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VERSITA

Ultrastructure of spermatogenesis of *Taenia taeniaeformis* (Batsch, 1786) (Cestoda, Cyclophyllidea, Taeniidae) and comparison of spermatological characters in the family Taeniidae Ludwig, 1886**

Jordi Miquel[1]*, Zdzisław Świderski[2,3], Pilar Foronda[4], Jordi Torres[1] and Carlos Feliu[1]

[1]Laboratori de Parasitologia, Departament de Microbiologia i Parasitologia Sanitàries, Facultat de Farmàcia, Universitat de Barcelona, Av. Joan XXIII, sn, 08028 Barcelona, Spain; [2]W. Stefański Institute of Parasitology, Polish Academy of Sciences, 51/55 Twarda Street, 00-818 Warsaw, Poland; [3]Department of General Biology and Parasitology, Warsaw Medical University, 5 Chałubińskiego Street, 02-004 Warsaw, Poland; [4]Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias, c. Astrofísico F. Sánchez, sn, 38206, La Laguna, Spain

Abstract

The ultrastructure of spermatogenesis of *Taenia taeniaeformis* is described for the first time by means of transmission electron microscopy (TEM). Mature testes contain all stages of spermatogenesis; primary spermatogonia are usually situated at the periphery and mature spermatozoa in the centre of testes. The general process is similar to that described in other cestodes. Six incomplete, synchronic cytokineses occur: four mitotic and two meiotic cell divisions. All these divisions occur simultaneously, resulting in a rosette cluster of four tertiary spermatogonia, then eight quaternary spermatogonia, and subsequently sixteen primary spermatocytes. All of these enter into a growth period and their enlarged nuclei move to the periphery of cells of the rosettes. The first meiotic division forms thirty-two secondary spermatocytes and after the second meiotic division, there are sixty-four spermatids. Spermiogenesis in *T. taeniaeformis* corresponds to the Bâ and Marchand's Type 3 and begins with the formation of a differentiation zone in the form of a conical projection of cytoplasm delimited by a ring of arching membranes and surrounded by submembranous cortical microtubules. Within this area, there are two centrioles, orthogonally disposed, and vestigial striated rootlets. Only one of the centrioles develops a flagellum that grows externally to the cytoplasmic extension. Posteriorly, a flagellar rotation inferior to 90º occurs and the flagellum becomes parallel to the cytoplasmic extension. Later, the two processes fuse during the so-called proximodistal fusion. The nucleus elongates and moves into the cytoplasmic extension. In the final stage of spermiogenesis, a single crested body appears at the base of the differentiating spermatozoon. Finally, the ring of arching membranes constricts and the young spermatozoon detaches from the residual cytoplasm. Ultrastructural aspects of spermatogenesis are compared with that of other cestodes studied to date, particularly of the family Taeniidae.

Keywords

Taenia taeniaeformis, Taeniidae, Cyclophyllidea, Cestoda, spermatogenesis, spermiogenesis, ultrastructure

Introduction

The taeniids represent the best known family of cestodes which comprises 44 species, including 5 of medical and about 20 of veterinary importance. They have been intensively studied because of this medical and veterinary importance. In spite of excellent taxonomic revisions of the genus *Taenia* Linnaeus, 1758 by Verster (1969) and its more recent up-date by Loos-Frank (2000), some disagreement still exists in the discrimination of genera in the Taeniidae, due to different opinions concerning the relative significance of taxonomic characters. Spermatological characters of cestodes have generally been accepted and widely used as valid criteria for analysis of cestode phylogeny and evolution, and generally for the interpretation of phylogenetic relationships within the Platyhelminthes (Świderski 1970, 1986; Euzet *et al*. 1981; Justine

*Corresponding author: jordimiquel@ub.edu

**Dedicated to the memory of Professor Krystyna Rybicka on the occasion of 85th Anniversary of her birthday

1991, 1998, 2001; Bâ and Marchand 1995; Hoberg *et al*. 1997). Currently, they are frequently applied in parallel with molecular data to provide reciprocal supporting arguments.

At present, there are ultrastructural studies on spermiogenesis or sperm of the following nine species of the Taeniidae: *Echinococcus granulosus*, *E. multilocularis*, *Taenia crassiceps*, *T. hydatigena*, *T. mustelae*, *T. parva*, *T. pisiformis*, *T. saginata* and *T. solium* (Morseth 1969; Featherston 1971; Barrett and Smyth 1983; Shi *et al*. 1994; Tian *et al*. 1998; Miquel *et al*. 2000; Ndiaye *et al*. 2003a; Willms *et al*. 2003, 2004). The purpose of the present paper is to describe the ultrastructure of spermatogenesis of *Taenia taeniaeformis* with emphasis on the early stages comprising 4 generations of spermatogonia, primary and secondary spermatocytes, spermatids and the entire process of sperm differentiation or spermiogenesis. We also compare our results with that of spermiogenesis of four other taeniids in order to draw a list of spermatological characters for the family Taeniidae Ludwig, 1886. Mature spermatozoon of *T. taeniaeformis* will be characterized only very briefly, as it was a subject of our previous paper (Miquel *et al*. 2009a).

