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The fine structure of the spermatheca of *Amaurobius fenestralis* (Stroem, 1768) (Amaurobiidae, Araneae)

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RIASSUNTO

Nella cuticola della spermateca di *Amaurobius* sono stati trovati due tipi di pori differenti. Sotto ogni piccolo poro primario sono presenti distinti complessi cellulari di una tetrade di cellule con un dotto cuticolare al centro.

La loro funzione rimane poco chiara: potrebbe trattarsi di ghiandole ectodermiche e/o sensilli. In tutte le specie di ragni i pori primari sono considerati come un carattere primitivo.

Inoltre, in ogni spermateca è presente un grande poro secondario, attraverso il quale delle cellule ghiandolari secernono probabilmente alcuni prodotti dentro il lume della spermateca stessa. Queste secrezioni possono svolgere un ruolo molto importante nella nutrizione e lo spostamento dello spermio.

La presenza di pori secondari in *Amaurobius* potrebbe essere importante nella tassonomia.

Parole chiave: Spermateca, *Amaurobius*, Pori primari e secondari.

SUMMARY

Two different types of pores have been found in the cuticle of female *Amaurobius* spermatheca. Distinct cell complexes of a cell tetrade with a cuticular duct in its centre are found below each small primary pore.

Their function remain unclear as they may be interpreted as ectodermal glands and/or as sensilla. Primary pores are suggested as a primitive character in all species of spiders. Further, in each spermatheca one large secondary pore is present, to which glandular cells lead and secretion of some product into the spermathecal lumen probably occurs. These secretions may play an important role in sperm nutrition and displacement.

The presence of secondary pores in *Amaurobius* may be of taxonomic importance.

Key words: Spermatheca, *Amaurobius*, Primary and secondary pores,

Introduction

As little is known about the function and morphology of female genitalia of spiders in relation to e.g. sperm manipulation we studied the spermatheca of *Amaurobius fenestralis* with its surrounding epithelium by means of scanning and transmission electron microscopy. As was shown by SIERWALD (1989) and BENNETT (1992) detailed observations on the female genitalia may also be of taxonomic importance.

Results

In the cuticle of the spermatheca two types of pores are revealed. Approximately twenty small (primary) pores containing cuticular ducts are found (Figs. 1, 2a-b) on the dorsal side, whereas at the end of the bulb one larger single pore (secondary pore) is located (Figs. 1, 2). The cuticle is surrounded by a strongly innervated epithelium of prismatic cells connected to the basement lamina by hemidesmosomes (Fig. 3). The cells exhibit a very characteristic basal labyrinth with rough endoplasmic reticulum, nuclei and mitochondria (Fig. 4).

Apically the cells narrow and enter the secondary pore (Fig. 5), where the cuticle does not seem to be extremely tight. In these apical regions of the cells many microtubules, various vesicles and microvilli are found (Fig. 6).

In the epithelium described above distinct cell complexes are found below each primary pore. These consist of a group of ciliated, secretory, connecting, canal and sheath cells distinguished by their relative position and structure.

The mostly two somata of the central ciliated cells are separated by the connecting and secretory cells (Fig. 7) and are connected to the secretory cells by septate junctions. Their cytoplasm is lucid and shows some mitochondria and a basal body complex (Fig. 8).

The apical cell processes of the ciliary cells are enveloped by a common cuticular wall with a dilated proximal portion (Fig. 7). Here, ciliary structures of $9 \times 2 + 0$ axonemal pattern are often seen (Fig. 10). The distal part of the duct is thick walled and has a narrow lumen. There, cell processes of the ciliated cell contain evenly distributed microtubules (Fig. 11).

In aged adult females the detection of cell organelles of the secretory cell is hampered as the cytoplasm is filled with electron dense material (Figs. 8, 9).

The connecting cell is wrapped around the two cell types mentioned and is connected to the proximal portion of the duct (Figs. 9, 10) whereas the canal cell envelopes the connecting cell and surrounds the distal part of the cuticular duct (Fig. 11).

The outer rim of the cell complex described is lined by several sheath cells. Together with the canal cell, they convey the cuticular duct into the primary pore (Fig. 12).

Discussion

Perforations similar to the primary pore have been described in many spider species. They occur in haplogynes (COOK, 1966; BRIGNOLI, 1976; COYLE *et al.*, 1983) as well as in entelegynes (SIERWALD, 1989; BENNETT, 1992). Observations of the primary pores of *Segestria senoculata* (Dysderidae) and *Antrodiaetus unicolor* (Antrodiaetidae) (unpubl.) showed a structure similar to that of *Amaurobius*. These studies provide further support for the hypothesis of primitive presence of primary pores in the vulva of all spiders as suggested by SIERWALD (1989).

