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A new family of lithophoran Proseriata (Platyhelminthes), with the description of seven new species from the Indo-Pacific and South America, and the proposal of three new genera

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In this contribution a new representative of the taxon *Meidiama* Marcus, 1946, ***Meidiama uruguayensis* sp. nov.**, from Uruguay, is described, as are six more new species, for which three new genera are proposed: ***Dreuxiola philippi* gen. nov. sp. nov.**, from the French subantarctic archipelago Kerguelen; ***Yorknia aprostatica* gen. nov. sp. nov.**; ***Serrula byronensis* gen. nov. sp. nov.**; ***Serrula maxillaria* sp. nov.**; ***Serrula concharum sp. nov.***; and ***Serrula acuta* sp. nov.**, from eastern Australia and Tasmania. Arguments are presented to propose a new taxon to contain these new species, rather than include them in the Archimonocelididae Meixner, 1938 (of which *Meidiama* has been considered a member so far), as well as to remove the Calviriinae Martens & Curini-Galletti from the Archimonocelididae to become a separate taxon Calviriidae. Possible autapomorphies for the three families are discussed. It is also concluded that, with the present state of our knowledge, no sound indications can be given about close relationships. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, **155**, 759–773.

ADDITIONAL KEYWORDS: Australia – *Dreuxiola* – *Meidiama* – *Serrula* – Kerguelen – subantarctic – systematics – Uruguay – *Yorknia*.

INTRODUCTION

Meixner (1938) introduced the taxon *Archimonocelidinae* as a subfamily of the Monocelididae to contain the new species *Archimonocelis mediterranea*. Karling (1966) rejected this taxon, but it was reintroduced by Martens & Schockaert (1988) at the family level, based on the election microscopic data of Martens (1984), and on the karyological data of Curini-Galletti *et al.* (1984). In 1993, Martens & Curini-Galletti split this family into the Archimonocelidinae, with two genera, *Archimonocelis* Meixner, 1938 and *Meidiama* Marcus, 1946, and the Calviriinae, also with two genera, *Asilomaria* Karling, 1966 and *Calviria* Martens & Curini-Galletti, 1993. In this contribution, we describe a new species of *Meidiama* from Uruguay, and six new species from the Indo-Pacific, showing a number of similarities with the species of *Meidiama*.

Phylogenetic analysis of the Proseriata, based on the DNA sequences of Curini-Galletti (2001) and of Willems *et al.* (2006), revealed that *Calviria solaris* Martens & Curini-Galletti, 1993 is not related to the species of *Archimonocelis*, but is found in the same

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clade as the Coelogynoporidae, although with very low support. It thus seems appropriate to remove the Calviriinae from the Archimonocelididae. On the other hand, including the new species described below into the Archimonocelididae would make this taxon very heterogeneous. Moreover, whether all of these species are indeed related to each other, and to the Archimonocelididae, and how they are related to the other taxa of Proseriata must be established by a thorough phylogenetic analysis. For the time being, and awaiting such an analysis, we therefore propose a separate taxon for these species, the Meidiamidae.

The former Archimonocelididae thus splits into three entities: Archimonocelididae, Calviriidae, and the new family Meidiamidae. We propose the 'family level' for the three taxa to avoid any suggestion of a close relationship, and to make their status within the lithophoran Proseriata clear. More arguments are given in the final discussion.

MATERIAL AND METHODS

Animals were extracted from the sediment using the $MgCl_2$-decantation method (see Martens, 1984), and were studied alive and mounted in lactophenol as whole mounts. If available, individuals were fixed with Bouin's fluid, sectioned at 4-μm thickness, and stained with Heidenhain's or Ehrlich's haematoxylin, using eosin or erythrosin as the counterstain. Freehand drawings are not to scale, and the scales for reconstructions are approximate. The holotypes of the Australian species are deposited in the Queensland Museum (QLDM; Brisbane, QLD, Australia); other holotypes are deposited in the collections of the Swedish Museum of Natural History (SMNH; Dept of Invertebrates, S-10405, Stockholm, Sweden); paratypes are kept in the SMNH and/or in the collections of the University of Hasselt (UH; Agoralaan, building D, B-3590 Diepenbeek, Belgium). The position of structures is described using the proportions of the body length, and indicates the distance from the anterior tip of the body.

TAXONOMY

MEIDIAMIDAE, NEW FAMILY

Diagnosis: Lithophoran Proseriata with an encapsulated brain, a precerebral gut diverticle, intraepidermal nuclei, and with the epidermis completely ciliated. Ovaries in front of the vitellaria, anterior of and close to the pharynx; a long female duct, the oviducts joining before the male copulatory organ, and with the female pore behind it (digonoporid condition). With a genito-intestinal connection close to the female pore, leading to a resorbing bursa incorporated in the gut. Testes: in front of the ovaries. Copulatory organ directed forwards, with a stylet and atrial needles, only needles, or only a stylet. One or a pair of seminal vesicles behind the copulatory organ. Accessory glandular organ, associated with the male atrium, present or not. Pharynx globular and directed ventrally.

Type genus: Meidiama Marcus, 1946.

MEIDIAMA MARCUS, 1946

Diagnosis (emended after Martens & Curini-Galletti, 1993): Filiform Meidiamidae with the prostate vesicle curved over about 180°, and with the proximal pole directed forwards, where the paired seminal vesicles enter; the distal pole, where the stylet is attached, is also directed forwards. The stylet is directed forwards and accompanied by the atrial needles. Accessory glandular organ absent. Genito-intestinal duct leading backwards from the female pore to a resorbing bursa in the gut. Female duct with a prepenial vagina, and functioning as a (prepenial) copulatory bursa.

Type species: Meidiama lutheri Marcus, 1946.
There are three species that are very similar, except for the hard parts of the copulatory organ and the number of testes. They are described together, mainly based on material of *Meidiama uruguayensis* sp. nov.

MEIDIAMA LUTHERI MARCUS 1946
MEIDIAMA URUGUAYENSIS SP. NOV.
MEIDIAMA SCHOCKAERTI MARTENS & CURINI-GALLETTI, 1993

Diagnoses: Meidiama lutheri: species of *Meidiama* with a curved stylet of about 60-μm long, accompanied by 10–12 needles of 30-μm long, with a small terminal hook of about one-third to one-quarter of the length of the needles; close to 100 testes.

Meidiama uruguayensis: species of *Meidiama* with a curved stylet of 80–90-μm long, accompanied by 19–21 needles of 30–45-μm long, with a small terminal hook of about one-quarter to one-fifth of the length of the needles; about 50 testes.

Meidiama schockaerti: species of *Meidiama* with a straight stylet of about 65-μm long, accompanied by 18–20 needles of 60 μm, without hook; 9–10 testes in a row.

Occurrence: Meidiama lutheri: Beach of Guarujà, near Santos, Brazil; coarse shell gravel (type locality).

Meidiama uruguayensis: Río de la Plata, Balneario Las Flores, Departamento de Maldonado (34°48′50″S, 55°20′03″W), Uruguay (type locality); Playa Grande, Uruguay; coarse sand between rocks (18/7/2004).

Meidiama schockaerti: Pingüinera beach (Seno Otway), Chili (Magellan Province); coarse sand and gravel (**not** Punta Arenas, Argentina, as mentioned in the original description of Martens & Curini-Galletti 1993).

Material studied: Meidiama lutheri: two whole mounts, one indicated as lectotype (SMNH 7348); two slides with dispersed sections of several individuals, and of very poor quality, containing very fragmentary information (paralectotypes: SMNH 7349–7350).

Meidiama schockaerti: holotype (SMNH 7351; whole mount).

Meidiama uruguayensis: four whole mounts and ten sectioned individuals (13 slides) from the type locality; one of the whole mounts is designated as the holotype (SMNH 7352); paratypes UH 371–380.

Etymology: Meidiama uruguayensis has been named after the country where it was found.

