

Ultrastructural study of the spermatogenesis of the free-living marine nematode *Steineridora borealis* Kito, 1977 (Chromadorida, Chromadoridae)

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Summary. Spermatogenesis in the free-living marine nematode, *Steineridora borealis* Kito, 1977, from the Sea of Japan has been studied with electron microscopy. Early spermatocytes are polygonal cells that have a large nucleus with nucleolus. The cytoplasm of early spermatocytes is filled with mitochondria, ribosomes, cisternae of rough endoplasmic reticulum (ER) and Golgi bodies. In late spermatocytes, a myelin-like structure appears surrounded by the Golgi bodies, the rest of the cytoplasm is filled with free ribosomes, cisternae of ER, mitochondria and osmiophilic inclusions. One large residual body joins a few main cell bodies (MCB) of spermatids. The latter are conical and comprise chromatin devoid of the nuclear envelope, fibrous body and mitochondria. Spermatozoa are similar to the MCB of spermatids. The spermatozoa of *S. borealis* exhibit the main ultrastructural features characteristic of many nematode spermatozoa: absence of an axoneme, an acrosome, and a nuclear envelope. However, *S. borealis* and other chromadorid nematodes lack aberrant membranous organelles, typical for nematode sperm cells, at any stage of spermatogenesis. In this respect, representatives of the order Chromadorida differ significantly from many other nematodes, except Desmodorida and Desmoscolecida.

Key words: chromadorids, electron microscopy, fibrous bodies, MSP, membranous organelles, ultrastructure.

The ultrastructure of nematode spermatozoa has already been studied for more than sixty years. The general concept of the spermatozoa structure, development and evolution has been established (Foor, 1983; Bird & Bird, 1991; Justine, 2002; Yushin & Malakhov, 2014). Aberrant spermatozoa of nematodes are characterised by the absence of an acrosome, an axoneme and a nuclear envelope (Foor, 1983; Justine, 2002). A typical spermatozoon of nematodes is a bipolar cell with an anterior pseudopodium and posterior main cell body (MCB). The latter contains a condensed nucleus, mitochondria and membranous organelles (MO) – unique organelles found exclusively in nematode spermatozoa (Justine & Jamieson, 1999; Justine, 2002). It has been shown for most of nematodes that MO derived from Golgi bodies and form complexes with fibrous bodies (FB) – another aberrant component of nematode sperm cells. These MO-FB complexes dissociate into separate MO and FB during spermiogenesis. MO join to the cell membrane of mature spermatozoa, while FB

transform into pseudopodium cytoskeleton (Justine & Jamieson, 1999; Justine, 2002; Yushin & Malakhov, 2014).

Such type of spermatogenesis was described for most of the nematode studied. However, in some free-living marine nematodes from the order Chromadorida (Chromadoria) either both MO and FB were not found during spermatogenesis (Yushin & Coomans, 2000; Yushin & Zograf, 2004), or modified FB without MO were found (Yushin & Zograf, 2002; Zograf & Yushin, 2004; Zograf *et al.*, 2004). Such deviation in gametes' formation of chromadorids may be interesting for nematologists and those who are interested in sperm evolution of multicellular organisms.

To date, spermatogenesis of three representatives of the family Chromadoridae has been studied. Two of them belong to the subfamily Hypodontolaiminae (*Neochromadora poecilosoma* and *Panduripharynx pacifica*) (Yushin & Zograf, 2002; Yushin & Coomans, 2000) and one to the subfamily Euchromadorinae (*Euchromadora robusta*) (Yushin

