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Ultrastructure of Spermatozoa in the Nematode *Halalaimus dimorphus* (Nemata: Oxystominidae)

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Abstract: The ultrastructure of spermatozoa in the free-living marine nematode *Halalaimus dimorphus* was studied with transmission electron microscopy. Spermatozoa in the posterior testis of the male had a large cavity filled with cellular processes, which contained a variable number of small tubules. Mitochondria and small tubules were the only cell structures observed in the cytoplasm. The spermatozoa had a bipolar structure. The anteriorly situated nucleus, which was electron-dense and homogeneous, was surrounded by a single membrane. The size of the small tubules in the cytoplasm (diam. 12-13 nm) and their relatively thick wall structure suggested that they were not normal microtubules (diam. 25 nm). The material of the small tubules was assumed to be major sperm protein (MSP). The cavity appeared to open on the surface of the spermatozoon at the posterior extremity of the cell, and also medially, at the level of the anterior end of the cavity. The pores apparently were closed by a special plug-like structure, which was an evagination of the cell. The wall of the cavity was characterized by longitudinal folds, which were mushroom-shaped in transverse section. Spermatids in the anterior testis of *H. dimorphus* were characterized by fibrous bodies packed with small tubules and by cellular processes also containing small tubules. *H. dimorphus* sperm seem to perform swimming movements based on liquid currents commonly present in turbin-like systems. Spermatogenesis resembled that found in ticks.

Key words: Halalaimus dimorphus, marine nematode, nematode, reproduction, sperm, spermatogenesis, tick, ultrastructure.

Nematode sperm is unique in lacking both flagellum and acrosome. Aflagellate sperm are common only in certain Platyhelminthes and Arthropoda and occasionally in a few other groups (Baccetti et al., 1983).

Morphologically, nematode sperm show a high degree of structural diversity (Baccetti et al., 1983; Bird and Bird, 1991; Foor, 1970; Mansir and Justine, 1995). Baccetti et al. (1983) divided nematode sperm into the following types: (i) sperm found in the enoploid genus *Mesacanthion,* characterized by a nuclear envelope, few mitochondria, and many membranous organelles (MO) (= membranous vesicles, for other synonyms see Bird and Bird, 1991; Takahashi et al., 1994); (ii) rounded, amoeboid spermatozoa devoid of a nuclear envelope but containing mitochondria, membranous organelles, filaments, microtubules, and often centrioles or ascaridin granules, found in more specialized Enoplida and in Rhabditida, Strongylida, Ascarida, Spirurida, and Trichinellida; and (iii) sperm devoid of membranous organelles (Tylenchida and Dorylaimida) or mitochondria (Monochida, Dioctophymatida, Rhigonematida). Sperm of the ascarid genus *Aspicularis* also lack MOs but have a large mitochondrial complement. Tylenchida usually lack MOs and are characterized by numerous filopodia covering the cell surface (Bird and Bird, 1991; Cares and Baldwin, 1994; Shepherd and Clark, 1983; Shepherd et al., 1973).

In nematode sperm a special protein (major sperm protein, MSP) has been described that has not yet been found in other animals. This protein may be involved in formation of the cytoskeleton and pseudopods in amoeboid sperm (Theriot, 1996). Compared with other phyla, nematode sperm structure is unusually diverse. A case in point is that of the free-living marine nematode *Halalaimus dimorphus* Turpeenniemi, 1997 (Enoplida), which was described from

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the Baltic Sea. This species is unique in having both egg and sperm dimorphism (Turpeenniemi, 1997). The anterior testis contains large, longitudinally striated sperm. Sperm in the posterior testis appear similar in LM but are smaller in size. The purpose of this study was to describe the ultrastructure of this sperm.

Materials and Methods

The material for this study was collected in the Bothnian Bay, northern Baltic Sea, at a depth of 12 m, close to Station 2 (Turpeenniemi, 1995). Fixation in glutaraldehyde, postfixation in OsO_4, dehydration in aceton, infiltration in epon, sectioning, and staining with lead citrate and uranyl acetate were as previously described (Turpeenniemi, 1993). Thin sections were viewed with a Zeiss EM 900 at 80 kV.

Results

The male reproductive system of the marine nematode *Halalaimus dimorphus* (Fig. 1) consisted of two outstretched testes of different sizes (Fig. 2). The anterior testis was larger and produced larger sperm than the posterior testis (Fig. 2). In LM, the large and small sperm types had a similar, bipolar structure (Figs. 3,4). The nucleus was situated at the anterior, more rounded end of the sperm (Figs. 2–5). The posterior end of the sperm was characterized by longitudinal striations (Figs. 3–5). In females, spermatozoa were arranged in parallel with the nuclear end toward the oocyte (Fig. 3). In vas deferens, the nuclear end of the spermatozoon was oriented toward the cloaca (Fig. 5).

The spermatogonia and spermatozoa were tightly packed within the posterior testis (Figs. 6,7). The spermatogonium was characterized by a large nucleus enclosed within a nuclear envelope (Fig. 6). Spermatids in the anterior testis contained cisternae, cellular processes, fibrous bodies, endoplasmic reticulum, and many vesicles (Fig. 8). Small tubules were arranged in parallel in fibrous bodies, and they occurred also in the cellular processes (Fig. 8). The nucleus

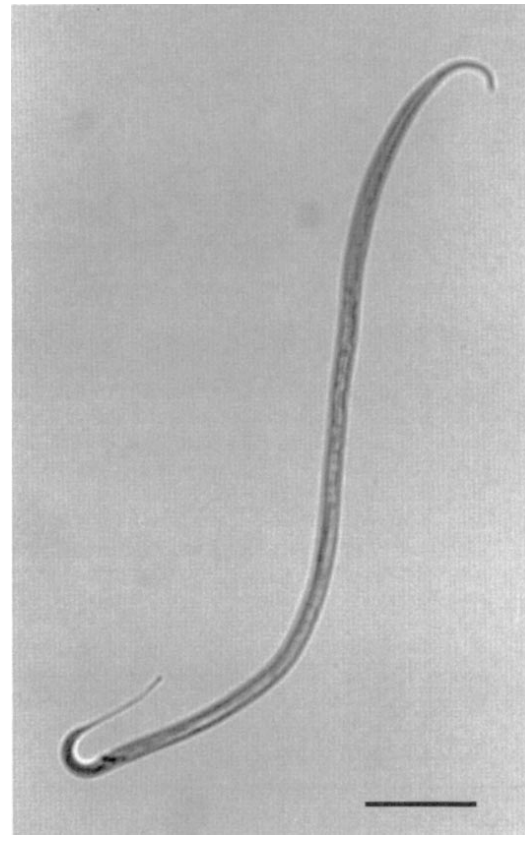

Fig. 1. *Halalaimus dimorphus.* Total view of male. Scale bar = 100 µm.

of spermatid was large, heterogeneous, and enclosed by a nuclear membrane connected to the rough endoplasmic reticulum (RER).

