

Spermatid and spermatozoon structure in fresh-water nematode *Paractinolaimus microdentatus* (Nematoda: Dorylaimida: Actinolaimidae)

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Summary. The nematode spermatozoa have been studied in many nematode taxa including the order Dorylaimida. However, all information on the dorylamid spermatozoa is based on the representatives of only one genus, *Xiphinema* (Longidoridae). The structure of spermatids and spermatozoa from male gonads of the fresh-water dorylaimid *Paractinolaimus microdentatus* (Actinolaimidae) were studied using transmission electron microscopy (TEM). An unusual spindle-shaped complex of nucleus with mitochondria is characteristic for spermatids and immature spermatozoa. The complex contains the nucleus consisting of intertwining threads of chromatin without a nuclear envelope, a monolayer of mitochondria with dense matrix, and a fibre layer which encloses the mitochondria; in *P. microdentatus* the fibre layer has a distinct annulated structure. The peripheral cytoplasm of the spermatid contains large amount of filamentous matter filling prominent pseudopods. The immature spermatozoa are unpolarised 8-10 µm long and 2 µm wide cells with filopodia covering the cell surface. Each spermatozoon contains the central complex of nucleus and mitochondria, which is surrounded by electron-light cytoplasm containing numerous bundles of filaments and microtubule-like fibres 16-18 nm in diameter. No inclusions resembling membranous organelles specific of other nematode spermatozoa were observed in the male germ cells of *P. microdentatus*. The spermatozoa of the dorylaimids from two families, Longidoridae and Actinolaimidae show close resemblance both in structure and development. The spermatozoa of the dorylaimids studied have very special internal structure, which differentiates them from other nematode spermatozoa and may be considered as the distinct character of the order.

Key words: fibrous bodies, Longidoridae, membranous organelles, MSP, spermatogenesis, ultrastructure, *Xiphinema*.

Spermatozoon morphology and development have potential to be used in taxonomic and phylogenetic analysis as clear and easily comparable morphological characters (Baccetti, 1985; Jamieson *et al.*, 1995). The nematode spermatozoa and spermatogenesis were studied in several species belonging to many orders of the phylum. Nematode spermatozoa represent an aberrant type of male gamete; they are characterised by the absence of an axoneme and an acrosome (Justine & Jamieson, 1999; Justine, 2002). The basic type of nematode spermatozoon is an amoeboid bipolar cell with an anterior pseudopod and posterior main cell body which includes a condensed nucleus lacking a nuclear envelope, mitochondria and so called 'membranous organelles' (MO). These are unique, aberrant organelles characteristic of developing and mature spermatozoa of many nematodes studied.

Usually, MO look like large (0.5-1.0 µm diam.) vesicles with dense content and a system of internal finger-like projections of the outer membrane. The MO are derived from the Golgi bodies and appear as a part of the complexes with paracrystalline fibrous bodies (FB) – another special component of developing spermatozoa. The prism-shaped FB are composed of densely packed parallel fibres consisting of the unique cytoskeleton protein MSP ('major sperm protein'). The complexes of FB and MO ('FB-MO complexes') during late stages of spermatogenesis dissociate into separate FB and MO. After sperm activation inside the female gonoduct, MO join to the spermatozoon plasmalemma and release their content into the uterus lumen. The empty MO, looking like membranous sacs continuous with plasmalemma, are retained as a constant feature of the mature

spermatozoa. Sperm activation is also accompanied by transformation of FB into the MSP-based cytoskeleton of a newly formed pseudopod. The pseudopod and amoeboid movement are well known special characteristics of nematode spermatozoa.

The Nematoda constitutes one of the most diverse and abundant phyla of Metazoa. In the classification based on morphological and molecular data proposed by De Ley and Blaxter (2002), the phylum is subdivided into two classes: Enoplea and Chromadorea. The outlined basic pattern of sperm structure and development is characteristic for representatives of the class Chromadorea, especially for the well studied order Rhabditida (Justine & Jamieson, 1999; Justine, 2002; Yushin & Malakhov, 2004). The class Enoplea comprises two subclasses, Enoplia and Dorylaimia, each with several orders in which spermatozoa are more diverse in structure than in Chromadorea and cannot be clearly defined by a common pattern possibly because many taxa have been studied less extensively (Justine & Jamieson, 1999; Justine, 2002; Yushin & Malakhov, 2004). A unique type of spermatozoa was described also for the order Dorylaimida (subclass Dorylaimia) but using representatives of only one family Longidoridae, namely several plant-parasitic species from the genus *Xiphinema* (Baccetti *et al.*, 1983; Kruger, 1991; Van de Velde *et al.*, 1991; Bleve-Zacheo *et al.* 1993). The spermatozoa of the species studied have no specific membranous organelles and anterior pseudopod, the FB-MO complexes and free FB with paracrystalline structure also have not been detected in spermatogeneous cells (Kruger, 1991). The general structure of the *Xiphinema* spermatozoa is unusual and represents a pattern that separates the dorylaimids from other nematodes (Justine & Jamieson, 1999). However, this large order includes three suborders with 16 families; it seems that the verification of the spermatozoon uniqueness together with its specificity for the whole order remains to be confirmed.

The fresh-water dorylaimid from the family Actinolaimidae, *Paractinolaimus microdentatus* (Thorne, 1939) Meyl, 1957, was chosen for a new study to elucidate all the structural details of the dorylaimid spermatozoon and to perform comparative analysis with other nematode sperm. The ultrastructure of spermatids and spermatozoa from the testes of *P. microdentatus* were studied.

