

FINE STRUCTURE OF MALE GENITAL SYSTEM AND SPERM IN SOLIFUGAE DOES NOT SUPPORT A SISTER-GROUP RELATIONSHIP WITH PSEUDOSCORPIONES (ARACHNIDA)

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ABSTRACT. Comparative spermatology may provide characteristics that can be useful in systematics. Previous observations on sperm structure of the solifugid *Eusimonia mirabilis* revealed that the most similar arachnid sperm cells are found within the Actinotrichida (Acari). The general morphology of the testis and the tendency to form sperm aggregates are also similar in both taxa. Since knowledge of sperm in Solifugae until now came only from one species, in contrast to Acari in which all the higher taxa have been investigated, these characters were difficult to assess with regard to systematical implications. The present paper confirms the derived, simple-aflagellate structure of sperm in Solifugae and the similarity with sperm of Actinotrichida, presenting results for two further species of another family (Ammotrechidae) from Argentina. Sperm cells of representatives of both taxa are small, devoid of a flagellum, contain a chromatin body that is penetrated and surrounded by circles of the acrosomal filament, and have a tendency to form peripheral protuberances. Sperm morphology does not support the frequently suggested sister-group relationship between Solifugae and Pseudoscorpiones.

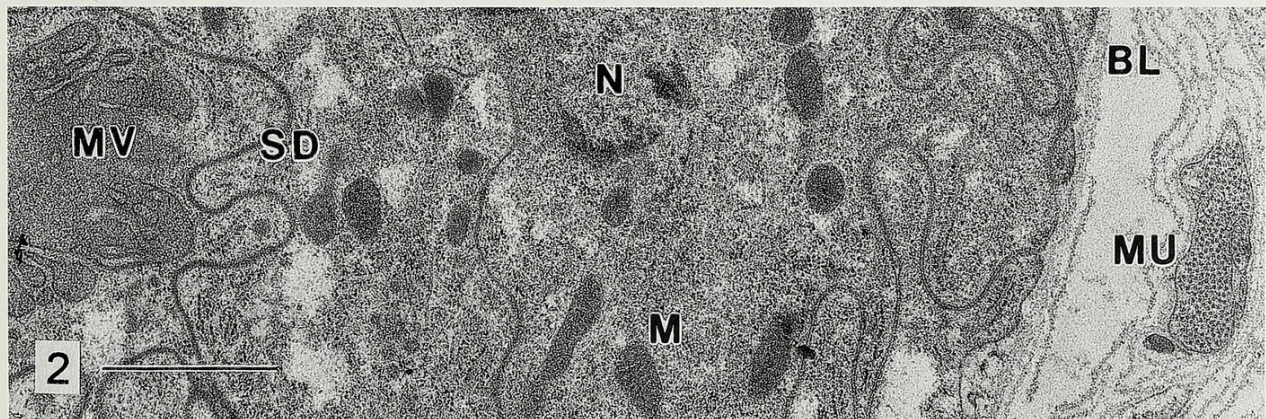
