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VERSITA

Ultrastructure of spermiogenesis and mature spermatozoon of *Angularella beema* (Clerc, 1906) (Cestoda, Cyclophyllidea, Dilepididae)

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Abstract

The ultrastructure of the spermiogenesis of a dilepidid cestode species is described for the first time. The spermiogenesis of *Angularella beema* is characterised by absence of both flagellar rotation and proximodistal fusion. The differentiation zone is surrounded by cortical microtubules and is delimited by a ring of arching membranes. It contains two centrioles, one of which develops the axoneme that grows directly into the elongating cytoplasmic protrusion. This pattern of spermiogenesis was described as the Type IV spermiogenesis of cestodes. Among cestodes, similar pattern of spermiogenesis is known in the family Hymenolepididae and in some representatives of the family Anoplocephalidae. The mature spermatozoon of *A. beema* consists of five regions differing in their ultrastructural characteristics. It is characterised by the presence of cortical microtubules (spirally arranged at angle of 30–40° to the spermatozoon axis) and a single crested body. There is a periaxonemal sheath in certain parts of the spermatozoon as well as glycogen-like granules between the periaxonemal sheath and the cortical microtubules. The comparisons of the mature spermatozoon of *A. beema* with those of other two dilepidid species (*Dilepis undula* and *Molluscotaenia crassiscolex*) demonstrate some variation within the family: presence of periaxonemal sheath in *A. beema* and *D. undula* and its absence in *M. crassiscolex*; presence of electron-dense rods in *D. undula* and their absence in *A. beema*.

Key words

Cestoda, Cyclophyllidea, Dilepididae, *Angularella beema*, spermiogenesis, spermatozoon, ultrastructure

Introduction

The ultrastructure of spermiogenesis and the mature spermatozoon provides useful information applicable in phylogenetic and taxonomic studies of cestodes (Świderski 1968, Justine 1991, 1998, 2001; Bâ and Marchand 1995; Hoberg *et al*. 1997, 1999, 2001). Out of 5,100–5,200 cestode species in the world, about 3,100 belong to the order Cyclophyllidea (Georgiev 2003). This order is subdivided into 15–18 families depending on taxonomic concepts adopted (Jones *et al*. 1994, Georgiev 2003). The phylogenetic relationships within this order are poorly resolved on the basis of the existing morphological and molecular datasets (Mariaux 1998; Hoberg *et al*. 1999, 2001). As demonstrated by an earlier summary paper (Bâ and Marchand 1995), the diversity in the sperm structure and formation patterns is considerable. However, the implementation of spermiological characters in phylogenetic analyses of cyclophyllideans is currently not possible because the information is unevenly distributed. The cyclophyllidean species studied belong to 9 families only (recently surveyed by Yoneva *et al*. 2006). Therefore, accumulation of ultrastructural data on the spermiogenesis and mature spermatozoa of representatives of the cyclophyllidean families is urgently needed.

The family Dilepididae is a diverse group parasitic in birds and mammals, which includes more than 100 genera (Bona 1994). The spermiological data about them are restricted to the ultrastructure of the mature spermatozoon of three species only: *M. crassiscolex* (see Świderski and Tkach 1996), *D. un-*

