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Ultrastructure of the spermatozoon of the bank vole tapeworm, *Paranoplocephala omphalodes* (Cestoda, Cyclophyllidea, Anoplocephalidae)

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Abstract The mature *Paranoplocephala omphalodes* spermatozoon is filiform, tapered at both ends and lacks mitochondria. Its anterior extremity exhibits an apical cone of electron-dense material measuring about 900 nm in length and 200 nm in width, and two crested-like bodies. The cortical microtubules follow a 25–35° helicoidal path along their whole length, except at the posterior extremity where they become parallel to the spermatozoon axis. They are arranged in a single or two fields which may cover each other partially. The axoneme, of the 9 + "1" pattern of the Trepaxonemata, lacks a peri-axonemal sheath and does not reach the extremity of the spermatozoon. The nucleus is a compact and irregular cord coiled in a spiral around the axoneme. Moreover, we report for the first time a nucleus in the spermatozoon of a Cyclophyllidea species which reaches beyond the axonemal posterior extremity. The cytoplasm, depending on the level where the section is cut, is slightly electron dense or electron lucent and contains numerous small electron-dense granules in regions III–V. In the posterior spermatozoon extremity, granular material is replaced by a terminal and compact electron-dense material.

Introduction

To date, only 8 of the 15 Cyclophyllidea families have been the subject of ultrastructural studies of spermiogenesis and/or the spermatozoon. These are the Anoplocephalidae, Catenotaeniidae, Davaineidae, Dilepididae, Dipylidiidae, Hymenolepididae, Nematotaeniidae and Taeniidae families (Bâ and Marchand 1995, 1996; Justine, 1995; Swiderski and Tkach 1996a, b; Miquel and Marchand 1997; Miquel et al. 1997).

For the Anoplocephalidae family, there are ultrastructural studies on the spermatozoon of species belonging to nine genera: *Aporina* (Bâ and Marchand 1994a), *Avitellina* (Bâ and Marchand 1994b), *Inermicapsifer* (Bâ and Marchand 1994c), *Mathevotaenia* (Bâ and Marchand 1994d), *Moniezia* (Bâ and Marchand 1992a), *Monoecocestus* (MacKinnon and Burt 1984), *Oochoristica* (Swiderski and Subilia 1985), *Stilesia* (Bâ and Marchand 1992b) and *Thysaniezia* (Bâ et al. 1991).

The aim of the present work is to describe the ultrastructure of the mature spermatozoon of another Anoplocephalidae species, *Paranoplocephala omphalodes*.

Materials and methods

The specimens of *P. omphalodes* were gathered live from the small intestine of naturally infested bank voles, *Clethrionomys glareolus* (Rodentia: Arvicolidae), coming from two Spanish localities: Granollers (Barcelona province) and Eugi (Navarra province). They were kept in a 0.9% NaCl solution. Portions of mature proglottides containing seminal vesicles and testes were removed under a binocular microscope and fixed for 1 h at 4 °C with 2.5% glutaraldehyde in 0.1 *M* sodium cacodylate buffer at pH 7.2, postfixed for 1 h at 4 °C with osmium tetroxide in the same buffer, then dehydrated with ethanol and propylene oxide before being embedded in Epon. Ultrathin sections were cut on a Reichert-Jung Ultracut E ultramicrotome, then stained with uranyl acetate and lead citrate. They were examined in a Hitachi H-600 electron microscope in Banyuls-sur-Mer (France) and Barcelona (Spain).

Results

From anterior to posterior of a spermatozoon we could distinguish five different regions (I–V); there was no