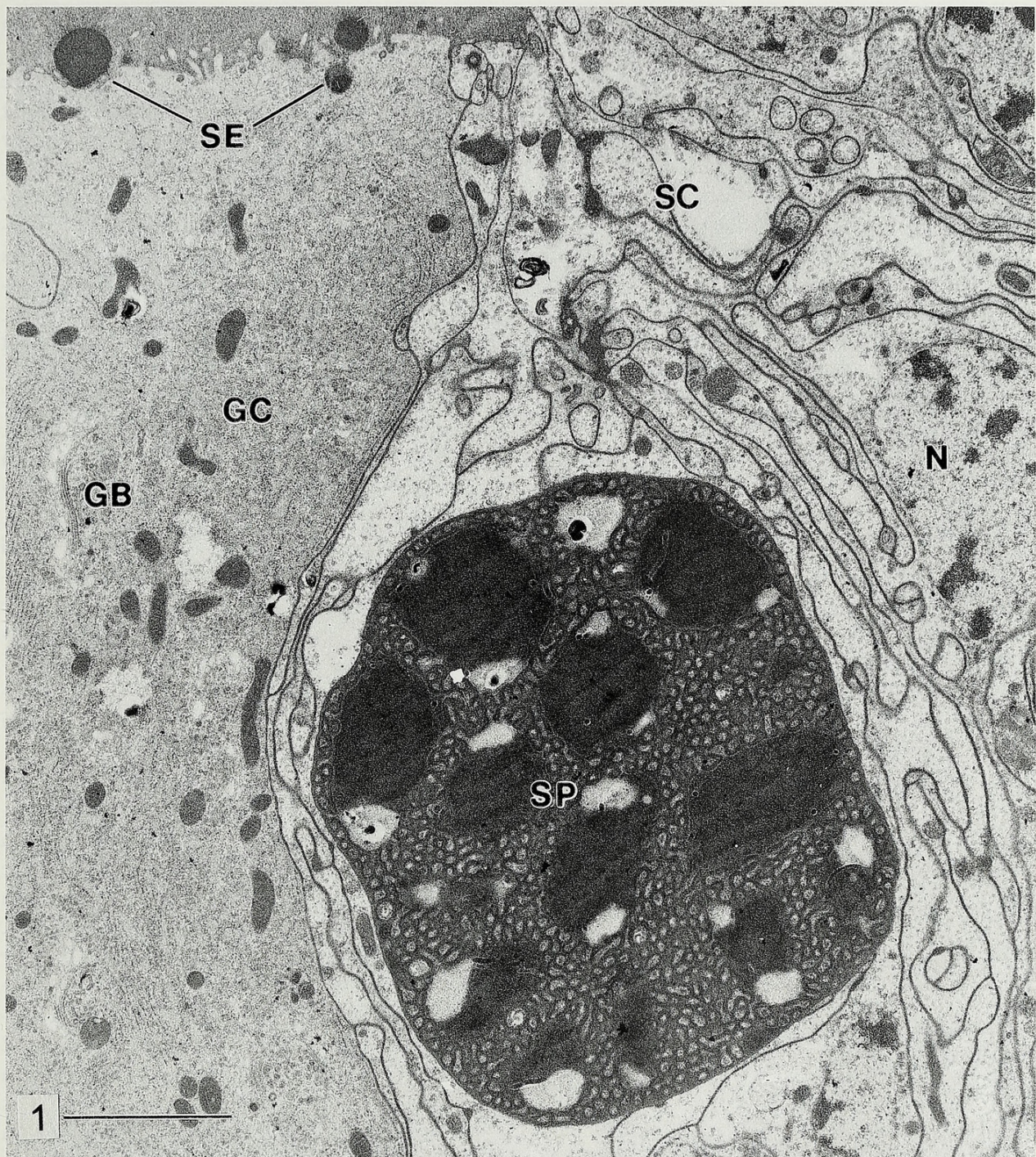
Keywords: Arachnid sperm, comparative spermatology, sperm aggregates, systematics

Solifugae present a number of peculiar characteristics that are considered to represent a mixture of plesiomorphies and autapomorphies (Moritz 1993). Hence the position of Solifugae within the Arachnida and their relationship with other taxa is difficult to define. Nevertheless, most authors who have considered the phylogenetic systematics of Arachnida regard Solifugae as most closely related to Pseudoscorpiones (e.g. Weygoldt & Paulus 1979a, b; Hammen 1989; Shultz 1990; Wheeler & Hayashi 1998; Weygoldt 1998). However, this putative sister-group relationship is based on only a few characteristics of debatable value, e.g. rostrum, two-jointed chelicerae and segmentation of the legs (Shultz 1990; Moritz 1993). A relationship between Solifugae and Acari

has frequently been suggested or discussed in the past, but it has never really been accepted (e.g. Hammen 1989; Evans 1992). Hammen (1989), who considered the Acari as being diphyletic, created two taxa Apatellata (Pseudoscorpiones and Solifugae) and Epimerata (Palpigradi and Actinotrichida), which he placed into a sister-group relationship. Dunlop (2000) recently accepted the sister-group relationship between Solifugae and Pseudoscorpiones (forming the Haplocnemata) and suggested Acari as the possible sister group of Haplocnemata.

