# Spermatogenesis of deep-sea nematode *Paramesacanthion* sp. (Enoplida: Thoracostomopsidae)

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**Summary.** The ultrastructure of spermatocytes, spermatids, immature and mature spermatozoa of the deep-sea nematode *Paramesacanthion* sp. was studied using a transmission electron microscope. Spermatocytes are large polygonal cells with a central nucleus with a nuclear envelope. The cytoplasm of cells is filled with typical structures, such as the endoplasmic reticulum, Golgi apparatus and mitochondria, as well as special structures, membranous organelles (MO). In spermatids, cell polarisation occurs: the nucleus, surrounded by mitochondria and MO, occupies the central part of the cell, while all elements of the synthetic apparatus are displaced to the periphery of the cell. Immature sperm are round cells with a central nucleus with a nuclear envelope. The sperm cytoplasm is filled with mitochondria and MO. Mature sperm are bipolar amoeboid cells with an anterior pseudopodium and a posterior main cell body containing a nucleus with a nuclear envelope, mitochondria and free MO not attached to the cell membrane. In general, spermatozoa of *Paramesacanthion* sp. are characterised by the main characteristics of enoplid spermatozoa: the presence of a nuclear envelope and MO. In this case, fibrous bodies, characteristic of most nematode spermatozoa, do not appear at any stage of spermatogenesis.

**Key words:** gametogenesis, spermatogenesis, spermatozoa, ultrastructure, nuclear envelope, membranous organelles.

The deep-sea environments with its extreme conditions always catch the attention of scientists. One of the actual questions is the adaptation of organism to these conditions, such as high pressure, shortage of organic matters and its seasonal fluxes (Eckelbarger & Watling, 1995). Although spermatozoa of nematodes are studied on a large number of species (Justine & Jamieson, 1999; Yushin & Malakhov, 2004), spermatogenesis of deep-sea nematodes has never been studied previously. Peculiarities of the development of germ cells of deep-sea nematodes may lift the curtain on the mystery of adaptation nematodes to the life at great depths.

Nematode spermatozoa are aberrant cells characterised by the absence of an acrosome, an axoneme and a nuclear envelope (Foor, 1983; Justine, 2002). In general, spermatozoon of nematodes is described as a bipolar cell with anterior pseudopodium and posterior main cell body. The latter contains nucleus, mitochondria and membranous organelles (MO). Membranous organelles are the unique structures found exclusively in nematode spermatozoa (Justine & Jamieson, 1999; Yushin & Malakhov, 2014). Membranous organelles are derived from Golgi bodies and form complexes with fibrous bodies (FB). These MO-FB complexes dissociate into separate MO and FB during spermiogenesis. MO join to the cell membrane of mature spermatozoa, while FB transform to pseudopodium cytoskeleton (Justine & Jamieson, 1999; Justine, 2002; Yushin & Malakhov, 2014).

Such type of spermatogenesis was described for most of nematodes studied. However, spermatozoa of representatives of order Enoplida have some differences. The enoplid spermatozoa retain a nuclear envelope (Baccetti *et al.*, 1983; Yushin & Malakhov, 1994; 1998; 1999; Yushin *et al.*, 2002; Yushin, 2003; Afanasiev-Grigoriev & Yushin, 2006; 2009; Yushin & Gliznutsa, 2021; Zograf *et al.*, 2022). It has also been shown that the MO and FB develop separately without formation of MO-FB complexes (Yushin & Malakhov, 1998; Yushin

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*et al.*, 2002). Spermatozoa of the only representative of the family Thoracostomopsidae, *Mesacanthion hirsutum*, were studied to date (Baccetti *et al.*, 1983). Only spermatozoon from the uterus was studied, so the information of spermatogenesis of this family is absent. The knowledge on the cytological differences may be useful for analyses of thoracostomopsid phylogeny.

The present work presents data on the ultrastructure of spermatogenesis and sperm in males and females of *Paramesacanthion* sp. (Enoplida: Thoracostomopsidae) to elucidate a new aspect of comparative cytology of thoracostomopsid nematodes.

## MATERIAL AND METHODS

Sediment sample was collected in the Sea of Japan using the remotely operated vehicle (ROV) Comanche-18 during cruise 93 of the R/V Akademik M.A. Lavrentyev from May to July 2021 (2051 m depth; 42.27° N, 131.373° E). On deck, the sediment was carefully sieved through 1000- and 500 μm mesh sizes and sorted using stereomicroscopes. The nematodes were identified as a new species, morphologically related to genus *Paramesacanthion* Wieser, 1953. Previously representatives of the genus *Paramesacanthion* have never been described from the Sea of Japan. The morphological and molecular characteristic of this species are currently under preparation.