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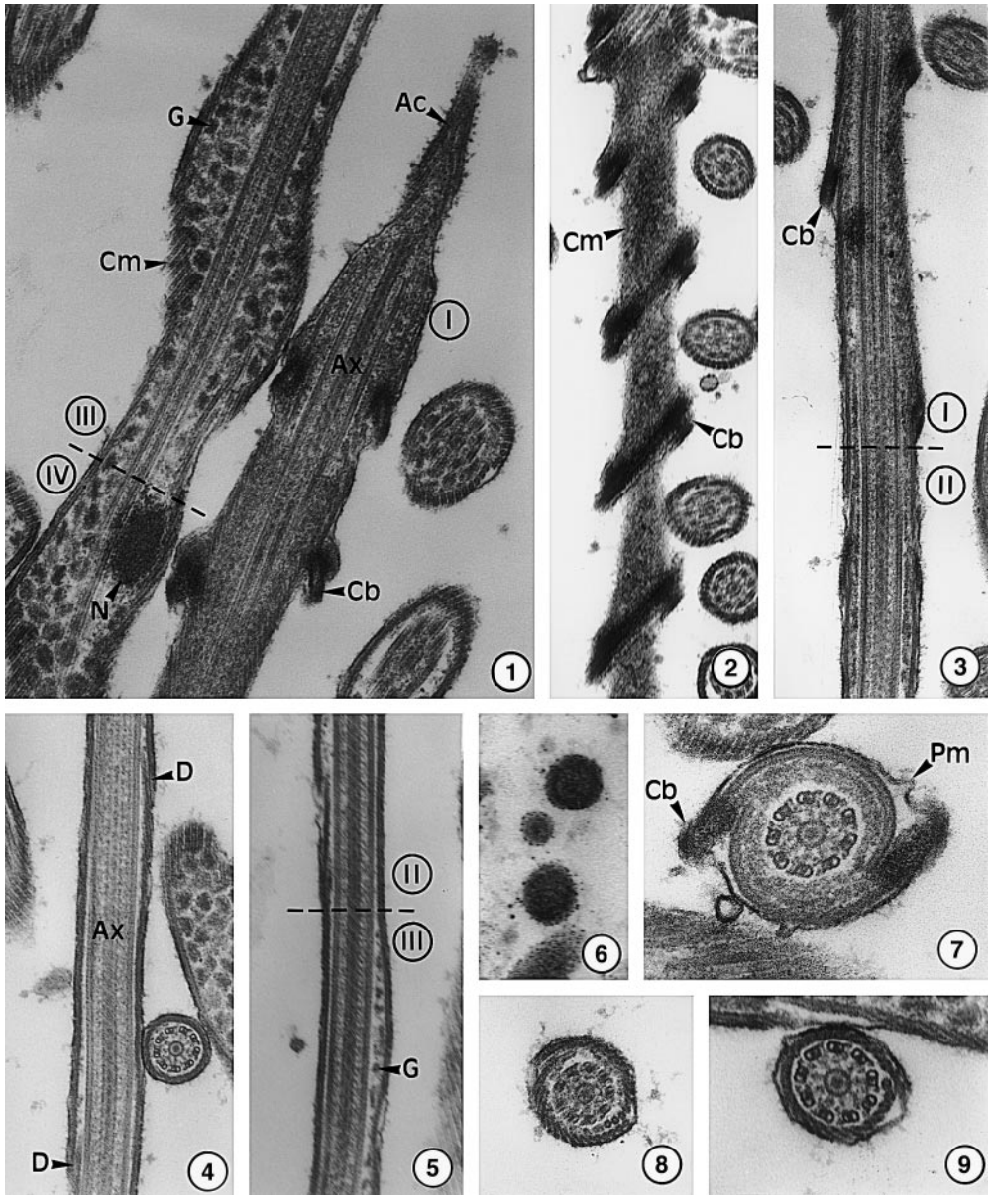