Description: The animals are very long and slender: adults of *M. lutheri* are around 4-mm long; adults of *M. schockaerti* are 2–3-mm long and adults of *M. uruguyaensis* are around 6-mm long (all measured on the whole mounts), with some anterior sensory bristles. Adhesive papillae were not seen in the whole mounts, nor in the sections, but are present in the caudal region of *M. lutheri*, according to Marcus (1946). The brain is encapsulated, and there is a clear extension of the gut over the brain. The pharynx is directed ventrally, is slightly lobate, and is roughly in the middle of the body (Fig. 1). The epidermis is 1.5–2-μm thick in *M. lutheri*, and the cilia are 3-μm long dorsally and 4-μm long ventrally; in *M. uruguayensis* the epidermis is 1–1.5-μm thick, and the cilia are 2 and 3-μm long, respectively.

The ovaries are just in front of the pharynx, and the vitellarian follicles are all behind the pharynx, extending over around two-thirds of the post-pharyngeal body part. Behind the last, most posterior follicle, the two ovovitelloducts join to form the common female duct. Slightly more posteriorly, this duct enlarges to form the copulatory bursa, in which a short vagina opens (Figs 1, 2). The female duct continues over a considerable distance (about 0.25 mm) to reach the female pore. From here departs a short genito-intestinal duct, which opens into a large resorbing bursa in the intestine. A connection with the gut is not seen, although some clusters of sperm are observed in the gut at the level of, and even anterior to, the copulatory organ. Very large cement glands run to the female pore, with the gland bodies lying mainly in the most caudal body part. The whole female duct is lined by a rather dense and nucleated epithelium, and is surrounded by spiral muscles. The epithelium is slightly higher in the copulatory bursa and in the most anterior part of the female duct. The muscle layer around the copulatory bursa is also slightly stronger than on the rest of the duct. The epithelium of the ovovitelloducts is very thin and sinuous, and no evidence of a resorbing function was seen.

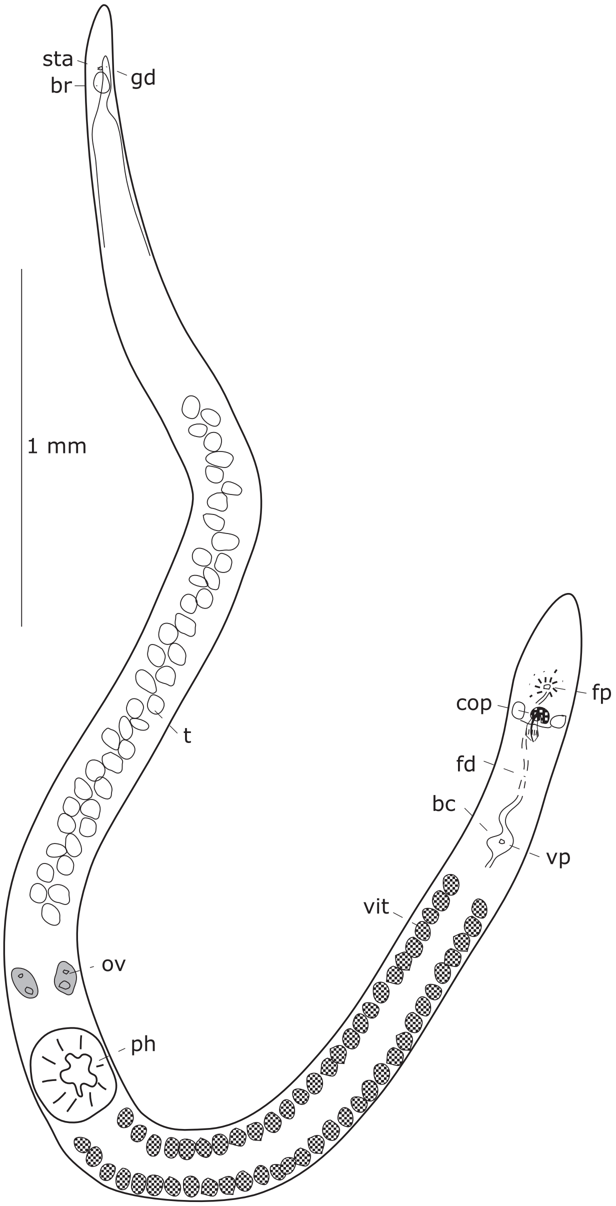

Figure 1. General appearance of a species of *Meidiama* combined from whole mounts of *Meidiama lutheri*, *Meidiama uruguayensis*, and fig. 120 of Marcus (1946). Refer to the Appendix for a list of abbreviations.

There are about 50 testes in *M. uruguayensis* (close to 100 in *M. lutheri*, according to Marcus

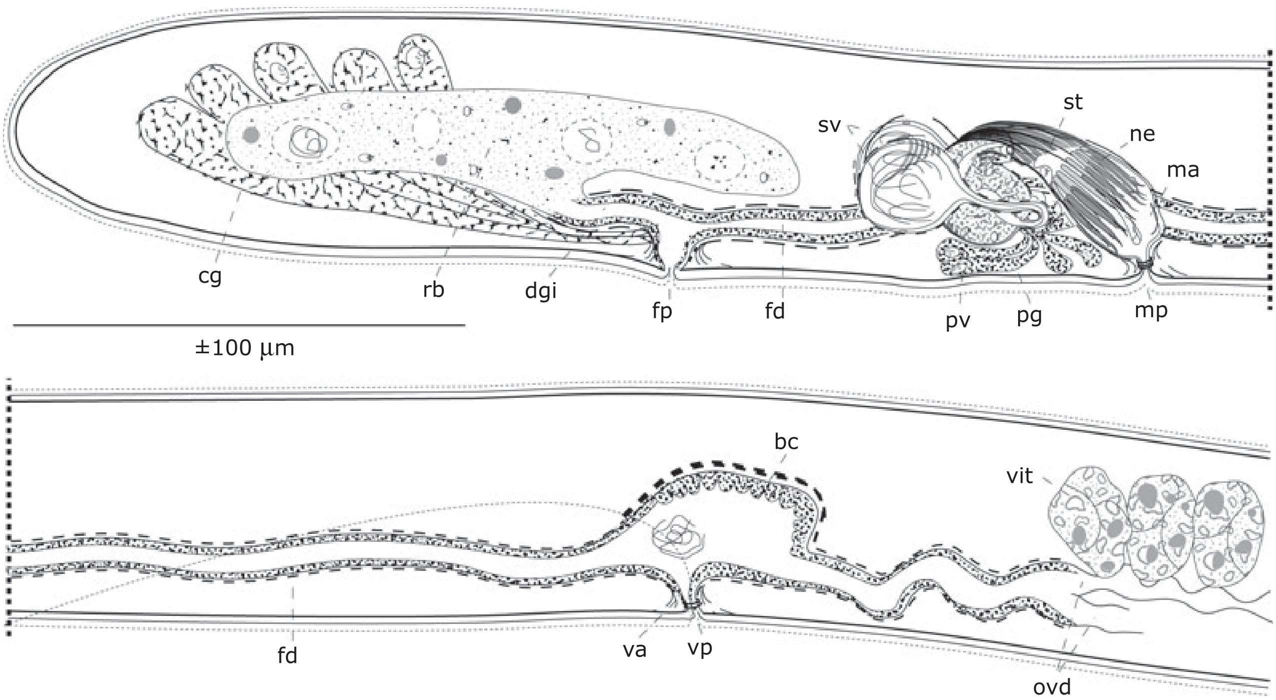

Figure 2. Sagittal reconstruction of the female system, seen from the left, of the species of *Meidiama*, mainly based on sections of ***Meidiama uruguayensis* sp. nov.** The lower figure is the continuation of the upper part. Refer to the Appendix for a list of abbreviations.