Five males and five females were cut at the head and tail region to improve impregnation and 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 21 mg $ml^{-1}$ NaCl. Post-fixation 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 (Spurr, Sigma). The series of thin sections cut with a Leica Ultracut UC6 using glass knives were stained with lead citrate and then examined with a Zeiss SIGMA 300VP electron microscope.

## RESULTS

Spermatogonia are polygonal cells 14-18 μm in diam. The huge spherical nucleus (6-8 μm in diam.) with nucleolus occupies most of the cell (Fig. 1A). The cytoplasm is filled with free ribosomes, cisterns of rough endoplasmatic reticulum and Golgi bodies (Fig. 1B). Spermatocytes are polygonal cells (Fig. 1C). As a result of the activity of the Golgi bodies, numerous membranous structures (0.6-1.2 μm in diam.) appear. These structures are characterised by the distinct polarisation of the osmiphilic part and the part consisting of the membranous system (Fig. 1D), and are similar to membranous organelles (MO) described for other nematodes.

We did not observe the meiotic process, which may be because of the speed of this process. Spermatocytes were followed by spermatids. Early spermatids are polygonal cells 9-13 μm in diam. (Fig. 2A). The central part of the cell is occupied by the nucleus with nuclear envelope. MO and mitochondria are concentrated around the nucleus, while the synthetic apparatus, including free ribosomes, cisterns of endoplasmatic reticulum and Golgi bodies, is shifted to the periphery of the cell (Fig. 2A). At this stage MO sink into the nuclear envelope forming pits in it (Fig. 2B).

In the late spermatids segregation of cytoplasm continues (Fig. 2C). At this stage the centrally situated main cell body is separated from the residual body by the layer of condensed cytoplasm (Fig. 2D). As the result of such segregation, the main cell body of the spermatid contains the nucleus with dispersed chromatin surrounded by the nuclear envelope, osmiophilic MO and mitochondria. The residual body evenly surrounds the main cell body and contains free ribosomes, cisterns of rough endoplasmatic reticulum and Golgi bodies.

Immature spermatozoa found in seminal vesicle are rounded cells with a centrally situated nucleus (Fig. 3A). Dispersed chromatin is surrounded by a nuclear envelope that forms irregular protrusions (Fig. 3B). The cytoplasm of immature spermatozoa is filled with numerous electron dense MO and mitochondria (Fig. 3B). Immature spermatozoa found in the most terminal part of the seminal vesicle undergo partial activation: a newly forming pseudopodium is situated at the edge of the cell and regions with the flaky material are found in the cytoplasm (Fig. 3C).

Mature spermatozoa are found in the uterus of females. Mature spermatozoon is a bipolar cell with anterior pseudopodia and posterior main cell body (Fig. 4A). The main cell body of the spermatozoon is *ca* 10 μm in diam. The nucleus with dispersed chromatin has a nuclear envelope. The cytoplasm of the main cell body is filled with MO of different morphology. Roundish electron dense granules are characterised by the light central part (Fig. 4A, D). Some MO are elongate, bent and form coiled lamellar structures (Fig. 4B, D). MO do not contact with plasmalemma. The rest of the cytoplasm is filled with flaky material similar to that found in immature