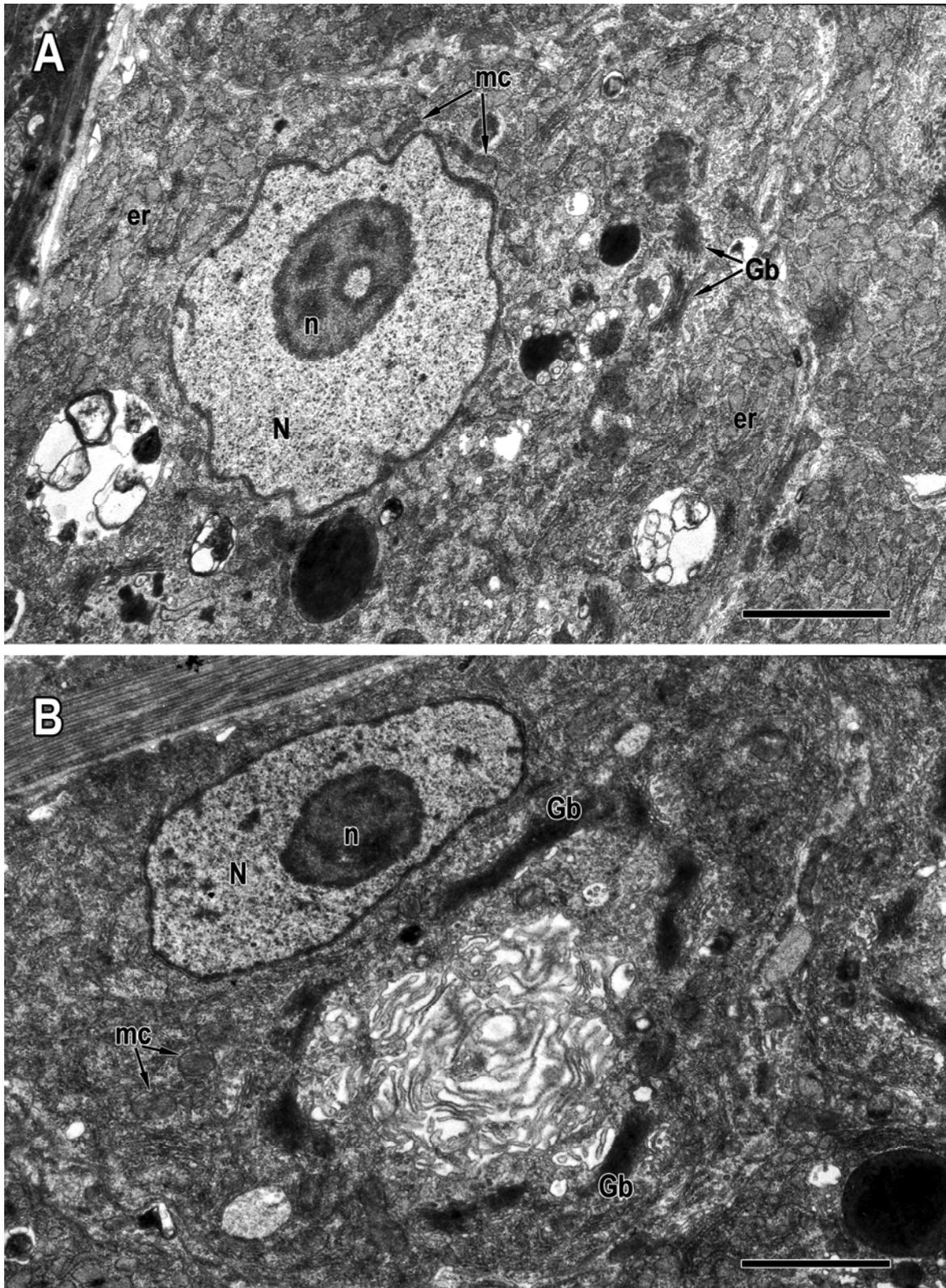


Fig. 1. Spermatocytes of *Steineridora borealis* (TEM). A. The cytoplasm of early spermatocytes is filled with mitochondria (mc) and cisterns of rough endoplasmic reticulum (er) and Golgi bodies (Gb). N – nucleus; n – nucleolus. B. Late spermatocyte. Area of the myelin-like cytoplasm surrounded with Golgi bodies (Gb) appears under the nucleus (N) with nucleolus (n). mc – mitochondria. Scale bars: 2 μ m.