The plasma membrane of spermatozoa was smooth, i.e. devoid of evaginations or invaginations (Figs. 4,7,9–12). Only occasionally were short evaginations observed between abutting cells (Figs. 9A,11A). Beneath the plasma membrane was a row of longitudinally oriented cortical small tubules (Figs. 4,7,9–12). The electron-dense granules observed in the testicular cells appeared to be absorbed by the spermatozoa (Figs. 7,10B). The cytoplasm of spermatozoa was characterized by many mitochondria and an extensive network of small tubules (Figs. 4,7,9–12).

The nucleus was enclosed by a single membrane, with an appearance similar to that of the plasma membrane (Figs. 4,7,9A). The content of the nucleus was homogeneous and electron-dense (Figs. 7,9A). Pos-

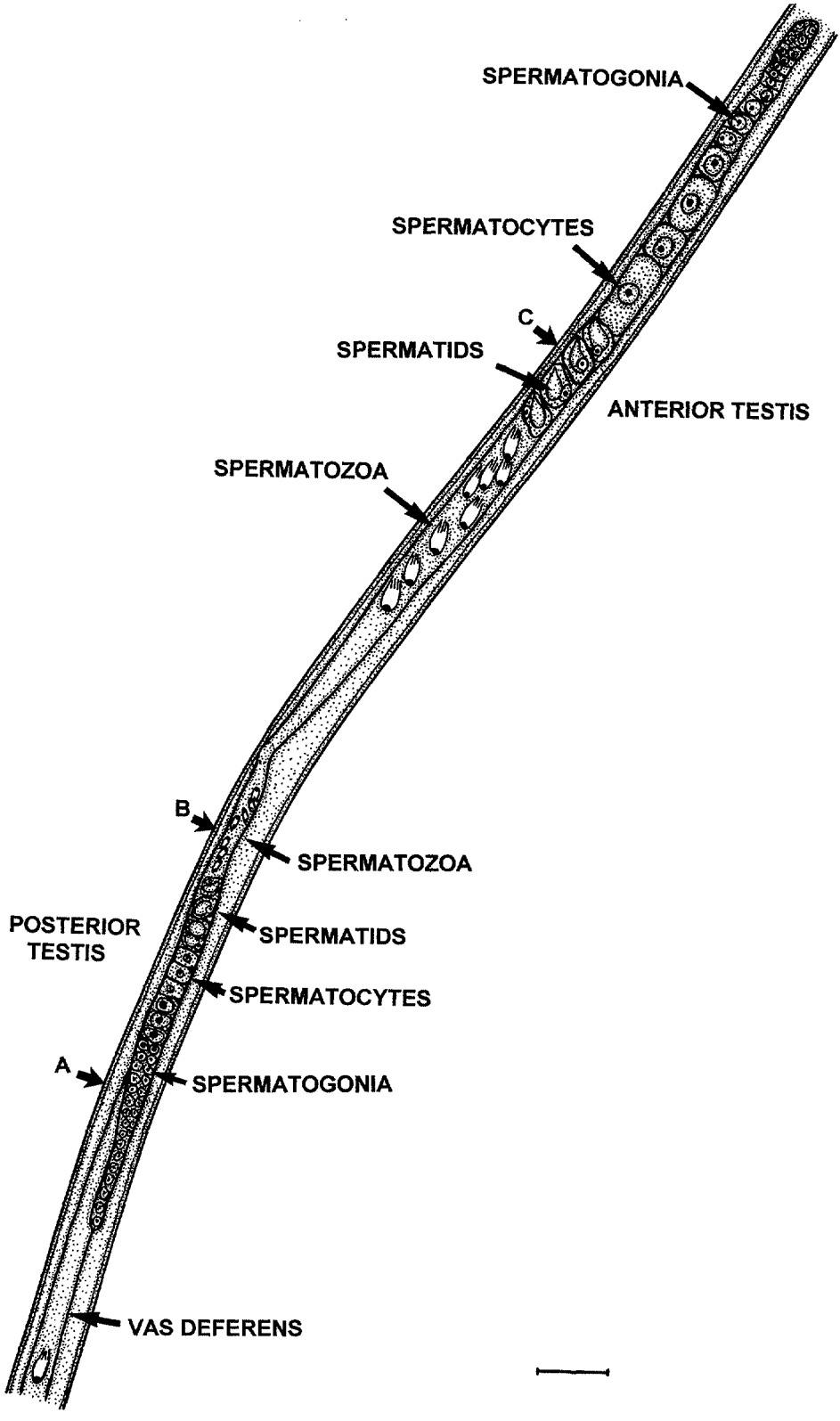

FIG. 2. *Halalaimus dimorphus.* Schematic drawing showing the anterior and posterior testis and part of vas deferens. Note a single spermatozoon in the vas deferens. Transverse sections for electron microscopy were taken at levels A, B, and C. Scale bar = 20 μm.

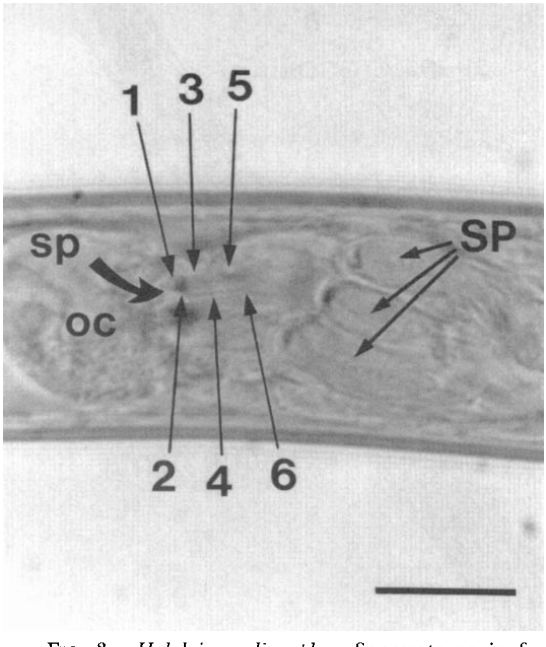

FIG. 3. *Halalaimus dimorphus.* Spermatozoa in female reproductive system. The numbers (1–6) indicate the regions shown in electron micrographs in Figs. 7, 12. (oc = oocyte, sp = small spermatozoon, SP = large spermatozoa). Scale bar = 10 µm.