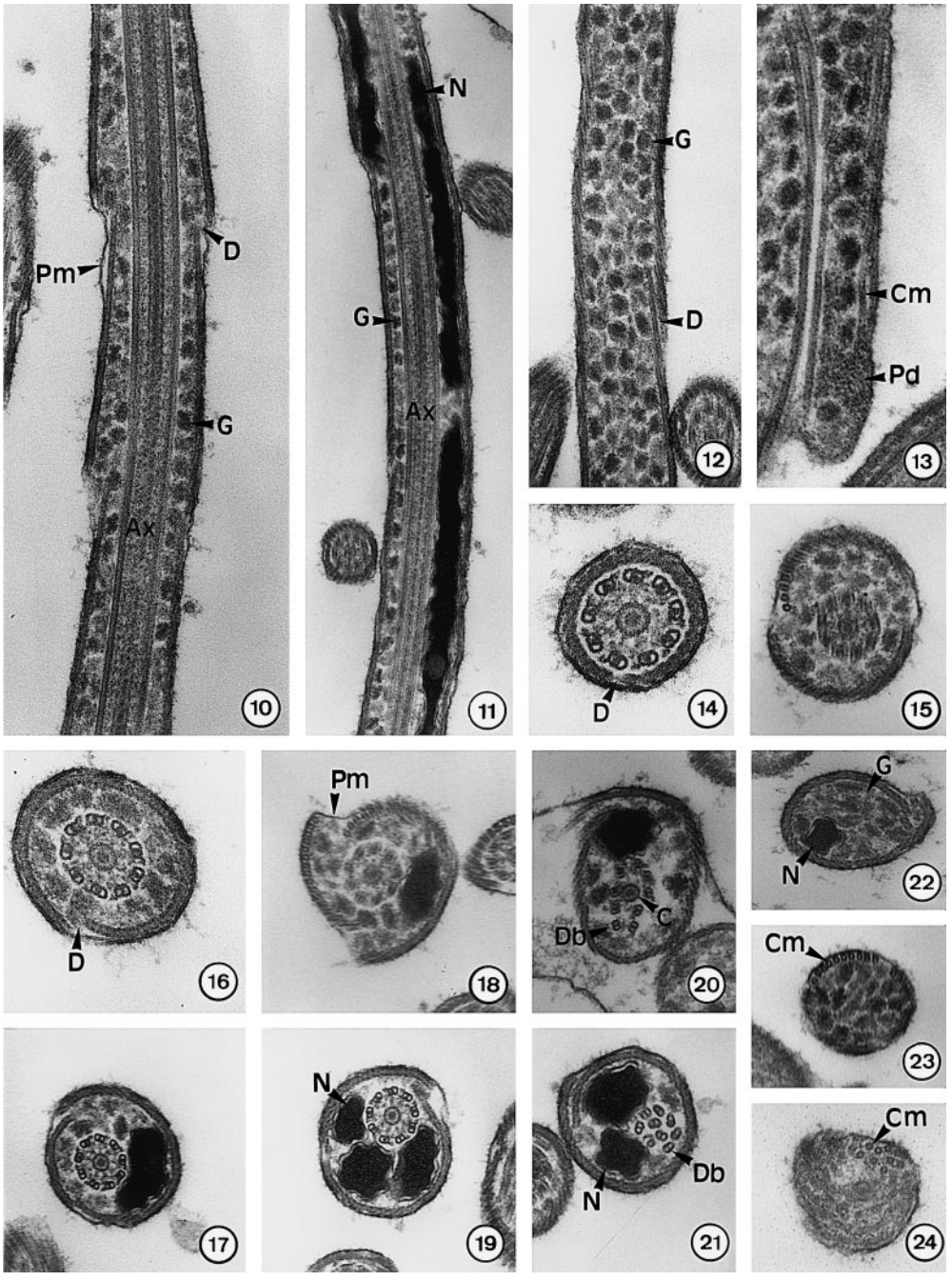
Fig. 1 Longitudinal sections of regions I, III and IV of the mature *Paranoplocephala omphalodes* spermatozoon (*Ac* apical cone of electron-dense material, *Ax* axoneme, *Cb* crested-like bodies, *Cm* cortical microtubules, *G* electron-dense granular material, *N* nucleus). ×37,500. **Fig. 2** Tangent section of region I of the mature *P. omphalodes* spermatozoon (*Cb* crested-like bodies, *Cm* cortical microtubules). ×35,000. **Fig. 3** Longitudinal section of regions I and II of the mature *P. omphalodes* spermatozoon (*Cb* crested-like bodies). ×35,000. **Fig. 4** Longitudinal sections of region II of the mature *P. omphalodes* spermatozoon (*Ax* axoneme, *D* discontinuity in the electron-dense layer of cortical microtubules). ×40,000. **Fig. 5** Longitudinal section of regions II and III of the mature *P. omphalodes* spermatozoon (*G* electron-dense granular material). ×35,000. **Fig. 6** Cross-section of the apical cone of region I of the mature *P. omphalodes* spermatozoon. ×65,000. **Fig. 7** Cross-section of region I of the mature *P. omphalodes* spermatozoon showing two crested-like bodies (*Cb*) (*Pm* plasma membrane). ×75,000. **Fig. 8** Cross-section of region II of the mature *P. omphalodes* spermatozoon showing two fields of cortical microtubules. ×50,000. **Fig. 9** Another cross-section of region II of the mature *P. omphalodes* spermatozoon showing a single field of cortical microtubules. ×70,000

marked morphological discontinuity between them but they exhibited distinctive ultrastructural features.