& Coomans, 2000). In the subfamily Hypodontolaiminae, two patterns of spermatogenesis were found: *i*) the absence of both MO and FB at all stages of sperm development; *ii*) the absence of MO and formation of free FB during sperm development. For the present work, we have chosen another representative of the subfamily Euchromadorinae to find out which pattern is represented in this subfamily. The free-living marine nematode, *Steineridora borealis*, was chosen for this study.

MATERIAL AND METHODS

Adult males of *S. borealis* were collected from silty sand at 1 m depth at the Vostok Marine Biological Station of A.V. Zhirmunsky National Scientific Center of Marine Biology (Vostok Bay, Sea of Japan, Russia). Live males were cut into pieces, each of which contained a whole testis.

The specimens were fixed for transmission electron microscopy (TEM) at 4°C in 2.5% glutaraldehyde in 0.05 M cacodylate buffer containing 21 mg ml⁻¹ NaCl and then postfixed in 2% osmium tetroxide in the same buffer containing 23 mg ml⁻¹ NaCl. Postfixation was followed by *en bloc* staining for 1 h in 1% solution of uranyl acetate in distilled water and then the specimens were dehydrated in ethanol and acetone series and embedded in Spurr resin. Thin sections were cut with a Reichert Ultracut E ultratome, stained with 1% uranyl acetate and lead citrate, and then examined with a JEOL JEM 100B or JEOL JEM 100S electron microscope. The testes of five specimens were observed.

RESULTS

Development of spermatozoa from spermatogonia to immature spermatozoa may be traced on the longitudinal section of testis of *Steineridora borealis*. Spermatogonia are situated in the distal part of the testis. They are small polygonal undifferentiated cells with large nucleus.

Early spermatocytes are polygonal cells 12 µm in diam. (Fig. 1A). The nuclei (4-5 µm in diam.) of spermatocytes contain diffused chromatin and large nucleoli, their nuclear envelopes penetrated with numerous pores. The cytoplasm of spermatocytes shows high metabolic activity, and is filled with numerous ribosomes, cisterns of rough endoplasmic reticulum (ER) and Golgi bodies, mitochondria, osmiophilic inclusions and lipid drops.

During spermatocytes ripening, their nuclei elongate and chromatin becomes more condensed.

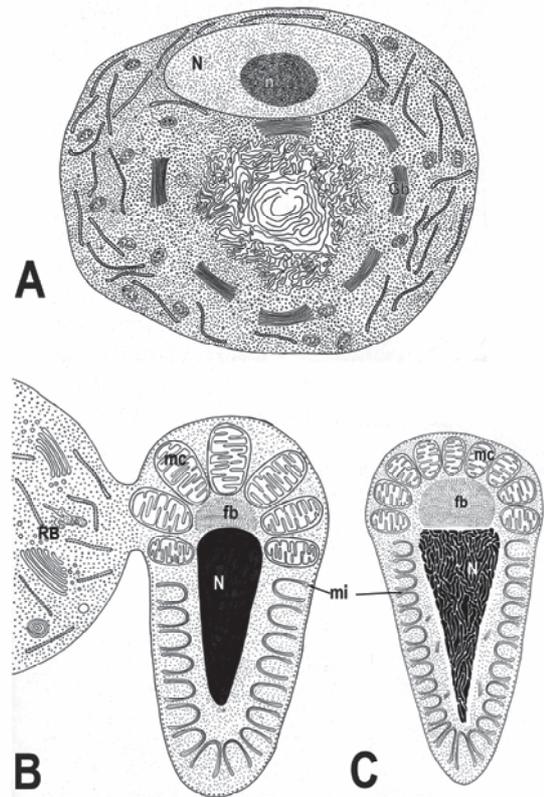


Fig. 2. Schematic representation of the spermatogenesis of *Steineridora borealis*. A. Late spermatocyte. Nucleus (N) with nucleolus (n) is shifted to the cell periphery in the late spermatocyte. Just under the nucleus, the area of the myelin-like cytoplasm surrounded with Golgi bodies (Gb) is located. B. Spermatid. The main cell body of the spermatid is connected with the residual body (RB) by the cytoplasmic bridge. There is conical nucleus (N) in the main cell body of the spermatid. Single fibrous body (fb) is surrounded with mitochondria (mc). The membrane of the cell forms deep invaginations (mi). C. Immature spermatozoa. Nucleus (N) is formed with particles of tightly condensed chromatin. Fibrous body (fb) is surrounded with mitochondria (mc).