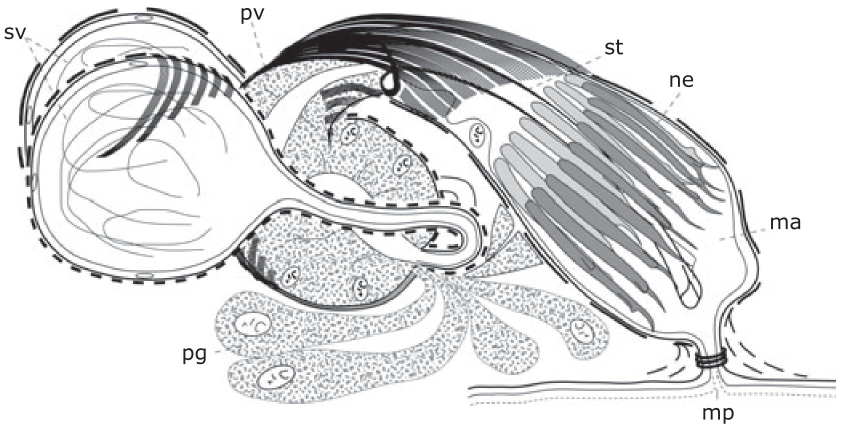

Figure 3. Reconstruction of the copulatory organ in *Meidiama lutheri* and ***Meidiama uruguayensis* sp. nov.**, seen from the left, based on sections of ***M. uruguayensis* sp. nov.** and the whole mounts of both species. Refer to the Appendix for a list of abbreviations.

1946: fig. 120), roughly arranged in two rows, and with the first testis found at one-third of the prepharyngeal region, and with the last testes just in front of the ovaries. In *M. schockaerti* there are only 9–10 testes in a row. The copulatory organ, just in front of the female pore, is directed forwards. It consists of a pair of spherical seminal vesicles, from which long narrow ducts depart (Fig. 3). These ducts join to form a single seminal duct, which enters the prostate vesicle at its proximal pole. The seminal vesicles and the ducts are all surrounded by a strong spiral muscle layer. The prostate vesicle tapers anteriorly, where the stylet is attached, and is recurved over 180°, with both proximal and distal poles directed forwards. The seminal duct can clearly be seen in the centre of the vesicle, with its epithelium forming the prostate glands, the nucleated gland bodies of which are outside and inside

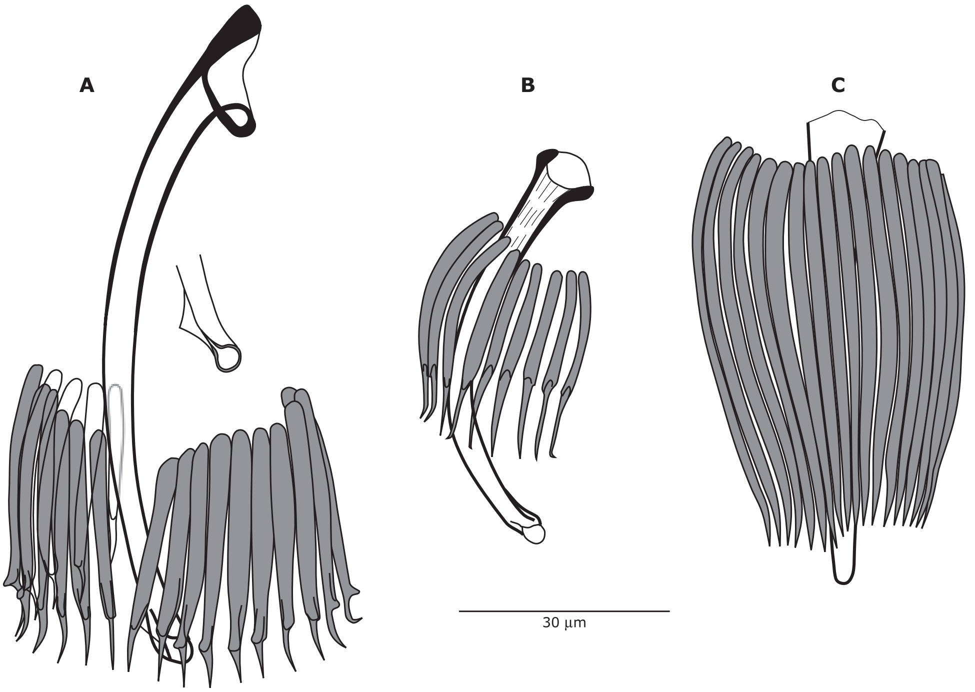

Figure 4. Hard parts of the copulatory organ of ***Meidiama uruguayensis* sp. nov.** (A; inset, terminal opening in the holotype), *Meidiama lutheri* (B), and *Meidiama schockaerti* (C).

the vesicle. In the large male atrium, the curved stylet and the atrial needles are found. The needles are situated in the distal half of the atrium, and are arranged in a half-open girdle, closed at the dorsal side (above the stylet), and open at the ventral side. The prostate vesicle is surrounded by very strong, spirally arranged muscles, which continue over the male atrium, and seem to be attached to the needles. A moderately strong sphincter surrounds the male pore.

In both individuals of *M. lutheri*, the curved stylet is about 60-µm long, the needles are 28–30-µm long, and are also slightly curved. The funnel-like proximal end of the stylet has an opening of 7–8 µm in diameter, with a strongly thickened wall, whereas the stylet diameter tapers from 5 µm proximally to 2 µm distally. The curvature of the very distal end is stronger than in the middle of the stylet, making a precise measurement difficult, as the entire length of the stylets in the whole mounts cannot be seen in the same plane. The terminal opening is oblique and tapering proximally. We counted nine needles, whereas Martens & Curini-Galletti (1993) counted ten, and Marcus (1946) mentions 12. Needles lying above each other are indeed often difficult to discern. Each needle ends in a slender 'hook', about one-third of the total length of the needle in the shortest needles, and about one-quarter of the total length in the longest needles.

In *M. uruguayensis* the stylet is also curved, and is about 90-µm long in the holotype. At the distal opening it bears a variably ornamented 'wing' (Fig. 4, inset). The obliquely-placed proximal opening, also with a strongly thickened wall, has a diameter of 20 µm, and the stylet has a diameter of slightly less than 5 µm distally. There are about 18 needles, which are 31–37-µm long, with the shortest needle located in the middle of the circle. The terminal 'hooks' have a strongly curved tip, and are a little less than between one-fifth and one-quarter of the total length of the needles. The length of the stylet varies from 76 to 90 µm ($n = 7$, mean = 84 µm); the shortest needles are 26–46-µm long ($n = 6$, mean = 32 µm), and the longest needles are 35–69-µm long ($n = 6$, mean = 44 µm). The individuals with the longest stylet also have the largest needles.

The copulatory organ of *M. schockaerti* deviates in a number of aspects from that of the other two species. The stylet is straight, close to 65-µm long, and gradually narrows from 10-µm wide at the proximal opening (without obvious thickening) to about 3-µm wide distally. The needles are about 60-µm long, and are without a terminal 'hook'. We counted about 18 needles, whereas Martens & Curini-Galletti (1993) depicted 21 needles in a regular arrangement around the stylet. We have the strong impression that the needles are concentrated at one side of the stylet, as in the other species of *Meidiama*.

DREUXIOLA GEN. NOV.

Diagnosis: Filiform Meidiamidae with many testes. The prostate vesicle has the proximal pole directed forwards, where the paired seminal vesicles enter. The distal pole is directed backwards, but at its end, where the stylet is attached, it turns sharply forwards, so that the stylet is directed forwards. It enters the male atrium next to the atrial needles. These needles are surrounded by a glandular epithelium with its own muscular envelope. Female duct with a prepenial vagina, functioning as a copulatory bursa. Genito-intestinal duct near the female pore leading to a resorbing bursa.

Type species: Dreuxiola philippi sp. nov.

DREUXIOLA PHILLIPI SP. NOV.

Diagnosis: Species of *Dreuxiola* with about 25 testes, a very long and coiled stylet, about 250-µm long, and two groups of four needles, each 35–37-µm long. The vagina ends with a sclerotized ('cuticular') tube.

Occurrence: Port aux Français, Kerguelen (Territoire Australe Français), on the flat beach east of the port; fine sand in the mid-littoral, dominated by nematodes.

Material studied: Observations were made on the living animals and two whole mounts (one of them indicated as the holotype, SMNH 7353, the other indicated as a paratype UH 381); four series of sections, from which only two contain relevant information (UH 382–385).

Etymology: Genus and species are named in honour of Prof. Philippe Dreux (Université Pierre et Marie Curie, Paris): entomologist and noted authority on the wingless Curculionidae (Coleoptera) of the French Austral Territories.

