Spermiogenesis, Spermatozoa and Phyletic Affinities in the Cestoda

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ABSTRACT

Comparative ultrastructural studies of spermiogenesis and/or spermatozoa of 43 species of cestodes lead us to conclude that flagellar rotation and the proximodistal fusion of one or two flagella with the median cytoplasmic extension is a plesiomorphic character in the Eucestoda and that the absence of flagellar rotation is a synapomorphy for the Cyclophyllidea. We consider the presence of the crested-like body at the anterior extremity of the spermatozoa of cestodes as a synapomorphy for the Eucestoda. We also confirm the absence of mitochondria as a synapomorphy for the Eucestoda. Previous phylogenetic diagrams are critically reviewed.

RÉSUMÉ

Spermiogenèse, spermatozoïdes et affinités phylétiques chez les Cestoda.

L'étude ultrastructurale comparée de la spermiogenèse et/ou du spermatozoïde de 43 espèces de cestodes nous a permis de considérer la rotation flagellaire et la fusion proximo-distale du ou des flagelles spermatiques avec une expansion cytoplasmique médiane comme un caractère plésiomorphe des Eucestodes et l'absence de rotation flagellaire comme une synapomorphie des Cyclophyllidea. Nous considérons la présence de corps en crête à l'avant du spermatozoïde comme une synapomorphie des Eucestodes. Nous confirmons également l'absence de mitochondrie comme une synapomorphie des Eucestodes. Les schémas phylétiques précédents sont révisés de manière critique.

Cestodes have been described in all vertebrates except agnathans [44]. They now comprise nearly 4 000 species spread over 600 genera, 63 families and 13 orders. The different authors interested in their phylogenesis on the basis of their morphological characters [14, 16, 19, 20, 22], frequently came to contradictory conclusions. The absence of mitochondria in spermatozoa has been considered as a synapomorphy of the Cestodes [17, 18], and the spiral coil of the cortical spermatic microtubules as a synapomorphy of the Cyclophyllidea [26]. In the present work, we propose two new synapomorphies, one for the Eucestoda and one for the Cyclophyllidea. Moreover, we critically debate the two last phylogenetic diagrams proposed by EUZET *et al.* [20] and BROOKS *et al.* [16].

BÂ, C. T., & MARCHAND, B., 1995. — Spermiogenesis, spermatozoa and phyletic affinities in the Cestoda. *In:* JAMIESON, B. G. M., AUSIO, J., & JUSTINE, J.-L. (eds), Advances in Spermatozoal Phylogeny and Taxonomy. *Mém. Mus. natn. Hist. nat.*, **166** : 87-95. Paris ISBN : 2-85653-225-X.

MATERIAL AND METHODS

We have studied the ultrastructure of spermiogenesis and/or the spermatozoa of 14 species of cestodes (Table 1). The specimens of the different species were gathered from the intestines of their respective hosts (birds or mammals), naturally infested, then placed, alive and active, in a physiological saline solution (9 ‰ NaCl). Portions of strobile, 3 to 6 cm long, consisting of mature proglottids, were quickly taken, then stretched out with a brush soaked in cold (4°C) 2.5 % glutaraldehyde in a 0.1 M sodium cacodylate buffer at pH 7.2. The genital apparatus was removed under a binocular microscope, fixed for about 24 hours in glutaraldehyde at 4°C, rinsed for one night in the sodium cacodylate buffer, post-fixed for one hour with cold 1% osmium tetroxide, dehydrated with ethanol and propylene oxide, then embedded in epon. Ultrathin sections were cut on a Porter-Blum MT1 and Reichert-Jung Ultracut-E ultramicrotomes, then stained with uranyl acetate and lead citrate. They were examined in Siemens Elmikop 101 and JEOL 100 CX II electron microscopes.

