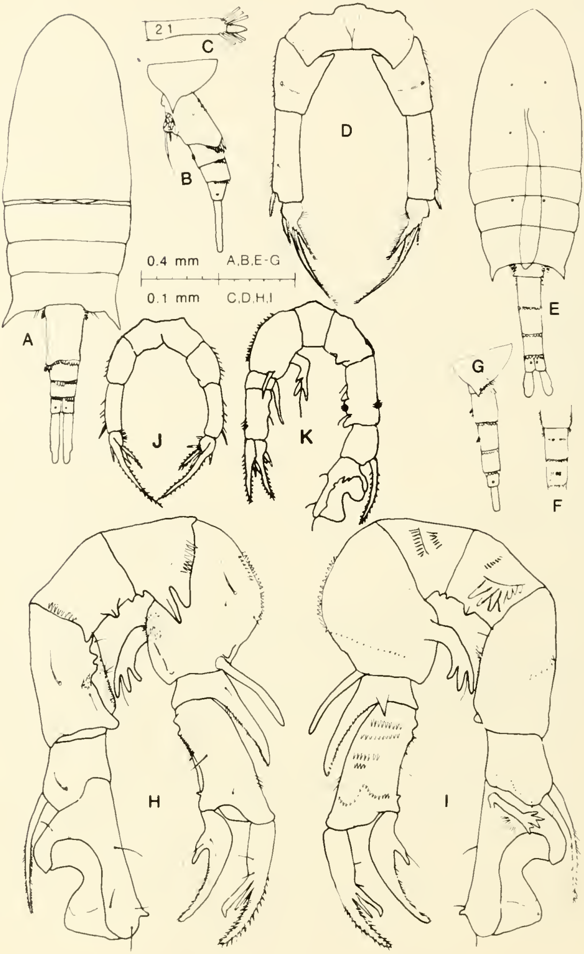

Fig. 7. *Pseudodiaptomus bispinosus,* new species. A–D, Adult female allotype, USNM 204905: A, Dorsal view; B, Lateral view of left side of Ur; C, Terminal segment of A1 showing short esthete; D, P5 posterior view. E–I, Adult male holotype, USNM 204904; E, Dorsal view; F, Ventral view of Ur1–3 showing spinule rows; G, Lateral view of left side of Ur; H, P5 posterior view; I, P5 anterior view. J–K, *Pseudodiaptomus incisus* Shen and Lee, J, Female P5 posterior view; K, Male P5 anterior view. Redrawn from Shen and Lee (1963).

of *P. incisus* are no longer extant. Based on their drawings (p. 579, figs. 15–19), the present species differs from *P. incisus* as follows: i) Left B1 with spatulate cluster. ii) Left Re2 with distolateral projection on inner medial margin and hand-like process at proximal corner. iii) Right B1 with bifid distomedial corner. iv) Se of B2 slightly longer. v) Right Re1 with larger plumose spine and auxiliary basal spine. vi) Right Re2 heavily ornamented with spinules and wider at distal end. vii) Female Ur1 with left posterodorsal margin swollen and abnormal spine rows on Ur1–3. viii) Genital boss with 2 pairs of ventral spines. ix) Female P5 with pointed proximomedial corners on B2. x) Pdg1 and head fused, not partly fused as indicated by Shen and Lee.

Females of *P. bispinosus* are distinguished from those of *P. trihamatus* by the absence of two large distal spines at swollen left posterodorsal margin of Ur1; males lack the large distal spines on left B1 and B2 of P5, the Ri is not as elongate in *P. trihamatus,* and the Se of right Re2 possess auxiliary medial spines, absent in *P. trihamatus.* Males of *P. sewelli* differ from *P. bispinosus* in that the Ri of P5 with widely spaced triangular points, Se on right Re2 with only one spine, while left Re2 lacks the deeply indented hyaline process.

Etymology.—The name *bispinosus* refers to the two medial spines present on the Se of right Re2 on male P5.

Pseudodiaptomus baylyi, new species
Fig. 8A–J

Pseudodiaptomus cf. *P. aurivilli.*—Bayly, 1966:54, 55, figs. 2d–f, 3c, d.
Pseudodiaptomus aurivilli.—Greenwood, 1977:64–65.
Pseudodiaptomus sp. 2.—Bayly, 1965:325, 327.

Material.—Australia: East Point, Darwin, surface, intertidal substrate and algal washings, 22 Aug 1982, 1 male, 0.94 mm, USNM 210669, holotype (P5 male on slide); 1 female, 0.17 mm, USNM 210670, allotype (P5 female on slide); coll. by J. L. Barnard.

Sex	#	Length	$\bar{x}$	Pr $\bar{x}$	Ur $\bar{x}$	Pr:Ur
Female	1	1.17	1.17	0.81	0.45	1.8:1
Male	1	0.94	0.94	0.62	0.34	1.8:1

Description.—This species is the same as *P. aurivilli* sensu Bayly (1966). Female Pdg4 and 5 fused (Fig. 8A), with additional pair of small dorsal spines and pair of fine hairs along distomedial margin. Ur1 with anterolateral patches of spinules and hairs; both lateral surfaces with small posteroventral protrusions (Fig. 8B–C) and long pair of ventral spines at genital boss. CR about 6× longer than wide. Ur segments and CR in the proportions 30:14:14:12:30 = 100. Terminal esthete of A1 elongate (Fig. 8D). P5 posterior view (Fig. 8E): B1 with triangular distomedial corners. B2 proximomedial corners rounded and extend past medial margin.

Male Pdg4 and 5 fused (Fig. 8F). Ur1 short and naked. Ur2 with anterolateral patches of fine hairs and spinules that extend dorsally (Fig. 8G–H). Ur2–3 with

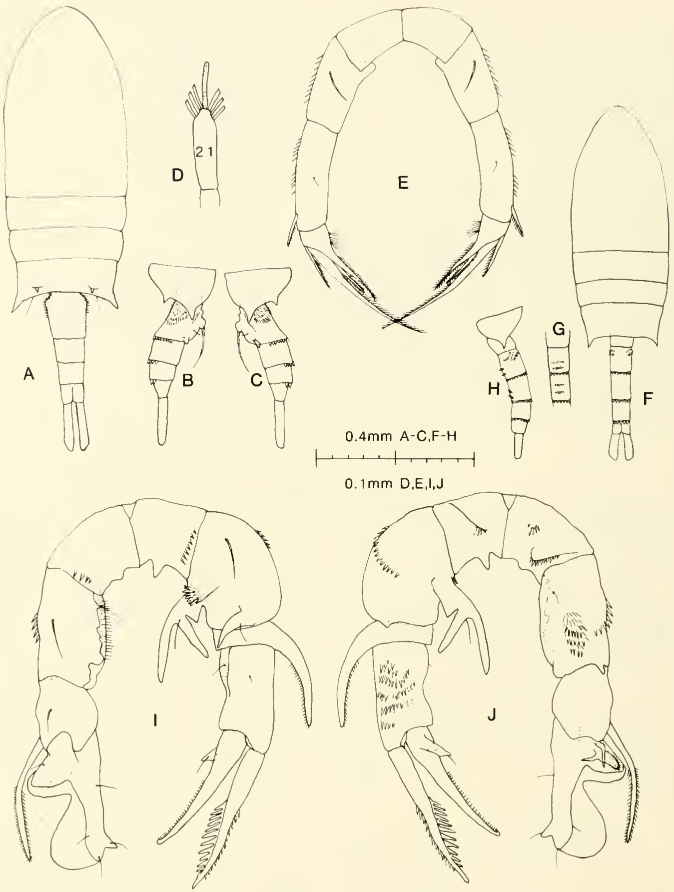

Fig. 8. *Pseudodiaptomus baylyi,* new species. A–E, Adult female allotype, USNM 210670: A, Dorsal view; B, Lateral view of right side of Ur; C, Lateral view of left side of Ur; D, Terminal segment of A1 showing elongate esthete; E, P5 posterior view. F–J, Adult male holotype, USNM 210669: F, Dorsal view; G, Ventral view of Ur1–3 showing spinule rows; H, Lateral view of left side of Ur; I, P5 posterior view; J, P5 anterior view.

ventral rows of fine spinules. CR 3× longer than wide. Ur segments and CR in the proportions 13:20:22:15:8:22 = 100.

P5 posterior view (Fig. 8I): Right leg, B1 medial margin with triangular projection. B2 with short curved Se bearing medial seta and spinules at Ri base. Re1 distolateral corner produced into attenuated large slightly curved projection, medially plumose. Re2 with 2 setae, proximomedial margin lined with fine hairs; Se heavily serrate on distomedial margin, distolateral margin lightly serrate. Re3 large pointed proximal process with distal seta. Left leg, B1 with small medial projection. B2 with raised posterior surface irregular in shape, 1 seta and fine hairs along medial margin. Re2 with 5 surface setae, proximal ear-shaped process, distomedial projection and large deeply excavated hyaline process. P5 anterior (Fig. 8J): Right leg, Ri of B2 trifid, though appears bifid, with small triangular proximal projection, outer branch slightly longer than inner, with 1 seta between branches. Left leg, B1 distomedial corner with raised surface bearing small spinules. B2 with 1 seta and surface spinule-hair patch. Re2 with proximal spine and Y-shaped process; lateral fork rounded and covered with fine hairs, medial fork truncate and pointed.

Remarks.—Bayly's (1966) specimens belong to the *trihamatus* group not to that containing *P. aurivilli* for the following reasons: Left Re2 hyaline membrane incised, right Re2 with large stout Se, and large Ri with prominent points. Although *P. baylyi* possesses P5 characters of both *P. trihamatus* and *P. sewelli,* it can be distinguished from the latter by: i) Absence of finger-like spine cluster on anterior surface of left B1. ii) Inner margin of right Re2 lacks irregular medial margin of *P. sewelli.* iii) Se of right Re2 heavily serrate and lacks basal spine. iv) Ri appears bifid in this species while trifid in *P. sewelli* and all other members of the Hyalinus group. v) Hyaline process on left Re2 deeply excavated. *Pseudodiaptomus baylyi* differs from *P. trihamatus* in Ri structure, possesses smaller medial projection on right B1, Se of right Re2 serrate and simple, and finger-like spine cluster of left B1 and distomedial spines of left B1 and B2 lacking on the former.

Bayly (1966) reported distinguishing this species from mixed collections with *P. colefaxi* and *P. mertoni* by the second CR setae which are longer and bent outwards at an angle of 90 degrees. This character, however, may be an artifact of preservation, as it was not observed in present female or any females of the Hyalinus group.

Etymology.—This species is named for Dr. I. A. E. Bayly, well-known for his work on Australian calanoids, who first reported this species.

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PROC. BIOL. SOC. WASH.
97(2), 1984, pp. 392–394

THREE NEW SPECIES OF THE GENUS *PROTOPTILA* FROM MEXICO AND COSTA RICA (TRICHOPTERA: GLOSSOSOMATIDAE)

Joaquin Bueno-Soria

Abstract.—Three new species of *Protoptila* (Trichoptera: Glossosomatidae) from the tropical regions of Mexico and Costa Rica are described—*P. pseudopiacha, P. tica,* and *P. ticumanensis.* The male genitalia are figured and described.

Protoptila is a very large genus found North, Central, and South America and is especially speciose in the tropical areas of Mexico. The larvae of *Protoptila* inhabit small streams with clean, clear, temperate waters.

The members of the genus found in the tropical areas have been studied by Mosely (1937, 1954) and Flint (1967, 1974); however, there are still many undescribed taxa of the genus from Mexico and Central America. The material described here will be deposited in the collections of Instituto de Biologia, Universidad Nacional Autonoma Mexico (IBUNAM) and the National Museum of Natural History, Smithsonian Institution (USNM).

Protoptila tica, new species
Fig. 1

Adult.—Length of forewing, 2.5 to 3 mm. Color unknown in alcohol. Sixth sternum with compressed midventral point.

Male genitalia: Eighth sternum with mesodorsal, pointed process; with rounded apical border; deeply and widely divided mesoventrally. Ninth sternum produced posteriorly to scooplike structure with pair of small apical lobes. Tenth tergum with somewhat rectangular basal section; apical section small, rather quadrate, bearing small, pointed, ventromesal process. Aedeagus with usual basal and mesal lobes and processes; central tube slightly curved, bearing apically pair of long, slender processes; apex membranous with central spine.

Material.—Holotype male: COSTA RICA, Corcovado, Estacion Sirena, 7 Feb 1981, J. Bueno; deposited in IBUNAM.

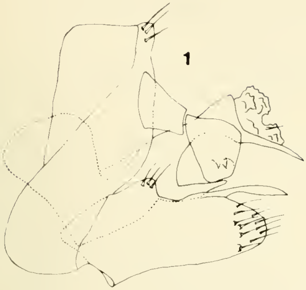
Paratypes: Same data as holotype; 2 males deposited in IBUNAM and 1 male deposited in USNM.

Remarks.—This species seems to be somewhat related to *P. chontala* Flint (1974), but differs from that species by the shape of the aedeagus, tenth tergum, and especially in the eighth sternum which has a broadly rounded ventral lobe and a pointed dorsal lobe only barely surpassing the ventral one.

Protoptila ticumanensis, new species
Fig. 2

Adult.—Length of forewings, 4 mm. Color reddish brown in alcohol. Sixth sternum with a small compressed apicomesal process.

Male genitalia: Eighth sternum emarginate apicomesially with each side of emargination ending in acute, sclerotized apex. Ninth sternum with two short,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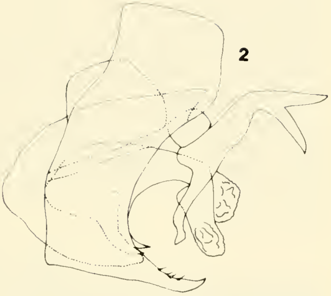
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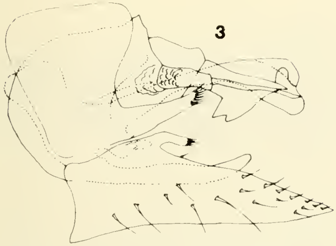
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Fig. 1. *Protoptila tica,* male genitalia, lateral view. Fig. 2. *Protoptila ticumanensis,* male genitalia, lateral view. Fig. 3. *Protoptila pseudopiacha,* male genitalia, lateral view.

sinuous, apicomesial spines produced posteriad. Tenth tergum with small, basal, cylindrical section; apical section with elongate dorsal and ventral arms; dorsal arm bilobed with both lobes tapering to apices; ventral arm sinuous, apex tapering and directed mesially. Aedeagus with pair of ventral sharply pointed appendages; central tube strongly angulate, apical portion wider and bilobed; with pair of ventromesial processes.

Material.—Holotype male: MEXICO, Morelos, Ticuman, 7 Feb 1981, L. Marino; deposited in IBUNAM.

Paratype: Same data as holotype, 1 male; deposited in USNM.

Remarks.—This species appears to be most closely related to *P. mayana* Flint (1974). From that species, *P. ticumanensis* may be recognized by the dorsolateral bifurcation of the tenth tergum and the shape of the aedeagus, especially the ventral processes.

Protoptila pseudopiacha, new species
Fig. 3

Adult.—Length of forewing, 3 mm. Color, reddish in alcohol. Sixth sternum with very long, cylindrical mesal process about as long as sternum.

Male genitalia: Eighth tergum with apically setose, posteroventral process. Eighth sternum elongate, tapering to narrow apex, with short, apically setose basodorsal process. Ninth sternum slender, elongate, produced posteriad. Tenth tergum with basal section rectangular; apical segment triangular and produced into posterodorsal point and two ventral processes. Aedeagus with typical basal lobes; with long, slender, central process arising from membranous base; central tube slender, apex enlarged, scooplike.

Material.—Holotype male: MEXICO, Oaxaca, Guelatao, 1800 m, 9 Mar 1978, J. Bueno; in the USNM.

Paratype: Mexico, Durango, Rio Mimbres, 18 Aug 1977, J. Bueno, 1 male; in the collection of IBUNAM.

Remarks.—This species is, perhaps, distantly related to *Protoptila piacha* Mosely (1954). From that species, *P. pseudopiacha* may be recognized by the ventrolateral process on the eighth tergum, the small basodorsal process with a number of setae on the eighth sternum, and the tenth tergum with two short, ventrally situated points.

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ON SMALL BATS OF THE GENUS *PTEROPUS* FROM THE PHILIPPINES

David Klingener and G. Ken Creighton

Abstract.—Analysis of cranial ontogeny in large series of *Pteropus* from the Philippine Islands indicates that bats previously allocated to three different species in the genus are conspecific. The name *Pteropus tablasi* Taylor was based on a very young individual, and the name *Pteropus balutus* Hollister on a very old one. Both are synonyms of *Pteropus pumilus* Miller. *Pteropus pumilus* is a member of the *hypomelanus* species group. *Pteropus tablasi,* when initially described, was mistakenly assigned to the *temmincki* group. *Pteropus pumilus* is distinct from *P. speciosus* and is sympatric with it on at least one island. Some allometric properties of skull growth are described.

In January 1906 Dr. Edgar A. Mearns collected three specimens of *Pteropus* on Miangas (Palmas) and Balut Islands southeast of Mindanao. Miller (1910:394) observed that the two specimens from Miangas resemble *P. speciosus* from the Sulu Archipelago, but are smaller, and based the name *Pteropus pumilus* on them. Andersen (1912:816) examined the paratype of *P. pumilus* and included the species in his *hypomelanus* group. Hollister (1913:111) based the name *Pteropus balutus* on the single specimen from Balut and observed that it approached *P. speciosus* in size, though it resembled *P. pumilus* in coloration of pelage. Taylor (1934:169) described *Pteropus tablasi* on the basis of a single specimen from Tablas Island, east of Mindoro. Taylor assigned *P. tablasi* to Andersen's *temmincki* group. Lawrence (1939:35) referred three specimens from Mindoro to *P. tablasi* and confirmed assignment of the species to the *temmincki* group. Our attempt to identify a small specimen of *Pteropus* from Negros Island in the University of Massachusetts Museum of Zoology (UMA) led to examination of Lawrence's material from Mindoro (Museum of Comparative Zoology, Harvard University, MCZ), the types of *P. pumilus* and *P. balutus* in the National Museum of Natural History (USNM), the type of *P. tablasi* in the American Museum of Natural History (AMNH), and large series of small *Pteropus* from various islands in the Philippine Archipelago housed in the Delaware Museum of Natural History (DMNH). In addition, series of *P. speciosus, P. griseus,* and *P. temmincki capistratus* were also studied.

Taxonomic Discussion

Taxonomic study of megachiropteran bats is complicated by the fact that the skull continues to change in dimensions and shape throughout life. Even when "adult" bats from different localities are compared, ontogenetic factors must be considered when evaluating differences observed. The large number of specimens of small Philippine *Pteropus* now available in collections allows reassessment of the morphological basis of previous taxonomic opinions.

The following measurements were taken by Klingener with dial calipers calibrated to 0.1 mm: greatest length of skull (GLS); diameter of orbit; interorbital

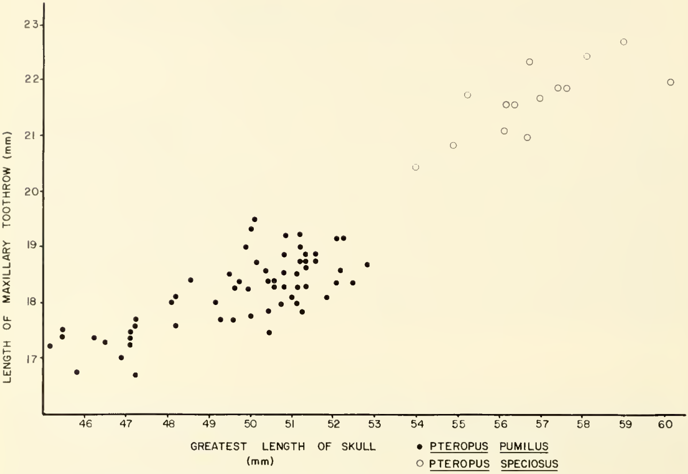

Fig. 1. Regression of maxillary toothrow length (C-M^2) on greatest length of skull.

width (IOW); postorbital width (POW); maximum width of braincase (WBC), taken above the squamosal roots of the zygomatic arches; length of maxillary toothrow, measured from the anterior surface of the upper canine tooth to the posterior surface of the second (last) upper molar; and length of molariform toothrow, measured from the anterior surface of the third upper premolar to the posterior surface of the second upper molar, excluding the diminutive second premolar. Few forearm lengths were obtained, as the majority of skins had been prepared in such a way that accurate measurement was impossible. Specimens examined are listed in the Appendix. Many specimens could not be included in the graphs or analyses owing to damage to the skulls during preparation.

In megachiropterans the skull continues to elongate in adults. This elongation may involve backward and dorsal movement of the braincase, as well as elongation of the rostrum in long-faced forms. Lanza (1961) described rostral elongation in *Epomophorus*, and Peterson and Fenton (1970) described changes in the braincase in *Harpyionycteris*. In *Pteropus* both rostral elongation and posterodorsal extension of the braincase occur. As the rostrum lengthens, the small upper second premolar may drop out, and a pronounced diastema appears between the upper canine and the third premolar. Lengthening of the rostrum and expansion of the toothrow produce an increase in maxillary toothrow length as the bat ages (see Felten 1964, fig. 4).

We plotted several dimensions against greatest length of skull. As in the *Harpyionycteris* described by Peterson and Fenton (1970) the postorbital width decreases with age as the braincase extends posteriad, and the ventral deflection of the braincase decreases. The width of the braincase is somewhat variable but

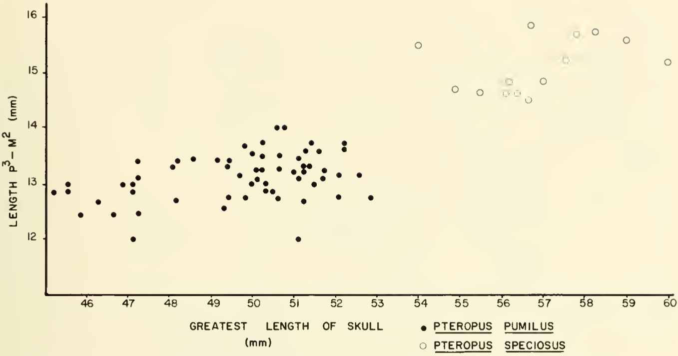

Fig. 2. Regression of molariform toothrow length (P^3-M^2) on greatest length of skull.

remains essentially constant. The maxillary toothrow length clearly increases with skull length (Fig. 1), but a similar increase is not obvious in length of the molariform toothrow (Fig. 2). Increase in the value of the former dimension is due to growth of the rostrum and forward movement of the canines. The skull of the type specimen of *P. tablasi* (AMNH No. 241737) is obviously that of a very young bat. The rostrum is short, the teeth are crowded together, there is no diastema, the cranial sutures are visible, and the braincase shows a pair of weak temporal lines rather than a median sagittal crest. Bats with a skull length of about 50 mm, including the type material of *P. pumilus,* are obviously more mature, with a long rostrum, an obvious diastema, fused sutures, and a variably developed sagittal crest. The older bats agree with the type specimen of *P. tablasi* in coloration of the mantle (yellowish buff) but tend to have darker fur on the body behind the mantle. Numerous specimens are intermediate in size, coloration, and morphology, and the differences are clearly ontogenetic. *Pteropus tablasi* is therefore conspecific with *P. pumilus.*

Pteropus speciosus is easily distinguished from *P. pumilus.* In *P. speciosus* the mantle is dark reddish brown, in contrast to the buffy mantle of *P. pumilus.* Molariform toothrow length in *P. speciosus* ranges from 14.5 to 16 mm; in *P. pumilus* from 12 to 14 mm. Further, bats identified as *P. speciosus* with a skull length of 54 or 55 mm are obviously young bats with short rostra and crowded toothrows. Bats with a skull length approaching 60 mm are obviously more mature. The type specimen of *P. balutus* (USNM No. 144760), with a skull length of 55.4 mm, falls within the size range of *P. speciosus.* The skull, however, is clearly that of a very old bat. The first and second upper molars on both right and left sides have been worn away or have dropped out, and the alveoli have closed over with bone. The upper fourth premolars are worn down to the roots, and the worn third premolars are the only intact molariform teeth in the skull. The mandibular dentition is also worn and lacking some teeth. Coloration of the pelage agrees with *P. pumilus,* and the specimen is certainly a very old individual

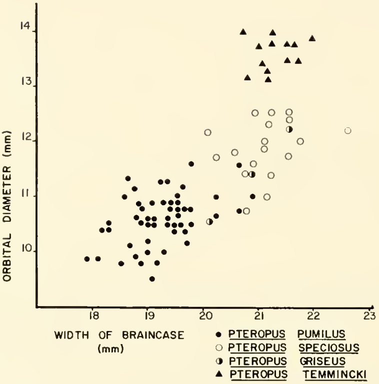

Fig. 3. Regression of orbital diameter on width of braincase.

of that species. (This specimen was not included in Figs. 1 and 2 because the dentition is incomplete.)

Andersen (1912:315, 822), in characterizing the *Pteropus temmincki* species group, stressed the short rostrum and large orbits as distinctive cranial characters. In young bats of other species groups, however, the rostra are short and the orbits large relative to skull length, and some confusion in assignment of bats to the *temmincki* group has resulted. Goodwin (1979:87f) discussed past misidentifications of young specimens of *P. griseus* from Timor as *P. temmincki.* Similarly, Taylor's (1934) assignment of *P. tablasi* to the *temmincki* group was based on his evaluation of the skull of a very young individual. We plotted orbital diameter against braincase width, which is not affected by growth, and found that specimens of *P. temmincki* from the Bismarck Archipelago cluster well above *P. pumilus* (sensu lato, including the type specimen of *P. tablasi*), *P. griseus,* and *P. speciosus* regardless of the age of the bat (Fig. 3). The last three species are all members of Andersen's *hypomelanus* group. *Pteropus pumilus,* then, includes bats previously described as *P. tablasi* and *P. balutus,* and is not a member of Andersen's *temmincki* group.