Description: The animals are very long and slender, 3–4-mm long, with some anterior sensory bristles. Adhesive papillae were not seen in the whole mounts, nor were they seen in the sections. The brain is encapsulated, and there is a clear extension of the gut over the brain. The pharynx is directed ventrally, is slightly lobate, and is placed at two-thirds of the body length (Fig. 5). The epidermis is 1-µm-thick ventrally and 1.5-µm-thick dorsally; cilia are 2-µm long.

The ovaries are just in front of the pharynx, and most vitellarian follicles are behind the pharynx, extending over about one-third of the post-pharyngeal body part. Behind the last follicle, the two ovovitelloducts join into the common female duct, which looks very muscular and swollen in living animals, is filled with sperm, and clearly functions as a copulatory bursa. The vagina opens roughly in its middle, with a little sclerotized tube that is about 50-µm long (Figs 6, 7). In the sections the vaginal duct appears as a narrow tube with a strongly muscular wall, surrounded by loose tissue that is also surrounded by some longitudinal muscles. In one of the sectioned animals this part is highly swollen, forming a vesicle that is also seen in the living animal and in the whole mounts (Fig. 6). Further backwards, the female duct narrows towards the female pore that is found at three-quarters of the postpharyngeal body part. From the female pore the genito-intestinal duct departs towards the resorbing bursa.

Figure 5. A living animal of ***Dreuxiola philippi* sp. nov.** Refer to the Appendix for a list of abbreviations.

The male system consists of about 25 testes in a row, extending from some distance behind the brain down to the level of the ovaries (Fig. 5). The copulatory organ lies between the female pore and the vagina, and has an astonishing construction (Figs 6–9). The prostate vesicle has the proximal pole directed

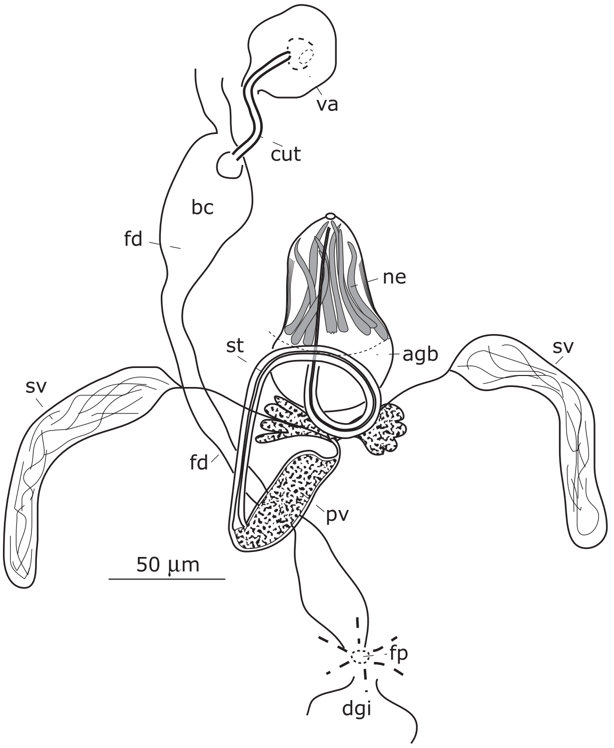

Figure 6. Postpharyngeal genital organs of ***Dreuxiola philippi* sp. nov.** as in the whole mount, but also as they have been seen in the living animal. Refer to the Appendix for a list of abbreviations.

forwards, where the paired seminal vesicles enter, and the distal pole is directed backwards; distally, the prostate vesicle tapers, and recurves by almost 180°. The stylet starts with a bent proximal end, so that the stylet becomes directed forwards. The seminal vesicles lie next to the prostate vesicle and join each other in a short seminal duct that can be followed in the prostate vesicle. Here, its epithelium forms the prostate glands, of which the cell bodies with nuclei are outside the vesicle, and some nuclei are inside the bulb. The stylet is very narrow and very long. It makes a loop and enters the expanded male atrium. The proximal part of the atrium is swollen and contains a net-like glandular tissue surrounded by a thin muscle layer. Two groups of needles seem attached to this accessory glandular bulb. The stylet enters the male atrium roughly in the middle of this glandular bulb. The stylet is about 250-µm long in the two whole mounts; the needles are 40–50-µm long. These needles seem to be very slightly sclerotized, and are rather difficult to discern in whole mounts. Nevertheless, it could be observed that the needles are arranged symmetrically in two groups, each consisting of a shorter, curved needle at the outside, and a thicker, straight needle in the middle (both about 40-µm long), and with two slender and moderately curved needles of about 50-µm long in between (measurements from the two whole mounts).

YORKNIA GEN. NOV.

Diagnosis: Elongated Meidiamidae with many testes. Copulatory organ without atrial needles, and without accessory glandular organ. Prepenial copulatory bursa.

Type species: Yorknia aprostatica sp. nov.

YORKNIA APROSTATICA SP. NOV.

Diagnosis: Species of *Yorknia* with 15 testes in a row, without either prostate glands or vesicle, and with an almost straight stylet of about 80-µm long, with a proximal 'cap' of 30–40 µm in diameter, and with a single large seminal vesicle. Female pore only slightly behind the male pore; prepenial copulatory bursa with two vaginas.

Occurrence: Cairns, Australia (Queensland), at Yorkney's Knob; intertidal in fine to medium-fine sand (type locality) (October 1993).

Material studied: A whole mount, designated as the holotype, (QM G 230107). A second whole mount and six sectioned animals (UH 386 and UH 387–392).

Etymology: The genus name is derived from the locality where the species was found; the species epithet is derived from the most striking character, namely the absence of prostate glands.

Description: The animals are long and slender, 3–4-mm long, with some anterior sensory bristles. Adhesive papillae were not seen in the whole mounts, nor were they seen in the sections. The brain is encapsulated, and there is a clear extension of the gut over the brain. The pharynx is directed ventrally, is slightly lobate, and is located at between two-thirds and three-quarters of the body (Fig. 10A). The epidermis is 1.5-µm thick, with 3-µm-long cilia.

The ovaries are just in front of the pharynx, and all vitellarian follicles are behind the pharynx, extending to the middle of the post-pharyngeal body part. Behind the last follicle the two ovovitelloducts join into the common female duct, which is swollen in the living animal, and clearly functions as a copulatory bursa. At about its middle, two vaginal pores can be seen (Fig. 10B). In the sections (Fig. 11), the two vaginas depart as a wide funnel from the dorsally-situated copulatory bursa. The female duct narrows towards the female pore, where the duct is enlarged

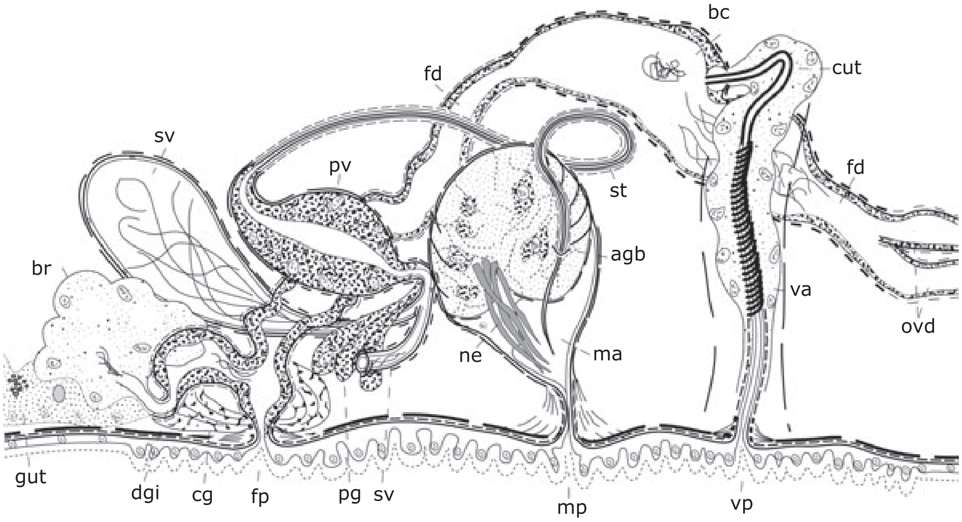

Figure 7. Reconstruction of the postpharyngeal genital organs of ***Dreuxiola philippi* sp. nov.**, seen from the right. Refer to the Appendix for a list of abbreviations.