In general, phylogenetic relationships within the Arachnida are still at least partly controversial. Hence, further characteristics are evidently necessary to improve or falsify suggested concepts. Comparative spermatology

Figures 1, 2.—Transmission electron micrographs. 1. *Oltacola gomezi* (Solifugae, Ammotrechidae), one group of sperm embedded in germinal layer. At left, glandular tissue. Scale bar = 2 μ m. 2. *Oltacola gomezi*, detail of seminal vesicle. Scale bar = 1 μ m. Abbreviations: BL = basal lamina, GB = Golgi body, GC = glandular cell, M = mitochondrion, MU = muscle, MV = microvilli, N = nucleus, SC = somatic cells, SD = septate desmosome, SE = secretion, SP = sperm cells.



may provide such characteristics (Jamieson 1987; Alberti 2000).

The only spermatozoa of Solifugae for which the fine structure has been described are those of *Eusimonia mirabilis* Roewer 1934 (Karschiidae) from Morocco (Alberti 1980a). Contrary to descriptions based on light microscopy (Roewer 1934), it was shown that they are highly derivative and differ strikingly from those of Pseudoscorpiones, which present a coiled-flagellate type of sperm and thus are more plesiomorphic (Alberti 1995, 2000). The sperm ultrastructure of *E. mirabilis* shows apomorphic similarities with sperm of actinotrichid mites (Alberti 1980a, b, 2000). The present paper intends to broaden our knowledge of the spermatological characteristics of Solifugae in order to establish whether the results obtained from the single previously investigated species apply more generally to this peculiar order.

METHODS

The following species, both belonging to the family Ammotrechidae, were used for this study: *Procleobis patagonicus* (Holmberg 1876) and *Oltacola gomezi* Roewer 1934. Specimens were captured in San José de las Salinas, Córdoba, Argentina. After dissection, they were fixed in ice-cold 3.5% glutaraldehyde buffered in Sörensen phosphate buffer (pH 7.4; 0.1M). They were then mailed in diluted glutaraldehyde to Germany, where further processing occurred, i.e. postfixation in OsO_4 (2%) and embedding in Araldite. Ultrathin sections were cut with a Leica Ultracut. Transmission electron microscopy was done with Zeiss transmission electron microscopes.

RESULTS

The male reproductive organs of *E. mirabilis*, *O. gomezi* and *P. patagonicus* are rather simple. They comprise a pair of tubular organs starting from a common genital chamber.

A wide seminal vesicle and a pair of long, thin testes is present on each side.

