

ORBINIIDAE (ANNELIDA: POLYCHAETA) FROM MANGROVE ROOT-MATS IN BELIZE, WITH A REVISION OF PROTOARICIIN GENERA

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Abstract. — Benthic samples taken in root-mats of *Rhizophora mangle* contain four species of orbiniid polychaetes including *Naineris setosa*, and three new taxa, *Protoaricia pigmentata*, new species, *Pettibonella multiuncinata*, new genus and new species and *Pararicia belizensis*, new genus and new species. Recognition of the new genera lead to a preliminary phylogenetic analysis of the genera of the subfamily Protoariciinae, brief characterizations of all genera in the subfamily and the development of a key to genera of the Protoariciinae from world-wide areas.

The mangrove fauna of Twin Cays, Belize, has been under study for several years by a team of scientists under the direction of Dr. Klaus Rützler of the Smithsonian Institution. As part of this overall program, a study of the fauna of the root-mats of red mangroves, especially where these are covered by the green alga, *Caulerpa verticillata* was undertaken by Brian F. Kensley and Kristian Fauchald. The ecological findings will be reported elsewhere (Kensley & Fauchald, in preparation). This paper is the first report on the polychaetes collected during the study; several additional papers are in preparation.

Members of the family Orbiniidae have been reported from sandy and muddy environments world-wide. The subfamily Orbiniinae has been revised repeatedly (Day 1977, and references therein). The subfamily Protoariciinae has been less comprehensively treated. The presence of three new protoariciin taxa in material collected in Belize, including two that did not belong to any known genus, caused us to review the generic subdivision of the subfamily, to update and clarify as much as possible definitions and to attempt a phylogenetic analysis of the subfamily. The subfamily is here

considered monophyletic; a dubious assumption, but without access to very much larger materials than was currently available a more detailed study is not possible.

Materials and methods. — The material was collected by K. Fauchald and B. F. Kensley as part of SWAMP (Smithsonian Western Atlantic Mangrove Program), directed by Dr. Klaus Rützler. The sample localities include West Bay, Twin Cays, and the mainland side of the middle islands in Blue Ground Range (Fig. 1). The habitat sampled was covered with red mangrove forest (*Rhizophora mangle*) varying in height from approximately 1.5 to 5 m and in density from open, isolated trees to dense forest with complete canopies. The microhabitat sampled was the root-mat where this mat was covered with a mat of *Caulerpa verticillata*. Part of the study includes a series of quantitative samples taken over a two-year period from 1979–1981. The samples were taken with a 10.4 cm diameter corer to a depth of approximately 10 cm in the substrate. The resulting core of the peat-like root-mat was gently broken up and screened through a 0.5 mm screen and preserved immediately in 10% neutralized formalin to which had been added Rose Bengal. After

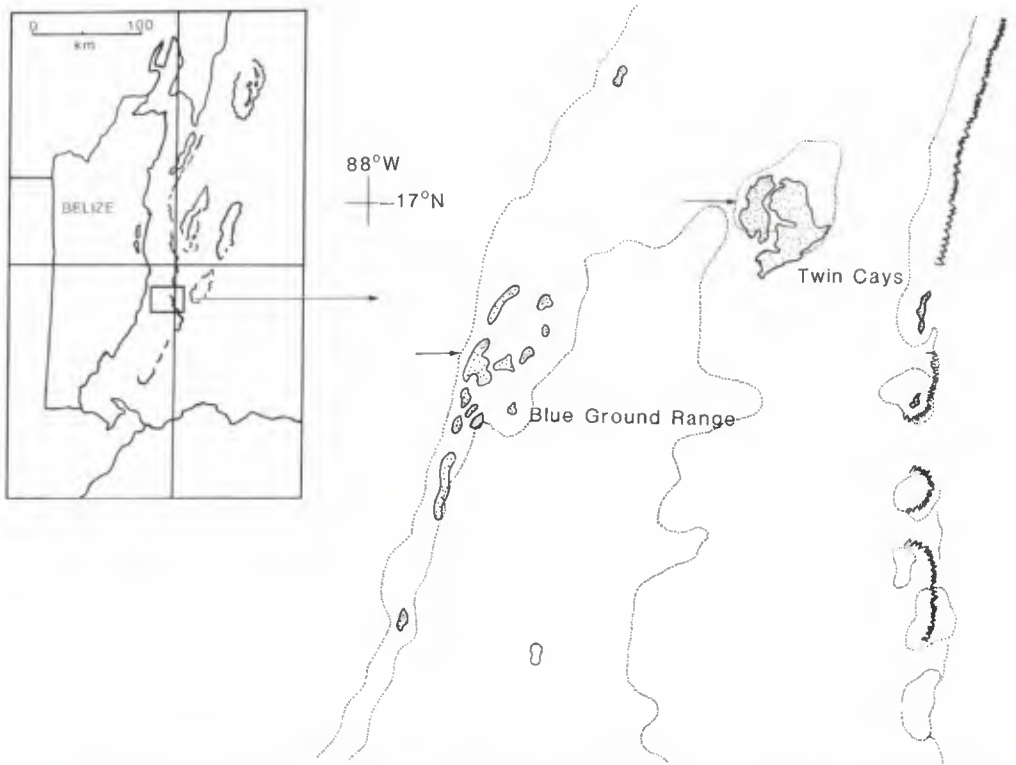


Fig. 1. Study area in Belize. The box to the left indicates the position of the study areas in relation to Belize; the study area is enlarged on the right. The two arrows in the enlargement indicates West Bay, Twin Cays and the un-named cay in the Blue Ground Range at which the collections were made.

24 hours in fixative, the samples were re-screened, and the specimens were sorted out in sea water, washed in freshwater and transferred to 70% alcohol. The samples were later sorted to family and counted.

All illustrations were made with the aid of a camera lucida attached to a stereo or compound microscope.

The morphological terminology is derived from Hartman (1957), Pettibone (1957) and Fauchald (1977). Any new terms used are explained in context. The literature cited include only papers directly used in this study; other papers can be found in the literature sections of the three papers mentioned above. The cladistic analysis was run using the IBM microcomputer version of PAUP 2.4; details are indicated below in the section on cladistic analysis of the genera. The terminology follows the one estab-

lished by Wiley (1981). The character-list is given in Appendix I and the original data table in Table 2.

Station list.—As indicated above, all stations were taken in two locations; each sample consisted of a single numbered core; the core numbers for each of the two localities are given below.

West Bay, Twin Cays, Belize, 10–50 cm water depth; root-mat of *Rhizophora mangle*, covered with *Caulerpa verticillata* core numbers M-1, M-2, M-3, M-5, M-9, M-10, M-11, M-12, M-27, M-32, M-35, M-50, M-51, M-55, M-58, M-59, M-70, M-71, M-88, M-90, M-95, M-96, M-102, M-105, M-107, M-133, M-136, M-137, M-139, M-140, M-142, M-143, M-144, M-145, M-146, M-147 and M-148.

West side of middle cay, Blue Ground Range, Belize, 10–50 cm water depth; root-

Table 1.—Variability of selected morphological features of *Pettibonella multiuncinata*. All specimens included.

| | Range | Mean | SD |
|---|--------|-------|-------|
| Length in mm | 1–20 | 8.01 | 5.21 |
| Number of setigers | 31–110 | 66.83 | 27.12 |
| Number of thoracic setigers | 7–18 | 12.34 | 3.36 |
| Branchiae from setiger number | 6–16 | 9.9 | 4.18 |
| Maximum number of rows of thoracic neuropodial uncini | 2–5 | 3.3 | 0.79 |
| Maximum number of uncini per row, thoracic neuropodia | 2–7 | 4.16 | 1.39 |
| Abdominal thin hooks first present from setiger number | 7–19 | 13.20 | 4.63 |
| Abdominal large hooks first present from setiger number | 6–22 | 14.57 | 3.69 |

mat of *Rhizophora mangle*, covered with *Caulerpa verticillata*, core numbers M-23, M-24, M-78 and M-79.