MATERIAL AND METHODS

Paractinolaimus microdentatus nematodes were extracted from the bottom mud collected in the swampy area created by natural spring in the

vicinity of the Marine Biological Station "Vostok" of the Institute of Marine Biology (Vostok Bay, Sea of Japan). Live males were cut in glutaraldehyde fixative to obtain a piece containing both testes and then each specimen was cut into halves. The specimens were fixed for transmission electron microscopy (TEM) at 4°C in 2.5% glutaraldehyde in 0.05 M cacodylate buffer (pH 7.4) with 0.25 mg ml⁻¹ MgCl₂, and were postfixed in 2% osmium tetroxide in the same buffer. Postfixation was followed by *en bloc* staining for 2 h in a 1% solution of uranyl acetate in distilled water and then the specimens were dehydrated in ethanol followed by an isopropanol series and embedded in Spurr resin. Thin sections, cut with a Leica UC6 ultratome and stained with uranyl acetate and lead citrate, were examined with a JEOL JEM 100S and JEOL JEM 2000EX electron microscopes. For low magnification panoramic views of sections the scanning transmission electron microscopy (STEM) was used with Zeiss Libra 120 electron microscope.

The testes of two males were examined for the present paper; the structure of spermatids and spermatozoa was studied. The end of the spermatid stage is marked by detachment of the residual body; sperm from testes and activated sperm from the uteri are termed as 'immature' and 'mature' spermatozoa, respectively (following Shepherd, 1981).

RESULTS

The male reproductive system of *P. microdentatus* comprises two opposite testes each as a simple epithelial tube filled with germ cells. The slightly dilated proximal half of each testis studied was filled with immature spermatozoa of uniform structure; distally the prominent zone of spermatids was observed (Fig. 1A).

The spermatids vary in shape but usually are elongated cells 7-8 µm long × 2-3 µm wide (Fig. 1B, 2A, B). Each spermatid has a characteristic arrangement of cell components: the opaque central complex of nucleus with mitochondria is surrounded by prominent peripheral cytoplasm; the cytoplasm forms large pseudopods devoid of organelles and filled with fibrous matter of a moderate density (Fig 1A, B, 2A, B). The central complex contains the nucleus surrounded by mitochondria (Fig. 2A, B). The nucleus is devoid of a nuclear envelope and consists of intertwining threads of condensed chromatin looking like separate chromatin particles on thin sections. Chromatin threads are embedded into the pale filamentous matter and are surrounded by a continuous monolayer of mitochondria with electron-dense matrix (Fig. 2A, B; 3A). The shape

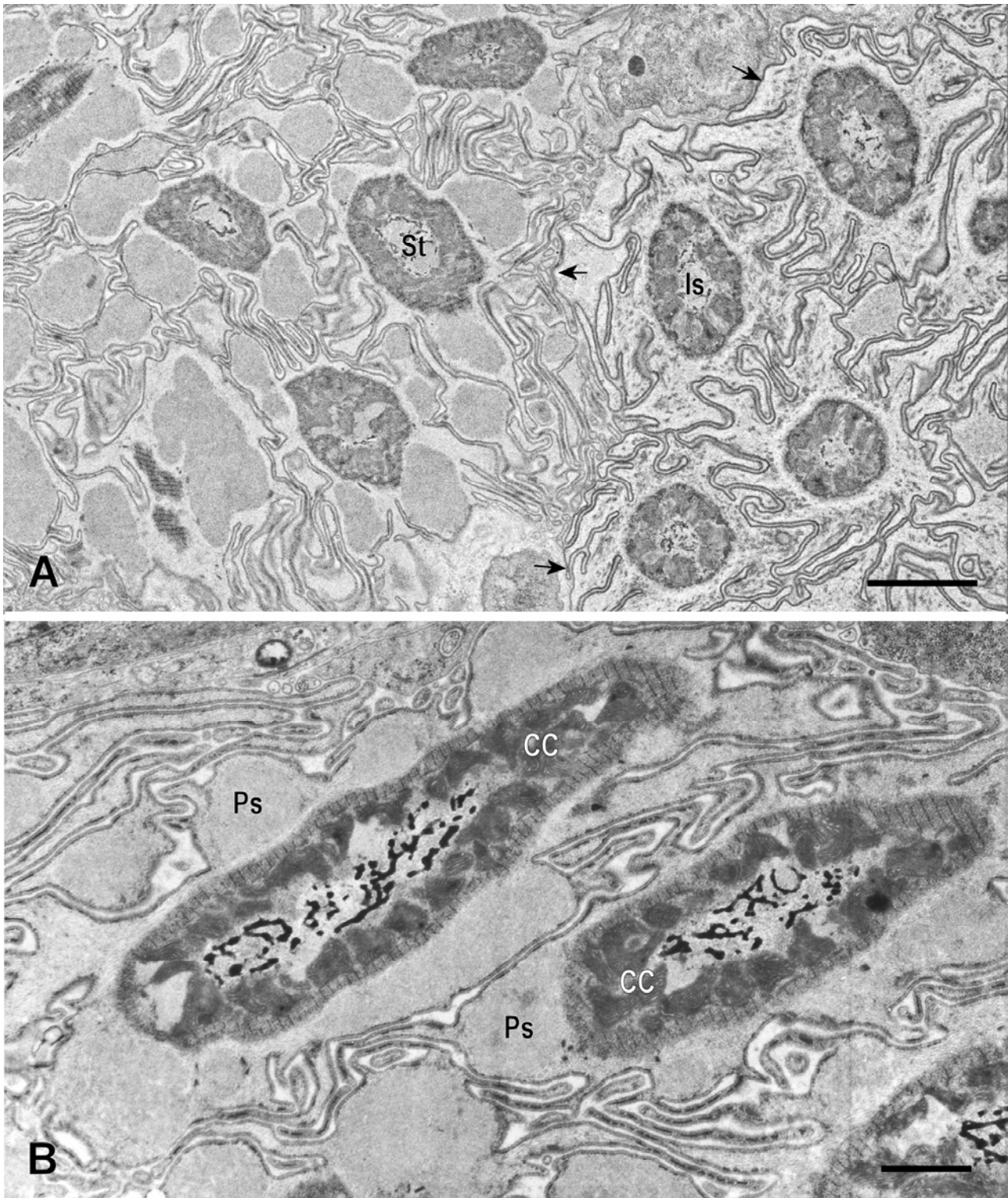


Fig. 1. *Paractinolaimus microdentatus*, spermiogenesis. A: Spermatids (St) and immature spermatozoa (Is) on the longitudinal section through the testis; note the sharp border between two cell clusters (arrows). STEM. B: Two spermatids cut longitudinally. TEM. The central opaque complex of nucleus with mitochondria (CC) is surrounded by pseudopods (Ps). Scale bars: A = 2 μm ; B = 1 μm .