terior to the nucleus was a large cavity filled with cellular processes containing various numbers of small tubules (Figs. 4,7,9B, 10,11). The cellular processes branched often (Figs. 7,10,11A). In the finest cellular processes small tubules were often irregular (Figs. 9B,10,11). The size of small tubules was clearly smaller than the size of the normal microtubules occurring in the longitudinal nerve (Fig. 11A). The diameter ofsmall tubules in spermatids and spermatozoa was 12–13 nm (Figs. 7–12). The wall of the internal cavity was characterized by longitudinal folds (Figs. 4,7,9B,10–11), which were mushroom like in transverse sections (Figs. 7,9B,10–12). The cavity appeared to open both medially and posteriorly to the surface of the spermatozoon through pores, which seemed to be closed by special plug-like structures, the evaginations of the cell (Figs. 11,12).

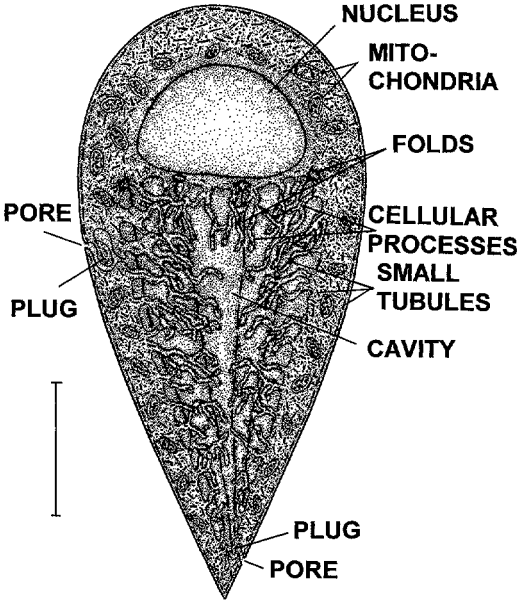

FIG. 4. *Halalaimus dimorphus.* Schematic drawing of small spermatozoon. Scale bar = 1 µm.

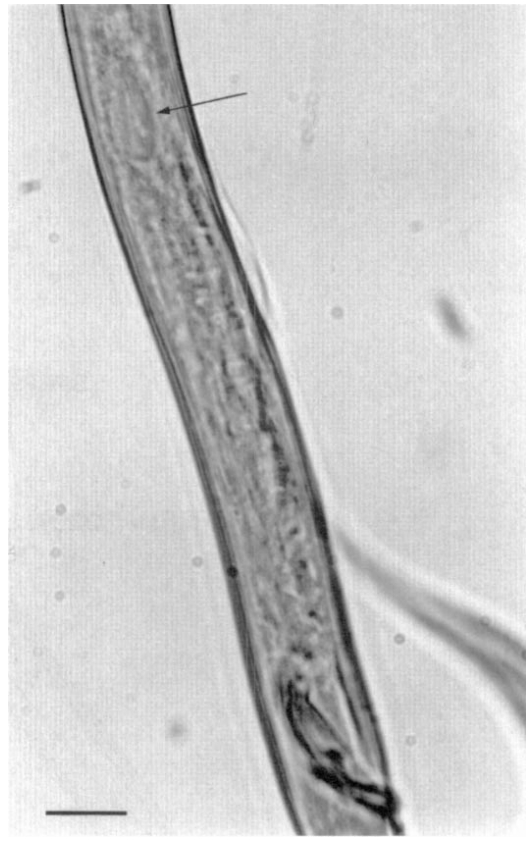

FIG. 5. *Halalaimus dimorphus.* Posterior region of male. Note a large spermatozoon (arrow) in vas deferens. Scale bar = 10 µm.

DISCUSSION

The ultrastructure of the spermatozoon in *Halalaimus dimorphus* indicates that it is