The occurence of secondary pores has only been reported in few spider species. In the spermatheca of *Agelena labyrinthica* (Agelenidae) Strand (1906) described a single perforation resembling that of *Amaurobius*. BENNETT (1992) described these pores as synapomorphic for dictynoid spiders (referring to Amaurobioidea, Dictynoidea sensu PLATNICK, 1989), hence he termed them dictynoid pores. However, occurring also in Amaurobiidae, in our opinion the secondary pore needs to be reevaluated as a taxonomic character state.

As the cells ending in the secondary pore contain vesicles and as the cuticle around this pore seems to be not extremely tight it may allow secretion of some product into the lumen of the spermatheca.

Till now, primary pores have been regarded as glandular ducts, too. However, in *Amaurobius* obvious similarities to typical arthropod sensilla were found:

- a small number of ciliated cells (receptor cells?), three or more auxiliary cells (secretory, connecting, canal cells).

- a ciliary region and a distal part with evenly distributed microtubules which might be a dendritic process of the ciliary (sensory?) cell.

- a cuticular duct that may correspond to the dendritic sheath.

As the spermathecal epithelium is strongly innervated, these cell complexes may have chemoreceptive sensory functions. These complexes may, however still be interpreted as ectodermal glands where temporary ciliary structures are important during the morphogenesis of the gland duct. After ecdysis cilia are used as a matrix for the newly emerging cuticular duct in crustaceans (DOUGHTIE and RAO, 1979) and in insects (SRENG and QUENNEDEY, 1976).

The organogenesis of epidermal glands and sensory organs begins rather similar, as both originate from a cellular tetrade (WIGGLESWORTH, 1953). This similarity is corroborated both by the presence of a process analogous to the dendritic ending of a sensory cell and by the presence of a ciliary region.

However, in evident glandular structures these cilia disappear during morphogenesis. In adult *A. fenestralis* cilia remain present, whereas no further moulting takes place. Therefore, a sensory or in analogy to termites a combined sensory and glandular function (NOIROT and QUENNEDY, 1972) may be ascribed to these organs.

Sensory systems in the female genitalia may play an important role in mating behaviour. In linyphiid spiders a typical female behaviour suppressing male courtship was only observed in females who had sperm-filled receptacula (Van HELSDINGEN, 1983). Furthermore, the sensory system may allow internal female choice as the female is able to interrupt copulation before sperm transfer takes place.

The gland(s?) found in *Amaurobius* might contribute directly to sperm transport, activation, and/or nutrition. Unfortunately none of the substances have been isolated and chemically or biologically characterized, and without more information, their precise contribution to reproduction must remain unsolved.

Fig. 1 - The two thick walled spermathecae of *Amaurobius* showing large secondary pores (300x).

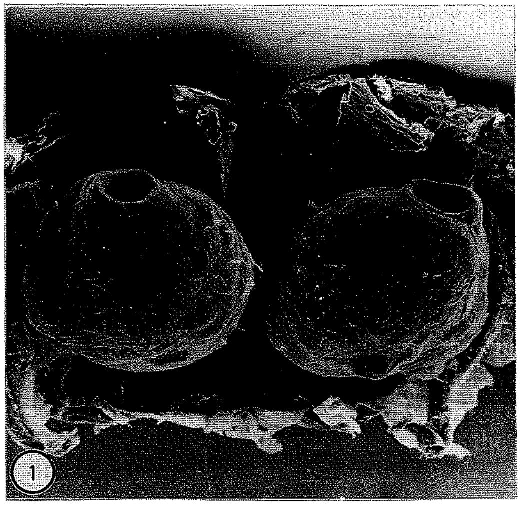


Fig. 2a - Higher magnification showing the large secondary pore (asterisk) and the smaller primary pores on the dorsal side of the spermatheca (arrows) (600x).
Fig. 2b - Primary pore with a cuticular duct (arrow) (7000x).