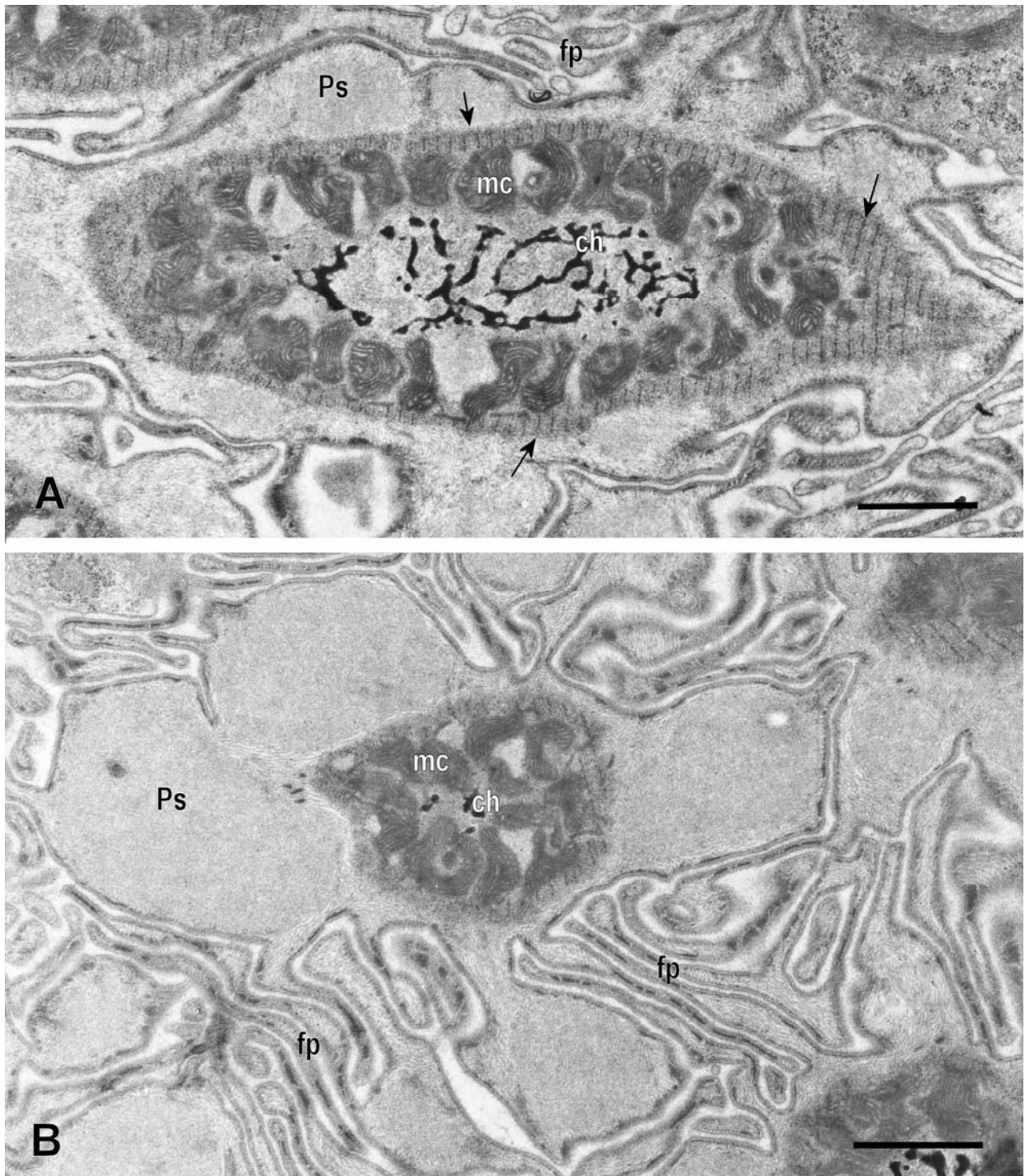


Fig. 2. *Paractinolaimus microdentatus*, spermatids. TEM. A: Longitudinal section through the central complex of the spermatid; the fibrous capsule enclosing the central complex (arrows) has characteristic striations. B: Cross section through the spermatid. Scale bars: 1 μm . Abbreviations: ch = threads of condensed nuclear chromatin; fp = filopodia; mc = mitochondria; Ps = pseudopod.