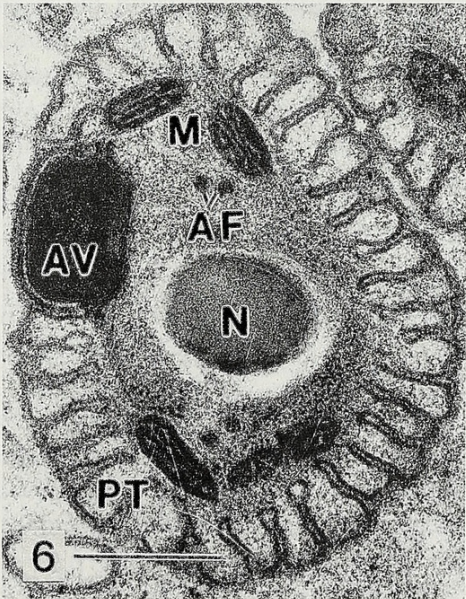
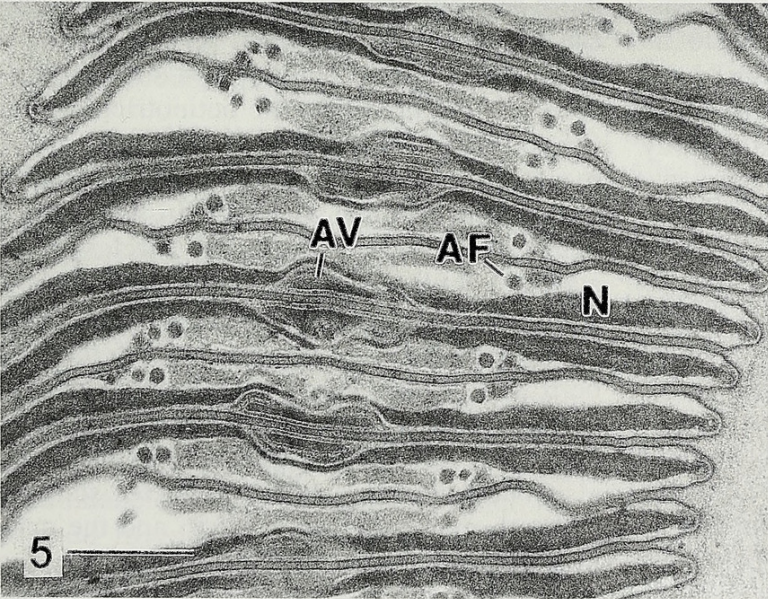
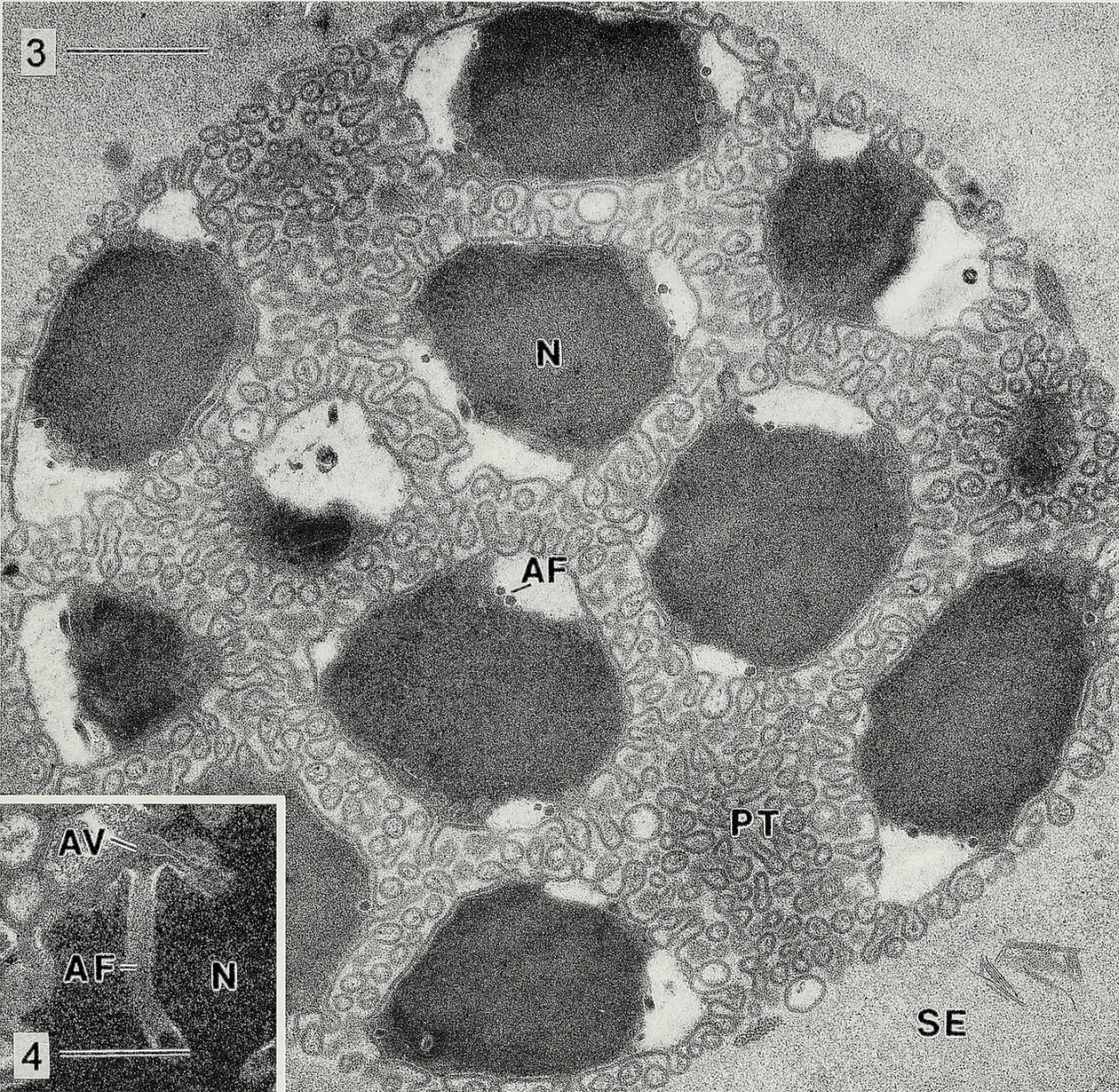
Each testis is composed of a spermatogenic part (germinal layer) and a glandular part that differ strikingly (Fig. 1). The germinal layer comprises somatic cells that form a meshwork in which groups of mature sperm cells are embedded. We did not find earlier stages of spermatogenesis. The larger part of the testis is composed of a glandular epithelium that produces the secretions, predominantly proteinic, found in the narrow testicular lumen and most likely present also in the seminal vesicle.