RESULTS

The figures 1 to 5 and Table 1 present our observations and those of other authors on spermiogenesis and/or the spermatozoa of cestodes. Whatever the cestode may be, spermiogenesis always begins by the formation of a differentiation zone (Figs 1a, 2a, 3a, 4a). This is delimited at the proximal extremity by arched membranes, and bordered by cortical microtubules. This contains one or two centrioles separated (Figs. 1a, 2a) or not (Figs 3a, 4a) by an intercentriolar body and surmounted (Figs. 1a, 2a) or not (Figs 3a, 4a) by striated roots or a centriolar-adjunct (Fig. 4a). Each centriole very rapidly gives rise to a flagellum that grows within (Figs 4b-c) or external to (Figs 1b, 2b, 3b) the differentiation zone. Subsequently, the flagellum (or the flagella) undergoes (Figs 1c, 2c) or not (Figs 3c, 4c) a rotation, becomes parallel to the cytoplasmic extension, and fuses with it. After the migration of the nucleus into the differentiation zone and the formation of one or many crested-like bodies, the ring of arched membranes narrows until the spermatid detaches itself from the residual cytoplasm. The mature spermatozoon of the cestodes lacks mitochondria, is filiform and is tapered at both extremities (Fig. 5). Its anterior extremity exhibits an apical cone of electron dense material and one or many crested-like bodies. The cytoplasm contains proteinaceous material and a nucleus coiled or not in a spiral around the axoneme. The proteinaceous material may be arranged in four different forms: granulations, rods making intracytoplasmic walls, a periaxonemal sheath, submicrotubular thickenings (Fig. 5).

DISCUSSION

During spermiogenesis of the Cercomeridea (Aspidobothrea, Digenea, Monogenea, Gyrocotylidea, Amphilinidea and Eucestoda), the flagellum (or the flagella) of old spermatids undergoes a rotation and becomes parallel to a median cytoplamic extension with which it fuses. This proximodistal fusion as it is termed [26, 27] is not found in the Turbellaria [26, 56]. In the cestodes in particular, it is encountered in the Tetraphyllidea-Onchobothriidae [33, 37], the Tetraphyllidea-Phyllobothriidae [36], the Tetrarhynchidea [51], the Proteocephalidea [50, 51], the Pseudophyllidea [54] and the Caryophyllidea [51]. The proximodistal fusion has recently been proposed as a synapomorphy for all the Cercomeridea [26]. Nevertheless, in three Cyclophyllidea, *Thysaniezia ovilla* [13], *Hymenolepis nana* [3] and *Aporina delafondi* [8], the single flagellum grows directly into the spermatid body. In three other Cyclophyllidea, *Nematotaenia chantalae* [38], *Mathevotaenia herpestis* [7] and *Raillietina (Raillietina) tunetensis* [9], the flagellum grows outside the differentiation zone, parallel to the cytoplasmic extension and then fuses with it before nuclear migration. Dealing with the existence or not of a flagellar rotation during spermiogenesis, we can distinguish in the Cercomeridea two types of spermiogenesis. The former which involves a flagellar rotation and a proximodistal fusion, has been supposed to exist in all the Cercomeridea [26]. The latter which is characterized by an absence of flagellar rotation, has been reported in the six Cyclophyllidea which we have previously cited [3, 7, 8, 9, 13, 38].
In the present work, we consider the absence of flagellar rotation as an apomorphic character for all the Cyclophyllidea.