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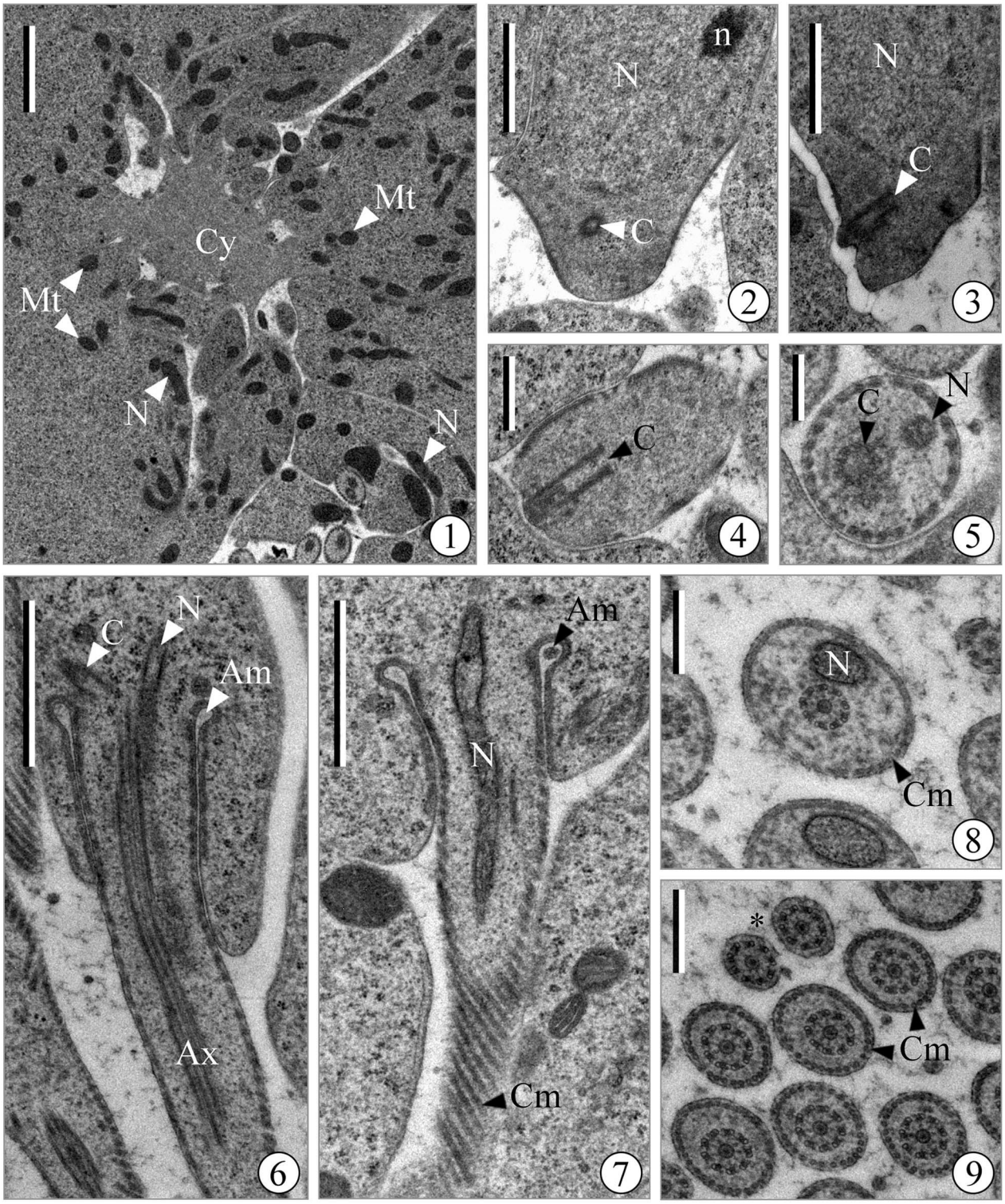
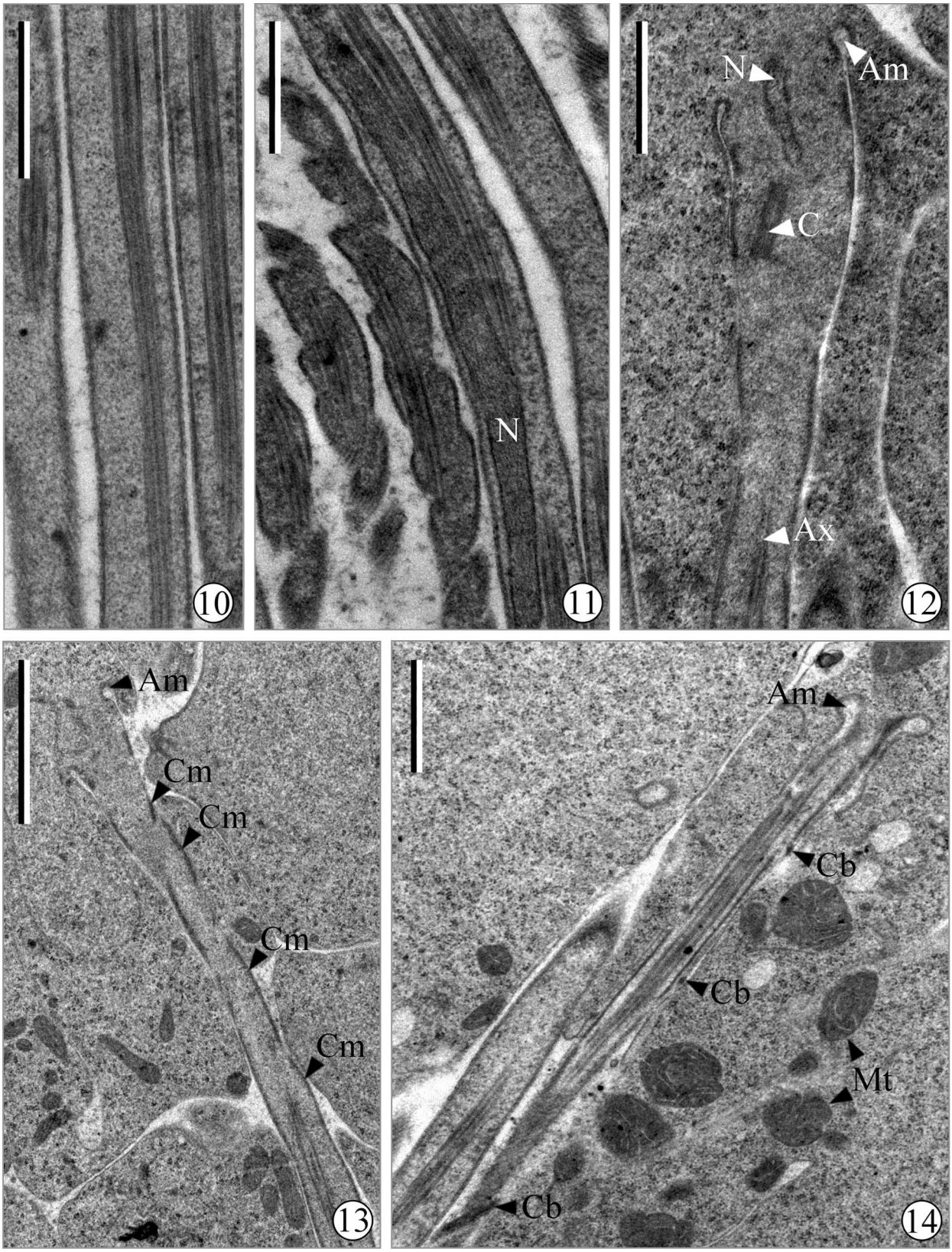
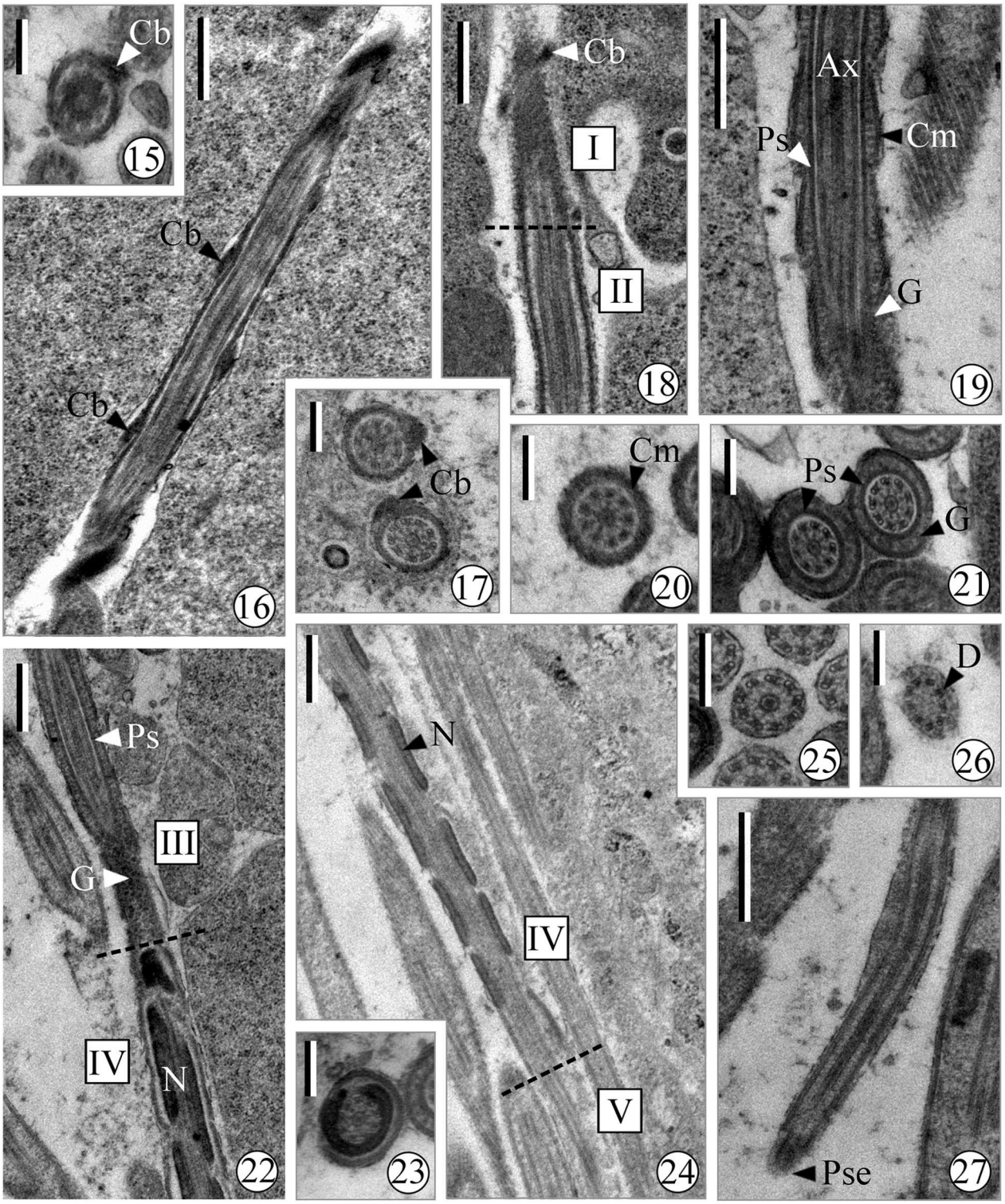


