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Ultrastructure of spermatogenesis and sperm of the free-living soil nematode *Panagrellus redivivus* (Rhabditida: Panagrolaimidae)

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Summary. Spermatogenesis and the structure of the mature spermatozoa were studied using TEM in a free-living nematode *Panagrellus redivivus*. In spermatocytes, complexes of fibrous bodies (FB) and membranous organelles (MO) develop; in spermatids, MO-FB complexes consist of typical paracrystalline FB, while free FB and MO are found in the cytoplasm of the cells. Immature spermatozoa from the proximal region of the testis are polygonal cells, the cytoplasm of which is filled with mitochondria and MO. The mature spermatozoa are polarized cells capable of forming chains. The main cell body of mature spermatozoa contains a nucleus without nuclear envelope, mitochondria and MO. Two types of MO are found in the mature spermatozoa: *i*) MO attached to the plasmalemma and opened to the exterior *via* pores; *ii*) MO in the cytoplasm with intact electron-dense content. The spermatozoa of *P. redivivus* show typical ultrastructural features of nematode sperm in general. The unusual early dissociation of FB separate *P. redivivus* from most rhabditids studied and resemble those described for steinernematids.

Key words: fibrous bodies, FB, membranous organelles, MO, pseudopod, spermatheca, spermatogenesis, Steinernematidae, TEM.

Spermatogenesis and ultrastructure of spermatozoa in representatives of the order Rhabditida are well known from numerous studies of parasitic species (Justine & Jamieson, 1999; Justine, 2002). The main features of the aberrant spermatozoa in nematodes are their amoeboid nature and the absence of an axoneme, an acrosome, and a nuclear envelope. A typical spermatozoon of nematodes is described as a bipolar cell with an anterior pseudopod and posterior main cell body (MCB). The latter comprises a condensed cell nucleus surrounded by mitochondria and membranous organelles (MO), the unique cell organelles that are characteristic of most studied spermatozoa of nematodes (Foor, 1983; Justine & Jamieson, 1999). Usually MO appear as vesicles with dense content and a system of internal, finger-like projections of the outer membrane. The MO are derived from the Golgi body and appear as a part of the complexes with fibrous bodies (FB) – another aberrant component of the nematode sperm.

During spermatogenesis, MO and FB complexes dissociate into separate MO and FB. After activation of spermatozoa in the female reproductive system, MO attach to the plasmalemma and release their content into the uterus lumen. Sperm activation is also accompanied by the transformation of FB into the cytoskeleton of a newly formed pseudopod.

Spermatogenesis in many taxa of soil and parasitic nematodes from the order Rhabditida *apud* De Ley & Blaxter (2002) proceeds as described above and results in a similar sperm structure (Justine, 2002; Yushin & Malakhov, 2004). However, the fate of the unusual organelles differs significantly in several taxa of Chromadorea. These cytological differences may be used for comparative analysis (Yushin & Malakhov, 2004), but such analysis across taxa is limited by the lack of ultrastructural data on spermatozoa of diverse taxa (Yushin, 2007).

A different type of spermatogenesis was described for the panagrolaimid species, *Panagrellus silusiae* (Pasternak & Samoiloff, 1972). Dissociation of FB in this nematode occur early in spermatogenesis, *i.e.* FB are not found in immature spermatozoa. This type of spermatogenesis is also

known for *Steinernema* species (Yushin *et al*., 2007b), representatives of the suborder Panadrolaimina *apud* Hodda (2007). This cytological difference may be useful for the analysis of panagrolaimid phylogeny, although data on many families of the suborder are poor or absent.

In this paper the author presents data on ultrastructure of spermatogenesis and sperm in males and females of *Panagrellus redivivus* (Linnaeus, 1767) Goodey, 1945 (Rhabditida: Panagrolaimidae) to elucidate a new aspect of the comparative cytology of panagrolaimid nematodes.

MATERIALS AND METHODS

Adult males and females of *P. redivivus* were picked with a fine tipped wire and transferred to washing buffer (100 mM NaCl; 20 mM KH_2PO_4, pH 5.7) using a stereomicroscope.

The males and females were fixed in 2.5% glutaraldehyde in 0.05 M sodium cacodylate buffer (pH 7.4). After 8 h animals were cut at the head and tail region to improve impregnation and left in the same fixative overnight at 4°C. Post-fixation took place in 1% osmium tetroxide for 12 h in the same buffer. 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 followed by an acetone series and embedded in low viscosity embedding medium Spurr resin (EMS, Hatfield, UK). Ultrathin (70 nm) sections were cut using a Leica Ultracut S ultratome (Leica, Vienna, Austria) with a glass knife and collected on formvar-coated copper single slot grids. Ultrathin sections were stained with uranyl acetate and lead citrate and examined with JEOL JEM 100S and Zeiss Libra 120 electron microscopes.