The known Philippine distribution of *P. speciosus* includes islands of the Sulu Archipelago and a small area of the Zamboanga Peninsula of Mindanao. Sanborn (1952:99) reported on two specimens in the Field Museum of Natural History, one from Dumaguete, Negros Island, and the other from Mactan Island near Cebu. We examined the former specimen, and Dr. Karl F. Koopman (pers. comm.) examined the latter. Both are young specimens of a larger species of *Pteropus,* probably *P. hypomelanus. P. speciosus* and *P. pumilus* are sympatric at least on Sanga-Sanga Island in the Sulu Archipelago.

Basic descriptive statistics for cranial measurements of specimens examined in this study are presented in Table 1. The "diastema" ("DIAS") was calculated by subtracting molariform toothrow length from maxillary toothrow length; increase in its value is an indication of rostral elongation. *Pteropus pumilus* and *P. speciosus* are apparently sexually dimorphic in size (males being slightly larger) and *P. pumilus* from different islands exhibit significant geographic variation in several cranial measurements. Two-way analyses of variance (by sex and locality) were computed for all cranial measurements of adult *P. pumilus. Pteropus pumilus* are significantly sexually dimorphic ($P < 0.005$) in GLS, maxillary toothrow length, and "diastema" length. Too few specimens of female *P. speciosus* were available to calculate a two-way analysis of variance by sex and locality; however, samples of male *P. speciosus* from four islands did not differ significantly (one-way ANOVA; $P > 0.1$). These samples were pooled and the composite sample ($n = 8$) was compared with adult female *speciosus* from Malanipa Island ($n = 6$). One-way ANOVA revealed significant sexual dimorphism in *P. speciosus* ($P < 0.05$) in GLS, maxillary toothrow length, "diastema" length, WBC, and POW. In both *P. pumilus* and *P. speciosus* males average slightly larger than females in all cranial measurements. Among the features evaluated, both species are most dimorphic in "diastema" length. A sample of twelve *P. temmincki* (4 males, 8 females) from New Britain was not significantly dimorphic in any of the cranial features measured, though males average larger for most traits (Table 1).

Secondary sexual dimorphism is marked in epomophorine pteropodids, the males being larger. Lanza (1961) documented almost complete nonoverlap of males and females in some cranial dimensions in *Epomophorus.* Our findings on *Pteropus* do not necessarily indicate true secondary sexual dimorphism, however. Larger bats with longer skulls and rostra tend to be male. That situation could be an effect of higher earlier mortality of females, possibly owing to stresses of pregnancy and lactation, or an effect of an intrinsic morphological difference between the sexes. Without an independent method of ageing our specimens, we cannot eliminate either alternative.

After accounting for sexual dimorphism, *P. pumilus* exhibit significant geographic variation in GLS, maxillary toothrow length, molariform toothrow length, "diastema" length, and POW ($P < 0.025$). Although specimens that were obviously immature were excluded from the statistical analyses, it seems likely that differences in age composition of local samples may account for much of the variation among the populations of *P. pumilus* studied. Coloration of pelage in *P. pumilus* is variable. The buffy mantle varies little with age or locality. The fur of the rest of the body, both dorsally and ventrally, varies in shade considerably within samples, although very young bats tend to be lighter. Individual adult bats from the Sulu Archipelago can be matched with individual adults from Mindoro and Negros Islands. Bats from Camiguin, however, differ in color pattern from all other populations in the species, having steel-gray fur on the head, shoulders in front of the mantle, and anterior part of the chest. This pattern is found in Camiguin specimens of all ages and is not seen in specimens from any other island. At present we do not choose to recognize the Camiguin population as a separate taxonomic entity.

We investigated the intraspecific scaling (size allometry) of three dimensions with cranial length for each species using least-squares regression (Ricker 1973) on log-transformed data. The allometric relationships among dimensions for each species are given by coefficients (slopes) of the regressions presented in Table 2.

Patterns of size allometry differ somewhat among the three species. All species

Table 1.—Cranial measurements of small *Pteropus*.†

Sex	(N)	GLS	Orb. Dia.	C–M^2	P^3–M^1	WBC	POW	'Diastema'
				Pteropus pumilus, type series, Palmas Island				
M	1	†51.3	11.2	18.8	12.7	19.3	8.0	6.1
F	1	—	10.5	17.8	12.8	—	—	5.0
				Pteropus tablasi, holotype, Tablas Island				
?	1	†45.2	9.8	17.2	12.9	18.6	9.0	4.3
				Pteropus balutus, holotype, Balut				
F	1	†55.4	11.6	—	—	20.7	6.8	—
				Pteropus pumilus, Mindoro				
M	1	†52.1	10.7	19.1	13.2	20.2	7.6	5.9
F	1	48.2	10.9	18.1	13.4	19.3	7.9	4.7
				Pteropus pumilus, Batu Batu				
M		†49.56 ± 1.91 (45.5–51.4) 7	10.65 ± .21 (10.4–10.9) 6	18.69 ± .71 (17.5–19.5) 7	13.51 ± .33 (13.0–14.0) 7	19.34 ± .79 (18.2–20.6) 7	8.00 ± .88 (7.1–9.4) 6	5.17 ± .63 (4.5–6.2) 7
F		48.71 ± 2.32 (45.9–51.7) 7	10.20 ± .66 (9.5–11.0) 5	17.76 ± .80 (16.7–18.8) 8	13.04 ± .63 (12.0–13.8) 8	18.81 ± .41 (18.1–19.4) 7	8.05 ± .79 (6.6–8.8) 6	4.72 ± .56 (4.1–5.6) 8
				Pteropus pumilus, Sanga Sanga				
M		†50.85 ± .88 (49.5–52.7) 18	10.79 ± .37 (9.9–11.6) 18	18.45 ± .44 (17.7–19.2) 19	13.31 ± .31 (12.8–14.0) 19	19.36 ± .62 (17.9–20.9) 19	7.83 ± .76 (6.4–9.1) 18	5.14 ± .31 (4.5–5.6) 19
F		50.6 ± 1.50 (48.2–52.2) 7	10.84 ± .05 (10.8–10.9) 5	18.12 ± .79 (16.5–19.1) 9	13.37 ± .33 (12.7–13.7) 9	19.14 ± .47 (18.4–19.6) 8	7.64 ± .87 (6.3–8.7) 7	4.75 ± .62 (3.5–5.5) 9
				Pteropus pumilus, Camiguin				
M		†49.73 ± 3.25 (46.4–52.9) 3	10.33 ± .31 (10.0–10.6) 3	18.50 ± .28 (18.3–18.7) 2	12.80 ± .14 (12.7–12.9) 2	19.40 ± .40 (19.0–19.8) 3	8.80 ± .61 (8.4–9.5) 3	5.70 ± .14 (5.6–5.8) 2
F	3	49.93 ± 1.01 (49.3–51.1)	10.43 ± .21 (10.2–10.6)	18.03 ± .35 (17.7–18.4)	12.46 ± .42 (12.0–12.8)	18.97 ± .15 (18.8–19.1)	7.37 ± .72 (6.9–8.2)	5.57 ± .45 (5.1–6.0)

Table 1.—Continued.

Sex	(N)	GLS	Orb. Dia.	$C–M^2$	$P^3–M^2$	WBC	POW	'Diastema'
Pteropus pumilus, Negros								
M		†49.23 ± 2.23 (45.5–51.5) 7	10.49 ± .51 (9.8–11.1) 9	18.14 ± .73 (17.0–19.0) 9	13.01 ± .20 (12.7–13.4) 9	19.23 ± .60 (18.3–20.3) 9	8.58 ± .78 (7.4–9.8) 9	5.13 ± .62 (4.3–5.8) 9
F	7	47.64 ± 1.63 (46.3–51.1) 7	10.47 ± .26 (10.1–10.9) 7	17.54 ± .46 (17.0–18.3) 7	12.94 ± .27 (12.5–13.3) 7	19.16 ± .30 (18.7–19.5) 7	9.16 ± .52 (8.5–9.9) 7	4.60 ± .38 (4.0–5.2) 7
Pteropus speciosus, Malanipa Island								
M	3	†57.1 ± 2.70 (54.0–59.0)	11.73 ± .86 (10.8–12.5)	21.93 ± 1.16 (20.6–22.7)	15.60 ± .20 (15.4–15.8)	21.00 ± .36 (20.6–21.3)	8.07 ± .57 (7.6–8.7)	6.33 ± 1.0 (5.2–7.1)
F	6	56.85 ± .67 (56.2–57.8)	11.70 ± .51 (11.0–12.5)	21.57 ± .66 (20.6–22.5)	15.17 ± .56 (14.5–15.9)	20.83 ± .30 (20.3–21.1)	7.43 ± .36 (7.0–7.9)	6.40 ± .30 (5.9–6.7)
Pteropus speciosus, Mindanao, Zamboanga Peninsula								
M	1	†60.3	12.4	22.0	15.2	21.6	7.2	6.8
Pteropus speciosus, Sanga Sanga								
M		†60.13 ± 3.05 (56.8–62.8) 3	12.2 1	22.63 ± .98 (21.5–23.2) 3	15.46 ± .85 (14.5–16.1) 3	22.00 ± .85 (21.4–22.6) 3	8.10 ± 1.13 (8.3–8.7) 3	7.17 ± .21 (7.0–7.4) 3
Pteropus speciosus, Sibutu								
M	2	†59.75 (58.6–60.9)	12.15 (11.8–12.5)	22.85 (22.5–23.2)	16.10 (16.0–16.2)	21.55 (21.5–21.6)	8.10 (7.9–8.3)	6.75 (6.5–7.0)
Pteropus temmincki, New Britain								
M	4	†57.05 ± 1.13 (55.5–58.0)	13.75 ± .17 (13.5–13.9)	20.90 ± .77 (20.0–21.8)	14.43 ± .17 (14.2–14.6)	21.42 ± .50 (20.8–22.0)	9.55 ± .78 (9.0–10.7)	6.48 ± .85 (5.6–7.6)
F		56.86 ± .79 (56.1–58.1) 7	13.62 ± .29 (13.2–14.0) 8	20.94 ± .70 (19.7–21.9) 7	14.93 ± .40 (14.3–15.4) 7	21.23 ± .38 (20.8–21.8) 7	8.77 ± 1.10 (7.5–10.6) 7	6.01 ± .64 (5.2–7.0) 7

† Table 1: Measurements (mm; $\bar{x}$ ± SD; range; sample size) of specimens of *Pteropus* examined.

Table 2.—Intraspecific scaling of cranial measurements.

Taxon	N	Dependent variable (log e)	Independent variable (log e)	R^2	Coefficient (slope)	$P\leq$*
P. pumilus	61	P^3–M^2	GLS	.16	.32	.0001
P. speciosus	20	P^3–M^2	GLS	.40	.64	NS
P. temmincki	13	P^3–M^2	GLS	.00016	.02	NS
P. pumilus	60	C–M^2	GLS	.61	.70	.001
P. speciosus	20	C–M^2	GLS	.70	.95	NS
P. temmincki	13	C–M^2	GLS	.55	1.55	NS
P. pumilus	60	"DIAS"	GLS	.42	1.64	.014
P. speciosus	20	"DIAS"	GLS	.58	1.71	.053
P. temmincki	13	"DIAS"	GLS	.63	5.05	.005

* Two-tailed 'T' test of H_0: observed slope = isometric slope = 1.0.

show positive allometry of "diastema" length with cranial length. Within each species, larger bats have absolutely and relatively longer "diastemata." To the extent that size allometry within species reflects the patterns of growth allometry it appears that rostral elongation occurs throughout life in these bats by elongation of the "diastema." In *P. temmincki,* though the rostrum is always short, relative growth in the rostral region anterior to the molariform teeth is pronounced. Length of the maxillary toothrow increases isometrically with cranial length in *P. speciosus,* with strong positive allometry in *P. temmincki,* and with negative allometry in *P. pumilus,* reflecting the pattern of relative scaling found for "diastema" length vs. GLS. Molariform toothrow length shows the lowest correlation with cranial length and the flattest slope of the three regressions for each species. In these pteropodids this dimension increases only minimally with increasing cranial length, and it also shows much less variation with age and sex within a species than the other measurements.

Our object in presenting this analysis of size allometry is to emphasize the need to account for continuous ontogenetic change when doing species level taxonomy of pteropodids. Exceptionally old individuals of one species may overlap in cranial measurements with young individuals of another. Very young specimens that appeared distinctive to the original describer are considerably less so when larger series are available for comparison. We found simple bivariate plots of cranial measurements to be adequate and effective for displaying the absolute and relative differences in cranial proportions among the species surveyed and the range of variation to be expected within each species.

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Appendix

List of Specimens Examined

Pteropus pumilus (93).—Palmas (Miangas) Island, 2 (USNM); Balut Island, 1 (USNM); Bongao Island, 4 (DMNH); Batu-Batu Island, 12 (DMNH); Sanga-Sanga Island, 30 (DMNH); Camiguin Island, 22 (DMNH); Negros Island, 1 (UMA), 17 (DMNH); Mindoro Island, 3 (MCZ); Tablas Island, 1 (AMNH).

Pteropus speciosus (21).—Mindanao, Zamboanga, 1 (AMNH); Malanipa Island, 10 (AMNH), 4 (USNM); Sanga-Sanga Island, 4 (DMNH); Sibutu Island, 2 (DMNH).

Pteropus griseus (3).—Timor, 3 (AMNH).

Pteropus temmincki capistratus (14).—New Britain, 12 (AMNH), 2 (USNM).

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OCCURRENCE OF THE SLIPPER LOBSTER *SCYLLARIDES HAANII* IN THE HAWAIIAN ARCHIPELAGO

Terrance D. Morin and Craig D. MacDonald

Abstract.—The regular occurrence of *S. haanii* (de Haan, 1841) throughout the Hawaiian Archipelago is documented and represents a major extension of the geographic range of this species, previously known only from the Indo-West Pacific region. Heretofore only one species of *Scyllarides, S. squammosus* (H. Milne Edwards, 1837), has been reported from the Hawaiian Islands and adjacent areas.

Eighty-two specimens of *Scyllarides* from Oahu (21°30′N, 158°W), Nihoa (23°03′N, 161°55′W), Necker (23°34′N, 164°42′W), and Kure Atoll (28°25′N, 178°25′W) in the Hawaiian Archipelago were examined and compared with published descriptions (Holthuis 1947; George and Griffin 1972, 1973). The materials consisted of live animals, including some that were marked and released as part of a capture-recapture study at Kure Atoll, and preserved specimens already deposited in the Bernice P. Bishop Museum (BPBM). Lengths are carapace length (cl), measured between the median point of the anterior part of the carapace (rostrum excluded) and the median point of the posterior margin.

Scyllarides haanii (de Haan)
Fig. 1a

Scyllarus haanii de Haan, 1841:152.
Scyllarides haanii.—Holthuis, 1947:96–99.

Material.—OAHU: Honolulu Market, 1 ♂, cl. 108 mm (BPBM, S172).—No data, 1 ♀, 115 mm (BPBM, S3206).—Kaneohe Bay, Jul 1955, C. S. Holmes, 2 ♀, 110 and 111 mm (BPBM, S 6312).—Makapuu Point, fish trap, 135 m, Jun 1979, E. Shallenberger, 1 live ♀, 44 mm; molt (BPBM, S8601).—No data, 1976, 3 ♀, 125–155 mm.—Waikiki, SCUBA, 10 m, Aug 1979, T. Morin, 1 live ♀, 86 mm.—NIHOA: lobster trap, 70 m, Feb 1980, S. Naftel, 1 live ♂, 130 mm.—NECKER ISLAND: lobster trap, 40 m, Nov 1979, S. Naftel, 1 ♀, 168 mm (BPBM, S8602).—KURE ATOLL: lobster trap, 5–10 m, Aug 1979–Jun 1980, C. MacDonald, 15 live ♀, 104–143 mm, 13 live ♂, cl. 121–147 mm.

Scyllarides squammosus (H. Milne Edwards)
Fig. 1b

Scyllarus squammosus H. Milne Edwards, 1837:284.
Scyllarides squammosus.—Edmondson, 1933:233; 1946:258.—Johnson, 1971:77, 97–98.
Scyllarides squamosus.—Holthuis, 1947:99–100.

Material.—OAHU: no data, 2 ♀, 51 and 73 mm, dry (BPBM, S5860).—Barbers Point, 33.5–35 m, 17 May 1964, R. Ridgeway and E. R. Cross, 1 ♂, 54 mm

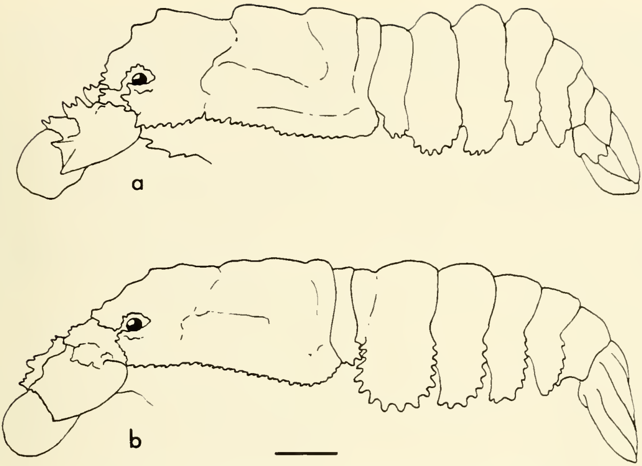

Fig. 1. Lateral view of: a, *Scyllarides haanii*; b, *S. squammosus*. Scale bar: 20 mm.

(BPBM, S6944).—NIHOA: lobster trap, 60 m, Feb 1980, S. Naftel, 7 live ♀, 89–96 mm, 11 live ♂, 86–98 mm.—NECKER: lobster trap, 36 m, Nov 1979, S. Naftel, 5 live ♀, 83–93 mm.—KURE ATOLL: lobster trap, 5–10 m, Aug 1979–Jun 1980, C. MacDonald, 9 live ♀, 75–96 mm, 8 live ♂, 40–95 mm.

Our records of *S. haanii* occurring throughout the Hawaiian Archipelago represent a major eastward extension of a broad geographic range. The previously known distribution of *S. haanii* includes the Red Sea, Mauritius, Singapore, Formosa, Japan, the Malay Archipelago, Western Australia and Lord Howe Island (Holthuis 1947, 1958; George and Griffin 1972, 1973). Heretofore, *S. squammosus* was the only species of *Scyllarides* reported from the Hawaiian Islands and adjacent areas (Edmondson 1933, 1946; Johnson 1971, 1977a, b).

Holthuis (1947) and George and Griffin (1972, 1973) reviewed the morphological characteristics of these species based on specimens from the Netherlands East Indies and Australia respectively, and established the most useful differences for distinguishing *S. haanii* from *S. squammosus.* The most obvious of these are illustrated in Fig. 1. Briefly, they are: 1) the dorsal midline of abdominal segments 2, 3, and 4 is strongly humped in *S. haanii* but is only a weak ridge in *S. squammosus*; 2) the cervical groove and constriction of the carapace behind the eyes is strong in *S. haanii* but weakly defined in *S. squammosus*; and 3) the anterior border of the third antennal segment has a median and terminal spine in *S. haanii* but is spineless in *S. squammosus.* Differences in the coloration pattern of the first abdominal tergite as noted by George and Griffin (1973) are not obvious and do not distinguish the species in our specimens.

In overall appearance the two species are much alike and easily confused. Rathbun (1906) very early suggested that *S. haanii* should be considered a variety of *S. squammosus,* but later authors (reviewed in Holthuis 1947; George and Griffin 1972, 1973) retained them as distinct. The presence of the morphological differences noted above, which are consistent across the wide geographic range of these species, supports this separation. Further, electrophoretic studies of *S. haanii* and *S. squammosus* from Kure Atoll revealed a suite of diagnostic isozymes that also separated the two species (J. Shaklee, pers. comm.).

Together, *S. haanii* and *S. squammosus* constitute an incidental but potentially valuable part of a recently developed commercial fishery for spiny lobsters in the Northwestern Hawaiian Islands. Also, *S. haanii* commmonly is caught by sport divers and commercial trap fishermen in the main Hawaiian Islands. The presence of these two species of *Scyllarides* in Hawaii should be recognized so that the relative contribution of each species to the commercial fishery can be assessed. This is important because potential differences in the population biology of the two species might influence how the fishery should be managed.

During the first year of a study of the population biology of these species at Kure Atoll conducted by one of us (CDM), *S. haanii* constituted 19.4% of 1,016 scyllarids caught by traps and divers. The remainder of the sample was *S. squammosus.* Preliminary results of this study indicate that these species may differ markedly in the nature of their sociality and reproductive seasonality. *Scyllarides haanii* apparently is a solitary species whereas *S. squammosus* tends to occur in groups. Using identical sampling methods and effort, *S. haanii* has been collected as adults but rarely as juveniles whereas *S. squammosus* has been caught as nisto stage postlarvae, juveniles, and adults. Additionally, only a single ovigerous female *S. haanii* has been collected, and that during winter, whereas the reproductive season of *S. squammosus* is well-defined and occurs during summer at Kure Atoll.

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NEW OBSERVATIONS ON *CLADOCARPUS FLEXUOSUS* NUTTING, 1900 (HYDROZOA: PLUMULARIIDAE), A BATHYAL HYDROID FROM THE GULF OF MEXICO

Dale R. Calder

Abstract.—The hydroid *Cladocarpus flexuosus* Nutting, 1900, is known from a single, fragmentary colony collected at a depth of 1719 m in the Gulf of Mexico. New material, obtained in deep water (788–1829 m) collections from DeSoto Canyon off the coast of Alabama, USA, is described and illustrated here. The gonothecae and phylactocarpia of this species are described for the first time. Phylactocarpia arise as hydrocladial appendages, confirming that the species belongs in the genus *Cladocarpus* Allman, 1874. The type of *C. flexuosus* differs from that of the related species *C. dolichotheca* Allman, 1877, in having cone-shaped instead of cylindrical hydrothecae, and more weakly developed septa in the internodes of the hydrocladia.

Cladocarpus Allman, 1874, is a widely distributed, largely deep water genus of hydroids extending to depths in excess of 5000 m. Of some 45 nominal species referred to the genus by Vervoort (1966), 11 were admitted with some reservation. Genera in the plumularian subfamily Aglaopheniinae, to which *Cladocarpus* belongs, are distinguished largely on the basis of their accessory reproductive structures (Millard 1975), and gonophores of these 11 species have not been described. One of those doubtfully included in *Cladocarpus* by Vervoort (1966) was *C. flexuosus* Nutting, 1900, a species known from a single, incomplete, sterile colony.

Several specimens of *C. flexuosus,* including a colony with gonophores, were recently identified in samples of deep water benthos from the northeastern Gulf of Mexico. The hydroid is redescribed here, and types of the morphologically similar species *C. flexuosus* and *C. dolichotheca* Allman, 1877, are compared.

Family Plumulariidae L. Agassiz, 1862

Subfamily Aglaopheniinae Stechow, 1911

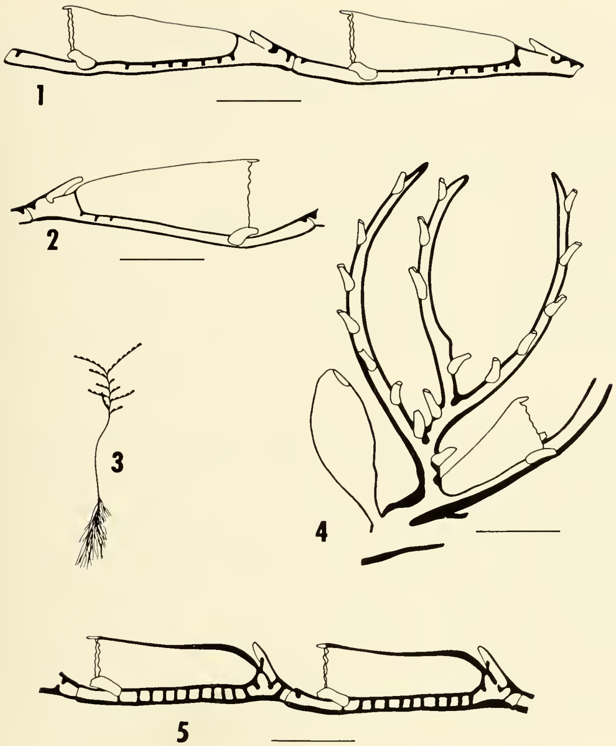
Genus *Cladocarpus* Allman, 1874

Cladocarpus flexuosus Nutting, 1900

Figs. 1–4

Cladocarpus flexuosus Nutting, 1900:114, pl. 27, figs. 11–13.

Material examined.—Northeastern Gulf of Mexico, *Albatross* sta 2384 (28°45′N, 88°16′W), 1719 m, type-slide of a single hydrocladium, USNM 18679.—DeSoto Canyon, N.E. Gulf of Mexico, *Alaminos* sta 67A5-6B (28°48′N, 87°03′W), 788 m, 16 Jul 1967, benthic skimmer, one infertile colony, 7 cm high, ROMIZ B307.—DeSoto Canyon, N.E. Gulf of Mexico, *Alaminos* sta 68A7-14B (28°56′N, 87°32.7′W), 1829 m, 8 Aug 1968, benthic skimmer, one fertile, fragmentary colony, 3 cm high; one hydrocaulus with hydrorhizal fibers, 5 cm high; ROMIZ B308.—DeSoto Canyon, N.E. Gulf of Mexico, *Alaminos* sta 66A9-XV (28°15′N,



Figs. 1–4. *Cladocarpus flexuosus*: 1, Hydrothecae, ROMIZ B309; 2, Hydrotheca from type-slide, USNM 18679; 3, colony, one-half life-size, ROMIZ B307; 4, Phylactocarp and gonotheca, ROMIZ B308; Fig. 5, *Cladocarpus dolichotheca*, hydrothecae, MCZ. Scale bars = 500 μm.

87°02′W), 1000 m, 11 Jul 1966, midwater trawl on bottom, two fragmentary, infertile colonies, 3 cm and 5 cm high; one hydrocaulus with hydrorhizal fibers, 7 cm high; ROMIZ B309.

