Mature spermatozoa of *Brevibucca* sp. (Nematoda: Rhabditida: Brevibuccidae)

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Summary. Mature spermatozoa found in the female gonoduct of the nematode *Brevibucca* sp. (Brevibuccidae, Rhabditida) were studied with transmission electron microscopy. As in other nematodes, the spermatozoa in *Brevibucca* sp. represent an aberrant type of male gametes characterised by the absence of an axoneme and an acrosome. Mature spermatozoa of *Brevibucca* sp. are amoeboid bipolar cells *ca* 4-4.5 µm diam.; each cell is subdivided into a main cell body and a pseudopod devoid of organelles. The main cell body includes a condensed nucleus, many mitochondria and so-called 'membranous organelles' (MO). These unique organelles are characteristic of developing, as well as of mature, spermatozoa of many nematodes. The MO in *Brevibucca* sp. sperm resemble large (*ca* 0.5 µm diam.) vesicles with transparent content and a system of internal finger-like projections of the outer membrane. Each MO is joined to the plasmalemma of the main cell body and is open to the intercellular exterior *via* a pore. Each spermatozoon has a prominent pseudopod filled with the filamentous components of the cytoskeleton. The structure and development of the rhabditid (order Rhabditida *apud* De Ley & Blaxter, 2002) sperm is somewhat conserved throughout the order. That is, the general pattern of spermatozoon recognized as "rhabditid" in *Brevibucca* sp. is similarly expressed in Spiruromorpha, Ascaridomorpha, Panagrolaimomorpha, Tylenchomorpha and Rhabditomorpha. Thus, such conservation lacks phylogenetic pointers at the scale of order. The spermatozoa of the rhabditid pattern observed also in *Brevibucca* sp. may be considered as an ancestral or symplesiomorphic character for several clades of the order Rhabditida.

Key words: female gonoduct, fibrous bodies, membranous organelles, mitochondria, phylogeny, pseudopod, spermatogenesis, ultrastructure.

The nematode family Brevibuccidae Paramonov, 1956 is usually considered as a taxon within the order Rhabditida in most nematode taxonomic systems based on molecular phylogeny, but the relationships of Brevibuccidae with other taxa within the order are obscure (De Ley & Blaxter, 2002, Meldal *et al*., 2007; van Megen *et al*., 2009). New comparative morphological data are desirable to contribute further to phylogenetic analysis of the rhabditids and other nematode taxa. 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 sperm structure and development have been observed in a variety of the rhabditid nematodes (order Rhabditida *apud* De Ley & Blaxter, 2002) and these suggest a general pattern of the nematode sperm for this order (Yushin & Malakhov, 2004).

Nematode spermatozoa represent an aberrant type of male gamete in that 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, as well as of mature, sperm of many nematodes. Usually, MO resemble 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 in the rhabditid sperm as part of complexes with paracrystalline fibrous bodies (FB), which are another aberrant component of developing sperm. The prism-shaped FB are composed from an 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 the plasmalemma of the sperm main cell body and release their content into the uterus lumen. The empty MO resemble membranous sacs continuous with the sperm plasmalemma and these are retained as a constant feature of mature sperm. Sperm activation is also accompanied by transformation of FB into the MSP-based cytoskeleton of a newly formed pseudopod. Pseudopodia and amoeboid movement are special characteristics of nematode sperm.

The order Rhabditida *apud* De Ley & Blaxter (2002) includes many taxa that have a deviation of sperm structure and development from the more general 'rhabditid' pattern (Shepherd & Clark, 1976; Justine & Jamieson, 1999; Yushin & Spiridonov, 2001; Justine, 2002). These cytological differences may be useful characters for analysis of rhabditid phylogeny (Yushin & Malakhov, 2004).

In this paper we present transmission electron microscope observations on mature sperm in the female gonoduct of the rhabditid *Brevibucca* sp. (Nematoda: Rhabditida: Brevibuccidae) to elucidate a new aspect of the comparative cytology of the rhabditid nematodes.