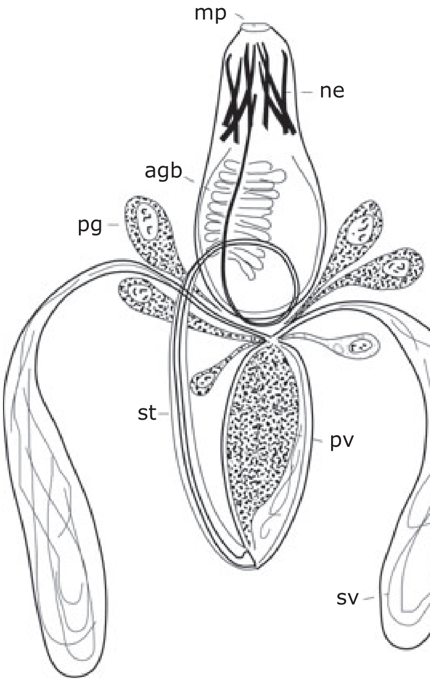

Figure 8. The copulatory organ of ***Dreuxiola philippi* sp. nov.**, as seen in the living animal. Refer to the Appendix for a list of abbreviations.

again, and continues backwards as a genito-intestinal duct communicating with a large resorbing bursa. The epithelium covering the female duct is ciliated. This epithelium is very low in the copulatory bursa, in the vaginas, and at the dorsal side of the swollen part at the pore, and is extremely thin in the genito-intestinal duct, where it is devoid of cilia. At their very end, the ovovitelloducts show aspects that suggest some resorbing function, but no degenerating sperm was observed. The cement glands, which open at the female pore, are very large and are found in the whole posterior part of the animal.

The copulatory organ is provided with an almost straight stylet, lying in a tubiform, narrow male atrium that enlarges proximally to a narrow space, which receives at its ventral side the wide opening of the seminal vesicle. Dorsally, this proximal space is covered by a sclerotized 'cap', which has a fan-like muscle, with its wider side attached to the cap, and its narrower side attached to the stylet (see also Fig. 12). The seminal vesicle is extremely large, occupying almost the whole postpenial part of the animal. One of the most striking characters of this species is the complete absence of any prostate glands (and vesicle). The stylet (Fig. 12) is about 80-μm long, with an almost constant diameter of 8–10 μm; the 'cap' is 45-μm long in the holotype, and is 30-μm long in the paratype. The fan-like muscle is clearly visible in the whole mount.

SERRULA GEN. NOV.

Diagnosis: Meidiamidae with a single pair of testes and the pharynx in the anterior part of the body. Copulatory organ with a pair of short atrial needles sitting on a muscular base. Without stylet and accessory glandular organ. Seminal vesicles paired or single. With or without prepenial vagina. Genito-intestinal connection absent?

Type species: Serrula byronensis sp. nov.
There are four species that are very similar, and these are described together.

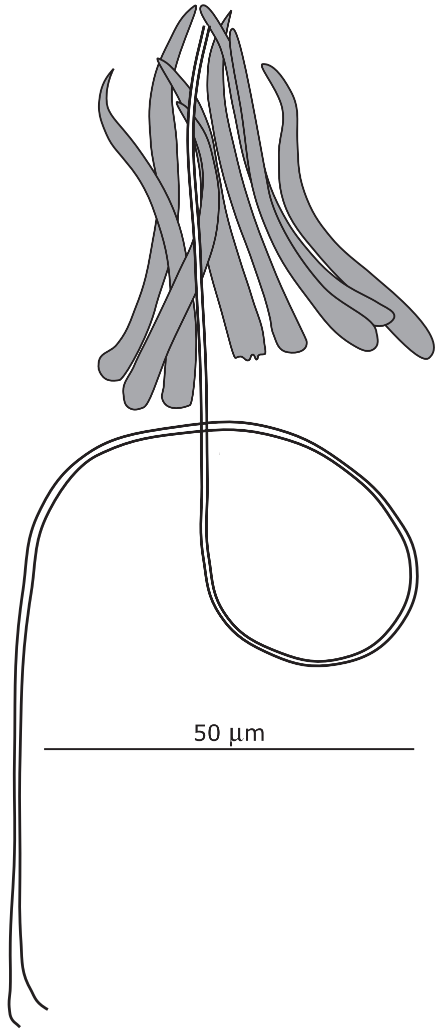

Figure 9. Hard parts of the copulatory organ in the holotype of ***Dreuxiola philippi* sp. nov**.

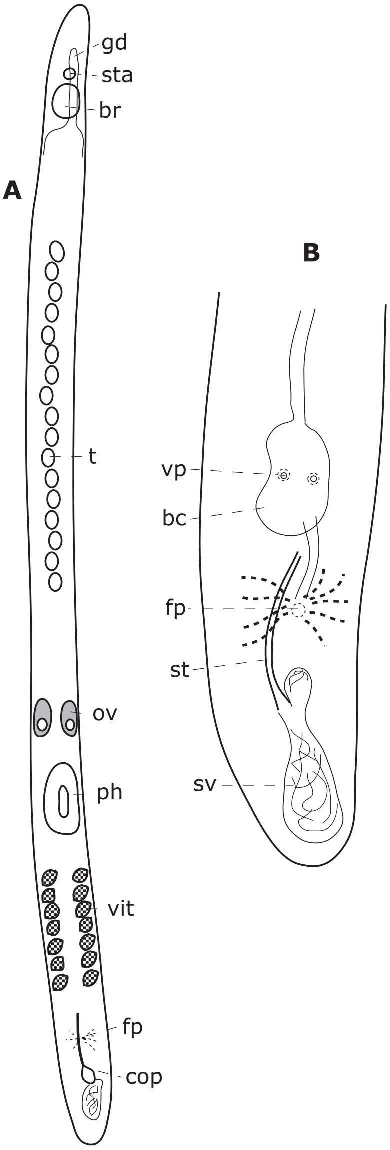

Figure 10. Drawings from a living animal of ***Yorknia aprostatica* sp. nov**. A, the whole animal; B, the post-pharyngeal genital organs. Refer to the Appendix for a list of abbreviations.

SERRULA BYRONENSIS SP. NOV.

SERRULA MAXILLARIA SP. NOV.

SERRULA CONCHARUM SP. NOV.

SERRULA ACUTA SP. NOV.

Diagnoses: Serrula byronensis: species of *Serrula* with an unpaired seminal vesicle, a prepenial vagina, and a copulatory bursa. The needles are pointed: 14-µm long, and 5–6-µm wide at the base. The precerebral diverticle ends at the statocyst.

Serrula maxillaria: species of *Serrula* with a single seminal vesicle. Atrial needles are 13-µm long and 3-µm wide over the whole length, and have a truncated and serrated distal end. The precerebral diverticle ends at the statocyst.

Serrula concharum: species of *Serrula* with paired seminal vesicles; needles are similar to those of *S. maxillaria*, 15-µm long and 5-µm wide. Pre-cerebral diverticle ends anteriorly of the statocyst.

Serrula acuta: species of *Serrula* with a single seminal vesicle?; slender pointed needles that are 25-µm long, and are 6-µm wide at the base. No data on the living animal.

Occurrence: Serrula byronensis: Byron Bay, Australia (New South Wales); exposed intertidal at Tallum Beach, mid-fine sand (October 1993).

Serrula maxillaria: Cairns, Australia (Queensland); protected beach at Yorkney's Knob, with fine to mid-fine sand (October 1993).