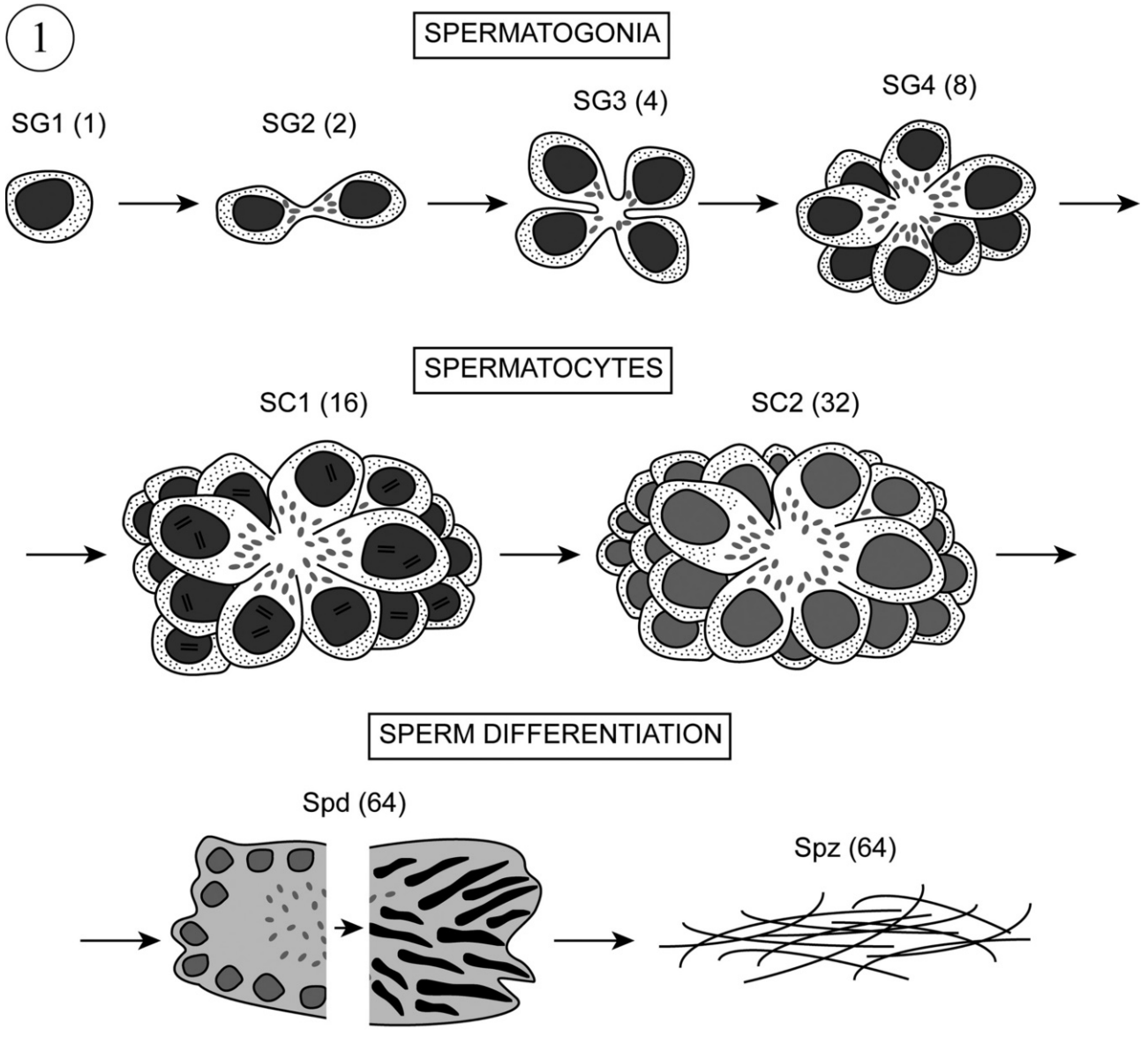
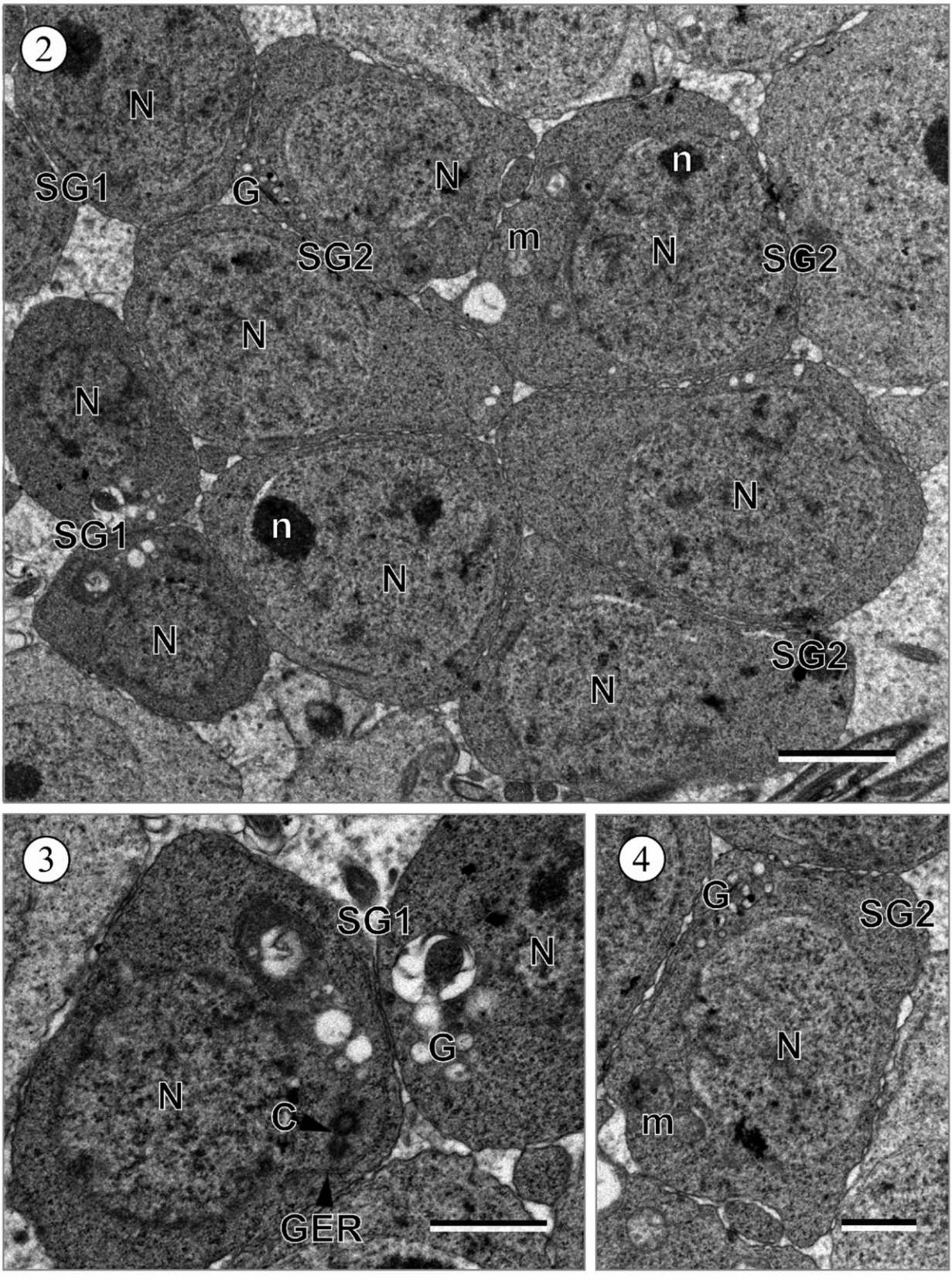


Fig. 1. Diagram illustrating the general pattern of the consecutive stages of spermatogenesis in *Taenia taeniaeformis*. The number of nuclei of each stage originating from six incomplete synchronic divisions of a single primary spermatogonium is indicated in brackets. **Abbreviations of all figures:** ac – abortive centriole, am – arching membranes, ax – axoneme, C – centriole, cb – crested bodies, ce – cytoplasmic extension, cm – cortical microtubules, cs – cytoplasmic stalk, cy – cytophore, dm – electron-dense material, F – flagellum, G – Golgi vesicles, GER – granular endoplasmic reticulum, m – mitochondria, Mp – medullar parenchyma, n – nucleolus, N – nucleus, np – nuclear pore, rc – residual cytoplasm, SC1 – primary spermatocytes, SC2 – secondary spermatocytes, SG1 – primary spermatogonia, SG2 – secondary spermatogonia, SG3 – tertiary spermatogonia, SG4 – quarternary spermatogonia, Spd – spermatids, Spz – spermatozoa, sy – synaptonemal complex, T – testes, vsr – vestigial striated rootlets, ZD – zone of differentiation



Figs 2–**4.** TEM micrographs of primary and secondary spermatogonia of *Taenia taeniaeformis*. **2.** General topography of primary and secondary spermatogonia. Note different electron density of their cytoplasm and nuclei. Scale bar = 2 μm. **3** and **4.** Details of primary (**3**) and secondary spermatogonia (**4**). Note their low cytoplasm:nucleus ratio. Scale bars = 1 μm

Materials and methods

Live adult specimens of *Taenia taeniaeformis* (Batsch, 1786) were collected from the small intestine of a naturally infected road-killed domestic cat, *Felis catus* from Breña Baja (La Palma, Canary Islands, Spain). The live cestodes were first placed in a 0.9% NaCl solution and different portions of mature proglottides were fixed in cold (4°C) 2.5% glutaraldehyde in a 0.1 M sodium cacodylate buffer at pH 7.2 for a minimum of 2 h, rinsed in a 0.1 M sodium cacodylate buffer at pH 7.2, post-fixed in cold (4°C) 1% osmium tetroxide in the same buffer for 1 h, rinsed in a 0.1 M sodium cacodylate buffer at pH 7.2, dehydrated in an ethanol series and propylene oxide, and finally embedded in Spurr's resin. Ultrathin sections were obtained using a Reichert-Jung Ultracut E ultramicrotome, placed on copper grids and double-stained with uranyl acetate and lead citrate. Ultrathin sections were examined using a JEOL 1010 TEM operated at an accelerating voltage of 80 kV.

Results

General pattern of spermatogenesis

The testes in mature proglottides of *Taenia taeniaeformis* contain all consecutive stages of spermatogenesis. As in most parasitic Platyhelminthes, spermatogenesis in *T. taeniaeformis* is of the rosette type (Fig. 1), with six incomplete synchronic cytokineses, four mitotic and two meiotic. The primary spermatogonium divides mitotically, producing two secondary spermatogonia that remain connected with one another by a cytoplasmic bridge or stalk. All further divisions occur simultaneously, resulting in a rosette of four tertiary (Fig. 1), then eight quaternary spermatogonia and subsequently the formation of sixteen primary spermatocytes. The spermatocytes enlarge, their nuclei move to the periphery and the syncitium takes on the form of a cluster. After the first meiotic division, a cluster of thirty-two secondary spermatocytes is formed. The latter cells exhibit smaller nuclei and have less granular cytoplasm. The cell membranes near the centre of the cluster become progressively indistinct as the nuclei continue to be displaced toward the periphery. The second maturation division results in sixty-four spermatids (Figs 1 and 12); their nuclei subsequently elongate and the cells differentiate into spermatozoa (Figs 14–22). The mature spermatozoa are released, leaving behind a large, deeply stained body as a residual mass of cytoplasm.