Description.—Colony with basal tuft of root-like fibers arising from hydrorhizal tubules. Hydrocaulus about 200–300 μm wide basally, unbranched, monosiphonic, lacking septa, separated into proximal and distal parts by 2–3 hinge-joints. Proximal part of hydrocaulus straight, nematothecae present at upper end only, nodes and hydrocladial apophyses absent, perisarc moderately thick. Distal part of hydrocaulus geniculate, nodes indistinct if detectable at all, internodes long, slender, each with lateral apophysis distally and a variable number of nemato-

Table 1.—Size comparisons of R/V *Alaminos* hydroids (ROMIZ) with type-specimens of *Cladocarpus flexuosus* (USNM 18679) and *C. dolichotheca* (MCZ, no catalog number). Measurements in μm.

	C. flexuosus USNM 18679	*C. flexuosus* ROMIZ B307	*C. flexuosus* ROMIZ B308	*C. flexuosus* ROMIZ B309	*C. dolichotheca* (MCZ)
Hydrocladium					
Internode length	1,681–1,723	1,394–1,574	1,532–1,681	1,574–1,702	1,085–1,404
Diameter at node	85–96	81–96	66–143	79–119	70–112
Hydrotheca					
Total length	968–1,042	936–1,021	874–1,032	915–1,042	746–960
Diameter at aperture	404–447	298–330	362–415	317–381	298–317
Median Nematotheca					
Total length	228–251	202–230	208–245	202–219	261–298
Lateral Nematotheca					
Total length	177–194	168–191	160–191	153–177	177–205

thecae, 1–3 along internode axis, one in axil of each apophysis, and one reduced nematotheca on apophysis. Apophyses moderately long, given off alternately from opposite sides of hydrocaulus, each supporting hydrocladium. Hydrocladia unbranched, inserted directly on apophysis without intermediate internodes, up to 22 mm long, divided into long, sinuous internodes by nearly transverse nodes. Internodes very slender, each with one frontally-placed hydrotheca, one median inferior nematotheca, one pair of lateral nematothecae, and variable number of internodal septa, usually 2 proximal to, 1 distal to, and 2–9 beneath the hydrotheca. Hydrothecae distant, elongate, cone-shaped but variable in outline, abcauline and adcauline walls varying from convex to concave, intrathecal septa lacking, perisarc moderately thin. Hydrothecal aperture oval, plane of orifice perpendicular to axis of internode, margins with linguiform median abcauline tooth, bordered on either side by about 6–7 teeth, teeth often little more than faint undulations, particularly away from abcauline wall. Median inferior nematotheca one-chambered, immovable, long, anvil-shaped, free from hydrotheca, aperture scoop-shaped. Lateral nematothecae one-chambered, immovable, sac-shaped, projecting beyond hydrothecal margin, aperture terminal.

Phylactocarpia about 2 mm long, dichotomously branched, antler-shaped, arising 1 per hydrocladium between, and lateral to, median inferior nematotheca and hydrotheca of first hydrocladial internode, forming double row over hydrocaulus and arching over gonothecae, bearing nematothecae similar in morphology to median inferior nematothecae of hydrocladia, faint nodes near base of each branch, septa lacking. Gonothecae elongate-oval, about 0.8 mm long, one per phylactocarp, arising from hydrocladial apophysis by short stalk, aperture oval, subterminal, sex indeterminable.

Remarks.—The presence of gonothecae and phylactocarpia in material of *C. flexuosus* from *Alaminos* station 68A7-14B (ROMIZ B308) removes any doubt about the generic identity of this species. In having gonothecae protected by phylactocarpia arising as appendages of alternately disposed hydrocladia, *C. flex-*

uosus conforms with contemporary diagnoses of the genus *Cladocarpus* (see Millard 1975). Two distinctly different types of phylactocarpia occur in *Cladocarpus,* a difference which suggests possible grounds for eventual subdivision of the genus. Phylactocarpia of *C. flexuosus* resemble those of *C. formosus* Allman, 1874, the type-species of *Cladocarpus* by monotypy.

A comparision of *Alaminos* hydroids from DeSoto Canyon (ROMIZ B307, ROMIZ B308, ROMIZ B309) with type-material of *Cladocarpus flexuosus* (USNM 18679) leaves little doubt that all belong to the same species. The aperture diameters of hydrothecae in the type-slide generally exceed those of *Alaminos* specimens (Table 1, Figs. 1, 2), but this difference is attributed to flattening of the hydrothecae by the coverslip. Median inferior nematothecae are somewhat closer to the hydrothecae in the type, although their position and length are variable in *Alaminos* material. Slight differences in such an inconstant morphological character are not considered to be taxonomically important. The number of internodal septa beneath the base of the hydrotheca is also variable in *Alaminos* hydroids, and apparent differences between these specimens and the type (Figs. 1, 2) are not regarded as significant either.

Hydroids of *C. flexuosus* bear considerable resemblance to *C. dolichotheca* Allman, 1877, and phylactocarpia of both species are antler-shaped. Specimens of *C. flexuosus,* including the type-material (USNM 18679), were compared with the probable type of *C. dolichotheca* (MCZ, no catalog number). From this comparison (Table 1, Figs. 1, 2, 5), it was evident that *C. flexuosus* differs from *C. dolichotheca* in having (1) cone-shaped instead of cylindrical hydrothecae, (2) fewer and less well developed septa in the hydrocladial internodes, (3) longer hydrocladial internodes, (4) median inferior nematothecae seated well below instead of adjacent to the hydrothecae. While acknowledging that species of *Cladocarpus* display considerable variability, none of the colonies of *C. flexuosus* examined here approached the form of *C. dolichotheca* in the characters listed above. Accordingly, Nutting's (1900) view that the two are closely related but distinct species is upheld here.

Nutting (1900) distinguished *C. flexuosus* from *C. tenuis* Clarke, 1879, based on hydrotheca shape. The abcauline wall of the hydrotheca is decidedly concave in *C. tenuis,* and convex to slightly concave in *C. flexuosus.* The phylactocarp of *C. tenuis,* as described by Vervoort (1966), is decidedly different from that of *C. flexuosus.*

Present records do little to extend the known range of *C. flexuosus.* All reported collections of this species are from the DeSoto Canyon area off the coast of Alabama.

Acknowledgments

Alaminos hydroids described in this note were collected by Dr. W. E. Pequegnat. I thank Dr. Linda Pequegnat for sending me the specimens and relevant collection data. Thanks are also due to Dr. F. M. Bayer of the United States National Museum of Natural History, Smithsonian Institution, and Dr. K. P. Sebens of the Museum of Comparative Zoology for allowing me to examine type-specimens from their collections.

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THE FIRST ZOEAL STAGE OF A HYDROTHERMAL VENT CRAB (DECAPODA: BRACHYURA: BYTHOGRAEIDAE)

Cindy Lee Van Dover, Austin B. Williams, and Jan Robert Factor

Abstract.—The first zoeal stage of a bythograeid crab is described. The zoea has numerous features that distinguish it from all known brachyuran larvae. These include the ornamentation of the carapace, abdomen, and telson, as well as details of the appendages. The zoeal morphology supports Williams' (1980) establishment of the superfamily Bythograeoidea.

The Bythograeidae comprise a new family of brachyuran crabs recently described from deep-sea hydrothermal vents in the eastern Pacific (Williams 1980). Adult, juvenile, and megalopal stages of *Bythograea thermydron* Williams have been collected from the "Galapagos Rift" study site (0°48.25′N, 86°13.48′W), where the adults are locally abundant. Adults of *B. thermydron* are also abundant at the "21°N" (20°49.6′N, 109°0.6′W) and "13°N" (12°48.85′N, 103°56.6′W) sites. Descriptions of two rare species in the family, one collected from both "13°N" and "21°N" and a second found only at "13°N," are in preparation (M. de St. Laurent, pers. comm.). The family Bythograeidae is the only family of brachyuran crabs known to occur in the vicinity of the vent sites.

A single brachyuran zoea attributable to this family was collected in a plankton tow 1 to 3 m above the area known as "Clam Acres" (20°49.6′N, 109°0.6′W; 2600 m) at the "21°N" vent site. The 35-minute multiple-circuit plankton tow was made by the DSRV *Alvin* (Dive 1218; 24 Apr 1982) using a Wishner (1980) opening-closing plankton net. Because of similarities between the morphology of the zoea and that of a prezoeal stage collected from a berried female bythograeid (as discussed below), this zoea is assigned to the family Bythograeidae. Identification to the specific level is not possible.

The zoea, mangled but nearly entire, was sorted from plankton and examined aboard the R/V *Melville* immediately after the sample arrived at the surface. Following preservation in buffered formalin, the zoea was stored in 70% ethyl alcohol. Illustrations were prepared with the aid of a Wild M-20 compound microscope with attached camera lucida. The zoeal and prezoeal specimens are deposited in the National Museum of Natural History, Washington, D.C. (USNM 210471, 210470, respectively).

Illustration of the general aspect of the zoea represents a composite of several drawings which rectify tortuous foldings of the body, appendages, and processes of the specimen. The presence of carapacial and telsonal spines or processes on the right or left sides was in some instances inferred by symmetry, as noted in the text.

Description of First Zoea

Carapace (Fig. 1).—Rostral-carapace length 0.48 mm; dorsal spine 0.36 mm. Rostral spine moderately elongate, extending beyond antennae; distal ⅔ bearing appressed spinules. Dorsal spine stout, elongate, bearing 4 spinulose processes. Multiple spinulose and simple lateral spines present on body; precise number undeterminable. Two posterolateral spines and single anterolateral spine observed on right side of carapace, assumed by argument of symmetry to occur on left side. Eyes fused to carapace, with at least 5 processes of varying lengths on or near circumcorneal margin. Posterolateral margin of carapace fringed with fine hairs, anterolateral margin minutely denticulate, as illustrated.

Abdomen (Fig. 1).—Five somites, 1st naked, 2nd to 5th with 3 to 7 lateral processes per somite (precise number and symmetry of processes undeterminable).

Telson (Fig. 1).—Broadly bifurcate, right branch with 7 lateral and dorsolateral spines of unequal lengths and 3 submedial, dentate setae extending nearly length of furca. Distal ⅓ of furca with minute mesial spines regularly spaced. Details of left furca assumed by symmetry.

Antennule (Fig. 2A).—Short, swollen, with 3 aesthetascs, 1 subterminal seta.

Antenna (Fig. 2B).—Protopodite slender, elongate, with 2 rows of minute teeth; exopodite shorter, with 2 terminal setae, 1 elongate seta at midlength.

Mandible.—Not dissected.

Maxillule (Fig. 2C).—Endopodite 3-segmented; setal formula progressing distally: 1, 1, 4; basal endite with 3 stout spinose setae and 1 slender seta terminally, 1 slender seta laterally, and numerous hairlike setae as illustrated; coxal endite with 4 terminal, 3 subterminal slender setae.

Maxilla (Fig. 2D).—Endopodite unsegmented, with 3 + 4 setae, pubescence as illustrated; basal endite with 3 and 2 setae on distal and proximal lobes, respectively; scaphognathite with 4 plumose setae distally, terminating in a hirsute apical process.

Maxilliped I (Fig. 2E).—Ventromesial margin of basipodite with 3 plumose, 3 simple setae; endopodite with indistinct segmentation, setal formula progressing distally: 2, 1, 2, 4; left exopodite with 1 natatory plus 4 simple terminal setae, right exopodite not observable.

Maxilliped II (Fig. 2F).—Ventromesial margin of basipodite with 3 setae; endopodite and exopodite nascent, former with 2 terminal, latter with 4 terminal plus 1 lateral short, simple setae.

Color.—Devoid of pigmentation with exception of dark brown eyes.

Comparison with Prezoeal Stage

Several post-emergent, prezoeal specimens (carapace length approximately 0.25 mm), free of the embryonic membrane, were found entangled in the egg mass of an unidentified bythograeid crab from "13°N." The appendages and carapacial ornamentation (including rostral, dorsal, and lateral spines) of the prezoeae were undeveloped. Certain features of the prezoeal morphology, in particular the size, the presence of long, filamentous processes on the abdominal segments, and the distinctive, slender furcae and elongate setae of the telson, correspond to those of the planktonic zoea collected at "Clam Acres."

Remarks

The bythograeid zoea has numerous features that distinguish it from all known brachyuran larvae. The appressed spinulate condition of the dorsal, rostral, and lateral carapacial spines is unique to this zoea, as are the circumocular processes

Fig. 1. Bythograeidae, first zoea. Dorsal view, with carapace flattened and extended anterolaterally. Scale bar represents 0.1 mm.

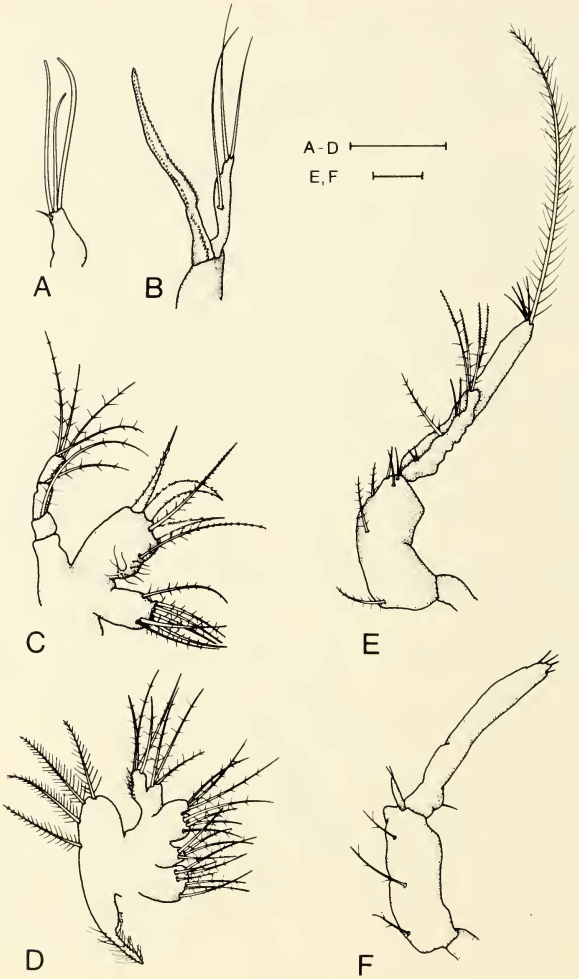

Fig. 2. Bythograeidae, first zoea. A, Antennule; B, Antenna; C. Maxillule; D, Maxilla; E, Maxilliped I; F, Maxilliped II. Scale bars represent 0.1 mm.

and paired posterolateral spines. Although multiple lateral spines occur in several species of Brachyura (e.g. ?*Dorynchus thomsoni* Norman (Williamson 1960, Rice 1980); *Cymonomus bathamae* Dell (Wear and Batham 1975)), details of the arrangement of these spines are not similar. Ornamentation of the carapacial margin in brachyuran zoeae is usually restricted to a sparse fringe of setae (e.g. *Thalamita danae* Stimpson (Fielder and Greenwood 1979)); marginal dentition is seen in a few brachyuran groups, including the Homolidae (e.g. *Homola barbata* (Fabr.), (Rice and Provenzano 1970)) and Raninidae (e.g., "raninid larva C," Rice 1970). The combination of a dense fringe of fine hairs posteriorly and fine dentition anteriorly, however, appears to be another character unique to the Bythograeidae. The asymmetric arrangement of the abdominal processes of the bythograeid zoea almost certainly reflects distortion of the specimen during collection. Although the precise arrangement of processes is undeterminable, it is clear that they are numerous and elongate. The abdomen of the zoea of ?*Dorynchus thomsoni* is superficially most similar to the bythograeid zoea in this respect. There is no counterpart to the telson of the bythograeid zoea among known brachyuran zoeae; the combination of elongate setae and numerous processes is unique. The obscure spination along the surface of the furcae is shared by the zoea of the raninid *Lyredius tridentatus* de Haan (Williamson 1965). Proportions of the antennal exopodite and spinous process correspond to those of the Cancridae, but details of the dentition and setation differ. The bythograeid maxillule is distinguished from that of other brachyuran zoeae by the 3-segmented endopodite. The 3 + 4 arrangement of setae on the endopodite of the maxilla is shared with certain members of the Cancridae (e.g. *Cancer productus* Randall; Trask 1970) and Xanthidae (e.g. *Cycloxanthops truncatus* (de Haan); Hong 1977). The maxillary scaphognathite is typical of the type found in the first zoeal stage of most Brachyura (type 7 of Van Dover, Factor, and Gore 1982). The single natatory seta of the exopodite and unsegmented condition of the endopodite of maxilliped I are uncertain features of the bythograeid zoea. It is possible that setae were lost during collection and that the segmentation of the endopodite is obscured by distortion of the specimen; alternatively, the zoea may be aberrant, displaying a combination of prezoeal and first zoeal characters with respect to the maxillipeds. The nascent condition of the endopodite of maxilliped II (assuming the specimen is a "mature" first zoea) is unique to the bythograeid zoea.

It is clear from the above discussion that the single known zoea of the Bythograeidae is not closely allied to any other brachyuran zoea. This larval evidence supports Williams' (1980) establishment of the superfamily Bythograeoidea based on features of the adult morphology of *Bythograea thermydron.*

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Addendum.—An additional larval specimen, sorted from washings of megafaunal material collected on *Alvin* Dive #1218 at "21°N," was received from Dr. Howard Sanders and Ms. Isabelle Williams, Woods Hole Oceanographic Institution. The larva, intermediate between a prezoea and first zoea, has morphological features which correspond in general to those of the bythograeid zoea described herein. Setal formula of basipodite, maxilliped I is 2,1,1,2; endopodite: 3,2,2,1,2,4 + 1; exopodite with 4 natatory setae. Maxilliped II lacks natatory setae, with 12–13 simple, short setae instead; endopodite with 1 basal, 1 subterminal seta, terminus damaged; basipodite naked. Variation between the two larval specimens probably reflects variation in abnormality rather than a difference in identity. Both larvae were collected on the same dive, from the same area, suggesting that they were from the same female and were collected only because they were abnormal and unable to swim away from the vent site.

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97(2), 1984, p. 419

SAIDOVINA NEW NAME FOR *LOXOSTOMINA* SAIDOVA, 1975 (NON SELLIER DE CIVRIEUX, 1968) AND THE STATUS OF *LOXOSTOMELLA* SAIDOVA, 1975 (FORAMINIFERIDA)

Drew Haman

Saidova (1975) established the genus *Loxostomina* (type-species *Bolivina karreriana* Brady, 1884) for specimens retrieved from Recent tropical Pacific Ocean sediments.

The same generic name, with type-species *Bolivina mayori* Cushman, 1923, had previously been used by Sellier de Civrieux (1968) to accommodate Recent Floridean specimens.

A new name is required for *Loxostomina* Saidova, 1975, a junior homonym of *Loxostomina* Sellier de Civrieux, 1968, ICZN (Art. 53), and *Saidovina* is herein proposed. The new name is constructed in honor of K. M. Saidova in recognition of her contributions to the knowledge of Quaternary Foraminifera.

Bolivina mayori Cushman, 1922, selected as type-species for the genus *Loxostomina* by Sellier de Civrieux (1968), was also selected by Saidova (1975) as the type-species for the genus *Loxostomella* (although erroneously ascribing authorship date to Cushman, 1924). *Loxostomella* is therefore a junior objective synonym of *Loxostomina* Sellier de Civrieux, 1968 (ICZN Art. 61b).

Acknowledgments

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A NEW "*METULA*" SPECIES FROM THE INDO-WEST PACIFIC (PROSOBRANCHIA: BUCCINIDAE)

Richard S. Houbrick

Abstract.—A new Indo-Pacific species, belonging to the "*Metula*" group, family Buccinidae, is described and allocated to the genus *Acamptochetus* Cossmann, herein considered synonymous with *Antemetula* Rehder. The new species, *Acamptochetus inflatus,* is larger and has more widely inflated whorls than any other living Indo-Pacific species. It closely resembles *Bartschia* Rehder, a *Metula*-like genus from the Western Atlantic.

Numerous specimens of a large "*Metula*" species, dredged by the R/V *Albatross* from deep water from a number of stations in the Philippines are in the mollusk collection of the National Museum of Natural History, Smithsonian Institution. Although none of the specimens was taken alive, the empty shells afford a range of shell variation and sufficient comparative material to establish that these specimens represent an undescribed species of "*Metula.*" A survey of the literature shows that nothing similar to these specimens has been previously described. The new taxon is described herein, and referred to the genus *Acamptochetus.* A review of the taxonomic problems of the "*Metula*" group follows.

Family Buccinidae
Subfamily Pisaniinae Tryon, 1881
Acamptochetus Cossmann, 1901

Acamptochetus Cossmann, 1901:123. Type-species by original designation: *Murex mitraeformis* Brocchi, 1814; mid-Pliocene of Europe.

Antemetula Rehder, 1943:199. Type-species by original designation: *Buccinum metula* Hinds, 1844; Recent, west coast of Panama.

Metula H. and A. Adams, 1853:84. Type-species by subsequent designation (Kobelt 1876): *Metula clathrata* Adams & Reeve = *Buccinum clathratum* Adams & Reeve, 1850 (not Kiener, 1834, nor Anton, 1839); Recent, Cape of Good Hope (erroneous citation—see Tomlin 1927 = Gorgona Is, off Colombia, west coast South America).

Remarks.—The problems surrounding the identity of the type-species of *Metula, Buccinum clathratum* Adams and Reeve, 1850, have been fully discussed by Rehder (1943), Regteren Altena (1949), Cernohorsky (1971), Olsson and Bayer (1972), and Kilburn (1975). I follow the solution of Cernohorsky (1971) who suggested using the generic name *Acamptochetus* Cossman, 1901, for *Metula* and *Antemetula* Rehder, 1943. Although *Acamptochetus* was proposed for mid-Tertiary European fossil species, I concur that it is congeneric with *Antemetula* and agree with Cernohorsky (1971) who was unable to find a single diagnostic character that would allow separation of *Antemetula* from *Acamptochetus.* Cernohorsky (1971) has provided an adequate diagnosis of the genus *Acamptochetus.*

The "*Metula*" group in the Indo-Pacific was reviewed by Regteren Altena (1949) who recognized nine Recent and fossil species. Since that review, another species has been described (Kilburn 1975:594). Olsson and Bayer (1972) reviewed Recent and fossil species known from the American faunas and recognized four subgenera and 16 species. As to the number of taxa in the group on a worldwide basis, the extent of available material is often insufficient to establish the range of variability of most species (Regteren Altena 1949:393); consequently, their number and validity is uncertain.

Although the anatomy of *Acamptochetus* (=*Metula*) is unknown, Ponder (1968) described the anatomy of *Ratifusus* Iredale, 1919, and *Iredalula* Finlay, 1927, which, according to Cernohorsky (1971:152), are closely related to the "*Metula*" group.

Very little is known of the biology of *Acamptochetus* species, but the anatomical information provided by Ponder (1968) on the closely related genera discussed above suggests that they are predators or scavengers. The radula of only one species, "*Metula*" *mitrella* (Adams & Reeve, 1848), is known and was figured by Troschel (1867). It is rachiglossate, has a rachidian tooth with five cusps, and laterals with three, of which the medial is the largest. According to Cernohorsky (1971:152), the radula is very similar to those of tropical Pisaniinae.

As Olsson & Bayer (1972:900–901) have pointed out, the fossil record of the "*Metula*" group is impressive, and the main occurrence, on a worldwide basis, is in the Upper Tertiary.

Acamptochetus inflatus, new species
Fig. 1

Description.—Shell (Table 1): Shell solid, fusiform-elongate, reaching 45.5 mm in length and 17 mm in width, comprising 9 moderately inflated whorls. Body whorl high, over half total shell length. Sculpture finely cancellate, produced by nearly equal, narrow axial and spiral cords, intersections of which beaded and intervals deeply pitted. Body whorl with 25 spiral cords; teleoconch with 9 spiral cords per whorl. First 4 spirals separated by wide interspaces but remaining spirals closer together. All spiral cords of equal size and no varices present save for thickened varix at edge of outer lip. Former resting marks evident. Suture distinct and impressed. Slight sutural ramp on posterior of each whorl. Protoconch of 2½ smooth whorls with sinuous lip. First 2 whorls of teleoconch nearly smooth but with weak axial ribs. Spiral elements appear on fourth whorl becoming progressively more distinct. Aperture narrow, acutely angled at each end, little less than one-half shell length. Siphonal canal narrow, slightly reflexed and twisted at end. Slight columellar keel present at siphonal constriction. Columella concave, angulate at center, with moderately enamelled callus. Outer lip sinuous, thickened at edge. Interior of outer lip with about 20 denticles. Ground color light chestnut with 2 lighter banded areas on body whorl. Darkest chestnut color at base of shell and at base of each whorl. All beads tan; interspaces lighter or white. Peristome white. Periostracum tan, moderately thick on upper whorls. Radula, operculum, and animal unknown.

Type-locality.—Off Lubigon, Bohol, Philippines, USFS *Albatross* Sta 5419 (9°58′30″N, 123°46′E), 320 m.

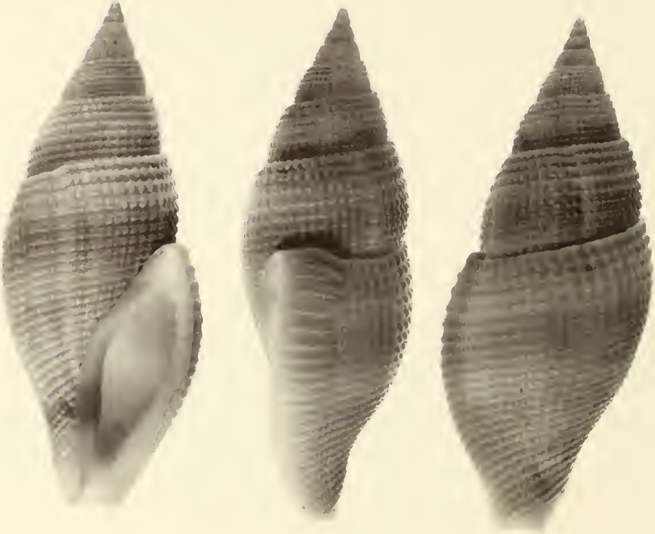

Fig. 1. Apertural, lateral, and dorsal views of holotype of *Acamptochetus inflatus,* USNM 229183, 38.8 × 15 mm.

Type-material.—Holotype (Fig. 1): USNM 229183, length 38.8 mm, width 15 mm; Paratype: USNM 820185, length 45.5 mm, width 16.9 mm. Locality as above.