Areas of the myelin-like cytoplasm surrounded with Golgi bodies appear (Figs 1B & 2A), while the rest of the cytoplasm is filled with free ribosomes, cisterns of ER, mitochondria and osmiophilic inclusions.

We did not observe the meiotic process, which may be because of the speed of this process. So, spermatocytes were followed by spermatids. The latter are segregated into MCB and residual bodies. One residual body unites a few MCB that are connected to the residual body by cytoplasmic bridges.

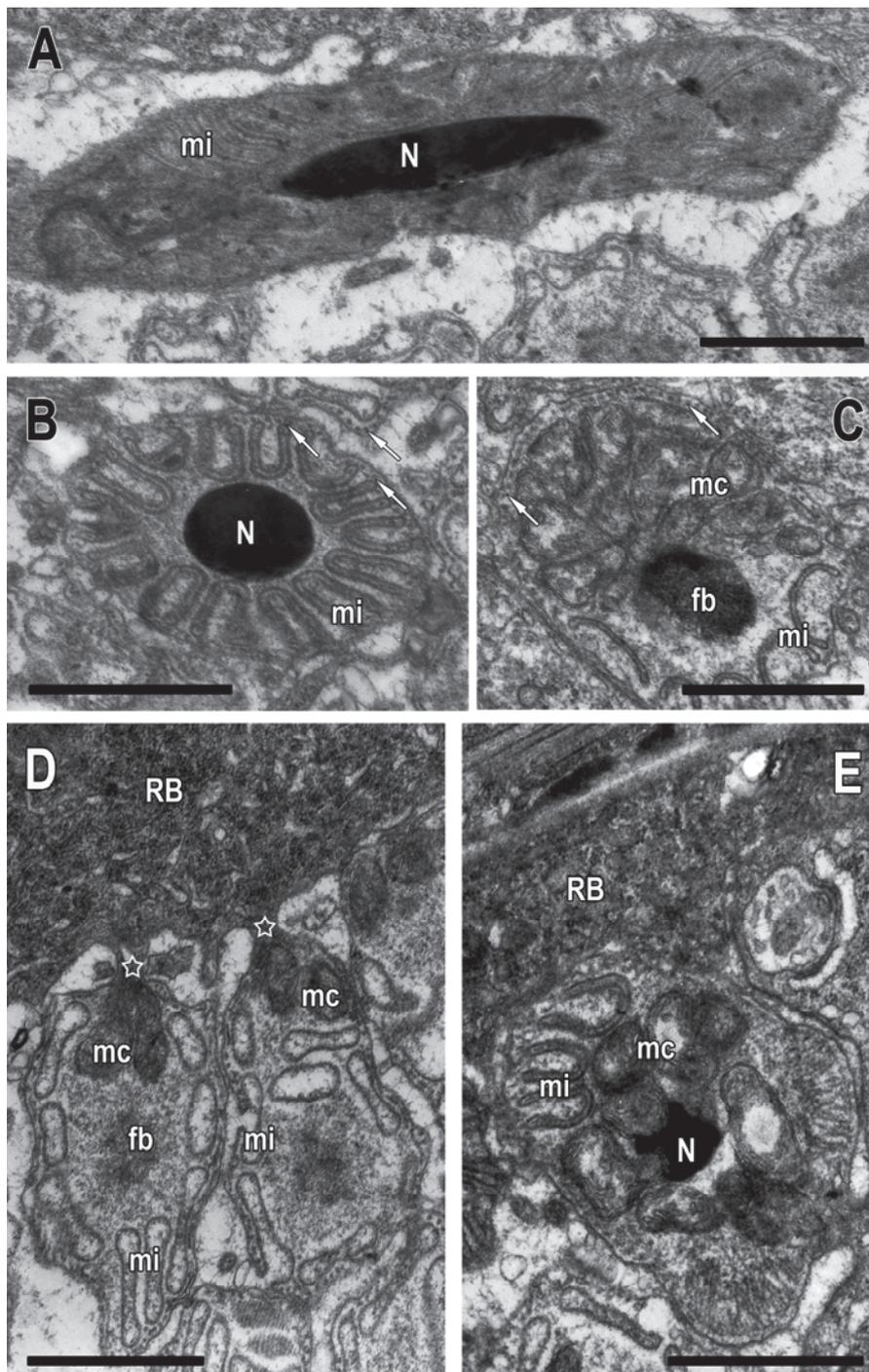


Fig. 3. Spermatids of *Steineridora borealis* (TEM). A. Longitudinal section through the main cell body of the spermatid. The nucleus (N) with tightly condensed chromatin is devoid of nuclear envelope. The outer membrane forms horseshoe-shaped invaginations (mi). B. Cross section through the middle part of the main cell body of the spermatid. A layer of microtubule-like filaments (arrows) underlays cell membrane. mi – membrane invaginations, N – nucleus. C. Cross section through the posterior part of the main cell body of the spermatid. Fibrous body (fb) is surrounded with mitochondria (mc). A layer of microtubule-like fibers (arrows) underlays the cell membrane. mi – membrane invaginations. D. Two main cell bodies of spermatid connected to the residual body (RB) through the cytoplasmic bridge (asterisk). fb – fibrous bodies, mc – mitochondria, mi – membrane invaginations. E. Main cell body of spermatid with nucleus (N) connected to the residual body (RB). mc – mitochondria, mi – membrane invaginations. Scale bars: 1 μ m.

