

# Ultrastructure of the female gonoduct of *Xiphinema theresiae* (Nematoda)

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## SUMMARY

The structure of the female gonoduct of *Xiphinema theresiae* was studied electron microscopically. The tubular part of the oviduct is narrow and contains sperm cells. It is followed by the wider *pars dilatata oviductus* which has a very plicated inner and outer wall. A well developed sphincter separates the oviduct from the uterus. The wider proximal part of the uterus, the *pars dilatata uteri*, is composed of a proximal glandular part and a distal spermatheca. In the glandular part, the lumen of the uterus is filled with highly secretory cells. The spermatheca contains sperm cells arranged in a single peripheral layer. The Z-differentiation contains several globular inclusions, as well as fibrillar inclusions which resemble the spiniform structures present in the rest of the uterus. These spiniform structures have a large forward pointing spine and a stellate base of radiating processes. They consist of a moderately electron-dense ground substance, in which electron-dense filaments are embedded.

## RÉSUMÉ

### *Ultrastructure du gonoducte femelle de Xiphinema theresiae (Nematoda)*

La structure du gonoducte femelle de *Xiphinema theresiae* a été étudiée en microscopie électronique. La partie tubulaire de l'oviducte est étroite et contient des cellules spermatiques. Elle est suivie par la large *pars dilatata oviductus* à parois interne et externe très plissées. Un sphincter très développé sépare l'oviducte de l'utérus. La partie élargie de l'utérus — ou *pars dilatata uteri* — est composée d'une partie proximale glandulaire et d'une spermatheque distale. Au niveau de cette partie glandulaire, la lumière de l'utérus est remplie de cellules à grande activité sécrétrice. La spermatheque renferme les spermatozoïdes, disposés en une couche unique périphérique. La différenciation Z comporte plusieurs inclusions globulaires ainsi que des inclusions fibrillaires ressemblant aux structures spiniformes présentes dans le reste de l'utérus. Ces structures spiniformes comportent une grande épine dirigée vers l'avant et une base à procès rayonnants formant une étoile; elles sont composées d'une substance de base moyennement dense aux électrons où sont inclus des filaments denses aux électrons.

The female reproductive system of dorylaims, which has since long proved to be of major diagnostic importance (Coomans, 1965), has recently gained renewed interest, as evidenced by the considerable attention devoted to representatives of the genus *Xiphinema*. In this genus the presence and structure of intra-uterine differentiations are under extensive investigation (for a recent review see e.g. Kruger, 1988). These differentiations appear to be either restricted to a well defined area, called the Z-organ, pseudo Z-organ or Z-differentiation, or they occur throughout a longer part of the uterus. The latter case includes crystal- and/or spine-like structures, randomly distributed in the uterus or attached to the uterine wall.

Earlier studies (Grimaldi-De Zio *et al.*, 1979; Bleve-Zacheo *et al.*, 1984; Bleve-Zacheo, Zacheo & Lamberti, 1985) primarily considered the ultrastructure of the Z-differentiation, while a recent study (Van de Velde *et al.*, 1990) describes the ultrastructure of almost the

entire female genital tract of *X. meridianum*. Until now the ultrastructure of a genital tract with intra-uterine spiniform differentiations has not yet been studied, although spiniform structures or spines have already been described in at least 23 *Xiphinema* species. *X. theresiae* Stocker & Kruger, 1988 is reported to have the largest spines hitherto observed (Kruger, 1988). In this study our goal was to elucidate the ultrastructure of the uterine spines, as well as of the remaining part of the female genital tract of *X. theresiae*.

## Materials and methods

Soil samples were collected in South Africa and shipped to Ghent. In the laboratory the nematodes were extracted from the soil by the centrifugal-flotation method, using a non-toxic silicagel (Ludox AS of DuPont de Nemours & Co.).

Adult females were picked out and placed in an ice bath for some minutes to stretch. Then they were killed and fixed in ice-cooled fixative, composed of 0.75 % acrolein, 1.5 % glutaraldehyde and 0.75 % paraformaldehyde in 0.1 M sodium cacodylate buffer. After approximately 15 h of fixation at 7 °C, they were rinsed in 0.2 M sodium cacodylate buffer for 8 h. During this rinsing the nematodes were cut into pieces of roughly 200–300 µm, to facilitate the penetration.

Postfixation took place in 2 % osmiumtetroxide in 0.2 M sodium cacodylate buffer for 36 h and was followed by an *en bloc* staining of 1 h in 2 % uranyl acetate. The specimens were dehydrated in a graded ethanol series and embedded in Spurr's resin.

Ultrathin sections were cut on a Reichert OMU-2 ultramicrotome and picked up on formvar coated slot grids. The sections were poststained in a LKB ultrastainer, for 30 min in uranyl acetate at 40 °C and 5 min in leadstain at 20 °C.

## Results

### GENERAL RECONSTRUCTION (Fig. 1)

Coomans (1965) developed a terminology for the different parts of the female gonads in Dorylaimidae. The applicability of this terminology is confirmed by its subsequent frequent use and we will also adopt it in this paper, except for the use of proximal/distal, as explained in Van de Velde *et al.* (1990).