Etymology.—From the Latin adjective *inflatus,* inflated, in reference to the wide, inflated lower whorls.

Material examined.—Philippines: United States National Museum 240424, USFS sta 5403, off Abgao, Leyte (11°10′N, 124°17′15″E), 333 m; 238660, 238671, USFS sta 5502, off Opol, Mindanao (8°37′37″N, 124°35′E), 391 m; 238823, USFS sta 5519, NE off Tagalo Pt., Mindanao (8°47′N, 123°31′15″E), 333 m; 238817, USFS sta 5517, off Tagalo Pt., Mindanao (8°45′30″N, 123°33′45″E), 309 m; 238812, USFS sta 5516, off Tagalo Pt., Mindanao (8°46′N, 123°32′30″E), 320 m; 238300, USFS sta 5409, W of Pacyan Is (10°38′N, 124°13′08″E), 346 m; 238103, USFS sta 5374, Tayabas Bay, Luzon (13°46′45″N, 121°35′08″E), 347 m; 235376, USFS sta 5118, Balayan Bay, Luzon (13°48′45″N, 120°41′51″E), 291 m; 238322, USFS sta 5411, off Lauis Pt., Cebu (10°10′30″N, 123°51′15″E), 265 m; 238387, USFS sta 5418, off Lauis Pt., Cebu (10°08′50″N, 123°52′30″E), 291 m; 230989, USFS sta 5412, SE of Tabisayo, Cebu (10°09′15″N, 123°52′E), 89 m; 237058, USFS sta 5222, Taybas Bay, off San Andreas Is (10°31′N, 122°18′45″E), 357 m.—Andaman Sea: Academy of Natural Sciences, Philadelphia 291929, *Anton Brunn* sta 22B, (10°39′N, 97°06′E), 30 m W Twin Is, S. Burma.

Table 1.—Statistical summary of shell parameters of *Acamptochetus inflatus.* (Measurements in mm).

Statistic (n = 20)	$\bar{x}$	SD	Range
Shell length	40.93	2.92	35.3–45.5
Shell width	14.58	3.39	13.2–17
Aperture length	21.55	1.41	18.1–23.4
Aperture width	8.26	0.68	6.6–9.2
Number of whorls	9	0	8–9

Remarks.—This species is easily separated from its Indo-Pacific congeners by the widely inflated body whorl and thick, heavy shell. It is one of the largest of *Acamptochetus* species. All other species of *Acamptochetus* are more narrowly fusiform, but the fine, lattice-like sculpture is typical of the genus. The shell shape and sculpture resemble those of two species assigned to the western Atlantic subgenus *Agassitula* Olsson and Bayer, 1972: *Acamptochetus* (*A.*) *agassizi* (Clench and Aguayo, 1941), and *Acamptochetus* (*A.*) *guppyi,* (Olsson & Bayer, 1972). The suture of *Acamptochetus inflatus,* is not as deeply impressed as in the latter two species, and, in contrast to *A. agassitula,* there is banding in the color pattern.

Western Atlantic species of *Bartschia* Rehder, 1943, have inflated, thick shells very similar in shape to *Acamptochetus inflatus,* but are heavier, wider, and have twisted siphonal canals that are less attenuated than in *Acamptochetus inflatus.* Cernohorsky (1971:151) suggested that *Bartschia* should be allocated to the Pisaniinae, near the "*Metula*" group.

Collection data indicate that *Acamptochetus inflatus* occurs on coarse, sandy substrates at an average depth of 284 m and a depth range of 89 to 391 m.

Acknowledgments

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CAECIDOTEA ROTUNDA, A NEW TROGLOBITIC ASELLID FROM INDIANA AND OHIO (CRUSTACEA: ISOPODA: ASELLIDAE)

Thomas E. Bowman and Julian J. Lewis[1]

Abstract.—*Caecidotea rotunda* is described from caves in southern Indiana and Ohio, along the northeastern fringe of the Interior Low Plateaus. It appears to be a relict descended from a formerly widespread ancestor that gave rise also to the widespread species *C. antricola* and *C. beattyi.*

Unlike the southern and western parts of the Interior Low Plateaus, where caves are inhabited by the common species *Caecidotea bicrenata* or *C. stygia* (Lewis and Bowman 1981; Lewis 1982a), along the northeastern fringes of the region are found an assemblage of rare, endemic species. Besides *Caecidotea stygia,* whose range also extends into this area (Steeves 1963; Bowman and Beckett 1978), four other species are known: *C. jordani* (Eberly, 1966), *C. barri* (Steeves, 1965), *C. teresae* Lewis (1982b), and *C. filicispeluncae* Bowman and Hobbs (1983). The species described herein is a new addition to this zoogeographically interesting group of subterranean asellids.

Caecidotea rotunda, new species

Figs. 1–5

Material examined.—OHIO: Pike Co., Frost Cave, coll. H. H. Hobbs, III, 11 Sep 1982, 6.0 mm male holotype (USNM 210515); 3 male, 11 female paratypes (USNM 210516).—INDIANA: Decatur Co., Faulty Cave, coll. J. Lewis, T. Lewis, 16 Jun 1979, 4 male, 2 female paratypes (USNM 210678); Horsethief Cave, coll. J. Lewis, T. Lewis, 16 Jun 1979, 7 male, 8 female paratypes (USNM 210679). Jennings Co., Cave Spring Cave, coll. J. Lewis, T. Everitt (Lewis), 31 Dec 1977, 3 male, 4 female paratypes (USNM 210680); Meek Cave, coll. J. Lewis, T. Everitt (Lewis), 31 Dec 1977, 1 male, 1 female paratype (USNM 210681).

All specimens are deposited in the National Museum of Natural History, Smithsonian Institution.

Description.—Eyeless, unpigmented, longest male (holotype) 6.0 mm, female 7.5 mm; body slender, about 5.8 × as long as wide. Head about 1.5 × as wide as long, anterior margin concave, postmandibular lobes moderately produced. Pleotelson about 1.5 × as long as wide, sides subparallel, caudomedial lobe moderately produced.

Antenna 1 reaching proximal end of last segment of antenna 2 peduncle, flagellum with 11 segments in holotype, 8 in 7.5 mm female, esthete formula 4–0. Antenna 2 with 53 segments in holotype and 7.5 female. Mandibles with 4-cuspate incisors and lacinia mobilis, palp with rows of plumose setae in distal segments.

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[1] Sequence of authors determined by toss of a coin.

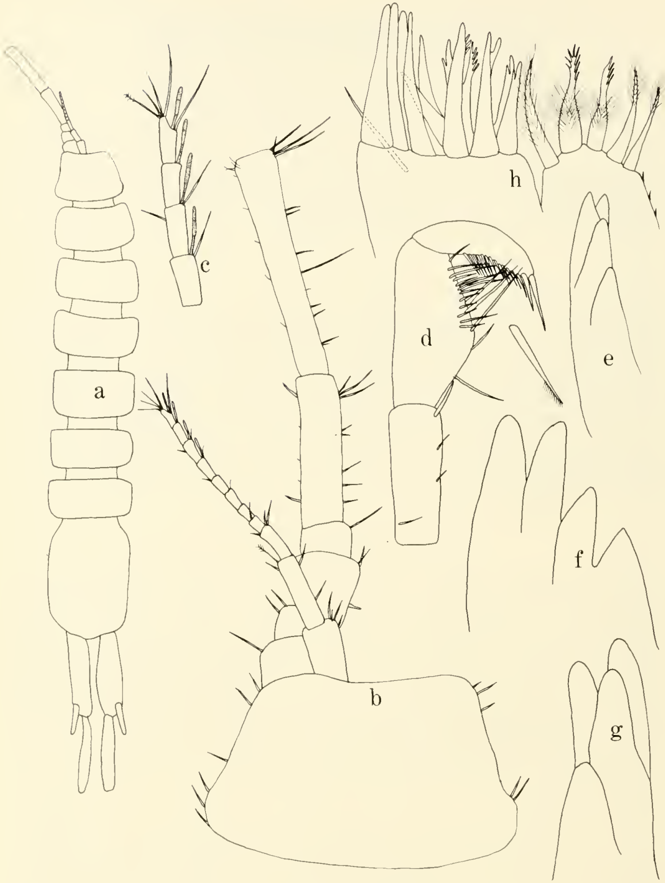

Fig. 1. *Caecidotea rotunda,* Frost Cave, Ohio: a, Habitus, dorsal, male paratype; b–h, Female paratype; b, Head, dorsal; c, Distal segments of antenna 1; d, Mandibular palp; e, Lacinia of left mandible; f, Incisor of left mandible; g, Incisor of right mandible; h, Maxilla 1.

Maxilla 1, outer lobe with 13 robust spines, inner lobe with 5 plumose setae. Maxilliped with 6 retinacula.

Male pereopod 1, propus about 1.3× as long as wide; palm with robust proximal spine, high subtriangular medial process separated by U-shaped cleft from lower,

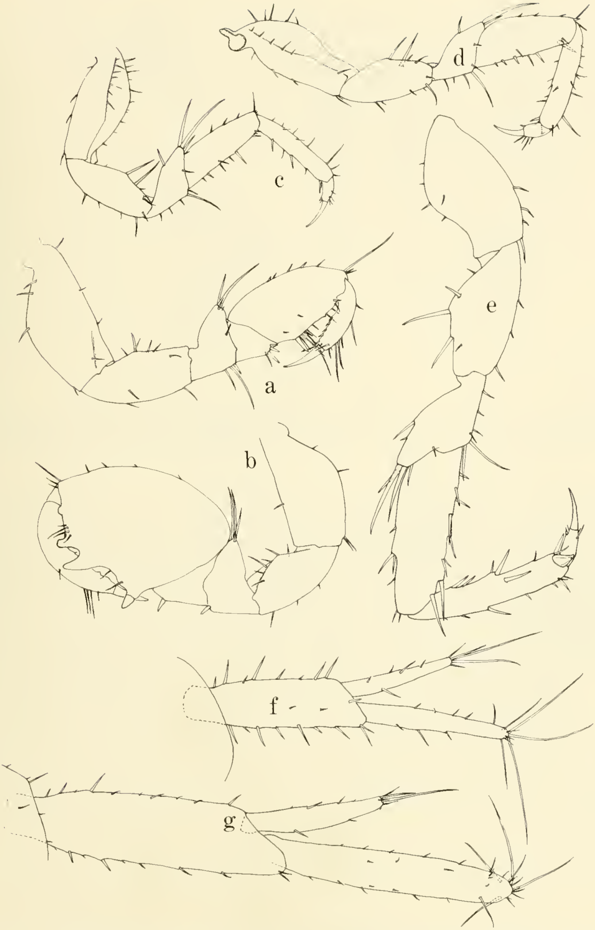

Fig. 2. *Caecidotea rotunda*, Frost Cave, Ohio: a, Pereopod 1, female; b, Pereopod 1, male; c, Pereopod 4, female; d, Pereopod 4, male; e, Pereopod 7, male; f, Uropod, female; g, Uropod, male.

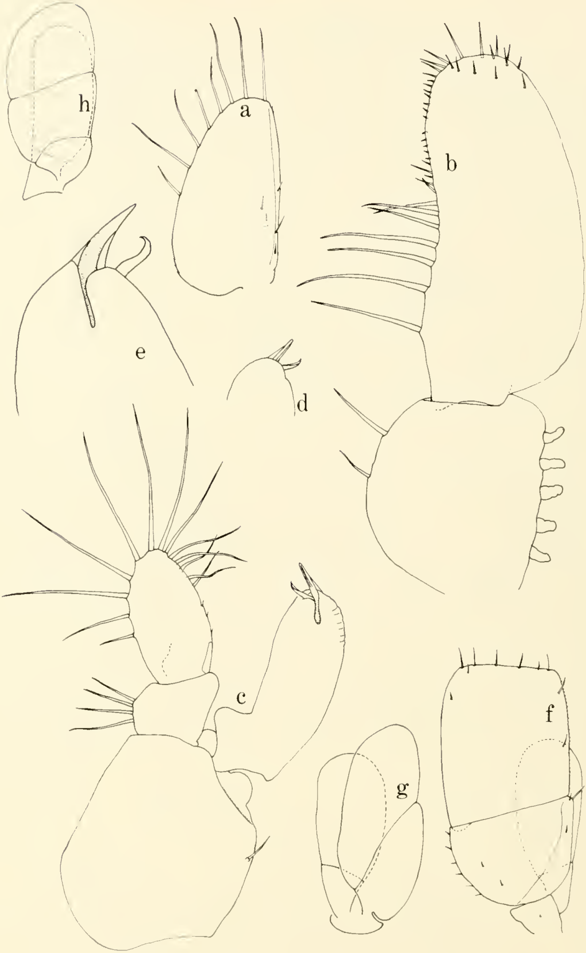

Fig. 3. *Caecidotea rotunda,* Frost Cave, Ohio: a, Pleopod 2, female; b, Pleopod 1, male; c, Pleopod 2, male, anterior; d, Pleopod 2, male, endopod tip, posterior; e, Same, anterior, from different specimen; f, Pleopod 3, male; g, Pleopod 4, male; h, Pleopod 5, male.

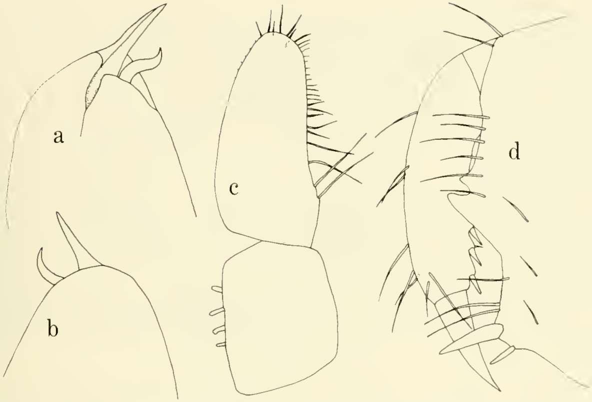

Fig. 4. *Cacidotea rotunda,* Faulty Cave, Indiana: a, Pleopod 2, male, endopod tip, anterior; b, Same, posterior; c, Pleopod 1, male; d, Pereopod 1, male.

blunt distal process; dactyl flexor margin without processes. Female pereopod 1 about 2× as long as wide, propus with large proximal spine, processes absent. Pereopod 4, carpus and propus slightly more robust in male.

Male pleopod 1 longer than pleopod 2; protopod about 0.5× length of exopod, with 5 retinacula; exopod about 2× as long as wide, apex broadly rounded, with numerous short setae, lateral margin concave, with about 7 long non-plumose setae in proximal ⅗. Male pleopod 2 exopod, proximal segment with 4 plumose lateral setae, distal segment with 9 plumose setae along lateral and distal margins, 4 non-plumose setae along mesial margin. Endopod with rounded basal apophysis, tip with 2 major processes extending subparallel to one another, nearly perpendicular to axis of endopod: (1) lateral process subterminal, tapering to recurved point, and (2) cannula elongate beak-shaped, endopodial groove separating 2 poorly defined processes. Pleopod 3 exopod distal margin with 6 plumose setae. Pleopod 4 exopod with single sigmoid suture. Pleopod 5 with 2 transverse sutures. Uropods about 1.5× as long as pleotelson in ♂, 1.1× in ♀; peduncle longer than rami, both rami slender in ♀, endopod broader in ♂.

Etymology.—From the Latin "rotundus," meaning "rounded," referring to the rounded distal margin of the male first pleopod.

Range.—Known from five caves adjacent to the northeastern fringe of the Interior Low Plateaus, from Pike Co., Ohio to Jennings Co., Indiana. Locations for the Indiana localities are given by Powell (1959).

Relationships.—The male first pleopod exopod, with elongate non-plumose setae along the lateral margin, and the second pleopod endopod tip processes extending perpendicular to the axis of the endopod indicate that the general

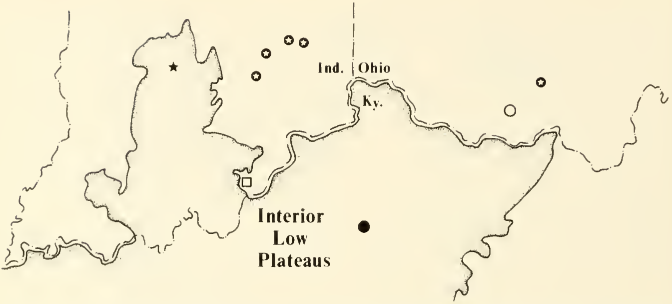

Fig. 5. Known distribution of *Caecidotea* spp. in the northwestern part of the Interior Low Plateaus. Open square, *C. teresae*; filled circle, *C. barri*; open circle, *C. filicispeluncae*; white star, *C. rotunda*, black star, *C. jordani*.

morphological affinities of *Caecidotea rotunda* lie with the Stygia Group. *Caecidotea rotunda* can be readily separated from other species found in the northeastern part of the Interior Low Plateaus (Fig. 5). *Caecidotea stygia* and *C. barri* each possess a distally truncate male first pleopod with a distolateral lobe; in *C. rotunda* the apex of the first pleopod is rounded and a distolateral lobe is absent. The male second pleopod endopod of *Caecidotea filicispeluncae* lacks the lateral process that is present in *C. rotunda*. The second pleopod endopod tip of *C. jordani* is similar to that of *C. rotunda*, but the lateral process of *C. jordani* is apically blunt; the lateral process of *C. rotunda* is curved and tapers to a point. The final species known from this part of the Interior Low Plateaus, *C. teresae*, is a member of the Hobbsi Group.

Thus, *Caecidotea rotunda* lies geographically among a group of species with which it has no more than a general affinity. However, the endopodal tip of *C. rotunda* closely resembles that of *C. beattyi* (a phreatobite inhabiting the glacial plains of Illinois) and *C. antricola* (an Ozark troglobite). In each of these three species the endopod tip consists of a beak-shaped cannula and a sigmoid lateral process, tapering distally to a point. The male first pleopods of *C. rotunda* and *C. antricola* closely resemble one another, with elongate exopods having rounded apices, but the first pleopod exopod of *C. beattyi* has a distinct distolateral lobe. The fourth pleopods of all three species have a single sigmoid suture. *Caecidotea rotunda* is clearly separated from *C. antricola* and *C. beattyi* by the structure of the male gnathopods. In both *C. antricola* and *C. beattyi*, the palm of the propodus has a triangular proximal and distal bicuspid process, while the medial process is absent. In *C. rotunda*, the proximal process is represented by a spine, which may be replaced by a process in larger individuals. A distinct medial process is present in *C. rotunda*, and the distal process is blunt, not bicuspid.

The similar morphology of *Caecidotea rotunda*, *C. antricola*, and *C. beattyi* suggests that these three species evolved from a common ancestor. In the Ozarks the result of this evolution is the common, widespread *C. antricola*. Similarly, *C.*

beattyi occurs over a large area of the Illinois Basin (Lewis and Bowman 1981). The presence of *C. rotunda* in Indiana and Ohio suggests that the ancestor of these species was once widespread over both the Ozarks and Interior Low Plateaus, and gave rise to successful species in the Ozarks and the adjacent Central Lowland, but for the most part failed to succeed in the Interior Low Plateaus, where *C. stygia* and *C. bicrenata* are now widespread (Lewis 1982a). *Caecidotea rotunda* is the only remnant along the northeastern fringe of the Interior Low Plateaus of the once widespread ancestor.

This idea is supported by the distribution of *Caecidotea teresae,* which occurs in southern Indiana at the base of the escarpment that separates the Interior Low Plateaus from the Central Lowland, and is the only member of the Hobbsi Group in the region. *Caecidotea teresae* is morphologically similar to *C. salemensis,* a common troglobite in the Ozark Plateau (Lewis 1981). The ancestor of these two species of the Hobbsi Group may have once had a distribution pattern similar to that of the three species of the Stygia Group discussed above.

Acknowledgments

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NEOTROPICAL MONOGENEA. 6. FIVE NEW SPECIES OF *DIPLECTANUM* (DIPLECTANIDAE) FROM FRESHWATER TELEOSTS, *PLAGIOSCION* SPP. (SCIAENIDAE), IN BRAZIL

Delane C. Kritsky and Vernon E. Thatcher

Abstract.—Five new diplectanid monogenes are described from the gills of *Plagioscion squamosissimus* (Heckel) and *Plagioscion* sp. (Perciformes, Sciaenidae) from Janauaća Lake, Manaus, Amazonas, Brazil, as follows: *Diplectanum decorum* n. sp., *D. gymnopeus* n. sp., and *D. piscinarius* n. sp. from *P. squamosissimus*; *D. hilum* n. sp. from *Plagioscion* sp.; and *D. pescadae* n. sp. from *P. squamosissimus* and *Plagioscion* sp.

Members of *Diplectanum* Diesing, 1858 (Diplectanidae), are predominantly gill parasites of marine perciform fishes of the families Serranidae, Sciaenidae, Polynemidae, Toxodidae, Percichthyidae, Sparidae, Sillanginidae, Centropomidae, and Theraponidae. While some *Diplectanum* species have been recorded from freshwater hosts, all freshwater forms are reported from perciform fishes with relatively recent marine origins.

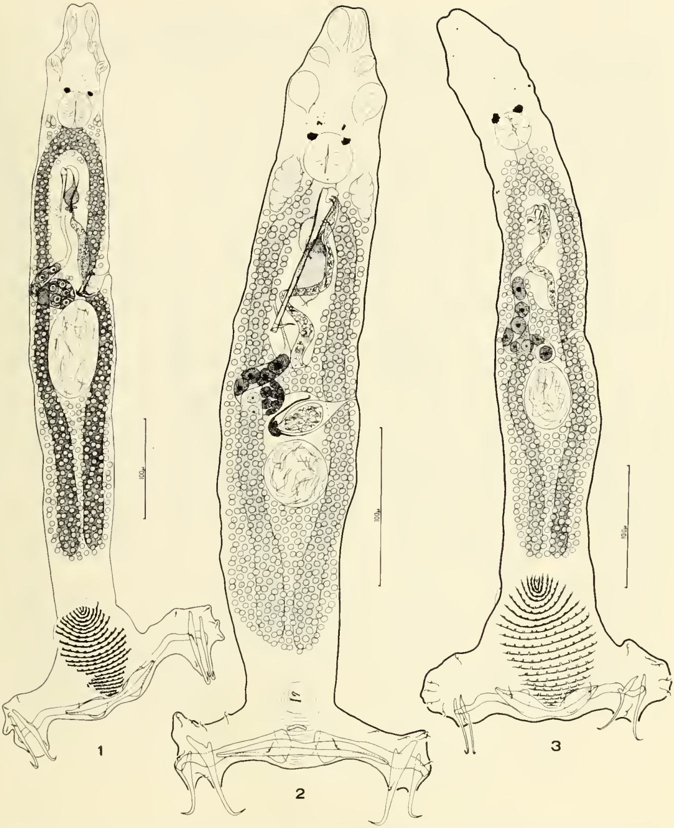
The host genus *Plagioscion* Gill consists of freshwater sciaenids inhabiting the larger rivers of South America; these fishes occasionally descend to marine waters along the coast (Jordan and Evermann 1896–1900). *Plagioscion squamosissimus* (Heckel) is the common sciaenid distributed throughout the Amazon Basin. *Plagioscion* sp. was described as a new species in an unpublished thesis by Soares (1978) at the Instituto Nacional de Pesquisas da Amazônia. The present study includes the description of five new species of *Diplectanum* from the gills of these hosts, three of which were found only on *P. squamosissimus,* and one of which occurred only on *Plagioscion* sp. One new species was collected from both hosts.

Hosts were collected from Janauaća Lake, near Manaus, Amazonas, Brazil on several occasions during 1978–80. The gills of each fish were removed and placed in finger bowls containing a 1:4000 formalin solution to kill and relax the helminth specimens. Monogenes were collected and prepared for study as described previously by Thatcher and Kritsky (1983). Measurements were made according to the procedures outlined by Mizelle and Klucka (1953); averages are followed by ranges in parentheses; all are in micrometers. The dimension of the ovary is the greatest diameter. Illustrations were prepared with the aid of a camera lucida or microprojector. Type-specimens were deposited in the collections of the Instituto Nacional de Pesquisas da Amazônia (INPA), the U.S. National Museum Helminthological Collection (USNM), and the University of Nebraska State Museum (UNSM) as indicated below.

Diplectanum decorum, new species
Figs. 1, 18–24

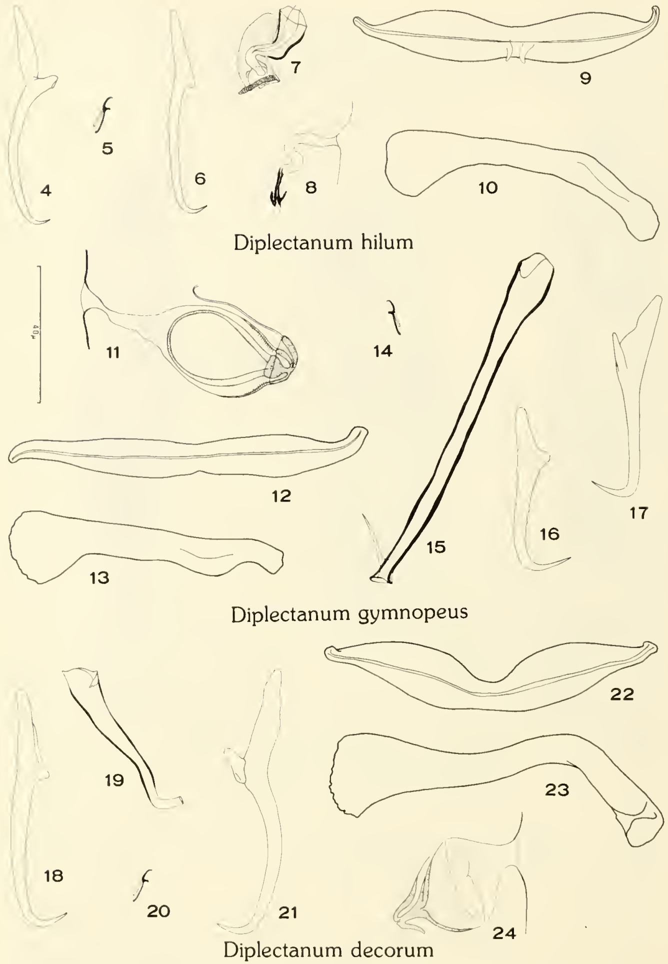
Host.—Gills of pescada, *Plagioscion squamosissimus* (Heckel) Sciaenidae.

