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

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Additional Keywords
Australia – *Dreuxiola* – *Meidiama*– *Serrula* –– Kerguelen ––Subantarctic – systematics – Uruguay – *Yorknia*

Running title
A new family of lithophoran Proseriata

ABSTRACT

In this contribution a new representative of the taxon *Meidiama* Marcus 1946, *M. uruguayensis* n.sp. (from Uruguay) is described, as are six more new species for which three new genera are proposed: *Dreuxiola philippi* n.g.n.sp. (from the French subantarctic archipelago Kerguelen), *Yorknia aprostatica* n.g.n.sp., *Serrula byronensis* n.g.n.sp., *S. maxillaria* n.sp., *S. concharum* n.sp. and *S. acuta* n.sp. (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, 1993 from the Archimonocelididae to become a separate taxon Calviriidae. Possible autapomorphies for the three families are discussed. It is also concluded that, at the present state of our knowledge, no sound indications can be given about close relationships.

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 P. Martens & Schockaert in 1988 at the family level, based on EM data of E. Martens (1984) and on karyological data of Curini-Galletti et al. (1984). In 1993, P. Martens & Curini-Galletti split this family into the Archimonocelidinae with two genera, *Archimonocelis* Meixner, 1938 and *Meidiama* Marcus, 1946, and the Calviriinae with two genera also, *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 DNA sequences by Curini-Galletti, (2001) and in 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 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 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 falls apart 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 with the $MgCl_2$-decantation method (see Martens, 1984), studied alive and mounted in lactophenol as whole mounts. If available, individuals were fixed with Bouin’s fluid, sectioned at 4 µm, and stained with Heidenhain’s or Ehrlich’s haematoxylin, using eosin or erythrosin as counterstain. Drawings without a scale are free hand; scales for reconstructions are approximate. The holotypes of the Australian species are deposited in the Queensland Museum (Brisbane, QLD, Australia - QLDM); 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). Position of structures is described as proportion of the body length, and indicates the distance from the anterior tip of the body.

ABBREVATIONS TO THE FIGURES

agb: accessory glandular bulb
ap: adhesive papilla
cg: cement glands
bc: copulatory bursa
br: brain
cap: “cap”
cn: cnidae
cop: copulatory organ
cut: sclerotised (“cuticular”) tube
dgi: genito-intestinal duct
fp: female pore
fd: female duct
gut: gut
gd: gut diverticle
ma: male atrium
mp: male pore
mu: muscle
ne: atrial needle
ov: ovary
ovd: ovo-vitelloduct
pg: prostate glands
ph: pharynx
pv: prostate vesicle
rb: resorbing bursa
st: stylet
sta: statocyst
sv: seminal vesicle
t: testis
va: vagina
vp: vaginal pore
vit: vitellaria

TAXONOMY

Meidiamidae, new family

Diagnosis
Lithophoran Proseriata with an encapsulated brain, a pre-cerebral gut diverticle, intraepidermal nuclei and the epidermis completely ciliated. Ovaries in front of the vitellaria, anteriorly of and close to the pharynx; a long female duct, the oviducts joining before the male copulatory organ, 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 or 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 recurved over about 180°, with the proximal pole directed forwards, the latter receiving the paired seminal vesicles enter; the distal pole, where the stylet is attached, is directed forwards also. 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, the female duct functioning as (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 *M. uruguayensis* n.sp.

Meidiama lutheri Marcus, 1946.
Meidiama uruguayensis n. sp.
Meidiama schockaerti Martens and Curini-Galletti, 1993.

Diagnoses
M. lutheri: species of *Meidiama* with a curved stylet of about 60 µm, accompanied by 10-12 spines of 30 µm with a small terminal hook about 1/3 of the length of the spines; close to 100 testes.
M. uruguayensis: species of *Meidiama* with a curved stylet of 80-90 µm, accompanied by 19-21 spines of 30-45 µm with a small terminal hook about 1/5 of the length of the spines; about 50 testes.
M. schockaerti: species of *Meidiama* with a straight stylet of about 65 µm, accompanied by 18-20 spines of 60 µm without hook; 9-10 testes in a row.

Occurrence

M. lutheri: Beach of Guarujà, near Santos, Brazil. Coarse shell gravel (type locality)
M. uruguayensis: Río de la Plata, Balneario Las Flores, Departamento de Maldonado (34º48´50"S, 55º20´03"W), Uruguay (type locality). Playa Grande, Uruguay. Coarse sand between rocks (18/7/2004).
M. 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

M. lutheri: two whole mounts, one indicated as lectotype (SMNH, nr 7348); two slides with dispersed sections of several individuals and of very poor quality, containing very fragmentary information (paralectotypes: SMNH, nr 7349-7350).
M. schockaerti: holotype (SMNH, nr 7351)(whole mount).
M. uruguayensis: four whole mounts and 10 sectioned individuals (13 slides) from the type locality, one of the whole mounts designated the holotype (SMNH, nr 7352 – paratypes: UH, nr 371-380).