MCB of spermatid is conical (Figs 2B & 3A), its length is 6–8 μm and diameter at the apical part is 1.5–2 μm . The conical nucleus ($2 \times 0.5 \mu\text{m}$) is devoid of nuclear envelope and is formed with strongly condensed chromatin. The cytoplasm of the spermatid MCB is electron transparent and filled with fibrous material. The sperm plasma membrane is arranged into deep infoldings that are open to the exterior by ‘pores’ (Fig. 3D). The cisterns look horseshoe-shaped on the sections; however, reconstruction of the several sections revealed that cisterns are cup-shaped (Figs 2B & 3B). Microtubule-like fibres (MLF) (16–18 nm thick) form a monolayer under the cell membrane of the MCB (Figs 2B & 3B, C).

In its expanded part, spermatid MCB connect with the residual body by cytoplasmic bridges where a few mitochondria are situated (Figs 2B & 3D, E). There is a bundle of fibrous material (0.6 μm in diam.) next to the mitochondria (Figs 2B & 3C, D). This structure is similar to FB described for other chromadorid spermatozoa. The large residual body of spermatid is filled with ribosomes, cisterns of ER and Golgi bodies (Figs 2B & 3D, E).

The immature spermatozoa are similar in their shape and size to spermatid MCB. The chromatin is segregated into numerous electron dense vermiform particles (Figs 2C & 4). These particles are oriented along the longitudinal axis of the nucleus (Figs 2C & 4A). The nucleus is surrounded with electron transparent cytoplasm filled with cup-shaped cisterns (Figs 2C & 4B). A single large FB (1.5 \times 0.9 μm) is situated above the broadened part of the nucleus (Figs 2C & 4A). The FB surrounded by large mitochondria (Figs 2C & 4C). Smaller FB scattered in the cytoplasm may be also found.

In general, the inner structure of immature spermatozoa is clearly polarised: there is a large FB at the apex of conical nucleus covered with mitochondria and rows of membranous cisterns are situated along the nucleus. A layer of MLF 18 nm thick located under the cell membrane. The distance between adjacent MLF is 50 nm (Fig. 3C).

