

Ultrastructure of the spermatozoon of *Paroniella reynoldsae* (Cyclophyllidea, Davaineidae) an intestinal parasite of *Corvus albus* (Aves, Corvidae)

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Abstract

The mature *Paroniella reynoldsae* spermatozoon exhibits an apical cone of electron-dense material about 2.2 µm long and 0.65 µm wide at its base and two helicoidal crest-like bodies roughly 100 to 150 nm thick. The latter are of different lengths, spiralled and make an angle of about 45° with the spermatozoon axis. The axoneme is of the 9 + '1' trepaxonematan pattern and does not reach the posterior extremity of the gamete. The nucleus is an electron-dense cord 0.25 µm thick coiled in a spiral around the axoneme. The cytoplasm exhibits a posterior densification and contains few small electron-dense granules in regions I, II and V of the spermatozoon. In regions III and IV, it is divided into irregular compartments by walls of electron-dense material. The cortical microtubules are spiralled at an angle of about 45°. The presence of an electron-lucent apical cone containing numerous small granules of electron-dense material has never, to our knowledge, been reported in a cestode. Likewise, a crest-like body forming a terminal spot of electron-dense material located in the prolongation of the apical cone has never been described before in a cestode. Moreover, in this study, we try to show the existence of tight reciprocal phylogenetic relationships between genera within the Davaineidae and the Anoplocephalidae.

Key words

Ultrastructure, spermatozoon, *Paroniella*, Cestoda, Cyclophyllidea, *Corvus albus*, Aves

Introduction

The order Cyclophyllidea comprises 15 families (Khalil *et al.* 1994) including the Davaineidae which are parasites of birds and mammals (Yamaguti 1959, Schmidt 1986). This family comprises four subgenera *Fuhrmannetta*, *Paroniella*, *Raillietina* and *Skrjabinia* (Schmidt 1986) which were elevated to generic rank by Movsesyan (1966). Khalil *et al.* (1994) considered the generic significance of the number of eggs and the disposition of genital pores. Consequently they consider the four subgenera as genera. To our knowledge, only three species of Davaineidae belonging to two genera, parasitic of birds, have been up until now the subject of ultrastructural study of spermiogenesis and/or the spermatozoon. These are *Raillietina carneostrobilata* (Polyakova-Krusteva and Vassilev 1973), *R. tunetensis* (Bâ and Marchand 1994d) and *Co-*

tugnia polyacantha (Bâ and Marchand 1994f). Nevertheless, within these ultrastructural works, the study of *R. carneostrobilata* is scarcely illustrated and lacks a complete description of the ultrastructural features of the spermatozoon. In the present study, we describe the ultrastructure of the spermatozoon of another davaineid species belonging to the genus *Paroniella* (*P. reynoldsae*).

Materials and methods

The specimens of *Paroniella reynoldsae* Meggitt, 1926 were gathered live from the small intestine of *Corvus albus* (Aves, Corvidae). Then, the worms were kept active in physiological saline solution (0.9% NaCl). Portions of strobila 3–6 cm long, made up of mature proglottids, were quickly taken and

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then stretched out with a brush soaked in cold (4°C) 2.5% glutaraldehyde buffered with 0.1 M sodium cacodylate solution at pH 7.2. The male genitalia were removed under a binocu-

lar microscope, fixed for about 24 h in glutaraldehyde, rinsed several times in a sodium cacodylate buffer, then left overnight in the same buffer, postfixed with cold (4°C) 1% os-