In addition to the material newly identified from the collections in Belize, we also examined type material and other materials as needed to verify our identifications and to clarify taxonomic uncertainties. This material is listed as previously identified material for each species.

Systematic Results

Family Orbiniidae Hartman, 1942

The two subfamilies, Orbiniinae and Protoriciinae are currently separated only by the presence of one or two asetigerous anterior segments (Fauchald 1977).

Subfamily Orbiniinae Hartman, 1957

Key to genera of this subfamily can be found in Day (1977).

Genus *Naineris* Blainville, 1828

Naineris setosa (Verrill, 1900)

Figs. 2–3

Aricia setosa Verrill, 1900:651–653.

Anthostoma latacapitata Treadwell, 1901: 203–205, figs. 61–65.

Naineris setosa.—Hartman, 1942:61, figs. 116–118.—Hartman 1951:67–70, pl. 17, figs. 1–6.—Hartman, 1957:305, pl. 41, figs. 1–6.

Material examined.—Previously identified material: Bermuda, Platts Inlet, 1898,

coll. A. E. Verrill and party (1 incomplete syntype, YPM 1242). Bermuda, 1901, coll. A. E. Verrill and party; id. M. Pettibone, 1962 (one incomplete specimen, YPM 1384). Bermuda, 1903, coll. W. R. Coc; id. M. Pettibone, 1962 (one complete specimen, YPM 1303). Bermuda; id. M. Pettibone (one incomplete specimen, USNM 34092). Bermuda, SE of Causeway, 1979, coll. & id. S. Gardiner (12 specimens).

Newly identified material: Belize, West Bay, Twin Cays and Blue Ground Range, 1979–1981, coll. K. Fauchald and B. F. Kensley M-11 (5, USNM 120928); M-12 (1, USNM 120932); M-23 (2, USNM 120935); M-24 (1, USNM 120938); M-90 (1, USNM 120955).

Description.—The description is based on the specimen referred as the syntype above, supplemented by notes on other material. No additional type material is currently available. The syntype is an incomplete fragment of 150 segments measuring 58 mm. It is widest at midthorax, 1.63 mm without, 3.83 mm with parapodia; the anterior abdomen is 1.53 mm without and 2.83 mm with parapodia; the posterior abdomen is 1.33 mm without and 2.4 mm with parapodia. Color as preserved, brown.

The prostomium is broadly truncate to T shaped (Fig. 2a). Two diffuse, deeply embedded eyespots are present. Two shallow, comma-shaped grooves are present dorsally at the posterior end of the prostomium.

The peristomium is a broad, asetigerous

Table 2.—Character-states scored for protoariciin genera. Inappropriate or missing information marked with a dash.

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|-----------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| <i>Orbiniella</i> | 1 | 1 | - | - | 1 | 2 | 0 | 0 | 0 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 0 | 1 | - | 2 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 |
| <i>Proscoplos</i> | 1 | 2 | 4 | 1 | 1 | 2 | 8 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 2 | 2 | - | 1 | 1 | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 2 |
| <i>Protoaricia</i> | 1 | 1 | 4 | 1 | 2 | 2 | - | 3 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | |
| <i>Protoariciella</i> | - | 1 | 6 | 1 | 2 | 2 | 6 | 4 | 2 | 2 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | - | 2 | - | 2 | 1 | 2 | 1 | 1 | - | 2 | 1 | 2 | 1 | |
| <i>Schroederella</i> | 1 | 1 | 4 | 1 | 2 | 1 | - | - | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 3 | 1 | 1 | 1 | 7 | 1 | 2 | 2 | 1 | 1 | 2 | 2 | 1 | 2 | 2 | |
| <i>Pettibonella</i> | 2 | 2 | 4 | 2 | 2 | 3 | 9 | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 3 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 |
| <i>Pararicia</i> | 1 | 2 | 4 | 1 | 3 | 2 | 6 | 3 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 2 | 2 | |
| <i>Scolopella</i> | 2 | - | - | - | 1 | 1 | - | 4 | - | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | - | - | 2 | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | |
| <i>Leitoscoplos</i> | 0 | 2 | 2 | 1 | 2 | 2 | 1 | 8 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 2 | 2 | 0 | 2 | 1 | 1 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | |



segment; the mouth is more than $\frac{2}{3}$ of the total width of the peristomium. The ever-visible pharynx is not everted in the syntype; it is everted and illustrated as present in another Bermudian specimen (YPM 1303, Fig. 2b).

The thorax consists of 20 biramous setigers, fully developed by setiger 5. The notopodial postsetal lobes are foliaceous, broadest at two-thirds distance from the base. The neuropodial postsetal lobes are shorter, broader and rounder than corresponding notopodial lobes. They bear an upper digitiform papilla which is longer anteriorly than posteriorly (Fig. 2c). Statocysts are visible as oval spots dorsally, anteromedial to the branchiae. Setigers 21 to 25 are transitional, characterized by a diminishing number of neuropodial setae both in number of rows and in number of setae in each row. The parapodia become gradually more dorsal. The abdomen begins at setiger 25. The notopodial postsetal lobes become slenderer and progressively shorter towards the posterior abdomen. The corresponding neuropodial lobes become sharply reduced in size and foliaceous in shape (Fig. 2d), instead of round. Low dorsal ridges are present from the beginning of the abdomen, becoming less conspicuous towards the end of the fragment. No neuropodial subpodial lobe is present either in anterior or middle abdominal segments.

Branchiae appear, in all specimens studied, in setiger 6. However, in the syntype, a stout, unpaired bifid structure is found on one side in the position where branchiae are located on later setigers. This feature seems to be an abnormality of the specimen rather than a feature normally associated with the

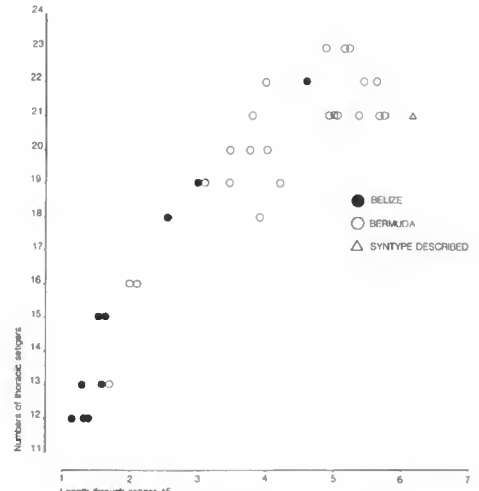


Fig. 3. Relationship between length through setiger 15 and number of thoracic setigers in *N. setosa* from Belize and Bermuda.

species (Fig. 2a). From setiger 6, normal paired branchiae appear. They are digitiform, elongate, held erect over the body or recumbent along the dorsum. They are similar in length to the notopodial lobes but slenderer in the thoracic region, whereas in the abdominal region they are longer and broader than the corresponding notopodial lobes. They are present to the end of the fragment, and to the end of the body in all the complete specimens.

The thoracic notopodia have long crenulate capillary setae aligned in about three irregular rows and totalling approximately 25 or 30 setae per notopodium. The neuropodial thoracic setae are all crenulate capillaries. They are shorter than the notopodial setae and positioned in two bundles: 1). Approximately eight irregular, longitudinal palisaded rows, each bearing about 25 such setae, and 2). Approximately four irregular

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Fig. 2. *Naineris setosa*: a, Anterior end of syntype, dorsal view; b, Anterior end of syntype, YPM 1303, showing evaginated pharynx; c, Right parapodium setiger 12, syntype, anterolateral view; d, Left parapodium, setiger 49, syntype, anterolateral view; e, Right parapodia, setigers 17–18, syntype, dorsal view; f, Abdominal uncinus, setiger 49, syntype; g, Furcate seta, abdominal setiger, CBC-M-11; h, Posterior end, CBC-M-11; i, Anterior end, dorsal view, CBC-M-11; j, Anterior end, dorsal view, CBC-M-90. Scales: a, b, e, 1 mm; c, d, h–j, 100 μ m; f, g 10 μ m.

diagonal palisaded rows, posterior to the first bundle, each bearing 14 to 18 setae (Fig. 2e). In the abdomen, the number of setae decreases to about a dozen or less in both rami, although they are more abundant in the notopodium than in the neuropodium. Furcate setae are present in some abdominal notopodia but are difficult to observe. They have a delicately spinous shaft and two distal tines of different length (Fig. 2g). In the abdominal neuropodia, in addition to the crenulate setae two or three straight, bluntly pointed uncini appear (Figs. 2d, f).