The testes of five males and the uteri of five females were examined.

RESULTS

The male reproductive system of *P. redivivus* consists of a single telogonic gonad. Male germ cells were joined together by a common rachis and could be found along the gonad. The seminal vesicle contains immature spermatozoa and is connected with the *vas deferens*.

Spermatogonia are polygonal cells situated at the distal tip of the testis. Large nucleus with nucleolus fills almost all space of the cell. In the cytoplasm endoplasmatic reticulum, Golgi body, free ribosomes and mitochondria are found.

Early spermatocytes are large (18-24 µm in diam.) polygonal cells. Spherical nucleus (6-8 µm in diam.) with nucleolus is situated in the central part of the cell and is surrounded with a nuclear envelope (Fig 1A). The rest of the cytoplasm is filled with free ribosomes, sparse mitochondria and Golgi body. As a progeny of Golgi bodies, electron transparent organelles (0.7-1.2 in diam.) in the shape of vesicles fill most of the cytoplasm. Each of these organelles contains electron dense particles of 0.25 µm in diam. and internal finger-like shaped projections of the outer membrane. These organelles must be considered as membranous organelles (MO) known from spermatozoa of other nematodes.

Late spermatocytes are similar to early ones. Most changes take place in the cytoplasm of the cells. In close contact with MO, oval dense bodies (*ca* 0.6 × 1 µm) with paracrystalline structure appear. These paracrystalline bodies are similar to fibrous bodies (FB) of other nematodes studied (Figs 1B, 2). Thus, the complexes of the FB-MO appear at this stage of spermatogenesis. The FB-MO complexes of the terminal spermatocyte include large (1.2 µm long and 0.6 µm wide) FB. The side of the FB opposite to a vesicle is exposed to the cytoplasm and is free of enveloping cisternae.

Meiosis was not observed in the testes studied, probable due to the rapidity of the process. The late spermatocytes adjoin with the spermatids. Each spermatid contains a nucleus without nuclear envelope (Figs 2, 3). The nucleus is surrounded by electron transparent cytoplasm filled with ribosomes and mitochondria. The mitochondria (0.7-1.2 µm in diam.) have a dense matrix and well developed system of lamellar cristae. Dissociation of FB-MO complexes takes place in the spermatids. As the result of this dissociation, free FB and free MO with the finger-like invaginations and electron dense particle could be found in the cytoplasm (Figs 2B, 3A).

All the testes studied contain uniform immature spermatozoa located just after the zone of spermatids. The spermatozoa (18-22 µm in diam.) are tightly packed inside the seminal vesicle and assume polygonal outlines (Figs 2, 4A). Nuclei of spermatozoa consist of heavily packed chromatin and are devoid of a nuclear envelope (Figs 2, 4B). Rounded mitochondria are about 1 µm in diam. randomly scattered through the electron light cytoplasm. MO (1-1.5 µm in diam.) became bipolarised. One part of this organelle contains numerous finger-like invaginations and the volume of organelles is filled with electron dense matrix; here in this part osmiophilic granules are always present (Figs 2, 4B). Another part of the organelle is electron translucent, free of any vesicles and always bears a membranous knob at the surface (Figs 2, 4C). Characteristically, the area subtending the knob