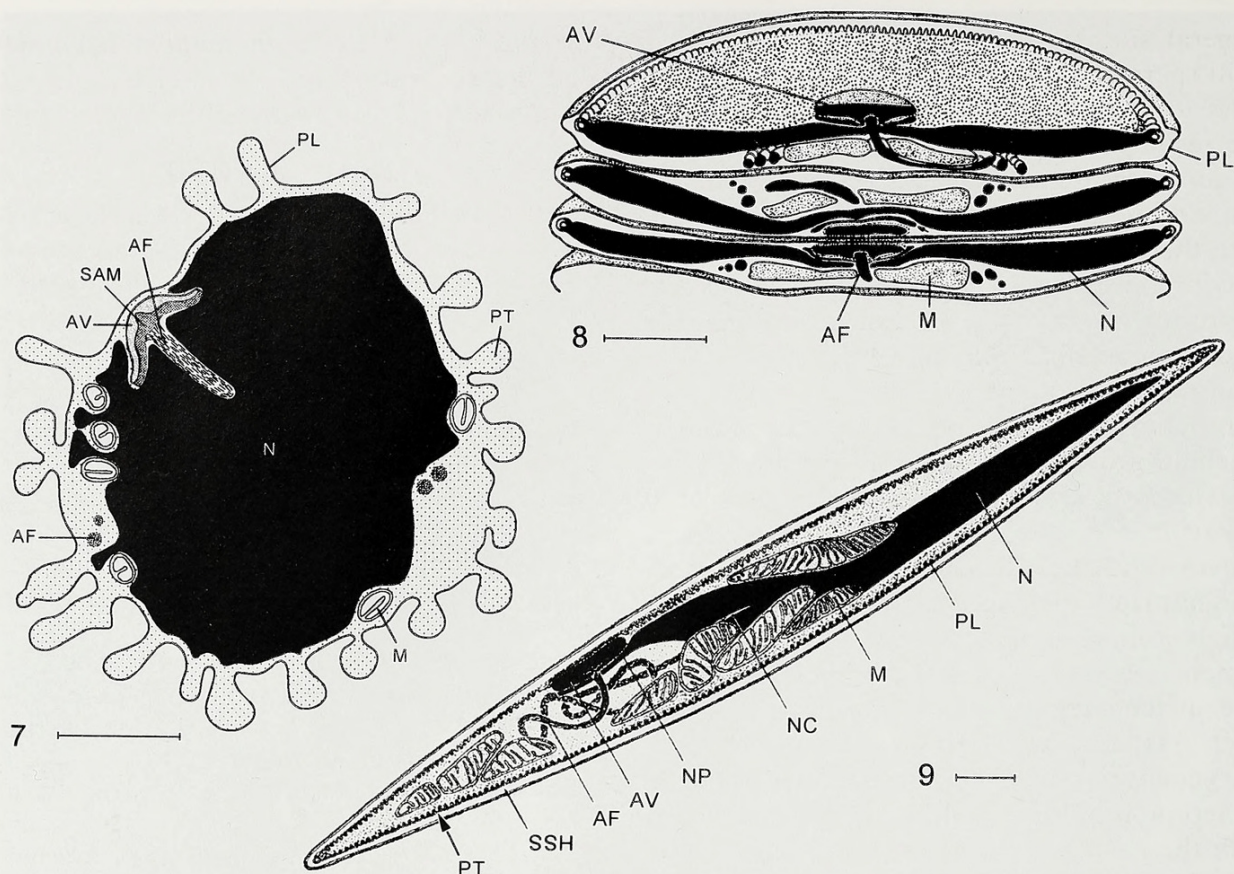
The vesicle wall is composed of a flat epithelium underlain by a few muscle cells (Fig. 2). The wide lumen of the vesicle is filled with secretions and groups of sperm cells. The secretions differ according to the species. In *O. gomezi* there are distinct globules embedded in a homogeneous matrix, whereas such globules are less obvious in *P. patagonicus*. The difference between these secretions may explain an observation during the fixation process: in *P. patagonicus* the tissue in each specimen changed colour, whereas in *O. gomezi* this did not happen.