The syntype is incomplete, and the only complete specimen from YPM, has a damaged pygidium. The pygidium in a complete specimen from Belize (CBC-M-11, Fig. 2h) is elongate with three (probably originally four) elongate distally tapering anal cirri. Anal aperture is terminal and central.

Comparison of specimens from Belize and Bermuda.—The specimens newly identified agree fairly well with both type material and earlier descriptions. The main differences noted are:

1) The prostomium can be either T shaped or rounded.

2) In specimens with rounded prostomia numerous eyes are present, scattered between the middle and the posterior end of the prostomium (Fig. 2i). In specimens with T shaped prostomia, the eyespots are formed into two to four sickle shaped dark areas located at the posterior end of the prostomium; occasionally some additional small isolated spots are present (Fig. 2j).

3) The number of thoracic setigers varies from 13 to 23.

4) The two separate groups of thoracic neurosetae are distinct only in larger specimens. Smaller specimens have only one bundle with fewer rows and fewer setae per row than in the syntype.

In order to determine if the number of thoracic setigers and the shape of the prostomium are size-related features, we did a least squares regression correlating the

number of thoracic setigers of the specimens with the length of the 15 first setigers. The results show a high correlation between the two ($r = 0.91$). There is no significant correlation between the different prostomial shapes and the size of the organism ($r = 0.37$).

Figure 3 shows that in general, the Belize specimens reach maximum number of thoracic setigers at a smaller size than do the Bermuda specimens. There is no consistent trend in relation between numbers of thoracic setigers and length in the material from Bermuda. Especially the syntype is very long in relation to the number of thoracic setigers. The differences among the populations are not sufficient to recognize them, even at the subspecies level, but are useful in allowing us to expand and quantify the description of the species.

Hartman (1957) stated that neuropodial subpodial lobes should be present in this species; a feature not mentioned by Verrill (1900) in the original description nor mentioned in any other review. We examined part of the material listed by Hartman (1957) including the specimens used to make the illustrations for that paper and failed to find subpodial lobes in any of the specimens. We assume that the subpodial lobes as mentioned and illustrated by Hartman (1957) represent a *lapsus calami*, and that such lobes are normally absent in the species.

Habitat.—Subtidal, probably euryhaline species associated with vegetation (*Thalassia testudinum* beds, algal mats and *Rhizophora mangle* root-mats). Substrate may be sandy, sandy mud, or mangrove root-mats with minimal sediment. Locally present both in West Bay, Twin Cays and at Blue Ground Range (Fig. 1).

Distribution.—*N. setosa* has been reported from Bermuda (type locality), various localities in the Gulf of Mexico (Perkins & Savage 1975; Hernandez-Alcántara & Solis-Weiss 1989), Puerto Rico (Treadwell 1901), and Acapulco, Mexico (Hartman 1957).

Subfamily Protoariciinae Hartman, 1957
Preliminary Phylogenetic Analysis of the
Protoariciin Genera

This analysis of putative relations among the protoariciin genera is based on several assumptions. First, the subfamily is assumed to be monophyletic; this assumption cannot be justified without a complete analysis of the whole family, or indeed the order to which the family will eventually be referred (its current assignment is unsatisfactory).

A second major set of assumptions can be summarized by the choice of the genus *Leitoscoloplos* among the Orbiniinae as outgroup. Members of this genus are characterized first and foremost by lacking all modified setae in the thorax, and by the extreme simplicity of the acicular spines in the abdomen, in addition to the simple structure of the parapodial lobes and branchiae. The choice thus polarizes all more complex features, such as the presence of complex parapodial lobes, the presence and structure of various kinds of thoracic hooks and even the loss of certain features, such as branchiae, as apomorphic features. The procedure has the advantage of simplicity: without information to the contrary, it appeared simpler to assume that all more complex features were apomorphic, rather than randomly select some as being plesiomorphic and others as apomorphic. Resolution of this issue cannot come until possible relations among all orbiniids and between the orbiniids and the related families have been analyzed in detail.

The features used to characterize the genera are those traditionally used in orbiniid systematics (Day 1954, Fauchald 1977). The initial list contained 41 characters; the list was reduced to 31 characters by exclusion of features invariant among the taxa considered (including the outgroup) and of certain features that were so poorly known for most members of the group that they could

not be coded (numbers of abdominal segments present for example). Appendix 1 lists the characters and character-states included in the analysis. Multistate characters are listed as transformation-series.

The character matrix was run on PAUP using the ALLTREES option (cfr. documentation for PAUP as issued with the program).

Four trees were found, the consistency index was 0.670 and length was 88 for all four. All four trees plus a consensus tree is presented in Fig. 4. The four trees have several features in common. *Protoariciella*, *Schroederella* and *Scoloprella* are grouped together in all four trees. *Orbiniella* which is mainly characterized by the loss of various features, nevertheless is defined by unique autapomorphies. In three of the four trees, *Protoaricia* and *Pararicia* show a unique synapomorphy and emerge jointly; in the last tree this character-state is interpreted as having being a reversal. In all four trees the two genera emerge next to each other. The presence of the curved hooks (called swan-shaped in *Proscoloplos*) is a unique synapomorphy joining *Pettibonella* and *Proscoloplos*.

All internal nodes are supported by various apomorphies in all four trees. All four trees are defined by synapomorphies. None of the nodes is exclusively supported by reversals or parallelisms, or exclusively by synapomorphies created by various states in transformation series. All tree-topologies and a strict consensus tree are shown in Fig. 4. All taxa, including the two genera are supported by autapomorphies.

The consensus tree demonstrates that the summary given above cannot be expanded upon. The character-sequence used to define the four trees differ and different transformation-series have been reversed in each tree. Without additional information the "correct" reading of this series cannot be confirmed.