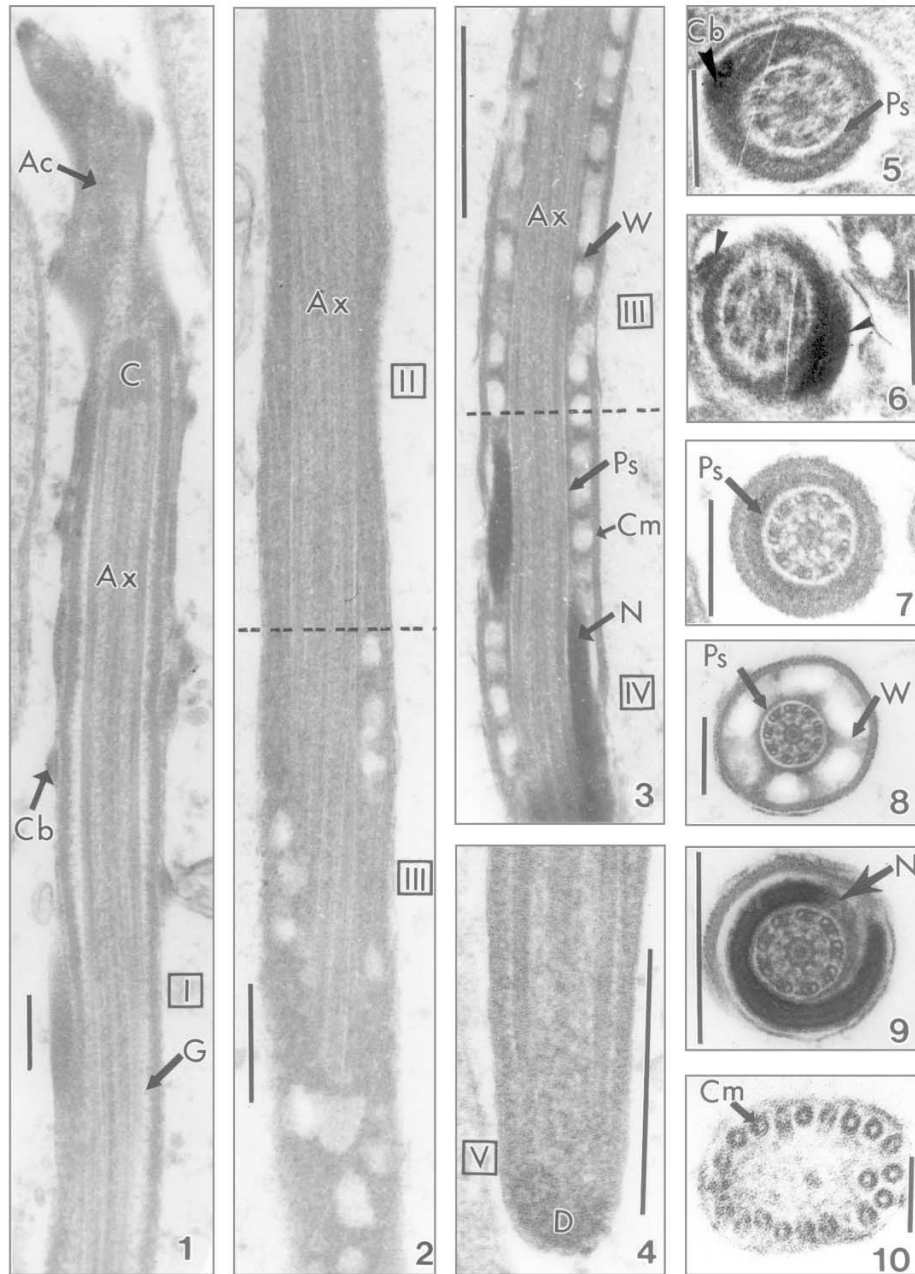


Fig. 1. Longitudinal section of region I of the mature *Paroniella reynoldsae* spermatozoon. Note the terminal densification of the crest-like bodies located at the front of the slightly electron-dense apical cone which is filled with numerous small granules of electron-dense material. **Fig. 2.** Longitudinal section of regions II and III of the mature spermatozoon. **Fig. 3.** Longitudinal section of regions III and IV of the mature spermatozoon. **Fig. 4.** Longitudinal section of region V of the mature spermatozoon. **Fig. 5.** Cross-section of region I of the mature spermatozoon showing one crest-like body. **Fig. 6.** Cross-section of region I of the mature spermatozoon showing two crest-like bodies (arrowheads). **Fig. 7.** Cross-section of region II of the mature spermatozoon. **Fig. 8.** Cross-section of region III of the mature spermatozoon. **Fig. 9.** Cross-section of region IV of the mature spermatozoon. **Fig. 10.** Cross-section of region V of the mature spermatozoon. Scale bars = 0.5 μm (Figs 1–10). **Abbreviations to all figures:** Aae – axonemal anterior extremity, Ac – apical cone, Ace – apical cone extremity, Ape – axonemal posterior extremity, Ax – axoneme, C – centriole, Cb – crest-like body, Cm – cortical microtubules, D – posterior densification, G – electron-dense granule, N – nucleus, Ps – periaxonemal sheath, W – intracytoplasmic walls