*X. theresiae* has an amphidelphic reproductive system, in which each branch has a reflexed ovary (Fig. 1 A). The ultrastructure of the germinal zone of the ovary has already been described elsewhere (Van de Velde & Coomans, 1988). The oviduct joins the ovarial sac subterminally. The oviduct itself consists of a long tubular proximal part and a short, much wider distal part, called the *pars dilatata oviductus*. A sphincter muscle forms the junction between the oviduct and the uterus. The wide proximal part of the uterus, the *pars dilatata uteri*, can be divided in two parts : (1) the

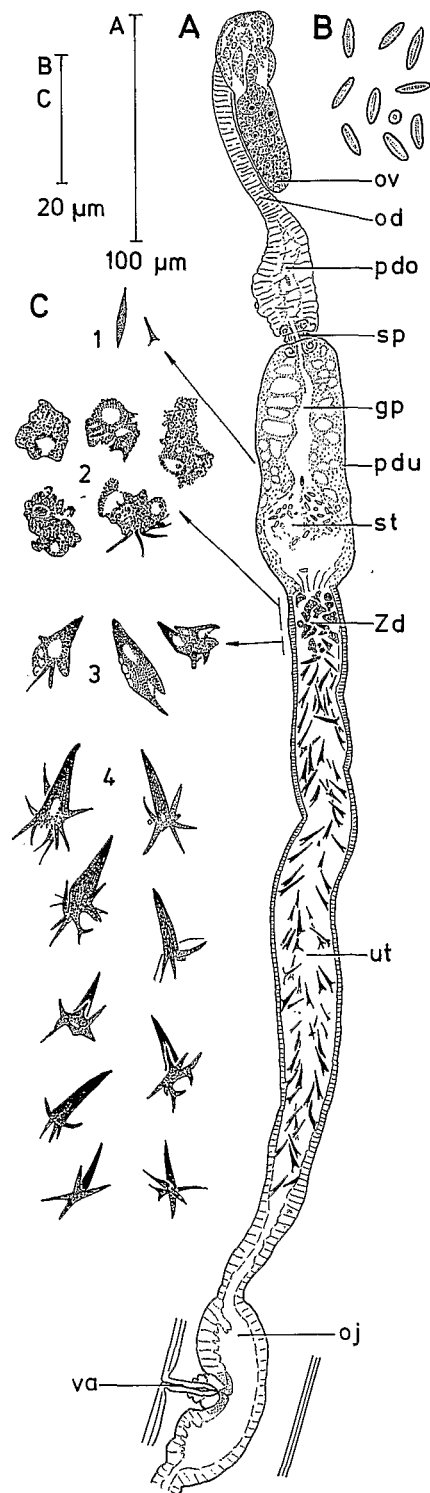


Fig. 1. A : Camera lucida drawing of a branch of the female reproductive system of *Xiphinema theresiae* with indication of the different parts; B : Sperm cells; C : 1, Inclusions in the spermatheca; 2, 3, Inclusions in the Z-differentiation; 4, Uterine spiniform structures.

*List of abbreviations* : bl : basal lamina; fi : fibrillar inclusion; gd & gp : glandular part; ger : granular endoplasmic reticulum; gi : glandular inclusion; gs : granular substance; l : lumen; m : mitochondrium; mf : muscle fibers; n : nucleus; ni : nucleus inside the lumen; nl : nucleolus; nw : nucleus in the wall; od : oviduct; oj : ovejector; ov : ovary; pdo : *pars dilatata oviductus*; pdu : *pars dilatata uteri*; pli : plication inner wall; plo : plication outer wall; ps : pseudocoelomic cavity; sb : stellate base; sc : sperm cell; sg : secretory granule; si : spine;

sm : somatic muscle; sp : sphincter; st : spermatheca; ut : uterus; va : vagina; Zd : Z-differentiation; → : points in the direction of the ovary.

proximal half, which has a glandular appearance, and (2) the distal half, which contains sperm in inseminated females, and is called spermatheca. The rest of the uterus is long and tubular. A short section located adjacent to the *pars dilatata uteri*, containing several irregular globules, represents the Z-differentiation (pseudo-Z-type). The remainder of the tubular part of the uterus is filled with numerous (up to 80) spines. It is followed by a short narrow part that joins the uterus with the ovejector. The latter is the unpaired structure that is connected to the vagina.

#### ULTRASTRUCTURE

##### *Oviduct* (Figs 2, 3, 5 A)

The long tubular part of the oviduct is at most about 10  $\mu\text{m}$  wide. It is composed of numerous, tightly packed small cells. The cell membranes between the neighbouring cells lie close to each other, are electron-dense and have a twisted course. There is no visible pre-formed lumen in the center. Sperm cells are frequently observed in this part of the oviduct (Fig. 2 A), and since there is no pre-formed lumen, they must have wedged their way between the cell membranes.

Towards the periphery of the tubular part of the oviduct, the cell membranes of neighbouring cells diverge, thereby creating a gap of 50 nm wide and 0.5 to 1.5  $\mu\text{m}$  deep (Fig. 3 A, B). The gap is usually filled with a rather electron-dense substance which resembles the basal lamina. The basal lamina entirely covers the outer surface and is about 130 nm thick (Fig. 3 A).

In the tubular part of the oviduct, the nuclei are usually located towards the periphery of the cells (Fig. 3 A, B). They are polygonal in shape, with dimensions of 1 by 1.5  $\mu\text{m}$  and contain a nucleolus and electron-dense chromatin accumulated against the inner nuclear membrane. The cytoplasm contains (Fig. 3 B) a full set of cell organelles, such as small mitochondria, small Golgi-dictyosomes, spherical, membrane bound secretory granules (0.7  $\mu\text{m}$  in diameter), free ribosomes and stacks of parallel granular endoplasmic reticulum.

Distally, a short section of the tubular part of the oviduct gradually widens and is connected to the *pars dilatata oviductus* (Fig. 2 B), which is about 35 to 40  $\mu\text{m}$  long and 15 to 20  $\mu\text{m}$  wide. Its most proximal part is characterized by a cup-shaped accumulation of electron-dense irregular inclusions (Figs 2 B and 3 C), situated in the cytoplasm of a large cell with a very strongly lobed nucleus (Fig. 3 C).