The analysis was undertaken to examine

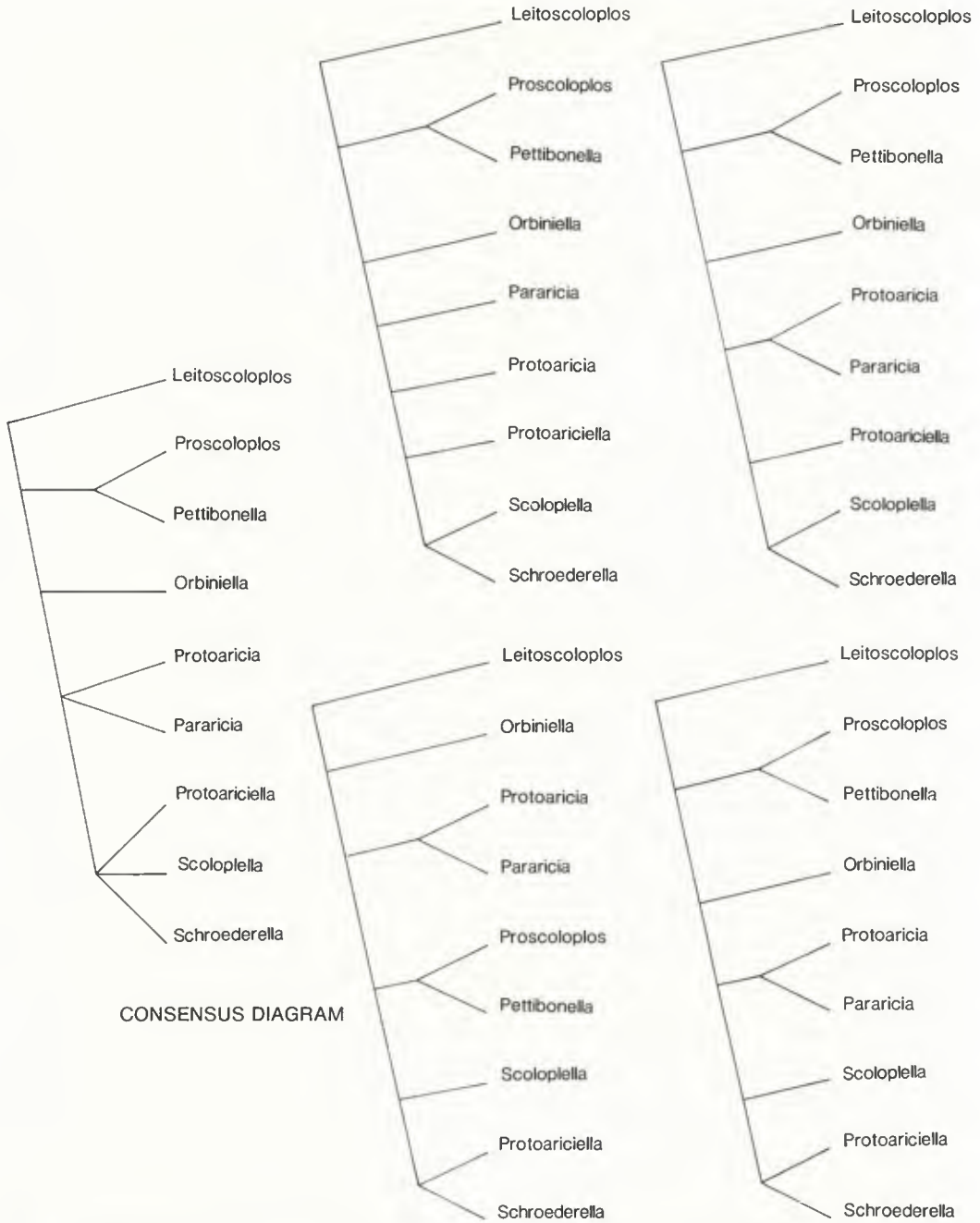


Fig. 4. Cladograms showing possibly phylogenetic relations among the genera of the Protoariciinae. Further explanation in the text.

the level of support for previously described genera and compare them to the newly described genera. We feel justified in erecting the new genera: They represent unique combinations of features otherwise not present in the subfamily, but recognize that the validity of all genera may again be tested when the whole family is being analyzed.

Key to Genera of Protoariciinae

- 1. Branchiae absent *Orbiniella*
- Branchiae present 2
- 2. Transition between thorax and abdomen indistinct *Protoariciella*
- Transition between thorax and abdomen distinct, transitional segments may be present 3
- 3. Only crenulated capillaries present *Scolopella*
- Crenulated capillaries and other kinds of setae present 4
- 4. Abdominal hooks acicular 5
- Abdominal hooks otherwise 7
- 5. Prostomium acutely pointed; anus dorsal *Schroederella*
- Prostomium distally rounded; or bluntly conical; anus terminal 6
- 6. Thorax with mucronate setae and subuluncini in addition to crenulated capillaries *Protoaricia*
- Thorax with crenulated capillaries only *Pararicia*
- 7. Abdominal hooks of a single kind *Proscoloplos*
- Abdominal hooks of two different kinds *Pettibonella*

Brief Generic Characterizations

The new genera are defined in place in the text.

Orbiniella Day, 1954, type species *O. minuta* Day, 1954. Prostomium rounded or pointed. Branchiae absent. All thoracic setae crenulate. Thoracic notopodial setal lobes indistinct; notopodial postsetal lobes reduced; neuropodial postsetal lobes single, rounded. Two transitional segments pres-

ent. Abdominal setae crenulated capillaries, acicular setae and sometimes furcate setae. Anus terminal.

Proscoloplos Day, 1954, type species *P. cygnochaetus* Day, 1954. Prostomium rounded. Eyes absent. Branchiae from setiger 8. All thoracic setae crenulated capillaries. Thoracic notopodial setal lobes indistinct. Notopodial and neuropodial postsetal lobes tapering. Abdominal setae crenulated capillaries and one or two swan-shaped hooks. Anus terminal with four tapering anal cirri.

Protoaricia Czerniawsky, 1881, type species *Aricia oerstedii* Claparède, 1864. Prostomium rounded. Two eyes. Branchiae limited to abdominal segments. Thoracic setae crenulated capillaries, hooks and subuluncini. Thoracic notopodial setal lobes distinct. Notopodial and neuropodial postsetal lobes tapering. No transitional segments present. Abdominal setae crenulated capillaries and neuropodial uncini. Anus terminal with four blunt anal papillae or anal cirri absent.

In the original description of the type species, Claparède (1864), stated that the dorsal (notopodial) rami in the abdomen were bifurcate; no types are available of any of Claparède's species (cfr. Fauchald, in prep.). Specimens from the Mediterranean Sea (off Málaga, Spain and off Marseille, France lack bifurcate abdominal notopodia (see discussion below).

Protoariciella Hartmann-Schröder 1962a, type species *P. uncinata* Hartmann-Schröder, 1962a. Prostomium rounded. Two eyes. Branchiae from setiger 6 or 8. Thoracic notosetae all crenulated capillaries. Abdominal notosetae crenulated capillaries and acicular setae. Neurosetae include crenulated capillaries, thick, tridentate hooks, slender acicular setae with flattened teeth and thick, smooth spines. Separation between thorax and abdomen indistinct. Anus terminal; anal cirri absent.

Schroederella Laubier, 1962, type species *S. pauliani* Laubier, 1962. Prostomium