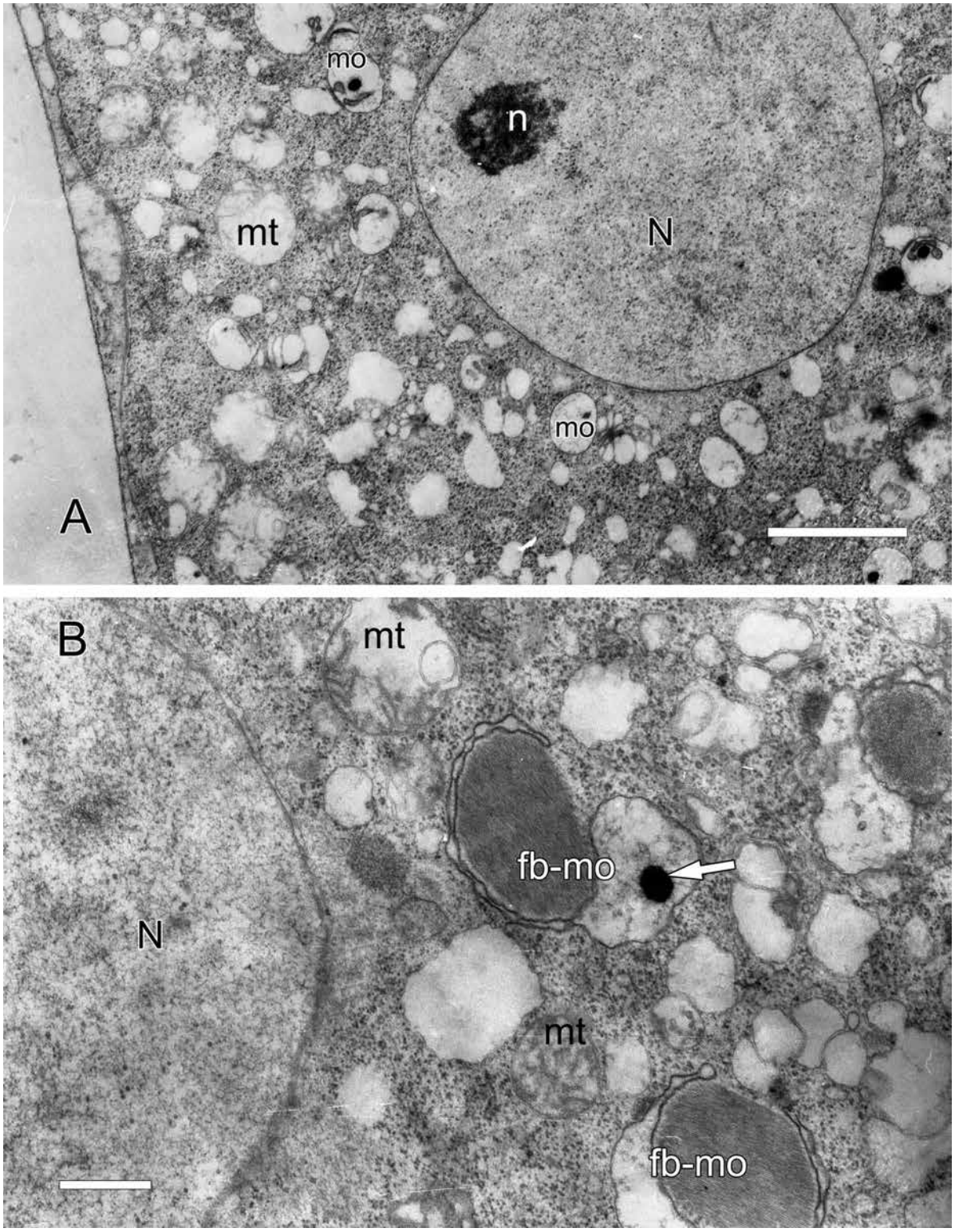

Fig. 1. Spermatocytes of *Panagrellus redivivus*. TEM. A. Early spermatocytes. Central nucleus with nucleolus surrounded with nuclear envelope. Cytoplasm of the spermatocytes filled with mitochondria, forming membranous organelles, and free ribosomes. B. Late spermatocyte. Membranous organelles and fibrous bodies form complexes. Note electron dense particle in membranous organelle (arrow). fb-mo – complex of fibrous bodies and membranous organelles; mo – membranous organelles; mt – mitochondria; N – nucleus; n - nucleolus. Scale bars: A – 2 μm; B – 0.5 μm.