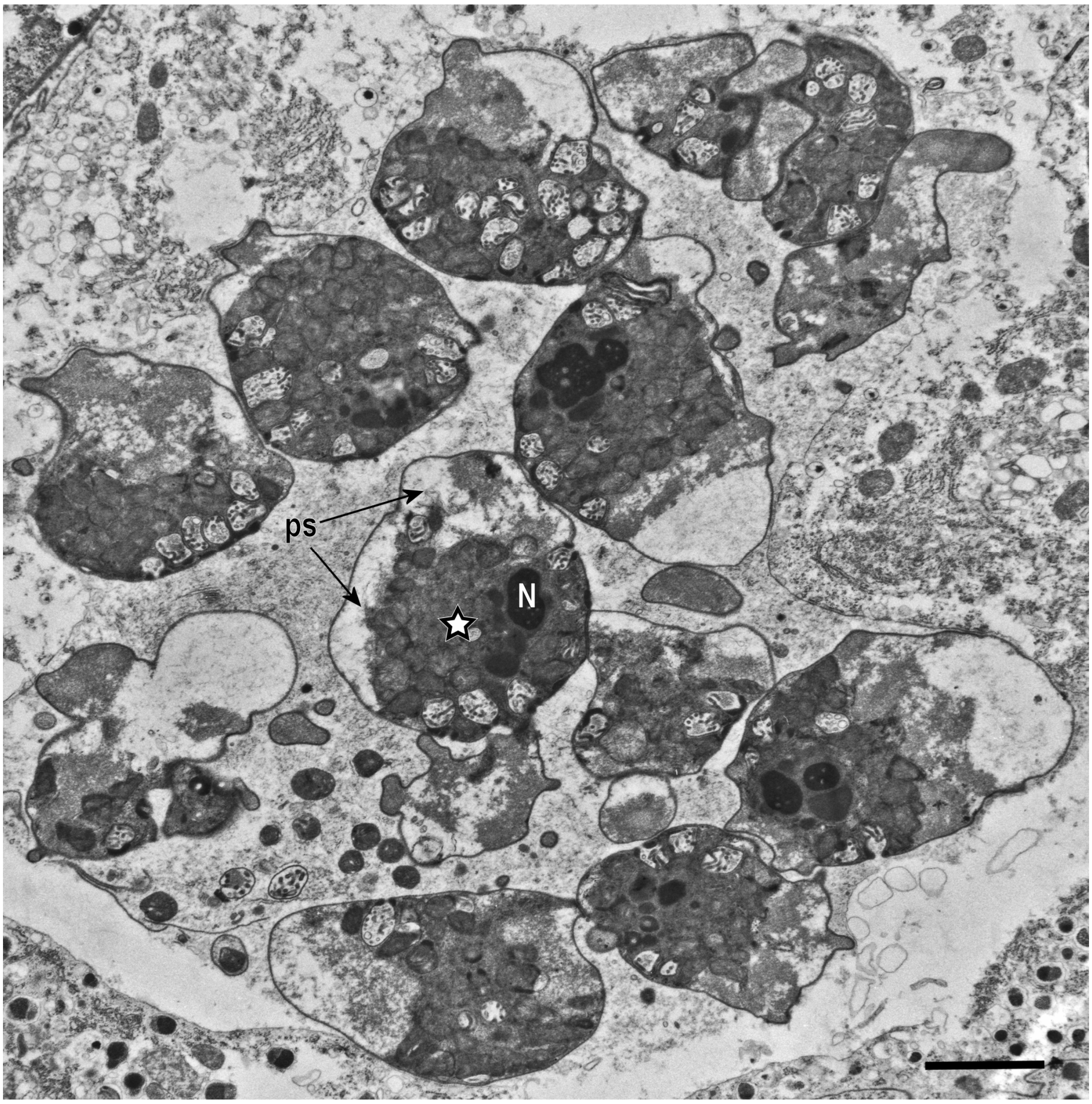

Fig. 1. TEM of *Brevibucca* sp., showing a cluster of mature spermatozoa stored in the spermatheca. Each spermatozoon is clearly subdivided into a main cell body (asterisk) with nucleus (N), and a pale pseudopod (ps). Scale bar = 2 μm.