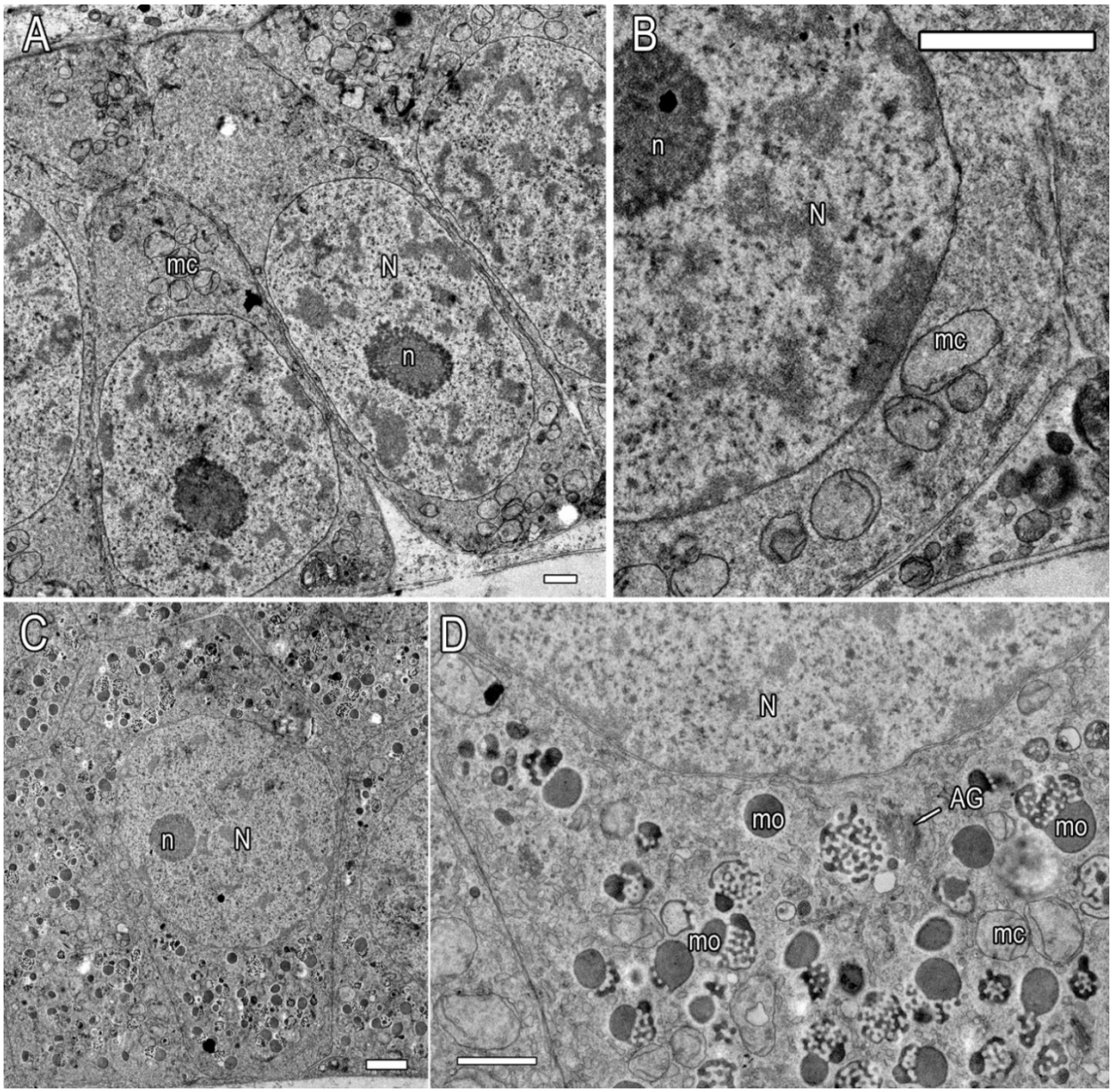


**Fig. 1.** Spermatogonia (A, B) and spermatocytes (C, D) of *Paramesacanthion* sp. A. General view of spermatogonia. Central nucleus (N) with nuclear envelope and nucleolus (n). B. Part of spermatogonium. Cytoplasm is filled with mitochondria (mc), free ribosomes and cisterns of rough endoplasmatic reticulum. C. Spermatocyte. Centrally located nucleus (N) with nucleolus (n) occupies most of the cell. D. As a result of Golgi bodies activity (AG) membranous organelles (mo) appear in cytoplasm. Abbreviations: AG – Golgi body; mc – mitochondria; mo – membranous organelles; N – nucleus, n – nucleolus. Scale bars: A, D – 1 μm; B, C – 2 μm.

spermatozoa. The main cell body is separated from the pseudopod by a layer of condensed cytoplasm. The pseudopodium is characterised by irregular shape (Fig. 4A, C). Its cytoplasm is filled with two types of material: *i*) homogenous material (Fig. 4C); and *ii*) fibrous microtubule-like material (Fig. 4C, insert). The sperm cell is enveloped with electron dense layer *ca* 70 nm thick. The cell membrane is also strengthened by the layer of submembrane osmiophilic material.