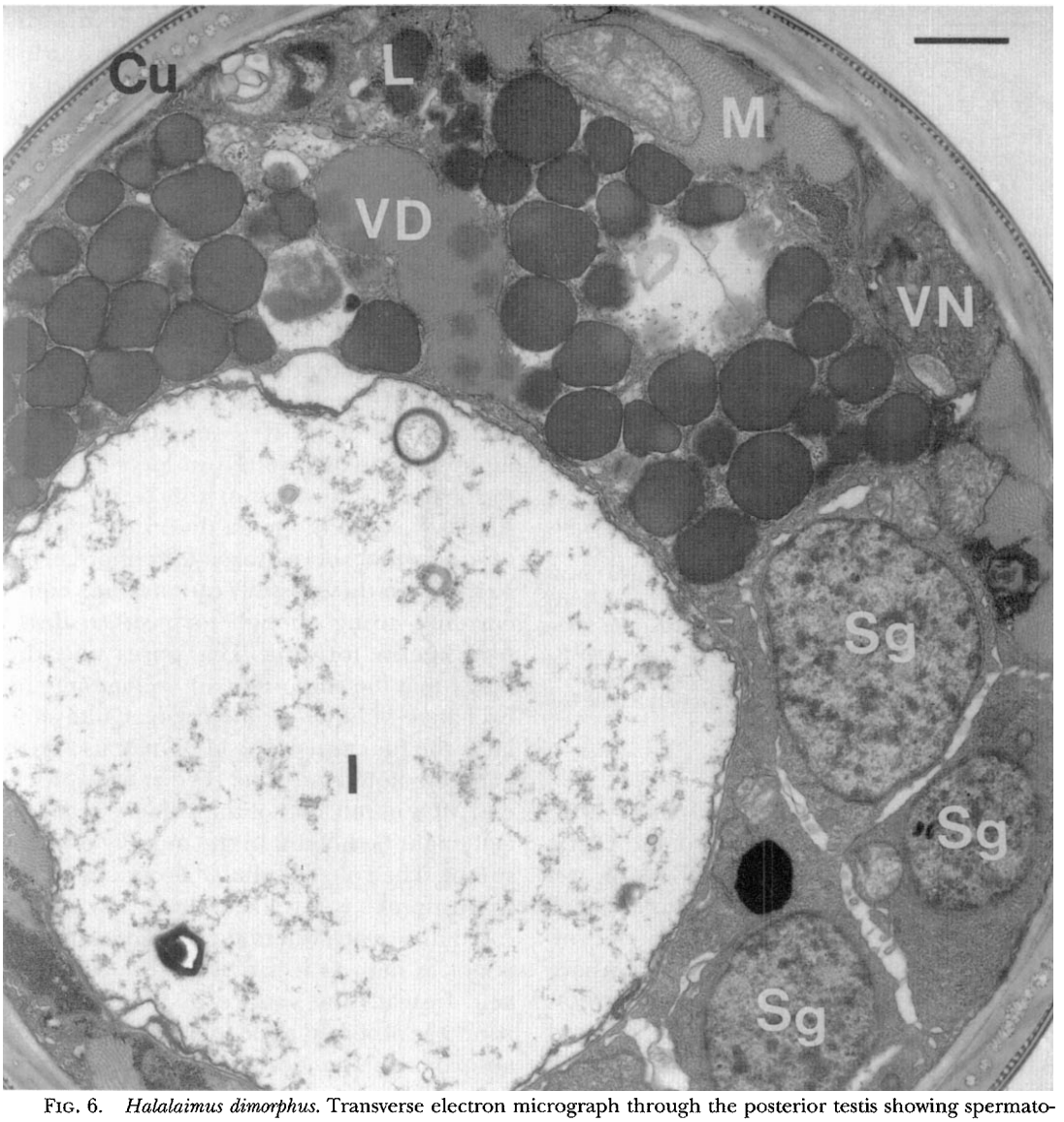

FIG. 6. *Halalaimus dimorphus.* Transverse electron micrograph through the posterior testis showing spermatogonia (Sg) and vas deferens (VD). Note the large nuclei in the spermatogonia and the degenerate epithelial cells of the intestine (I). (Cu = cuticle, L = lateral cord, M = muscle cell, VN = ventral nerve cord.) Scale bar = 1 μm.

aflagellate (Baccetti and Afzelius, 1976). In LM the spermatozoa resemble "flagellate" or striated sperm, which is very rare in nematodes (Bird and Bird, 1991). The striated sperm have been previously described in *Tobrilus* spp., *Syringolaimus* spp., and in some members of trichodorids (Bernard, 1992; Bird and Bird, 1991; Chitwood, 1931; Riemann, 1983).

The spermatozoa of *H. dimorphus* differ from all other studied nematode sperm in having a large internal cavity filled with cellular processes. The membranous organelles (MO) typical of such groups as Ascarida, Enoplida, Rhabditida, and Monhysterida (Baccetti et al., 1983; Hess and Poinar, 1989; Nicholas and Stewart, 1997; Noury-Srairi et al., 1993; Yushin and Malakhov, 1994) also contain microvillus-like structures (Beams and Sekhon, 1972; Bird and Bird, 1991; Foor, 1968; Shepherd et al., 1973; Yushin and Malakhov, 1994), which resemble the finest cellular processes of *H. dimorphus* and the filopodia of plant-

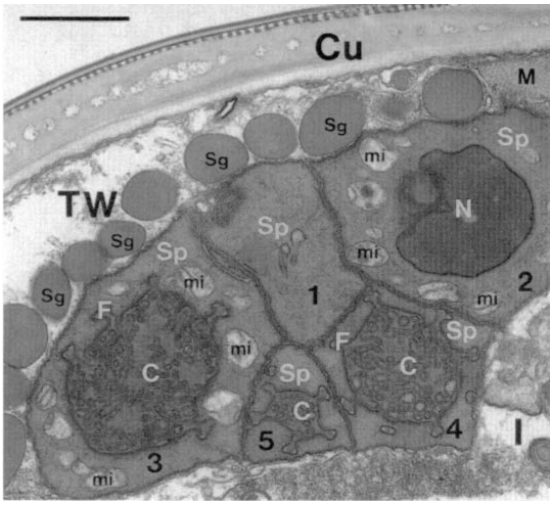

FIG. 7. *Halalaimus dimorphus.* Transverse electron micrograph showing spermatozoa (Sp) from the posterior testis. The two uppermost spermatozoa are sections through the anterior (left) and posterior (right) margin of the nucleus (N). The lowest three spermatozoa represent sections posterior to the nucleus (the numbers indicate levels in Fig. 3). (C = cavity, Cu = cuticle, F = fold, I = intestine, mi = mitochondrion, M = muscle cell, Sg = secretory granule, TW = testis wall.) Scale bar = 1 μm.

parasitic nematodes (Bird and Bird, 1991; Shepherd et al., 1973; Shepherd and Clark, 1983). These structures are all 60–80 nm wide and provided with one tubule. Thick cellular processes with more than one tubule and branched cellular processes have occasionally been described also in the MOs or filopodia of other nematodes (Cares and Baldwin, 1994; Neill and Wright, 1973; Noury-Srairi et al., 1993; Shepherd and Clark, 1983). In living spermatozoa the filopodia flicker continuously, resembling ciliary movement (Shepherd et al., 1973).

The function of the membranous organelles and filopodia is not known (Baccetti et al., 1983; Bird and Bird, 1991). In inseminated sperm the MOs migrate to the periphery of the cell and open on the surface of the spermatozoon through a pore, the pseudopod enlarges, the cell becomes bipolar, and the sperm become motile (Shepherd and Clark, 1983; Ward and Carrel, 1979; Ward et al., 1983; Wright and Sommerville, 1984). There seem to be three functions of the large pseudopod: (i) to attach the spermatozoon to the uterine wall; (ii) to attach, push, and puncture the oolemma in fertilization; and (iii) to pull the sperm during amoeboid locomotion (Foor, 1968; Theriot, 1996). In some species that lack MOs, e.g. *H. dimorphus, Aspicularis tetraptera,* and some Tylenchida, the sperm become bipolarized in males (Lee and Anya, 1976; Shepherd and Clark, 1983).

The function of the internal cavity of *H. dimorphus* sperm is not known. It differs from an acrosome by lacking the unit-enclosing membrane, having cellular processes, and being located at the posterior end of the sperm. It is supposed that the internal cavity is involved in locomotion. If the cellular processes in the cavity flicker similarly as the filopodia do on the surface of some other spermatozoa (Shepherd et al., 1973), then they possibly can produce liquid currents strong enough to push *H. dimorphus* sperm forward. The pores and the plugs may be important in facilitating the exchange of liquid in the cavity. Quite similarly, the function of the MOs may also be to generate liquid currents. The activity of several MOs in one end of the amoeboid sperm cell might be helpful in the motility of these sperm. The role of cellular processes in nutrient uptake is not likely since they are located in a cavity, where the level of nutrients is not as high as it is on the surface of the cell. Instead, the surface of the spermatozoon was observed to be involved in material absorption. The occurrence of mitochondria in *H. dimorphus* sperm supports the opinion that these cells are motile cells. In general, sperm types devoid of mitochondria seem to be nonmotile in other groups (Baccetti and Afzelius, 1976). The energy produced by mitochondria is evidently used in the movements of cellular processes since pseudopod formation is low or totally absent. The evidence indicates that there might be an evolution toward increased motility in nematode sperm.