Ultrastructure of consecutive stages of spermatogenesis

The primary spermatogonia of *T. taeniaeformis* (Figs 1–3) are oval in shape, approximately 7 to 8 μm in diameter, and

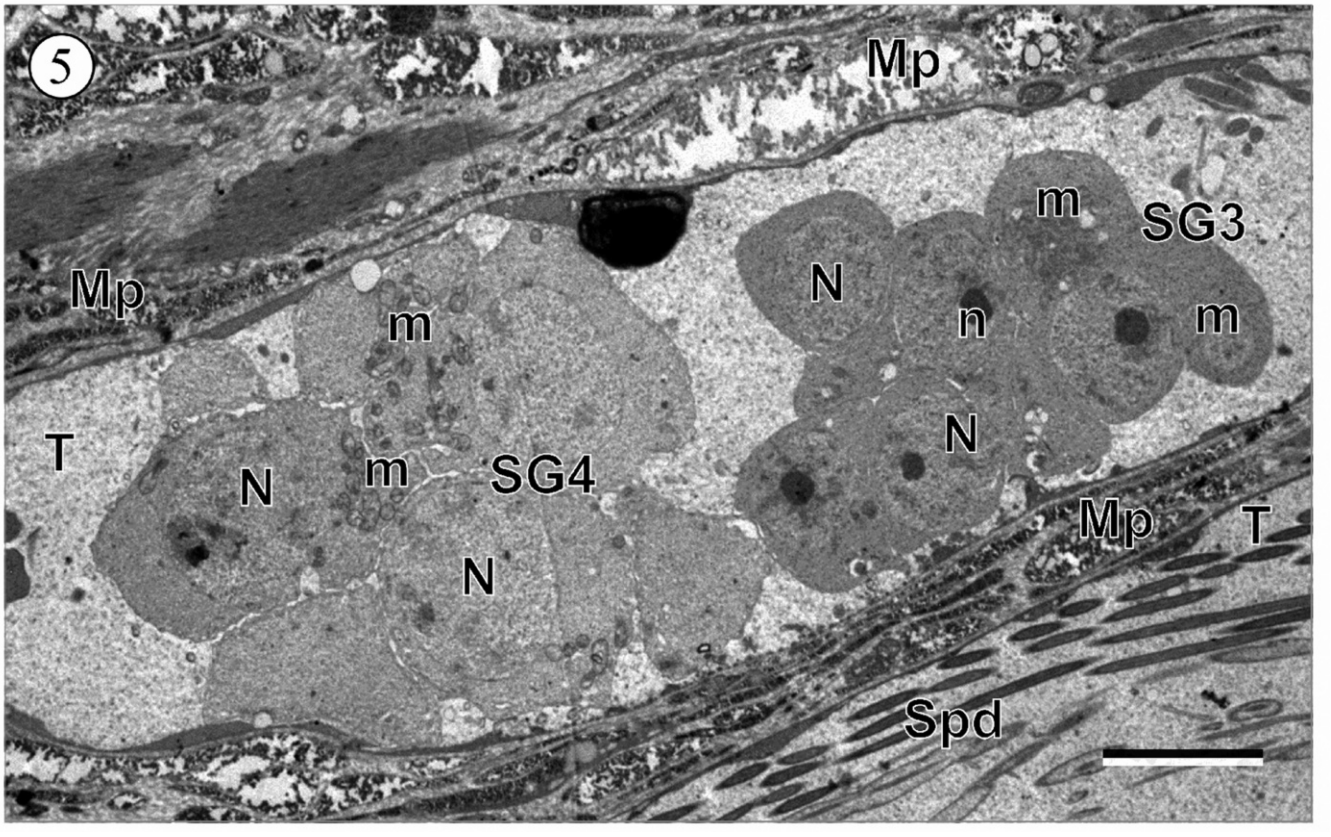
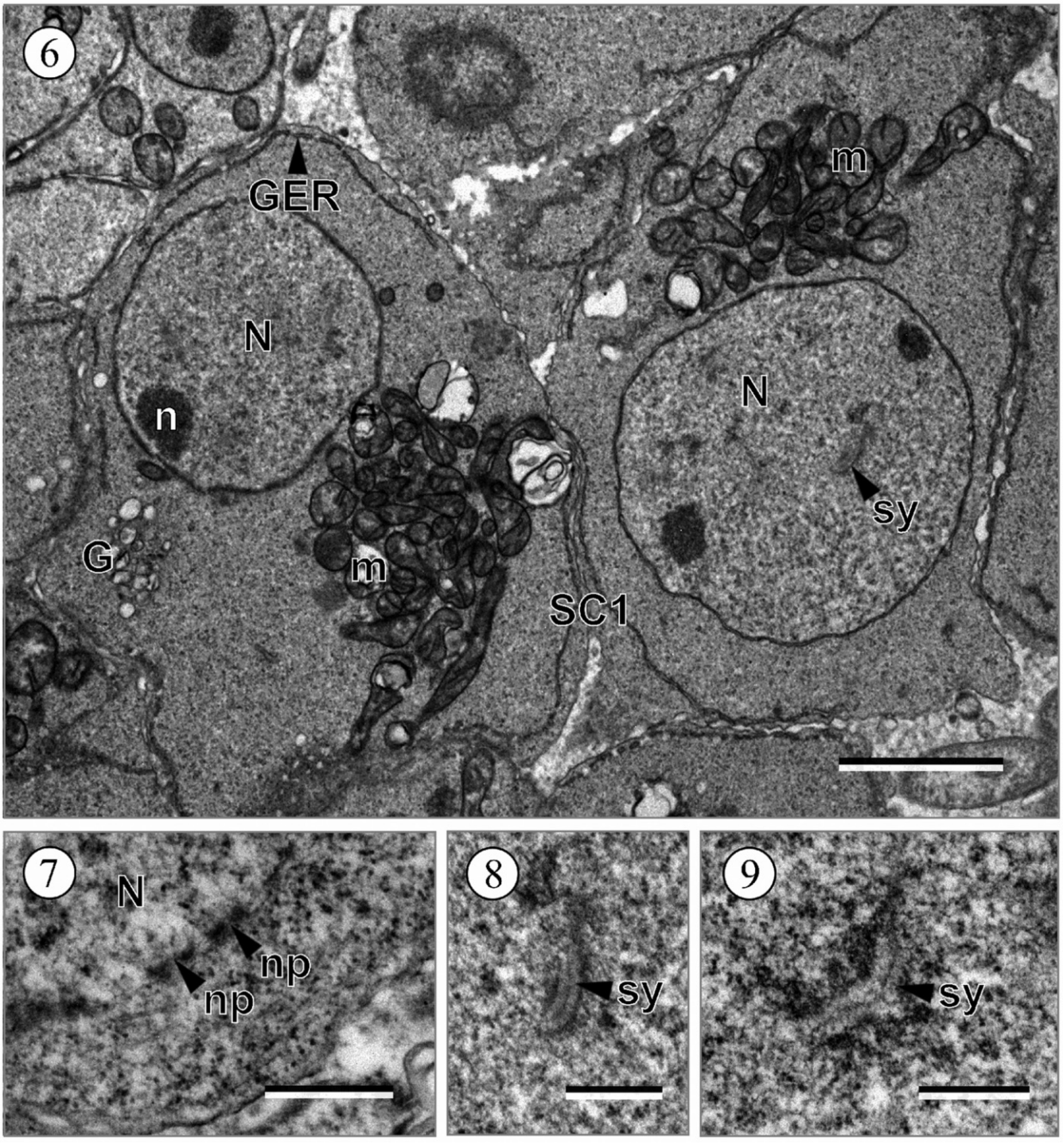
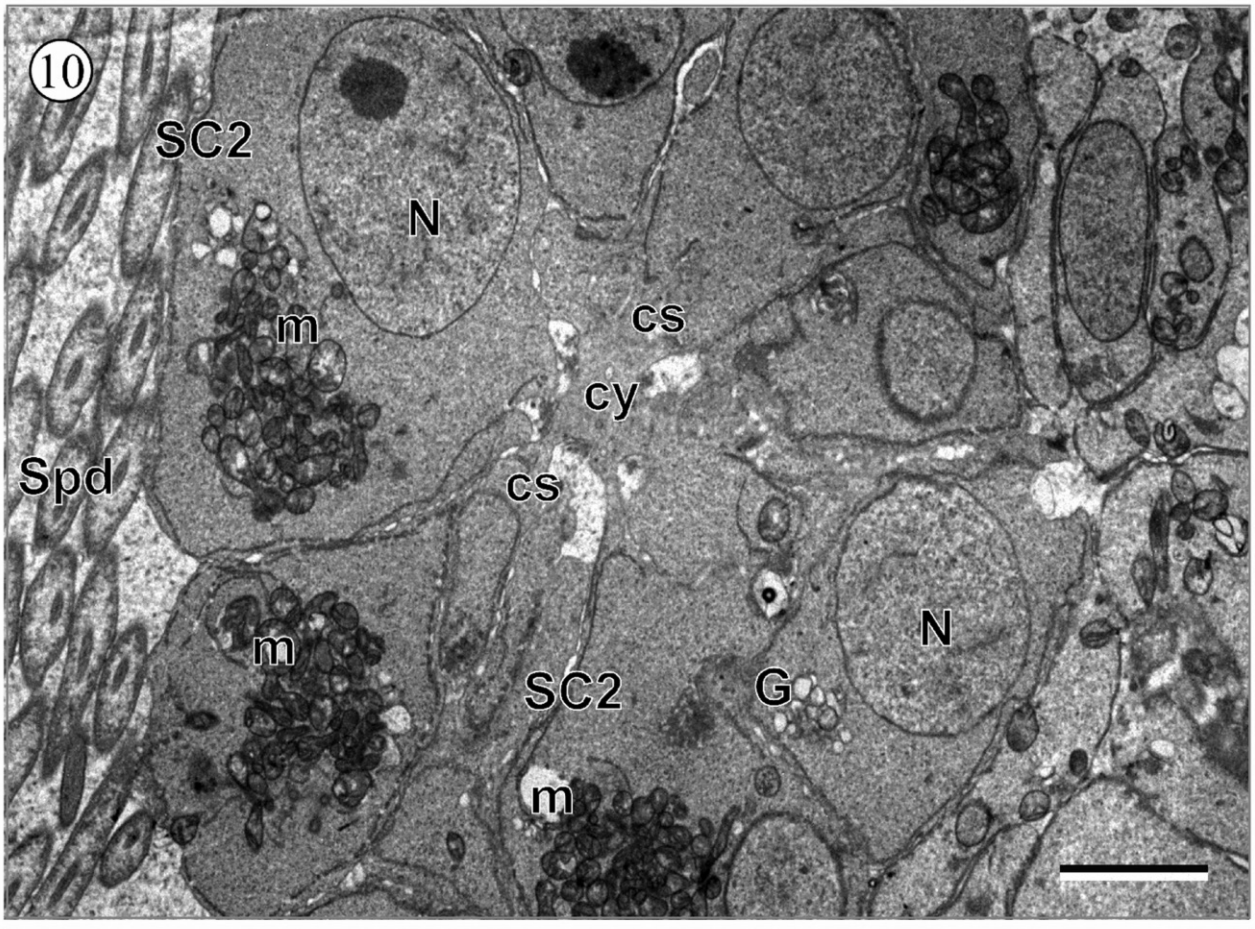