## DISCUSSION

In general, spermatozoa of *Paramesacanthion* sp. are similar to those described for other nematodes. They are amoeboid bipolar cells with anterior pseudopod and posterior main cell body and

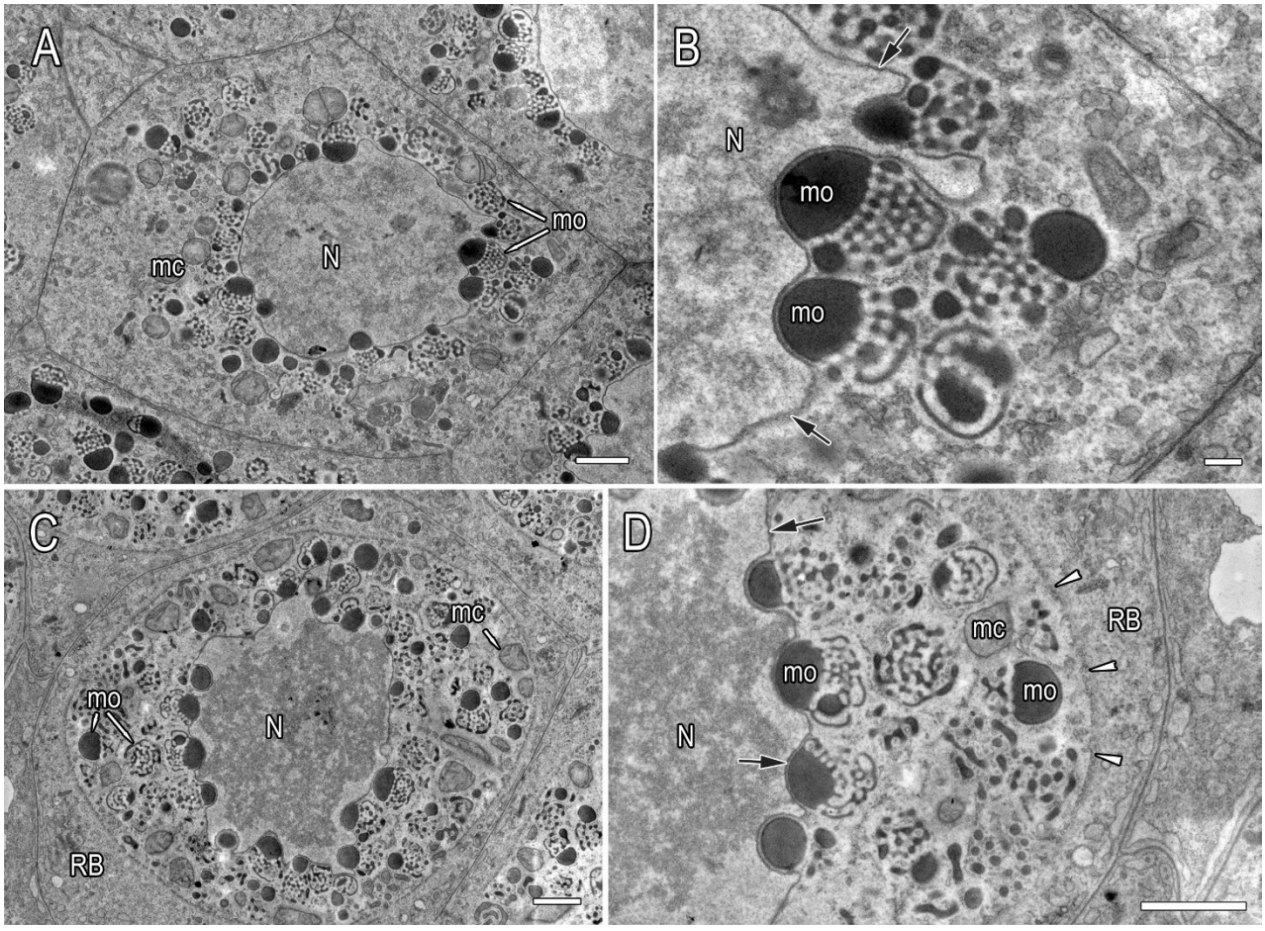


**Fig. 2.** Spermatids of *Paramesacanthion* sp. A. Early spermatid. Nucleus (N) with nuclear envelope. Mitochondria (mc) and membranous organelles (mo) concentrate around the nucleus. B. MO are in contact with the nuclear envelope (black arrows) forming pits in it. C. Late spermatid. Main cell body of spermatid contains nucleus (N) with nuclear envelope, mitochondria (mc) and membranous organelles (mo). Residual body (RB) with free ribosomes, cisterns of rough endoplasmatic reticulum and Golgi body surrounds the main cell body. D. Part of spermatid with clear border (arrowheads) between main cell body and residual body of spermatid. Abbreviations: mc –mitochondria, mo – membranous organelles; N – nucleus, RB – residual body; black arrows – nuclear envelope. Scale bars: A, C, D – 1 μm; B – 200 nm.