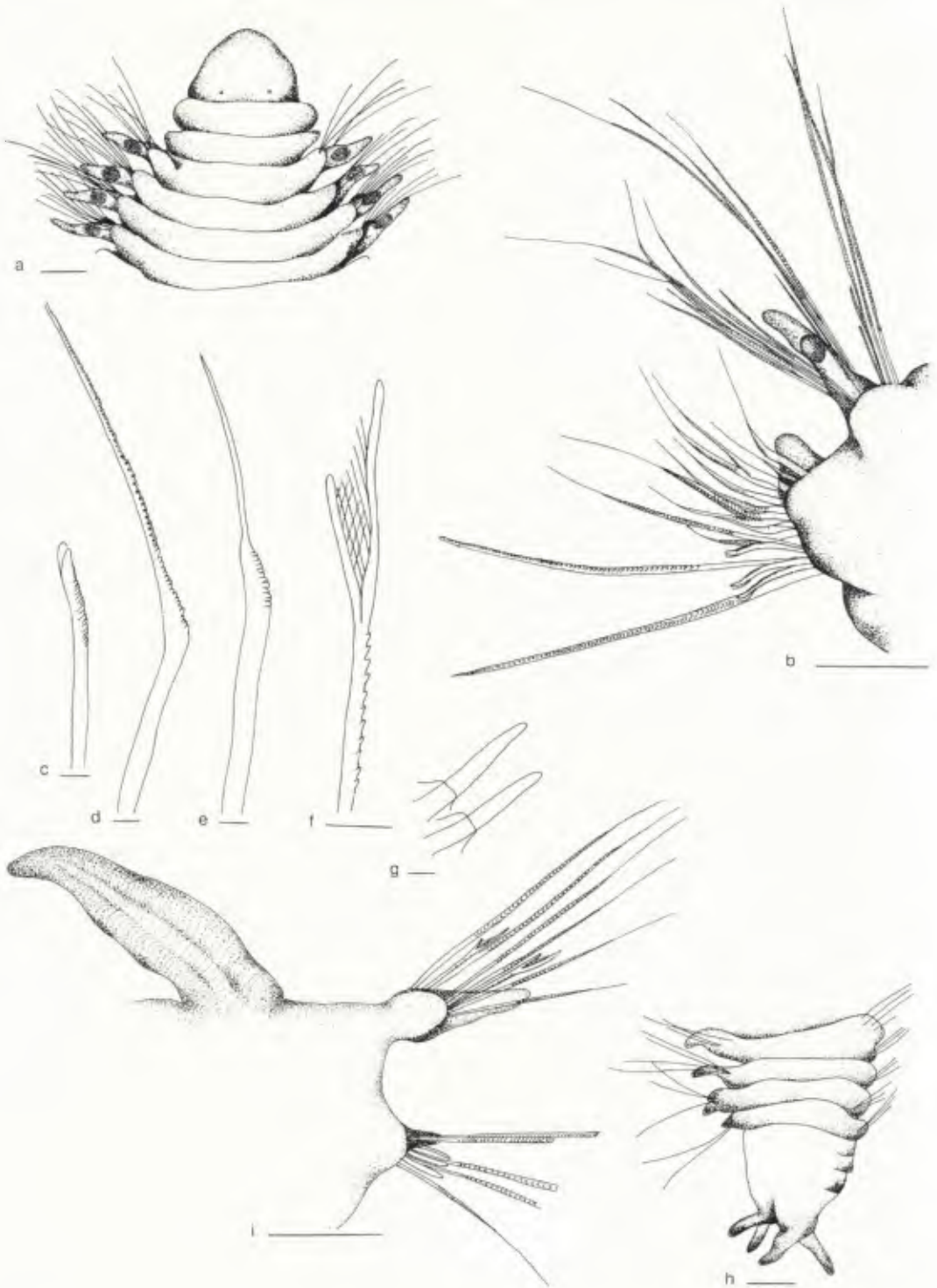


Fig. 5. *Protoaricia pigmentata*: a, Anterior end, holotype, dorsal view; b, Left parapodium, setiger 6, holotype, anterolateral view; c, Hooded hook, setiger 5, holotype; d, Subuluncinus, setiger 5, holotype; e, Mucronate seta,

acutely pointed. Two eyes. Branchiae on abdomen only. Parapodia poorly developed; thoracic notopodial postsetal lobes digitiform, increasing in size posteriorly; thoracic neuropodial postsetal lobes single, rounded. Thoracic setae crenulated capillaries and straight neuropodial uncini. Abdominal notopodial and neuropodial postsetal lobes tapering. Abdominal setae crenulated capillaries and slender, pointed notopodial aciculae and hooded, thick neuropodial aciculae. Transitional segments present. Anus distinctly dorsal with 4 anal lobes.

Scolopella Day, 1963, type species *S. capensis* Day, 1963. Prostomium pointed. Eyes absent. Branchiae present from mid-abdominal segments. All postsetal lobes rounded. Parapodial rami reduced. All setae crenulated capillaries. Anus terminal.

The genus *Scoloplosia* proposed by Rulier, 1972, was synonymized with *Protoaricia* by Ben-Eliahu (1976). This synonymy is here accepted.

Genus *Protoaricia* Czerniawsky, 1881

Protoaricia pigmentata, new species

Fig. 5

Material examined.—M-78 (one, holotype, USNM 120950, two paratypes, USNM 120951); M-79 (three paratypes, USNM 120952, one paratype Australian Museum; three paratypes British Museum (NH) and two paratypes Zoological Museum Hamburg).

Description.—Holotype with 8 thoracic and 55 abdominal setigers for a total of 63; transitional setigers absent. Total length 5.4 mm; width at midthorax 0.8 mm and 0.54 mm in posterior abdomen. Length of other types 3 to 6.5 mm. Body somewhat flattened dorsoventrally; widest at midthorax. Color, as preserved, white with scattered

brown dorsal pigmentation in branchial region to mid-abdomen in some specimens. Brown, circular postsetal patch on each notopodial thoracic lobe about two thirds from base, through mid-abdomen in most specimens (Fig. 5a, b).

Prostomium frontally round and wider at base. Two small round eyes deeply embedded, occasionally very difficult to see; located towards peristomial boundary (Fig. 5a). Peristomium and asetigerous segment clearly defined on all sides. Mouth, with lateral lips more than two thirds of ventral peristomial width. Pharynx not everted in any specimen.

All parapodia biramous. Thoracic notopodial postsetal lobes elongate, cirriform; widest at proximal two-thirds of length (Fig. 5b). Thoracic neuropodial postsetal lobes shorter, wider and rounder than corresponding notopodial lobes; upper digitiform papillae present on lobes (Fig. 5b). Abdominal parapodia located slightly more dorsally than thoracic ones (Fig. 5i). Abdominal notopodial postsetal lobes similar to thoracic notopodial postsetal lobes; becoming reduced in far posterior setigers. Abdominal notopodial and neuropodial postsetal lobes reduced last one to four setigers; upper papillae of neuropodia elongate; cirriform in anterior and mid-abdomen; shorter in far posterior setigers.

Branchiae in holotype from setiger 8; missing on last two setigers; in paratypes from setigers 6–9 and missing in last two to four setigers; foliaceous, spionid-like, elongate, never overlapping; recumbent (Fig. 5i). First pair shorter and slenderer than other branchiae. Branchiae longer and wider than notopodial lobes through mid-abdomen; thereafter distinctly reduced and more cirriform.

Thoracic notopodial setae distinctly long-

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setiger 5, holotype; f, Abdominal furcate notoseta, holotype; g, Abdominal neuropodial uncinus, holotype; h, Posterior end, dorsal view, holotype; i, Right parapodium, setiger 36, from one of the paratypes, anterolateral view. Scales: a, b, h, i, 100 μ m; c–g, 10 μ m.

er than abdominal notopodial setae; capillary crenulate setae long, slender and more abundant in thorax than in abdomen; furcate setae present from thorax (Fig. 5f); single or at most two in a notopodium. Thoracic neuropodial capillary crenulate setae shorter than corresponding notosetae; three or four mucronate setae, up to five subuluncini and up to three thinly hooded, distally tapering hooks present in thoracic neuropodia (Figs. 5c–e). Mucronate setae in upper end of setal bundles; subuluncini in middle and hooks in lower end of bundles (Fig. 5b). In the abdomen only three to five crenulate and one or two furcate neurosetae present; subuluncini, mucronate setae and hooded hooks absent; two to three slightly sigmoid, distally tapering hooks without hoods present (Figs. 5i, g).

Pygidium elongate with four large papillae; each terminated by a slender digitiform cirrus of variable length (Fig. 5h). The anal aperture is central and terminal. Tubes absent.

Etymology.—The specific name refers to the characteristic brown color patterns present in specimens of this species.

Discussion.—Among the described species of *Protoaricia*, this species resembles *P. oerstedii* (Claparède) and *P. capsulifera* (Bobretzky) more than *P. minima* (Rullier). The types of *P. oerstedii* and *P. capsulifera* are unavailable. The discussion is based on the original descriptions and illustrations and in the case of *P. oerstedii*, on observations on specimens from the Mediterranean Sea (Cap Couronne, near Marseille, France and near Málaga, Spain).

According to the literature (Claparède 1864, Bobretzky 1870, Eisig 1914, and Fauvel 1927), *P. oerstedii* and *P. capsulifera* are much larger (13 to 15 mm) than *P. pigmentata*. *P. capsulifera* and *P. pigmentata* have very short segments, up to 77 for 6 mm in length; in contrast *P. oerstedii* has only 52 segments for the same length.

In descriptions of *P. oerstedii*, branchiae are said to begin on the first abdominal se-

tiger, reported as setiger 12, the abdomen is flattened posteriorly, notopodial lobes are bifurcate and two or three straight aciculae are present in the posterior notopodia; only one to two uncini are reported present in each abdominal neuropodium (Claparède 1864, Eisig 1914, Fauvel 1927). In the Mediterranean material however, branchiae begin well after the first abdominal setiger (12–14, but the thorax has only six to nine setigers).

In *P. pigmentata* the abdomen is nearly cylindrical; the notopodial lobes are never bifurcate; distinct abdominal aciculae are absent and we commonly found three abdominal neuropodial uncini, even in small specimens. Branchiae are present from the last thoracic setiger.