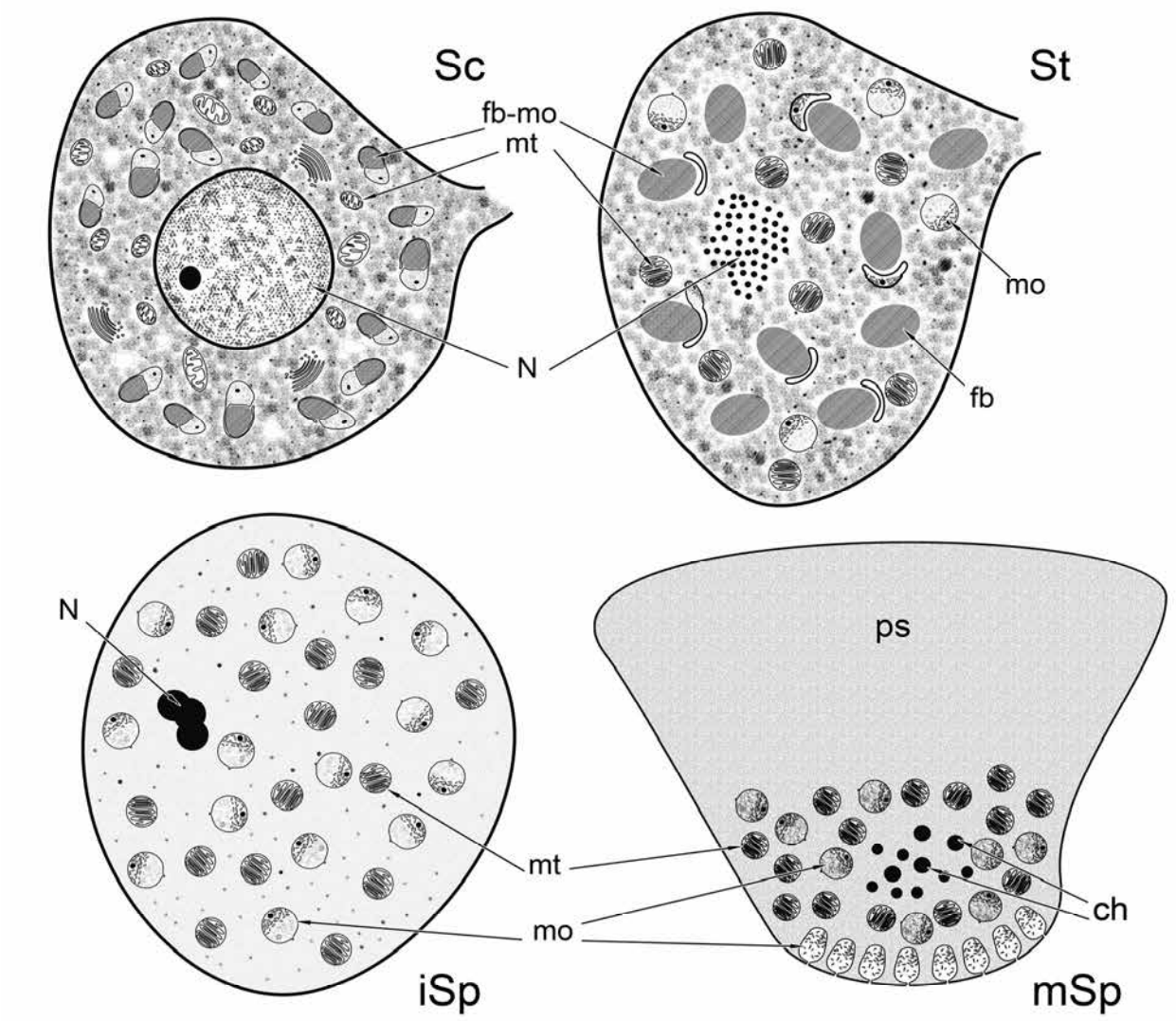

Fig. 2. Schematic representation of spermatogenesis in *Panagrellus redivivus*. In spermatocytes (Sc) cell synthetic apparatus well developed. As result, complexes of membranous organelles and fibrous bodies (fb-mo) appear. Spermatid (St) contains nucleus (N) without nuclear envelope. Cytoplasm of spermatid filled with complexes of membranous organelles and fibrous bodies (fb-mo), mitochondria (mt), free membranous organelles (mo) and free fibrous bodies (fb). Cytoplasm of immature spermatozoa (iSp) contains mitochondria (mt) and free membranous organelles (mo). Fibrous bodies absent. Mature spermatozoa (mSp) from females bipolar cells with anterior pseudopodium (Ps). In the posterior part nuclear material in form of separate chromosomes (ch) present. Mitochondria (mt) and membranous organelles (mo) also found in the main cell body of spermatozoa.

is free of finger-like invaginations. FB are not found in immature spermatozoa.

Mature spermatozoa could be found in spermathecae of females. These are bipolar cells with anterior pseudopodium and posterior main cell body. Spermatozoa form chains consisting of 7-12 cells attached to each other by tight contacts (Figs 2, 5A). The maximum width of the spermatozoa in the chain varies from 18 to 22 µm. After activation in the female reproductive system, nuclear material dissociates and appears in the form of separate chromosomes in the main cell body (Figs 2, 5A). Rounded mitochondria (0.9-1.2 µm in diam.) fill the cytoplasm of the main cell body of sperm cells. There are two types of MO found in cytoplasm of mature spermatozoa. The first group is composed of the MO attached to the outer membrane of the main cell body (Figs 2, 5B). These are electron transparent organelles about 0.6-0.9 µm in diam. with a well developed system of finger shaped