The groups of sperm cells are highly ordered in *E. mirabilis*, forming piles of regularly arranged sperm cells (Figs. 5, 8). In both the species from Argentina, these groups are less complex. In *O. gomezi*, the spermatozoa collectively form distinct spheres (Fig. 3), whereas in *P. patagonicus* the groups appear less compact. In general, the sperm of all three species investigated are very simple, representing a small (diameter approximately 2 μm) disc- or ovoid-shaped cell devoid of a flagellum (Figs. 3, 7, 8). The cell surface is provided with conspicuous protuberances in the ammotrechid species (Figs. 3, 7), there being less obvious in *E. mirabilis* (Fig. 5, 8). The electron-dense chromatin body (nuclear derivative) is relatively large. It is surrounded

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Figures 3–6.—Transmission electron micrographs. 3. Spherical sperm aggregate of *Oltacola gomezi*, from vesicle. Note distinct protruberances of plasmalemmae of the sperm cells. Scale bar = 1 μm . 4. *Procleobis patagonicus*, sperm cell from testis showing acrosomal complex. Scale bar = 0.5 μm . 5. Detail of a sperm aggregate of *Eusimonia mirabilis*, from testis lumen. Note regular arrangement of sperm cells. Two discoid sperms form a pair with opposed acrosomal vacuoles. Scale bar = 0.5 μm . 6. Sperm cells from germ layer of testis of *Cyta latirostris* (Actinotrichida, Bdellidae). Scale bar = 0.5 μm . Abbreviations: AF = acrosomal filament, AV = acrosomal vacuole, M = mitochondrion, N = nucleus, PT = protuberances, SE = secretion.