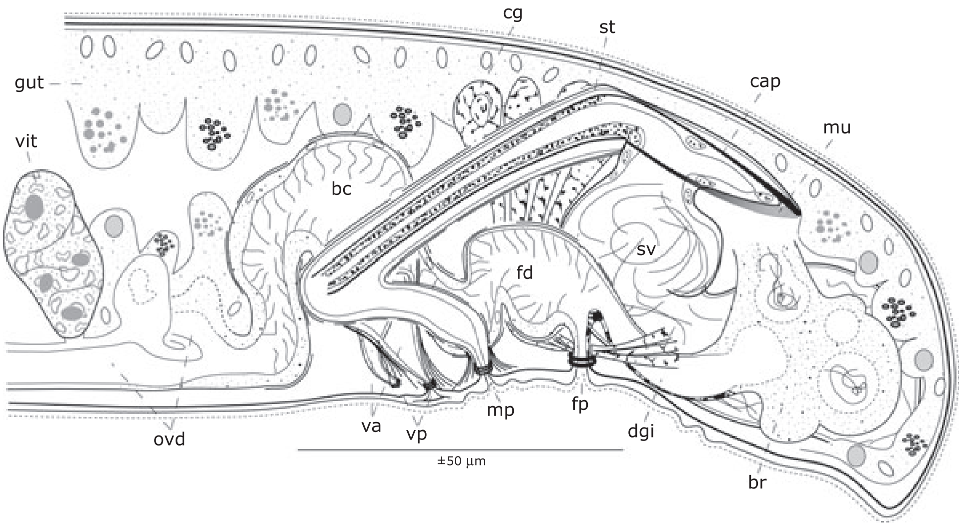

Figure 11. Sagittal reconstruction of the postpharyngeal genital organs of ***Yorknia aprostatica*** **sp. nov.**, seen from the left. Refer to the Appendix for a list of abbreviations.

Serrula concharum: Eaglehawk Neck, Australia (Tasmania); exposed intertidal, with fine sand, and with a high density of Mesodesmatidae bivalves of the genus *Paphies* Lesson, 1830 (October 1993).

Serrula acuta: same locality as *S. maxillaria*.

Material studied: Drawings from the living animals, except for *S. acuta*. One whole mount of each species (designated as holotypes, QM G 230108–230111). Sections of one individual of *S. byronensis* of very poor quality, and without relevant information (except the epidermis) (UH 393).

Etymology: The genus name refers to the serrate end of the needles in two of the species (Latin *serrula*: little saw). The species epithet of *S. byronensis* refers to the place where it has been found; that of *S. concharum* refers to the co-occurrence with many shells (Latin *concha*: shell); the needles of *S. maxillaria* show some resemblance to the maxillae of crustaceans; the needles of *S. acuta* are very slender and pointed (Latin *acuta*: pointed).

Description: These four species are described from only one living individual of each species, and from the whole mounts. Therefore, our knowledge of a number of important characters is lacking. Nevertheless, we consider it worthwhile to describe them, hoping that more abundant material may be found in the future.

The four species are relatively small: only about 1-mm long. They have the usual anterior sensory bristles, but also have long bristles at the caudal end. *Serrula byron* also has prominent adhesive papillae (Figs 13, 14). The precerebral gut diverticle reaches far in front of the statocyst in *S. concharum*, whereas it ends roughly above the statocyst in *S. byronensis* and *S. maxillaria* (and is unknown in *S. acuta*). Cnidocysts were seen in the anterior part of the gut in *S. maxillaria*.

The globular and ventrally directed pharynx is placed at the first quarter of the body; the ovaries, located anterior to the pharynx, are preceded by a single pair of testes. All vitellarian follicles are behind the pharynx, and the posteriormost follicles are found in front of the copulatory bursa in *S. byronensis*, and in front of the copulatory organ in the other species. The female pore is located at some distance behind the seminal vesicle (Fig. 14). The copulatory organ is directed forwards, with a small prostate vesicle on which the two needles are attached. *Serrula concharum* has a pair of seminal vesicles; the other species have an unpaired seminal vesicle. Only in *S. byron* has a prepenial copulatory bursa been observed, with a vagina just in front of the copulatory organ. We could not determine whether the vagina and the male pore are combined or not. As far as the whole mount reveals, *S. acuta* has a single seminal vesicle, whereas a copulatory bursa is absent. Without sections, it cannot be said if a genito-intestinal connection or a resorbing bursa is present.

The hard parts of the copulatory organ (Fig. 15) consist of two spines that we interpret as the equivalent of the needles in the male atrium of the other representatives of Meidiamidae. Except in *S. acuta*, each of the two needles sits on a base, evidently formed by two muscles that 'flank' the prostate vesicle at either side. Because of the lack of sections, the hypothesis that these bases are muscles is yet to be confirmed. The form and size of the needles are given in the diagnoses.

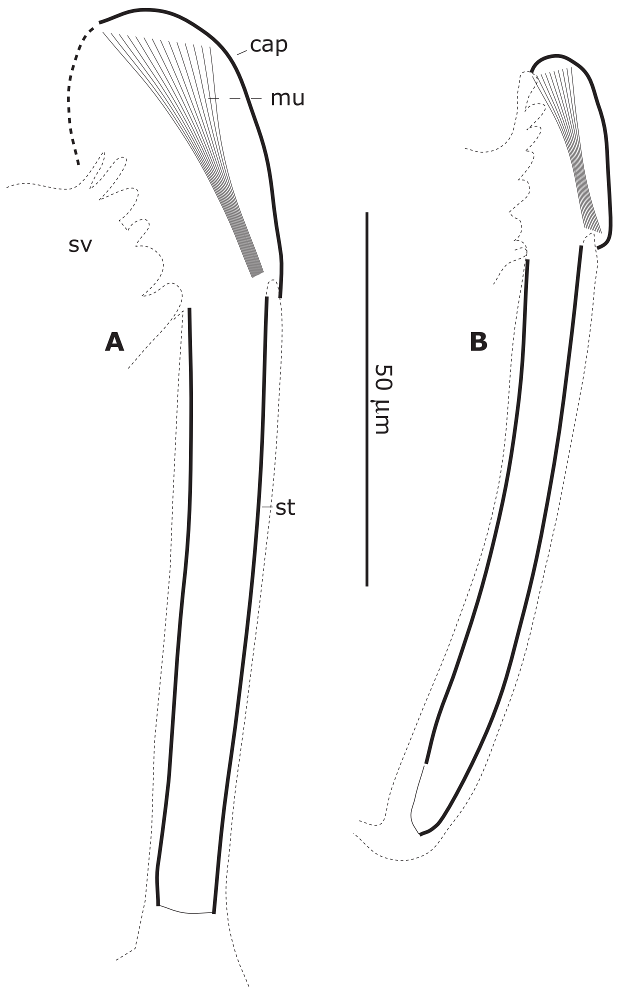

Figure 12. Copulatory organ of ***Yorknia aprostatica* sp. nov.**, as seen in the whole mounts. A, in the holotype; B, in the paratype. Refer to the Appendix for a list of abbreviations.

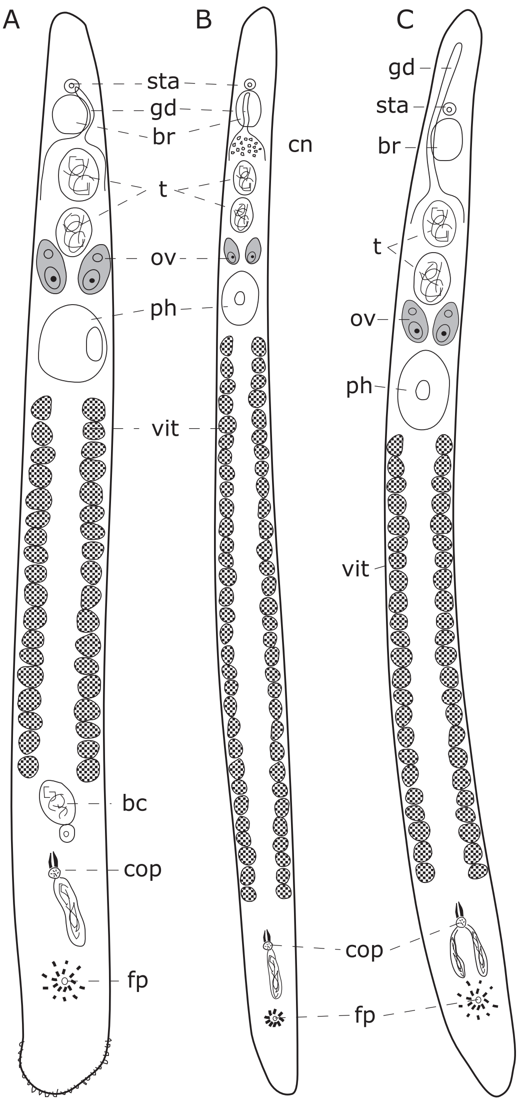

Figure 13. Living specimens of the species of *Serrula*. A, ***Serrula byronensis* sp. nov.**; B, ***Serrula maxillaria* sp. nov.**; C, ***Serrula concharum* sp. nov.** Refer to the Appendix for a list of abbreviations.