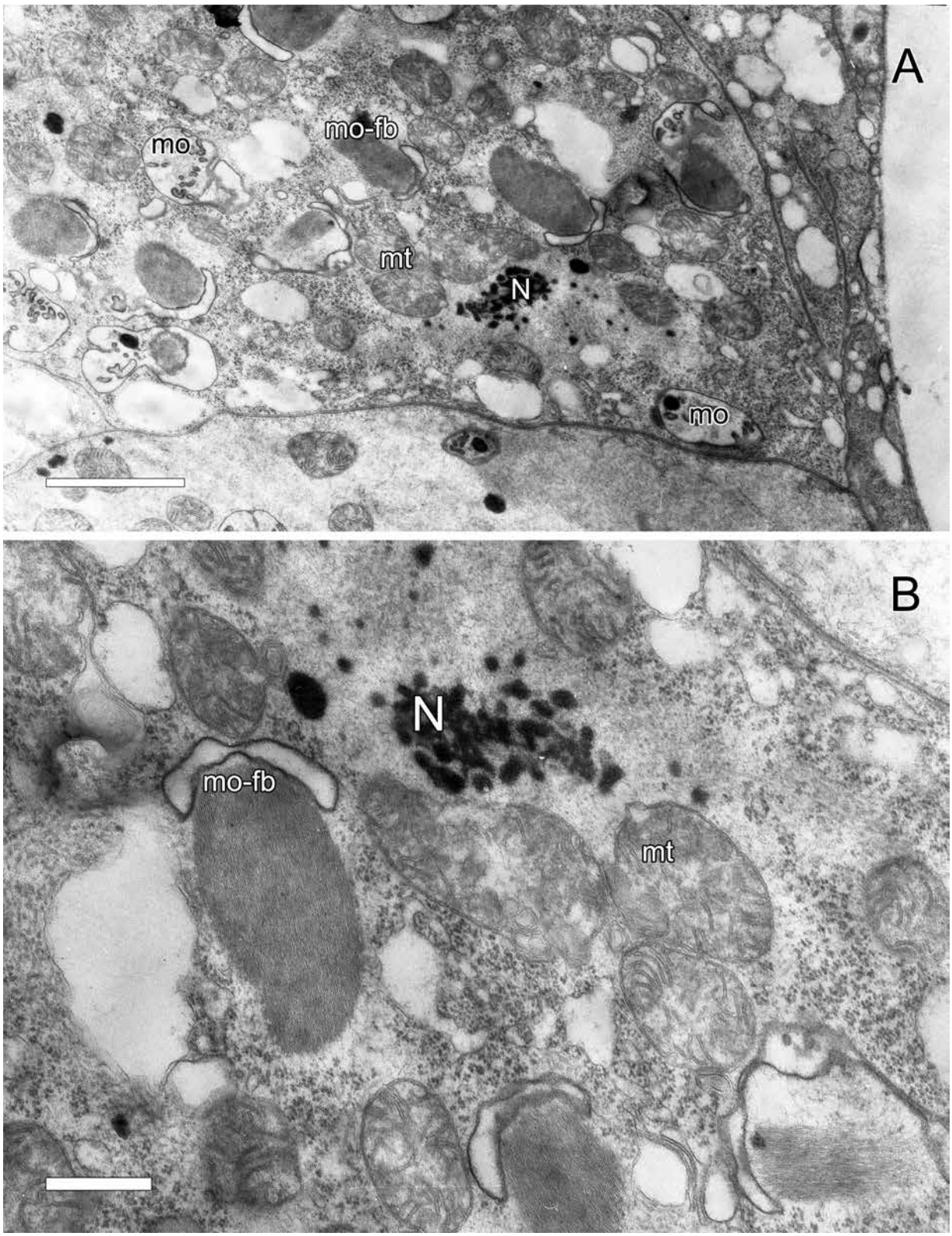

Fig. 3. Spermatids of *Panagrellus redivivus*. TEM. A. Cytoplasm of spermatid filled with free ribosomes, free membranous organelles, and mitochondria. Nucleus devoid of nuclear envelope. B. Central part of spermatid. mo – membranous organelles; fb-mo – complexes of fibrous bodies and membranous organelles; mt – mitochondria; N – nucleus. Scale bars: A – 2 μm; B – 0.5 μm.