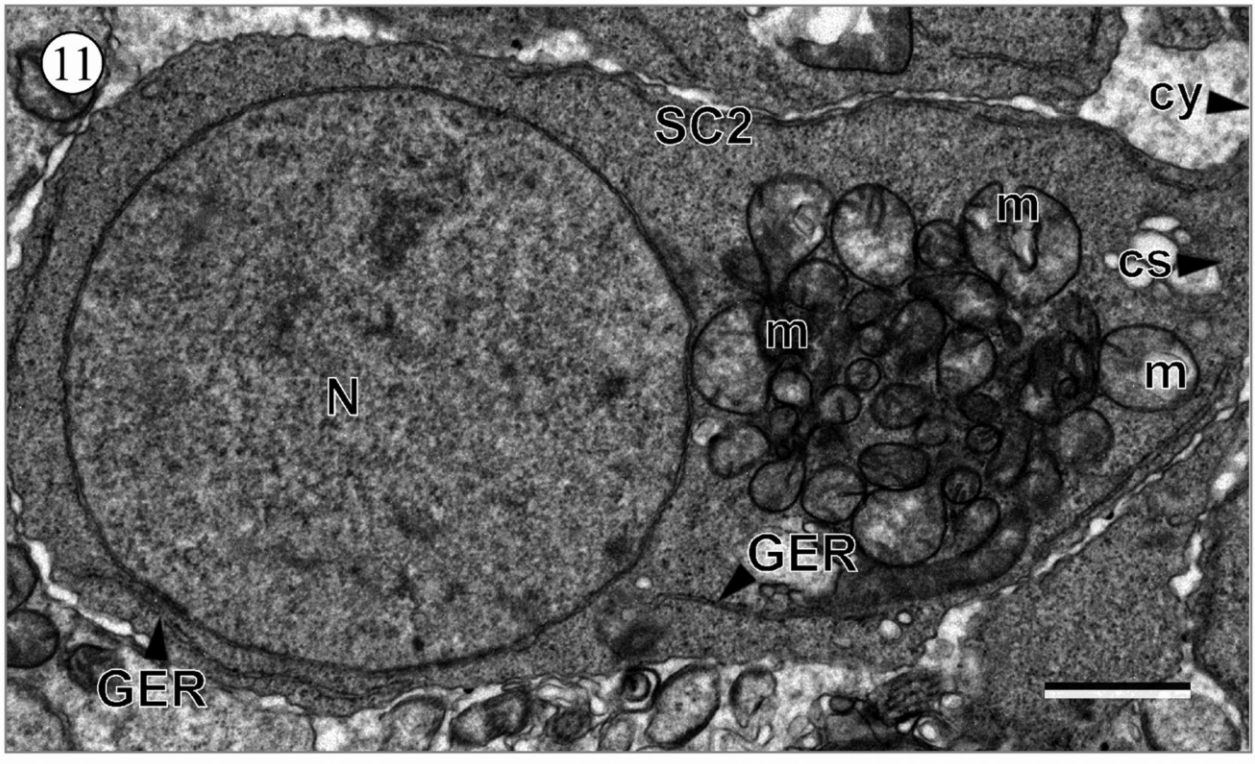
Fig. 5. Low power TEM micrograph of the general topography of a testis showing peripheral parts of two rosettes; tertiary spermatogonia on the right side and quarternary spermatogonia on the left side. Scale bar = 5 μm



Figs 6–**9.** TEM micrographs of primary spermatocytes of *Taenia taeniaeformis*. **6.** General view of two primary spermatocytes. Scale bar = 2 µm. **7.** Detail of the nuclear membrane of a primary spermatocyte showing nuclear pores. Scale bar = 0.5 µm. **8** and **9.** Details of two synaptonemal complexes. Scale bars = 0.5 µm

with a large nucleus and a thin layer of cytoplasm, thus showing a low cytoplasm:nucleus ratio. Starting from the two secondary spermatogonia (Figs 1 and 4), all subsequent stages to the spermatids share a common cytoplasm. The cytoplasm of the rosette of tertiary spermatogonia on the right side of Figure 5 is evidently more granular and contains a much higher concentration of free ribosomes than the lighter rosette of quaternary spermatogonia on the left side. Primary spermatocytes (Fig. 6) have nuclei that contain moderately electron-dense, homogeneous nucleoplasm and are usually with nucleoli and dense heterochromatin islands. The most characteristic feature of the nuclei at this stage is the presence of nu-