devoid of acrosome and axoneme. At the same time, spermatozoa of *Paramesacanthion* sp. preserve a nuclear envelope – a unique character for nematode spermatozoa found exclusively in order Enoplida. In contrast with most nematode studied, spermatozoa of *Paramesacanthion* sp. are devoid of aberrant organelles, and fibrous bodies.

The presence of the nuclear envelope in nematode spermatozoa was shown to be exceptionally present in enoplids studied to date (Yushin & Malakhov, 2004, 2014; Yushin & Gliznutsa, 2021). It has been demonstrated that the nuclear envelope in enoplids is reconstructed after the last meiotic division and may be traced through all stages of spermatogensis (Yushin & Malakhov, 1998; Yushin *et al.*, 2002; Yushin, 2003; Afanasiev-Grigoriev & Yushin, 2006). The present study confirms these observations. Such a clear character as the presence of the nuclear envelope in spermatozoa supports the separation of the order Enoplida as a separate clade, as shown by molecular phylogeny studies (Bik *et al.*, 2010; Yushin & Gliznutsa, 2021).

The aberrant organelles (MO and FB) are considered as unique characteristic of nematode spermatozoa (Justine & Jamieson, 1999; Yushin & Malakhov, 2004, 2014). Both types of organelles or only MO are found in enoplid spermatozoa (Turpeenniemi, 1998; Justine & Jamieson, 1999; Yushin & Malakhov, 1999; Yushin *et al.*, 2002; Yushin, 2003; Afansiev-Grigoriev & Yushin, 2009; Yushin & Gliznitsa, 2021). Nevertheless, although usual for most nematodes, MO-FB complexes have never been found in enoplids (Justine & Jamieson,