The remaining part of the *pars dilatata oviductus* consists of a mass of cytoplasm without pre-formed lumen. Centrally, the inner cell membranes are highly intertwined, while peripherally the outer cell membranes surround lobes of cytoplasm. The outer cell membrane is in turn covered by a thin basal lamina (Figs 2 B, 3 C). The peripheral lobes occasionally contain a nucleus (Figs 2 B, 5 A).

##### *Sphincter* (Fig. 4)

The sphincter is the cylindrical constriction between the *pars dilatata oviductus* and the *pars dilatata uteri*, about 10  $\mu\text{m}$  long and 8  $\mu\text{m}$  in diameter. Its inner wall is highly plicated, which gives rise to predominantly longitudinal ridges. The lumen is the irregular space between the plications of the wall, and is filled with an indistinct, moderately electron-dense substance. Nuclei can be found in the lumen, as well as closely anterior and posterior to the sphincter (Fig. 4), but an immediately detectable cytoplasmic link with the sphincter musculature was not found.

The sphincter musculature consists of a 1 to 1.5  $\mu\text{m}$  thick layer of oblique and predominantly transverse muscle filaments. The insertions of the muscle filaments are situated at the very electron-dense bands near the outer sphincter wall. The outer sphincter wall consists of a cell membrane which is covered by a basal lamina about 80 nm thick, and shows thin, about 1  $\mu\text{m}$  long irregular protrusions (Fig. 4).

##### *Uterus* (Figs 5-9)

The wide proximal part of the uterus, the *pars dilatata uteri*, is about 90 to 100  $\mu\text{m}$  long and 30  $\mu\text{m}$  wide (Fig. 5 A). The proximal part of the *pars dilatata uteri* (about 50 to 60  $\mu\text{m}$  long) is highly glandular. The outer cell membrane of this part is covered with a thin (60 nm) basal lamina and possesses irregular outward protrusions about 0.5  $\mu\text{m}$  long (Fig. 5 B). The muscle filaments are arranged in a relative thin layer (about 0.5  $\mu\text{m}$  thick) and have an oblique or transverse orientation (Fig. 5 A, B). Their insertion on the outer cell membrane causes electron-dense spots near this cell membrane. The major part of the slightly stained cytoplasm of these muscular cells, as well as their lobulated nuclei (with dimensions of 1 by 2  $\mu\text{m}$ ), are situated inwardly, and fill the spaces in the protrusions of the inner uterine wall (Fig. 5 B). The inner uterine wall exhibits long (up to 2  $\mu\text{m}$ ) irregular protrusions towards the center (Figs 5 A, B).

As a consequence, the central space with irregular protrusions towards the periphery represents the lumen. These peripheral protrusions are filled with electron-dense cytoplasm (which indicates the presence of a high amount of ribosomes) with stacks of granular endoplasmic reticulum (Fig. 5 B). Nuclei are situated closely adjacent to the protrusions and are surrounded by a thin layer of cytoplasm (Fig. 5 A, B). The nuclei of these cells can clearly be distinguished from the muscle cell nuclei since they are larger (up to 3  $\mu\text{m}$ ) and are far more electron-dense (Fig. 5 B).

Each of these cells contains a few very large secretory granules (about 3 by 8  $\mu\text{m}$ ) which extend towards the center. These secretory granules have a moderate electron-dense overall appearance in which a variety of rounded or rod-like inclusions are embedded (Fig. 5 A, B). Since these inclusions completely fill the central