Figs 10 and **11.** TEM micrographs of secondary spermatocytes of *Taenia taeniaeformis*. **10.** Middle part of the rosette of secondary spermatocytes. Scale bar = 3 μm. **11.** Secondary spermatocyte attached to the cytophore by an elongated cytoplasmic stalk. Scale bar = 1 μm

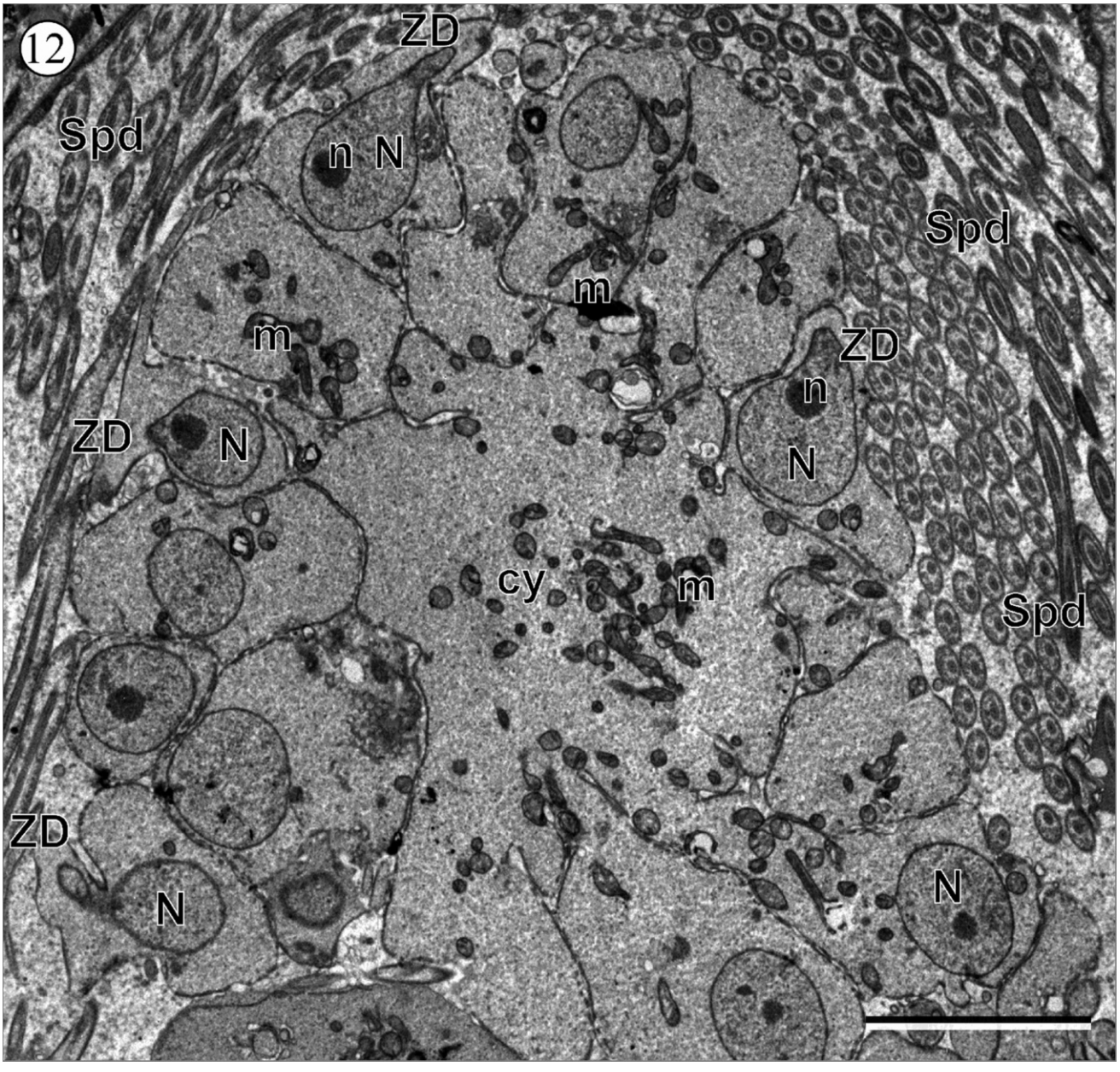


Fig. 12. TEM micrograph of a rosette of spermatids of *Taenia taeniaeformis*. Scale bar = 5 µm

merous synaptonemal complexes (Figs 6, 8 and 9), which confirm the first division of meiosis. Each synaptonemal complex consists of a pair of coarse filaments separated by a clear space, through which runs a dense central element or medial complex (Figs 8 and 9). Transverse fibres cross the central region and connect with lateral filaments on each side of the complex (Figs 8 and 9). Another characteristic of primary spermatocytes is the large nuclear pores (Fig. 7). The granular cytoplasm of secondary spermatocytes is rich in numerous free ribosomes, very large, densely packed mitochondria, several Golgi vesicles and a few elongated but very narrow cisternae of granular endoplasmic reticulum (Fig. 10). The cytophore is clearly evident in the central part of the rosette of secondary spermatocytes (Fig. 11) that are linked together to the cytophore by elongated cytoplasmic stalks or bridges resulting from five consecutive and incomplete cytokineses. The granular cytoplasm of the secondary spermatocytes, like that of the primary spermatocytes, contains a large, densely packed accumulation of mitochondria, a few Golgi complexes and short profiles of GER (Fig. 11). Their ovoid nuclei usually contain spherical, homogeneously electron-dense nucleoli but no heterochromatin islands. The spermatid cluster (Fig. 12), with a much enlarged volume of the cytophore, shows numerous spermatid nuclei at the periphery. Some of the spermatids show the initial stages of their elongation and migration towards the newly formed zones of differentiation. The sper-