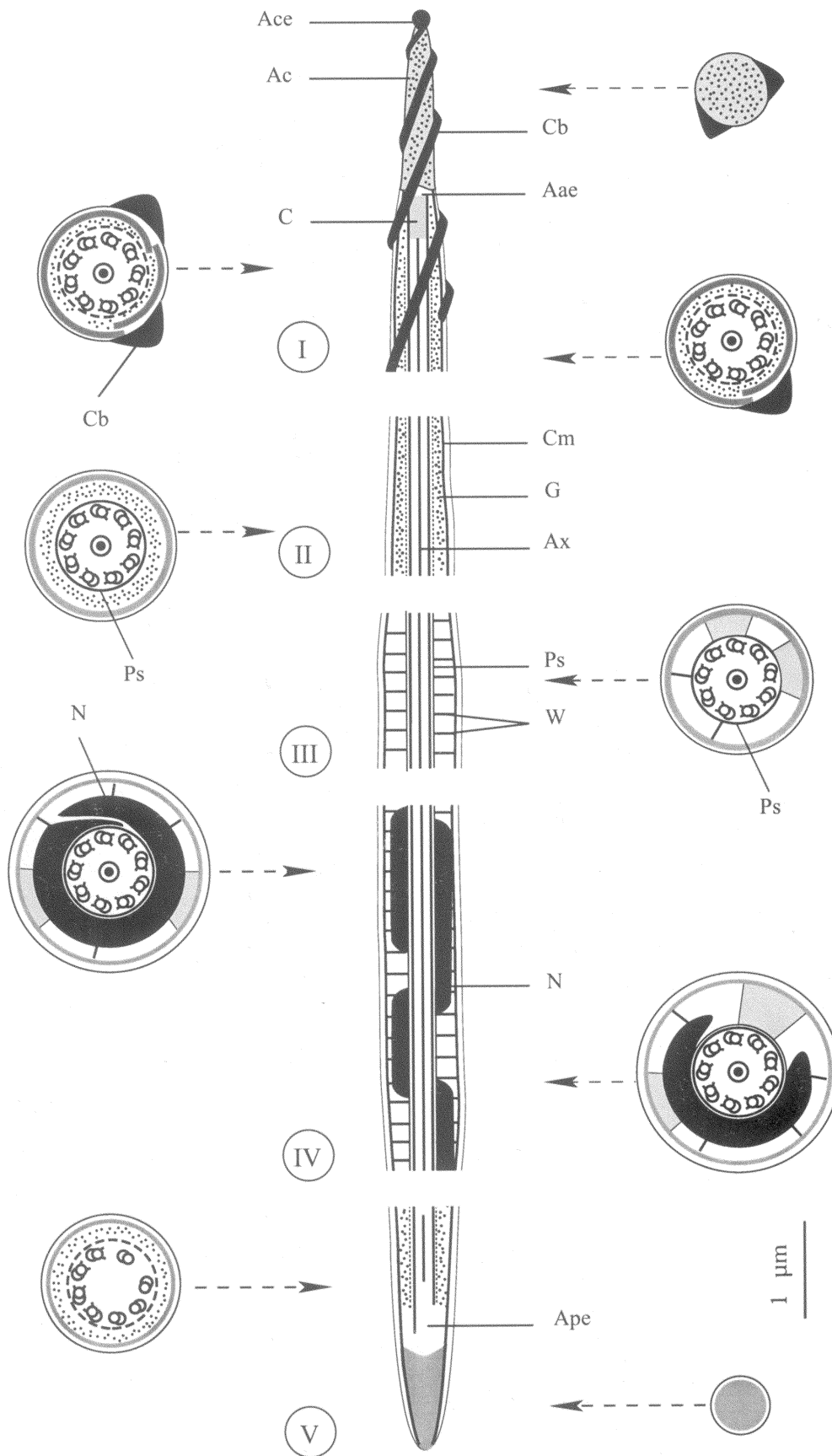


Fig. 11(I-V). Attempted reconstruction of the mature *P. reynoldsae* spermatozoon

mium tetroxide for 1 h, dehydrated in an ethanol series and propylene oxide, and then embedded in Epon. Ultrathin sections (50–60 nm thick) were cut on a LKB Ultramicrotome with diamond knife, then stained with uranyl acetate and lead citrate. They were examined in a Hitachi H-600 electron microscope at 75 kV.

Results

The mature *Paroniella reynoldsae* spermatozoon has no mitochondria, and is filiform and tapered at both ends (Figs 1, 4 and 11I). We were able to distinguish five regions (I–V) along the longitudinal axis exhibiting distinctive ultrastructural characters.