Type-specimens.—INPA (holotype, PA-245-1; paratypes, PA-245-2 to PA-245-3), UNSM (paratypes, 21635), USNM Helm. coll. (paratypes, 77917).



Figs. 1–3. Composite drawings of *Diplectanum* species (ventral). 1, *Diplectanum decorum*; 2, *Diplectanum gymnopeus*; 3, *Diplectanum hilum.*

Description (based on 8 specimens).—Diplectanidae, Diplectaninae. Body 776 (701–860) long, slender, fusiform; greatest width 94 (86–105) near level of testis. Tegument smooth. Two terminal, 2 bilateral cephalic lobes moderately developed; head organs conspicuous, lying in cephalic lobes and adjacent cephalic area; small group of unicellular cephalic glands lying posterolateral to pharynx. Usually 2 eyes; anterior pair, when present, poorly developed or represented by scattered granules, members closer together than those of posterior pair; eyespot granules subovate, variable in size; accessory granules present in cephalic area. Mouth



Figs. 4–24. Sclerotized parts of *Diplectanum* species. Figs. 4–10, *Diplectanum hilum*: 4, Ventral anchor; 5, Hook; 6, Dorsal anchor; 7, Copulatory complex; 8, Vagina; 9, Ventral bar; 10, Dorsal bar. Figs. 11–17, *Diplectanum gymnopeus*: 11, Vagina (dorsal); 12, Ventral bar; 13, Dorsal bar; 14, Hook; 15, Copulatory complex; 16, Dorsal anchor; 17, Ventral anchor. Figs. 18–24, *Diplectanum decorum*: 18, Dorsal anchor; 19, Copulatory complex; 20, Hook; 21, Ventral anchor; 22, Ventral bar; 23, Dorsal bar; 24, Vagina.

subterminal, ventral; pharynx subspherical, 37 (34–39) in diameter; esophagus short to absent; crura blind posteriorly.

Peduncle broad, elongate; haptor 248 (221–290) wide, 95 (89–101) long, with two conspicuous bilateral lobes. Squamodiscs ovate, overlying distal peduncle and medial portion of haptor; ventral squamodisc 91 long, 73–74 wide, with 23–24 curved rows of rods; dorsal squamodisc 103–104 long, 72–73 wide, with 24 curved rows of rods. Squamodisc rods sclerotized, easily lost in preserved specimens; marginal rods with pointed lateral and enlarged medial terminations; medial rods with anterior projections on each enlarged termination; rods of posteriormost rows scale-like. Anchors dissimilar; ventral anchor 78 (75–82) long, with large elongate deep root, knob-like superficial root, curved shaft, short point; dorsal anchor 69 (66–70) long, with tapered deep root, incipient superficial root, straight shaft, short point. Ventral bar 96 (88–109) long, with tapered ends, constricted medial portion, ventral groove; dorsal bar 105 (95–127) long, with spathulate medial end. Six pairs of hooks lying on lateral haptoral lobes, one pair near tips of ventral bar; hooks similar, each 11–12 long, with curved shank, perpendicular thumb, delicate shaft and point. FH loop ⅞ shank length.

Cirrus 53 (50–55) long, an elongate, tapered tube with sigmoid or straight distal end; accessory piece absent. Gonads slightly overlapping. Testis postovarian, subovate, 53 (45–60) wide, 87 (83–90) long; vas deferens conspicuous anteriorly, lying sinistral to midline; seminal vesicle a conspicuous dilation of vas deferens; prostatic reservoir pyriform. Ovary pyriform, looping right intestinal crus; greatest diameter 41. Oviduct, ootype not observed; uterus delicate, extending along midline; genital pore midventral; vagina sinistral, comprising a distal unsclerotized pouch with proximal sclerotized cup-like sheath; vitellaria coextensive with intestine.

Remarks.—*Diplectanum decorum* resembles several species of the genus parasitizing sciaenid fishes (i.e., *D. sciaenae* van Beneden and Hesse, 1863; *D. bocqueti* Oliver, 1980; *D. dollfusi* Oliver, 1980; *D. chabaudi* Oliver, 1980; *D. grassei* Oliver, 1974; *D. gymnopeus* and others) by possessing a simple tubular cirrus which is not associated with an accessory piece. All of these species can be distinguished from *D. decorus* by the comparative morphology of the vagina.

Etymology.—The specific name is from Latin *decoris* = elegant.

Diplectanum gymnopeus, new species
Figs. 2, 11–17

Host.—Gills of pescada, *Plagioscion squamosissimus* (Heckel), Sciaenidae.

Type specimens.—INPA (holotype, PA-243-1); UNSM (paratype, 21640); USNM Helm. Coll. (paratypes, 77921).

Description (based on 4 specimens).—Diplectanidae, Diplectaninae. Body robust, fusiform, 619 (553–666) long; greatest width 90 (81–98) near level of gonads. Tegument smooth. Cephalic lobes incipient, 2 terminal, 2 bilateral; head organs large, 2 pairs lying in cephalic lobes and adjacent cephalic area, one pair in cephalic region between lobes; cephalic glands comprising 2 large distinct bilateral groups of unicellular glands posterolateral to pharynx. Eyes usually 4; members of anterior pair poorly developed or absent, closer together than those of posterior pair; eyespot granules large, subovate; few accessory granules in cephalic area. Mouth subterminal, ventral; pharynx spherical, 33 (28–37) in diameter; esophagus short to absent; crura blind posteriorly.

Peduncle broad; haptor 199 (179–223) wide, 82 (79–84) long, with 2 bilateral lobes. Squamodiscs reduced; all available specimens having lost most sclerotized rods. Medial rods with enlarged terminations; small bar-like structure probably associated with haptoral musculature present beneath ventral squamodisc. Anchors dissimilar; ventral anchor 61 (59–63) long, with lateral superficial root, large deep root, straight shaft, short point; dorsal anchor 51 (44–55) long, with elongate deep root, incipient superficial root, straight shaft, short point. Ventral bar 108 (106–110) long, slender, elongate, with tapered ends, inconspicuous medial constriction, ventral groove; dorsal bar 75 (71–80) long, robust, with spathulate medial end, subterminal lateral inflation. Six pairs of hooks on lateral haptoral lobes, one pair near medial terminations of dorsal bars; hooks similar, each 11–12 long, with curved shank, erect thumb, delicate point and shaft. FH loop ¾ shank length.

Cirrus 104 (94–108) long, an elongate sclerotized tube with terminal reflexed spike; accessory piece absent. Gonads separated by large vagina. Testis postovarian, spherical to subovate, 43 (38–49) wide, 44 (39–49) long; vas deferens conspicuous anteriorly, with loop near base of prostatic reservoirs; seminal vesicle an indistinct dilation of terminal vas deferens. Two prostatic reservoirs; anterior reservoir lunate, simple; posterior reservoir elongate ovate, usually with two areas of density. Ovary pyriform, lying to right of midline, looping right intestinal crus; greatest diameter 28 (27–30). Oviduct, ootype not observed; uterus delicate, extending anteriorly to right of midline; genital pore midventral; vagina sinistral, comprising a large terminal pouch containing sclerotized seminal receptacle filled with sperm; vitellaria throughout trunk except absent in areas of reproductive structures.

Remarks.—This species resembles *D. aequans* (Wagener, 1857) Diesing, 1858, by the comparative morphology of the haptoral armament and copulatory complex. In *D. gymnopeus,* the vagina encloses an obvious seminal receptacle, whereas the seminal receptacle in *D. aequans* occurs as a simple dilation of the duct of the vagina. The species also can be separated by subtle differences in the morphology of the anchors and bars (compare Figs. 2, 11–17 *nobis* and Figs. 2–5 in Oliver, 1968).

Etymology.—The species name is from Greek *gymno/o* = naked + *peos* = penis, and refers to the absence of an accessory piece in the copulatory complex.

Diplectanum hilum, new species
Figs. 3–10

Host.—Gills of pescada, *Plagioscion* sp., Sciaenidae.

Type specimens.—INPA (holotype, PA-246-1; paratypes, PA-246-2 to PA-246-4); UNSM (paratypes, 21636); USNM Helm. Coll. (paratypes, 77916).

Description (based on 12 specimens).—Diplectanidae, Diplectaninae. Body robust, tapered anteriorly; length 591 (548–706), greatest width 87 (65–112) usually at level of testis. Tegument smooth. Cephalic margin with 2 terminal, 2 bilateral cephalic lobes incipient; head organs, cephalic glands weakly developed. Eyes 2, large; eye granules small, elongate ovate; accessory granules present. Mouth subterminal, ventral; pharynx subspherical, 27 (23–32) in diameter; intestinal crura blind posteriorly.

Peduncle broad; haptor 179 (148–207) wide, 86 (72–101) long, with 2 large bilateral lobes. Squamodiscs ovate, with 18–23 rows of sclerotized rods; ventral disc 94 (77–110) long, 69 (59–74) wide; dorsal disc 94 (87–100) long, 69 (57–78) wide. Three types of squamodisc rods; marginal rods with tapered lateral and enlarged medial end, medial rods with bilateral anterior projections; posterior rods scale-like. Rods become more delicate posteriorly. Anchors delicate, dissimilar; ventral anchor 66 (58–71) long, with elongate deep root, depressed superficial root, curved shaft, short point; dorsal anchor 61 (58–65) long, with long tapered deep root, erect superficial root, straight shaft, short point. Ventral bar 83 (73–90) long, with tapered ends, constricted midregion, ventral longitudinal groove, 2 posteromedial processes; dorsal bar 78 (68–90) long, rod-shaped with spathulate medial termination. Six pairs of hooks lying on lateral haptor lobes, 7th pair usually located near terminations of ventral bar; hooks similar, each 11–12 long, with curved shank, erect thumb, delicate curved shaft and point; FH loop ⅞ shank length.

Cirrus 22 (18–25) long, a contorted tapered tube, usually sigmoid, acessory piece 21 (18–22) long, slightly sclerotized, with flat base, terminal aperture functioning as cirrus guide. Gonads tandem. Testis postovarian, ovate, 43 (40–45) wide, 51 (46–54) long; vas deferens with conspicuous loop posterior to level of cirrus; seminal vesicle an inconspicuous dilation of vas deferens; prostatic reservoirs comprising 2 indistinct vesicles lying near cirrus base. Ovary elongate, approximate equal diameter, 20 (18–23), throughout. Oviduct, ootype, uterus not observed; genital pore ventral, immediately posterior to cirrus; vagina sinistral, comprising a distal unsclerotized chamber, proximal sclerotized valve; vitellaria coextensive with intestinal crura.

Remarks.—This species is separated from its sibling, *D. pescadae,* by the comparative morphology of the vagina, haptoral armament, and copulatory complex.

Etymology.—The specific name is from Latin *hilum* = a little thing.

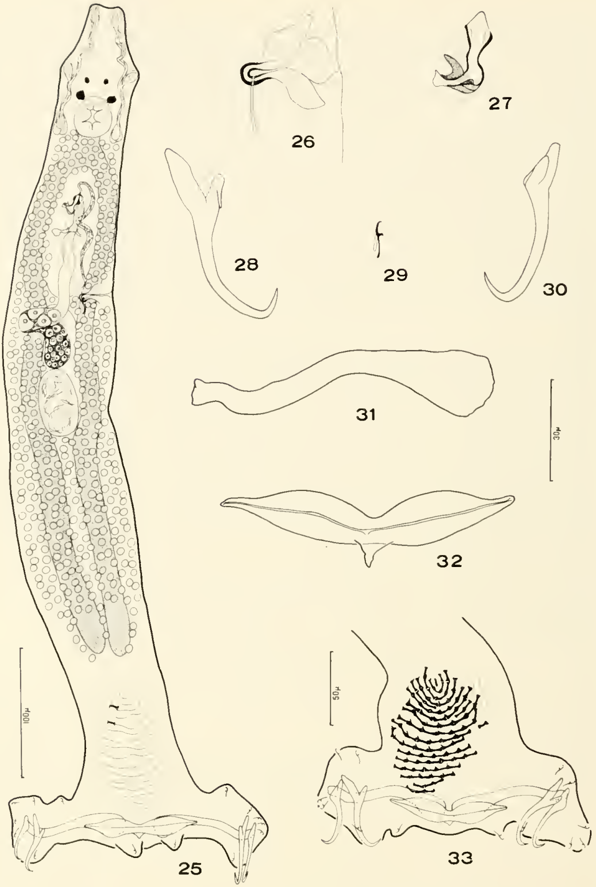
Diplectanum pescadae, new species
Figs. 25–33

Host.—Gills of pescada, *Plagioscion squamosissimus* (Heckel) (type host) and *Plagioscion* sp., Sciaenidae.

Type specimens.—INPA holotype, PA-242-1; paratypes, PA-242-2 to PA-242-12); UNSM (paratypes, 21637); USNM Helm. Coll. (paratypes, 77918, 77919).

Description (based on 52 specimens, 20 measured).—Diplectanidae, Diplectaninae. Body slender, fusiform; length 638 (502–837) greatest width 93 (74–106) usually at level of testis. Tegument smooth. Two terminal, 2 bilateral cephalic lobes poorly developed; head organs small, lying in cephalic lobes and adjacent cephalic area; cephalic glands inconspicuous, comprising 2 groups of unicellular glands posterolateral to pharynx. Eyes 4; members of anterior pair smaller, closer together than members of posterior pair; eye granules variable to ovate; accessory granules usually present in cephalic area. Mouth subterminal, ventral; pharynx subspherical, 32 (25–37) in diameter; intestinal crura blind posteriorly.

Peduncle broad, elongate; haptor 188 (160–237) wide, 78 (69–88) long, with 2 bilateral lobes. Squamodiscs ovate, lying in peduncle and anteromedial haptor; ventral squamodisc 105 (95–117) long, 77 (74–82) wide, with 16–20 rows of sclerotized rods; dorsal disc 102 (93–115) long, 75 (64–82) wide, with 19–22 rows



Figs. 25–33. *Diplectanum pescadae*: 25, Composite illustration of whole mount (ventral); 26, Vagina; 27, Copulatory complex; 28, Ventral anchor; 29, Hook; 30, Dorsal anchor; 31, Dorsal bar; 32, Ventral bar; 33, Haptor (ventral).

of rods. Three types of rods; lateral rods with pointed lateral and enlarged medial terminations; medial rods with enlarged ends possessing short anterior projections; rods of posterior rows scale-like. Anchors dissimilar; ventral anchor 53 (47–57) long, with well developed roots, bent shaft, short point; dorsal anchor 46 (43–50) long, lacking superficial root, with evenly curved shaft, short point. Ventral bar 78 (70–84) long with tapered ends, medial construction, posteromedial projection, ventral longitudinal groove; dorsal bar 77 (67–83) long, with spathulate medial termination. Six pairs of hooks located on lateral haptoral lobes, one pair on small lobes on posterior haptoral margin; hooks similar, each 11–12 long, with slightly curved shank, perpendicular thumb, delicate shaft and point; FH loop ⅘ shank length.

Cirrus 21 (17–24) long, shaped as inverted Greek letter gamma (Γ), with varying diameter along length, distal sheath present; accessory piece absent. Gonads tandem. Testis postovarian, ovate, 41 (33–54) wide, 63 (53–78) long; vas deferens delicate, with loop posterior to cirrus; seminal vesicle absent or represented by inconspicuous dilation of vas deferens; prostatic reservoir with bilateral basal ducts. Ovary pyriform, anterior end looping right crus, greatest diameter 25 (24–27). Oviduct, ootype not observed; uterus delicate, extending anteriorly along midline; genital pore midventral, immediately posterior to cirrus; vagina sinistral, comprising a distal unsclerotized cavity, proximal sclerotized sheath, and fine tube; vitellaria coextensive with intestine.

Remarks.—The closest relative of this species is *Diplectanum hilum.* They are easily distinguished by the comparative morphology of the vagina and cirrus.

Etymology.—The specific name is derived from the local name of the fish host.

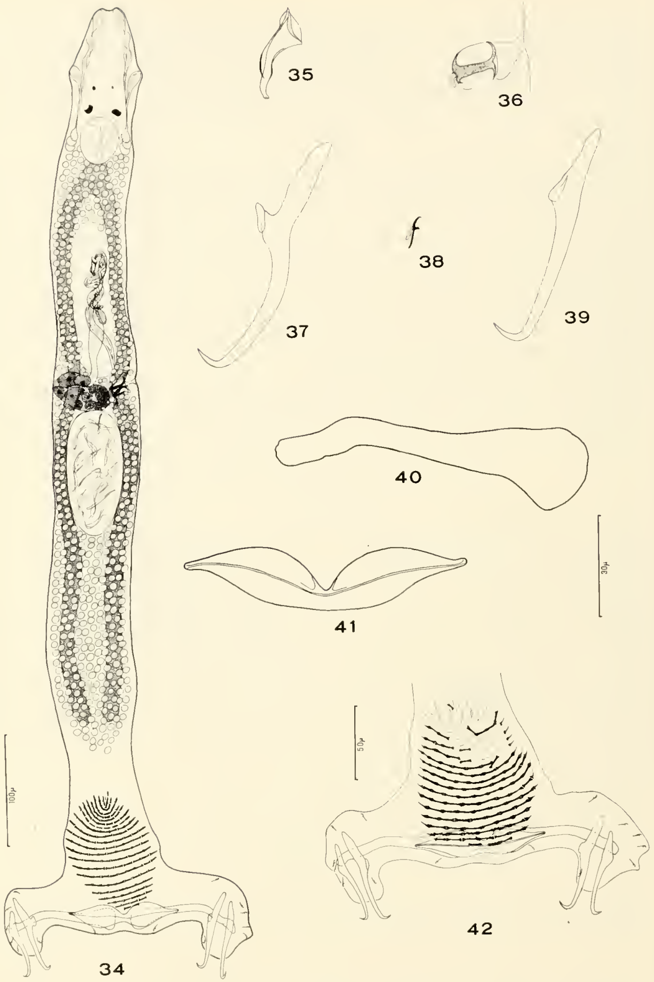
Diplectanum piscinarius, new species
Figs. 34–42

Host.—Gills of pescada, *Plagioscion squamosissimus* (Heckel), Sciaenidae.

Type specimens.—INPA (holotype, PA-244-1; paratypes, PA-244-2 to PA-244-5); UNSM (paratypes, 21639); USNM Helm. Coll. (paratypes, 77920).

Description (based on 13 specimens).—Diplectanidae, Diplectaninae. Body elongate, rod-shaped; length 728 (537–869), greatest width 86 (69–98) near level of testis. Tegument smooth. Cephalic lobes poorly developed, 2 terminal, 2 bilateral; heads organs well developed, one lying in each cephalic lobe and adjacent cephalic area; cephalic glands comprising 2 indistinct bilateral groups of unicellular glands posterolateral to pharynx. Eyes 4, members of anterior pair smaller, closer together than those of posterior pair; eyespot granules subspherical to irregular, small; accessory granules rare. Mouth ventral, subterminal; pharynx spherical, 35 (29–39) in diameter; crura blind posteriorly.

Peduncle broad, elongate; haptor 206 (191–228) wide, 86 (81–92) long, with two bilateral lobes. Squamodiscs subovate with approximately 19–21 rows of sclerotized rods; ventral disc 106 (103–108) long, 80–81 wide; dorsal disc 97–98 long, 80–81 wide. Two types of rods; marginal rods with pointed lateral and enlarged medial ends; medial rods with enlarged terminations. Anchors dissimilar; ventral anchor 71 (66–77) long, with elongate deep root, knob-like superficial root, bent shaft, short point; dorsal anchor 64 (59–68) long, with elongate deep root, straight shaft and point, lacking superficial root. Ventral bar 84 (77–91) long with tapered ends, deep medial indentation of anterior margin, ventral groove; dorsal bar 88 (76–97) long, with spathulate medial termination. Six hook pairs lying in lateral haptoral lobes, 7th pair posterior to ventral bar; hooks similar, each 10–11 long, with delicate shank, perpendicular thumb, tapered shaft and point; FH loop ¾ shank length.



Figs. 34–42. *Diplectanum piscinarius*: 34, Composite drawing of whole mount (ventral); 35, Copulatory complex; 36, Vagina; 37, Ventral anchor; 38, Hook; 39, Dorsal anchor; 40, Dorsal bar; 41, Ventral bar; 42, Haptor (ventral).

Cirrus 23 (20–26) long, funnel-shaped with delicate lateral flange; accessory piece absent. Gonads tandem. Testis postovarian, intercecal, ovate, 42 (35–47) wide, 87 (61–115) long; vas deferens conspicuous, with 2 loops posterior to cirrus; seminal vesicle absent or represented by inconspicuous dilation of vas deferens; prostatic reservoir an elongate structure with 2 bulbous portions. Ovary pyriform, loops right crus; greatest diameter 33 (31–34). Ootype not observed; uterus delicate, extending anteriorly along midline; genital pore midventral; vagina sinistral, comprising a distal unsclerotized pouch, proximal sclerotized dumbbell-shaped valve; vitellaria throughout trunk except absent in regions of reproductive structures.

Remarks.—*Diplectanum piscinarius* most closely resembles *D. cayennensis* Euzet and Durette-Desset, 1973, which was described from *Plagioscion auratus* (Castelnau) from the coast of Guyana. These species are differentiated by the comparative morphology of the dorsal anchors, which in *D. cayennensis* possess a subterminal projection near the union of the shaft and point (compare Figs. 34–42 *nobis* and Figs. 1–5 in Euzet and Durett-Desset, 1973).

Etymology.—The species name is from Latin *piscinarius* = fish loving.

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OPHIODERMA DEVANEYI AND *OPHIODERMA ENSIFERUM,* NEW BRITTLESTAR SPECIES FROM THE WESTERN ATLANTIC (ECHINODERMATA: OPHIUROIDEA)

Gordon Hendler and John E. Miller

Abstract.—Two new western Atlantic brittlestars are described and illustrated in color. *Ophioderma devaneyi* n. sp., is a large (up to 39.6 mm disc diameter), robust, red-spotted species collected from the outer continental shelf and upper slope between Cape Hatteras and central Florida, and observed in situ from the Research Submersible *Johnson-Sea-Link.* It has also been identified in seafloor photographs from the Gulf of Mexico, off southern Florida. *Ophioderma devaneyi* is distinguished from its congeners by a combination of characters including subdivided dorsal arm plates, radial and adoral shields bare of granules, and truncate ventralmost arm spines. *Ophioderma ensiferum* n. sp., is a moderate-sized (up to 22.0 mm disc diameter), fragile species with a splendid pink or reddish disc and yellow- or orange-colored arms, collected by divers on the reef slope of the Belize Barrier Reef, off Carrie Bow Cay, Belize. It differs from other *Ophioderma* species with unfragmented dorsal arm plates in having arm spines that cover the tentacle scale and reach the base of the ventralmost arm spine of the adjacent arm segment.

In his review of the genus *Ophioderma,* Ziesenhenne (1955) recognized 21 constituent species. A majority of them (11 species) occurs in the western Atlantic region and one species, *Ophioderma elaps,* is known from moderately deep waters of the Caribbean region and the Galapagos Islands. Of the remainder, one species is eastern Atlantic, four Panamic, two southern African, and two of uncertain systematic status and questionable provenance have been reported from the Pacific. Since Ziesenhenne's (1955) study, three additional species of *Ophioderma* have been described, *Ophioderma besnardi* Tommasi, 1970, and *Ophioderma divae* Tommasi, 1971, from Brazil, and *Ophioderma anitae* Hotchkiss, 1982, from Belize. In this paper we describe two new and quite distinctive species of *Ophioderma* that we collected from Florida and Belize. Thus, our increasing knowledge of the genus confirms that the greatest diversity of *Ophioderma* species occurs in the western Atlantic region.

The coasts of Florida and Belize, though comparatively well explored, have continued to yield novel species of echinoderms in recent years. To an extent, this growth in apparent echinoderm diversity may reflect the application of recently developed collecting techniques and an increasing accessibility of poorly explored collecting sites. For example, one species in this contribution was taken using a research submersible on the Florida shelf-slope break, and the other by using a diver-applied ichthyocide solution on the steep seaward wall of the Belize Barrier Reef.

Specimens from such unfamiliar biotopes might be sampled with conventional gear but taken so seldom that they would not be recognized as new taxa. Indeed, the species studied from the shelf-slope break has been sampled previously with standard trawling equipment and deposited unidentified in the collections of the National Museum of Natural History and the University of Miami. Additionally, specimens and photographs were sent to us for identification from the Outer Continental Shelf Survey of Duke University sponsored by the United States Bureau of Land Management, and by Continental Shelf Associates Southwest Florida Shelf Ecosystems Study.

We expect that the diversity of the relatively well-known western Atlantic echinoderm fauna will continue to grow as a function of increasing attention from biologists employing conventional as well as state-of-the-art oceanographic gear especially in difficult-to-sample habitats. Therefore, although we are preparing a more detailed treatment of the genus *Ophioderma,* we offer this preliminary contribution to facilitate and encourage the identification of brittlestars in old and new collections of echinoderms from the western Atlantic region.