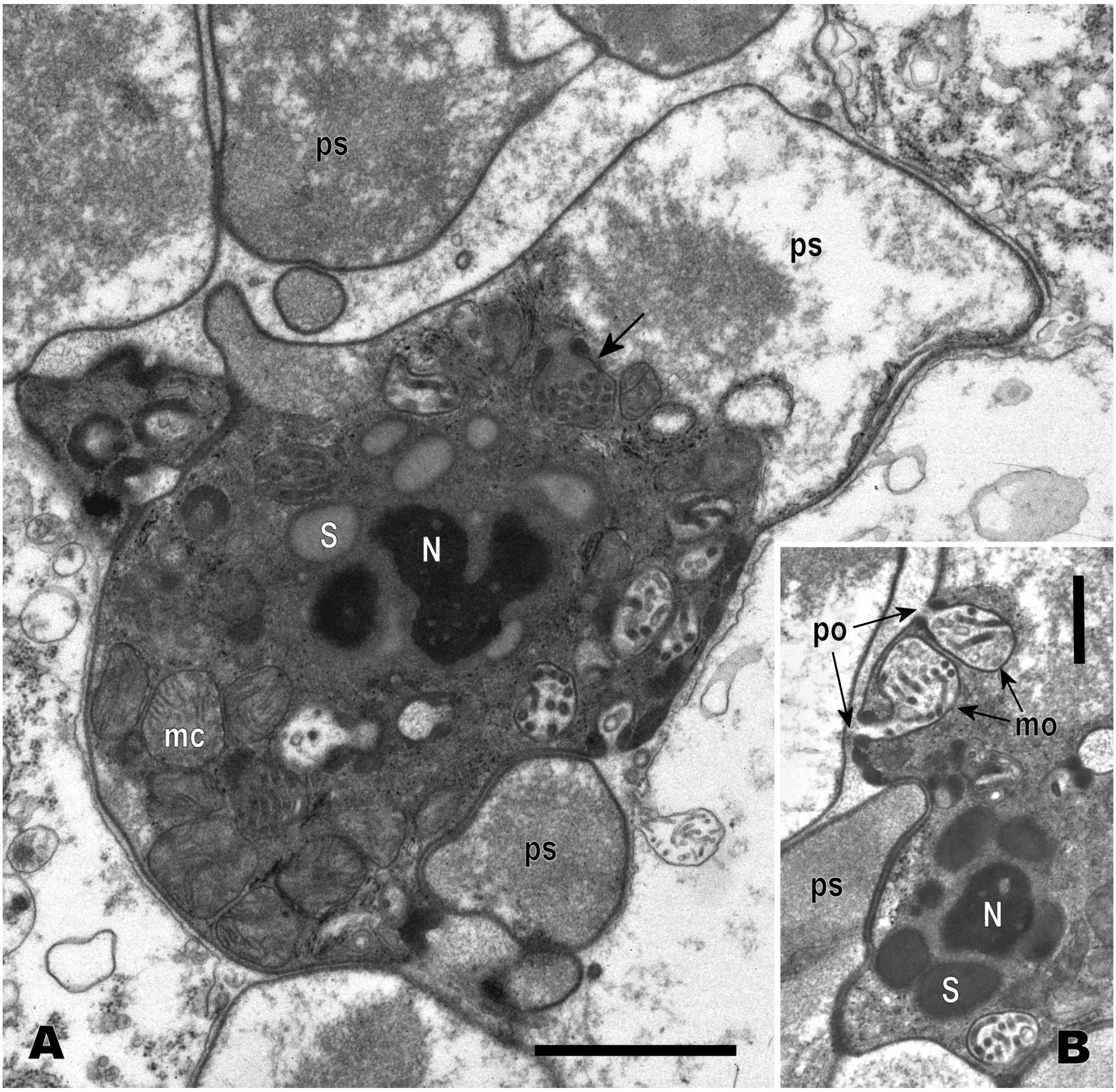

Fig. 2. TEM of *Brevibucca* sp., mature spermatozoa. A: General view of spermatozoon; arrow shows the free membranous organelle with dense content. B: The spermatozoon main cell body. Scale bars: A = 1 μm; B = 0.5 μm. Abbreviations: mc = mitochondria; mo = membranous organelles; N = nucleus; po = pores of membranous organelles; ps = pseudopods; S = nuclear satellites.