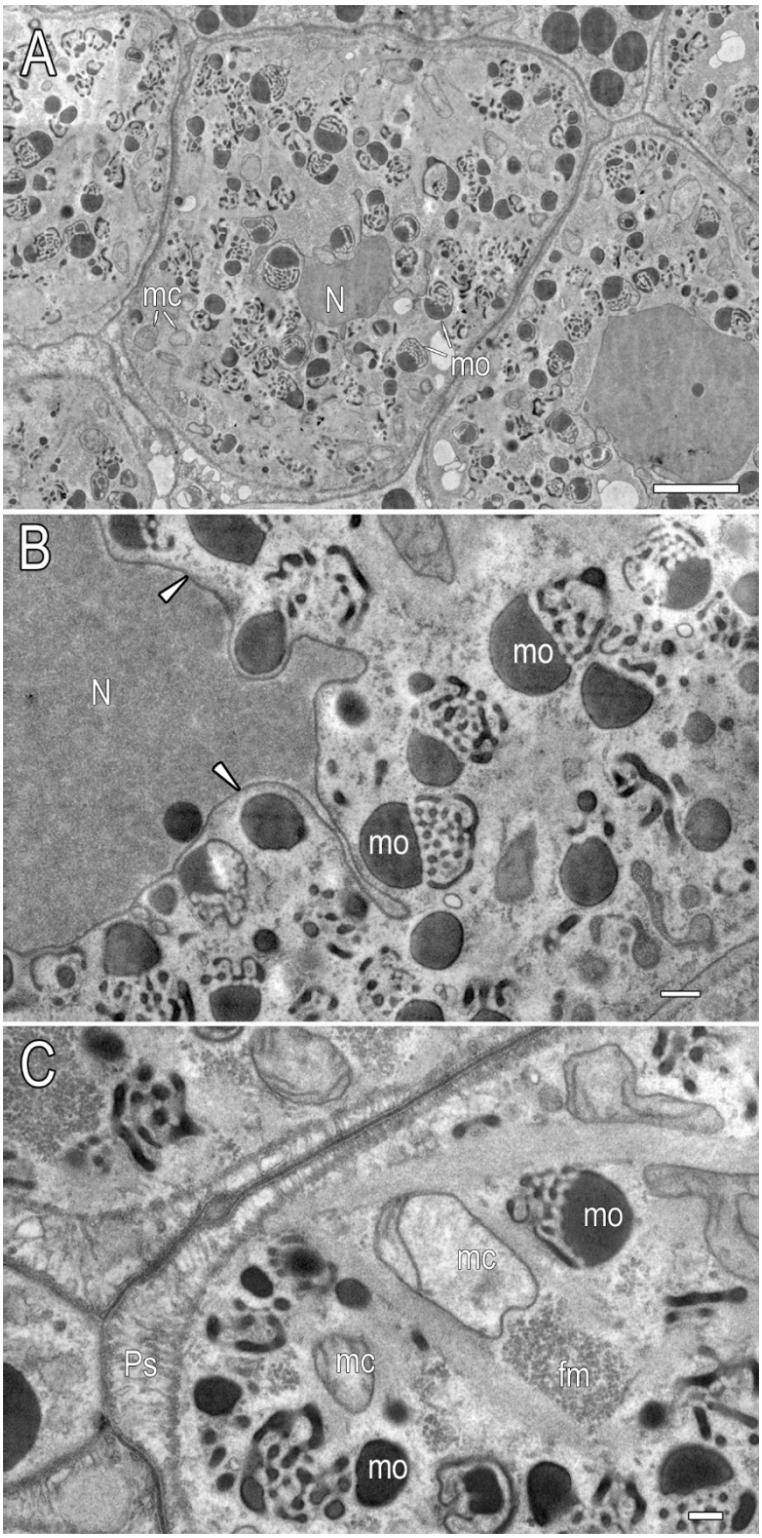


**Fig. 3.** Immature spermatozoa of *Paramesacanthion* sp. A. General view of spermatozoa. Centrally located nucleus (N) surrounded by membranous organelles (mo) and mitochondria (mc). B. Part of immature spermatozoon. Homogenous chromatin is surrounded by the nuclear envelope (arrowheads). C. Partially activated spermatozoon with newly emerging pseudopod (Ps). Regions of cytoplasm with flaky material (fm) can be found in cytoplasm of sperm cell. Abbreviations: fm – flaky material; mc – mitochondria; mo – membranous organelles; N – nucleus; Ps – pseudopod. Scale bars: A – 2 μm; B – 300 nm; C – 200 nm.