DISCUSSION

With the introduction of the new family and the promotion of the archimonocelidid subfamilies to the family level, as prosposed here, the lithophoran Proseriata (with a statocyst) comprise six families: Coelogynoporidae, Otoplanidae, Monocelididae, Archimonocelididae, Calviriidae, and Meidiamidae. Proseriata without a statocyst are united in the Unguiphora Sopott-Ehlers, 1985, with two families, Nematoplanidae and Polystylophoridae.

Several contributions have been made to elucidate the phylogenetic relations within the Proseriata: Sopott-Ehlers (1985), Martens (1984), and Martens & Schockaert (1986), based on ultrastructural data, Tajika (1982); Martens & Schockaert (1988), Martens, Curini-Galletti & van Oostveldt (1989), and Martens & Curini-Galletti (1993), based on on light microscopic and karyological analyses; Curini-Galletti *et al.* (1984), Curini-Galletti, Puccinelli & Martens (1989), and Curini-Galletti & Martens, 1990), based on karyological data; and a number of smaller contributions by these and other authors. More recently, two contributions have been presented based on DNA sequences (Curini-Galletti, 2001; Willems *et al.*, 2006). However, the hypotheses of relationships proposed by all of these authors are often very contradictory. For example, among other contradictions, Ehlers (1985) and Sopott-Ehlers (1985) consider the Unguiphora as the sister taxon of all lithophoran Proseriata, whereas Martens & Schockaert (1988) consider the Monocelididae as the sister taxon of all

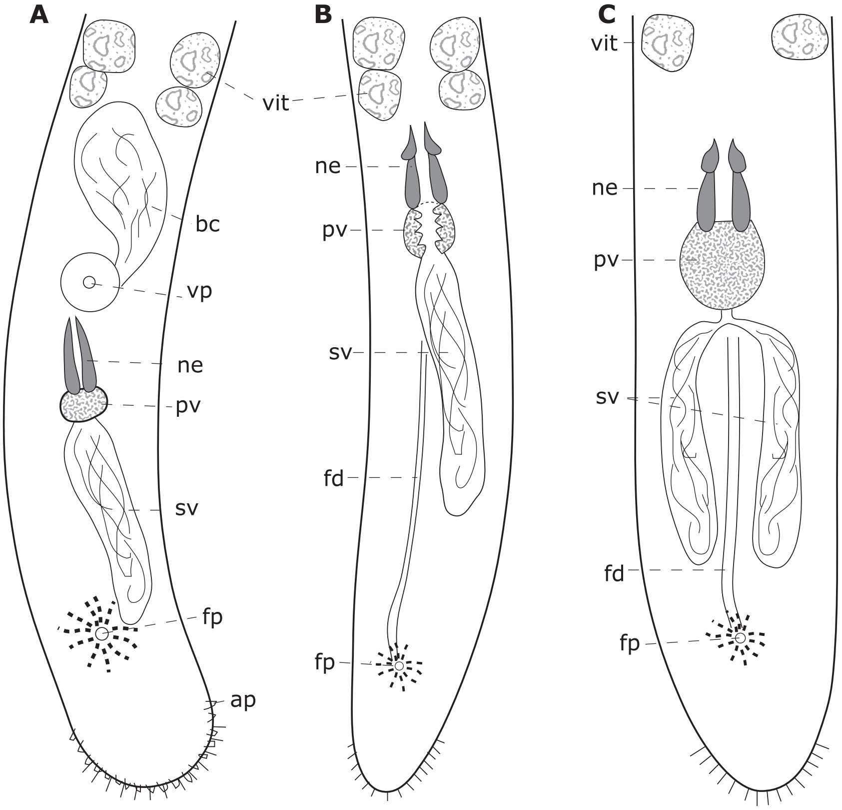

Figure 14. Posteriormost body part in live animals. A, ***Serrula byronensis* sp. nov.**; B, ***Serrula maxillaria* sp. nov.**; C, ***Serrula concharum* sp. nov.** Refer to the Appendix for a list of abbreviations.

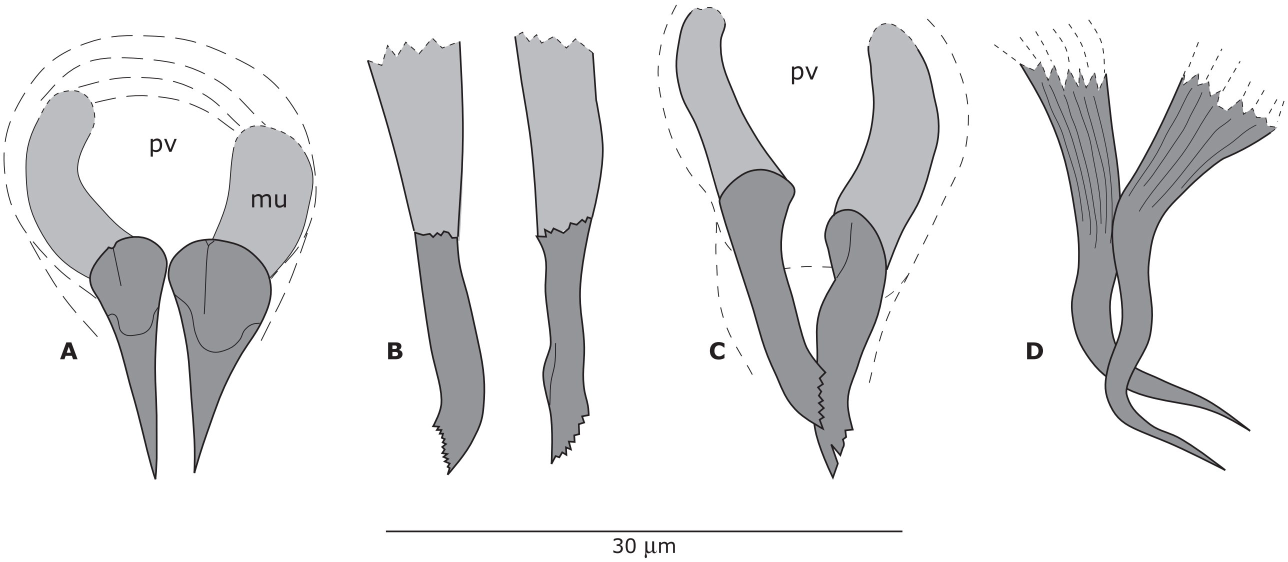

Figure 15. The needles and the muscular supports of the copulatory organ in the species of *Serrula*. A, ***Serrula byronensis* sp. nov.**; B, ***Serrula maxillaria* sp. nov.**; C, ***Serrula concharum* sp. nov.**; D, ***Serrula acuta* sp. nov.** Refer to the Appendix for a list of abbreviations.

other Proseriata, and the Unguiphora as the sister taxon of the Archimonocelididae. On the other hand, the molecular data indicate that *Calviria solaris* (originally considered a member of the Archimonocelididae) is not closely related to the species of *Archimonocelis*, whereas these are found in the same clade as the Monocelididae and – rather unexpectedly – the Otoplanidae species used in the analyses. It is thus clear that the phylogenetic relationships among the Proseriata are far from being resolved. Therefore, any speculation on the relationships of the Meidiamidae is premature at this stage of our knowledge, and is also beyond the scope of this contribution. In what follows, we reformulate the diagnoses of the Archimonocelididae and of the Calviriidae; the diagnosis of the Meidiamidae has been given in the taxonomic section, and is repeated here for the sake of the clarity of this discussion. We also compare a number of characters in the various proseriate taxa in an attempt to find autapomorphies that may indicate the monophyly of these three taxa.