Possible differences in pygidial structures present a problem: Bobretzky's illustration of *P. capsulifera*, shows the pygidium to be very similar to that of *P. pigmentata*. Fauvel's illustration of the pygidium of *P. oerstedii* is in lateral view, making it impossible to determine accurately the distribution and length of various papillae; Fauvel's description is uninformative in that it only refers to the pygidium as having four short round cirri. The Mediterranean specimens have all short anal papillae rather than distinct cirri. Statocysts are present in both *P. oerstedii* and *P. capsulifera* and absent in *P. pigmentata*. In the description of *P. capsulifera*, no mention is made of the mucronate setae or subuluncini, nor are they illustrated.

Rullier (1972) did not mention the number of thoracic setigers, the shape of the thoracic region, or the shape of the pygidium for *P. minima*. Rullier (1972) reported branchiae absent and on the strength of this feature created a new genus, *Scoloplosia* for it: Ben-Eliahu (1976) synonymized it with *Protoaricia* since her largest specimen of the same species had branchiae "from setigers 13 to 16"; that is, from one of the abdominal setigers as in the other species of *Protoaricia*. In addition, *P. minima* differs from our specimens in the following characters: Eyes

are absent in *P. minima*. The branchiae, are fingerlike from the start in *P. minima*, not foliaceous as in *P. pigmentata*. Ben-Eliahu (1976) did not mention presence of mucronate setae for *P. minima* and Rullier (1972) specifically stated that subuluncini and mucronate setae were absent in his material. *P. minima* also has one or two abdominal neuropodial uncini rather than three as present in *P. pigmentata*.

Distribution.—The species is known only from Blue Ground Range, Belize (Fig. 1).

Pettibonella, new genus

Diagnosis.—Prostomium rounded or conical, usually with two eyespots. Two anterior asetigerous segments. Branchiae deciduous, present from thoracic region, becoming longer than notopodial postsetal lobes in abdominal region. Notopodial postsetal lobes well developed in thorax and abdomen, neuropodial postsetal lobes well developed only in thorax. Notosetae include crenulate capillaries only. Neurosetae in thorax and abdomen include crenulate capillaries (shorter than notosetae) and uncini in thorax; a few crenulate capillaries and two different kinds of dentate hooks in abdomen. The pygidium with four digitiform anal cirri.

Because of obvious close similarities between *Proscoloplos* and *Pettibonella*, we compared *Proscoloplos cygnochaetus*, the type species, and *P. confusus* Hartmann-Schröder, 1962b, the only other species in the genus, to our new species. The type material of *P. cygnochaetus* (British Museum (Natural History), ZK 1955.3.20.1–6) was examined as were the types of *P. confusus*.

In *Proscoloplos* eyes are absent, rather than present. Branchiae are rounded, with glandular cells and much shorter than in *Pettibonella*. Only a few crenulate capillaries are present in the thoracic setigers in *Proscoloplos*; these setae are abundant in *Pettibonella*, and in the latter there are, in addition, several neuropodial thoracic uncini. The dis-

tinctive swan-shaped hooks are present singly or at most paired in *Proscoloplos* and they differ little in size or shape where paired; in *Pettibonella* two kinds of hooks, differing in size and shape are present.

Etymology.—This genus is named in honor of Dr. Marian H. Pettibone, Emeritus Zoologist of the Smithsonian Institution, in recognition of her excellent work on polychaete systematics.

Type species.—*Pettibonella multiuncinata*, new species.

Pettibonella multiuncinata, new species

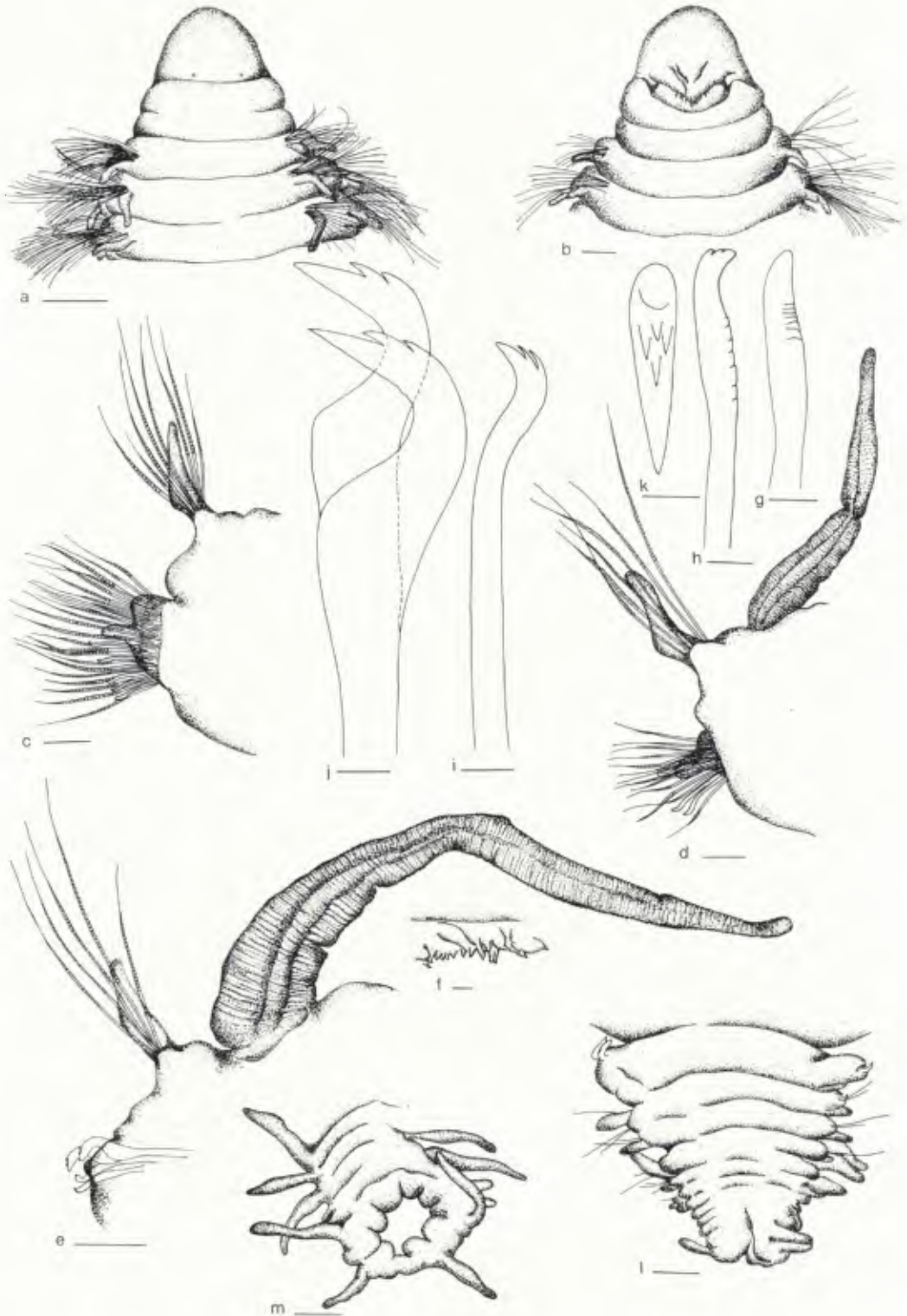
Fig. 6, Table 1

Material examined.—M-1 (one specimen); M-2 (1); M-3 (1); M-9 (one paratype, USNM 120926); M-11 (1); M-12 (8); M-23 (13); M-24 (1); M-27 (5); M-32 (1); M-35 (4); M-50 (2); M-51 (2); M-55 (8); M-59 (1); M-70 (1); M-71 (1); M-88 (4); M-90 (2); M-95 (3); M-96 (6); M-102 (1); M-105 (1); M-107 (1); M-139 (4); M-140 (3); M-142 (1); M-143 (3); M-144 (4); M-145 (1, holotype, USNM 120971, one paratype USNM 120972); M-146 (three paratypes, USNM 120973); M-147 (4); M-148 (1).

Description.—Holotype with 15 thoracic and 75 abdominal setigers, for a total of 90; total length 16mm, greatest width (in thorax) approximately 0.8 mm excluding parapodia. Body somewhat flattened dorsoventrally, especially in anterior region. Color as preserved, white.