Spermatogenesis in the nematode *H. dimorphus* resembles that found in ticks, which indicate that Nemata and Acarina might be remarkably convergent taxa. Ticks have motile, aflagellate sperm with cellular processes and ultrastructure (Feldman-Muhsam and

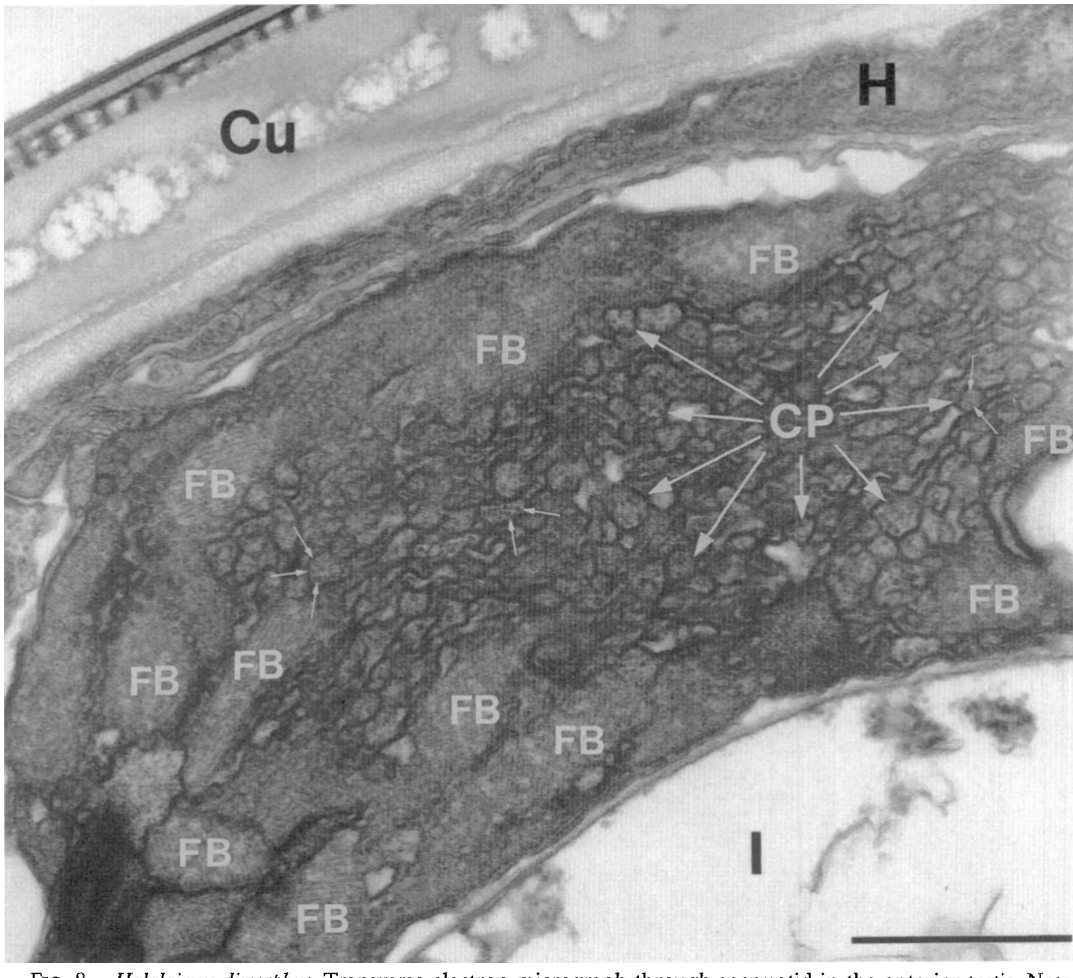

FIG. 8. *Halalaimus dimorphus.* Transverse electron micrograph through spermatid in the anterior testis. Note small tubules in fibrous bodies (FB) and in cellular processes (CP) (small arrows). (Cu = cuticle, H = hypodermis, I = intestine.) Scale bar = 0.5 μm.

Filshie, 1976; Reger, 1961, 1962, 1963), much like those of the finest cellular processes (1–2 tubules) of *H. dimorphus.* The diameters of the cellular processes (50–100 nm) and their tubules (6–9 nm) indicate a close functional relationship between these processes and cellular processes of *H. dimorphus* (Feldman-Muhsam and Filshie, 1976; Reger, 1961; Rothschild, 1961). The cytoskeleton beneath the cellular processes is strikingly similar in the nematode *H. dimorphus* and in ticks. Both contain a mass of anastomosing tubules of almost the same size (Reger, 1962). The spermatids in the anterior testis of *H. dimorphus* resemble tick spermatids in that the cytoplasm contains cellular processes, cisternae, endoplasmic reticulum, mitochondria, and fibrous (nematode) or multivesicular (tick) bodies (Reger, 1962). During spermatogenesis in the tick, Golgi-complex-derived subplasmalemmal cisternae fuse to form a common large cisternum, into which the cellular processes extend from the inside wall of the cisternum (Breucker and Horstmann, 1972; Reger, 1962, 1974). Morphologically, this stage resembles the *H. dimorphus* sperm. Mature tick sperm, however, shows a different morphology (El Shoura, 1986; Feldman-Muhsam and Filshie, 1976; Reger, 1974).

The small tubules in *H. dimorphus* sperm are thinner (diam. 12–13 nm) than normal microtubules (diam. 25 nm), and, probably for this reason, they often have been re-