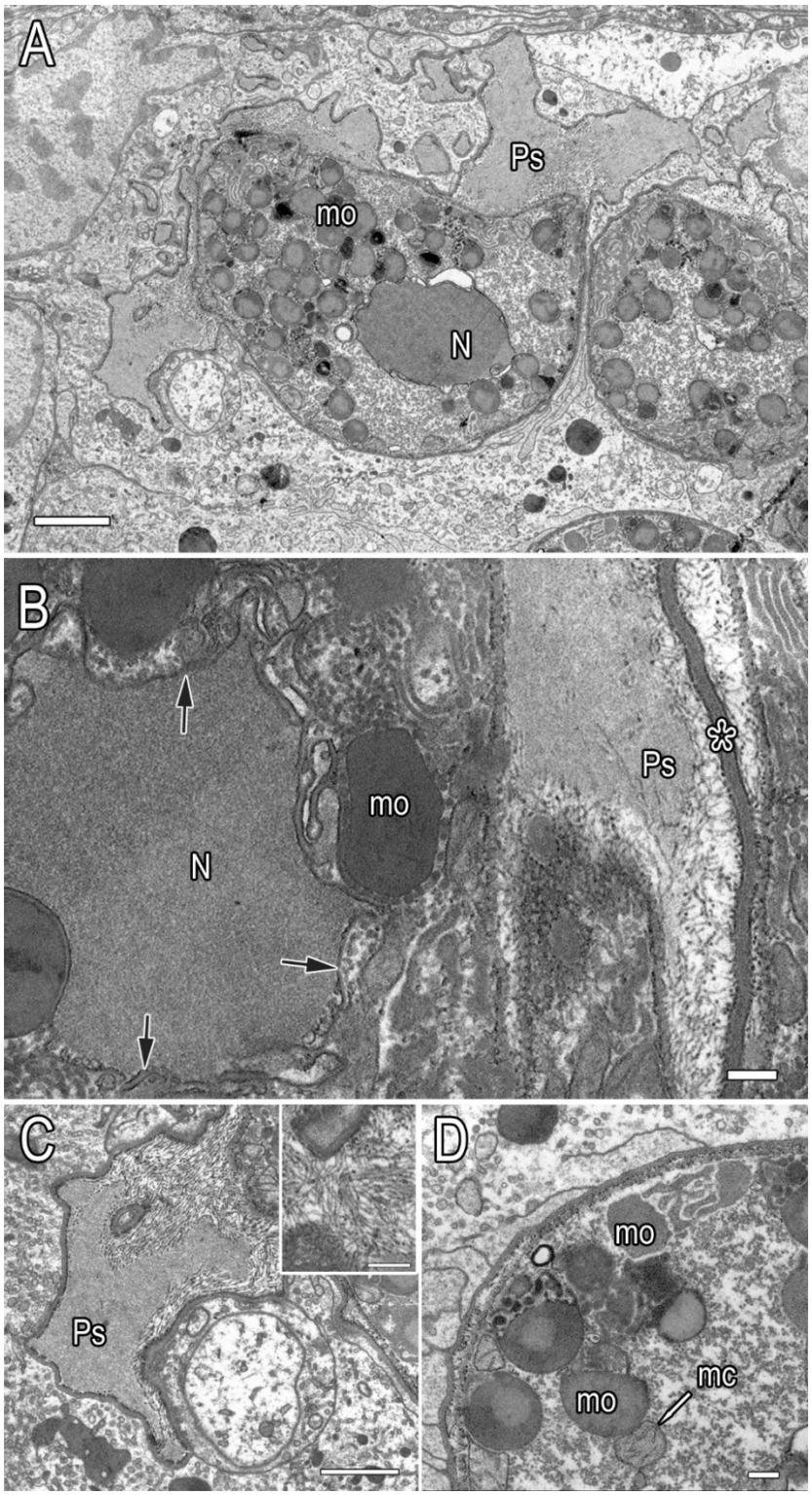


**Fig. 4.** Mature spermatozoon from uterus. A. General view. Posterior main cell body contains nucleus (N), membranous organelles (mo) and mitochondria. B. Part of mature spermatozoa with nucleus (N) with nuclear envelope (black arrows), membranous organelles (mo) and pseudopod (Ps). C. Pseudopod (Ps) is filled with homogenous material and fibrous microtubule like material (insert). D. Part of mature spermatozoa with membranous organelles (mo) and mitochondria (ms). Abbreviations: mc – mitochondria; mo – membranous organelles; N – nucleus; Ps – pseudopod; asterisk – cell sheath. Scale bars: A – 2 μm; B, D, insert – 300 nm; C – 1 μm.

1999; Yushin & Malakhov, 2004, 2014). In all cases of enoplids studied MO and FB are developed separately (Turpeenniemi, 1998; Yushin & Malakhov, 1998; Justine & Jamieson, 1999; Yushin *et al.*, 2002; Afanasiev-Grigoriev & Yushin, 2009). In *Paramesacanthion* sp. development of MO is not accompanied by the formation of FB. Previously such pattern of spermatogenesis was shown for several representatives of the subclass Enoplia (Neill & Wright, 1973; Poinar & Hess-Poinar, 1993; Takahashi *et al.*, 1994; Justine & Jamieson, 1999; Yushin, 2003). Such pattern of spermatogenesis may be considered as a case of secondary simplification of spermatogenesis.

Another remarkable difference of spermatozoa of *Paramesacanthion* sp. is the absence of contact between MO and cell membrane in mature spermatozoa. Usually, each MO in spermatids and immature spermatozoa bears a characteristic head, which is the future place of fusion with the sperm plasmalemma during activation in the female gonoduct (Justine & Jamieson, 1999; Justine, 2002; Yushin *et al.*, 2016). However, MO of *Paramesacanthion* sp. spermatids and spermatozoa lack these heads. Previously, examples where all MO lack heads have been described in *Mesacanthion hirsutum* (Baccetti *et al.*, 1983), *Anticoma possjetica* (Yushin, 2003), *Acrobeles complexus* (Yushin *et al.*, 2016) and *Admirandus multicavus* (Yushin & Gliznutsa, 2021). In all these cases, the absence of such heads in MO has led to the absence of the contact between MO and plasmalemma in mature spermatozoa. Thus, we suppose that the presence of MO heads is crucial for the formation of the contact between MO and plasmalemma. The release of MO content onto the surface of spermatozoon is considered as a key phenomenon for egg fertilisation and sperm-egg fusion (Roberts *et al.*, 1986; Chu & Shakes, 2013; Marcello *et al.*, 2013; Ellis & Stainfield, 2014; Yushin *et al.*, 2016). On the other hand, MO were not detected in several groups of nematodes (Justine, 2002; Yushin & Malakhov, 2014), which suggest that sperm physiology of nematodes differs and needs further investigation.