Etymology

M. uruguayensis has been named after the country where it was found.

Description

The animals are very long and slender, adults of *M. lutheri* around 4 mm in length, those of *M. schockaerti* 2-3 mm and *M. uruguyaensis* around 6 mm (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, slightly lobate and about in the middle of the body (Fig. 1). The epidermis is 1.5-2 μm thick in *M. lutheri*, cilia 3 μm dorsally and 4 μm ventrally; in *M. uruguayensis* the epidermis is 1 and 1.5 μm thick and the cilia 2 and 3 μm, respectively?

The ovaries are just in front of the pharynx and the vitellarian follicles are all behind the pharynx, extending over about 2/3rd of the post-pharyngeal body part. Behind the last, most posterior follicle the two ovo-vitelloducts 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 and 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, though 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, 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 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 ovo-vitelloducts is very thin and sinuous and no evidence of a resorbing function was seen.

There are about 50 testes in *M. uruguayensis* (close to 100 in *M. lutheri,* according to fig. 120 of Marcus, 1946), roughly arranged in two rows, the first testis found at 1/3 of the prepharyngeal region, the last ones 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^o, with both proximal and distal poles directed forwards. The seminal duct can clearly be seen in the centre of the vesicle, its epithelium forming the prostate glands, whose nucleated gland bodies are outside and inside 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 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, the needles 28 to 30 µm, also slightly curved. The funnel-like proximal end of the stylet has an opening of 7-8 µm with a strongly-thickened wall, while 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, since the whole 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 10 and Marcus (1946) mentions 12. Needles lying above each other are indeed often difficult to discern. Each needle ends in a slender “hook”, about 1/3 of the total length of the needle in the shortest needles and about ¼ in the longest needles.

In *M. uruguayensis* the stylet is also curved, about 90 µm 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 slightly less than 5 µm distally. There are about 18 needles, 31 to 37 µm long, the shortest located in the middle of the circle. The terminal “hooks” have a strongly curved tip and are a little less than 1/5 to 1/4 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 to 46 µm (n=6, mean=32 µm) and the longest needles are 35-69 µm (n=6, mean= 44 µm). The individuals with the longest stylet also have the larger 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, gradually narrowing from 10 µm at the proximal opening (without obvious thickening) to about 3 µm distally. The needles are about 60 µm long, without a terminal “hook”. We counted about 18 needles, while Martens & Curini-Galletti (1993) depict 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 nov. gen.

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, the female duct functioning as a copulatory bursa. Genito-intestinal duct near the female pore leading to a resorbing bursa.

Type species: *Dreuxiola philippi* n. sp.

Dreuxiola phillipi n.sp.

Diagnosis

Species of *Dreuxiola* with about 25 testes, and 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 sclerotised (“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 on the living animals, two whole mounts (one of them indicated holotype, SMNH, nr 7353, the other indicated paratype UH, nr. 381), four series of sections of which only two contain relevant information (UH, nr 382-385).

Etymology

Genus and species are named in honour of Prof. Dr. 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, with some anterior sensory bristles. Adhesive papillae were not seen in the whole mounts, nor in the sections. The brain is encapsulated and there is a clear extension of the gut over the brain. The pharynx is directed ventrally, slightly lobate and placed at 2/3rd of the body length (Fig. 5). The epidermis is 1 µm thick ventrally and 1.5 µm 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 1/3rd of the post-pharyngeal body part. Behind the last follicle the two ovo-vitelloducts join into the common female duct, which looks very muscular and swollen in living animals, filled with sperm, clearly functioning as a copulatory bursa. The vagina opens about in its middle with a little sclerotised tube, about 50 µm long (Figs 6 and 7). In the sections, the vaginal duct appears as a narrow tube with a strongly muscular wall, surrounded by a loose tissue that itself surrounded itself 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 the whole mounts (Fig. 6). More backwards, the female duct narrows towards the female pore that is found at ¾ of the postpharyngeal body part. From the female pore departs the genito-intestinal duct towards the resorbing bursa.