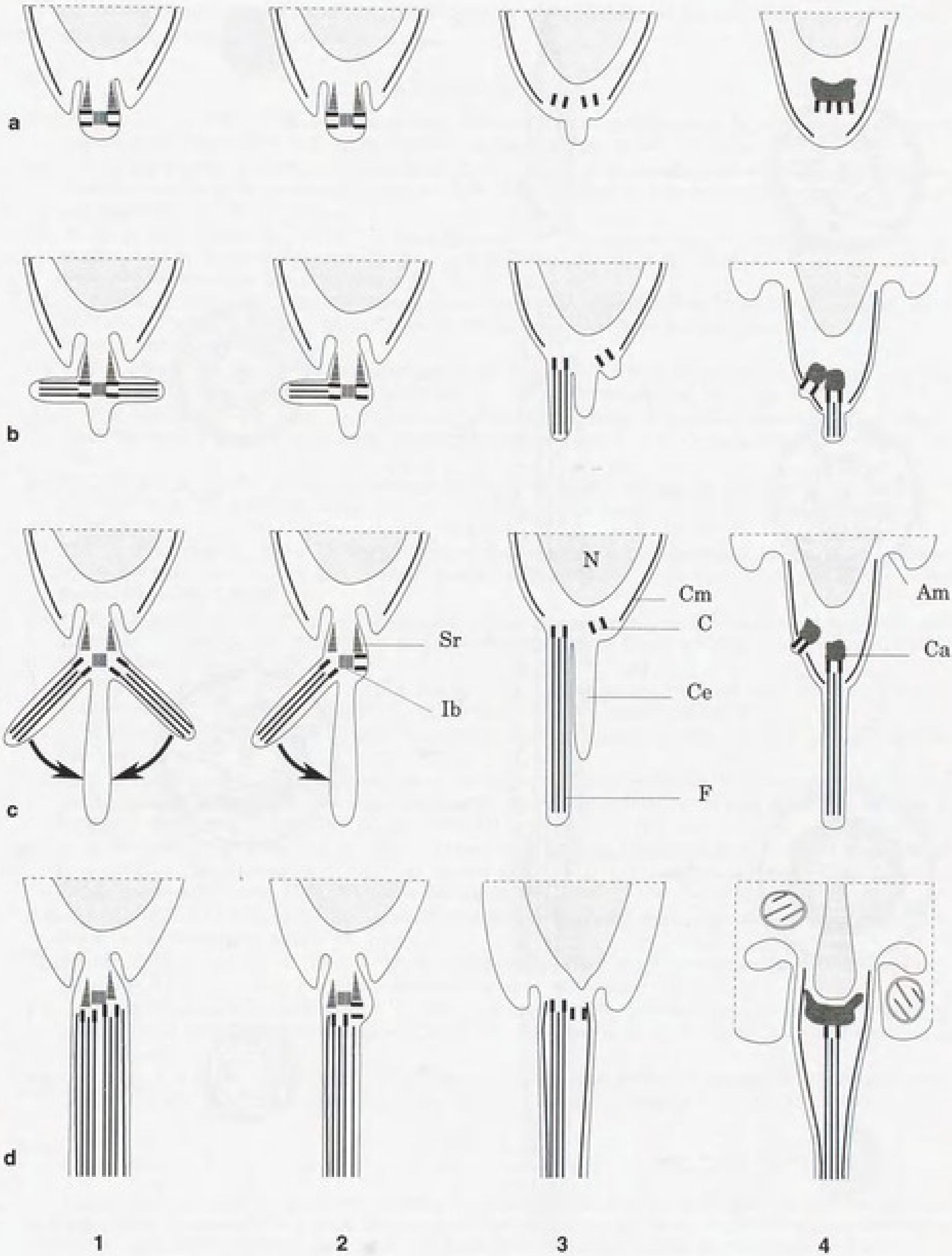
TABLE 1. — Cestodes whose spermatozoa have been studied by electron microscopy. The references quoted contain data on spermiogenesis (*), the presence of one (+) or more than one (++) crested-like bodies and the presence of two axonemes (2a).