In *Paramesacanthion* sp. FB were not found at any stage of spermatogenesis. However, mature spermatozoa from uterus posses a well developed pseudopod filled with threads of microtubule like material. FB accumulate specific nematode sperm protein MSP (major sperm protein). This protein is synthesised in rough endoplasmic reticulum and forms the bulk of the pseudopod cytoskeleton of the mature sperm cells (Justine & Jamieson, 1999; Zograf *et al.*, 2022). To date several species from very distant taxa are known to form pseudopod without the intermediary condensed stages resembling FB (Justine & Jamieson, 1999; Yushin & Coomans, 2002; Yushin, 2003; Yushin & Malakhov, 2004; Yushin & Zograf, 2004). The lack of FB during spermatogenesis suggests that MSP accumulates in cytoplasm but is not visible under TEM (Zograf *et al.*, 2022).

The present study is the second report on ultrastructure of spermatozoa of the representatives of the family Thoracostomopsidae. Forty years ago Baccetti and co-authors (1983) described mature spermatozoon from the uterus of *Mesacanthion hirsutum* as an aflagellate cell with nucleus and the nuclear envelope. Cytoplasm of cells contained spheroid membranous vesicles that could be considered as MO. Spermatozoa of *Paramesacanthion* sp. is similar to those described by Baccetti and co-authors (1983). They are both retain the nuclear envelope and contain MO not connected with plasmalemma. However, in contrast with *M. hirsutum*, mature spermatozoa of *Paramesacanthion* sp. are bipolar cells with anterior pseudopod and posterior main cell body.

There are no significant differences in spermatogenesis of deep-sea *Paramesacanthion* sp. and shallow water *M. hirsutum*. Such similarity was also shown for different groups of marine invertebrates, such as echinoids (Eckelbarger *et al.*, 1989), gastropods (Eckelbarger & Young, 1997; Hodgson *et al.*, 1997) and bivalves (le Pennec *et al.*, 2002; Yurchenko *et al.*, 2020). So, deep-sea nematodes confirm the hypothesis proposed by Eckelbarger and Watling (1995) that each species possesses a unique suite of life-history characteristics that had been compiled throughout a long evolutionary history and that impart selective advantages under given set of environmental conditions. Because the reproductive capability of a given species is phylogenetically constrained, its response to conditions in the deep sea reflects its ancestry (Eckelbarger & Watling, 1995).

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**Ю.К. Зограф и В.В. Мордухович.** Сперматогенез глубоководной нематоды *Paramesacanthion* sp. (Enoplida: Thoracostomopsidae).

**Резюме.** С помощью трансмиссионного электронного микроскопа изучена ультраструктура сперматоцитов, сперматид и сперматозоидов глубоководной нематоды *Paramesacanthion* sp. Сперматоциты представляют собой крупные полигональные клетки с центральным ядром с ядерной оболочкой. Цитоплазма клеток заполнена типичными структурами, такими как эндоплазматический ретикулюм, аппарат Гольджи и митохондриями, а также особыми структурами – мембранными органеллами. В сперматидах происходит поляризация клетки: ядро, окруженное митохондриями и мембранными органеллами, занимает центральную часть клетки, тогда как все элементы синтетического аппарата смещаются на периферию клетки. Незрелые сперматозоиды представляют собой округлые клетки с центральным ядром с ядерной оболочкой. Цитоплазма сперматозоидов заполнена митохондриями и мембранными огранеллами. Зрелые сперматозоиды представляют собой биполярные амебоидные клетки с передней псевдоподией и задним главным телом клетки, содержащими ядро с ядерной оболочкой, митохондрии и свободные мембранные органеллы, не прикрепленные к клеточной мембране. В целом сперматозоиды *Paramesacanthion* sp. характеризуются основными признаками сперматозоидов эноплид: наличием ядерной оболочки и мембранных органелл. При этом волокнистые тела, характерные для большинства сперматозоидов нематод, не появляются ни на каком этапе сперматогенеза.