Figs 1–9. Spermiogenesis of *Angularella beema*. **1.** Low magnification of testes tissue showing a rosette of spermatids. Scale bar = 2 μm. **2** and **3.** Zones of differentiation demonstrating initial stages of spermiogenesis. Scale bars = 1 μm. **4.** Cross-section of a zone of differentiation showing a centriole. Scale bar = 0.5 μm. **5.** Cross-section of a spermatid at the level of centriole showing the migration of nucleus. Scale bar = 0.3 μm. **6** and **7.** Longitudinal sections of spermatids showing nuclear migration. Scale bars = 1 μm. **8.** Cross-section of a spermatid during nuclear migration. Scale bar = 0.3 μm. **9.** Several cross-sections of spermatids before the twisting of cortical microtubules. Scale bar = 0.3 μm. Note the terminal sections (*) without cortical microtubules. **Abbreviations to all the figures:** Am – arched membranes, Ase – anterior spermatozoon extremity, Ax – axoneme, C – centriole, Cb – crested body, Ce – cytoplasmic extension (cytoplasmic protrusion), Cm – cortical microtubules, Cy – cytophore, D – doublets, G – granules; Mt – mitochondria, n – nucleolus, N – nucleus, Pm – plasma membrane, Ps – periaxonemal sheath, Pse – posterior spermatozoon extremity