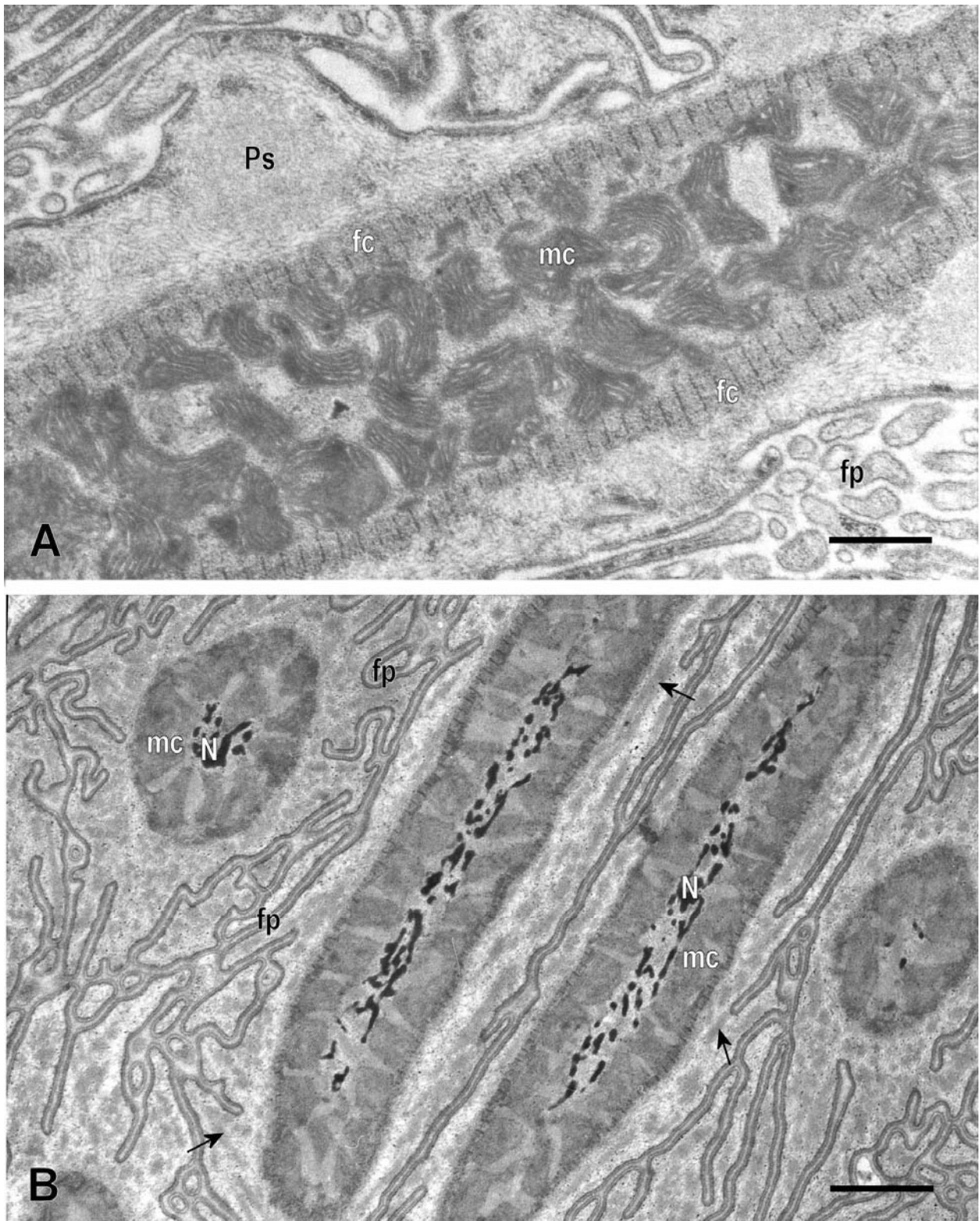


Fig. 3. *Paractinolaimus microdentatus*, spermiogenesis. TEM. A: Tangential section through the spermatid went through the mitochondrion layer and enclosing fibrous capsule (fc); the capsule has characteristic striations. B: Immature spermatozoa, longitudinal and cross sections; the central complex of nucleus (N) with mitochondria (mc) is surrounded by pale cytoplasm and filopodia (fp). Arrows show bundles of fibres. Scale bars: A = 0.5 μm ; B = 1 μm . Abbreviations: fc = fibrous capsule; fp = filopodia; mc = mitochondria; Ps = pseudopod.