Region I (Figs. 1–3, 6, 7, 25), roughly 375–650 nm wide, corresponds to the anterior extremity of the spermatozoon. It is capped by an apical cone of electron-dense material with a base of roughly 200 nm and a length of about 900 nm (Fig. 1). It exhibits two helicoidal crested-like bodies associated with the subjacent microtubules (Figs. 1, 7). The thickness of the crested-like bodies gradually decreases towards the beginning of region II (Fig. 3). The axoneme, of the 9 + "1" pattern of the Trepaxonemata, is located centrally. It lacks a peri-axonemal sheath and is surrounded by a thin layer of slightly electron-dense cytoplasm (Figs. 1, 7). The cortical microtubules spiral at an angle of about 25–35° to the spermatozoon axis (Fig. 2). In longitudinal sections, they form a discontinuous layer of electron-dense and submembranous material (Figs. 1, 3). In transverse section, they form two fields and meet, once or a more than once, the periphery of the spermatozoon at the level of the crested-like bodies (Fig. 7).

Region II (Figs. 3–5, 8, 9, 14, 25) is between 275–450 nm wide. It lacks crested-like bodies but exhibits a central axoneme, a thin layer of electron-lucent cytoplasm and a single or two bundles of spiralled cortical microtubules, which sometimes cover each other partially, and form a discontinuous layer of electron-dense and submembranous material (Figs. 8, 9, 14).

Region III (Figs. 1, 5, 10, 15, 16, 25) is about 350–575 nm wide. It is characterized by the presence of a central axoneme enveloped by a thick layer of electron-lucent cytoplasm with numerous granules of electron-dense material (Figs. 1, 10, 15, 16). The cytoplasm is surrounded by the spiralled cortical microtubules. These



cortical microtubules are organized in a single field or two fields of electron-dense and submembranous material (Figs. 10, 15, 16).

Region IV (Figs. 1, 11, 17–22, 25) is about 475–600 nm wide. This region is characterized by a nucleus coiled in an irregular spiral around the central axoneme that becomes disorganized. The doublets lose their arms and become disorganized around the central core (Fig. 20), which then disappears, and the doublets transform into singlets before their disappearance (Fig. 21). The nucleus appears as a compact cord, irregular in section, and exhibits a different morphology in diverse cross-sections (Figs. 17–22). It stops after reaching the posterior extremity of the axoneme (Fig. 22). The flagellum is also enveloped by a thick layer of electron-lucent cytoplasm showing electron-dense granular material (Figs. 1, 11, 17, 18). The twisted cortical microtubules are constituted by a single or two bundles of electron-dense and submembranous material, cover which sometimes each other partially (Figs. 17–22).

Region V (Figs. 12, 13–25), which is 300–500 nm wide, corresponds to the posterior extremity of the spermatozoon. It has neither axoneme nor nucleus. The electron-lucent cytoplasm shows numerous electron-dense granules and the cortical microtubules are