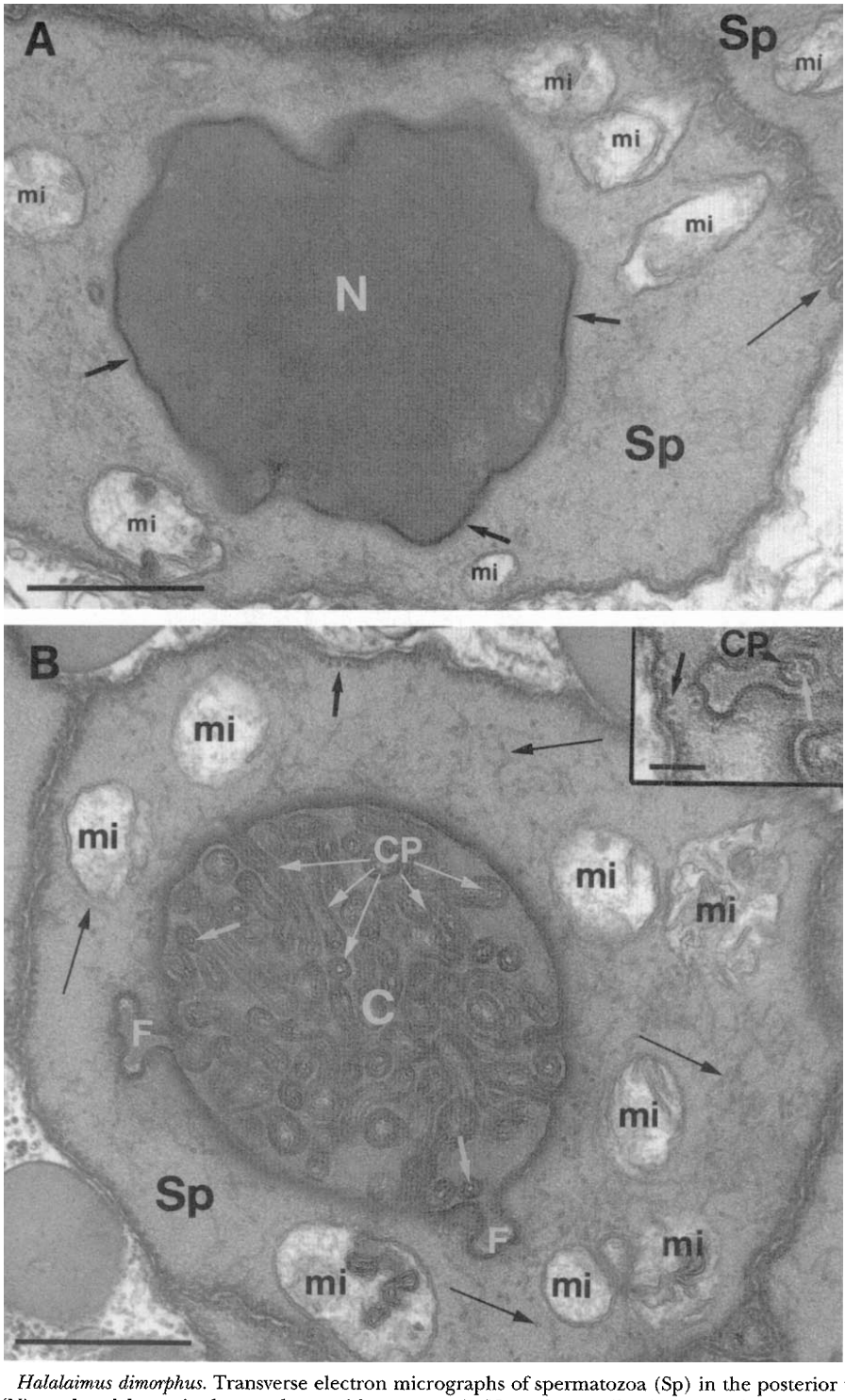

FIG. 9. *Halalaimus dimorphus*. Transverse electron micrographs of spermatozoa (Sp) in the posterior testis. A) Nucleus (N) enclosed by a single membrane (short arrows). Note the small tubules inside a pseudopod-like evagination (long arrow). B) Cavity (C) filled with cellular processes (CP). Small tubules in cellular processes (white arrows), in the cortical cytoplasm (short black arrow), and in other cytoplasm (long black arrows) are also indicated. Scale bar = 0.5 µm. Inset: High magnification showing the identical size of small tubules in the cytoplasm (black arrow) and in the cellular processes (white arrow). Scale bar = 100 nm. (F = fold, mi = mitochondrion, TW = testis wall.)