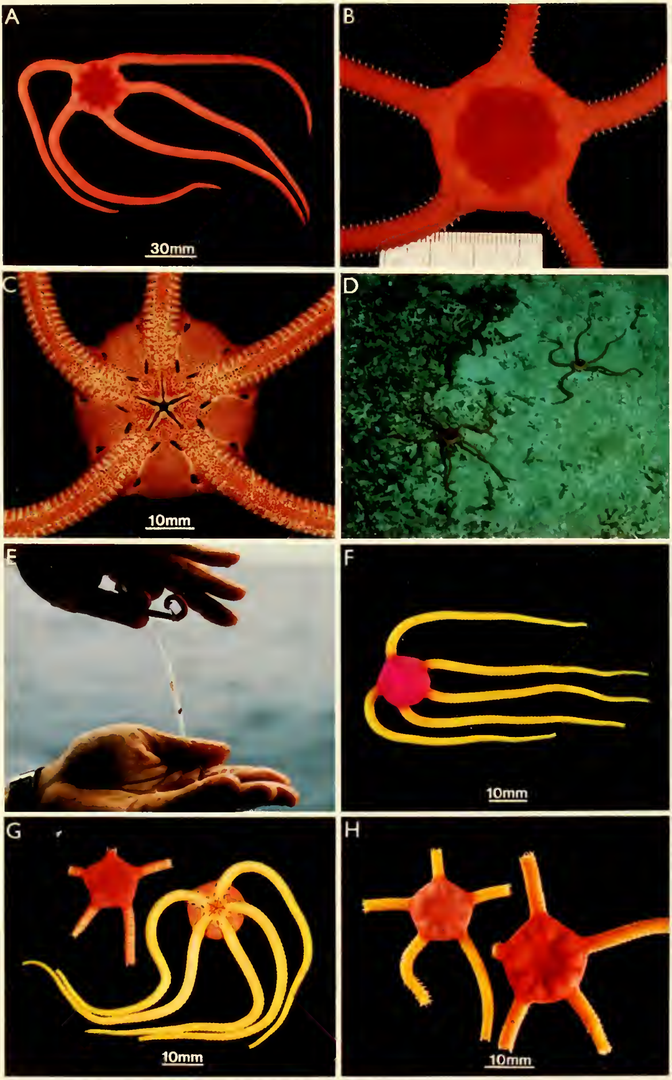
Ophioderma devaneyi, new species
Figs. 1–3.

Etymology.—This handsome species is named for the late Dr. Dennis M. Devaney, in recognition of his outstanding contributions to echinoderm biology.

Material examined.—All specimens in this series other than the holotype are paratypes.

FLORIDA: East of Sebastian Inlet: R/V JOHNSON Cr. 147, Sta. JSL-I-1267, 23 Sep 1982, 27°46.30′N, 79°58.52′W, 56 m, submersible manipulator, coll. J. E. Miller; HOLOTYPE—disc diameter (d.d.) 32.4 mm, dry (USNM E30565); Paratypes—d.d. 36.7 mm, alcohol (USNM E30566) [dissected], and d.d. 32.6 mm, alcohol (USNM E30567) [dissected]. R/V GOSNOLD, Cr. 248, Sta. 734, 18 Sep 1974, 27°49.7′N, 79°57.4′W, 76–80 m, box dredge, coll. L. E. Scotto; d.d. 13.0 mm, dry (USNM E30568). R/V GOSNOLD, Cr. 250, Sta. 759, 18 Feb 1975, 27°49.6′N, 79°58.9′W, 75–85 m, box dredge, coll. R. M. Avent; d.d. 27.1 mm, dry (USNM E30569). R/V JOHNSON, Cr. 062, Sta. JSL-I-583, 31 Aug 1978, 27°45.78′N, 79°56.79′W, 61 m, lock-out dive, coll. M. Mitchell; d.d. 38.9 mm, dry (USNM E30570). R/V JOHNSON, Cr. 147, Sta. JSL-I-1266, 22 Sep 1982, 27°46.30′N, 79°58.52′W, 56 m, submersible manipulator, coll. G. Hendler; d.d. 39.7 mm, 39.2 mm, 36.7 mm, 36.6 mm, and 35.5 mm, alcohol (USNM E30571), d.d. 34.9 mm, and 31.6 mm, dry (USNM E30572), and d.d. 34.6 mm, dry (British Museum Natural History 1984.2.16.1). R/V JOHNSON, Cr. 153, Sta. JSL-I-1323, 14 Mar 1983, 27°46.07′N, 79°58.52′W, 54 m, submersible manipulator, coll. J. E. Miller; d.d. 39.5 mm, dry (Indian River Coastal Zone Museum 074:00467), and d.d. 35.7 mm [damaged], dry (USNM E30573). FLORIDA: East of Key Largo (Straits of Florida): R/V COMBAT Sta. 457, 26 Jul 1957, 25°16′N, 80°07′W, 117 m; d.d. 29.7 mm, dry (USNM E30574). FLORIDA: Northeast of Cape Canaveral: R/V COMBAT Sta. 90, 3 Sep 1956, 28°52′N, 80°05′W, 117 m, from H. R. Bullis; d.d. 25.6 mm, alcohol (University of Miami Marine Laboratory 41.245). R/V JOHNSON, Cr. 141, Sta. JSL-I-1209, 17 Jun 1982, 28°46.7′N, 80°04.7′W, 76 m, submersible manipulator, coll. W. Japp; d.d. 39.6 mm, dry (USNM E30575).

SOUTH CAROLINA: R/V SILVER BAY Sta. 1393, 26 Oct 1959, 32°32′N, 78°40′W, 72–80 m, from H. R. Bullis; d.d. 33.3 mm, alcohol (UMML 41.246).


A
30mm
B
C
10mm
D
E
F
10mm
G
10mm
H
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NORTH CAROLINA: Off Cape Fear: R/V EASTWARD Sta. OS05, sample no. 818055, 3 Mar 1981, 33°48.1′N, 76°34.7′W, 77 m, trawl, Dr. W. Kerby-Smith—Bureau of Land Management Outer Continental Shelf Survey (BLM); d.d. 32.5 mm, dry (USNM E30576). R/V DAN MOORE Sta. OS05, sample no. 818101, 14 May 1981, 33°48.3′N, 76°33.9′W, 104 m, Cerame-Vivas dredge, BLM; d.d. 27.1 mm, alcohol (USNM E30577). R/V CAPE HATTERAS Sta. OS05, sample no. 818318, 11 Nov 1981 33°48.3′N, 76°34.3′W, 100 m, Cerame-Vivas dredge, BLM; d.d. 29.9 mm and 25.6 mm, alcohol (USNM E30578).

PUERTO RICO TRENCH [Station data doubtful; sample label likely incorrect]: R/V PILLSBURY Sta. 1384, 6 Jul 1971, 19°09′N, 66°57.5′W, 7956 m, 41′ otter trawl; d.d. 28.0 mm, alcohol (UMML 41.247).

Additional locality data (based on examination of photographs made from Continental Shelf Associates Southwest Florida Shelf Ecosystems Study).—FLORIDA: Gulf Coast shelf-break between Naples, Florida and Dry Tortugas Islands: Jul 1981—Transect C, Sta. +694, 25°45′30″N, 83°48′08″W, 106 m; Transect D, Sta. +841, 25°16′48″N, 83°57′01″W, 126 m; Sta. +839, 25°16′48″N, 83°56′50″W, 126 m; Sta. +769, 25°16′52″N, 83°50′35″W, 115 m; Sta. +843, 25°16′49″N, 83°57′12″W, 126.5 m; Transect F, Sta. +1013, 25°58′55″N, 83°44′43″W, 92 m; Sta. +130, 24°56′42″N, 83°47′05″W, 95 m; Sta. +675, 25°34′38″N, 83°47′59″W, 106 m; Sta. +670, 25°34′14″N, 83°47′50″W, 105 m; Sta. 36, 25°16′50″N, 83°57′21″W, 126 m. Nov 1981—Transect L, Sta. 21, 24°49′58″N, 83°56′27″W, 119.5 m; Sta. 27, 24°50′52″N, 83°57′21″W, 126 m; Sta. 28, 24°50′59″N, 83°57′33″W, 126.5 m; Sta. 30, 24°51′13″N, 83°57′51″W, 126.5 m; Sta. 31, 24°51′22″N, 83°58′02″W, 128 m; Sta. 48, 24°53′47″N, 84°00′40″W, 135.5 m; Sta. 62, 24°55′08″N, 84°01′57″W, 138 m; Sta. 76, 24°56′19″N, 84°03′31″W, 139 m; Sta. 88, 24°57′59″N, 84°05′25″W, 137 m.

Description of holotype.—Disc diameter 32.4 mm, longest arm 133.0 mm, broken just before tip.

Disc circular, periphery scalloped; inflated area at base of each arm. Rounded granules covering disc, not densely aggregated, extending to arm base; some granules between proximal-most dorsal arm plates. Radial shields bare, about 2.7 mm long × 1.6 mm wide; distance between paired shields about 1.6 times length of shield. Granules on aboral surface at center of disc approximately 54/mm^2, 85 ± 7 μm diameter ($\bar{x}$ ± s.d., n = 31); size increasing towards periphery of disc, largest at base of arms. Granules between paired radial shields approximately 45/mm^2, 122 ± 14 μm diameter (n = 31); those in ventral interbrachial area approximately 44/mm^2, 99 ± 9 μm diameter (n = 31).

Jaws bearing 16 to 20 oral papillae: outer papillae broadest, subtriangular; 1 to

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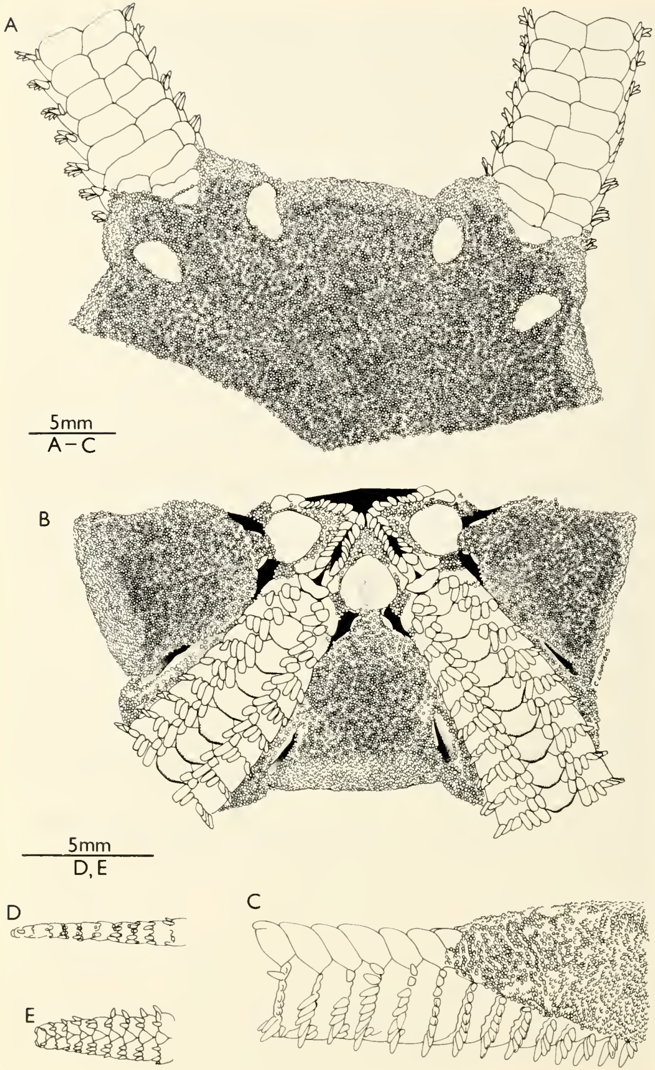
Fig. 1. A, *Ophioderma devaneyi* n. sp., holotype, USNM E30565, disc diameter 34.6 mm; B, *O. devaneyi* n. sp., holotype, dorsal view; C, *O. devaneyi*, n. sp., paratype, IRCZM 074:00467, disc diameter 39.5 mm, ventral view; D, *O. devaneyi* n. sp., in situ, *Oculina varicosa* coral bank, East of Sebastian Inlet, Florida, 56 m; E, *O. devaneyi* n. sp., mucous secretion flowing from broken arm fragment; F, *Ophioderma ensiferum* n. sp., holotype, USNM E30579, disc diameter 14.0 mm; G, *O. ensiferum* n. sp., (right) holotype, ventral view, (left) paratype USNM E30580, disc diameter 13.6 mm, dorsal view; H, *O. ensiferum* n. sp., paratypes, dorsal view, (right) USNM 30582, disc diameter 18.0 mm, (left) BMNH 1984.2.16.2, disc diameter 13.0 mm.


A
5mm
A–C
B
5mm
D, E
D
E
C

2 papillae at jaw apex irregularly spade-shaped, bluntly pointed, broad surface parallel with major plane of disc; lateral series of oral papillae irregularly shaped, their broad surfaces overlapping at an angle to plane of disc. Ventral buccal tentacle scale at jaw angle originating from adoral shield, extending into oral slit below oral papillae.

Oral shield about as wide as long; distal edge slightly concave; lateral edges nearly parallel; proximal, convex edges forming broadly rounded point. Granules border periphery of oral shields except for small gap along each genital slit. Madreporite slightly larger than oral shields, with median distal excavation.

Two pairs of genital slits per arm. Proximal slits extending from base of adoral shield to second arm-segment; shorter than distal pair. Indentation at disc margin running between end of distal genital slit and corresponding radial shield.

Granule cover extending from jaw apex, around oral shield to first lateral arm plate, into spaces between proximal lateral arm plates, across ventral interbrachial surface, around distal genital slits, over scales between edge of arm and distal slit. Thickened lateral area of adoral shield free of granules.

Arms ovoid in cross section near disc, tapering gradually, dorso-ventrally flattened near tip.

Dorsal arm plates with thickened distal edge; subdivided except near arm tip; fissures completely dissect subdivisions of dorsal arm plates: larger component pieces lateral, smaller pieces near central axis of the arm. Composite dorsal arm plates near disc arched, much wider than long (3.54:1 = length : width); distal medial edge slightly concave. Viewed laterally, dorsal arm plates occupying one-half height of arm; dorsal edge of lateral arm plate only reaching middle of arm.

Distal edge of lateral arm plate thickened, bearing up to 9 spines and 2 tentacle scales (Table 1), plate scalloped at base of each spine. Triangular ends of lateral arm plate inserting between successive dorsal and ventral arm plates.

Proximal, ventral arm plates somewhat wider than long (1.33:1 at ventral arm plate 10); most about as wide as long; proximal edges and lateral edges slightly indented; distal edges convex to semicircular. Paired pore-like gaps between distal edges of first proximal 2 to 3 ventral arm plates. Distal ventral arm plates longer than wide. Near arm tip, dorsal and ventral arm plates triangular; lateral arm plates massive, nearly hemispherical.

Tentacle scales near base of arm of nearly equal length; paired; inner scale subtriangular, slightly longer than outer scale. Beyond disc, inner scale becoming slender, ovoid, exceeding length of outer scale by up to one-third. At distal tip of arm, number of scales reduced to one; this remaining scale spine-like.

Dorsal arm spines thick, wedge-shaped in lateral aspect, with broad base and blunt tip. Ventral spines broader, with truncate tip. Most spines extending half way across adjacent lateral arm plate, length increasing slightly dorsad to ventrad. Ventral-most arm spine noticeably broadest and longest especially on proximal segments, partly overlapping tentacle scale of adjacent arm segment.

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Fig. 2. *Ophioderma devaneyi* n. sp., holotype, USNM E30565: A, portion of disc, dorsal view; B, portion of disc with madreporite, ventral view; C, arm base, lateral view; D, arm tip, lateral view; E, arm tip, ventral view.

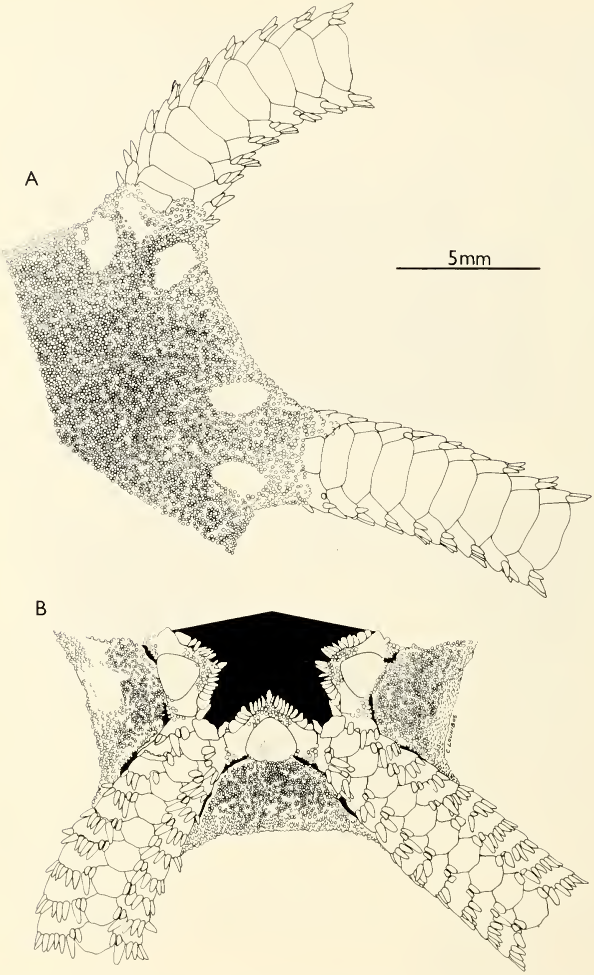

Fig. 3. *Ophioderma devaneyi* n. sp., paratype, USNM E30568: A, portion of disc, dorsal view; B, portion of disc with madreporite, ventral view.

Color: Ground color of living specimen reddish-pink, covered by regularly-spaced deep-reddish spots. Ground color on dorsal surface, especially arms and radial shields, darker red and more intense than color on ventral surface. On ventral surface, jaws and arms more intensely pigmented than disc. Towards center of dorsal surface of disc, spots merge, forming a reticulate pattern, and then an irregular, stellate reddish-brown patch that covers middle of disc. Spots on disc have a more diffuse border than those on arms and radial shields. Spots cover remainder of animal except for distal portions of tentacle scales, oral papillae and arm spines. The white tips of these elements are strongly accentuated by the darker overall coloration of the animal. After preservation in alcohol, dried holotype shows same pattern of pigmentation, but pink and red coloration is replaced by pale tan and brown.

Variations in the Type-Series

Dimensions.—Disc diameters of the type-series range from 13.0 to 39.6 mm and maximum arm length from 47.0 to 193.0 mm. Ratios of arm length/d.d. range from 4.3 to 5.4 for specimens with intact arms.

Disc.—Number of granules/mm^2 at the center of the disc ranges from 43 to 88 ($\bar{x} \pm$ s.d. = 67.5 ± 14.3, n = 22). The granules range from 83 to 107 μm diameter ($\bar{x} = 92$ μm), based on measurements of 31 mid-disc granules from each of 23 paratypes. In several of the paratypes, the granules between the first few dorsal arm plates are very few or missing entirely from all but one arm.

Radial shields.—Dimensions generally correlated with disc diameter. For the smallest specimen (13.0 mm d.d.) shield length is 0.88 mm and for the largest (39.7 mm d.d.), shield length is 1.16 mm, however the longest radial shields (1.96 mm) were measured on a 38.9 mm d.d. specimen.

Jaw.—There are 20 to 23 oral papillae on a jaw, exclusive of the buccal tentacle scale. Usually, there are 2 apical oral papillae, more rarely 1 or 3.

Oral shields.—Length/width ratio of the oral shield ranges between 0.88 and 1.13 ($\bar{x} = 0.99 \pm 0.08$, n = 23). In two specimens a genital scale adjacent to the oral shield is enlarged, resembling an accessory oral shield.

Adoral shields.—Only 2 of 23 paratypic specimens have any adoral shields completely covered by granules. One of these specimens has 1 of 10 shields covered, and the other has 2 of 10 shields covered and several that are partially concealed by granules.

Genital slits.—Proximal slits generally shorter, length rarely equal to or greater than, that of distal slits.

Dorsal arm plates.—All specimens with d.d. greater than 25 mm have numerous subdivided dorsal arm plates. A single specimen of 13.0 mm d.d. has only a few subdivided dorsal arm plates, but its arms are otherwise similar to those of larger specimens. Three of the arms (with 46, 49, and 52 segments) lack subdivided dorsal arm plates. A 31-segment arm has one subdivided plate and a 54-segment arm has 2 subdivided plates.

Arm spines.—The maximum number of arm spines of individuals in the type-series ranges from 7 to 10 (mode = 9, n = 23). The first arm segment with the maximum number is between segments 6 and 22 (mode = 10, n = 23) (Table 1).

Ventral arm plates.—Most paratypes have pairs of pore-like gaps between the

Table 1.—Numbers of arm spines per lateral arm plate presented for both sides of each arm segment of the holotype and for one side of the longest arm of a representative size-series of paratypes of *Ophioderma devaneyi* and *Ophioderma ensiferum.*

		Ophioderma devaneyi																								
		Arm segment																								
d.d.	Arm	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
32.4	1-A	2	3	5	5	5	6	7	8	9	9	9	8	8	9	8	8	8	8	7	8	7	7	7	7	7
	1-B	2	3	4	5	4	6	7	8	9	9	9	9	8	9	8	8	8	8	8	8	7	7	7	7	7
	2-A	3	3	4	5	5	5	6	8	8	9	8	8	8	8	8	8	8	8	8	8	7	8	8	7	8
	2-B	3	3	4	4	6	5	6	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	7	7
	3-A	2	3	4	5	5	6	7	8	9	8	9	8	8	8	8	8	8	8	8	8	7	7	8	7	7
	3-B	2	4	4	4	5	6	7	8	9	9	9	7	8	8	8	8	8	7	8	8	8	7	7	8	7
	4-A	2	3	4	5	6	6	7	8	9	9	9	8	9	8	9	8	8	8	8	8	8	7	6	6	6
	4-B	2	3	5	5	5	7	7	8	9	9	9	9	9	9	9	9	8	8	8	8	8	8	5	6	7
	5-A	3	3	4	4	5	6	7	8	9	9	9	8	7	9	9	8	8	7	8	8	8	8	8	8	7
	5-B	3	4	4	4	5	6	7	8	8	9	9	9	8	9	8	8	8	8	8	8	8	8	7	8	8
13.0		3	4	4	5	5	6	7	7	7	7	7	7	7	6	6	7	7	7	7	7	7	7	7	7	7
24.9		1	3	4	5	6	6	7	8	9	9	8	8	9	8	7	8	8	8	7	7	7	7	7	7	7
25.6		3	3	5	5	6	7	8	8	9	9	9	8	9	8	8	9	10	10	8	8	8	8	9	9	8
28.0		3	3	4	4	5	6	7	7	8	8	8	8	8	8	8	8	8	8	8	8	8	9	7	7	7
29.7		3	4	4	5	5	6	7	8	8	8	8	9	8	8	8	8	8	8	8	8	8	8	7	7	8
31.6		3	4	4	5	6	5	6	8	8	9	9	9	9	9	8	10	8	9	8	8	8	8	8	7	8
34.6		3	3	3	4	5	6	6	8	8	8	8	8	8	8	8	7	7	7	8	8	7	8	7	7	7
36.6		3	3	4	5	5	5	6	7	8	8	8	8	8	9	8	8	8	8	8	8	8	8	7	7	7
39.6		3	3	4	5	5	6	5	6	7	8	9	8	9	8	8	8	8	8	8	8	8	8	7	6	7

Table 1.—Continued.

		Ophioderma ensiferum																								
		Arm segment																								
d.d.	Arm	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
14.0	1-A	2	2	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	6	6	6
	1-B	1	2	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	5	5	6
	2-A	2	2	3	3	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
	2-B	2	2	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	6
	3-A	2	2	3	4	4	5	6	6	7	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5
	3-B	1	2	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	6
	4-A	2	3	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
	4-B	2	2	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5
	5-A	3	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	6	5	5	5
	5-B	3	3	3	4	4	5	6	6	6	6	6	6	6	6	6	6	6	6	6	5	5	5	5	6	5
13.0		2	3	3	4	5	6	7	7	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
13.6		2	3	3	4	5	5	6	6	6	6	6	6	6	6	6	6	6	6		B	R	O	K	E	N
18.0		3	2	3	4	4	5	5	6	7	7	7	7	6	6	6	6	6	6	6	7	6	7	6	6	6
19.5		2	3	3	3	4	5	5	6	6	7	7	7	6	7	7	5	5	6	7	7	7	7	6	6	6
22.0		3	4	4	4	4	5	6	6	7	7	7	7	7	7	7	7	7	7	7	7	7	7	6	7	6

first 4 ventral arm plates (a few specimens have pores between the first proximal 2 and 3 plates or between the first proximal 5 plates).

Tentacle scales.—Over half of the paratypes have 1 to 4 lateral arm plates with 3 (rather than 2) tentacle scales. The supernumerary scale is generally thinner than the flanking scales. Most extra scales are within 4 segments of the disc but some occur at least to segment 33.

Color.—The color pattern of the paratypes is similar to that of the holotype. Specimens briefly fixed in formaldehyde or in alcohol and dried retain much of their red pigmentation. Those preserved in alcohol for more extended periods are leached to varying degrees, and the pink and red coloration is replaced by pale tan and brown. In preserved material, the more intense ground coloration and the spots on the dorsal surface remain darker than the ventral color pattern. In faded specimens, the characteristic central patch remains evident on the dorsal surface of the disc, and even in severely faded specimens it is present as a pale gray area. This patch may cover from one-third to nearly the whole dorsal surface of the disc. The oocytes and ovaries have a reddish-pink color, similar to the pigmentation of the disc; the testes are white.

Relationships

In life, *Ophioderma devaneyi* is easily differentiated from all congeners by its distinctive red-spotted color pattern. In comparison with other western Atlantic congeners, preserved specimens even with leached pigmentation can be recognized as follows. Only four western Atlantic species have subdivided dorsal arm plates. Two of them, *Ophioderma guttatum* Lütken and *Ophioderma squamosissimum* Lütken, have flattened disc granules, while those of *Ophioderma devaneyi* and *Ophioderma cinereum* Müller and Troschel are round. Unlike *O. devaneyi, O. cinereum* has bare rather than granule-bearing scales bordering the dorsal base of the arm, tapered and pointed rather than truncate ventralmost arm spines, adoral shields generally covered with granules rather than with a bare spot, and oral shields markedly wider than long. *Ophioderma brevicaudum* Lütken and *Ophioderma elaps* Lütken, which rarely have subdivided dorsal arm plates, consistently have their radial shields covered by granules, while the radial shields of *O. devaneyi* are bare of granules. Care should be taken to differentiate faded, preserved specimens of *Ophioderma guttatum* and possibly *O. divae* from similarly stippled, preserved specimens of *O. devaneyi.*

Ecological Observations

Habitat.—The known range of *Ophioderma devaneyi* extends from North Carolina (East of Cape Fear) to the Straits of Florida (East of Key Largo), in depths between 54 and 117 m. The species has been identified from underwater photographs taken in the Gulf of Mexico at points west of Naples, Florida and the Dry Tortugas in depths between 92 and 139 m (see "Material examined" section).