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Fig. 10 Longitudinal section of region III of the mature *P. omphalodes* spermatozoon (*Ax* axoneme, *D* discontinuity in the electron-dense layer of cortical microtubules, *G* electron-dense granular material, *Pm* plasma membrane). ×40,000. **Fig. 11** Longitudinal section of region IV of the mature *P. omphalodes* spermatozoon (*Ax* axoneme, *G* electron-dense granular material, *N* nucleus). ×30,000. **Fig. 12** Longitudinal section of region V of the mature *P. omphalodes* spermatozoon (*D* discontinuity in the electron-dense layer of cortical microtubules, *G* electron-dense granular material). ×35,000. **Fig. 13** Another longitudinal section of region V of the mature *P. omphalodes* spermatozoon at the level of the posterior spermatozoon extremity. The cortical microtubules (*Cm*) become parallel to the spermatozoon axis (*Pd* posterior electron-dense material). ×55,000. **Fig. 14** Cross-section of region II of the mature *P. omphalodes* spermatozoon showing a single field of cortical microtubules. They still form a discontinuous layer under the plasma membrane but do not cover each other (*D* discontinuity in the electron-dense layer of cortical microtubules). ×87,500. **Fig. 15** Cross-section of region III of the mature *P. omphalodes* spermatozoon showing two fields of cortical microtubules. ×52,500. **Fig. 16** Another cross-section of region III of the mature *P. omphalodes* spermatozoon showing a single field of cortical microtubules (*D* discontinuity in the electron-dense layer of cortical microtubules). ×75,000. **Fig. 17** Cross-section of region IV of the mature *P. omphalodes* spermatozoon showing a single field of cortical microtubules. ×47,500. **Fig. 18** Another cross section of region IV of the mature *P. omphalodes* spermatozoon showing two fields of cortical microtubules. (*Pm* plasma membrane). ×47,500. **Fig. 19** A further cross-section of region IV of the mature *P. omphalodes* spermatozoon showing a single field of cortical microtubules and the irregular arrangement of the nucleus (*N*) around the axoneme. ×47,500. **Fig. 20** Cross-section of region IV of the mature *P. omphalodes* spermatozoon. The doublets (*Db*) lose their arms and become disorganized (*C* central core). ×47,500. **Fig. 21** Cross-section of region IV of the mature *P. omphalodes* spermatozoon (*Db* doublets, *N* nucleus). ×52,500. **Fig. 22** Cross-section of region IV of the mature *P. omphalodes* spermatozoon. The nucleus (*N*) reaches beyond the axonemal posterior extremity (*G* electron-dense granular material). ×47,500. **Fig. 23** Cross-section of region V of the mature *P. omphalodes* spermatozoon. The cortical microtubules (*Cm*) become parallel to the spermatozoon axis. ×47,500. **Fig. 24** Another cross-section of region V of the mature *P. omphalodes* spermatozoon. In the posterior spermatozoon extremity, electron-dense granules disappear and are replaced by other electron-dense material (*Cm* cortical microtubules). ×47,500