RESULTS

Mature (activated) spermatozoa found in the female gonoduct were positioned mainly as a cluster of uniform amoeboid cells in the spermatheca, a special dilated region in the distal part of the uterus adjoining the oviduct (Fig. 1). The spermatozoa are not squeezed tightly but some of them are in intimate contact. Several spermatozoa were also observed proximally in the uterus lumen.

The spermatozoa found in the female gonoduct are clearly polarised irregular cells *ca* 4-4.5 μm diam (Figs 1; 2A; 4A). Each cell is clearly subdivided into a pseudopod and a main cell body. The main cell body contains a nucleus, mitochondria and MO. The lobate nucleus, roughly 1 μm diam, has no nuclear envelope; the highly condensed nuclear chromatin has a clear-cut boundary; small pale lacunae result in a spotted appearance of the nucleus in thin sections (Figs 1; 2A; 3A; 4A). Each nucleus is accompanied by 0.4 μm long oval satellites embedded in a fibrous matrix (Figs 2A, B; 3C; 4A). The satellites are easily recognised

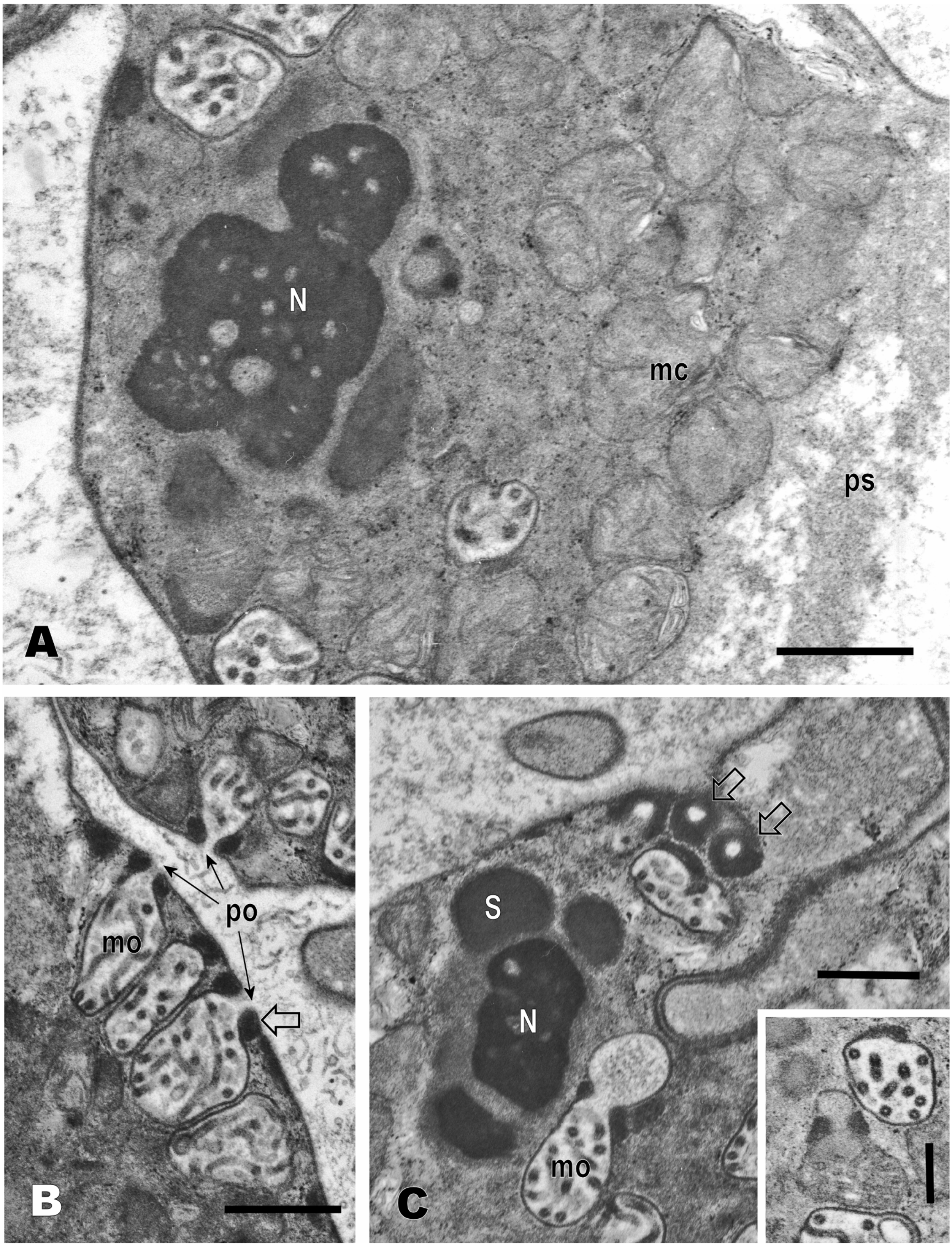

Fig. 3. TEM of *Brevibucca* sp., mature spermatozoa. A: The spermatozoon main cell body with lobate nucleus (N) and cluster of mitochondria (mc) at the base of the pseudopod (ps). B: Empty membranous organelles (mo) opened to the exterior *via* pores (po); note osmiophilic material (hollow arrow) at the base of each pore. C: Spermatozoon main cell body; hollow arrows show tangential sections through osmiophilic rings surrounding ducts of membranous organelles. Abbreviations: mo = membranous organelle; N = nucleus; S = nuclear satellite. Inset in C: the intact membranous organelle with dense content. Scale bars: A-C = 0.5 μm; inset in C = 0.25 μm.