DISCUSSION

The ultrastructure of the male germ cells of a representative of the order Chromadorida, *S. borealis*, has been investigated. The cells represent the typical pattern of nematode spermatozoa and are devoid of an acrosome, an axoneme and a nuclear envelope. In contrast with most nematodes studied, spermatozoa of *S. borealis* are also devoid of aberrant organelles, membranous organelles (MO), which are unique for most rhabditids.

The absence of typical MO is evident for *S. borealis* spermatozoa. Such a situation is present in a number of species of the subclass Chromadoria. Total absence of MO was described in Rhabditida (Oxyuridomorpha and Haplolaimina *sensu* Siddiqi (2000)) and free-living marine nematodes from the orders Chromadorida, Desmodorida and Desmoscolecida (Shepherd *et al.*, 1973; Goldstein & Triantaphyllou, 1980; Shepherd & Clark, 1983; Cares & Baldwin, 1995; Endo *et al.*, 1998; Yushin & Zograf, 2002; Zograf & Yushin, 2004; Zograf *et al.*, 2004, 2008, 2016; Yushin & Coomans, 2005). In some cases of simplification, complete reduction of aberrant sperm components have also been observed (Justine, 2002; Yushin & Malakhov, 2004, 2014).

The fibrous body (FB) is known to accumulate the specific nematode sperm protein (MSP) that is synthesised in the rough ER and forms the bulk of the pseudopod cytoskeleton of the mature spermatozoon (Scott, 1996; Justine, 2002). In many rhabditids, the FB appears first as the integral part of the FB-MO complexes in the spermatocyte cytoplasm (Justine, 2002). In some tylenchomorphs and some chromadorids, FB are free of MO but they also appear in the spermatocytes (Goldstein & Triantaphyllou, 1980; Shepherd & Clark, 1983; Cares & Baldwin, 1995; Yushin & Zograf, 2002; Zograf & Yushin, 2004).

Spermatocytes of *S. borealis* have no FB, although spermatocytes have a large nucleus with nucleolus and a voluminous cytoplasm in which the cell synthetic apparatus is well developed. The late FB formation in spermatids has also been reported in the spermatogenesis of some Enoplida, Chromadorida, Desmodorida and Tylenchomorpha (Shepherd *et al.*, 1973; Cares & Baldwin, 1994, 1995; Yushin & Malakhov, 1998; Justine & Jamieson, 1999; Zograf *et al.*, 2004; Yushin & Coomans, 2005). The late FB formation shows the capability of a haploid cell (spermatid) to perform synthesis as a result of activities of the residual body (Yushin & Coomans, 2005). It should be pointed out that all the cases of late FB appearance are known for spermatogenesis with FB that never associate with MO (Shepherd *et al.*, 1973; Cares & Baldwin, 1994, 1995; Yushin & Malakhov, 1998, 2004; Justine & Jamieson, 1999; Zograf *et al.*, 2004; Yushin & Coomans, 2005).

The microtubule-like fibres (MLF) of *S. borealis* are especially obvious at the submembrane position. Very similar fibres have been found in the spermatozoa of many other nematodes from a variety of diverse orders: Tylenchomorpha, Rhabditida, Strongylida, Enoplida, Mermithida, Trichurida, Desmoscolecida, Desmodorida, Dorylaimida (Zograf *et al.*, 2016; Yushin *et al.*, 2018).