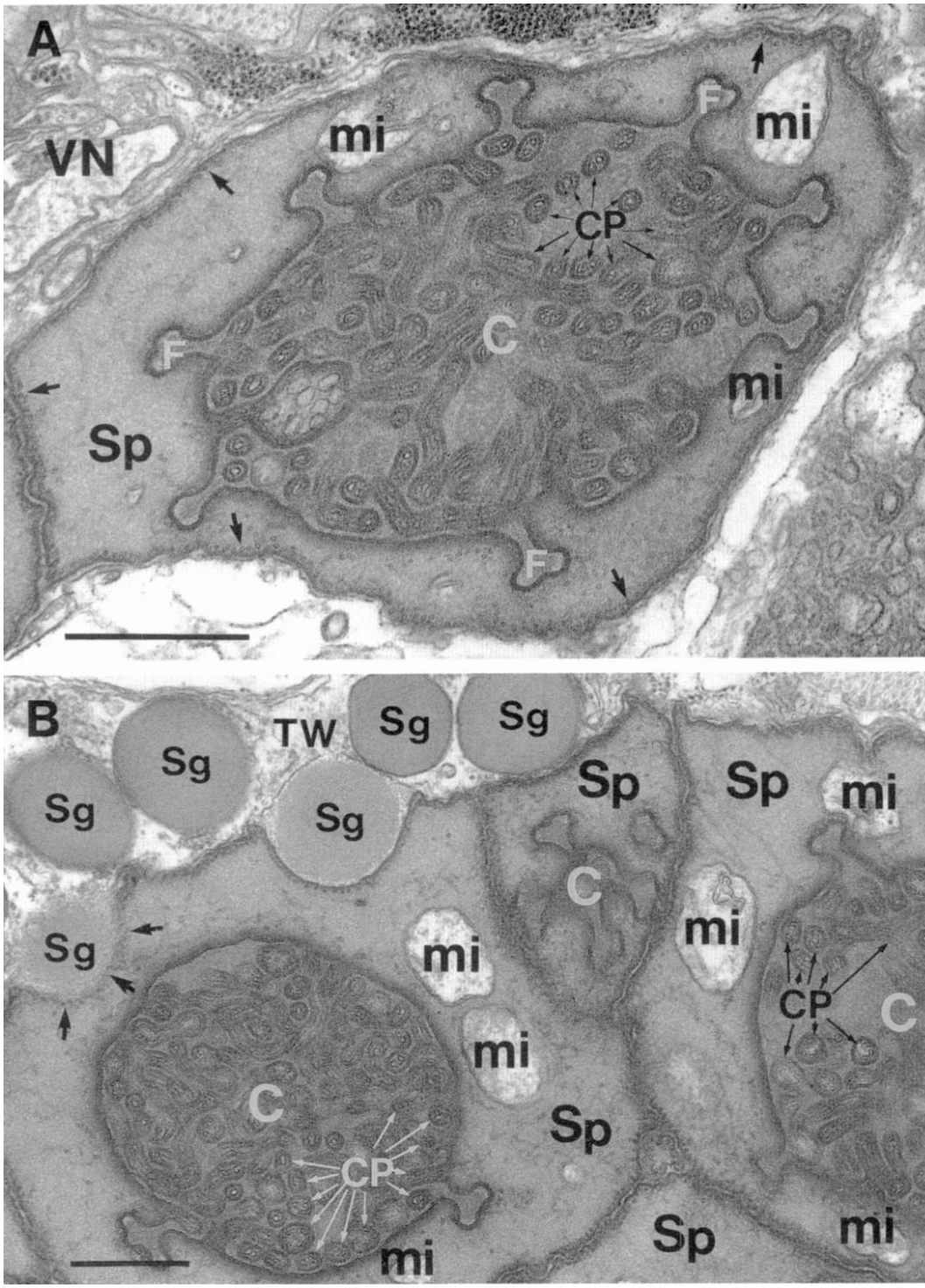

FIG. 10. *Halalaimus dimorphus*. Transverse electron micrographs through the posterior testis. A) Star-shaped cavity (C) containing cellular processes (CP). Note cortical small tubules (short arrows). B) Secretory material (Sg) of the testis wall (TW) absorbed by spermatozoa (Sp). (F = fold, mi = mitochondrion, VN = ventral nerve cord.) Scale bar = 0.5 μm.

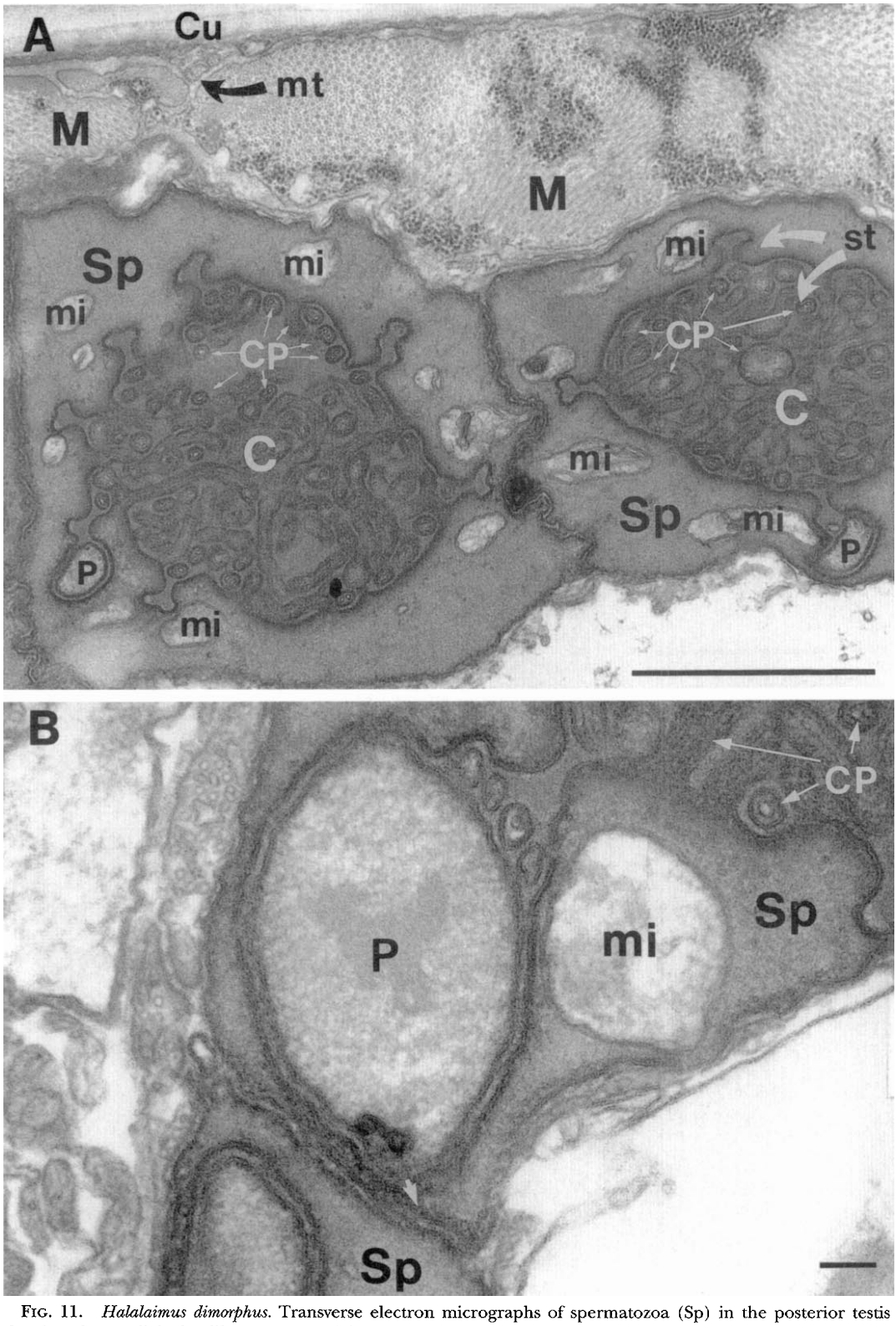

FIG. 11. *Halalaimus dimorphus.* Transverse electron micrographs of spermatozoa (Sp) in the posterior testis showing the medial plug-like structures (P) and the pore. A) Medial plug. Note the size difference between microtubules (mt) (nerve) and small tubules (st) (spermatozoa). Scale bar = 1 µm. B) Medial pore (arrowhead) and the plug. (C = cavity, CP = cellular processes, Cu = cuticle, mi = mitochondrion, M = muscle cell.) Scale bar = 100 nm.