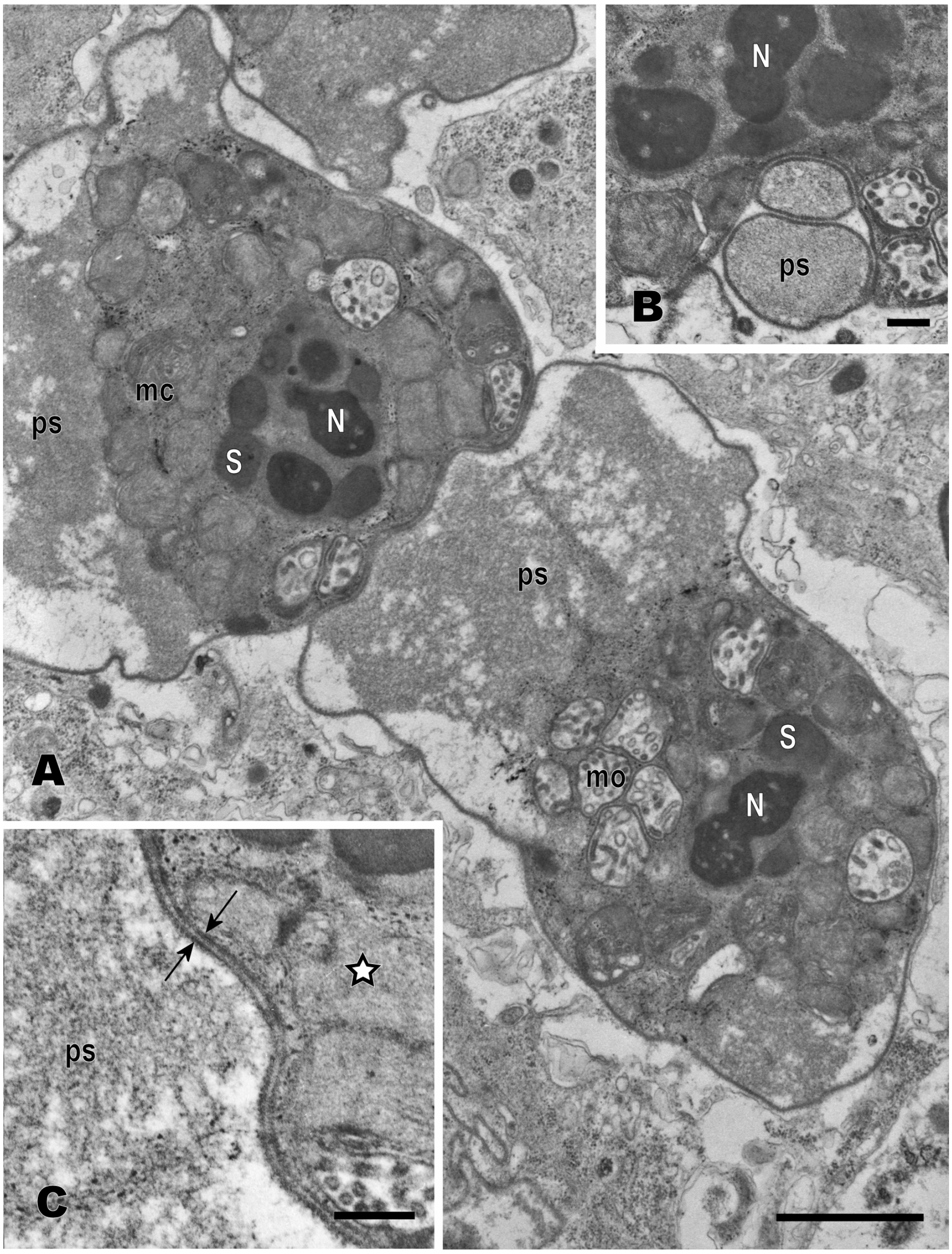

Fig. 4. TEM of *Brevibucca* sp., mature spermatozoa. A: Two spermatozoa in the uterus lumen forming a chain. B: Pseudopod protuberances (ps) in close contact with neighbouring spermatozoon within the spermatheca. C: Border (arrows) between the pseudopod (ps) and the main cell body (asterisk) of two spermatozoa forming a chain within the uterus lumen. Scale bars: A = 1 µm; B, C = 0.25 µm. Abbreviations: mc = mitochondria; mo = membranous organelles; N = nucleus; ps = pseudopod; S = nuclear satellites.

in that they are less dense than the nuclear chromatin.

The spherical or polygonal mitochondria are 0.4-0.5 µm diam. and have a dense matrix crossed by lamellar cristae (Figs 2A; 3A). Mitochondria occur throughout the cytoplasm of the main cell body and tend to be clustered at the base of the pseudopod (Fig. 3A).

The membranous organelles (MO) are empty peripheral vesicles *ca* 0.5 µm diam. with finger-like invaginations of the outer membrane (Figs 2B; 3B). Usually each MO is joined to the plasmalemma of the main cell body and opens to the exterior *via* a pore. The short duct joining the MO with an opening is surrounded by a thick osmiophilic ring 0.3 µm diam. (Fig. 3B, C). The cytoplasm of the main cell body also contains occasional MO with intact electron-dense content and a characteristic knob (Fig. 2A; inset in 3C).

The pseudopod is a well-defined part of each spermatozoon characterised by pale cytoplasm devoid of organelles (Figs 1, 2 A; 3 A; 4 A). The pseudopods have irregular contours and contain only fibrous material; they may be in close contact with neighbouring spermatozoa within the spermatheca (Figs 2A, B; 4B).

The spermatozoa found in the uterus lumen are capable of forming a chain of several cells where each pseudopod (except the leading cell) joins with the main cell body of an adjacent spermatozoon (Fig. 4A). The place of adhesion of each pseudopod to the adjacent cell is organised as a specialised cell junction where the intercellular space is only 10 nm wide and adjoining membranes seem to be thickened (Fig. 4C).