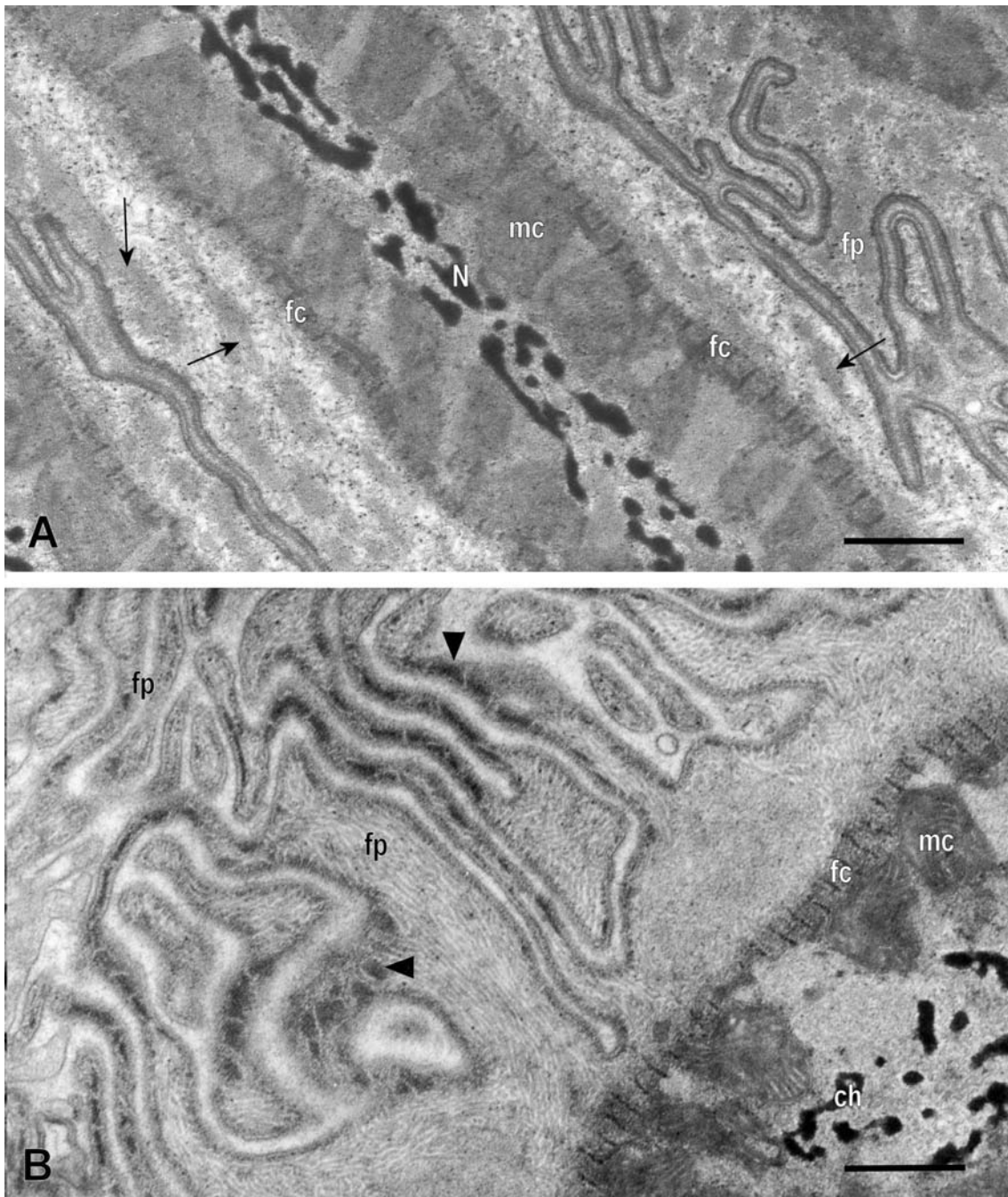


Fig. 4. *Paractinolaimus microdentatus*, immature spermatozoa. TEM. A: Central complex of nucleus (N) with mitochondria (mc); enclosing fibrous capsule (fc) has characteristic striations. Arrows show bundles of fibres. B: The sperm central complex and peripheral cytoplasm; arrowheads show osmiophilic particles under plasmalemma. Note parallel arrays of fibres inside the filopodia. Scale bars: 0.5 μm . Abbreviations: ch = threads of condensed nuclear chromatin; fc = fibrous capsule; fp = filopodia; mc = mitochondria.

of mitochondria is variable, they may curve and branch; the system of lamellar cristae is well developed. The nucleus-mitochondria cluster is enclosed by a 0.12 μm thick capsule of dense fibrous layer of annulate structure (Fig. 2A, 3A). Regular interchange of 0.1 μm wide fibrous rings and 25 nm wide dense rings, like barrel bands,

isolate the central complex from surrounding filamentous cytoplasm. Peripheral cytoplasm is arranged as prominent pseudopods and numerous thin filopodia (Fig. 1B; 2A, B; 3A). The spermatid plasmalemma is underlain by osmiophilic particles.

Each spermatid is connected by cytoplasmic bridge to a residual body accommodating the

synthetic apparatus of the cell (ribosomes, rough endoplasmic reticulum, Golgi bodies). The residual body detaches close to the zone of immature spermatozoa. The border between spermatids and immature spermatozoa is sharp: cluster of spermatids with lobate pseudopodia is followed by tightly packed mass of spermatozoa with more transparent cytoplasm and thick filopodia (Fig. 1A, 3B). The spermatozoa are tightly packed, their filopodia are interdigitated and separated by only a 50 nm wide space (Fig. 5A, B). The spermatozoa vary in outline but in many cases these are spindle-shaped cells 8-10 µm long and 2 µm wide (Fig. 3B). The characteristic complex of nucleus with mitochondria observed in the spermatid also persists in the immature spermatozoa (Fig. 3B, 4A). The mitochondria with dense matrix assume more or less uniform shape and are separated by pale fibrous matter. The fibrous capsule consisting of fibrous and dense rings encloses the central complex (4A, B). The peripheral cytoplasm and filopodia contain randomly orientated bundles of fibres (3B, 4A). The cytoplasm is also filled with parallel arrays of 16-18 nm thick fibres which run longitudinally inside the filopodia (Fig. 4B, 5A); each fibre has a transparent core and looks like a microtubule (Fig. 5B, C). The spermatozoon plasmalemma is underlain by an electron dense 30 nm thick layer separated from the plasmalemma by a narrow light space (Fig. 5A-C). The microtubule-like fibres are in close contact with this layer. Osmiophilic particles occur under the plasmalemma of filopodia (Fig. 4B).

DISCUSSION

The dorylamid spermatozoa were observed with TEM in three plant-parasitic species belonging to the genus *Xiphinema* (Longidoridae). The immature and mature spermatozoa were observed in *X. diversicaudatum* (Baccetti *et al.*, 1983; Bleve-Zacheo *et al.*, 1993); mature spermatozoa were examined in details in *X. theresiae* and *X. pinoides* (Van de Velde *et al.*, 1991); the only description of the dorylamid spermatogenesis from spermatocytes through immature spermatozoa was made on males of *X. theresiae* (Kruger, 1991).

The nucleus and mitochondria in the immature and mature spermatozoa of *Xiphinema* spp. were observed as an opaque cluster surrounded by voluminous peripheral cytoplasm without organelles (Baccetti *et al.*, 1983; Kruger, 1991; Van de Velde *et al.*, 1991). The nucleus represented by clumps of chromatin embedded in transparent matrix is devoid of a nuclear envelope and is protected by a capsule made up of mitochondria enclosed by a fibrous layer (Baccetti *et al.*, 1983; Kruger, 1991; Van de Velde

et al., 1991; Bleve-Zacheo *et al.*, 1993). The peripheral cytoplasm is arranged as prominent pseudopods or filopodia filled with cytoskeletal components; it may contain 'bundles of microtubules' (Baccetti *et al.*, 1983) or packets of dense fibres (Kruger, 1991; Van de Velde *et al.*, 1991).

In general, details of the spermatozoon structure in *P. microdentatus* and *Xiphinema* are the same. The nucleus of *P. microdentatus* spermatozoa is formed of clumps of chromatin isolated from the peripheral cytoplasm by a capsule made up of a tightly packed monolayer of mitochondria and a distinct external fibrous layer. In *P. microdentatus* the external fibrous layer covering the mitochondria has a distinct annulate structure, which possibly reflects a structural function of the capsule analogous to barrel bands. This characteristic central complex is well developed in spermatids and then persists in immature and mature spermatozoa up to fertilisation (Kruger, 1991; Van de Velde *et al.*, 1991; Bleve-Zacheo *et al.*, 1993). It seems that the complex is an original and easily recognisable character of the dorylamid spermatozoa; the less opaque and organised sperm structure where mitochondria encircle the nucleus was observed also in some other taxa from both classes of Nematoda (Justine & Jamieson, 1999; Justine, 2002; Yushin & Coomans, 2005; Yushin, 2008).