All stations where *Ophioderma devaneyi* has been identified are on the edge of the continental shelf. At these depths, sunlight is considerably dimmer than at the surface. It is sufficient for visual navigation at close range, but for detailed observations artificial lighting is necessary. Light intensity may fluctuate drastically due to localized phytoplankton blooms and to turbidity from sediments suspended by rough seas. Bottom currents also create sediment scour at the sampling sites (G.H. and J.E.M., pers. obs.).

Probably attributable to influence of the Gulf Stream, bottom temperatures from the northern end of the species' range are similar to those at the southern end and temperatures at both sites show definite seasonality. MacIntyre and Milliman (1970) reported mean monthly temperatures ranging from 17°–22.5°C off Cape Fear, North Carolina, and Reed et al. (1982) recorded a 7.5°–26.5°C annual range off Sebastian Inlet, Florida.

The shelf-break habitat of *Ophioderma devaneyi,* between North and South Carolina (the northern end of the species' range) has been characterized by MacIntyre and Milliman (1970) as a zone with variable development of terraces and ridges, and with rock surfaces protruding through a gravel-sand sediment. They noted an epifauna consisting of tube-building polychaetes, barnacles, bryozoans, and Foraminifera. A rich macrofauna including demosponges and crinoids is found there as well (W. Kerby-Smith, pers. comm.).

Further south, the habitat of *Ophioderma devaneyi* is markedly different. A dominant feature of the shelf-break of the East Coast of Florida is steeply sloping banks covered with thickets of the branching coral, *Oculina varicosa* Lesueur (Reed 1980). The substratum that is not occupied by coral in this region is covered with greenish silty sand and coral rubble. Numerous fish and dense invertebrate assemblages of hydrozoans, actinarians, and echinoderms inhabit the coral banks. South of the *Oculina* ridges, between Palm Beach and Fort Lauderdale, Florida, there is a narrow continental shelf and a shallow shelf-break supporting an "inactive" coral reef system (MacIntyre and Milliman 1970). *Ophioderma devaneyi* has not been sampled here, but it occurs at approximately the same latitude at the edge of the broad Gulf Coast shelf. There the bottom is sandy with chunks of rubble and occasional rock outcrops. Seafloor photographs of the area show fishes, numerous comatulid crinoids, gorgonian fans, antipatharian whips, some actinarians and tunicates, and an encrusting biota that appears to consist of calcareous algae, bryozoans and sponges.

Distribution.—Although the shallow, landward portions of the continental shelf have been sampled off North Carolina, and the Atlantic and Gulf Coasts of Florida, *Ophioderma devaneyi* has been collected only from a narrow zone spanning the continental slope break (J. Reed, W. Kerby-Smith, K. D. Spring, pers. comm.; G. H. and J. E. M., pers. obs.). In addition, the species was not observed during extensive series of submersible dives at depths where it might be expected to live off Grand Bahama and San Salvador Islands in the Bahama Islands. That *Ophioderma devaneyi* does not have a wider distribution is remarkable considering the broad temperature range, stressful conditions, and the variety of reef and hard bottom habitats occupied by the species.

Ophioderma devaneyi was consistently found on the upper 10 meters of the *Oculina* ridges off Sebastian Inlet, Florida, during a series of vertical transects run with the *Johnson-Sea-Link* submersible between 56 and 86 m depth. Extensive operations with the submersible on a number of the Florida slope-break ridges have shown that the distribution of *O. devaneyi* is not uniform. There are extensive areas where the brittlestar is not seen, but where it does occur, densities of 3 to 4 individuals per m^2 are common.

Typically, large individuals are observed in the open or less frequently, under coral colonies or rubble with several arms completely exposed (Fig. 1D). Limited examinations of *Oculina* thickets and rubble revealed no small *Ophioderma devaneyi* or concealed adults. In photographs of the Gulf Coast population specimens were usually located near areas with rubble or rock outcrops. In photographs showing contiguous expanses of sand and of rubble, *O. devaneyi* was always near the rubble rather than on the comparatively featureless terrain nearby. They resembled deep-sea ophiuroids rather than their shallow-water congeners in that they remained in the open rather than concealed, even when shelter was available nearby. In New Zealand, *Pectinura maculata* (Verrill), a reddish species similar in size to *O. devaneyi* lives in the same way in some areas (D. L. Pawson, pers. comm.).

Most specimens had a disc diameter (d.d.) exceeding 25.0 mm, and specimens reached 39.6 mm d.d. and an arm length of 193.0 cm. The only small specimen examined (13.0 mm d.d., 47.0 mm arm length) was recovered from a box dredge sample that included a specimen of *Ophioderma elaps.* Since we found *O. elaps* under clumps of *Oculina,* the dredge observation suggests that small *O. devaneyi* may be more cryptic than large specimens.

Behavior.—Shallow-water reef-associated ophiuroids show a spectrum of behavioral and morphological types from extremely agile and delicate species such as *Ophioderma appressum* (Say) to sluggish, heavily calcified species such as *Ophioderma brevicaudum. Ophioderma devaneyi* is much larger but similar to the latter species in that it is heavily calcified and responds with slow movements to mechanical stimulation (e.g., prodding with a submersible manipulator). When the submersible manipulator suction tube was applied to *O. devaneyi,* specimens invariably extended and stiffened their arms.

Only one specimen was seen actively crawling without artificial provocation. This observation was made during the afternoon. At night, *Ophioderma devaneyi* occupied similar positions and showed similar postures as in the day. They usually were situated on the sediment with one or several arm tips slightly raised, and sometimes with their disc somewhat raised off the bottom (Fig. 1D).

The arms of some specimens were regenerated, indicating that *Ophioderma devaneyi* is subject to predation; arm damage from physical stress is unlikely in these resilient ophiuroids. How their vulnerability can be reconciled with their tendency to remain in the open is unclear. Although their red speckling and red disc stand out in artificial illumination, under natural light their pigmentation pattern and slow movement could provide camouflage, and their large size could deter some predators. The ability of *O. devaneyi* to produce mucus may also provide some defense. Injured animals, specimens that were roughly handled, and specimens subjected to fresh-water shock exuded copious quantities of mucus that was so viscous it could be cut with scissors (Fig. 1E). Since the mucus was tasteless (to G.H.) it is likely that its slipperyness acts as a mechanical defense rather than as an irritant to predators. Two shallow-water congeners, *Ophioderma guttatum* and *O. squamosissimum,* also produce mucus when injured, but tests for copious mucus production in other *Ophioderma* species (*O. appressum, O. brevicaudum, O. brevispinum, O. cinereum, O. phoenium* H. L. Clark, and *O. rubicundum* Lütken) gave negative results (G. H., pers. obs.).

Ophioderma devaneyi also differs from reef-associated congeners in its unresponsiveness to fresh bait. Specimens offered crushed sea urchins (*Centroste-*

phanus longispinus rubricingulus H. L. Clark) in situ showed no feeding response, even when in direct contact with echinoid tissue. Fishes were attracted to the area and fed on the urchins within 15 sec. The stomach contents of two *O. devaneyi* were examined. In addition to the largest item, a 2.3 mm long gastropod, the stomachs contained 2–3 gastropod postlarvae or veligers, remains of several copepods and an amphipod carrying eggs, a fecal pellet, a few unidentifiable crustacean parts, and some shell fragments. These items are not revealing of the feeding habits of the species. They not only resemble items ingested by the carnivorous, shallow-water *Ophioderma brevispinum,* but also the stomach contents of *Ophioderma longicaudum* (Retzius), a microphagous feeder (Deschuyteneer and Jangoux 1978; Hendler 1982). *Ophioderma devaneyi* more closely resembles the latter species in that its lack of response to bait is like the negative chemosensory response of *O. longicaudum* and completely unlike the ravenous feeding behavior and positive chemosensory reactions of *O. brevispinum* and reef-dwelling congeners (Reimer and Reimer 1975; G.H., pers. obs.). Although the stomachs examined were not filled with sediment, evidence of selective feeding suggested by the stomach contents of *O. devaneyi* cannot be reliably gauged on the basis of only two specimens.

Reproduction.—Shallow-water, reef-dwelling *Ophioderma* species (*O. appressum, O. brevicaudum,* and *O. rubicundum*) have oocytes about 0.3 mm in diameter (Hendler 1979). *Ophioderma devaneyi* of 36.0 mm d.d. and 32.6 mm d.d., collected 23 Sep 1982, had oocytes about the same size ($\bar{x} \pm$ s.d. = 0.32 ± 0.02 mm and 0.32 ± 0.03 mm, n = 30 for each). Other *Ophioderma* species that have been reared (*O. brevispinum, O. cinereum,* and *O. longicaudum*) have eggs of the same size and all produce rapidly-developing, lecithotrophic vitellaria larvae (Hendler 1979). Considering the agreement found between ophiuroid oocyte size and mode of reproduction (Hendler 1975), it seems likely that *O. devaneyi* has a vitellaria larval form.

Ophioderma ensiferum, new species

Figs. 1, 4.

Etymology.—The specific epithet is derived from the Latin words ensis, "sword" and fero, "to bear," referring to the long, pointed arm spines of the species.

Material examined.—BELIZE: ESE of Carrie Bow Cay on the seaward forereef slope of the Belize Barrier Reef. Sta. Belize-83 No. 02, 2 Apr 1983, 24 m, poison station, coll. G. Hendler, B. Littman, B. Spracklin; HOLOTYPE—disc diameter (d.d.) 14.0 mm, dry (USNM E30579) and paratype, d.d. 13.6 mm, alcohol (USNM E30580). Sta. Belize-83 No. 10, 7 Nov 1983, 24 m, poison station, coll. G. Hendler, B. Littman, B. Sullivan; paratypes, d.d. 22.0 mm, and 19.5 mm, alcohol (USNM E30581). Sta. Belize-83 No. 11, 8 Nov 1983, 24 m, poison station, coll. M. Byrne, M. Carpenter, G. Hendler, B. Littman, B. Sullivan; paratypes, d.d. 18.0 mm, dry (USNM E30582) and 13.0 mm, dry (British Museum Natural History 1984.2.16.2).

Description of holotype.—Disc diameter 14.0 mm; longest arm 66.0 mm, all arms broken before tip.

Disc subpentagonal, covered with rounded granules; about 160 granules/mm^2, diameter 61 ± 4 μm ($\bar{x} \pm$ s.d., n = 31) at center of upper surface of disc. Granules slightly larger but less numerous around the dorsal periphery of the disc and on

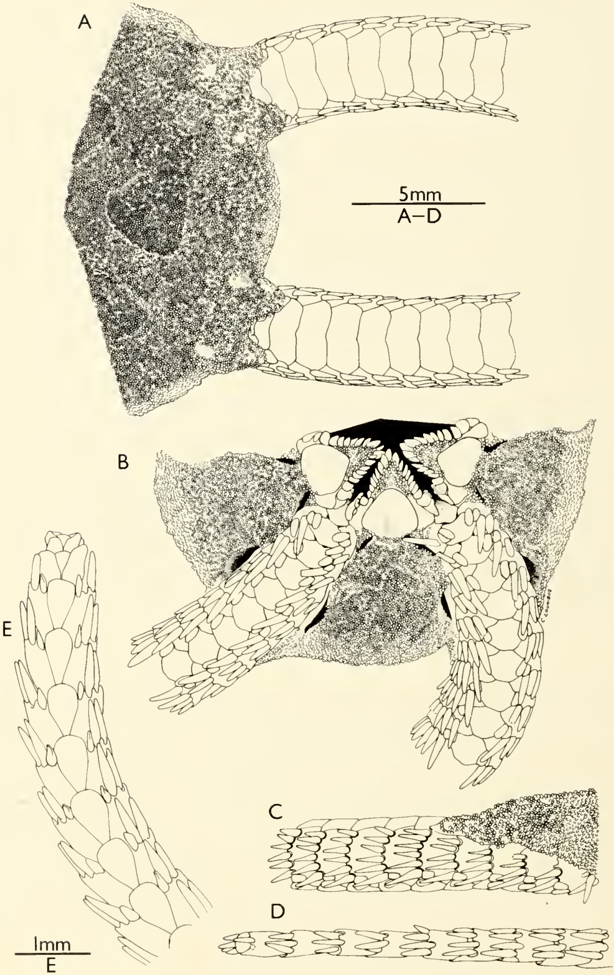

Fig. 4. *Ophioderma ensiferum* n. sp., holotype, USNM E30579: A, portion of disc, dorsal view; B, portion of disc with madreporite, ventral view; C, arm base, lateral view; D, arm tip, lateral view; E, arm tip, ventral view.

scales at arm base. Approximiately 79 granules/mm^2, diameter 70 ± 6 μm (n = 31) between paired radial shields; approximately 110/mm^2, diameter 69 ± 7 μm (n = 31) in ventral interbrachial region. Radial shields small (mean length × width = 0.75 × 0.48 mm) and with very few attached granules. Paired radial shields separated by gap about 2.9 × shield length.

Jaws bearing 16 to 19 oral papillae. Two to 3 apical papillae and distalmost 2 to 3 papillae largest; broad surface of apical papillae and 3 to 4 distal papillae parallel to major plane of disc; plane of proximal papillae perpendicular to disc plane. Ventral buccal tentacle scales at jaw angle attached to adoral shields, projecting into oral slit below oral papillae.

Oral shields pentagonal, slightly wider than long (length : width = 1:1.26); broad base almost straight; short lateral edges nearly parallel; proximal edges convex; apex rounded. Madreporite slightly larger, more irregular in outline than oral shields; lateral ends of base convex; medial distal surface slightly depressed.

Two pairs of genital slits per arm; proximal slit extending from base of oral shield to first arm segment; distal slit longer than proximal, separated from arm by narrow portion of genital plate bare of scales and granules.

Most of surface of adoral shields free of granules. Widely spaced granules, taller than interbrachial granules, covering jaw from base of oral papillae just to proximal edge of oral shield; band of smaller granules along distal edge of oral shield and proximal end of genital slit to first lateral arm plate; granules covering ventral interbrachial surface.

Arms tapering gradually, proximal portion flattened-ovoid in cross section; dorsal surface slightly arched near disc, flattened near tip of arm.

Dorsal arm plates not fragmented; L:W ratio = 1:2.1 at base of arm; distal edge slightly concave and not thickened, often with small medial notch; lateral edges rounded, with curved postero-lateral corners and antero-lateral corners converging proximally to meet the preceding dorsal arm plate. Distal dorsal arm plates with long, convex antero-lateral edges; plates triangular near tip of arm.

Lateral arm plates covering nearly entire side of the arms; triangular ends of plate insert between dorsal and ventral arm plates; thickened distal edge, scalloped at base of arm spines, bearing maximum of 7 arm spines and 2 tentacle scales (Table 1).

Paired pore-like gaps between edges of first proximal 2 to 3 ventral arm plates. Beyond pores, proximal ventral arm plates octagonal, slightly wider than long (ratio 1:1.1), proximal and lateral edges slightly concave. Distal ventral arm plates longer than wide, hexagonal; posterior edge convex, lateral edges concave, slightly concave proximal edges converging towards preceding ventral arm plate.

Inner tentacle scales ovoid to spatulate, longer and thinner than polygonal outer tentacle scale, increasingly more slender towards tip of arm. At distal end of arm number of scales reduced to one; this remaining scale elongate, with sharp tip.

Arm spines thin, slightly flattened laterally, gradually tapering to blunt tip; length increasing from dorsal to ventral end of lateral arm plate: dorsal spine spanning one-half width of adjacent lateral arm plate, penultimate ventral spine touching edge of adjacent ventral arm plate. Ventralmost spine similar but thicker and longer than those dorsad, extending beyond tentacle scale of adjacent segment to base of ventralmost arm spine.

Color: In life, holotype brilliantly pigmented with deep-pink disc and yellow arms. Under low-power magnification, disc granules pale pink, almost white; disc scales and radial shields pink with minute, deep pink flecks. Minute pink flecks along lateral and distal edges of bright yellow dorsal arm plates. Lateral arm plates yellow. Ventral arm plates pale yellow flecked with microscopic orange spots, border of plates golden-yellow. Near distal tip of arm microscopic flecks disappear, yellow color more intense. Ventral surface of disc slightly more pale than dorsal surface, especially near oral frame. Yellow color of arms less intense ventrally than dorsally. Arm spines banded with yellow and white at base and tip. Tube foot shaft pale reddish-orange, tip red. Oral and adoral shields pale orange, speckled with microscopic red spots; edge of oral shield pink. Jaws pink, flecked with red specks; oral papillae pink.

Holotype preserved in alcohol and dried: granulose portion of disc very pale tawny off-white color, arms and oral frame and radial shields white.

Variations in the Type-Series

Disc.—Disc diameters of paratypes range from 13.0 to 22.0 mm. Shape and granulation of paratype discs similar to holotype. On one large specimen, a few scales near the arm base lacked any granules. For paratypes, the density of mid-disc granules ranges from 104 to 165/mm^2, and the diameter of granules from 56 to 84 μm.

Radial shields.—The density of granules on the radial shields is lower than elsewhere on the disc. One paratype (19.5 mm d.d.) has radial shields that partly lack granules; about one-half of each shield is bare. Dimensions of the radial shield are proportional to the size of the specimen. The smallest specimen (13.0 mm d.d.) has radial shields 0.79 mm long; the largest (22.0 mm d.d.) has shields 1.17 mm in length.

Jaws.—All paratypes have 16 to 18 oral papillae (excluding the buccal tentacle scales) per jaw.

Oral shields.—Widths range from 1.15 to 1.37 times the length of the shield. In the larger specimens, the oral shield is more subpentagonal than subcordate, with the proximal edges nearly straight rather than convex.

Genital slits.—Relative length of the proximal and distal slits is variable, even within a single specimen. Proximal slits are more often smaller or equal in size rather than longer than distal slits. There are a few granules occupying the space between the distal genital slit and the arm in only 3 slits of the largest (22.0 mm d.d.) specimen. Other specimens consistently lack granules in this region.

Arms.—One paratype with arms broken just before the tip has 90.0 mm arms and a 19.5 mm disc, arms of other paratypes broken near disc. Ratio of arm length to disc diameter in the relatively undamaged specimen (4.6:1) is similar to that of the holotype.

Dorsal arm plates.—For paratypes, L:W ratio near disc ranges from 1:1.91 to 1:2.70 ($\bar{x}$ = 1:2.32).

Ventral arm plates.—Several paratype specimens have paired pore-like gaps between only one pair of proximal ventral arm plates rather than between several plates.

Arm spines.—Only one specimen has a maximum of more than 7 arm spines. It has 8 arm spines on only one lateral arm plate (Table 1).

Tentacle scales.—In a single case, 3 scales are found on one arm segment near the disc. All other proximal arm segments of the paratypes have paired tentacle scales.

Color.—In life, the color of the disc may vary according to the size of the specimen, and the color of the arms is more variable than that of the disc. Individuals 13.0 to 14.0 mm d.d. had a deep-pink disc, and the specimens 18.0 to 22.0 mm d.d. had dark reddish-pink discs. The arms of one small paratype were pale pink, but the other small specimens had bright yellow arms. One large specimen had orange arms, and the arms of another large paratype were reddish-orange. The colors on the ventral side of the discs and arms of all specimens were paler than those described for the dorsal surface. As in the holotype, the oral shields of other examples in the type series were tinted pale orange to pale red, and the jaws were pink.

The pigments of *Ophioderma ensiferum* are rapidly leached by ethanol. Alcoholic specimens and dry specimens initially preserved in alcohol have white arms and a gray disc. Two specimens held in formaldehyde overnight prior to drying lost some orange pigment during preservation, but they retained much the same color they had in life.

Relationships

The gaudy pigmentation of living *Ophioderma ensiferum* type specimens is unique in the genus, but it is a variable and labile characteristic. Only 6 other western Atlantic species of *Ophioderma* with unfragmented dorsal arm plates and bare radial shields have been described. None of these species: *O. anitae, O. besnardi, O. divae, O. pallidum, O. phoenium,* and *O. rubicundum* have ventral arm spines that cover the tentacle scale and reach the base of the ventral spine on the adjacent arm segment. *Ophioderma ensiferum* also is unique in lacking bare scales at the base of the arms and in lacking scales between the arm and distal genital slit (these characters were not discussed in the descriptions of *O. besnardi* and *O. divae*).

Ecological Observations

The six specimens of the type series were collected on the seaward face of the Belize Barrier Reef. The habitat, a section of the reef about 24 m deep on a 50° to 70° slope, was characterized by mounds of shelflike coral colonies of *Montastrea annularis* (Ellis and Solander), and by large plates of *Agaricia lamarcki* Milne Edwards and Haime, distributed every few meters. The living and dead coral structures were surrounded by a dense cover of algae (especially *Halimeda* and *Lobophora* spp.) and separated by patches of coarse calcareous sand. Also at this depth were numerous, scattered small colonies of platy, foliose and massive corals (e.g., *Mycetophyllia, Diploria, Agaricia,* and *Siderastrea* spp.), small branching gorgonians (e.g., *Pseudoplexaura* and *Pseudopterogorgia* spp.) and a variety of desmosponges. Invariably, we noted a slow current moving along the face of the reef slope and found that visibility varied on different days from about 10 to over 30 m. This biotope is further illustrated and described by Rützler and MacIntyre (1982:30–37).

Ophioderma ensiferum was collected at 3 of 6 poison stations in this area. The specimens were forced from interstices under coral colonies by applying a commercial ichthyocide ("Noxfish", Peneck Corp.). They were acutely affected by the ichthyocide, remaining inactive after capture. The predominant associated organisms driven from the reef were other brittlestars, mostly *Ophioderma rubicundum* and *Ophiurochaeta* spp., and modest numbers of small fish and crustaceans.

Acknowledgments

We dedicate this contribution to Mr. S. Dillon Ripley, Secretary of the Smithsonian Institution, in gratitude for his efforts to foster field research in systematic biology.

The basis for naming a new species *Ophioderma devaneyi,* briefly alluded to in the etymology, merits elaboration. The late Dennis Devaney served as Chairman of the Department of Zoology at the Bernice Pauahi Bishop Museum and was a major contributor to echinoderm biology, particularly the systematics of Ophiuroidea. Dennis Devaney disappeared while diving off the island of Hawaii, near Mahukona, on 13 August, 1983. We very deeply regret the loss of an invaluable and highly esteemed colleague.

The crews of the R/V JOHNSON and JOHNSON-SEA-LINK I of Harbor Branch Foundation, Inc. (HBF) offered indispensable assistance during our *Oculina* reef dives. Mr. John Reed (HBF) was of great help in providing specimens of *Ophioderma devaneyi* and advice based on his extensive work on the offshore coral pinnacles.

Dive buddies in Belize who assisted in the pursuit of *Ophioderma ensiferum,* included Dr. Maria Byrne, Messrs. Michael Carpenter, Barry Spracklin and Brian Sullivan. Special thanks are due to Ms. Barbara Littman who collected half the specimens herein described and helped ably in many other aspects of the field program.

Mr. Keith D. Spring of Continental Shelf Associates, Inc., placed at our disposal an invaluable series of underwater photographs from the Southwest Florida Shelf Ecosystems Study-Year 2 (Contract No. AA851-CT1-45 through Mineral Management Service).

The following colleagues made specimens available to us: Dr. David L. Pawson and Ms. Maureen Downey (Smithsonian Institution), Dr. Gilbert Voss (University of Miami), and Dr. William Kerby-Smith (Duke University Marine Lab.) who provided material from a United States Bureau of Land Management Continental Shelf Survey.

Mr. George Steyskal (U.S. Dept. Agriculture) generously shared his knowledge of the classical languages to clarify nomenclatorial questions arising from this study. Dr. David L. Pawson reviewed the manuscript. Mrs. Charissa B. Lounibos prepared the line drawings, and Mr. Tom Smoyer (HBS) helped produce the color plate.

We are indebted to all these colleagues for their cooperation.

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A NEW CATFISH OF THE GENUS *EPAPTERUS* (SILURIFORMES: AUCHENIPTERIDAE) FROM THE ORINOCO RIVER BASIN

Richard P. Vari, Susan L. Jewett, Donald C. Taphorn,
and Carter R. Gilbert

Abstract.—A new species of auchenipterid catfish, *Epapterus blohmi,* is described from the central portion of the llanos of the Orinoco River basin. It is distinguished from *E. dispilurus* and *E. chaquensis,* the only other described species of the genus, by the presence of a dusky band that extends across the dorsal portion of the procurrent caudal-fin rays and dorsal lobe of the caudal fin. The congeneric species have a discrete pigmentation patch in the center of each caudal-fin lobe. Meristic and morphometric differences further separate the species. Both *E. blohmi* and *E. dispilurus* demonstrate pronounced sexual dimorphism in the form of the anterior rays of the anal fin, position of the urogenital opening, form of the dorsal-fin spine, and the degree of ossification of the maxillary barbel. *Epapterus dispilurus,* previously known only from the upper Rio Solimoẽs is reported from the central portion of the Rio Amazonas basin. The known range of *E. chaquensis,* described from Argentina, is extended into Paraguay.

Among the fishes described by Cope (1878) based on the Orton collection of fishes from the Peruvian Amazon was a monotypic genus of auchenipterid catfish, *Epapterus,* that was distinguished by its endentulous jaws, lack of an adipose dorsal fin, and high number of anal-fin rays. Only two subsequent collections of the single contained species, *E. dispilurus,* were reported on during the next century. *Euanemus longipinnis,* described by Steindachner (1881) from the Peru-Brazil border region, was placed into the synonymy of *Epapterus dispilurus* by Eigenmann and Eigenmann (1888) who, in a subsequent paper (1890), redescribed *E. dispilurus* on the basis of Steindachner's specimens. More recently, Fowler (1939) recorded a single specimen from Cantamana in the Río Ucayali drainage of Peru. The other citations of *E. dispilurus* were typically literature compilations based on the above records. A second species, *Epapterus chaquensis,* endemic to the Río Paraguay basin, was described from the Chaco Province of Argentina by Risso and Risso (1962). Recent collecting activities in the central portions of the llanos (savannas) of the Orinoco River basin have revealed a third species of *Epapterus,* described herein, that is evidently broadly distributed in the sampled region.