Figs 10–14. Spermiogenesis of *Angularella beema*. **10.** Longitudinal section of an anuclear area of spermatid. Scale bar = 1 μm. **11.** Longitudinal section of a nuclear region of spermatid. Scale bar = 1 μm. **12.** Longitudinal section of a differentiation zone in the final stage of nuclear migration. Scale bar = 1 μm. **13.** Longitudinal section of a zone of differentiation showing the twisting of cortical microtubules. Scale bar = 2 μm. **14.** Longitudinal section of a zone of differentiation in a final stage of spermiogenesis. Note the presence of a single crested body. Scale bar = 1 μm



Figs 15–27. Mature spermatozoon of *Angularella beema*. **15.** Cross-section of region I at the level of centriole. Scale bar = 0.2 µm. **16.** Longitudinal section of region I. Scale bar = 0.5 µm. **17.** Cross-section of region I. Scale bar = 0.2 µm. **18.** Longitudinal section showing the transition between region I and region II. Scale bar = 0.5 µm. **19.** Longitudinal section of region III. Scale bar = 0.5 µm. **20.** Cross-section of region II. Scale bar = 0.2 µm. **21.** Cross-sections of region III. Scale bar = 0.2 µm. **22.** Longitudinal section showing the transition between region III and region IV. Scale bar = 0.5 µm. **23.** Cross-section of region IV. Scale bar = 0.2 µm. **24.** Longitudinal section showing the transition between region IV and region V. Scale bar = 0.5 µm. **25.** Cross-section of region V showing the absence of cortical microtubules. Scale bar = 0.2 µm. **26.** Cross-section of region V during the disorganization of the axoneme. Scale bar = 0.2 µm. **27.** Longitudinal section of region V showing the posterior spermatozoon extremity. Scale bar = 0.5 µm

dula (see Świderski *et al*. 2000) and *Kowalewskiella glareola* (see Świderski *et al*. 2002). There are not any data on the spermiogenesis of dilepidid species.

The aim of the present study is to provide an ultrastructural description of the spermiogenesis and the mature spermatozoon of the dilepidid cestode *Angularella beema* (Clerc, 1906).