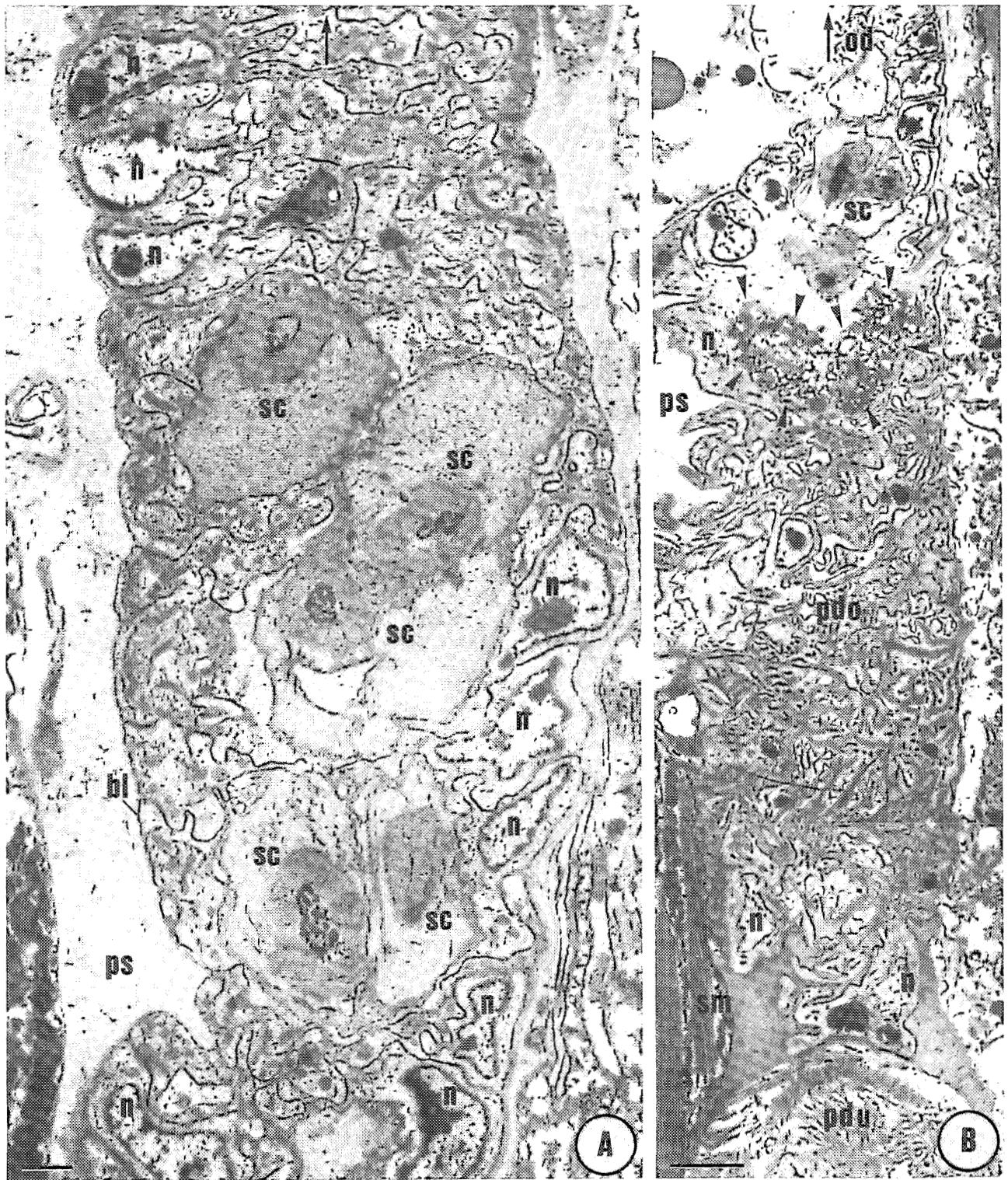


Fig. 2. A : Longitudinal section through the tubular part of the oviduct containing a few sperm cells; B : Lower magnification of a longitudinal section, showing the distal end of the tubular part of the oviduct, the *pars dilatata oviductus* (with proximal cup-shaped accumulation of inclusions (arrowheads)), and the proximal part of the *pars dilatata uteri*. (Bars equivalent : A = 1  $\mu$ m; B = 3  $\mu$ m). For abbreviations see Fig. 1.