Taxon	Reference
Haplobothrioidea	
Haplobothriidae	
Haplobothrium globuliforme (2a)*	[32]
Pseudophyllidea	
Bothriocephalidae	
Bothriocephalus clavibothrium (2a)*	[54]
Cyathocephalidae	
Bothrimonas sturionis	[31]
Caryophyllaeidae	
Monobothrium wageneri	[34]
Glaridacris catostomi	[53]
Diphyllobothriidae	
Diphyllobothrium latum (2a)	[15]
Duthiersia fimbriata + (2a)	[25]
Proteocephalidea	
Proteocephalidae	
Proteocephalus longicollis (2a)	[52]
Sandonella sandoni +	[10]
Tetrarhynchidea	
Lacistorhynchidae	
Lacistorhynchus tenuis (2a)	[48]
Diphyllidea	
Echinobothriidae	
Echinobothrium typus +*	[1]
Echinobothrium brachysoma +*	[1]
Echinobothrium affine (2a)*	[1]
Echinobothrium harfordi +*	[1]
Tetraphyllidea	
Phyllobothriidae	
Pseudanthobothrium hanseni +	[31]
Phyllobothrium gracile +*	[36]
Echeneibothrium beauchampi +	[40]
Onchobothriidae	
Acanthobothrium filicolle filicolle + (2a)*	[35, 37]
Acanthobotrium filicolle benedenii + (2a)	[39]
Onchobothrium uncinatum + (2a)	[39]
Trilocularia acanthiaevulgaris + (2a)*	[33]
Cyclophyllidea	
Anoplocephalidae	
Inermicapsifer madagascariensis ++	[11, 12, 49]
I. guineensis ++	[11, 12]
Moniezia expansa ++	[4, 46]
M. benedeni ++	[4]
Monoecocestus americanus	[31]
Stilesia globipunctata +	[2]
Avitellina centripunctata +	[6]
Thysaniezia ovilla +*	[13]
Mathevotaenia herpestis +*	[7]
Aporina delafondi +*	[8]
Oochoristica agamae	[55]
Catenotaeniidae	
Catenotaenia pusilla	[47]
Hymenolepididae	
Hymenolepis diminuta *	[2, 6, 30, 42, 43, 45]
Hymenolepis nana ++*	[3, 43]
H. microstoma	[47]
Retinometra serrata ++	[5]
Taeniidae	
Echinococcus granulosus	[41]
Taenia hydatigena *	[21]
Davaineidae	
Raillietina (Raillietina) tunetensis ++*	[9]
Cotugnia polyacantha ++	[11]
Nematotaeniidae	
Nematotaenia chantalae +*	[38]
Cylindrotaenia hickmani	[23, 24]

One or many crested-like bodies have been described at the anterior extremity of the spermatozoa of 26 species of cestodes: one Pseudophyllidean, one Proteocephalidean, three Diphyllidea, seven Tetraphyllidea and 14 Cyclophyllidea (Table 1). Although their presence has not been reported by some authors [24, 29, 42, 43], we have observed them in their illustrations. In a Caryophyllidean, *Glaridacris catostomi* [53], a Haplobothrioidean, *Haplobothrium globuliforme* [32] and a Tetrarhynchidean, *Lacistorhynchus tenuis* [48], these formations have neither been described nor figured. In fact, it is not easy to detect them owing to their very small size. Thus, in spite of these few "exceptions", and although our knowledge is still limited to a small number of species, we believe that the crested-like body should be considered as a synapomorphy for all cestodes. Moreover, we consider the presence of a crested-like body in the spermatozoa of one species of monopistocotylean Monogenea, *Calceostoma* sp. [28], as a simple phenomenon of convergence.