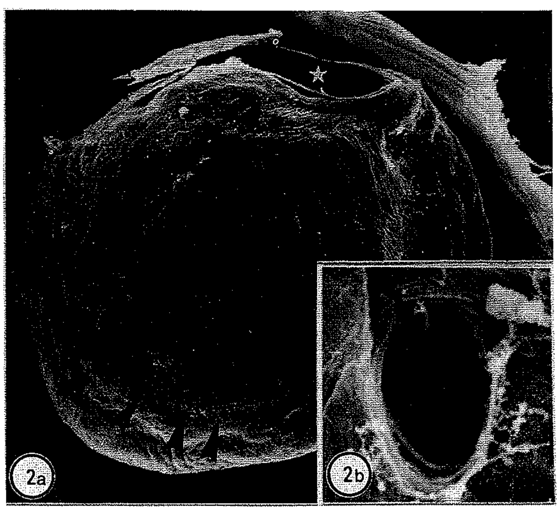


Fig. 3-6 -Epithelial cells leading to the secondary pore.

Fig. 3 - Axons are often seen in the basal labyrinth of the epithelium. The epithelial cells are connected to the basement lamina by hemidesmosomes (10150x).

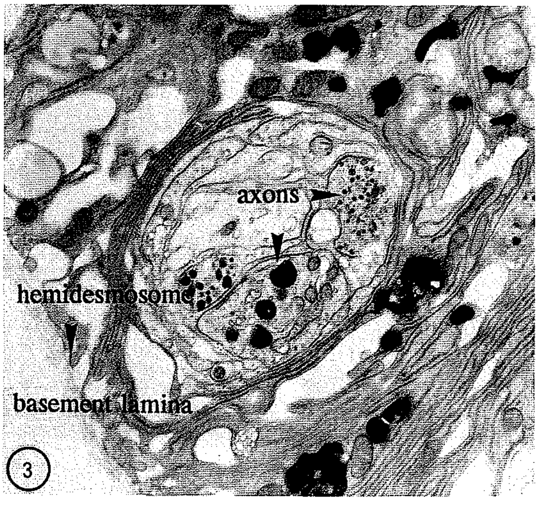


Fig. 4 - The spermathecal epithelium shows a very characteristic basal labyrinth with RER, nuclei and numerous mitochondria. Blood cells lying next to the basement lamina (7000x).

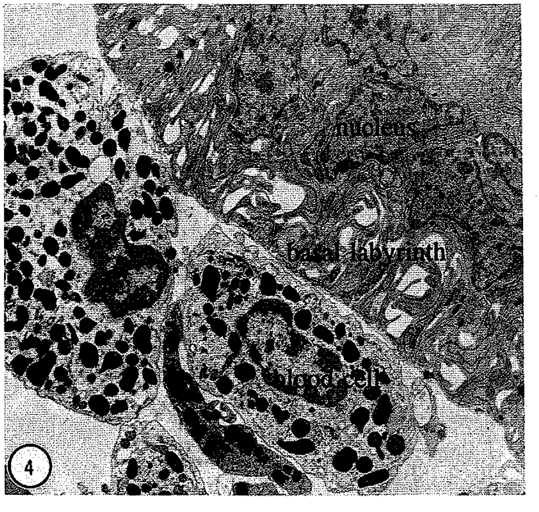


Fig. 5 - The apical region of the epithelial cells narrows and enters the secondary pore (6000x).

Fig. 6 - Near the secondary pore the cells contain many microtubules, various vesicles and microvilli (14200x).

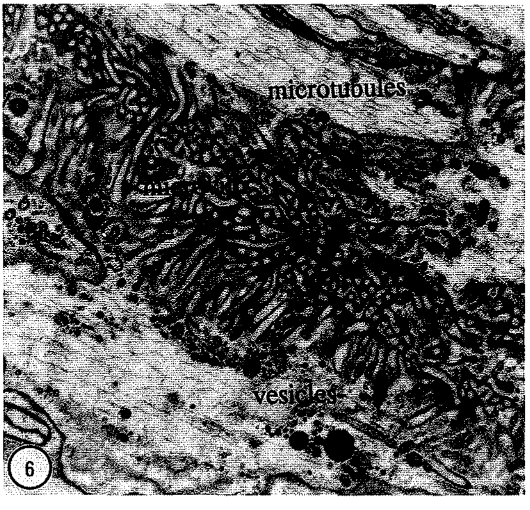


Fig. 7-12 - Cell complexes leading to the primary pore.

Fig. 7 - The somata of the central ciliated cells surrounded by a connecting cell. The nuclei of the connecting, canal and sheath cells are visible. Only the microvilli of the secretory cell can be seen. Cell processes of the ciliated cell in the lumen of the cuticular duct (7100x).