Prostomium conical, with two deeply embedded eyespots near peristomial boundary (Fig. 6a). Peristomium partially fused ventrally to next segment. Mouth two-thirds of ventral width of peristomium; lips lateral (Fig. 6b). Pharynx not seen in any specimen. Division between asetigerous segments distinct laterally, indistinct dorsally or ventrally, but never simultaneously on both sides.

Branchiae from setiger 9; missing in last two setigers; elongate, flattened, broad based.



Some branchiae with middle constrictions (Fig. 6d). Branchiae deciduous with no obvious glandular cells; branchial surface with minute digitiform papillae (Fig. 6f). First branchiae shorter than notopodial lobes; increasing in length towards posterior end, becoming between three and five times longer than notopodial lobes (Fig. 6e). Most branchiae held erect over the dorsum; some recumbent. All parapodia biramous.

First notopodium with filiform postsetal papillae; first neuropodium with similar, somewhat shorter postsetal lobes. Following notopodial postsetal lobes increasing in length. From setiger 2 neuropodial postsetal lobes unequally bilobed; superior part distally rounded; inferior part digitiform and longer than superior part (Fig. 6c). Bilobed neuropodial postsetal lobes best developed at about setiger 5–6, decreasing towards end of thorax. Inferior part disappearing gradually towards end of thorax (Fig. 6d); absent in abdomen.

Thoracic setae of two kinds: crenulate capillary noto- and neurosetae, and neuropodial uncini. First setiger with a bundle of approximately 10 notopodial crenulate capillary setae, and 15 or more neuropodial crenulate setae in a fan-shaped array. Notopodial crenulate setae increasing in length, but numbers remaining roughly constant through thorax. Crenulate neurosetae increasing dramatically in numbers; becoming arranged in irregular rows forming fan-shaped total arrays. Four rows of crenulated neurosetae present in setigers 5–6. In setigers 13–15 number of crenulate neurosetae decreasing to six or seven. In abdomen two short crenulate neurosetae present. From setiger 2 to end of thorax, up to five uncini

in a vertical row ventralmost in each neuropodium. Uncini yellow, shafts straight; distally bent, blunt tipped; with 7–12 flattened transverse scales (Fig. 6g); tips sometimes worn resulting in tooth-like structures being formed (Fig. 6h). In transitional segments (13–15) uncini with two terminal teeth.

Transition from thorax to abdomen marked at setiger 16 by reduction in number of neuropodial crenulate setae and replacement of thoracic uncini by two tridentate hooks (Fig. 6i). Transition region also with reduction of postsetal lobes and progressively more dorsal position of parapodia.

Tridentate hooks without hoods located ventrally with cutting edges facing dorsally (Fig. 6i). Hooks of setiger 16 intermediate in shape between thoracic uncini and fully formed hooks of middle abdomen (i.e. teeth present but hooks more elongate than in following setigers). From setiger 17, another kind of hook present, facing the other two hooks in a vis-a-vis position. In setigers 17–20, all hooks increasing gradually in width, especially subterminally. Where fully developed, large hooks with large main fangs surmounted by four denticles in a rhomboid arrangement (Fig. 6j, k); shafts distinctly inflated below rostrum. Usually one large hook and two slender hooks in a setiger; occasionally and scattered, some setigers with two large hooks parallel to each other; facing either two or three slender hooks. Branchiae distinctly reduced and hooks are absent in last three parapodia and last two parapodia asetigerous.

Pygidium elongated with four slender, digitiform cirri; two dorsal cirri longer than ventral ones. Pygidial cirri retracted or

Fig. 6 *Pettibonella multiuncinata*: a, Anterior end, holotype, dorsal view; b, Anterior end, holotype, ventral view; c, Left parapodium, setiger 6, holotype, anterolateral view; d, Left parapodium, setiger 12, holotype, anterolateral view; e, Left parapodium, setiger 60, holotype, anterolateral view; f, Branchial edge, setiger 60, holotype; g, Thoracic uncinus, setiger 6, holotype; h, Thoracic uncinus, setiger 12, holotype; i, Slender neuropodial abdominal hook, setiger 82, holotype; j, Large neuropodial abdominal hook, setiger 82, holotype; k, Large neuropodial abdominal hook, setiger 82, holotype, view from distal end; l, Posterior end, ventral view, holotype; m, Pygidium, CBC-M-9. Scales: a–c, l, m, 100 μ m; f–k, 10 μ m.

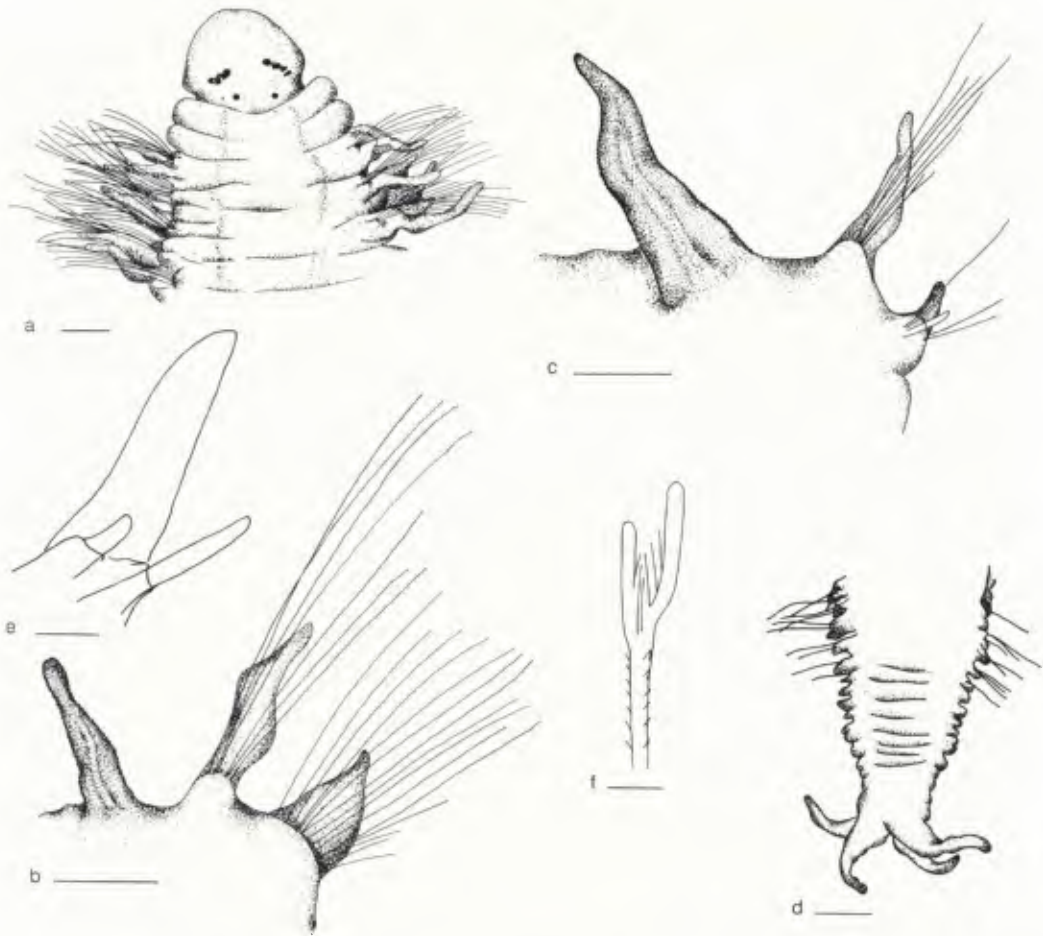


Fig. 7. *Pararicia belizensis*: a, Anterior end, holotype, dorsal view; b, Right parapodium, setiger 8, holotype, anterolateral view; c, Right parapodium, setiger 33, holotype, anterolateral view; d, Posterior end, holotype, dorsal view; e, Abdominal uncini, setiger 33, holotype; f, Furcate notoseta, setiger 9, holotype. Scales: a-d, 100 μ m; e, f, 10 μ m.

damaged (Fig. 6l) in some specimens. Anal aperture terminal, central; surrounded by about nine papillae (Fig. 6m).