The phylogenetic systematics of the cestodes are still poorly understood and are much debated. EUZET *et al.* [20] thought that the presence of a single axoneme in the cestode spermatozoon is an evolved character. Thus, they considered the Cyclophyllidea as derived from the Proteocephalidea, then the Proteocephalidea and the Tetraphyllidea-Phyllobothriidae as issued from the Tetraphyllidea-Onchobothriidae and lastly the Pseudophyllidea and the Tetrarhynchidea as coming from the Haplobothrioidea. The Caryophyllidea and the Diphyllidea were of unknown origin. On the other hand, FREEMAN [22] estimated the Tetraphyllidea-Phyllobothriidae as the ancestors of the Cyclophyllidea, taking into consideration their post-embryonic development. Schmidt [44], considered the Haplobothrioidea and the Tetrarhynchidea respectively as families belonging to the Pseudophyllidea and the Trypanorhynchidea. BROOKS *et al.* [16], using 12 synapomorphic characters, subdivided the cestodes into five orders: Pseudophyllidea, Nippotaeniidea, Proteocephalidea, Lecanicephalidea and Tetraphyllidea. Additionally, they included the Caryophyllidea, the Cyclophyllidea and the Trypanorhynchidea, respectively, in the Pseudophyllidea, the Proteocephalidea and the Tetraphyllidea. The phylogenetic systematic diagram of BROOKS *et al.* (1991) [16] involves the coexistence of spermatozoa bearing one or two axonemes in the same order (Table 1), thus showing a contradiction between spermatological and morphological characters. Moreover, their propositions do not clarify the evolution of the number of axonemes within the Cestodes. When considering the pattern of the posterior extremity of the spermatic flagella, some important differences between the Proteocephalidea and the Cyclophyllidea can be pointed out. In the Cyclophyllidea *Thysaniezia ovilla* [13], *Stilesia globipunctata* [2], *Hymenolepis nana* [3], *Moniezia expansa* and *Moniezia benedeni* [4], *Retinometra serrata* [5], *Aporina delafondi* [8] and *Raillietina (R.) tunetensis* [9], the central element of the axoneme disappears before the simplification of doublets into singlets. On the other hand, in the Proteocephalidean *Sandonella sandoni* [10], the posterior extremity of the spermatozoon consists of the axonemal central element, surrounded by nine singlets that correspond to the A microtubules which are in close contact with the plasmic membrane.