Region I (Figs 1, 5, 6 and 11I) varies in width from 0.65 to 1 μm . It corresponds to the anterior extremity of the spermatozoon. It exhibits an apical cone of electron-lucent material about 2.2 μm long and 0.65 μm wide at its base, filled with numerous small granules of electron-dense material, and two helicoidal crest-like bodies of about 100–150 nm thick. The latter lie outside the cortical microtubules on a distance of about 5–6 μm long, form a terminal densification at the front of the apical cone (Fig. 1) and are of different lengths. Thus, in cross-sections, depending on the level of the section, their number varies between 1 and 2 (Figs 5 and 6). The axoneme is of the 9 + '1' trepaxonematan pattern and centrally located. It is surrounded by a sheath of electron-dense material and a thin layer of slightly electron-dense cytoplasm that contains few granules of electron-dense material (Fig. 1). The cortical microtubules are spiralled at an angle of about 45° and appear in longitudinal and transverse sections in the form of a layer of continuous dense material in close contact with the plasma membrane (Figs 1, 5 and 6).

Region II (Figs 2, 7 and 11II) is approximately 1 μm wide at the most. It lacks crest-like bodies. As the preceding region, it exhibits spiralled cortical microtubules and a central axoneme surrounded by a periaxonemal sheath of electron-dense material (Fig. 7). The cytoplasm contains few small granules of electron-dense material.

Region III (Figs 2, 3, 8 and 11III) is between 0.5 to 1 μm in wide. The axoneme is central and surrounded by a periaxonemal sheath of electron-dense material and a lucent cytoplasm (Figs 3 and 8). The latter is divided into compartments by irregularly spaced partitions of electron-dense material (the transverse intracytoplasmic walls), which join the periaxonemal sheath of electron-dense material to the cortical microtubules (Figs 3 and 8).

Region IV (Figs 3, 9 and 11IV) is between 0.5 to 1 μm wide. It is characterized by the presence of a nucleus which is a fine compact cord of electron-dense material, approximately 0.25 μm thick, coiled in a helix around the axoneme (Fig. 3). In cross-section, depending on the level where the section is cut, it envelops more or less entirely the axoneme (Figs 9 and 11). The cytoplasm is slightly electron-dense and contains numerous walls of electron-dense material between

the periaxonemal sheath and the spiralled cortical microtubules (Fig. 3).

Region V (Figs 4, 10 and 11V) is between 0.5 to 0.25 μm wide. It corresponds to the posterior end of the gamete. It lacks walls of electron-dense material and crest-like bodies. Nevertheless, the cytoplasm exhibits few small granules of electron-dense material, a central axoneme surrounded by a periaxonemal sheath and a posterior densification (Figs 4 and 11). The cortical microtubules become parallel to the spermatozoon axis (Fig. 10).

Discussion

The crest-like body or bodies always marks the anterior extremity of the cestode spermatozoon (Bâ *et al.* 1991). Consequently, the extremity with crest-like bodies of the *Paroniella reynoldsae* spermatozoon corresponds to its anterior extremity and the extremity without crest-like bodies to its posterior extremity.

In most of the Cyclophyllidea and the Proteocephalidea (*Nomimoscolex* sp. and *Sandonella sandoni*), the crest-like body initiates its helicoidal course as soon as it reaches the apical cone base (Table I). On the other hand, in the Catenotaeniidae (Miquel *et al.* 1997, Hidalgo *et al.* 2000), the Anoplocephalidae (Bâ and Marchand 1992a, b, 1994e, 1995) and the Taeniidae (Miquel *et al.* 2000, Ndiaye *et al.* 2003a), it runs along one part or the whole length of the apical cone. In *P. reynoldsae*, the crest-like body forms a terminal densification at the front of the apical cone. As far as we know, such a terminal electron-dense spot has never been reported before in a cestode spermatozoon.

The angle of spiralization of crest-like bodies in the cestode's spermatozoon varies according to the species. It has been estimated at 20° in *Mesocestoides litteratus* (Miquel *et al.* 1999), 35° in *Avitellina centripunctata* (Bâ and Marchand 1994a), 40° in *Moniezia expansa* and *M. benedeni* (Bâ and Marchand 1992a), *Dipylidium caninum* (Miquel and Marchand 1997), *Catenotaenia pusilla* (Hidalgo *et al.* 2000) and *Echinocotyle dolosa* (Bâ *et al.* 2002), 50° in *Stilesia globipunctata* (Bâ and Marchand 1992b), and between 40 and 50° in *Thysaniezia ovilla* (Bâ *et al.* 1991). It is about 45° in *P. reynoldsae*.