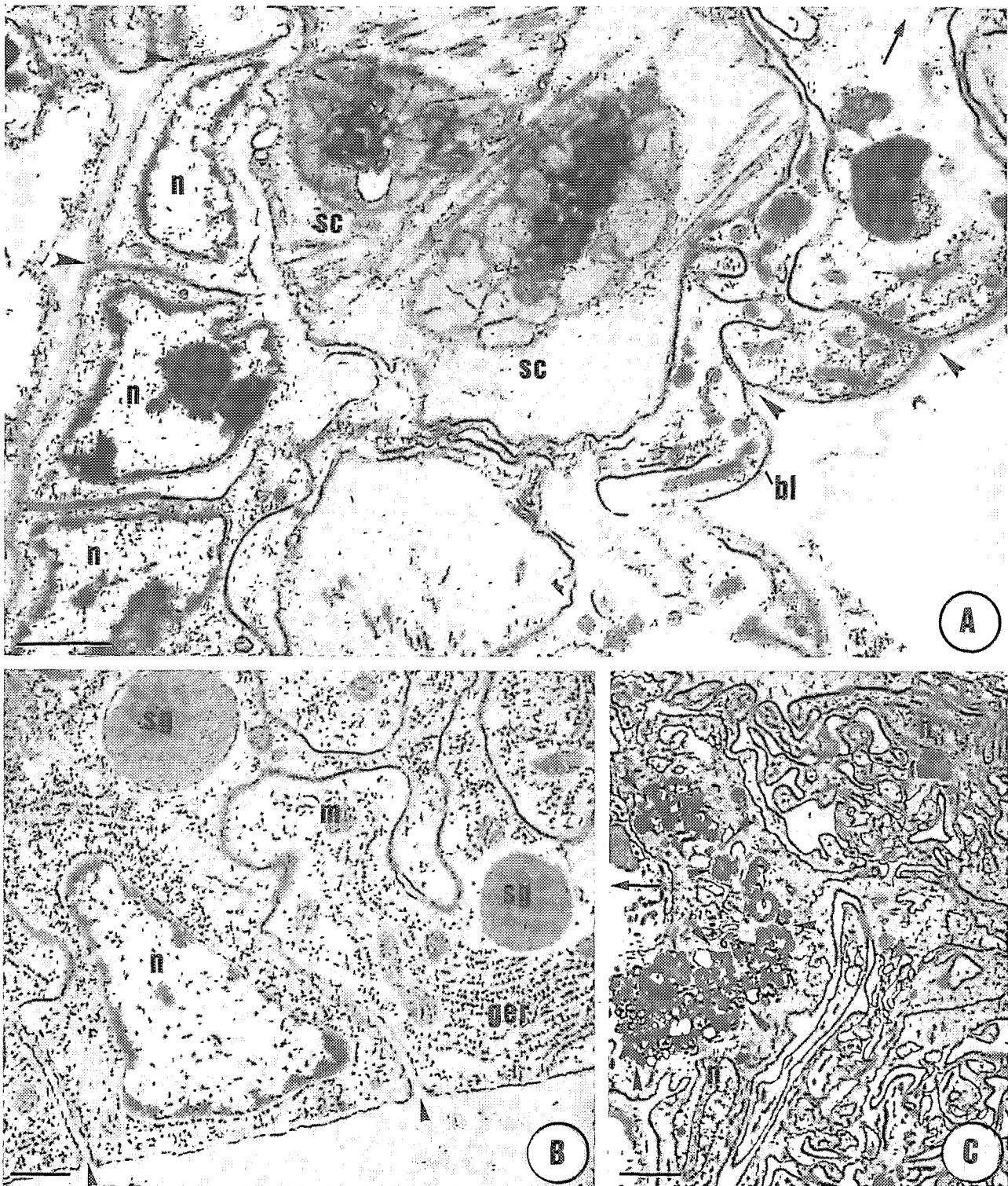


Fig. 3. A : Longitudinal section through the tubular part of the oviduct containing some sperm cells. The arrowheads indicate the gaps between neighbouring cell membranes; B : Higher magnification of the wall of the tubular part of the oviduct, showing the gaps between the neighbouring cell membranes (arrowheads); C : Proximal part of the *pars dilatata oviductus* with the cup-shaped accumulation of inclusions (arrowheads). (Bars equivalent : A = 1  $\mu$ m; B = 0.3  $\mu$ m; C = 2  $\mu$ m). For abbreviations see Fig. 1.



Fig. 4. Longitudinal section through the sphincter, showing three associated nuclei (*Bar equivalent : 1  $\mu$ m*). For abbreviations see Fig. 1.

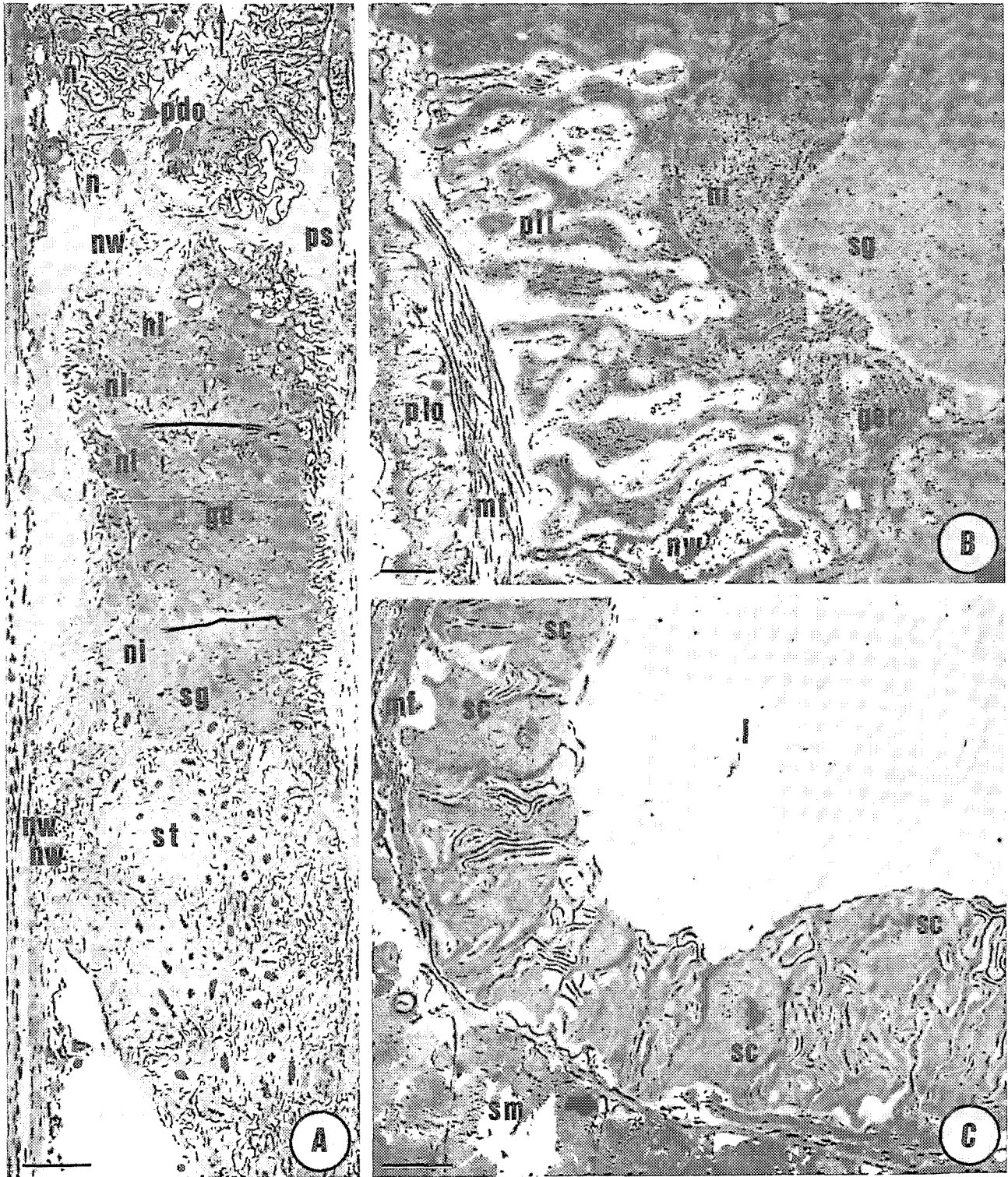


Fig. 5. A : Low magnification of a longitudinal section showing the *pars dilatata oviductus* and the *pars dilatata uteri*. In the latter, the glandular part and the spermatheca are recognizable; B : Higher magnification of the glandular part of the *pars dilatata uteri*; C : Transverse section through the spermatheca. (Bars equivalent : A = 4  $\mu$ m; B = 0.5  $\mu$ m; C = 2  $\mu$ m). For abbreviations see Fig. 1.



space of this granular part of the *pars dilatata uteri*, no pre-formed lumen is apparent.