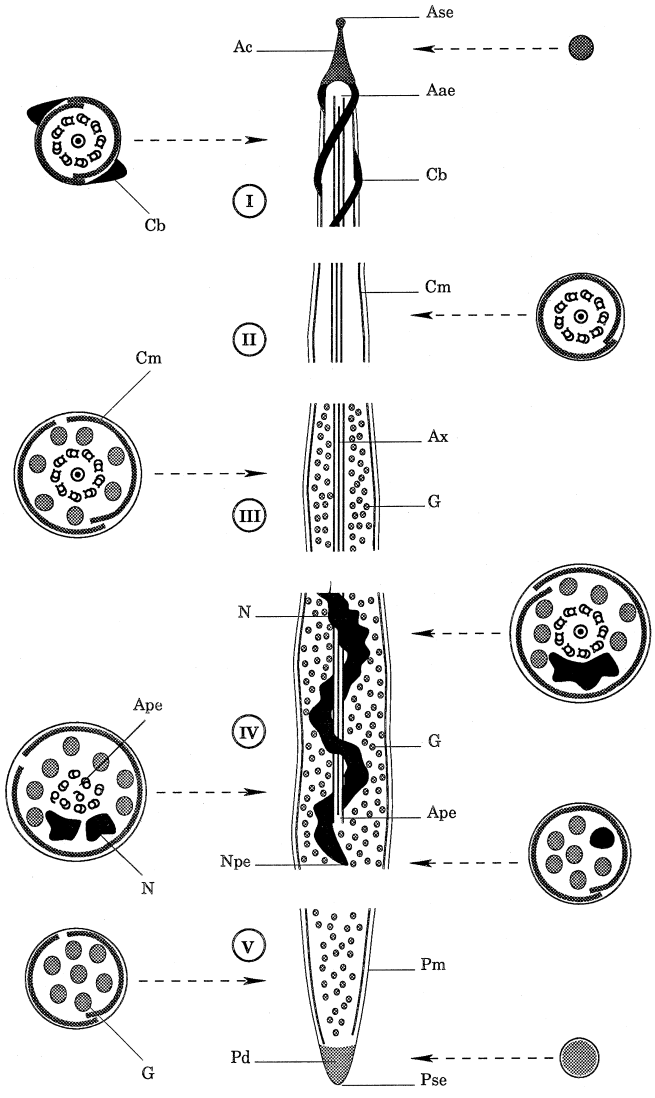

Fig. 25 Attempted reconstruction of the mature *P. omphalodes* spermatozoon with five regions (I–V) distinguished from apex to posterior. To make the diagram clearer, the spiral coil around the axoneme of the cortical microtubules has not been shown (*Aae* axonemal anterior extremity, *Ac* apical cone, *Ape* axonemal posterior extremity, *Ase* anterior spermatozoon extremity, *Ax* axoneme, *Cb* crested-like bodies, *Cm* cortical microtubules, *G* electron-dense granular material, *N* nucleus, *Npe* nuclear posterior extremity, *Pd* posterior electron-dense material, *Pm* plasma membrane, *Pse* posterior spermatozoon extremity)

spiralled, forming a discontinuous layer of electron-dense and submembranous material (Fig. 12). They end their helicoidal course by becoming parallel to the spermatozoon axis (Figs. 13, 23, 24). At the level of the posterior spermatozoon extremity, granules of electron-dense material are replaced by a compact electron-dense material (Fig. 24).

Discussion

The presence of a crested-like body (or bodies) in Cestoda spermatozoa always marks the anterior extremity of the gamete (Bâ et al. 1991). The extremity with the crested-like bodies in the *P. omphalodes* spermatozoon therefore corresponds to its anterior end and the extremity without crested-like bodies to its posterior end. To date, in the Cyclophyllidea, a crested-like body (or bodies) has been described on the spermatozoa of 18 species belonging to six families. These are 9 species of the Anoplocephalidae family (*Aporina delafondi*, *Avitellina centripunctata*, *Inermicapsifer madagascariensis*, *I. guineensis*, *Mathevotaenia herpestis*, *Moniezia expansa*, *Moniezia benedeni*, *Stilesia globipunctata* and *Thysaniezia ovilla*; Table 1), one Catenotaeniidae species (*Skrjabinotaenia lobata*, Miquel et al. 1997), two Davaineidae species (*Raillietina tunetensis*, Bâ and Marchand 1994e; and *Cotugnia polyacantha*, Bâ and Marchand 1994f), one Dipylidiidae species (*Dipylidium caninum*, Miquel and Marchand 1997), three Hymenolepididae species (*Hymenolepis nana*, Bâ and Marchand 1992c; *H. straminea*, Bâ and Marchand 1996;

Table 1 Variation in some features of the spermatozoon of diverse Anoplocephalidae species (an *asterisk* indicates observations made on the illustrations in the previously published papers, + presence of considered character, − absence of considered characters)

Anoplocephalidae subfamily Anoplocephalidae species Reference	Crested-like bodies		Apical cone (length × width) (nm)	Cortical microtubules		Peri-axonemal sheath	Electron-dense granules	Electron-dense posterior extremity
	Number	Thickness (nm)		Angle	Fields			
Anoplocephalinae								
Aporina delafondi Bâ and Marchand 1994a	5	15–40	300 × 150	15°		−	+	+
Moniezia benedeni Bâ and Marchand 1992a	2	30–40	1,000 × 250		2–4	−	+	−
Moniezia expansa Bâ and Marchand 1992a	2	30–60	1,000 × 250	45°	2–4	−	+	−
Monoecocestus americanus MacKinnon and Burt 1984				30–35°*	2*	−	+	−
Paranoplocephala omphalodes Present paper	2	180	900 × 200	25–35°	1–2	−	+	+
Inermicapsiferinae								
Inermicapsifer guineensis Bâ and Marchand 1994c	2	40*		30–35°*		+	−	+
Inermicapsifer madagascariensis Bâ and Marchand 1994c	2	40*		30–35°*		+	−	+
Linstowiinae								
Mathevotaenia herpestis Bâ and Marchand 1994d	1	70*		40°		+	−	+
Thysanosomatinae								
Avitellina centripunctata Bâ and Marchand 1994b	1	150–200	700 × 300	35°		+	−	−
Stilesia globipunctata Bâ and Marchand 1992b	1	150*	1,250 × 500	50°		+	−	−
Thysaniezia ovilla Bâ et al. 1991	2	80	600 × 200	40–50°	2–4	−	+	−

Retinometra serrata, Bâ and Marchand 1993) and two Nematotaeniidae species (*Nematotaenia chantalae*, Mokhtar-Maamouri and Azzouz-Draoui 1990; *Cylindrotaenia hickmani*, Jones 1994). In the present study, we describe for the first time the existence of crested-like bodies in a species of the genus *Paranoplocephala*. The *P. omphalodes* spermatozoon exhibits two crested-like bodies.