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 forwards, where the paired seminal vesicles enter, and the distal pole directed backwards; distally, the prostate vesicle tapers and recurves almost 180^{o}. 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 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 latter 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 about in the middle of this glandular bulb. The stylet is about 250 µm in the two whole mounts; the needles are between 40 to 50 µm long. These needles seem to be very slightly sclerotised and are rather difficult to discern in whole mounts. Nevertheless, it could be observed that the needles are in two symmetrically arranged groups, each consisting of a shorter, curved needle at the outside and a thicker straight needle in the middle (both about 40 µm) and two slender and moderately curved needles of about 50 µm in between (measurements from the two whole mounts).

Yorknia nov. gen.

Diagnosis

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

Type species: *Yorknia aprostatica* n. sp.

Yorknia aprostatica n. sp.

Diagnosis

Species of *Yorknia* with 15 testes in a row, without prostate glands nor vesicle, with an almost straight stylet about 80 µm long with a proximal “cap” of 30-40 µm and 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 designed holotype, (QM, nr G 230107). A second whole mount and six sectioned animals (UH, nr 386 and 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 in length, with some anterior sensory bristles. Adhesive papillae were not seen in whole mounts, nor in sections. The brain is encapsulated and there is a clear extension of the gut over the brain. The pharynx is directed ventrally, slightly lobate and located at 2/3rd to 3/4 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 ovo-vitelloducts join into the common female duct, which is swollen in the living animal, clearly functioning 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 again and continues backwards as 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 extremely thin in the genito-intestinal duct, where it is devoid of cilia. At their very end, the ovo-vitelloducts 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 sclerotised “cap”, which has a fan-like muscle with its wider side attached to the cap and its narrower side to the stylet (see also Fig. 12). The seminal vesicle is extremely large, occupying almost the whole post-penial 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 with an almost constant diameter of 8-10 µm; the “cap” is 45µm long in the holotype and 30 µm in the paratype. The fan-like muscle is clearly visible in the whole mount.

Serrula nov. gen.

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* n.sp.

There are four species that are very similar and are described together.

***Serrula byronensis* n.sp.**
***Serrula maxillaria* n.sp.**
***Serrula concharum* n.sp.**
***Serrula acuta* n.sp.**

Diagnoses

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

Serrula maxillaria: species of *Serrula* with a single seminal vesicle. Atrial needles 13 µm long and 3 µm broad over the whole length and with a truncated and serrated distal end. Pre-cerebral diverticle ends at the statocyst.

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

Serrula acuta: species of *Serrula* with a single seminal vesicle (?); slender pointed needles of 25 µm long and 6 µm 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).

Serrula concharum: Eaglehawk Neck, Australia (Tasmania). Exposed intertidal, with fine sand, with 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 holotypes, QM, nr G 230108-230111). Sections of one individual of *S. byronensis* of very poor quality and without relevant information (except the epidermis) (UH, nr 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* 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 and from the whole mounts. Therefore, 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 long bristles at the caudal end. *S. byron* also has prominent adhesive papillae (Figs 13, 14). The precerebral gut diverticle reaches far in front of the statocyst in *S. concharum*, while it ends about above the statocyst in *S. byronensis* and *S. maxillaria* (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 ¼ of the body; the ovaries, located in anterior to the pahrynx, are preceded by a single pair of testes. All vitellarian follicles are behind the pharynx and the most posterior 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. *S. 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 while 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 two muscles that “flank” the prostate vesicle at either side. Because of the lack of sections, the hypothesis that these bases are muscles has to be confirmed. The form and size of the needles are given in the diagnoses.

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) and E. Martens (1984), E. Martens & Schockaert (1986) based on ultrastructural data, Tajika (1982), P. Martens & Schockaert (1988), P. Martens & Curini-Galletti and other co-authors (1989, 1993) on light microscopic and karyological analyses, Curini-Galletti et al. (1984, 1989, 1990) 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 these authors are often very contradictory. For example, among other contradictions, Sopott-Ehlers (1985) and Ehlers (1985) consider the Unguiphora as the sister-taxon of all lithophoran Proseriata, while Martens & Schockaert (1988) consider the Monocelididae as the sister-taxon of all 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*, while 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 also beyond the scope of this contribution. In what follows, we re-formulate 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 readability 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 completely ciliated epidermis. Ovaries in front of the vitellaria, anteriorly of and close to the pharynx. A long female duct, with the oviducts joining before the male copulatory organ, 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 or only needles or 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 not. Pharynx globular and directed ventrally.