The distal part of the *pars dilatata uteri* (about 40  $\mu\text{m}$  long) contains many sperm cells (Fig. 5 A) and can therefore be called spermatheca. The sperm cells are generally arranged peripherally, side by side, in a single layer (Fig. 5 C). The lumen of the spermatheca is the central space (up to 20  $\mu\text{m}$  in diameter), filled with a moderate electron-dense granulated substance (Fig. 6) or a less electron-dense more amorphous substance (Fig. 5 C, wrinkles appear during electron microscopical examination). Both the inner and outer wall of the spermatheca are only slightly undulating, with a thin (0.5  $\mu\text{m}$  thick) layer of transverse muscle filaments between them (Fig. 5 C). The nuclei of the muscle cells are lightly stained and are situated towards cytoplasmic lobes projecting towards the center, in between the sperms (Fig. 5 A).

The distal end of the spermatheca abruptly narrows towards the long tubular part of the uterus. The most proximal part of the latter forms a cylinder, about 20  $\mu\text{m}$  long and 15  $\mu\text{m}$  in diameter and represents the Z-differentiation (Fig. 6). It is characterized by the presence of several globular inclusions in the lumen and therefore belongs to the pseudo-Z-organ type. These inclusions have a varied appearance (Fig. 6). Some are composed of an electron-dense ground substance with electron transparent holes in it, others are composed of a moderate electron-dense fibrillar substance. Towards the distal region of the Z-differentiation, the fibrillar substance is aggregated into thick, blunt spiniform structures (Fig. 6).

The inner wall of the Z-differentiation shows an undulating, more or less longitudinal plicateness. The muscle layer is relatively thick (about 3  $\mu\text{m}$ ) and composed of predominantly transverse muscle filaments. The nuclei of the muscle cells are numerous. They are rounded (about 2.5  $\mu\text{m}$  in diameter) and situated between the packets of muscle filaments, sometimes bulging out a bit towards the outer surface of the Z-differentiation. The outer cell membrane is covered with a thin basal lamina and has a more or less even appearance (Fig. 6, insert).

The Z-differentiation is followed by a 200  $\mu\text{m}$  long and slightly wider (15  $\mu\text{m}$ ) part of the uterus that is characterized by the presence of many spiniform structures (Figs 1, 7). The tips of these spiniform structures are orientated towards the Z-differentiation (Fig. 1). They gradually decrease in size towards the distal end.

Each spiniform structure consists of a large conical part, the proper "spine", inserted on a base composed of many radiating processes, the so-called stellate base (Fig. 7). High magnification reveals that the spiniform structures are composed of an amorphous moderately electron-dense ground substance in which more electron-dense filaments are embedded (Fig. 8 A). The filaments vary in thickness between 15 and 60 nm (Fig.

8 A). The majority of the filaments are rather thin, and the thicker ones are often situated in the center of a spine or close to the radiating processes of the base (Figs 7, 8 A).

The filaments run lengthwise, mostly parallel to each other, but sometimes at small angles to one another (Fig. 8 B). They cross each other with larger angles at the transition between spine and base, and in the radiating processes of the base (Figs 7, 8 B). The spine and its base are not separate parts, since there is a continuity in ground substance and many filaments are overlapping (Figs 7, 8 B). Sometimes a narrow longitudinal inner cavity is observed in the center of a spine, extending from the base region to about the middle of the spine (Fig. 9). This cavity is filled with a finely granular, moderately electron-dense substance resembling the substance is also present in a layer around the spines probably continuous with the lumen, to which it is connected by narrow, meandering channels at the transition from the spine to the base (Figs 7, 8 B, 9 A). The rather thin endings of the radiating processes of the base are situated in between the protrusions of the inner uterine wall, thus anchoring the spiniform structures (Fig. 7).

The inner uterine wall (composed of the inner cell membrane covered by an amorphous layer of about 60 nm) shows many irregular plications, with up to 1.5  $\mu\text{m}$  long protrusions (Fig. 7). The open space of the lumen in between these plications is either filled with the radiating processes of spine bases, or a finely granular, moderately electron-dense substance (Fig. 7). This substance is also present in a layer around the spines (Figs 7, 8 A), and appears as small patches distributed in the less electron-dense granular substance that occupies most of the lumen (Fig. 7).

The muscle layer of the uterus is about 1  $\mu\text{m}$  thick, and is composed of predominantly transverse muscle fibers (Fig. 7). The muscle cell nuclei are situated between the muscle filaments. The outer cell membrane is covered by a basal lamina about 80 nm thick, and shows small outward protrusions (Fig. 7).

A short (40-50  $\mu\text{m}$  long) part of the uterus without spines is connected to the ovejector (Fig. 1). It is about 8  $\mu\text{m}$  in diameter. The muscle layer is relatively thick (1.5  $\mu\text{m}$ ) and contains predominantly transverse muscle fibers (Fig. 9 B). The nuclei of the muscle cells lie in cytoplasmic lobes inward to the muscle filament layer. They are lobed, lightly stained and surrounded by a thin layer of cytoplasm (Fig. 9 B).

The outer cell membrane is covered by a thick basal lamina (150 nm) and is only lightly plicated (Fig. 9 B). The inner cell membrane is strongly plicated, with long irregular projections towards the center. In this part, the lumen of the uterus is the irregular space between these projections. It is filled with a moderately electron-dense substance (Fig. 9 B).





Fig. 6. Longitudinal section showing the distal end of the spermatheca and the Z-differentiation. Insert : Longitudinal section through Z-differentiation (*Bars equivalent : 2  $\mu$ m*). For abbreviations see Fig. 1.



Fig. 7. Longitudinal section through the uterus showing two spiniiform structures and the meandering channels (\*) at the transition between the spine and the stellate base (Bar equivalent : 1  $\mu$ m). For abbreviations see Fig. 1.