FIGS 1-4. — Attempted reconstruction of the different types of spermiogenesis in the Cestodes. Am, arched membranes; C, centriole; Ca, centriolar-adjunct; Ce, cytoplasmic extension; Cm, cortical microtubules; F, flagellum; Ib, intercentriolar body; Sr, striated root. **1 a-d:** First type of spermiogenesis with flagellar rotations (c) and proximodistal fusions (d) as described in the Tetraphyllidea-Onchobothriidae [30, 33], the Proteocephalidea [48, 49] the Tetrarhynchidea [49] and the Pseudophyllidea [52]. **2 a-d:** Second type of spermiogenesis with a flagellar rotation (c) and a proximodistal fusion (d) as described in the Tetraphyllidea-Phyllobothriidae [32] and the Caryophyllidea [49]. **3 a-d:** Third type of spermiogenesis without flagellar rotation but with a proximodistal fusion (d). The single flagellum grows outside but parallel to the cytoplasmic extension (c) then fuses with it (d) as described in some species of the Cyclophyllidea: *Nematotaenia chantalae* [34], *Mathevotaenia herpestis* [7] and *Raillietina (R.) tunetensis* [9]. **4 a-d:** Fourth type of spermiogenesis with neither flagellar rotation nor proximodistal fusion. The single flagellum grows inside the cytoplasmic extension (b-d) as described in some other species of the Cyclophyllidea: *Thysaniezia ovilla* [13], *Hymenolepis nana* [3] and *Aporina delafondi* [8].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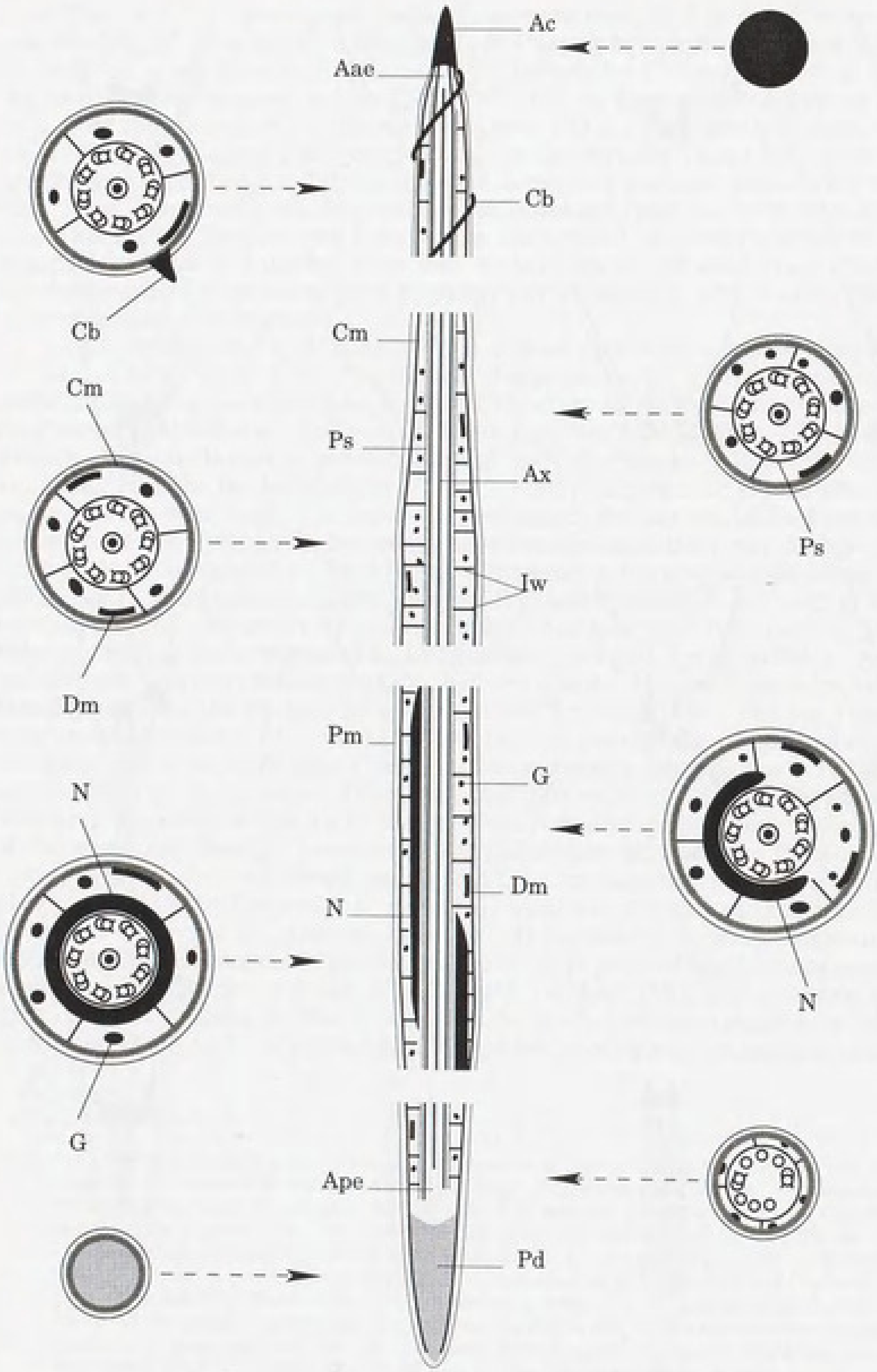

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Thus, it becomes obvious that the phylogenetic systematics of the Cestodes is a complex subject and requires serious revision.

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Fig. 5. — Longitudinal and cross sections of the different constitutive elements of the spermatozoa of the cestodes. Aae, axonemal anterior extremity; Ac, apical cone; Ape, axonemal posterior extremity; Ax, axoneme; Cb, crested-like body; Cm, cortical microtubules; Dm, submicrotubular electron dense material; G, proteinaceous granules; Iw, intracytoplasmic walls; N, nucleus; Pd, posterior electron dense material; Pm, plasma membrane; Ps, periaxonemal sheath.

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