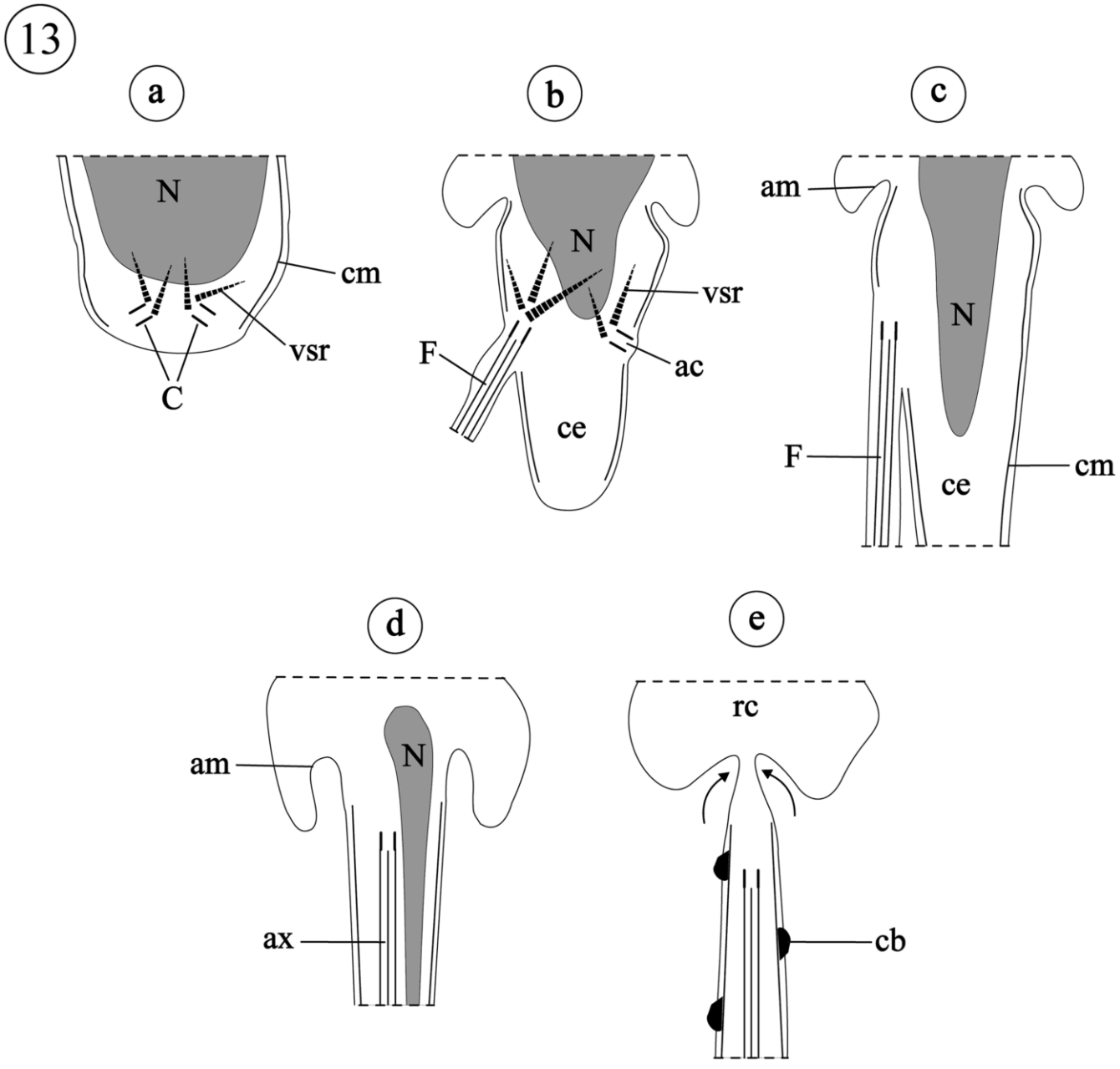
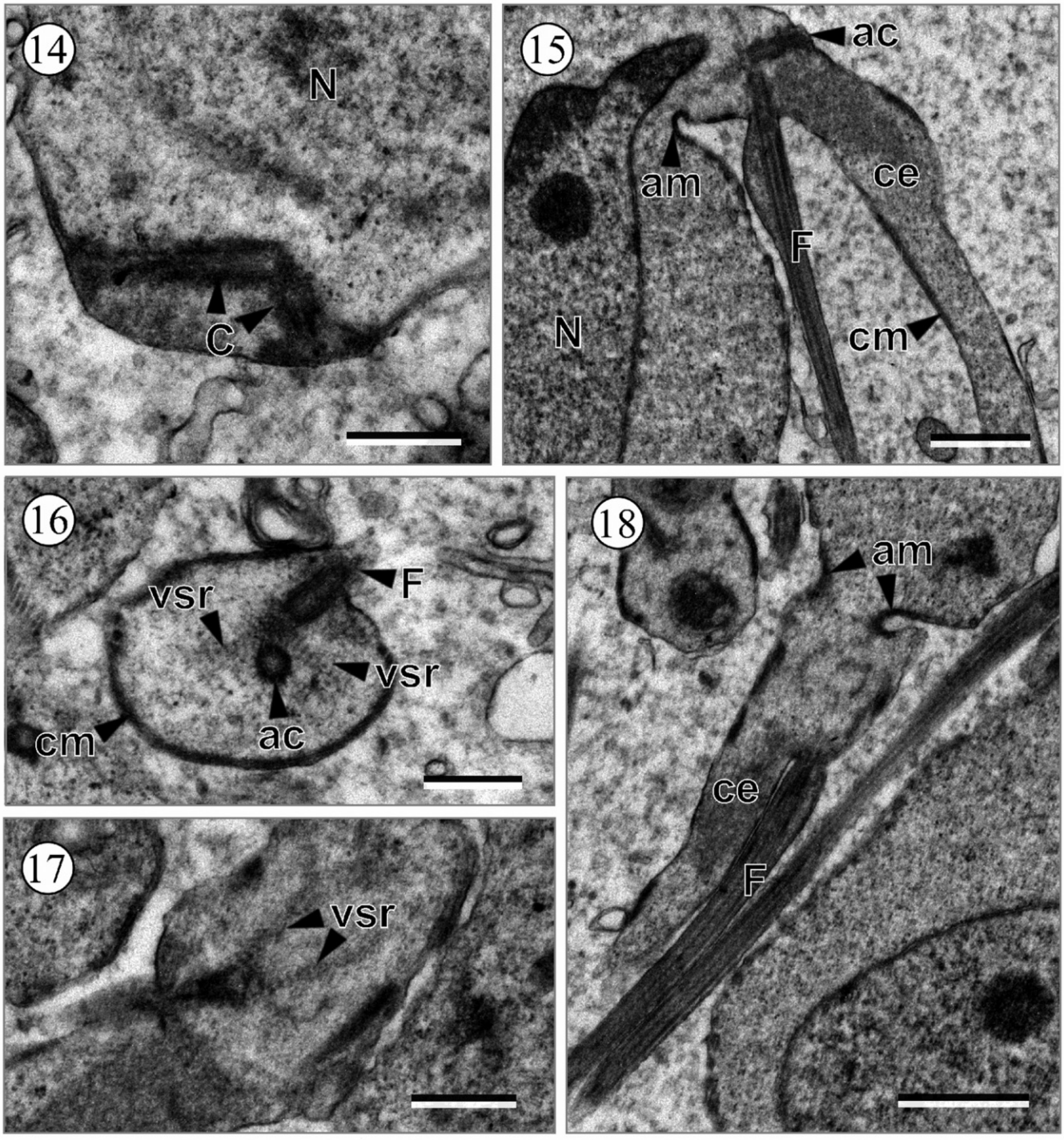


Fig. 13a-e. Diagram illustrating the main stages of spermiogenesis in *Taenia taeniaeformis*

matid nucleoplasm is still moderately electron-dense, uncondensed and usually contains high electron-dense, spherical nucleoli. This stage represents the initial phase of sperm differentiation or spermiogenesis.