The thickness of crest-like body or bodies also varies according to the cestode species ranging from 15 to 200 nm. Thus, the crest-like bodies are thin (15–40 nm) in the spermatozoon of *Aporina delafondi* (Bâ and Marchand 1994b) whereas their maximal thickness (up to 200 nm) has been shown in spermatozoa of *Raillietina tunetensis* (Bâ and Marchand 1994d), *Rodentolepis microstoma* (= *Vampirolepis microstoma*) (Bâ and Marchand 1998) and *Avitellina centripunctata* (Bâ and Marchand 1994a). It is between 100 to 150 nm in *P. reynoldsae*.

An apical cone has been described in the front of the spermatozoon of 26 cyclophyllidean and two proteocephalidean cestodes (*Nomimoscolex* sp. and *Sandonella sandoni*). Its

Table I. Comparison of few characters present in anterior extremity of the spermatozoon (crest-like body and apical cone) of cestodes belonging to the Proteocephalidea and Cyclophyllidea orders

Order	Family	Genus and species	Crest-like body			Apical cone			References
			angle of spiralization	thickness (nm)	anterior extremity	aspect of constitutive material	length (µm)	width at its base (µm)	
Cyclophyllidea	Anoplocephalidae	<i>Anoplocephaloides dentata</i>	–	140	B	D	1.40	0.35	Miquel and Marchand 1998a
		<i>Aporina delafondi</i>	–	15–40	B	D	0.3	0.15	Bâ and Marchand 1994b
		<i>Avitellina centripunctata</i>	35°	150–200	B	D	0.7	0.3	Bâ and Marchand 1994a
		<i>Gallegoides arfaai</i>	–	140	B	L	1	0.275	Miquel <i>et al.</i> 2004
		<i>Inermicapsifer guineensis</i>	–	–	A	D	–	0.15	Bâ and Marchand 1995
		<i>I. madagascariensis</i>	–	–	A	D	–	0.20	Bâ and Marchand 1995
		<i>Moniezia benedeni</i>	40°	30–60	A	D	1	0.25	Bâ and Marchand 1992a
		<i>Mathevotaenia herpestis</i>	–	–	A	D	–	0.1	Bâ and Marchand 1994e
		<i>Moniezia expansa</i>	40°	30–60	B	D	1	0.25	Bâ and Marchand 1992a
		<i>Paranoplocephala omphalodes</i>	–	180	B	D	0.90	0.20	Miquel and Marchand 1998b
		<i>Stilesia globipunctata</i>	50°	–	A	D	1.25	0.5	Bâ and Marchand 1992b
		<i>Sudarikovina taterae</i>	–	50–100	B	D	0.5	0.1	Bâ <i>et al.</i> 2000
		<i>Thysaniezia ovilla</i>	40–50°	802	B	D	0.6	0.2	Bâ <i>et al.</i> 1991
		Catenotaeniidae	<i>Catenotaenia pusilla</i>	40°	75	A	D	1.75	0.225
	<i>Skrjabinotaenia lobata</i>		–	–	A	D	2.5	0.20	Miquel <i>et al.</i> 1997
	Davaineidae	<i>Paroniella reynoldsae</i>	45°	100–150	A	L	2.2	0.6	present study
		<i>Raillietina tunetensis</i>	–	100–200	B	D	–	0.3	Bâ and Marchand 1994d
	Dipylidiidae	<i>Dipylidium caninum</i>	40°	150	B	D	0.6	0.4	Miquel and Marchand 1997
		<i>Joyeuxiella echinorhyncoides</i>	–	150	B	D	2.0	0.285	Ndiaye <i>et al.</i> 2003b
	Hymenolepididae	<i>J. pasqualei</i>	–	75	B	D	2.0	0.285	Ndiaye <i>et al.</i> 2003b
		<i>Echinocotyle dolosa</i>	40°	100	B	D	0.1	0.3	Bâ <i>et al.</i> 2002
<i>Rodentolepis straminea</i>		–	50–100	B	D	0.75	0.1	Bâ and Marchand 1996	
(= <i>Hymenolepis straminea</i>)		–	–	–	–	–	–	–	
<i>Rodentolepis microstoma</i> (= <i>Vampirolepis microstoma</i>)		–	100–200	–	–	–	–	Bâ and Marchand 1998	
	<i>Cladogynia serrata</i> (= <i>Retinometra serrata</i>)	–	–	B	L	0.5	0.35	Bâ and Marchand 1993	
Mesocestoididae	<i>Mesocestoides litteratus</i>	20°	100–150	B	D	–	–	Miquel <i>et al.</i> 1999	
Taeniidae	<i>Taenia mustelae</i>	–	75	A	D	1.9	0.25	Miquel <i>et al.</i> 2000	
	<i>T. parva</i>	–	60	A	D	1.9	0.225	Ndiaye <i>et al.</i> 2003a	
Monticellidae	<i>Nomimoscolex</i> sp.	–	–	B	D	–	–	SÐne <i>et al.</i> 1997	
Proteocephalidae	<i>Proteocephalus torulosus</i>	–	80–100	–	–	–	–	Bruňanská <i>et al.</i> 2003a	
	<i>P. longicollis</i>	–	60–100	–	–	–	–	Bruňanská <i>et al.</i> 2003b	
	<i>Electrotaenia malopteruri</i>	–	60–150	–	–	–	–	Bruňanská <i>et al.</i> 2004a	
	<i>Corallobothrium solidum</i>	–	30–200	–	–	–	–	Bruňanská <i>et al.</i> 2004b	
	<i>Sandonella sandoni</i>	–	50–100	B	D	1	–	Bâ and Marchand 1994c	