Voluminous peripheral cytoplasm as the base for formation of large pseudopods or filopodia also is characteristic for *Xiphinema* and *P. microdentatus* spermatozoa. The pseudopods or thick irregular filopodia provide no distinct polarity to spermatozoa even after activation (Van de Velde *et al.*, 1991; Bleve-Zacheo *et al.*, 1993). The peripheral cytoplasm contains bundles of fibres, which may be randomly or radially distributed.

The presence of bundles of microtubules was reported for immature spermatozoa of *X. diversicaudatus* (Baccetti *et al.*, 1983). The peripheral cytoplasm and filopodia of *P. microdentatus* also contains arrays of fibres closely resembling the cytoskeleton microtubules of Metazoa (Fig 4B; 5A, B), but these microtubule-like fibres have a diameter of 16-18 nm and cannot be identified as classic tubulin-containing microtubules, which have a normal diameter of 24-25 nm (Stephens & Edds, 1976). The microtubules and tubulin are absent in nematode spermatozoa (Justine, 2002), where the prevalent protein MSP is the base for structure and movement function of a pseudopod (Scott, 1996). The fibres morphologically resembling cytoskeleton microtubules (microtubule-like fibres) have been observed in spermatozoa of many nematodes

representing very distant taxa from both classes of the phylum, Enoplea and Chromadorea (Beams & Sekhon, 1972; Shepherd *et al.*, 1973; Shepherd & Clark, 1983; Hess & Poinar, 1989; Poinar & Hess-Poinar, 1993; Cares & Baldwin, 1994, 1995; Takahashi *et al.*, 1994; Endo *et al.*, 1998; Turpeenniemi, 1998; Yushin, 2004, 2007, 2008; Yushin & Zograf, 2004; Zograf *et al.*, 2004). The microtubule-like fibres observed in different species may be very abundant in order to fill the peripheral cytoplasm; they may also underlay the sperm plasmalemma or form a core of filopodia.

The microtubule-like fibres are distinctly less thick (13 to 20 nm, 16-18 in *P. microdentatus*) than the tubulin-containing microtubules (24-25 nm); this was reasonably interpreted by Turpeenniemi (1998) as the evidence of a difference in their protein nature. It is very likely that the microtubule-like fibres of nematode spermatozoa are assembled from the MSP-based filaments. However, there is no direct evidence of the presence of MSP in spermatozoa of the enoplean taxa; all the protein analyses were based on studies of several chromadorean species (Justine & Jamieson, 1999; Justine, 2002).

The only study of the dorylaimid spermatogenesis made on *X. theresiae* contains information on the presence of membranous organelles and fibrous bodies in spermatocytes. The membranous organelles were not detected in spermatids, whilst bundles of fibres persist in immature and mature spermatozoa (Kruger, 1991; Van de Velde *et al.*, 1991). The bundles which were also observed in *P. microdentatus* (Fig. 3B, 4A) may be likened to the usual fibrous bodies containing cytoskeleton proteins, which are used for pseudopod arrangement in many nematodes especially in the rhabditids. Dissolving fibrous body sometimes looks like fibre bundles (Justine, 2002; Zograf *et al.*, 2004; Yushin & Coomans, 2005).

The usual membranous organelles are abundant; they are considered as definitive characters of nematode spermatozoa which persist in spermatids and spermatozoa. However, the MO are undoubtedly absent in spermatids and spermatozoa of *P. microdentatus* and *Xiphinema* spp. This absence prevents the formation of well known FB-MO complexes; the components resembling FB, bundles of filaments, appear only at late stages of sperm development. This aberrant and possibly reduced pattern of sperm development and structure of the dorylaimids resembles many cases of MO absence known for distant taxa of Enoplea and Chromadorea (Justine, 2002; Yushin & Malakhov, 2004).

The spermatozoa of the nematode orders related to Dorylaimida (i.e. taxa united as subclass

Dorylaimia) are diverse and have no unequivocal resemblance with *P. microdentatus* and *Xiphinema* spp. spermatozoa. Possibly the most similar pattern was documented in the mononchid *Mylonchulus nainitalensis* (Mononchida, Mylonchulidae), where the central complex of nucleus with mitochondria is enclosed by a fibre layer; the spermatozoa bear characteristic filopodia (Baccetti *et al.*, 1983). However, data on *M. nainitalensis* are poor and ambiguous; it seems that a full investigation of the mononchid spermatogenesis and sperm structure will be useful for more substantial analysis. The mature spermatozoa of another mononchid, *Mononchus niddensis* (Mononchidae), are small and simple; they have only a nucleus, several mitochondria and a pseudopod (Yushin, 2004). The data available on other dorylaimian orders show very diverse spermatozoa and spermatogeneses, which cannot be fruitfully compared with the dorylaimid spermatozoa (Justine, 2002). However, all these spermatozoa are characterised by the absence of distinct FB and presence of MO, whose structure and development differ greatly from membranous organelles of Chromadorea and Enoplea (Yushin & Malakhov, 2004).

Together with the study of *P. microdentatus*, the data on the dorylaimid spermatozoa are based on the representatives of two genera belonging to two families of the order, Longidoridae and Actinolaimidae. The uniform spermatozoon pattern, differing only in small details, was observed in both families, which recently have been placed into different superfamilies (Hodda, 2007). It may be hypothesised that this original and easily recognizable spermatozoon pattern is a cytological character of the whole order Dorylaimida.

CONCLUSIONS

The spermatozoa of the dorylaimids from two families, Longidoridae and Actinolaimidae show close resemblance both in structure and development. These are unpolarised cells with filopodia covering the cell surface. The central complex of the spermatozoa contains:

- 1 - nucleus consisting of intertwining threads of chromatin without a nuclear envelope;
- 2 - monolayer of mitochondria with dense matrix;
- 3 - specific fibre layer, which encloses the mitochondria. In *P. microdentatus* the fibre layer has an annulated structure.