The surface of the spermatozoa is smooth; filopodia were never observed extending from the main cell bodies or pseudopods.

DISCUSSION

The size, shape and general structure of mature spermatozoa found in *Brevibucca* sp. are usual for many rhabditid nematodes. This type of sperm structure has been described in representatives of several higher taxa of the 'rhabditids': Spiruromorpha, Ascaridomorpha, Panagrolaimomorpha, Tylenchomorpha, Rhabditomorpha (Justine & Jamieson, 1999; Justine, 2002; Yushin & Malakhov, 2004; Yushin *et al*., 2006, 2007A, B; Yushin & Ryss, 2011). Usually these are amoeboid cells about 5 μm diam. (4-4.5 μm in *Brevibucca*) with distinct polarization into a pseudopod and a main cell body. The standard main cell body components include a nucleus, mitochondria and membranous organelles.

Each nucleus is usually a bean-shaped or lobated body composed of highly condensed chromatin. In some rhabditids and several other nematode taxa the nuclear chromatin may be less condensed and consist of particles or threads (Justine & Jamieson, 1999). In the spermatozoa of some rhabditids the special dense matter enveloping the nucleus contains nuclear satellites as homogeneous oval bodies (Yushin *et al*., 2006, 2007A, B). The satellites also surround the nucleus of each *Brevibucca* sp. sperm.

A large number of mitochondria of usual structure that are found in *Brevibucca* sp. sperm is also characteristic of many rhabditid nematodes as well as for nematodes of other taxa (Justine & Jamieson, 1999; Justine, 2002). The spherical or polygonal mitochondria with distinct lamellar cristae tend to be concentrated at the pseudopod base, possibly reflecting their metabolic role in pseudopod motility (McLaren, 1973; Burghard & Foor, 1975; Shepherd & Clark, 1976; Wolf *et al*., 1978; Sepsenwol *et al*., 1989; Yushin & Malakhov, 1994; Yushin, 2003; Yushin *et al*., 2006; 2007B).

Usually membranous organelles (MO) of nematode mature spermatozoa are 0.4-1.0 μm diam. (0.5 μm in *Brevibucca* sp.) empty sacs that open into the exterior *via* pores. The transparent content of each sac is crossed by specific finger-like projections of the outer membrane which thus provides the membranous organelles with a unique cytological character. It is interesting that these nematode MO resemble the membranous components of highly modified spermatozoa of mites and diplopods (Baccetti *et al*., 1974; Alberti & Coons, 1999). In nematodes the neck that joins the MO to a pore may provide strength as a dense collar (Justine, 2002). In *Brevibucca* sp. these collars are well developed and appear as osmophilic doughnut-shaped rings each with a narrow opening (Fig. 3C).

Intact MO with characteristic knob and dense content, as found in the mature spermatozoa of *Brevibucca* sp., have also been observed in activated spermatozoa of some other nematodes (Justine & Jamieson, 1999; Yushin & Ryss, 2011).

The prominent pseudopod of *Brevibucca* sp. sperm is devoid of cytoplasmic components except the cytoskeleton fibres. The pseudopods of this type are well known for spermatozoa of the rhabditids and other nematode taxa; the fibres of the cytoskeleton are composed of specific protein (MSP) basic for the cell amoeboid movement (Justine, 2002).

The spermatozoa found in the spermatheca and the uterus of *Brevibucca* sp. were in close contact. The pseudopods possibly have adhesive properties that join to the main cell body of a neighbouring spermatozoan; these adhesive properties unite *in utero* spermatozoa into chains. The characteristic sperm chains are composed of up to 25 spermatozoa and are capable of coordinated movement toward the spermatheca, as observed in the rhabditid nematodes from the genus *Steinernema* (Hess & Poinar, 1989; Spiridonov *et al*., 1999, 2004). This close cooperation of male gametes was possibly the basis of the development of giant movable spermatozeugmata in several species of Steinernematidae (Spiridonov *et al*., 1999; Yushin *et al*, 2007B).