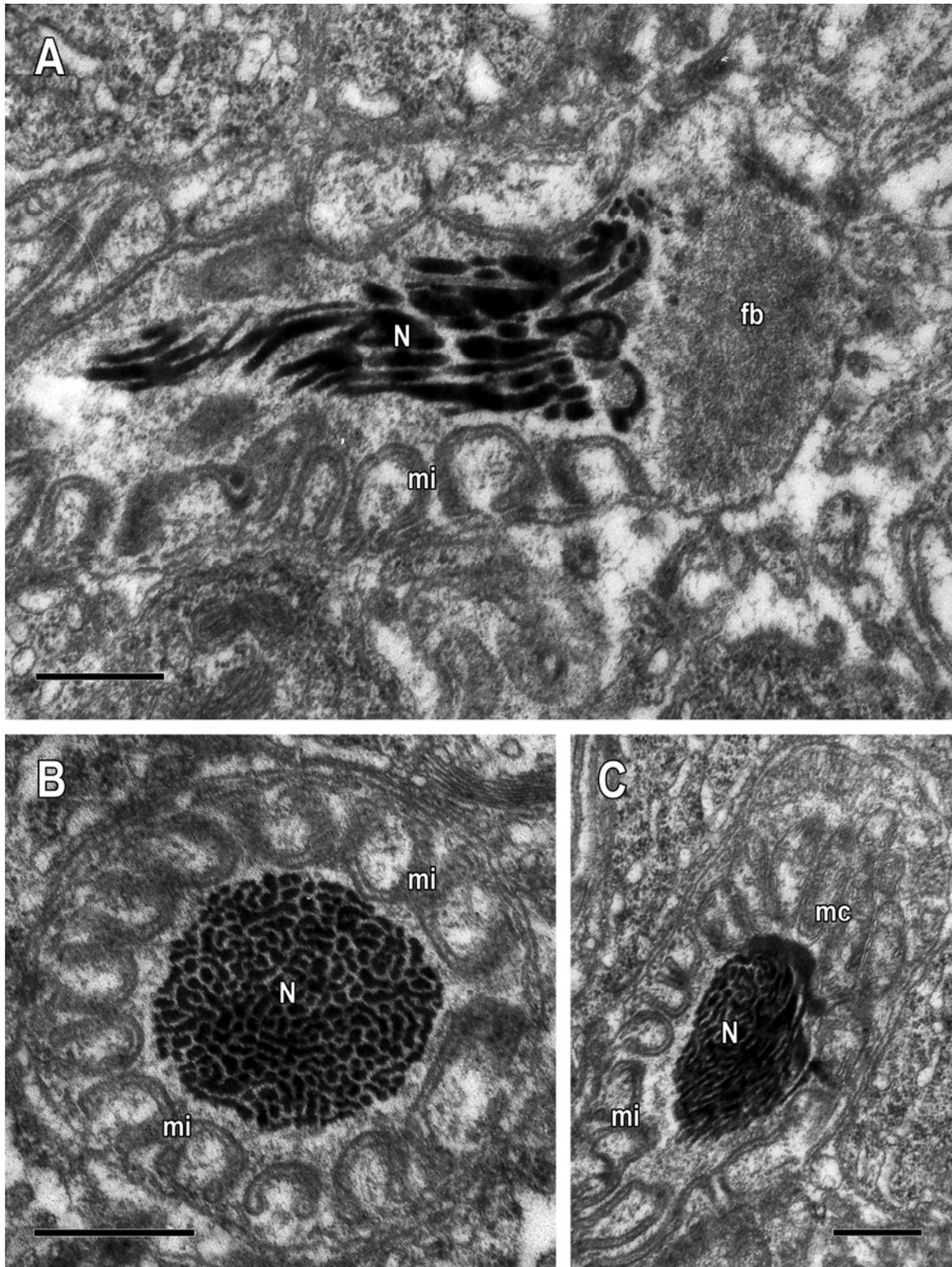


Fig. 4. Immature spermatozoa of *Steineridora borealis* (TEM). A. Longitudinal section through the spermatozoon. Conical nucleus (N) is surrounded with membrane invaginations (mi). Fibrous body (fb) is located above the nucleus. B. Cross section of the spermatozoon through the middle part. Nucleus (N) is round in the cross section. The surface of the cell forms numerous membrane invaginations (mi). C. Cross section of the spermatozoon at the level of mitochondria (mc). mi – membrane invaginations, N – nucleus. Scale bars: 0.5 μm .