Materials and methods

Live specimens of *Angularella beema* (Clerc, 1906) were obtained from the small intestine of a naturally infected bird *Riparia riparia* (Passeriformes, Hirundinidae) collected from the village of Krapec, Bulgarian Black Sea coast. The mature proglottides were fixed in 4% glutaraldehyde in 0.2 M sodium cacodylate buffer at pH 7.2 for 4 h, rinsed in 0.2 M cacodylate buffer, post-fixed in cold (0–4°C) 1% OsO_4 for 1 h, dehydrated in ethanol series and propylene oxide and embedded in Durcupan. Ultrathin sections were cut on Ultratome LKBIII and stained with uranyl acetate and lead citrate. The grids were examined under a JEOL 1010 transmission electron microscope at the "Serveis Científicotècnics" of the University of Barcelona.

Results

Spermiogenesis

The early spermatids are organized in rosettes with central cytophore (Fig. 1). The spermiogenesis starts with the forma-

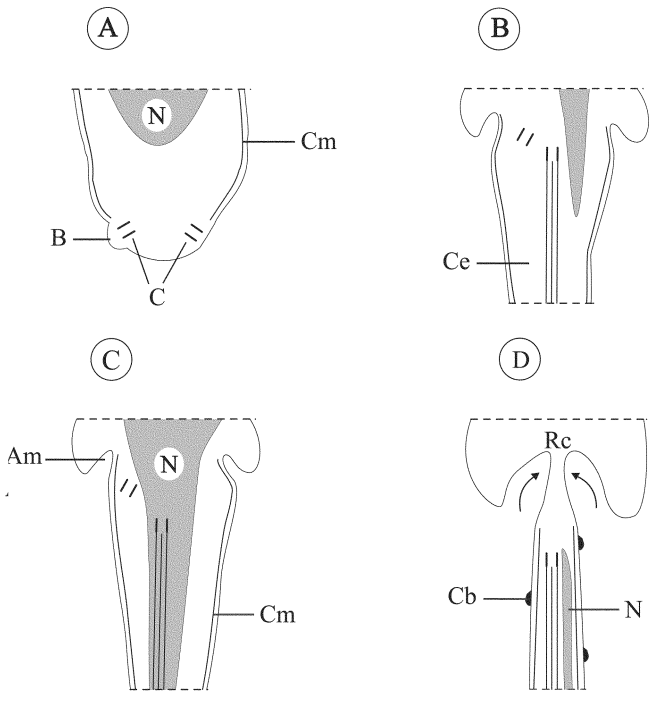


Fig. 28A-D. Schematical drawing showing the main stages of spermiogenesis in *Angularella beema*