The Archimonocelididae are lithophoran Proseriata with an encapsulated brain, a precerebral gut diverticle, intraepidermal nuclei and completely ciliated epidermis. Ovaries in front of the vitellaria, anteriorly of the pharynx; a long female duct, the oviducts joining before the male copulatory organ, 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 mostly also behind the ovaries. Copulatory organ directed forwards with stylet and atrial needles or 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 not. 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 completely ciliated epidermis. Ovaries located about in the middle of the vitellaria, anteriorly of and close to the pharynx; a very short female duct, the oviducts joining behind the male copulatory organ, the female pore behind it (digonoporid condition). With a resorbing bursa close to the female pore (but 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 and sphincter above the pharynx can divide 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 intraepithelial nuclei. Only the Monocelididae have no brain capsule and no gut diverticle. Monocelididae also have the epidermis nuclei insunk under the body musculature and have no cilia at their very caudal part. The Otoplanidae have only cilia in the ventral "creeping sole" (except in the species of *Archotoplana* Ax, 1956), some lack the gut diverticle and some have epidermal insunk nuclei as well.

Ovaries are mostly situated in front of the pharynx, with vitellarian follicles in front 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 have the 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 related in the past (Meixner, 1938; Marcus, 1946, Karling, 1966), though 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, 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, though 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 (E. Martens & Schockaert, 1985; Bruggemann, 1985, 1986). Even though this character has been detected by electron microscopy, it can very well be seen in light microscopic sections and even in the living animal. In Monocelididae hard parts are absent or are basement membrane derivatives (E. Martens & Schockaert, 1985). The presence of an accessory glandular organ is considered 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 *Dreuxiola philippi*.

Which characters are left that may be considered autapomorphies for each of the three families and which character might indicate a relationship of 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* have only needles in the copulatory organ as do the Calviriidae.

In view of the above it is here concluded that, for the time being, no sound indication can be given for a relationship between the three taxa, and therefore we consider them all “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, while 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 must be postponed until more new taxa become known.

ACKNOWLEDGMENTS

E.S. acknowledges the “Territoires Australes et Antartiques Francaises” and the Fund for Scientific Research, Flanders for enabling collection at the islands of Kerguelen and in Uruguay, Prof. Dr. R. Ponce de Leon for his help in collecting material in Uruguay and for providing part of the material of *Meidiama uruguayensis*. M. C-G. is indebted to Dr. L.R.G. Cannon, for providing opportunity for research in Australia, and to Dr. M. Potter (Northern Fisheries Centre, Cairns) and A.M.M. Richardson (University of Tasmania, Hobart) for their hospitality and provision of research facilities. We wish to thank Dr. Nikki Watson for the critical reading of the manuscript.

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Legends to the figures

Fig. 1. General appearance of a species of *Meidiama* combined from whole mounts of *M. lutheri*, *M. uruguayensis* and fig. 120 of Marcus (1946).

Fig. 2. Sagittal reconstruction of the female system, seen from the left, of the species of *Meidiama*, mainly based on sections of *M. uruguayensis*. The lower figure is the continuation of the upper part.

Fig. 3. Reconstruction of the copulatory organ in *M. lutheri* and *M. uruguayensis*, seen from the left, based on sections of *M. uruguayensis* and the whole mounts of both species.

Fig. 4. Hard parts of the copulatory organ of *M. uruguayensis* (A; inset: terminal opening in the holotype), *M. lutheri* (B) and *M. schockaerti* (C).

Fig. 5. A living animal of *Dreuxiola philippi*.

Fig. 6. Post-pharyngeal genital organs of *Dreuxiola philippi* in the whole mount, as they also have been seen in the living animal.

Fig. 7. Reconstruction of the post-pharyngeal genital organs of *Dreuxiola philippi*, seen from the right.

Fig. 8. The copulatory organ of *Dreuxiola philippi* as seen in the living animal.

Fig. 9. Hard parts of the copulatory organ in the holotype of *Dreuxiola philippi*.

Fig. 10. Drawings from a living animal of *Yorknia aprostatica*. A: the whole animal; B: the post-pharyngeal genital organs.

Fig. 11. Sagittal reconstruction of the post-pharyngeal genital organs of *Yorknia aprostatica*, seen from the left.

Fig. 12. Copulatory organ of *Yorknia aprostatica*, as seen in the whole mounts (A: in the holotype, B: in the paratype)

Fig. 13. Living specimens of the species of *Serrula*. A. *S. byronensis*, B. *S. maxillaria*. C. *S. concharum.*

Fig. 14. Most posterior body part in live animals. A. *S. byronensis*, B. *S. maxillaria*. C. *S. concharum.*

Fig. 15. The needles and the muscular supports of the copulatory organ in the species of *Serrula*. A. *S. byronensis,* B. *S. maxillaria,* C. *S. concharum,* D. *S. acuta.*