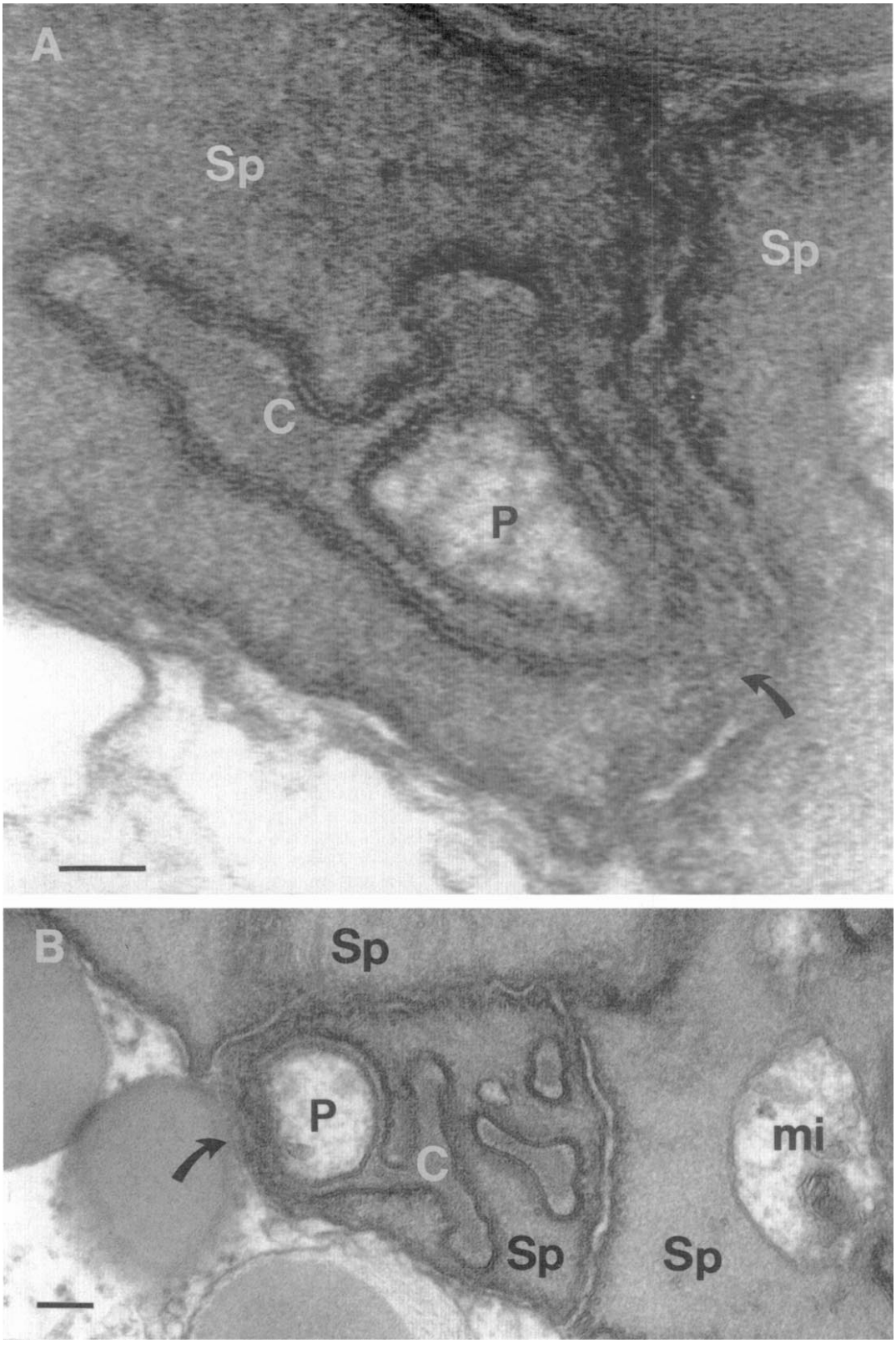

FIG. 12. *Halalaimus dimorphus.* Transverse electron micrographs through posterior ends of spermatozoa (Sp) (section 6 in Fig. 3), posterior testis. A) High magnification indicating the posterior pore aperture (arrow) and the posterior plug (P). Scale bar = 50 nm. B) Posterior plug (P) and the posterior pore (arrow). Scale bar = 100 nm. (C = cavity, mi = mitochondrion.)

ferred to as filaments (Baccetti et al., 1983), fibers (Yushin and Malakhov, 1994), or cytoplasmic tubular elements (Neill and Wright, 1973; Shepherd and Clark, 1983; Takahashi et al., 1994). They seem to be connected to the plasma membrane by fine filaments, resembling the Y-links of the flagella (Baccetti and Afzelius, 1976). The cortical tubules of *H. dimorphus* and other nematode sperm appear to be a general feature of all aflagellate sperm (Baccetti and Afzelius, 1976; Baccetti et al., 1983). Actin filaments are not present in the cytoplasm of *H. dimorphus* sperm. There is general agreement that nematode sperm contain almost no actin (Mansir and Justine, 1996; Theriot, 1996), comprising only 0.5% of the total sperm protein in a few 5-nm-wide filaments (Baccetti et al., 1983). In addition, it is widely accepted that normal microtubules are rare in mature nematode sperm (Baccetti et al., 1983; Mansir and Justine, 1995, 1996).

Nematode sperm contain a special protein commonly identified as major sperm protein (MSP), which has been studied mainly in ascarids and rhabditids (Mansir and Justine, 1996; Roberts and Stewart, 1995; Theriot, 1996). MSP has not yet been found in other cell types or in other animals but is the most abundant protein in nematode sperm, making up about 15% of the total cell protein in both *Caenorhabditis elegans* and *Ascaris* sp. (Theriot, 1996). In amoeboid nematode sperm the early stages of development contain actin and microtubules, but actin and tubulin are discarded in a residual body during spermatogenesis (Roberts and Stewart, 1995). MSP is not synthesized until the midpoint of spermatogenesis, in spermatocytes, where it is packed in fibrous bodies and released at the spermatozoon stage to make the cytoskeleton of the cell and pseudopods (Mansir and Justine, 1996; Roberts and Stewart, 1995; Theriot, 1996). Structurally, MSP is formed from 2- to 3-nm-thick primary filaments (Kimble and Ward, 1988). It is assumed that small tubules are formed from these primary filaments.

Halalaimus dimorphus sperm is similar to the enoplid sperm of *Mesacanthion* spp. and *Enoplus* spp. in having a nucleus enclosed by an envelope (Nicholas and Stewart, 1997; Yushin and Malakhov, 1994). Nematode sperm usually is devoid of a nuclear envelope (Baccetti and Afzelius, 1976). In *H. dimorphus* sperm, however, the nuclear membrane is a single membrane and clearly differs from the usual nuclear envelope.

In conclusion, these studies indicated that *H. dimorphus* has a sperm type that has not been described earlier. The spermatozoa contain an anterior nucleus bound by a single membrane and a voluminous cavity filled with numerous cellular processes containing small tubules that may be formed from MSP. The cavity apparently opens both posteriorly and medially to the surface of the spermatozoon, allowing liquid input and output from the cavity. These cells may have a unique mode of locomotion; they seem to perform swimming movements based on liquid currents commonly present in turbinlike systems.

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