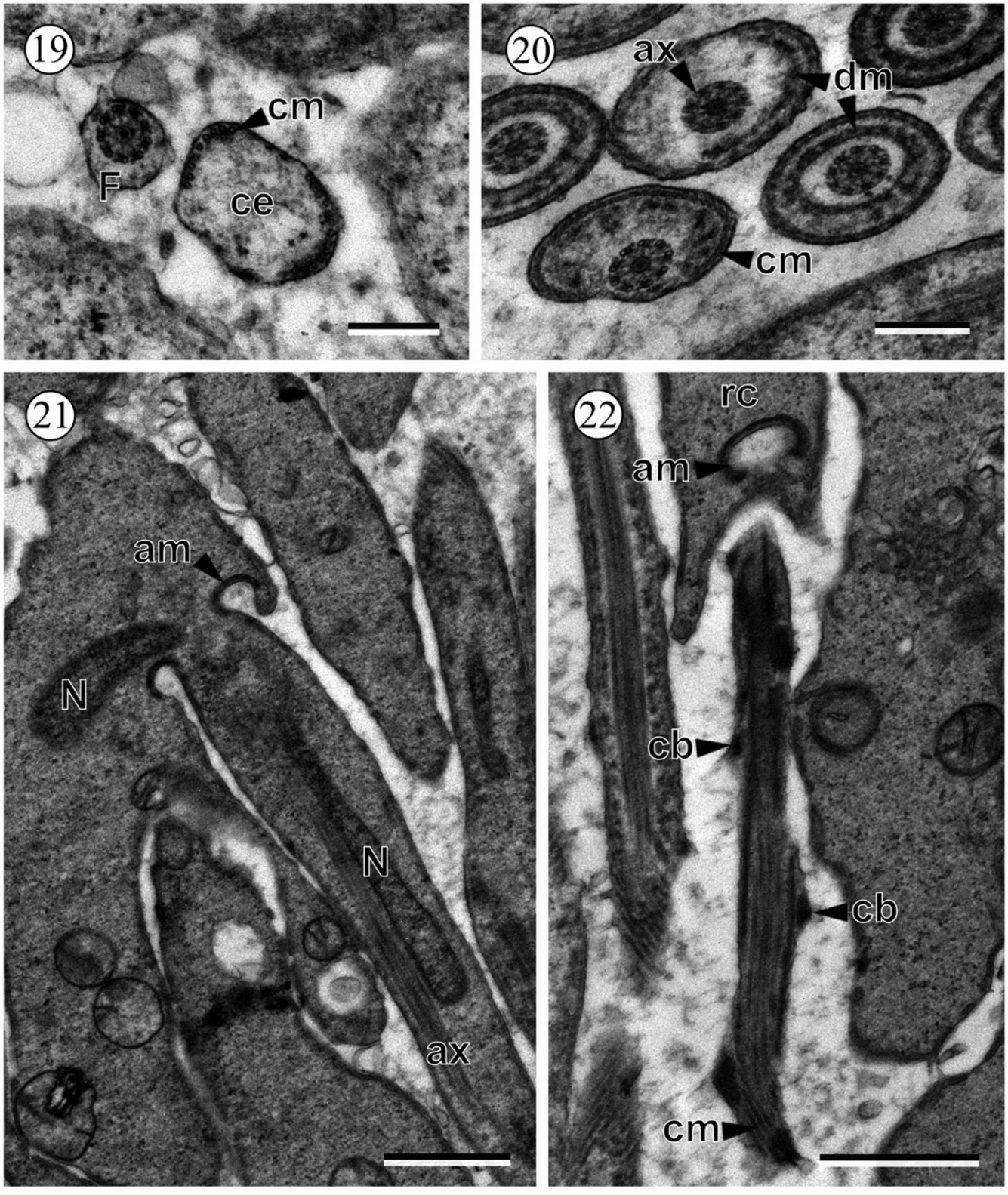
Spermiogenesis

The general pattern of spermiogenesis in *T. taeniaeformis* is illustrated in Figures 13–22. The initial stage of spermiogenesis begins with the formation of the differentiation zone (Figs 12, 13a and 14). The plasma membrane of the spermatid cluster invaginates into its cytoplasm, partially or completely encircling the spermatid nuclei, forming pockets of arching membranes that are later transformed into differentiation zones from which the spermatozoa develop (Figs 12, 13a and 14). The differentiation zone appears as a cone-shaped cytoplasmic projection supported by peripheral microtubules and delimited at its base by a ring of arching membranes (Fig. 12). This zone is also characterized by a change in the shape and density of the spermatid nucleus (Figs 12 and 14). Within the differentiation zone, there are two orthogonally disposed centrioles, both associated with "vestigial striated rootlets" (Figs 13a, 14, 16 and 17). During spermiogenesis, only one of the centrioles forms a flagellum that grows externally to the cytoplasmic ex-



Figs 14–**18.** TEM micrographs showing the initial stages of spermiogenesis in *Taenia taeniaeformis*. **14.** Zone of differentiation showing the orthogonal arrangement of the two centrioles. Scale bar = 0.5 µm. **15.** Longitudinal section of a differentiation zone showing the growth of the flagellum. Scale bar = 1 µm. **16** and **17.** Longitudinal and cross-sections showing centrioles associated with vestigial striated rootlets. Scale bars = 0.5 µm. **18.** Longitudinal section of a zone of differentiation after the flagellar rotation of the flagellum. Scale bar = 1 µm

tension (Figs 13b, 15 and 16). This flagellum forms an angle <90° relative to the cytoplasmic extension (Figs 13b and 15). Cortical microtubules elongate along this cytoplasmic process (Figs 13b, c, 15, 16 and 18). The other centriole aborts in a later stage of spermiogenesis (Figs 13c and 18). Later, the flagellum rotates and becomes parallel to the cytoplasmic extension (Figs 13c, 18 and 19). Subsequently there is a proximodistal fusion of the flagellum and the cytoplasmic extension (Figs 13d, 20 and 21). The nucleus elongates and moves into the differentiating spermatozoon (Figs 13d and 21). In the final stage



Figs 19–**22.** TEM micrographs showing the advanced stages of spermiogenesis in *Taenia taeniaeformis*. **19.** Cross-sections of the free flagellum and the cytoplasmic extension before the proximodistal fusion of both processes. Note the parallel disposition of cortical microtubules. Scale bar = 0.3 µm. **20.** Cross-sections of spermatids after the proximodistal fusion. Note the appearance of an electron-dense material when cortical microtubules are already twisted. Scale bar = 0.3 µm. **21.** Longitudinal section showing the migration of the nucleus along the spermatid body. Scale bar = 1 µm. **22.** Longitudinal section showing the final stage of spermiogenesis. Note the constriction of the ring of arching membranes and the appearance of a spiralled crested body. Scale bar = 1 µm

of spermiogenesis, a single crested body appears at the base of the differentiating spermatozoon near the arching membranes (Figs 13e and 22). Finally, the ring of arching membranes constricts and the young spermatozoon detaches from the residual cytoplasm (Figs 13e and 22).

Discussion

Spermatogenesis

The ultrastructural pattern of spermatogenesis in *T. taeniaeformis* is generally similar to that described for other cestodes (for review, see Świderski and Mackiewicz 2002, Miquel *et al*. 2005a). This cestode pattern differs from that of trematodes where there are only three mitotic divisions of spermatogonia, with a single primary spermatogonium giving rise to a single cluster of 32 spermatozoa (Justine 1980, Świderski and Tsinonis 1986). The formation of multicellular rosettes and clusters, as described here for *T. taeniaeformis*, appears typical for most flatworms. There are, however, some exceptions from this rosette-type spermatogenesis in some schistosome species. In *Schistosoma bovis* and *S. mattheei*, spermatogenic cells always remain separated throughout their development and differentiation into spermatozoa (Justine 1980, 1995; Świderski and Tsinonis 1986). On the other hand, in *Schistosomatium douthitti* and *Schistosoma magrebowiei*, there is the rosette-type spermatogenesis (Nez and Short 1957, Awad and Probert 1989). In *T. taeniaeformis* as in most of other Platyhelminthes, all cell divisions within rosettes are synchronic and allow formation of a large number of spermatozoa. It is generally accepted that rosette and cluster formation results from incomplete cell divisions. It should be noted, however, that there still remains some controversy regarding the nature and precise timing of rosette formation. For example, according to Taneya (1973), a true rosette appears at the primary spermatocyte stage only as a result of secondary fusion of initially separated cells. However, our results on *T. taeniaeformis* support the interpretation of the previous studies on parasitic Platyhelminthes, namely that a series of incomplete cytokineses is the major mechanism leading to rosette formation. Mitotic figures were never observed in *T. taeniaeformis* as it was the case in the anoplocephalid cestode, *Gallegoides arfaai* (see Miquel *et al*. 2005a). It is difficult to explain their absence in these two species, while they were usually the common features of the testes of caryophyllideans *Hunterella nodulosa* and *Glaridacris catostomi* (Kazacos and Mackiewicz 1972, Świderski and Mackiewicz 2002).

Spermiogenesis

The spermiogenesis in *T. taeniaeformis*, as in other cestodes examined so far, is initiated by a migration of the nuclei towards periphery of the cluster, progressive elongation of spermatid nuclei, formation of the zone of differentiation, and simultaneous condensation of their nucleoplasm (Świderski 1986, Świderski and Mackiewicz 2002, Miquel *et al*. 2005a).