The family Brevibuccidae was considered as the *insertae sedis* taxon by De Ley and Blaxter (2002) and cannot be unequivocally positioned with any other taxa of the rhabditids using morphological and molecular analysis (Lorenzen, 1994; Felix *et al*. 2000; Holterman, 2006; Meldal *et al*., 2007; Van Megen *et al*., 2009). However, Hodda (2007) proposed placing within the order Diplogasterida, the isolated suborder Brevibuccina containing Brevibuccidae.

Comparative analysis of the rhabditid spermatozoa shows little potential for phylogenetic conclusions including support for the phylogenetic position of *Brevibucca* sp. within the order Rhabditida. The structure and development of the rhabditid sperm is somewhat conserved with a general pattern of spermatozoon recognized as "rhabditid" and as described in Spiruromorpha, Ascaridomorpha, Panagrolaimomorpha, Tylenchomorpha and Rhabditomorpha with variations providing few pointers for phylogenetic analysis (Justine & Jamieson, 1999; Justine, 2002; Yushin *et al*., 2006, 2007A, B; Yushin & Ryss, 2011). The spermatozoa of the rhabditid pattern observed also in *Brevibucca* sp. may be considered as the ancestral or symplesiomorphic character for several clades of the order Rhabditida. As a result, the male gamete structure cannot elucidate well the taxonomical position of Brevibuccidae.

Notably, however, several rhabditid taxa demonstrate a high degree of deviation in spermatozoon structure and spermatogenesis; these deviations may be considered as cytological features of great importance for phylogenetic analysis. In the rhabditid superfamily Tylenchoidea (Tylenchomorpha) MO were not found in the mature spermatozoa; numerous fibrous bodies fill the spermatozoon cytoplasm (Justine, 2002). The absence of MO is a distinct cytological feature that separates Tylenchoidea (Hoplolaimidae, Meloidogynidae, Pratylenchidae) from related superfamilies of the tylenchomorphs such as Aphelenchoidea and Sphaerularioidea, where the typical rhabditid pattern of spermatozoa has been observed (Shepherd & Clark, 1976; Yushin *et al*., 2006, 2007A, B; Yushin & Ryss, 2011). The unique structure and development of spermatozoa in Oxyuridomorpha and Rhigonematomorpha also may be used for demarcation of these taxa inside the order Rhabditida (Justine & Jamieson, 1999; Yushin & Spiridonov, 2001; Justine, 2002).

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V. V. Yushin, M. Claeys, W. Houthoofd. Зрелые сперматозоиды *Brevibucca* sp. (Nematoda: Rhabditida: Brevibuccidae).

Резюме. Строение зрелых сперматозоидов нематоды *Brevibucca* sp. (Brevibuccidae, Rhabditida) изучено с помощью электронного микроскопа. Как и у других нематод, сперматозоиды *Brevibucca* sp. представляют собой аберрантный тип мужских гамет, характеризующийся отсутствием аксонемы и акросомы. Зрелые сперматозоиды *Brevibucca* sp. – это амебоидные биполярные клетки диаметром около 4-4.5 мкм, подразделяющиеся на главное тело клетки (ГТК) и псевдоподию, лишенную органелл. ГТК включает компактное ядро, множество митохондрий и т.н. «мембранные органеллы» (МО). Эти уникальные органеллы характерны как для развивающихся, так и для зрелых сперматозоидов самых разных нематод. МО у *Brevibucca* sp. – это довольно крупные (диаметром 0.5 мкм) пузырьки с прозрачным содержимым и системой внутренних пальцевидных выростов наружной мембраны. Каждая МО примыкает к плазмалемме ГТК сперматозоида и открывается наружу порой. Сперматозоид имеет хорошо развитую псевдоподию, заполненную волокнами цитоскелета. Сперматозоиды описанного типа характерны для множества таксонов «рабдитид»; такой «рабдитидный» тип сперматозоидов следует рассматривать как симплезиоморфный для целого ряда клад отряда Rhabditida.