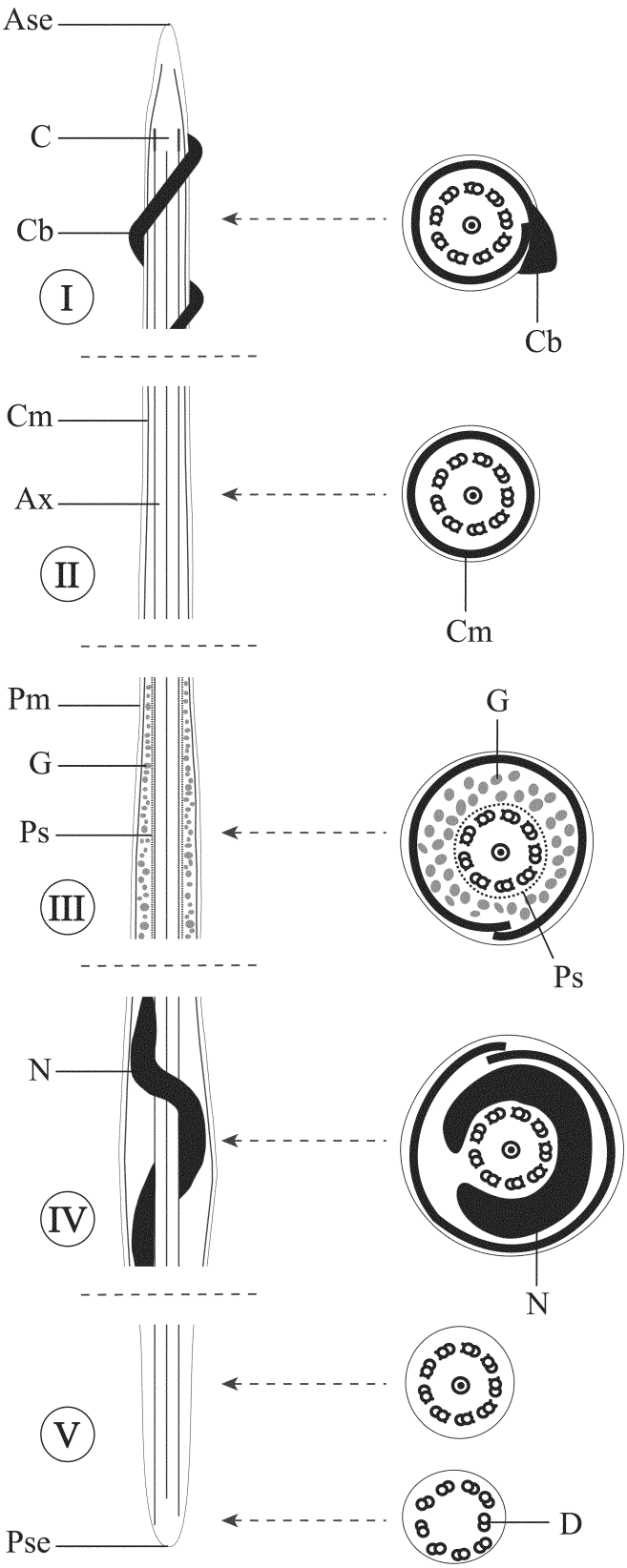


Fig. 29I–V. Schematical reconstruction of the mature spermatozoon of *Angularella beema*

tion of a differentiation zone, which is a conical area bordered by submembranous microtubules and containing two centrioles (Figs 2 and 3). One of the centrioles develops an axoneme (Fig. 4) that grows directly into the cytoplasmic protrusion (Fig. 6). The nucleus is initially located in the differentiation zone (Figs 2 and 3) and contains well-developed nucleolus (Fig. 2); later, it becomes elongate and initiates its migration into the spermatid body (Figs 5, 6 and 12). Initially, the cortical microtubules are parallel to the axis of the cytoplasmic protrusion (Fig. 9); they become twisted simultaneously with the migration of the nucleus (Figs 7, 8 and 13). At this stage, sections through the differentiation zone without nucleus (Fig. 10) and containing nucleus (Fig. 11) can be observed. After the incorporation of the nucleus, a single electron-dense crested body is formed externally to cortical microtubules (Fig. 14).

At the end of the spermiogenesis, the ring of arching membranes becomes narrower (Fig. 14), which precedes the detachment of the spermatozoon from the residual cytoplasm.

Spermatozoon

The mature spermatozoon can be subdivided into five regions with different ultrastructural characteristics.

Region I corresponds to the anterior extremity of the spermatozoon. This region contains the centriole (Fig. 15) and a single helically-coiled crested body (Figs 16 and 17). The axoneme is 9 + '1' pattern, lacks a periaxonemal sheath and is surrounded by a layer of electron-lucent cytoplasm. Submembranous cortical microtubules are twisted to the spermatozoon axis at angle of approximately 30–40°.

Region II is characterised by the lack of a crested body. It contains only the axoneme and a discontinuous layer of twisted peripheral microtubules (Figs 18 and 20).

Region III differs from the remaining regions by the presence of a periaxonemal sheath. In this region, glycogen-like granules appear; they are localised between the periaxonemal sheath and the cortical microtubules (Figs 19–22).

Region IV is the nucleated portion of the spermatozoon. The electron-dense nucleus is spirally surrounding the axoneme. There is no periaxonemal sheath in this region (Figs 22–24).

Region V is the posterior terminal part of the spermatozoon. It lacks nucleus. The axoneme progressively becomes disorganized: The central core unit disappears, followed by disintegration of doublets into singlets (Figs 24–27).

Discussion

Spermiogenesis

The spermiogenesis of *A. beema* is characterised by the lack of both flagellar rotation and proximodistal fusion. Flagellum is not formed externally to the cytoplasmic protrusion and the axoneme is directly formed within the body of the spermatid. This pattern of spermiogenesis was described as Type IV spermiogenesis of cestodes (Bâ and Marchand 1995). Until now, it has been described for all the examined members of the family Hymenolepididae [*Dicranotaenia coronula*, see Chomicz and Świderski 1992a; *Hymenolepis diminuta*, see Kelsoe *et al*. 1977; *Rodentolepis nana* (= *Hymenolepis nana*), see Bâ and Marchand 1992a; *Rodentolepis microstoma* (= *Vampirolepis microstoma*), see Bâ and Marchand 1998] and in some representatives of the family Anoplocephalidae [*Thysaniezia ovilla*, see Bâ *et al*. 1991; *Killigrewia delafondi* (= *Aporina delafondi*), see Bâ and Marchand 1994a; *Anoplocephaloides dentata*, see Miquel and Marchand 1998a; *Sudarikovina taterae*, see Bâ *et al*. 2000; *Moniezia expansa*, see Li *et al*. 2003; *Gallegoides arfaai*, see Miquel *et al*. 2005b; *Mosgovoyia ctenoides*, see Eira *et al*. 2006]. However, in other species of Anoplocephalidae, a proximodistal fusion of the flagellum and the cytoplasmic protrusion occurs and their spermiogenesis corresponds to the Type III (see Bâ and Marchand 1995). These are *Mathevotaenia herpestis*, *Avitellina centripunctata*, *Stilesia globipunctata* (see Bâ and Marchand 1992b, 1994b, d). Therefore, the Type IV of spermiogenesis is a putative synapomorphy for the group consisting of Dilepididae plus Hymenolepididae plus part of the Anoplocephalidae. This hypothesis questions the monophyly of Anoplocephalidae in the currently accepted taxonomic concept (Beveridge 1994) and the distant position of the Anoplocephalidae to the clade containing the Hymenolepididae and the Dilepididae (see Hoberg *et al*. 1999). The possible polyphyletic origin of the Anoplocephalidae was emphasized by Beveridge (1994).