A – stops after it runs along the apical cone; B – stops as soon as it reaches the apical cone base; D – electron-dense; L – electron-lucent or slightly electron-dense; “–” lack of information on the considered character.

length varies between 0.1 and 2.5 μm and its width is from 0.1 to 0.5 μm (see Table I). In *P. reynoldsae*, the apical cone is about 2.2 μm long and 0.65 μm wide at its base.

In most cases, the apical cone of the cestode spermatozoon is made up of material which may be electron-dense, slightly electron-dense or electron-lucent (Table I). In *P. reynoldsae* spermatozoon the apical cone is electron-lucent, but distinguishes from that in other cestodes by the fact that it contains numerous small granules of electron-dense material.

The width of the nucleus varies according to the cestode species. It has been estimated to be between 10 to 75 nm in *Inermicapsifer guineensis* (Bâ and Marchand 1995), 30 to 150 nm in *I. madagascariensis* (Bâ and Marchand 1995), and 300 to 700 nm in *Echinocotyle dolosa* (Bâ et al. 2002). It is approximately 250 nm wide in *P. reynoldsae*.

Schmidt (1986), taking into consideration the number of eggs per uterine capsule and the disposition of genital pores, identified four subgenera in the genus *Raillietina*. These are *Fuhrmannetta*, *Paroniella*, *Raillietina* and *Skrjabinia*. However, Khalil et al. (1994) recognized these subgenera as genera "following recognition of the generic significance of the number of eggs per capsule plus genital pores unilateral or irregularly alternating". Nevertheless, when we compare the spermatozoon of *P. reynoldsae* to that of *R. tunetensis* (Bâ and Marchand 1994d), we can see that they are so similar to each other that it is impossible to make any ultrastructural differences between the genera *Paroniella* and *Raillietina*.

In the same manner, when we compare ultrastructural characters of the spermatozoon of the davaineids *R. tunetensis* (Bâ and Marchand 1994d), *Cotugnia polyacantha* (Bâ and Marchand 1994f) and *P. reynoldsae* (present study) to those of the anoplocephalidaeans *Avitellina centripunctata* (Bâ and Marchand 1994a), *I. guineensis* and *I. madagascariensis* (Bâ and Marchand 1995), we can put into evidence many similarities between them. In fact, the spermatozoon of all these species exhibits an apical cone of more or less electron-dense material, two crest-like bodies of different lengths, spiralled cortical microtubules, an electron-dense nucleus, a periaxonemal sheath of electron-dense material, intracytoplasmic walls of electron-dense material, a slightly electron-dense cytoplasm containing granules of electron-dense material and a posterior densification.

All these common characters seem to show close phylogenetic relationships between the genera *Raillietina* (Bâ and Marchand 1994d), *Cotugnia* (Bâ and Marchand 1994f) and *Paroniella* (present study) on the one hand, between the *Avitellina* and the *Inermicapsifer* on the other hand. They also confirm the existence of phylogenetic affinities between the Davaineidae and the Anoplocephalidae (Baer 1927, Schmidt 1986).

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