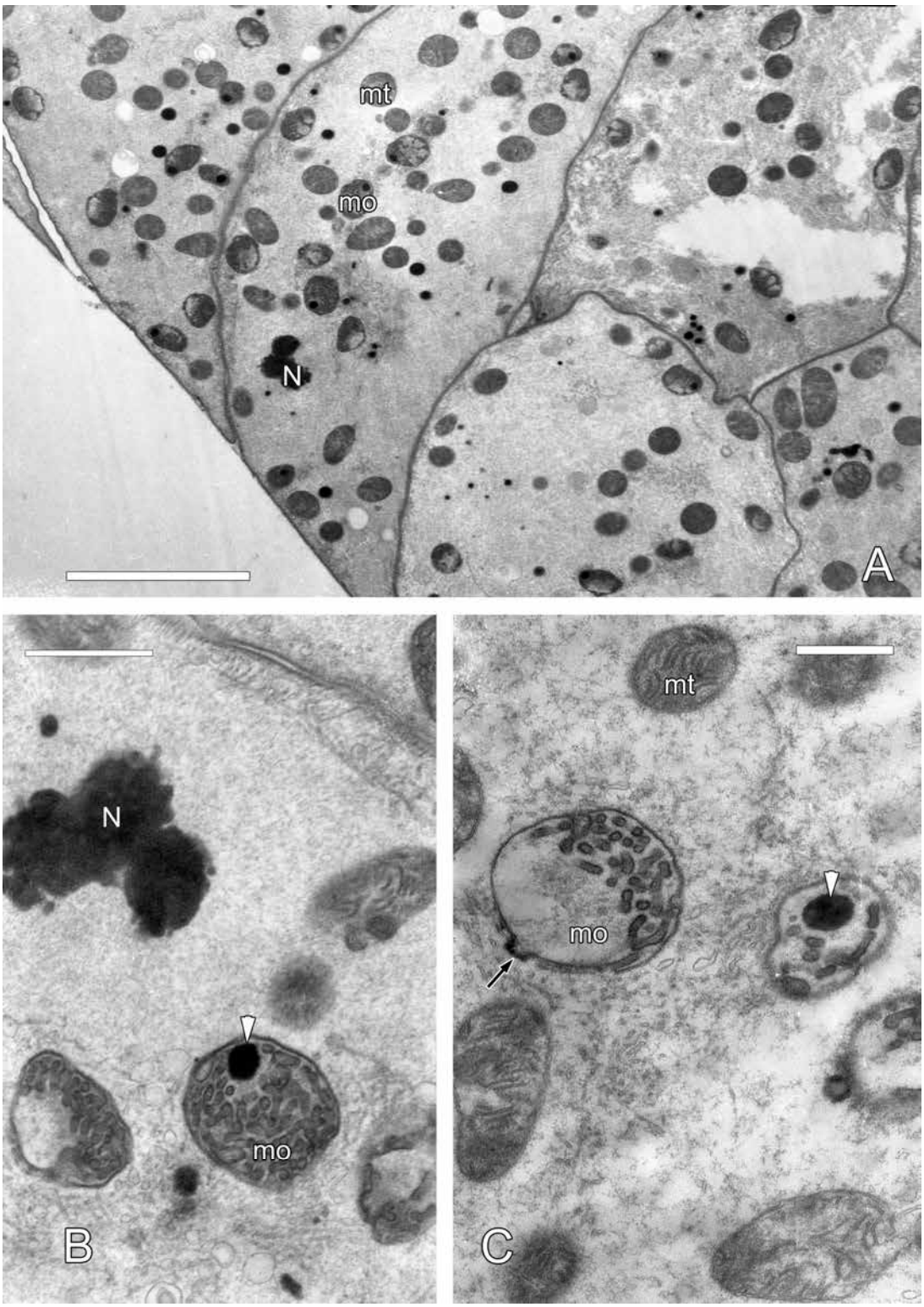

Fig. 4. Immature spermatozoa from testis of *Panagrellus redivivus*. TEM. A. Spermatozoa in testis. General view. Nucleus devoid of nuclear envelope. Electron light cytoplasm filled with mitochondria and free membranous organelles. B. Immature spermatozoon. Note electron dense particle (arrowhead) in free membranous organelle. C. Immature spermatozoon. Free membranous organelle with membranous knob (arrow). mo – membranous organelles; mt – mitochondria; N – nucleus; arrow – membranous knob; arrowhead – electron dense particle in membranous organelle. Scale bars: A – 5 μm; B, C – 0.5 μm.