In the Cyclophyllidea, the nucleus coils in a more or less tight spiral around the axoneme (Bâ and Marchand 1995). Nevertheless, in *R. serrata* (Bâ and Marchand 1993), the nucleus has a rectilinear disposition in the cytoplasm. The nucleus of the *P. omphalodes* spermatozoon shows the typical spiralled pattern of the Cyclophyllidea spermatozoon, but exhibits an irregular morphology in diverse cross-sections. To our knowledge, in the Cyclophyllidea, this morphological feature has only been described in *T. ovilla* (Bâ et al. 1991). However, in the *P. omphalodes* spermatozoon, the nucleus reaches beyond the axonemal posterior extremity. As far as we know, this character has never been reported before in the gamete of a Cyclophyllidea cestode. So far, a similar organization has only been observed in the *D. caninum* spermatozoon (Miquel and Marchand 1997). Nevertheless, in this Dipylidid, the nucleus stretches down to the disorganized axoneme, but does not reach beyond the axonemal posterior extremity.

Granular electron-dense material in the cytoplasm of spermatozoa has been described in nine Cyclophyllidea species belonging to three families: *A. delafondi*, *M. expansa*, *M. benedeni*, *Monoecocestus americanus* and *T. ovilla* (Anoplocephalidae); D. *caninum* (Dipylidiidae), and *H. nana*, *H. straminea* and *R. serrata* (Hymenolepididae). *M. americanus* exhibits granules of electron-dense material in the spermatozoon cytoplasm throughout its length (MacKinnon and Burt 1984). On the other hand, in *H. nana* (Bâ and Marchand 1992c), these electron-dense granules are present in all the gamete regions except that of the crested-like bodies. In contrast, in *D. caninum* mature spermatozoa, these granules of electron-dense material appear only after axonemal disorganization (Miquel and Marchand 1997). Finally, in *P. omphalodes* as in *M. expansa*, *M. benedeni*, *R. serrata*, *A. delafondi*, *H. straminea* and *T. ovilla* spermatozoa (Bâ et al. 1991; Bâ and Marchand 1992a, 1993, 1994a, 1996), this granular electron-dense material is distributed along all gamete regions except at their anterior and posterior extremities. In the Anoplocephalinae species, the presence of electron-dense granules and the absence of a peri-axonemal sheath appear to be constant features (see Table 1). These two characters seem to be of potential interest for discriminating between species of Anoplocephalinae and the other subfamilies.

Cortical microtubules arranged in two fields have been described in the spermatozoon of the Cyclophyllidea species. *M. americanus* (MacKinnon and Burt 1984) is the sole species that always shows two bundles of cortical microtubules (observation of published micrographs seems to indicate this fact). On the other hand, two to four fields of cortical microtubules partially covering each other have been reported for other Cyclophyllidea (Bâ et al. 1991; Bâ and Marchand 1992a) (Table 1). In the particular case of *P. omphalodes*, the cortical microtubules are arranged in a single or two fields forming a circle, and may or may not cover each other partially. To our knowledge, in the Cyclophyllidea, the present work constitutes the first report of this particular disposition of cortical microtubules.

In the ultrastructural organization of the spermatozoon, diverse characters vary according to the species. For representatives of the Anoplocephalidae, Table 1 summarizes some features observed in ultrastructural studies of the spermatozoon. It seems that the thickness of the crested-like bodies, the length of the apical cone and the presence of one or two discontinuous fields of cortical microtubules are the most clear criteria to distinguish the *P. omphalodes* spermatozoon from that of the other species. Nevertheless, we think that it is necessary to carry out a more complete study of different species to establish possible synapomorphic characters for the Cyclophyllidea families and/or subfamilies.

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