Holotype without tube; some paratypes are covered with fragments of tubes in middle abdominal region. Fragments thin, transparent and covered with sand grains of varying sizes; very small shell fragments and vegetal debris.

Etymology.—The specific name refers to the very distinctive hooks present in this species.

Discussion.—The occurrence of some fea-

tures is size dependent: The total number of setigers can vary from 32 to 106. The branchiae usually appear at setiger 9 but may be present from setiger 6 to 8. The number of thoracic segments and hence the first appearance of the abdominal hooks, is also size dependent. The variation of these and other characters is summarized in Table 1.

Habitat.—The species is equally well represented both at Twin Cays and Blue Ground Range (Fig. 1), taking the relative sample density into account.

Pararicia, new genus

Diagnosis.—Prostomium rounded, with two to numerous eyes, two asetigerous thoracic segments present; branchiae from one of the thoracic setigers. Notopodial setae include crenulate capillaries and furcate setae. Thoracic neuropodial setae shorter than crenulate capillary setae; thoracic uncini absent. Abdominal neuropodial setae, a few crenulate capillaries in addition to smooth acicular uncini. Four fingerlike anal cirri present.

Etymology.—Derived from the old generic name *Aricia* used in this family.

Type species.—*Pararicia belizensis*, new species.

Pararicia belizensis, new species

Fig. 7

Material examined.—M-3 (one specimen); M-5 (4); M-10 (1); M-11 (one, holotype, USNM 120930, one paratype, USNM 120931); M-12 (2); M-23 (5); M-24 (one paratype, USNM 120939); M-35(1); M-88 (two paratypes, USNM 120953); M-133 (one paratype, USNM 120962); M-135 (1); M-136 (1); M-147 (1).

Description.—Holotype complete with 68 setigers; length 4 mm, greatest width, in thorax, approximately 470 μm , without parapodia. Body slightly more flattened dorso-ventrally and wider in thoracic than in abdominal region. Abdomen tapering posteriorly with reduced parapodia in last 15 setigers. Length of other complete specimens from 2 to 9 mm; number of setigers from about 30 to 70. Color as preserved white. Thorax with 10 setigers; abdomen with 58 setigers, including first four transitional setigers.

Prostomium rounded with many eyespots. Two of those are round, clearer and present at the posterior end of the prostomium. The rest are divided in two roughly comma-shaped groups of eyespots at the middle region of the prostomium. No ap-

pendages are present (Fig. 7a). In smaller specimens, only two small, round, widely separated eyes are present, near the posterior boundary with the peristomium.

The first two asetigerous segments are distinctly separated from each other and from the prostomium. Mouth about $\frac{1}{2}$ of peristomial width, with lateral lips. Pharynx not everted in any specimens.

Branchiae from setiger 6 in all specimens; becoming reduced in last 15 setigers and absent in last 2–3 setigers; flattened, elongate, triangular, widely separated, never overlapping and recumbent. Mid-abdominal branchiae somewhat larger than other branchiae; otherwise all branchiae similar in size; slightly shorter than notopodial lobes in thorax (Fig. 7b); not deciduous. The last few branchiae are rudimentary and are not visible in the illustration.

All parapodia biramous. Thoracic notopodial postsetal lobes elongate, cirriform, broader in proximal $\frac{2}{3}$ of length; slightly increasing in length in first setigers. Thoracic neuropodial postsetal lobes shorter, wider, distally more rounded than corresponding notopodial lobes. Median papillae present; tapering distally (Fig. 7b). Setigers 11 to 14 transitional, characterized by gradual reduction in number of neurosetae and by dorsal shift in neuropodia. Abdominal notopodial postsetal lobes similar to thoracic notopodial postsetal lobes. Abdominal neuropodial postsetal lobes increasingly reduced in length; retaining the same shape (Fig. 7c). Low, dorsal transverse ridges present on abdominal segments.

Both rami with bundles of capillary crenulate setae; thoracic notopodia with about 8–10 setae; thoracic neuropodia with usually 12–18 up to 30 setae; neuropodial fascicles in rows of spreading setae. Notopodial crenulate capillaries longer than neuropodial ones throughout. Uncini absent in thoracic region. Abdominal setigers with reduced numbers of crenulate setae; neuropodia with only four or five setae. Some abdominal notopodia with furcate se-

tae (Fig. 7f). Each abdominal neuropodium with one or two stout hooks. Hooks straight to slightly sigmoid, bluntly pointed, without hoods (Fig. 7e). Small specimens (M-133, M-136, M-147) with hooks from first abdominal setiger. Larger specimens with hooks from the first post-transitional setiger.

Pygidium elongate with four cirriform, distally tapering anal cirri; all anal cirri similar in size. Anal aperture central; terminal (Fig. 7d).

Tubes absent.

Discussion.—The species differs from related taxa as indicated in the discussion of the protoariciini genera.

Etymology.—The specific name refers to the country of origin of the type material.

Habitat.—The species was found mainly in Twin Cays with the exception of M23 and M24 at Blue Ground Range (Fig. 1).

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Appendix 1.—Character-list for protoariciine genera.

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- | | |
|--|---|
| 1. Prostomial shape | 15. Number of transitional segments |
| 1. pointed or conical | 0-7. number of transitional segments |
| 2. rounded or truncate | 16. Abdominal setal lobes |
| 3. both | 1. distinct |
| 2. Branchial start | 2. indistinct |
| 0. branchia absent | 17. Abdominal neuropodial postsetal lobes |
| 1-8. setiger on which branchia begin | 1. tapering |
| 3. Shape of branchiae | 2. rounded |
| 0. branchia absent | 18. Abdominal notopodial furcate setae |
| 1. triangular (flattened) | 1. present |
| 2. fusiform | 2. absent |
| 3. foliaceous | 19. Abdominal notopodial acicular setae |
| 4. cirriform | 1. present |
| 4. Anterior and posterior branchiae | 2. absent |
| 0. all branchiae absent | 20. Abdominal neuropodial crenulate setae |
| 1. similar | 1. present |
| 2. dissimilar | 2. absent |
| 5. Glandcells in branchial walls | 21. Abdominal neuropodial acicular setae |
| 0. all branchiae absent | 1. present |
| 1. present | 2. absent |
| 2. absent | 22. Abdominal neuropodial subuluncini |
| 6. Thoracic furcate notosetae | 1. present |
| 1. present | 2. absent |
| 2. absent | 23. Abdominal neuropodial uncini |
| 7. Thoracic acicular notosetae | 1. present |
| 1. present | 2. absent |
| 2. absent | 24. Abdominal swan-shaped hooks |
| 8. Thoracic acicular neurosetae | 1. present |
| 1. present | 2. absent |
| 2. absent | 25. Abdominal crested hooks |
| 9. Thoracic neuropodial subuluncini | 1. present |
| 1. present | 2. absent |
| 2. absent | 26. Abdominal hooks |
| 10. Thoracic neuropodial uncini | 1. of a single kind |
| 1. present | 2. of two kinds in vis-a-vis rows |
| 2. absent | 27. Pygidium |
| 11. Thoracic notopodial setal lobes | 1. with short, blunt projections |
| 1. distinct | 2. with distinct pygidial cirri |
| 2. indistinct | 28. Number of anal projections or cirri |
| 12. Thoracic notopodial postsetal lobes | 0-6. number of anal cirri |
| 1. tapering | 29. All anal cirri |
| 2. fusiform | 1. similar |
| 3. digitiform (increasing in length through tho- rax) | 2. of two or more different kinds |
| 13. Thoracic neuropodial postsetal lobes | 30. Eyes |
| 1. single | 1. absent |
| 2. double | 2. paired |
| 14. Thoracic neuropodial postsetal lobes | 3. more than a pair |
| 1. rounded | 31. Distinct nuchal organs |
| 2. tapering | 1. present |
| | 2. absent |
-