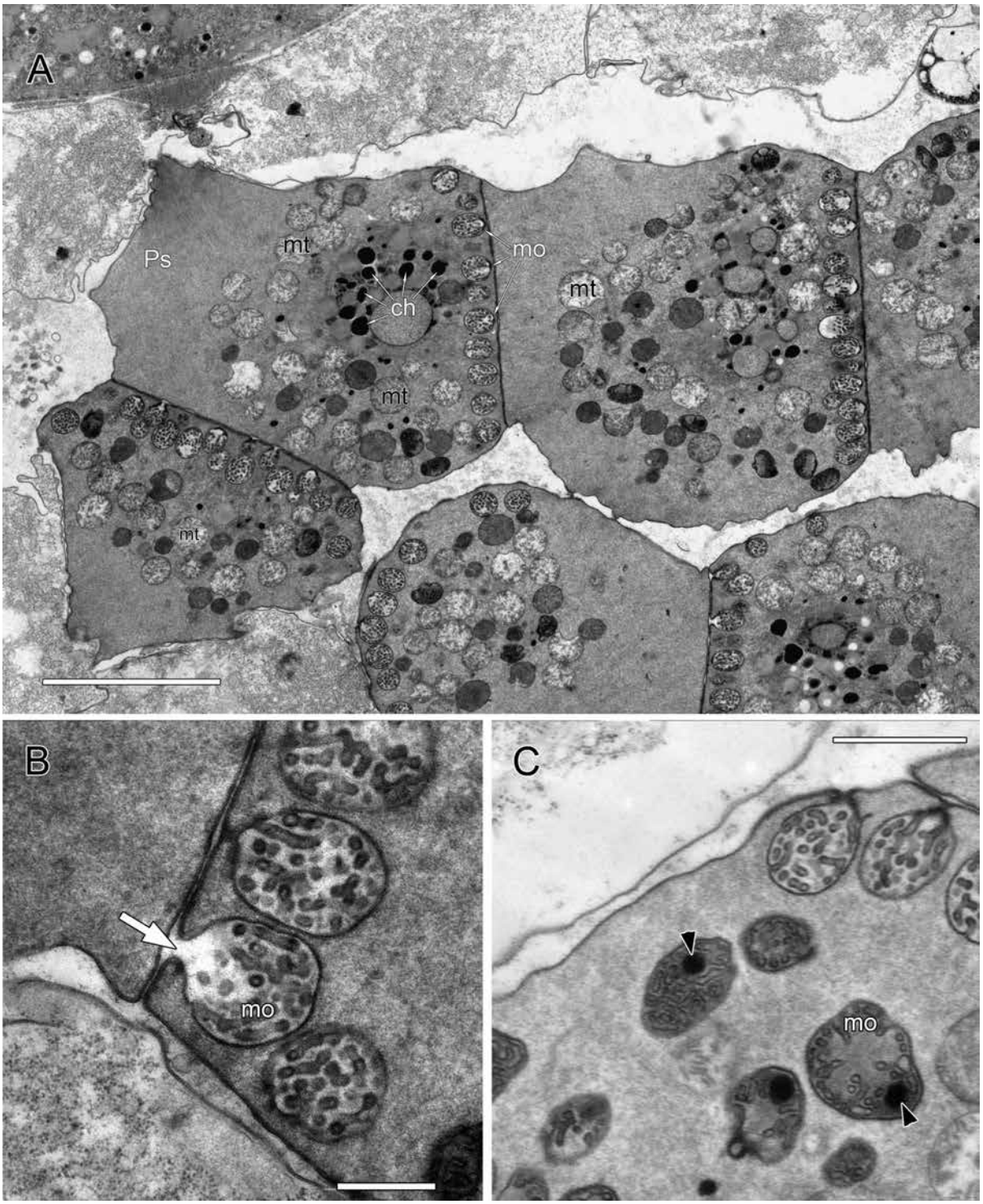

Fig. 5. Mature spermatozoa from female of *Panagrellus redivivus*. TEM. A. General view. Chain of spermatozoa in the uterus. Anterior pseudopodium form tight contacts with leading spermatozoon. Main cell body contains chromatin, mitochondria and membranous organelles. B. Membranous organelles attached to plasmalemma and open to the exterior *via* pore (arrow). Note electron transparent inner space of membranous organelles. C. Membranous organelles in cytoplasm of main cell body of spermatozoon. Note osmiophilic granule (arrowhead) inside membranous organelle. Inner space of membranous organelles filled with dense material. ch – chromatin; mo – membranous organelles; mt – mitochondria; Ps – pseudopodium; Scale bars: A – 5 μm; B – 0.5 μm; C – 1 μm.

invaginations. MO open to the exterior *via* pores. The second type of MO are electron dense organelles (0.8-1.0 µm in diam.) containing osmiophilic granules (Figs 2, 5C). These organelles are not attached to the plasmalemma. The anterior pseudopodium of spermatozoa is devoid of any organelles and is filled with an electron dense matrix.

DISCUSSION

The electron microscope study of the sperm development in *P. redivivus* shows the typical sperm development known for many taxa (Justine & Jamieson, 1999; Justine, 2002). The spermatozoa of *P. redivivus* are unpolarized cells in the seminal vesicle (immature spermatozoa) and, after activation in the uterus, are subdivided into the main cell body containing organelles and a prominent pseudopodium (mature spermatozoa). The central nucleus of the immature spermatozoa is devoid of a nuclear envelope and is surrounded by mitochondria and MO. The MO have a typical structure and are spherical vesicles with an internal system of finger-like invaginations of the membrane and a characteristic knob, which is the future place of fusion with the sperm plasmalemma during activation in the female gonoduct (Pasternak & Samoiloff, 1972; Shepherd & Clarck, 1976; Wolf *et al*., 1978; Justine & Jamieson, 1999; Justine, 2002; Yushin *et al*., 2007a; Yushin & Ryss, 2011).

To the date, the spermatogenesis of panagrolaimids were studied by the example of two species: *P. silusiae* (Pasternak & Samiloff, 1972) and *P. redivivus* (present work). Spermatogenesis of both species is similar and resembles those described for many nematode studied. Nevertheless, Pasternak and Samoiloff (1972) describe mature spermatozoa from females of *P. silusiae* as rounded unpolarized cells with MO situated around the entire outer cell boundary. In fact, the authors only observed part of the cell seen at the thin section, whereas the pseudopodium was not in the plane of the section.