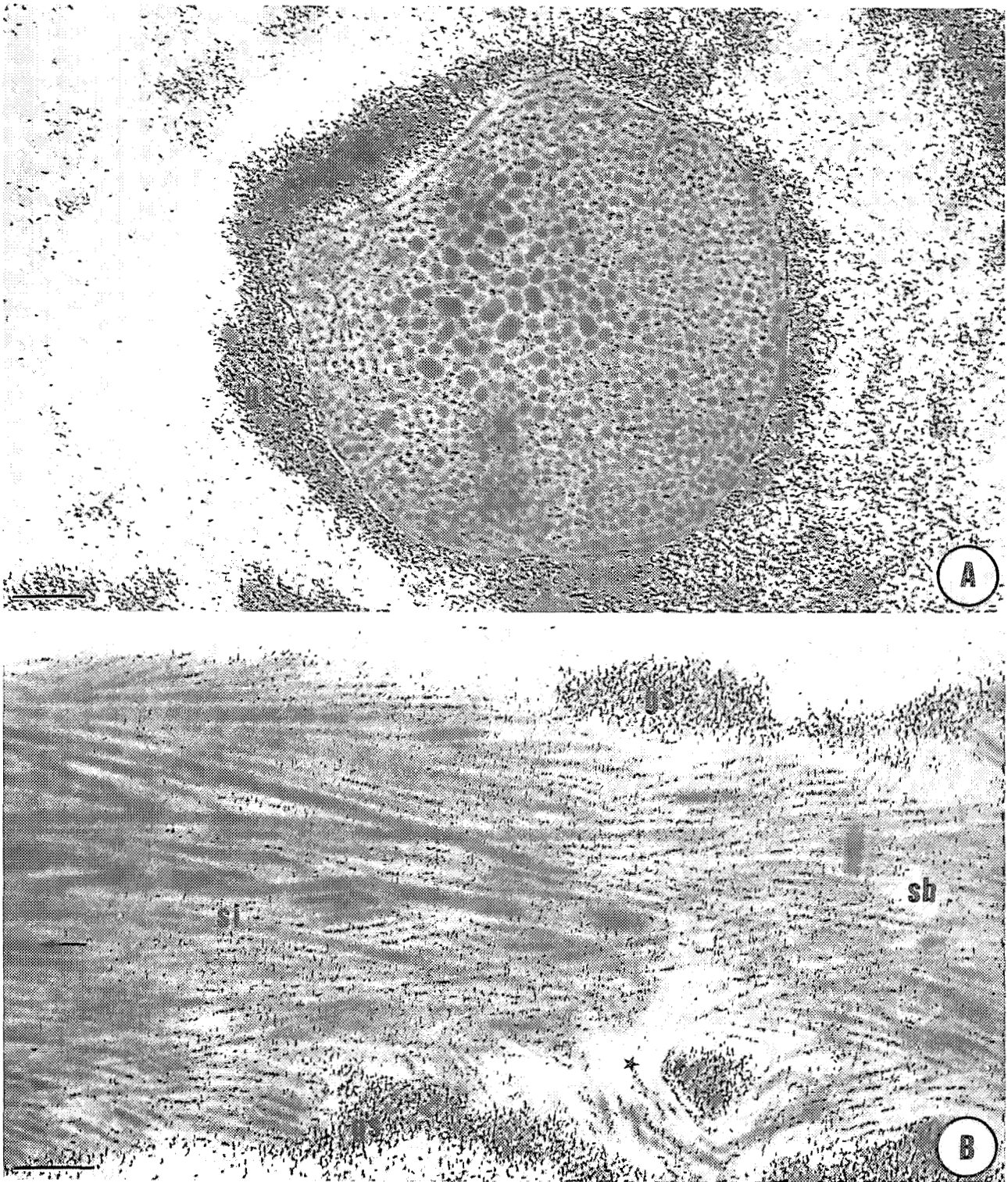


Fig. 8. A : High magnification of a transverse section through a spine showing its composition and the layer of moderately electron-dense granular substance around the spine; B : High magnification of a longitudinal section through a spine and the transition towards the stellate base. The (\*) indicate sections through the meandering channels (Bars equivalent :  $0.2 \mu m$ ). For abbreviations see Fig. 1.