Vertebral counts were taken from radiographs and include all free elements posterior of the Weberian apparatus inclusive of the complex terminal vertebra. Numbers in parentheses after a particular vertebral count are the number of specimens with that count. The anteriormost two anal-fin rays of males are not apparent when counts are made directly from the specimen but can be seen on radiographs. Greatest body depth was taken slightly anterior of the anal-fin origin. Gill-raker, branchiostegal ray, and rib counts were taken from cleared and stained specimens. Length of the maxillary barbel and subunits of the head are presented

Fig. 1. *Epapterus blohmi*, holotype, MBUCV V-14100.

as proportions of head length (HL). Head length and other measurements of body parts are discussed as proportions of standard length (SL). Holotype counts and proportions are presented in square brackets.

Specimens examined for this study are deposited in the following institutions: American Museum of Natural History, AMNH; Academy of Natural Sciences of Philadelphia, ANSP; British Museum (Natural History), BMNH; Field Museum of Natural History, FMNH; Museo de Biologia, Universidad Central de Venezuela, MBUCV; Museo de Ciencias Naturales de Guanare (at Universidad Nacional Experimental de los Llanos Occidentales Ezequiel Zamora, UNELLEZ), MCNG; Museum of Comparative Zoology, MCZ; Florida State Museum, University of Florida, UF; and National Museum of Natural History, Smithsonian Institution, USNM.

Epapterus blohmi, new species

Fig. 1

Holotype.—MBUCV V-14100, 74.3 mm SL, female, collected by R. P. Vari, S. L. Jewett, A. Machado-Allison, L. Aguana and O. Flint, 19 Jan 1983, in Laguna Los Guácimos, a broad shallow lagoon located on Fundo Pecuario Masaguaral, Guarico State, Venezuela (approx. 08°34'N, 67°35'W).

Paratypes.—46 specimens, 55.9–85.1 mm SL, all females unless otherwise noted. 19 specimens taken with holotype: MBUCV V-14101, 3 specimens, 1 male, 65.5–67.0 mm SL; AMNH 55210, 2 specimens, 69.0–75.0 mm SL; ANSP 152045, 2 specimens, 65.5–72.0 mm SL; BMNH 1983.9.20:1–3, 3 specimens, 65.3–67.3 mm SL; FMNH 94854, 2 specimens, 69.3–74.3 mm SL; USNM 260637, 7 specimens (2 cleared and counterstained for cartilage and bone), 2 males, 65.3–74.7 mm SL. 13 specimens collected by A. Machado-Allison, L. Aguana and R. P. Vari, 20 Jan 1983, Río Portuguesa at Camaguan, Guarico State, Venezuela (approx. 08°07'N, 67°36'W): MBUCV V-14102, 5 specimens, 64.3–69.8 mm SL; USNM 260638, 8 specimens (3 cleared and counterstained for cartilage and bone), 2 males, 61.6–68.8 mm SL. 9 specimens, UF 32119, 1 male, 59.2–85.1 mm SL, collected by C. R. Gilbert and D. C. Taphorn, 22 Mar 1981, Caño el Ajero at bridge on road to Guayabal, 11 km NNE of San Fernando de Apure, Guarico State, Venezuela. 5 specimens, MCNG 3760, 55.9–63.1 mm SL, collected by D. C. Taphorn, C. G. Lilyestrom, C. R. Gilbert and R. Franz, 20 Mar 1981, Modulo de la UNELLEZ, pond along southern dike, Apure State, Venezuela.

Non-type specimens examined.—103 specimens, all females or immatures un-

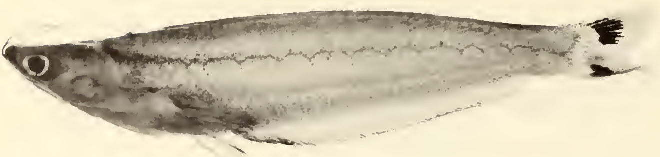

Fig. 2. *Epapterus dispilurus,* USNM 261422, 73.9 mm SL.

less otherwise noted. 77 specimens collected by O. Castillo, R. P. Vari and crew, 24 Jan 1983, Modulos de Mantecal, Apure State, Venezuela (approx. 07°39′N, 69°00′W): USNM 257985, 66 specimens, 9 males, and USNM 257983, 11 specimens, 5 males. 17 specimens, 4 males, USNM 257984, collected by O. Castillo, R. P. Vari, S. L. Jewett and crew, 22 Jan 1983, Río el Canito where crossed by road from San Fernando de Apure to Cunaviche, Apure State, Venezuela (approx. 07°28′N, 67°39′W). 2 specimens, MCNG 3599, collected by D. C. Taphorn, C. S. Lilyestrom and C. Olds, 16 Mar 1981, Modulo de la UNELLEZ, pond along southern dike, Apure State, Venezuela. 7 specimens, MCNG 4103, collected by D. C. Taphorn and C. G. Lilyestrom, 16 Jun 1981, locality as for preceding.

Diagnosis.—*Epapterus blohmi* shares a suite of distinctive characters with *E. dispilurus* and *E. chaquensis* that is evidently derived within the Auchenipteridae. These characters include: the edentulous premaxillae and dentaries, the reduced rayed dorsal fin, the elongate body, the absence of an adipose dorsal fin, and a high number of anal-fin rays. Although the above characters are specialized relative to the generalized conditions in the Auchenipteridae, at least two, the absence of an adipose dorsal fin and the high anal-fin ray count, have evidently been achieved independently in some other lineages of the family (see "Remarks").

Epapterus blohmi has a distinctive band of dark pigmentation that extends from the dorsal margin of the caudal peduncle, along the dorsal procurrent rays and across the dorsal lobe of the caudal fin to its posterior margin (Fig. 1). The caudal pigmentation pattern in *E. dispilurus* and *E. chaquensis,* in contrast, consists of a discrete patch of dark chromatophores in the center of each caudal-fin lobe (Figs. 2 and 3). *Epapterus blohmi* is also distinguishable by its long maxillary barbel (1.66–1.85 in HL versus 1.46 in *E. chaquensis* and 1.35–1.58 in *E. dispilurus*). The 49 to 57 anal-fin rays in *E. blohmi* further separate that species from *E. dispilurus,* which has 58 to 63 anal fin rays.

Description.—Body elongate, distinctly compressed, head depressed. Dorsal profile of head flat or barely convex, dorsal profile of body from rear of head to end of caudal peduncle slightly convex. Ventral profile of head slightly convex. Ventral profile of body gently curved to anal-fin origin. Pseudopenis of male extending along proximal three-quarters of anterior margin of third anal fin ray (Fig. 5). Anal-fin base gently convex to caudal peduncle.

Greatest body depth at anal-fin origin 0.17–0.22 [0.19], males typically more slender than comparably sized females of similar condition; snout tip to dorsal-fin origin 0.20–0.23 [0.20]; snout tip to pelvic-fin origin 0.31–0.35 [0.33]; snout tip to anal-fin origin 0.42–0.46 [0.44]. Dorsal fin greatly reduced overall, with a

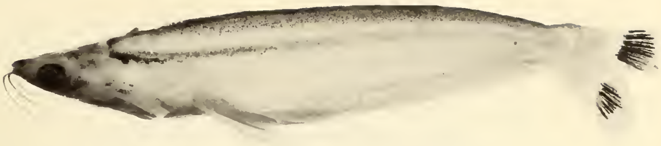

Fig. 3. *Epapterus chaquensis,* USNM 232304, 85.2 mm SL.

spine and two rays, second ray often reduced. Dorsal-fin spine non-serrate, sexually dimorphic, slender in females, much thicker in males, particularly proximally; length of spine 0.03–0.05 [0.03]. First dorsal-fin ray typically slightly longer than spine. Adipose dorsal fin absent. Pectoral fin with 1 spine and 9 to 11 rays [10]; pectoral-spine length 0.12–0.14 [0.13], medial margin of spine with series of serrations along its distal three-quarters; rayed portion of fin pointed; longest pectoral-fin ray typically longer than spine, length of longest pectoral-fin ray 0.12–0.15 [0.14]; tip of pectoral fin not reaching to origin of pelvic fin. Pelvic fin pointed, with 14 to 16 rays [15], lateralmost ray longest, length of longest pelvic-fin ray 0.18–0.23 [0.22]; pelvic fin with broad posteroventrally sloping base; origin distinctly dorsal of ventral margin of body. Anal-fin margin in females smoothly convex anteriorly, straight for much of its length and convex posteriorly; third and fourth anal-fin rays in males greatly developed (see "Sexual dimorphism"), remainder of fin as in females; length of base of anal fin 0.51–0.56 [0.52]; anal-fin rays 49 to 57 [57]. Caudal fin distinctly emarginate; principal caudal-fin rays 9 + 8; 12 to 18 dorsal procurrent rays of caudal fin evident in cleared and stained specimens, 7 to 12 visible in unstained specimens; 10 to 12 ventral procurrent rays of caudal fin, of which 4 to 7 are visible externally. Ribs on each side 5. Number of vertebrae 42 (9), 43 (28), 44 (6) [44].

Head depressed, anterior margin broadly rounded in dorsal view; head length 0.16–0.21 [0.18]. Lower jaw very slightly longer than upper; no teeth present on premaxillae, dentaries, vomer, palatines or lower pharyngeals; a broad patch of conical teeth on round, convex fifth upper pharyngeal tooth plate. Snout length 0.36–0.43 [0.39]. Orbital margin not free, horizontal width of orbit 0.25–0.32 [0.30]. Length of bony postorbital portion of head 0.34–0.40 [0.36]. Interorbital region gently convex, width 0.39–0.46 [0.44]. Nostrils of each side of head separated by a distance equal to 4.5 times diameter of posterior nostril; anterior nostril somewhat tubular, located on dorsal surface of snout, above lip; posterior larger, oval. Gill rakers on first arch (in cleared and stained specimens) long, slender; 12 to 15 above, 18 to 20 below, total 31 to 35. Branchiostegal rays 7. Gill membranes broadly attached to isthmus. Maxillary barbels rounded in cross section, elongate, length 1.66–1.83 of HL [1.75], reaching nearly to or beyond origin of pelvic fin; degree of ossification of proximal portion of barbel sexually dimorphic (see "Sexual dimorphism"). Mental barbels four, rounded, arranged in arch along ventral surface of jaw, barbels reaching nearly to vertical through pelvic-fin origin.

Lateral line complete, dendritic, with short side branches at irregular intervals, divided on caudal fin into 2 or 3 branches that run through lightly ossified tubes.

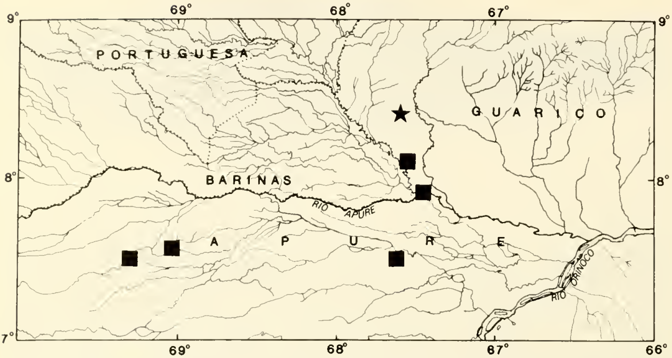

Fig. 4. Geographic distribution of *Epapterus blohmi*, new species, in the central portions of the Río Orinoco basin (Star = type locality; some symbols represent more than one lot of specimens).

Color in preservative.—Overall coloration tan, recently preserved specimens with distinct yellow fat deposits along base of anal and caudal fins. Dorsal surface of head with scattered chromatophores other than along middorsal line. Dense patch of pigmentation on area between each anterior and posterior nostril; patch sometimes partially envelopes anterior nostril. Large, irregular middorsal patch of pigmentation posterior to fontanel. Region proximate to middorsal line of body relatively densely marked with a band of discrete chromatophores; chromatophore field denser in region of dorsal-fin origin. Dorsal chromatophore field continuous posteriorly with pigmented band on dorsal procurrent rays and dorsal caudal-fin lobe. Elongate discrete patch of pigmentation typically present along anterior section of lateral line; line of pigmentation of varying degrees of intensity and development sometimes extending posteriorly along lateral line, reaching to base of middle rays of caudal fin in some individuals. Barbels pigmented, more so proximally. Caudal fin with distinct band of chromatophores extending from dorsal procurrent rays to posterior margin of middle rays of dorsal lobe of fin (Fig. 1). Smaller individuals (MCNG 4103) with a crescent-shaped pigmentation field along base of ventral lobe of caudal fin; pigmentation patch continuous with band across dorsal lobe of fin. Other fins of adults hyaline or with only few scattered chromatophores, particulary on pectoral fin. Some smaller individuals with series of chromatophores along anal-fin margin, and band of large chromatophores along ventral portion of body wall above anal fin.

Color in life.—Overall coloration whitish, somewhat translucent, with a slight greenish tint in some individuals; pigmentation otherwise as in preserved specimens.

Sexual dimorphism.—*Epapterus blohmi* demonstrates a high degree of sexual dimorphism in a number of the morphological systems described above. Differences between the sexes in the greatest depth of the body, although obvious within population samples, does not always discriminate the sexes from different pop-

Fig. 5. Geographic distribution of *Epapterus* species (Square = *E. blohmi* [see also Fig. 4]; Diamonds = *E. dispilurus*; Stars = *E. chaquensis*).

ulations. The three most obvious sexual differences involve the form of the dorsal-fin spine, degree of ossification of the maxillary barbel, and the modifications of the anterior portion of the anal fin in males.

The dorsal-fin spine in females of *E. blohmi* tapers rapidly from its base to a relatively slender non-serrate spine with a somewhat blunt tip. The males of that species, in contrast, have a dorsal-fin spine that is about twice as thick proximally as that in the females, and only tapers in its distal one-quarter. Although the spines in the sexes do not differ in relative length in the available specimens, the differences in overall spine form are sufficiently pronounced to permit sexing of individuals based solely on dorsal-fin spine form.

Sexual dimorphism in the maxillary barbel of auchenipterids was commented upon in *Ceratocheilus* (=*Auchenipterus*) (Miranda Ribeiro, 1918) and *Auchenipterus* (Myers 1947; Boeseman 1952; Miranda Ribeiro 1968; Mees 1974). *Epapterus blohmi* also demonstrates a marked degree of sexual dimorphism in the degree of maxillary barbel ossification. In females the ossified portion of the barbel does not extend posteriorly beyond the vertical through the posteroventral margin of the ventral process of the lateral ethmoid. The ossified section of the barbel in females is relatively slender with no external demarcation at the terminus of the ossified region. Males of *E. blohmi,* in contrast, have a more pronounced ossification of the barbel. The ossified region of the barbel extends posteriorly to the posterior third of the orbit and is distinctly thickened proximally, with a well-marked transition in the thickness of the barbel at the posterior limit of the ossification. This transition is comparable to that illustrated in *Auchenipterus nuchalis* by Mees (1974, Fig. 3), but differs in not having the barbel of males shortened.

The final and most complex of the noted sexually dimorphic characters in *Epapterus blohmi* involves the form of the anterior anal-fin rays. Sexual dimorphism in the external morphology of the anterior portion of the anal fin was reported in the auchenipterid genera *Auchenipterichthys* (Kner, 1858), *Pseudauchenipterus* (Fisher, 1917), *Ceratocheilus* (=*Auchenipterus*) (Miranda Ribeiro, 1918), *Auchenipterus* (Miranda Ribeiro, 1968), and *Asterophysus, Pseudauchenipterus, Auchenipterichthys, Tatia* and *Ceratocheilus* von Ihering, 1937). More recently Mees (1974) cited many of those reports, expanded on some, and also noted the presence of a less pronounced form of the modification in *Pseudotatia,* without, however, analyzing the associated osteological alterations.

Females of *Epapterus blohmi* do not possess any alterations of the form of the anterior anal-fin rays (Fig. 6A). The anal-fin rays in females of that species increase in size from the first to the third or fourth, with the latter elements similar in size to the neighboring posterior rays. Other than for the conjunction of the first and second proximal pterygiophores, all of those supporting elements are separate and of approximately the same size. Males of the species have dramatic modifications of the system (Fig. 6B). The first and second anal-fin rays are notably smaller than their counterparts in females and the other anal-fin rays in males. The most pronounced modifications involve the third and fourth anal-fin rays, which are greatly enlarged both relative to the remaining anal-fin rays and to their homologues in females. Each ray is thickened and has a fusion of its segments that results in a total absence of externally visible junctions between the segments of the third ray, and with only slight residual demarcations of the regions of contact apparent on the fourth ray (Fig. 6B). Proximally both of the rays have enlarged posterior processes which serve as expanded areas of attachment for the muscles associated with the movement of the rays. The proximal pterygiophores are also modified with the five anteriormost elements being conjoined, thickened and lengthened relative to their more posterior counterparts.

Associated with this modification of the anal-fin rays is a shift in the position of the genital pore of the male onto the distal portion of the third ray, resulting in a pseudopenis. A similar development of the pseudopenis has been noted in *Auchenipterus nuchalis* (Mees, 1974), and is evidently a modification permitting oviducal fertilization as discussed in the auchenipterid genus *Trachycorystes* by von Ihering (1937).

Relationships.—Our present understanding of phyletic relationships within the Auchenipteridae is quite nebulous, with generic definitions an apparent amalgam of generalized and specialized characters that may not define natural assemblages. The only evidently specialized characters unique to the three species of *Epapterus* within the Auchenipteridae are the lack of dentition on the premaxillae and dentaries, and the reduction in degree of development of soft portions of the dorsal fin. *Epapterus* also has several other specializations, including the absence of an adipose dorsal fin, lengthening of the anal fin, and the dorso-ventral depression of the cranium. Although these latter three characters are evidently derived

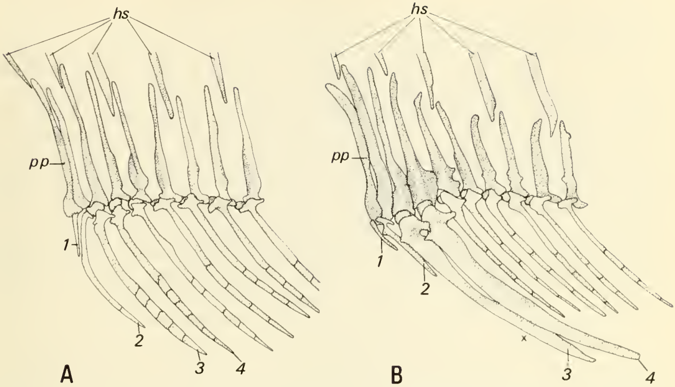

Fig. 6. Anterior portion of anal fin of (A) female and (B) male *Epapterus blohmi*, USNM 260638. Anal fin rays 1 to 4 numbered. Position of genital pore of male (B) indicated by an x. Abbreviations: pp - anteriormost proximal pterygiophore; hs - hemal spine.

relative to the conditions most common in the Auchenipteridae, they also occur incongruently in other assemblages of genera in the family.

An adipose dorsal fin is similarly absent in the nominal auchenipterid genera *Trachelyopterus* Valenciennes (in Cuvier and Valenciennes 1840), *Trachelopterichthys* Bleeker (1863), *Trachelyichthys* Mees (1974) and *Ceratocheilus* Miranda Ribeiro (1918). The type specimen of *Ceratocheilus* is apparently an aberrant individual of *Auchenipterus nuchalis*, a species that typically has an adipose fin (Mees 1974:17, 20), and *Ceratocheilus* is thus not pertinent to this discussion. Although the absence of an adipose dorsal fin is a derived condition within the Auchenipteridae, Mees questioned the naturalness of the subgroup of auchenipterids defined by the absence of an adipose fin. He rather suggested that the relationships of *Epapterus*, which lacks an adipose fin, were with *Auchenipterus* Valenciennes (in Cuvier and Valenciennes, 1840) and *Pseudepapterus* Steindachner (1915), both of which possess an adipose fin, rather than with *Trachelyopterus, Trachelopterichthys*, and *Trachelyichthys* in which the fin is absent. Evidently derived characters common to *Epapterus, Pseudepapterus*, and *Auchenipterus* include an increased number of anal-fin rays, a dorso-ventrally depressed cranium and an elongate body, modifications that are specialized relative to the typical conditions in the Auchenipteridae. Furthermore, as noted by Mees (1974:112), both *Pseudepapterus* and *Auchenipterus* have a reduced adipose dorsal fin. Such a condition may be an intermediate state in the transition series that culminates in the absence of the fin in *Epapterus*. The other auchenipterid genera in which the adipose dorsal fin is absent (*Trachelyopterus, Trachelopterichthys*, and *Trachelyichthys*), in contrast, have the rounded cranial form generalized for the family. Of these genera, only *Trachelopterichthys* has an increase in the number of anal-fin rays and a moderate elongation of the body reminiscent of the condition in *Epapterus* and its hypothesized close relatives. There is, therefore, some incongruity in the distribution of these sets of evidently derived characters within the Auchenipteridae. Nonetheless, Mees' hypothesis of a close relationship between *Epapterus, Auchenipterus,* and *Pseudepapterus* is reasonable within the context of our present knowledge of relationships within the Auchenipteridae, particularly in light of the problems inherent in uniting groups on the basis of loss characters (e.g., absence of an adipose dorsal fin). Further studies involving more inclusive phylogenetic hypotheses are necessary to analyze the significance of these evident homoplasies within the Auchenipteridae.

The lack of comparative material of *Pseudepapterus* makes it impossible to analyze possible phyletic relationships among that genus, *Auchenipterus* and *Epapterus,* or to comment further on the question of the distinctiveness of *Pseudepapterus* versus *Auchenipterus* that was raised by Böhlke (1951).

Remarks.—Sexual dimorphism has not been previously reported in *Epapterus.* Both of the specimens available to Cope (1878) when he first described *Epapterus* and its single contained species, *E. dispilurus,* were males. Fowler (1939) apparently did not notice the differences between his specimen from Contamana, a female, and the male ANSP syntypes of Cope. The type series of Steindachner's (1881) *Euanemus longipinnis,* alternatively, were all females. A comparison of the Cope and Fowler specimens and recently collected individuals from Peru and Brazil (see "Comparative material examined") reveals that *Epapterus dispilurus* shares the sexually dimorphic modifications of the dorsal and anal fins, and maxillary barbel form described above for *E. blohmi.* A single, very large male *E. dispilurus* (USNM 261388, 103.8 mm SL) differs from the smaller available males of that species and *E. blohmi* in having the dorsal spine distinctly lengthened in addition to being thickened. Such a lengthening of the spine is not apparent in similarly-sized *E. dispilurus* females. The extent of the maxillary-barbel ossification is also more pronounced in the large male specimen of *E. dispilurus* in which the ossified portion of the barbel extends posteriorly beyond the vertical through the posterior limit of the orbit. Risso and Risso (1962) did not note any sexual dimorphism in *E. chaquensis,* although the examination of a larger series of specimens would presumably reveal modifications in the males of that species comparable to those in *E. blohmi* and *E. dispilurus.*

All specimens of *E. dispilurus* previously reported upon (Cope 1878; Steindachner 1881 [as *Euanemus longipinnis*]; Eigenmann and Eigenmann 1888; and Fowler 1939) are from the western portions of the Rio Solimoẽs (upper Rio Amazonas), either in Peru or in the region along the Peruvian-Brazilian border. Two individuals examined (USNM 261422) extend the range of the species to the Manaus area, approximately 1400 kms downstream. A single specimen of *Epapterus chaquensis* from the Río Negro of the Río Paraguay system of Paraguay (USNM 232304) represents the first record of the genus in that country.

Ecology.—*Epapterus blohmi* was collected from a variety of aquatic habitats in the central llanos of the Río Orinoco basin. These included the margin of the main stream of the Río Portuguesa, small drying stream beds, artificial ponds in gravel excavations, and a large shallow lagoon (the holotypic locality). The water in all settings was turbid with little visibility and was either still or slow-flowing. The presence of *E. blohmi* in gravel excavations distant from natural permanent standing waters indicates that the species disperses across the flooded llanos during high-water periods. Examination of stomach contents of a limited number of specimens indicated that the species feeds extensively on filamentous algae and other small-sized plant matter during the dry season.

Etymology.—The specific name, *blohmi*, honors Sr. Tomas Blohm of Caracas, Venezuela, whose generosity in making available the facilities of his ranch, Fundo Pecuario Masaguaral, greatly facilitated research associated with this study.

Comparative material examined.—Epapterus dispilurus: ANSP 21353–4, 2, Peru, Nauta, syntypes of *E. dispilurus*; ANSP 103412, 1, Peru, Contamana; USNM 263114, 1, Peru, Río Ucayali, Pucallpa; USNM 263115, 5, Peru, Río Ucayali, Utoquinia; USNM 261388, 6, Peru, Río Aguaytia, Nuevo Requena; MCZ 9834 and 33450, 4, Brazil, Rio Hyavary [=Rio Javari], syntypes of *Euanemus longipinnis* (=*Epapterus dispilurus*); USNM 261422, 2, Brazil, Ilha da Marchantaria. *Epapterus chaquensis*: USNM 232304, 1, Paraguay, Río Negro.

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Resumen

Una nueva especie de bagre auchenipterido del género *Epapterus* es descrita de la región central de los Llanos de Venezuela pertenecientes a las cuenca del río Orinoco. *Epapterus blohmi* se distingue de *E. dispilurus* y *E. chaquensis*, por la presencia de una banda oscura que se extiende a través de la porción dorsal de los radios procurrentes y del lóbulo dorsal de la aleta caudal. Las especies congenéricas poseen una pigmentación discreta en forma de mancha en el centro de cada lóbulo caudal. Diferencias morfométricas y merísticas permiten diferenciar mas aún las especies. *Epapterus blohmi* y *E. dispilurus* poseen un pronunciado dimorfismo sexual en la forma de los radios anteriores de la aleta anal, la posición de la apertura urogenital, la forma de la espina dorsal y el grado de osificación de la barbilla maxilar. *Epapterus dispilurus*, previamente conocida solo de la

región alta del río Solimoes, es reportada por primera vez para la región central del río Amazonas. La distribución conocida de *E. chaquensis* descrita para Argentina, es extendida para incluir los ríos de Paraguay.

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