The species of the families Metadilepididae and Dipylidiidae were previously classified among dilepidids (Schmidt 1986). However, both *Skrjabinoporus merops* (Metadilepididae) and the species of the Dipylidiidae are characterised by the Type III spermiogenesis (Miquel *et al*. 1998, 2005a; Ndiaye *et al*. 2003b; Yoneva *et al*. 2006). The record of the Type IV spermiogenesis in a dilepidid species provides an additional support of considering Metadilepididae and Dipylidiidae as distinct families as suggested by Jones *et al*. (1994).

In the order Cyclophyllidea, a variation is described in relation to the presence and morphology of striated roots associated with centrioles in the differentiation zone. The presence of typical striated roots was reported for two of the three dipylidiids studied until now, *Joyeuxiella echinorhynchoides* and *J. pasqualei* (see Ndiaye *et al.* 2003b, Miquel *et al*. 2005a). The third dipylidiid examined, *Dipylidium caninum* (see Miquel *et al*. 1998, 2005a), as well as the anoplocephalid *A. dentata* (see Miquel and Marchand 1998a) possess 'thin striated roots' associated with the centrioles. In *G. arfaai* (Anoplocephalidae), up to six striated roots (believed to be vestigial) arranged in two groups (each consisting of 3 roots) at each side of the centrioles were observed (Miquel *et al*. 2005b). The latter authors recognised all these reduced striated roots under the name 'vestigial striated roots'. Recently, Eira *et al*. (2006) have also described these structures in another anoplocephalid species, *Mosgovoyia ctenoides*. No striated roots were observed in *A. beema*, which seems to be the most common case in the Cyclophyllidea.

The presence of a single axoneme in the differentiation zone and the absence of flagellar rotation were considered as synapomorphies for the Cyclophyllidea (Justine 2001). The former synapomorphy is confirmed by the present study. However, a slight rotation of the flagellum was reported for the catenotaeniid *Catenotaenia pusilla* (see Hidalgo *et al*. 2000), the taeniid *Taenia parva* (see Ndiaye *et al*. 2003a) and the metadilepidid *S. merops* (see Yoneva *et al*. 2006). There is no flagellar rotation in *A. beema*, which rather suggests that this character is a possible synapomorphy for the group of more evolved cyclophyllideans (including Davaineidae, Dilepididae, Anoplocephalidae and Hymenolepididae).

Spermatozoon

The present results are in agreement with the previous studies of spermatozoa of dilepidid cestodes (Świderski and Tkach 1996, Świderski *et al*. 2000); an exception is the lack of a periaxonemal sheath in *M. crassiscolex* (see Świderski *et al*. 2000) and its presence in *A. beema*. Therefore, this character seems to be of limited value for studying phylogenetic relationships among cyclophyllidean families. Further studies are needed to show the variation of the presence/absence of periaxonemal sheath among the dilepidid genera.

The ultrastructure of the mature spermatozoon of *A. beema* exhibits several characters, which are believed to be synapomorphies for superior taxa. These are the lack of mitochondria (synapomorphy for the Eucestoda, see Justine 1991), the spiral twisting of the cortical microtubules and the presence of periaxonemal sheath (synapomorphies for Cyclophyllidea plus Tetrabothriidea, see Justine 2001).