Figures 7–9.—Line drawings of sperm cells. 7. *Procleobis patagonicus*. 8. *Eusimonia mirabilis*, detail of a longitudinally sectioned sperm aggregate (from Alberti 1980a). 9. *Bdella septentrionalis* (Actinotrichida, Bdellidae) in longitudinal section (from Alberti & Storch 1976). Scale bars = 0.5 μ m. Abbreviations: AF = acrosomal filament, AV = acrosomal vacuole, M = mitochondrion, N = nucleus, NC = nuclear canal, NP = nuclear prolongation, PL = plasmalemma, PT = protuberances, SAM = subacrosomal material, SSH = secretion sheath.

by only a small amount of cytoplasm, containing small mitochondria. A small, flat acrosomal vacuole is located close to the plasmalemma (Figs. 4, 7). The vacuole is underlain by subacrosomal material, from which arises an acrosomal filament (*perforatorium*) that penetrates the chromatin body and finally encircles the chromatin body.

DISCUSSION

Our observations agree with the light microscopic results obtained by Vachon (1945) and Junqua (1966) for species of Galeodidae. Contrary to these authors, Roewer (1934), following Birula (1893–94), also illustrated a number of small accessory glands connected to the genital chamber in *Galeodes araneoides* (Pallas 1772). We have not yet studied this area in our specimens. The fine structure of the male system and spermatozoa of the ammotrechid species is in accordance with that of the karschiid species investigated by Al-

berti (1980a). Hence it is now possible to compare the sperm structure of Solifugae more reliably with that of other arachnid taxa. Earlier statements (Alberti 1980a, b, 1984, 1991, 1995, 2000) that the most similar sperm cells are found within the actinotrichid mites are confirmed (Figs. 6, 9). Sperm cells of representatives of both taxa are small, devoid of a flagellum, contain a chromatin body that is penetrated and surrounded by circles of the acrosomal filament, and have a tendency to form peripheral protuberances. Sperm cells of Anactinotrichida are profoundly different (Alberti 1980b, c, 1984, 1991, 2000; Alberti & Coons 1999). Thus, sperm morphology reflects the remarkable differences that occur also between many other character states of the both major groups of Acari and the question whether Acari represent a monophylum or not has been discussed by several authors (see Lindquist 1984; Hammen 1989; Evans 1992; Alberti & Coons 1999). Because of the

general simplicity of solifugid and actinotrichid sperm cells, we cannot categorically dismiss the possibility that these similarities are the result of convergence. However, the similarity in the fundamental organization of the testis tissue seems to be noteworthy: in both taxa there is a large glandular area that probably produces secretions needed for spermatophore formation. This has not been observed in other arachnids (Alberti 1991, 1995, 2000). Sperm aggregates are also found in certain actinotrichid mites, but may also occur in other arachnid groups (Alberti 1988; Peretti & Batán-Horenstein 2000). Evidently, a close relationship with Pseudoscorpiones, which have coiled-flagellate spermatozoa, is not supported by spermatological results. Except for the peculiar coiling of the flagellate spermatids at the end of spermiogenesis, a process found also in the Megoperculata (Uropygi, Amblypygi, Araneae) and Ricinulei, the sperm cells of Pseudoscorpiones are most similar to those of Scorpiones. Remarkably, the sperm cells of both these latter taxa have strongly modified mitochondria and retain a flagellar tunnel (Alberti 2000). If the similarities between Solifugae and Actinotrichida pointed out here are considered to be result of convergence, one needs to develop a hypothesis about selective forces that could favor evolution of these characteristics. Remarkably, a simple correlation between sperm morphology and sperm transfer, which might be expected, is not yet evident (see Schaller 1979; Weygoldt 1990; Alberti 2000). Alternatively, the assumption of monophyly for Haplocnemata and Acari should be reconsidered.

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