Turpeeniemi (1998) pointed out that the diameter of 'microtubules' in sperm cells of *Halalaimus dimorphus* is less than diameter of tubulin containing microtubules (13-18 nm vs 24-25 nm). The author made a supposition that nematode 'microtubules' do not contain tubulin (Turpeeniemi, 1998). It has also been shown that tubulin is only found in nematode spermatozoa in the centrioles (Justine, 2002). So, the MLF may contain major sperm protein that is found in the spermatozoa of nematodes and is capable of forming tubular structures (Justine, 2002; Yushin *et al.*, 2016). Single MSP filaments 2 nm thick may form fibre complexes resembling MLF. However, a final conclusion of the composition of MLF will be valid only when definitive immunocytochemical analysis has been carried out.

The deep infoldings of the membrane of germ cells of *S. borealis* resemble to some extent the MO of many other nematodes but cannot be interpreted as homologous with true MO. Typical MO appears in the spermatocytes as complexes with FB. After dissociation into free FB and MO, the latter adjoins to the cell membrane only after sperm activation in the uterus. The membrane infoldings in *S. borealis* have a distinctly divergent structure. They are found in germ cells and never form complexes with FB, and they are open to the exterior *via* pores in spermatids and immature spermatozoa. Similar structures were described for immature spermatozoa of *P. pacifica* (Yushin & Coomans, 2000).

To date, two patterns of sperm development have been described for representatives of the order Chromadorida: *i*) spermatogenesis with formation FB, while MO are not found at any stage of spermatogenesis (Justine, 2002; Yushin & Zograf, 2002; Yushin, 2003; Zograf & Yushin, 2004; Zograf *et al.*, 2004; present study); *ii*) spermatozoa devoid of aberrant organelles at all stages of development (Yushin & Coomans, 2000; Yushin & Zograf, 2004). However, the presence of membrane infoldings in two species of Chromadoridae (*S. borealis* and *P. pacifica*), belonging to two different subfamilies, gives a reason to highlight the third pattern of spermatogenesis in this group: spermatozoa with free fibrous bodies and membrane cisterns in cell cytoplasm.

Thus, species of chromadorids studied represent two different subfamilies of the family Chromadoridae – Euchromadorinae (*E. robusta* and *S. borealis*) and Hypodontholaiminae (*N. poecilosoma* and *P. pacifica*). Three proposed patterns of spermatogenesis have been found in both subfamilies and could be considered as characteristic of the family.

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Ю.К. Зограф. Ультраструктурное исследование сперматогенеза свободноживущей морской нематоды *Steineridora borealis* Kito, 1977 (Chromadorida, Chromadoridae).

Резюме. Сперматогенез свободноживущей морской нематоды *Steineridora borealis* Kito, 1977 из Японского моря был изучен с помощью электронной микроскопии. Ранние сперматоциты – это полигональные клетки с большим ядром и ядрышком. Цитоплазма ранних сперматоцитов заполнена митохондриями, рибосомами, цистернами эндоплазматического ретикулума и аппарата Гольджи. В поздних сперматоцитах появляются миелоноподобные структуры, которые окружены аппаратом Гольджи. Остальная часть цитоплазмы заполнена рибосомами, цистернами эндоплазматического ретикулума, митохондриями и осмиофильными гранулами. Одно большое резидуальное тело объединяет несколько главных тел сперматид. Последние содержат коническое ядро без ядерной оболочки, фиброзные тела и митохондрии, в то время как весь синтетический аппарат клетки вынесен в резидуальное тело. Сперматозоиды из семенника *S. borealis* сходны с главным телом клетки сперматиды. В целом сперматозоиды *S. borealis* характеризуются основными признаками сперматозоидов нематод: отсутствием акросомы, аксонемы и ядерной оболочки. В то же время сперматозоиды *S. borealis*, как и других изученных к настоящему времени хроматорид, лишены мембранных органелл. Такой паттерн сперматогенеза отличает хроматорид от других изученных нематод, за исключением десмодорид и десмосколецид.