Despite the overall similarity in spermatogenesis of the two *Panagrellus* species, few differences in sperm structure are present. There is difference in the size of the aberrant organelles. MO in *P. silusilae* are about 0.5 µm in diam. whereas MO in *P. redivivus* are about 0.7-1.2 µm in diam. The mature spermatozoa in *P. redivivus* are almost twice as big as those from *P. silusiae* (based on the diameter of main cell body of spermatozoa: 10.5 µm in *P. redivivus vs* 5.3 in *P. silusiae*). Such difference in the size of spermatozoa in closely related species has been described earlier. Mature spermatozoa described for three *Halichoanolaimus* species differ in size (spermatozoa of *Halichoanolaimus* sp. are twice as big as those in *H. sonorus* and *H. possjetiensis*) (Yushin, 2001). Immature spermatozoa of several rhabitid species (*Caenorhabditis* species, *Rhabditis* species, and *Pelodera* species) differ significantly in size (LaMunyon & Ward, 1999). According to LaMunyon and Ward (1999), larger sperm have evolved where competition is more important; smaller sperm have evolved where competition is less important.

The remarkable character of the mature spermatozoa of *P. redivivus* is their tendency to be aggregated into a chain by attachment of the pseudopodium to the main cell body of the preceding spermatozoon. Similar chains were previously described for several species representing the families Steinernematidae (Bovien, 1937; Hess & Poinar, 1989; Spiridonov *et al*., 1999; Yushin *et al*., 2007b) and Brevibuccidae (Yushin *et al*., 2011). These chains are motile and either move conjointly towards the oviduct or stick to the uterine wall (Yushin *et al*., 2007b), and the number of spermatozoa usually corresponds with number of oocytes in the female reproductive system (Spiridonov *et al*., 1999). This close cooperation of male gametes was possibly at the basis of the development of giant movable spermatozeugmata in several species of Steinernematidae (Spiridonov *et al*., 1999; Yushin *et al*., 2007b; Yushin *et al*., 2011).

The immature spermatozoa of *P. redivivus* contain only nucleus, mitochondria and MO filled with the dense matter. Usually, FB are also present in immature spermatozoa of rhabditids (Yushin *et al*., 2007a). The total dilution of FB in most cases coincides with a dramatic change in sperm morphology only after activation in the female reproductive system (Hess & Poinar, 1989; Justine & Jamieson, 1999). Observation of the sperm development of *P. redivivus* shows that formation of FB, typical for rhabditids, takes place in spermatocytes and their development and transformation continues in the spermatids. However, the FB dissociate to fill the cytoplasm of spermatozoa much earlier than in other rhabditids, *i.e*. in the immature spermatozoa. This unusual fate of the FB was earlier described for another representative of the order Panagrolaimida *apud* Hodda (2007), *Steinernema feltiae* (Yushin *et al*., 2007b). According to Yushin *et al.* (2007b), cytoskeleton proteins stored in the cytoplasm of spermatozoa are morphologically indistinct. Although the biology of these two groups of

nematodes (Steinernematidae and Panagrolaimidae) is different (free-living *P. redivivus* and entomopathogenic *S. feltiae*), certain molecular biological analyses confirm a close relationship of panagrolaimids and steinernematids (Nadler *et al*., 2006; Holterman *et al*., 2006; Meldal *et al*., 2007; Hodda, 2007). The distinct ultrastructural feature such as early dissociation of FB may be considered as an additional support for phylogenetic closeness of these groups. On the other hand, in different analyses this relation appears weakly supported (Bert *et al*., 2008; van Megen *et al*., 2009) indicating that additional data are needed to resolve the relationship of these two groups.

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J.K. Zograf. Ультраструктура сперматогенеза и спермиев у почвенной свободноживущей нематоды *Panagrellus redivivus* (Rhabditida: Panagrolaimidae).

Резюме. Сперматогенез и строение зрелых сперматозоидов *Panagrellus redivivus* были изучены с использованием трансмиссионной электронной микроскопии. В сперматоцитах формируются комплексы волокнистых тел (ВТ) и мембранных органелл (МО). В сперматидах обнаруживаются свободные МО, в то время как в МО-ВТ комплексах МО представлены в виде крайне уплощенных цистерн. В цитоплазме незрелых сперматозоидов присутствует ядро без ядерной оболочки, МО и митохондрии. Зрелые сперматозоиды из самки – это амебоидные клетки, способные образовывать цепочки клеток. В главном теле клетки сперматозоида располагается ядро, митохондрии и два типа МО: свободные МО и МО, присоединенные к плазмалемме клетки, открывающиеся наружу через пору. Необычная ранняя диссоциация ВТ и способность сперматозоидов формировать цепочки отличает *P. redivivus* от большинства изученных рабдитид и напоминает спермии, описанные для представителей семейства Steinernematidae.