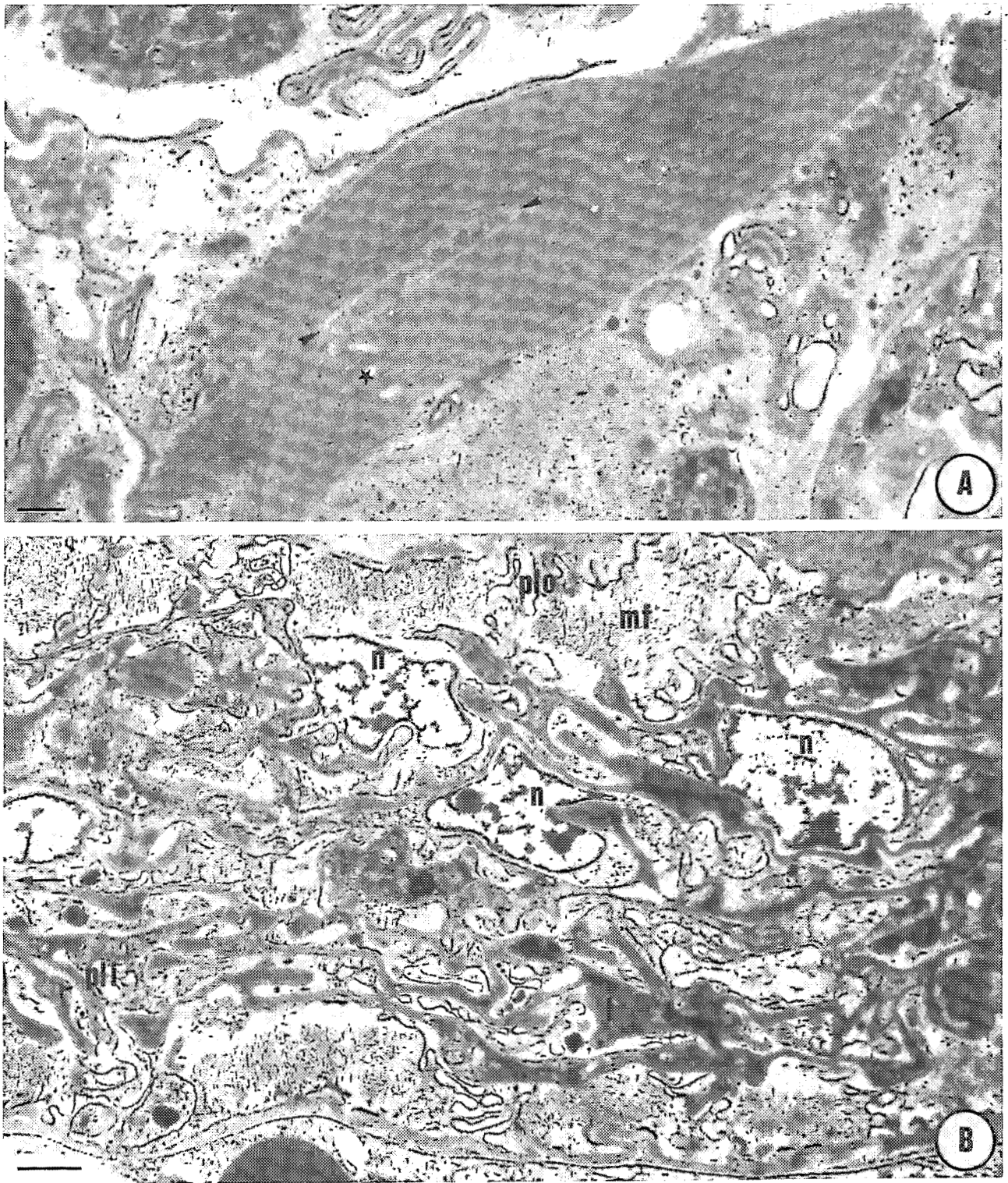


Fig. 9. A : Longitudinal section through a spine with an inner cavity (arrowheads) and meandering channel (\*); B : Longitudinal section through the distal, spineless part of the uterus. (Bars equivalent : A = 0.5  $\mu$ m; B = 1  $\mu$ m). For abbreviations see Fig. 1.



## Discussion

It comes as no surprise to learn that the ultrastructure of the female gonoducts hitherto studied (*X. meridianum*, Van de Velde *et al.*, 1990 and *X. theresiae*, present investigation) have so much in common. This might lead us to the conclusion that the general structure of the gonoduct is quite uniform in *Xiphinema*, although the different species remain recognizable by their difference in ultrastructural characteristics. Since the resemblance with *X. meridianum* is so prominent, we restrict ourselves here to a discussion of the differences observed in *X. theresiae*, and the spiniform structures.

Whereas in *X. meridianum* the arrangement of the nuclei in the tubular part of the oviduct is not regular, in *X. theresiae* on the other hand, the nuclei are arranged regularly along the periphery of the oviduct. This could explain the light microscopical interpretation that the oviduct of *Xiphinema* species would consist of a single row of disc-shaped cells (Kruger & Heyns, 1989). But the ultrastructural observation of highly intertwined cell membranes in the oviduct of *X. theresiae* does not corroborate with the above-mentioned light microscopical interpretation.

There is no pre-formed lumen in the oviduct of *X. theresiae*, and neither is there one in the oviduct of *X. meridianum*. This had led us to propose the hypothesis that a functional lumen would only appear when oocytes wedge their way between the oviduct cells (Van de Velde *et al.*, 1990). This mechanism is demonstrated in this paper by the passage of sperm cells in the oviduct. The relatively much more voluminous oocytes could pass through the oviduct by the same mechanism, but would cause a much higher strain on the oviduct cells.

The structure of the *pars dilatata uteri* in *X. meridianum* (Van de Velde *et al.*, 1990) and the glandular part of it in *X. theresiae* is essentially similar. The cytological differences mainly concern the dimensions of the secretory granules: several small ones in *X. meridianum* and only a few large ones in *X. theresiae*. These differences could represent a species specific cytological difference, but it could as well be due to different reproductive stages of the examined specimens.

The present ultrastructural study revealed that at least two types of inclusions are found in the Z-differentiation of *X. theresiae*: the globular ones and the fibrillar ones. The composition of the latter resembles the composition of the spiniform structures. The exact three-dimensional association between globular and fibrillar inclusions could not be reconstructed from the ultrathin sections. But our light microscopical observations illustrate the existence of composite inclusions (Fig. 1 C). The existence of "a gradual transition from spines to globular structures" was already mentioned by Kruger (1988) on a light microscopical basis. To determine

whether we are dealing with just a co-existence of different inclusions, or a gradual transition from one to the other (as Kruger, 1988 puts it), the formation of inclusions should be studied sequentially, e.g. by time-lapse video-microscopy in living specimens or labelling. The latter techniques will however not be available as long as the chemical composition of the globular inclusions of the Z-differentiation and the spines remains unknown.

The ultrastructure of the uterine spiniform structures of *X. theresiae* suggests that we are dealing with rather rigid structures, which can only be moved passively, by e.g. contraction of the uterine musculature or egg passage. This ultrastructural study could however not elucidate the true functional significance of the uterine spines.

## ACKNOWLEDGEMENT

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