THE DIAGNOSES

The Meidiamidae are lithophoran Proseriata with an encapsulated brain, a precerebral gut diverticle, intraepidermal nuclei, and a completely ciliated epidermis. Ovaries are in front of the vitellaria, anterior of, and close to the pharynx. A long female duct, with the oviducts joining before the male copulatory organ, and the female pore behind it (digonoporid condition). With a genito-intestinal connection close to the female pore, leading to a resorbing bursa incorporated in the gut. Testes in front of the ovaries. Copulatory organ directed forwards with a stylet and atrial needles, with only needles, or with only a stylet. One or a pair of seminal vesicles behind the copulatory organ. An accessory glandular organ, associated with the male atrium, is present or absent. Pharynx globular and directed ventrally.

The Archimonocelididae are lithophoran Proseriata with an encapsulated brain, a precerebral gut diverticle, intraepidermal nuclei, and with a completely ciliated epidermis. Ovaries are in front of the vitellaria, and are anterior of the pharynx. A long female duct, with the oviducts joining before the male copulatory organ, and with the female pore behind it (digonoporid condition). With a genito-intestinal connection close to the female pore, leading to a resorbing bursa incorporated in the gut. Testes in front of and also mostly behind the ovaries. Copulatory organ directed forwards with stylet and atrial needles, or with only a stylet. One or a pair of seminal vesicles behind the copulatory organ. An accessory glandular organ, associated with the male atrium, is present or absent. Horizontal, very long pharynx, with a prominent glandular proximal section. With cnidosacs (mostly) in one dorsal row.

The Calviriidae are lithophoran Proseriata with an encapsulated brain, a precerebral gut diverticle, intraepidermal nuclei, and with a completely ciliated epidermis. Ovaries are located roughly in the middle of the vitellaria, anterior of, and close to the pharynx. A very short female duct, with the oviducts joining behind the male copulatory organ, and with the female pore behind it (digonoporid condition). With a resorbing bursa close to the female pore (but with no genito-intestinal connection). Testes in front of the ovaries. Copulatory organ directed forwards, with only atrial needles or unarmed. A single seminal vesicle behind the copulatory organ. Accessory glandular organ present, separated from the copulatory organ, or combined with it. Horizontal pharynx not elongated, nor with a long prominent glandular proximal section; a septum before and a sphincter above the pharynx divides the gut into an anterior and a posterior part.

CHARACTER COMPARISONS

The majority of the Proseriata have the brain enclosed in a connective tissue capsule; they all have a gut diverticle that extends over the brain and the statocyst (in the Lithophora), and have a completely ciliated epidermis with an intraepithelial nuclei. Only the Monocelididae have no brain capsule and no gut diverticle. Monocelididae also have the epidermis with nuclei insunk under the body musculature, and have no cilia at their very caudal part. The Otoplanidae only have cilia in the ventral ‘creeping sole’ (except in the species of *Archotoplana* Ax, 1956); some lack the gut diverticle and some also have epidermal insunk nuclei.

Ovaries are mostly situated in front of the pharynx, with vitellarian follicles both in front of and behind them. Meidiamidae and Archimonocelididae have all vitellaria behind the ovaries, which was considered a synapomorphy by Martens & Schockaert (1988). However, a number of representatives of the Otoplanidae also have vitellaria behind the ovaries.

Meidiamidae, Archimonocelididae, and Calviriidae have the female and male pore separated, as have the Monocelidae, which is also the main reason why these taxa have been considered to be related in the past (Meixner, 1938; Marcus, 1946; Karling, 1966), athough Martens & Schockaert (1988) considered this character as the plesiomorphic situation for the Proseriata. Also, the Unguiphora have separated genital pores. The DNA data show that the Calviriidae are probably not related to the other three taxa. As stated by Curini-Galletti (2001), ‘the monogonoporid condition may have been overrated’. On the other hand, the

DNA data also suggest that Archimonocelididae, Monocelididae, and Otoplanidae are related. The representatives of Archimonocelididae, Monocelididae, and a number of Otoplanidae have a long female duct, which is perhaps a character that might indicate a relationship, according to Curini-Galletti (2001). Also, the Meidiamidae have a long female duct. Can this common character be considered a synapomorphy for Monocelididae, Archimonocelididae, and Meidiamidae? The genito-intestinal connection may also be a synapomorphy, although it also occurs in many Coelogynoporidae and Unguiphora.

Hard parts of the copulatory organ have an intracellular origin in the vast majority of the Platyhelminthes (Bruggeman, 1985, 1986; Martens & Schockaert, 1985). Even though this character has been detected by electron microscopy, it can clearly be seen in light-microscopic sections, and even in the living animal. In Monocelididae, the hard parts are either absent or are basement membrane derivatives (Martens & Schockaert, 1986). The presence of an accessory glandular organ is considered to be an apomorphy for the Archimonocelididae *sensu* Martens & Curini-Galletti (1993), i.e. a synapomorphy for the three families under discussion. However, if the Calviriidae are not closely related to the Archimonocelididae, as the DNA analyses indicate, this character loses much of its significance as an indication for relationship. Moreover, such an accessory glandular organ is lacking in many species of Archimonocelididae, and in most species of Meidiamidae, where it is only present in *Dreuxia philippi*.

Of the characters remaining, which can be considered as autapomorphies for each of the three families, and which character might indicate the relationships between the three families?

All Archimonocelididae have a long tubiform pharynx with a prominent glandular proximal part (which is not found in all other Proseriata), and cnidocysts of prey stored in cnidosacs, mostly arranged in one dorsal row. These characters consistently co-occur with ovaries in front of the vitellaria.

A unique character of the Calviriidae is the absence of a stylet in the copulatory organ (where only atrial needles occur, or it is unarmed). Also, the septum and sphincter in the gut is a unique character. Obvious differences of the Calviridae with both other taxa are the position of the ovaries, the very short female duct, and no genito-intestinal connection. The main common character shared with the other two taxa is the separate male and female pores.

Unambiguous autapomorphies cannot be given for the Meidiamidae. Members of the Meidiamidae share several (unusual) characters with the Archimonocelididae, but can be distinguished from them by the ovaries close to the pharynx (exceptional in Archimonocelididae), the absence of cnidosacs, and the globular pharynx directed ventrally. Archimonocelididae and Meidiamidae also have a long female duct. The species of *Serrula* only have needles in the copulatory organ, as do the Calviriidae.

In view of the above, we conclude here that, for the time being, no sound indication can be given for a relationship between the three taxa, and therefore we consider them all to be 'families', next to the other families of Proseriata. Moreover, indications for the monophyly of the new taxon Meidiamidae are very weak, and a close relationship of its representatives is yet uncertain. Nevertheless, we prefer not to include them into the Archimonocelididae (where the taxon *Meidiama* was placed originally), because this would make the Archimonocelididae extremely heterogeneous, whereas without *Meidiama* it is a very homogeneous taxon. Hopefully, molecular data will give us more indications on the correctness of our taxonomic proposals. A cladistic analysis, based on morphological characters, would be premature, and thus must be postponed until more new taxa are known.

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APPENDIX

Abbrevations used in the figures: agb, accessory glandular bulb; ap, adhesive papilla; bc, copulatory bursa; br, brain; cap, ‘cap’; cg, cement glands; cn, cnidae; cop, copulatory organ; cut, sclerotized (‘cuticular’) tube; dgi, genito-intestinal duct; fd, female duct; fp, female pore; gd, gut diverticle; gut, gut; ma, male atrium; mp, male pore; mu, muscle; ne, atrial needle; ov, ovary; ovd, ovovitelloduct; pg, prostate glands; ph, pharynx; pv, prostate vesicle; rb, resorbing bursa; st, stylet; sta, statocyst; sv, seminal vesicle; t, testis; va, vagina; vit, vitellaria; vp, vaginal pore.