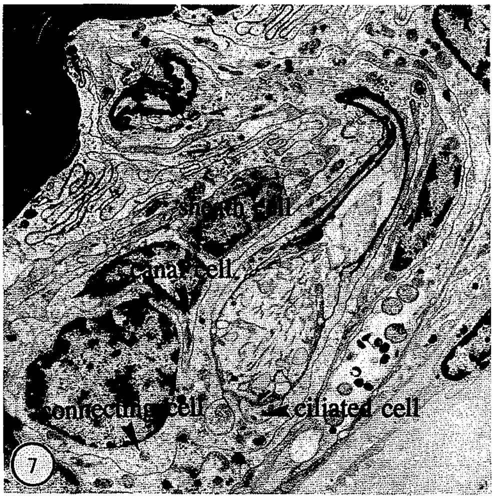


Fig. 8 - The cytoplasm of the ciliated cell is lucid and shows some mitochondria and a basal body complex (14200x).

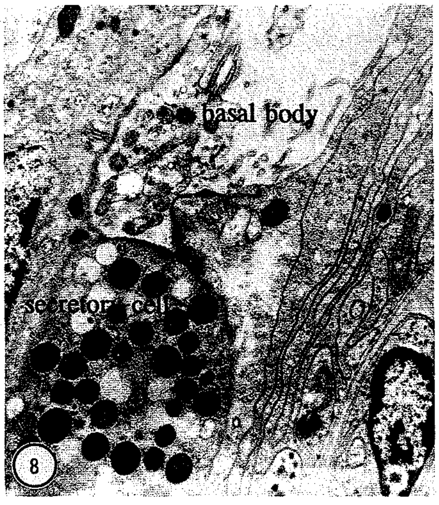


Fig. 9 - The proximal portion of the duct surrounded by the connecting cell is dilatated and shows a thin cuticular layer. In aged adult females the cytoplasm of the secretory cell is filled with electron dense material (4500x).

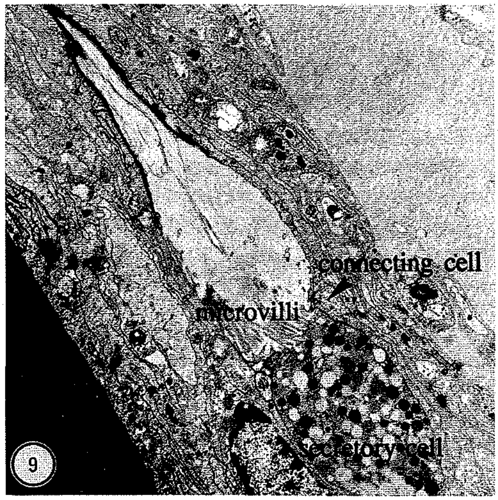


Fig. 10 - Ciliary cell processes of the ciliated cell showing a 9 x 2+0 axonemal pattern (arrows). The connecting cell surrounds the proximal portion of the thin layered cuticular duct (13500x).

Fig. 11 - Distal part of the duct showing a thick wall and a narrow lumen. The cell processes of the ciliated cell contain evenly distributed microtubules. A canal cell surrounding the distal part of the cuticular duct (12000x).

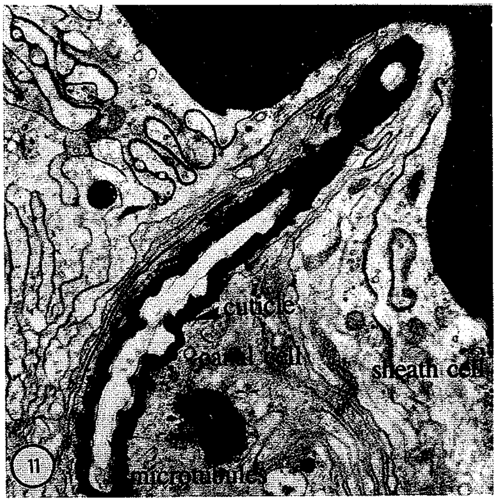
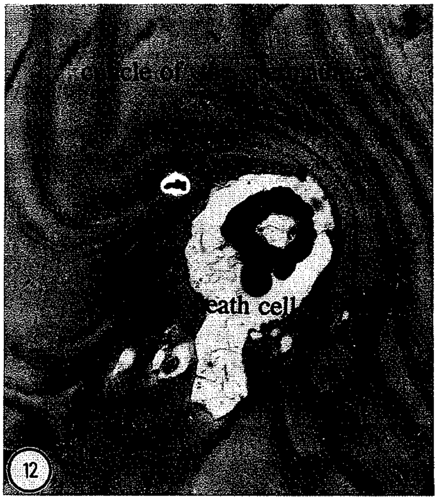


Fig. 12 - Sheath cells conveying the cuticular duct into the primary pore (14200x).



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