The voluminous peripheral cytoplasm is devoid of organelles but is filled with components of the cytoskeleton, including bundles of filaments and microtubule-like fibres. No inclusions resembling membranous organelles of other nematode spermatozoa

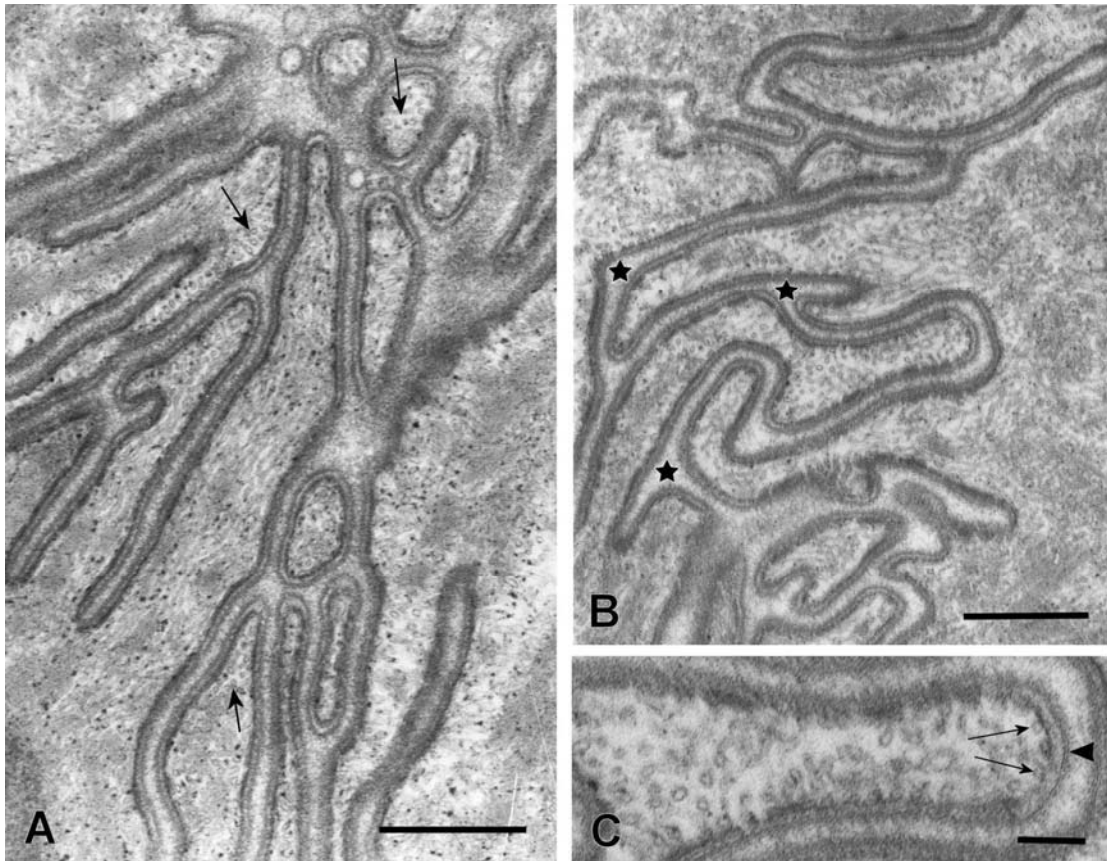


Fig. 5. *Paractinolaimus microdentatus*, immature spermatozoa. TEM. A: Filopodia filled with microtubule-like fibres; note the transverse cut fibres (arrows) and dense layer underlying the sperm plasmalemma. B: Interdigitating filopodia of neighbouring spermatozoa; the microtubule-like fibres fill the peripheral cytoplasm; note dense layer underlying the sperm plasmalemma. Asterisks show narrow space between neighbouring spermatozoa. C: The microtubule-like fibres (arrows) are in close contact with dense layer underlying the sperm plasmalemma (arrowhead). Scale bars: A, B = 0.5 μm ; C = 0.1 μm .

were observed in the male germ cells of *Xiphinema* spp. and *P. microdentatus*. The spermatozoa of the dorylaimids studied have very special internal structure, which differentiates these spermatozoa from others and may be considered as the distinct character of the order.

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REFERENCES

- BACCETTI, B. 1985. Evolution of the sperm cell. In: Metz, C.B. & Monroy, A. (Eds). *Biology of fertilization. Vol. 2. Biology of the sperm*, pp. 3-58. Orlando, FA, USA, Academic Press
- BACCETTI, B., DALLAI, R., GRIMALDI DE ZIO, S. & MARINARI, A. 1983. The evolution of the nematode spermatozoon. *Gamete Research* 8: 309-323.
- BEAMS, H.W. & SEKHON, S.S. 1972. Cytodifferentiation during spermatogenesis in *Rhabditis pellio*. *Journal of Ultrastructure Research* 38: 511-527.
- BLEVE-ZACHEO, T., MELILLO, M.T. & ZACHEO, G. 1993. Ultrastructural study of the nematode *Xiphinema diversicaudatum*: oogenesis and fertilization. *Tissue Cell* 25: 375-388.
- CARES, J.E. & BALDWIN, J.G. 1994. Comparative fine structure of sperm of *Verutus volvingentis* and *Meloidodera floridensis* (Heteroderinae, Nematoda). *Canadian Journal of Zoology* 72: 1481-1491.
- CARES, J.E. & BALDWIN, J.G. 1995. Comparative fine structure of sperm of *Heterodera schachtii* and *Punctodera chaltoensis*, with phylogenetic implications for Heteroderinae (Nemata: Heteroderidae). *Canadian Journal of Zoology* 73: 309-320.
- DE LEY, P. & BLAXTER, M. 2002. Systematic position and phylogeny. In: *The biology of nematodes* (D.L. Lee, Ed.), pp. 1-30. London and New York, Taylor and Francis.
- ENDO, B.Y., ZUNKE, U. & WERGIN, W.P. 1998. Spermatogenesis in the lesion nematode, *Pratylenchus*