The spermatozoon of *A. beema* has a single crested body, as it is in the cyclophyllidean families Taeniidae (see Miquel *et al*. 2000, Ndiaye *et al*. 2003a, Willms *et al*. 2004), Mesocestoididae (see Miquel *et al*. 1999), Nematotaeniidae (see Mokhtar-Maamouri and Azzouz-Draoui 1990), Dilepididae (see Świderski *et al*. 2000, 2002), Dipylidiidae (see Miquel and Marchand 1997, Ndiaye *et al*. 2003b, Miquel *et al*. 2005a) and Metadilepididae (see Yoneva *et al*. 2006). Two families, Catenotaeniidae and Davaineidae, are characterised by the presence of two crested bodies on the mature spermatozoon (Miquel *et al*. 1997; Hidalgo *et al*. 2000; Bâ and Marchand 1994c; Bâ *et al*. 2005a, b). The spermatozoa of the Hymenolepididae possess multiple (6–12) crested bodies, while the species of the Anoplocephalidae are characterised by 1 or 2 crested bodies (in two species only, *K. delafondi* and *S. taterae*, 5 and 7 crested bodies, respectively, were described, see Bâ and Marchand 1994a, Bâ *et al*. 2000). When data about the remaining cyclophyllidean families are accumulated, the number of crested bodies may be justified as a useful character from phylogenetic point of view.

In *A. beema*, similarly to many cyclophyllideans studied, no intracytoplasmic walls were observed in mature spermatozoon. Intracytoplasmic walls were described in all the Davaineidae studied (*Raillietina tunetensis*, see Bâ and Marchand 1994c; *Raillietina baeri*, see Bâ *et al*. 2005a; *Paroniella reynoldsae*, see Bâ *et al*. 2005b), in three anoplocephalid species (*Inermicapsifer guineensis* and *I. madagascariensis*, see Bâ and Marchand 1994e; *A. centripunctata*, see Bâ and Marchand 1994b). Similar structures, electron-dense rods, were observed in the dilepidid *D. undula* (see Świderski *et al*. 2000) and in the species of the genus *Taenia* (see Tian *et al*. 1998, Miquel *et al*. 2000, Ndiaye *et al*. 2003a, Willms *et al*. 2004).

The presence of electron-dense granular material is frequent in the spermatozoon of cyclophyllideans. Two types of inclusions were registered in the mature spermatozoa of cyclophyllideans, glycogen and proteinaceous granules. The latter were proved in the anoplocephalids *T. ovilla* and *K. delafondi* (see Bâ *et al*. 1991, Bâ and Marchand 1994a), and in the hymenolepidid *Cladogynia serrata* (= *Retinometra serrata*) (see Bâ and Marchand 1993). On the other hand, glycogen granules were evidenced for the hymenolepidid *H. diminuta* (see Robinson and Bogitsh 1978) and for the mesocestoidid *Mesocestoides litteratus* (see Miquel *et al*. 1999). Other species that exhibit glycogen-like granules (not corroborated by the Thiéry's test) in their spermatozoa are the dipylidiids *Joyeuxiella pasqualei* and *J. echinorhynchoides* (see Ndiaye *et al*. 2003b, Miquel *et al*. 2005a), and the nematotaeniid *Nematotaenia chantalae* (see Mokhtar-Maamouri and Azzouz-Draoui 1990). Numerous species of the Anoplocephalidae (*A. dentata, G. arfaai, M. expansa, M. benedeni, M. ctenoides* and *P. omphalodes*, see Bâ and Marchand 1992c; Miquel and Marchand 1998a, b; Bâ *et al*. 2000; Miquel *et al*. 2004; Eira *et al*. 2006) exhibit granular electron-dense material similar to the proteinaceous granules but not confirmed by any cytochemical test. The dilepidid *D. undula* (see Świderski *et al*. 2000) and various species of hymenolepidids also possess electron-dense inclusions with size intermediate between those of the proteinaceous particles and the glycogen granules. These hymenolepidids are *Echinocotyle dolosa*, *Rodentolepis straminea* (= *Hymenolepis straminea*), *R. nana*, *R. microstoma*, *Cladogynia guberiana* (= *Retinometra guberiana*), *Diorchis parvogenitalis* and *D. coronula* (see Bâ and Marchand 1992a, 1996, 1998; Chomicz and Świderski 1992a, b; Świderski and Chomicz 1994; Bâ *et al*. 2002). Granular inclusions found in the spermatozoon of *A. beema*, which probably are of glycogenic nature, were similar to those present in the dipylidiids, nematotaeniids, mesocestoidids and hymenolepidids. Inclusions are lacking in the spermatozoa of the Metadilepididae (see Yoneva *et al*. 2006), Davaineidae (see Bâ and Marchand 1994c; Bâ *et al*. 2005a, b), Catenotaeniidae (see Miquel *et al*. 1997, Hidalgo *et al*. 2000) and Taeniidae (see Miquel *et al*. 2000, Ndiaye *et al*. 2003a). For the moment, the presence and the character of the inclusions seem to be of limited value for the purposes of phylogenetic studies but their possible implication should be revisited when more data are accumulated.

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