According to the four spermiogenesis patterns established by Bâ and Marchand (1995), Type 1 spermiogenesis occurs in the Tetraphyllidea-Onchobothriidae, Proteocephalidea, Trypanorhyncha and Pseudophyllidea. With respect to the "Pseudophyllidea", which has recently been divided into Bothriocephalidea and Diphyllobothriidea, both orders exhibit Type 1 spermiogenesis (see Levron *et al*. 2006a, b). Recently, Bruňanská *et al*. (2006) reported Type 1 spermiogenesis in the spathebothriidean *Cyathocephalus truncatus*. Tetraphyllidea-Phyllobothriidae and Caryophyllidea typically present Type 2 spermiogenesis. Subsequently, Stoitsova *et al*. (1995) reported Type 2 spermiogenesis in the Tetrabothriidea (*Tetrabothrius erostris*) and Miquel *et al*. (1999, 2007) also reported Type 2 spermiogenesis in the cyclophyllideans mesocestoidids *Mesocestoides litteratus* and *M. lineatus*. According to Bâ and Marchand (1995), cyclophyllideans present either Type 3 or Type 4 spermiogenesis. Type 3 is characterized by an external single flagellum growing parallel to the cytoplasmic extension. In this type, a proximodistal fusion occurs. On the other hand, Type 4 also gives origin to a spermatozoon with a single axoneme but, in this case, the axoneme grows directly into the cytoplasmic extension. Type 4 spermiogenesis has been described by Yoneva *et al*. (2006a) in the dilepidiid *Angularella beema*, by Yoneva *et al*. (2008) in the gryporhynchid *Valipora mutabilis* and by several authors in the hymenolepidids and in all the anoplocephalids except for *Mathevotaenia herpestis* (Linstowiinae) (see Bâ and Marchand 1994a), which exhibits Type 3 spermiogenesis (for a review, see Miquel *et al*. 2005a).

Species belonging to the other examined families of Cyclophyllidea follow Type 3 spermiogenesis. This is the case of the catenotaeniid *Catenotaenia pusilla*, the davaineids, the dipylidiids, the metadilepidid *Skrjabinoporus merops*, the nematotaeniid *Nematotaenia chantalae*, and the taeniids (Featherston 1971; Mokhtar-Maamouri and Azzouz-Draoui 1990; Bâ and Marchand 1994b; Miquel *et al*. 1998, 2005b, 2009b; Hidalgo *et al*. 2000; Ndiaye *et al*. 2003a, b; Willms *et al*. 2003, 2004; Yoneva *et al*. 2006b). In the present study, we demonstrate that *T. taeniaeformis* also exhibits Type 3 spermiogenesis.

Most cyclophyllideans, including all the studied taeniid species, lack "typical striated rootlets", a condition that has been postulated as a synapomorphy for the cyclophyllideans (Justine 2001). There are some exceptions, however, such as the dipylidiids *Joyeuxiella pasqualei* and *J. echinorhynchoides* (Ndiaye *et al*. 2003b, Miquel *et al*. 2005b) and the mesocestoidids *M. litteratus* and *M. lineatus* (Miquel *et al*. 1999, 2007) that present typical striated rootlets associated with centrioles. The presence of typical striated rootlets in spermiogenesis of *Mesocestoides* is yet further evidence of the controversial position of mesocestoidids within the cyclophyllideans, as widely discussed by several authors (see Rausch 1994; Mariaux 1998; Miquel *et al*. 1999, 2007; Justine 2001). The

Table I. Ultrastructural characters of the spermiogenesis in *Taenia* species

Taenia species	Type	FR	PF	SR	IB	References
T. crassiceps	3	–	+	–	–	Willms *et al.* (2004)
T. hydatigena	3	–	+	–	–	Featherston (1971)
T. parva	3	<90°	+	–	–	Ndiaye *et al.* (2003a)
T. solium	3	–	+	–	–	Willms *et al.* (2003)
T. taeniaeformis	3	<90°	+	vsr	–	present paper

FR, flagellar rotation; IB, intercentriolar body; PF, proximodistal fusion; SR, striated rootlets; vsr, vestigial striated rootlets; +/–, presence/absence of considered character.

term "typical striated rootlets" was proposed by Justine (2001) in order to distinguish the particular pattern of striated rootlets found in certain cyclophyllideans. Earlier, Miquel and Marchand (1998) had demonstrated the presence of thin striated rootlets in the differentiation zone of the anoplocephalid *Anoplocephaloides dentata*. Additionally, thin striated rootlets have been reported in the dipylidiid *Dipylidium caninum* by Miquel *et al*. (1998, 2005b). These two findings have resulted in the recodification of the character "absence of striated rootlets" to "absence of typical striated rootlets" in order to consider the synapomorphy for the Cyclophyllidea (see Justine 2001). Moreover, recently Li *et al*. (2003) have examined spermiogenesis in the anoplocephalid *Moniezia expansa* and described the presence of a third type of rootlets, the so-called "spiral rootlets" that are very different from the typical, well-developed striated rootlets and thin striated rootlets. These spiral rootlets may represent an intermediate state between the other two other rootlet conditions. In our opinion, the plesiomorphic striated rootlets may have undergone a progressive reduction in the cyclophyllideans, leading towards their total absence in the more evolved cestodes. Finally, Miquel *et al*. (2005a) and Eira *et al*. (2006) describe structures similar to thin striated rootlets in the anoplocephalids *G. arfaai* and *Mosgovoyia ctenoides*. In order to increase homogeneity, Miquel *et al*. (2005a) has proposed to group all the previously described "non-typical striated rootlets" under the common designation of "vestigial striated rootlets". Later, similar structures were described in the metadilepidid *Skrjabinoporus merops* and in the paruterinid *Anonchotaenia globata* (Yoneva *et al*. 2006b, 2009). In the present study, vestigial striated rootlets associated with the centrioles are also observed in the differentiation zone of *T. taeniaeformis*. According to Miquel *et al*. (2005a), typical striated rootlets are degenerated and divided, forming several thin striated rootlets arranged in groups. Considering the type of rootlet development particular situation found in the mesocestoidids *M. litteratus* and *M. lineatus* and the dipylidiids *J. echinorhynchoides* and *J. pasqualei* (see Miquel *et al*. 1999, 2005b, 2007; Ndiaye *et al*. 2003b), their structure may represent an intermediate state between the typical well-developed striated rootlets in digeneans and non-cyclophyllidean cestodes and its absence in cyclophyllideans, the most evolved cestodes.

Similar variation in the range of expression of a character state occurs in the case of flagellar rotation. Four cyclophyllideans, the catenotaeniid *C. pusilla*, the metadilepidid *S. merops*, the paruterinid *A. globata* and the taeniid *T. parva* show a flagellar rotation inferior to 90° before the proximodistal fusion of the free flagellum with the cytoplasmic extension (Hidalgo *et al*. 2000; Ndiaye *et al*. 2003a); Yoneva *et al*. 2006b, 2009). This is also the case for *T. taeniaeformis*. Taking into account the recent observations of flagellar rotations of up to 120° in the Fasciolidae, Dicrocoeliidae, Monorchiidae, Opecoelidae and Allocreadiidae digeneans (Ndiaye *et al*. 2003c; Levron *et al*. 2003, 2004; Agostini *et al*. 2005; Quilichini *et al*. 2007a, b), and described in the caryophyllidean *Wenyonia virilis* and in the spathebothriidean *C. truncatus* (Bruňanská *et al*. 2006, Miquel *et al*. 2008), it appears that there may be a gradual reduction of the rotation angle until there is no rotation, a state that is considered the apomorphic condition of this character (Justine 1998, 2001).

The above analysis of our results and of certain ultrastructural features common in the spermiogenesis of taeniid species supports the homogeneity of the spermiological characters within the genus *Taenia* (Table I). Characters common in all five taeniid species are: (1) presence of the Type 3 of spermiogenesis; (2) presence of a proximodistal fusion during spermatozoon differentiation; and (3) absence of the intercentriolar body in the early stage of sperm differentiation. The two other characters, which appear variable are: (1) presence of flagellar rotation inferior to 90° described in *T. parva* by Ndiaye *et al*. (2003a) and observed in the present study on *T. taeniaeformis*; and (2) presence of vestigial striated rootlets in *T. taeniaeformis* but never mentioned in studies of four other taeniid species.

Because information on taeniid spermiogenesis is incomplete, general conclusions regarding relationships or significance of structures should be made with caution. For this reason, new and more complete TEM data on a greater variety of taeniid species are urgently needed not only for establishing more accurate analysis of spermatological characters in the family Taeniidae but also for a better understanding of cestode phylogeny and evolution.

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