- penetrans* (Nemata, Pratylenchidae). *Journal of Helminthological Society of Washington* 65: 227-242.
- HESS, R. & POINAR, G.O., JR. 1989. Sperm development in the nematode *Neoaplectana intermedia* (Steinernematidae: Rhabditida). *Journal of Submicroscopical Cytology and Pathology* 21: 543-555.
- HODDA, M. 2007. Phylum Nematoda. *Zootaxa* 1668: 265-293.
- JAMIESON, B.G.M., AUSTO, J. & JUSTINE, J.-L. (EDS). (1995). *Advances in spermatozoal phylogeny and taxonomy. Mémoires du Muséum National d'Histoire Naturelle* 166: 119-128.
- JUSTINE, J.-L. 2002. Male and female gametes and fertilization. In: *The Biology of Nematodes*. (D.L. Lee. Ed.). pp. 73-119. London and New York, Taylor & Francis.
- JUSTINE, J.-L. & JAMIESON, B.G.M. 1999. Nematoda. In: *Reproductive Biology of Invertebrates*. Vol. IX, part B. (B.G.M. Jamieson. Ed.). pp. 183-266. New Delhi, Oxford & IBH.
- KRUGER, J.C. DE W. 1991. Ultrastructure of sperm development in the plant parasitic nematode *Xiphinema thersiae*. *Journal of Morphology* 210: 163-174.
- POINAR, G.O. JR. & HESS-POINAR, R.T. 1993. The fine structure of *Gastromermis* sp. (Nematoda: Mermithidae) sperm. *Journal of Submicroscopic Cytology and Pathology* 25: 417-431.
- SCOTT, A.L. 1996. Nematode sperm. *Parasitology Today* 12: 425-430.
- SHEPHERD, A.M. 1981. Interpretation of sperm development in nematodes. *Nematologica* 27: 122-125.
- SHEPHERD, A.M. & CLARK, S.A. 1983. Spermatogenesis and sperm structure in some *Meloidogyne* species (Heteroderoidea, Meloidogynidae) and a comparison with those in some cyst nematodes (Heteroderoidea, Heteroderidae). *Revue de Nématologie* 6: 17-32.
- SHEPHERD, A.M., CLARK, S.A. & KEMPTON, A. 1973. Spermatogenesis and sperm ultrastructure in some cyst nematodes, *Heterodera* spp. *Nematologica* 19: 551-560.
- STEPHENS, R. & EDDS, K.Y. 1976. Microtubules: structure, chemistry and function. *Physiological Reviews* 56: 709-777.
- TAKAHASHI, Y., GOTO, C. & KITA K.K. 1994. Ultrastructural study of *Trichinella spiralis* with emphasis on adult male reproductive organs. *Journal of Helminthology* 68: 353-358.
- TURPEENIEMI, T.A. 1998. Ultrastructure of spermatozoa in the nematode *Halalaimus dimorphus* (Nemata: Oxystominidae). *Journal of Nematology* 30: 391-403.
- VAN DE VELDE, M.-C., COOMANS, A., VAN RANST, L., KRUGER, J.C.D. & CLAEYS, M. 1991. Ultrastructure of sperm cells in the female gonoduct of *Xiphinema*. *Tissue and Cell* 23: 881-891.
- YUSHIN, V.V. 2004. New data on sperm structure in mononchid nematodes (Enoplia, Mononchida). *Russian Journal of Nematology* 12: 139-142.
- YUSHIN, V.V. 2007. Spermatogenesis in the free-living marine nematode of the family Linhomoeidae (Nematoda, Monhysterida). *Russian Journal of Nematology* 15: 109-116.
- YUSHIN, V.V. 2008. Sperm dimorphism in the free-living marine nematode *Terschellingia glabricutis* (Nematoda: Monhysterida: Linhomoeidae). *Nematology* 10: 189-205.
- YUSHIN, V.V. & COOMANS, A. 2005. Ultrastructure of sperm development in the free-living marine nematode *Metachromadora itoi* (Chromadoria, Desmodorida). *Acta Zoologica* 86: 255-265.
- YUSHIN, V.V. & MALAKHOV, V.V. 2004. Spermatogenesis and nematode phylogeny. In: *Proceedings of the Fourth International Congress of Nematology, June 2002, Tenerife, Spain. Nematology Monographs and Perspectives, Vol. 2* (R.C. Cook & D.J. Hunt. Eds.). pp. 655-665. Leiden, The Netherlands, Brill Academic Publishers.
- YUSHIN, V.V. & ZOGRAF, J.K. 2004. Ultrastructure of spermatozoa in the free-living marine nematode *Paracanthochus macrodon* (Nematoda, Chromadorida). *Invertebrate Reproduction and Development* 45: 59-67.
- ZOGRAF, J.K., YUSHIN, V.V. & MALAKHOV, V.V. 2004. Ultrastructure of spermatogenesis in the free-living marine nematode *Halichoanolaimus sonorus* (Chromadorida: Selachinematidae). *Nematology* 6: 797-809.

В.В. Юшин. Строение сперматид и сперматозоидов пресноводной нематоды *Paractinolaimus microdentatus* (Nematoda: Dorylaimida: Actinolaimidae).

Резюме. Сведения о сперматозоидах нематод отряда Dorylaimida ограничиваются данными по роду *Xiphinema* (Longidoridae). Изучено строение сперматид и сперматозоидов пресноводной дорилеймиды *Paractinolaimus microdentatus* (Actinolaimidae). В сперматиде и незрелых сперматозоидах описан веретеновидный ядерно-митохондриальный комплекс. Периферическая цитоплазма сперматид содержит волокнистый материал, наполняющий псевдоподии. Незрелые сперматозоиды - неполяризованные клетки размером 8-10 мкм × 2 мкм с центральным ядерно-митохондриальным комплексом и периферической цитоплазмой, содержащей пучки филаментов и микротрубочко-подобные волокна диаметром 16-18 нм.