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The ultrastructure of the anterior sensory anatomy of the marine monhysterid nematode *Geomonhystera disjuncta*

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Summary — The sensory anatomy of the monhysterid nematode *Geomonhystera disjuncta* is studied electron-microscopically. The somatic post-foveal sensilla are composed of two dendritic processes, in which a modified ciliary structure is developed. The shorter of these processes ends in the body cuticle, at the base of the seta. The longer process runs inside the seta towards the pore at its apex. The lateral sense organ, the amphid, is composed of fourteen dendritic processes with modified ciliary structures, and a short fifteenth dendrite, without ciliary structure. The latter leaves the *fusus amphidialis* to become situated and to terminate beside the *canalis amphidialis*. The terminal regions of the fourteen dendritic processes run inside the *canalis amphidialis* and reach the *fovea amphidialis* through the dorsally situated *porus canalis amphidialis*. The terminal regions of the dendrites make a double helicoidal winding inside the *fovea amphidialis*. The cephalic and labial sensilla are composed of three dendrites, one short, poorly developed, and two with a modified ciliary structure. The shorter of the latter ends in the head cuticle, while the longer enters the setae (cephalic and external labial sensilla) or setiform papillae (internal labial sensilla). Each setiform papilla of the internal labial sensilla is surrounded by a crater-shaped elevation of the lip cuticle.

Résumé — ***Ultrastructure des dispositifs sensoriels antérieurs du nématode Monhystéride marin* Geomonhystera disjuncta** — Les dispositifs sensoriels du nématode Monhysteride *Geomonhystera disjuncta* sont étudiés en microscopie électronique. Les sensilles somatiques post-fovéales sont composées de deux procès dendritiques contenant une structure ciliaire modifiée. Le procès le plus court se termine dans la cuticule du corps, à la base de la soie. Le procès le plus long se poursuit à l'intérieur de la soie jusqu'au pore situé à l'apex de celle-ci. L'organe sensoriel latéral, ou amphide, est composé de quatorze procès dendritiques comportant des structures ciliaires modifiées, et d'un quinzième dendrite, court et dépourvu de structure ciliaire. Ce dendrite quitte le *fusus amphidialis* pour se loger et se terminer à côté du *canalis amphidialis*. Les parties terminales des quatorze procès dendritiques parcourent l'intérieur du *canalis amphidialis* et atteignent la *fovea amphidialis* à travers le *porus canalis amphidialis* situé dorsalement. Les parties terminales des dendrites ont une double courbure hélicoïdale à l'intérieur de la *fovea amphidialis*. Les sensilles céphaliques et labiales sont composées de trois dendrites, l'un court et peu développé, les deux autres pourvus d'une structure ciliaire modifiée. Le plus court de ces deux derniers se termine dans la cuticule de la tête tandis que le plus long pénètre dans les soies (sensilles céphaliques et sensilles labiales externes) ou les papilles sétiformes (sensilles labiales internes). Chaque papille sétiforme de la sensille labiale interne est entourée par une élévation de la cuticule labiale en forme de cratère.

Key-words : *Geomonhystera*, ultrastructure, receptors, sensilla, amphids.

The current knowledge of the sensory anatomy of nematodes acquired until now is predominantly based on ultrastructural studies of secernenteans. Studies on the detailed structure of the sensory anatomy of adenophorean nematodes have remained fragmented. This study is presented to elucidate the ultrastructure of the sensory anatomy in the anterior region of the monhysterid nematode *Geomonhystera disjuncta* (Bastian, 1865) Jacobs, 1987.

Terminology

While in earlier studies the terminology used to describe the sensorial structures in nematodes was often confusing, review articles (McLaren, 1976; Coomans, 1979; Wright, 1980; Coomans & De Grisse, 1981) have resulted in a more consistent terminology. This terminology will be used in the present description of the ultrastructure of the sensory structures in *G. disjuncta*, but it seems useful to briefly recapitulate the basic descriptive terms.

The basic arrangement of receptors in the anterior end of nematodes is represented in the now generally accepted scheme of De Coninck (1942, 1965). The primitive pattern would consist of twelve labial sensilla, four cephalic sensilla and two amphids. The labial sensilla are situated in the medioradial plane of each lip, and can be subdivided in an inner circlet of six inner labial sensilla and an outer circlet of six outer labial sensilla. The four cephalic sensilla occur in the middle of each body quadrant and the amphids occupy a lateral position. Apart from the above mentioned sensilla, there may be somatic sensilla situated just behind the amphidial fovea (see below for a definition of the term), which we will call the post-foveal sensilla.

The term sensillum designates a receptor organ as a whole, and consists of " a simple type of sense organ involving only a few neurons " (Bullock & Horridge, 1965). The basic internal structure of a nematode sensillum typically consists of a neuronal and a non-neuronal part. The neuronal part comprises one or more bipolar neurons, of which the terminal receptorial parts, the

dendritic processes, often have a modified ciliary structure. The non-neuronal part consists of two components : a sheath cell and a socket cell. The distal (anteriad) differentiation of the sheath cell surrounds the more proximal (posteriad) parts of the modified ciliary structure(s), while the distal differentiation of the socket cell forms a socket-like end that surrounds the more terminal parts of the modified ciliary structure(s). The terms " seta " and " papilla " frequently used in nematology, have only a descriptive significance, as they only concern the outer differentiation of the receptors (Coomans & De Waele, 1979; Malakhov & Ovchinnikov, 1980).

The terminology of the typical sensillum is also applicable to the lateral receptor organs, the amphids. The neuronal part comprises several dendrites whose processes are again surrounded by the two components of the non-neuronal part, the sheath cell and the socket cell. Riemann (1972) developed a consistent terminology for the light-microscopically discernable parts of the amphids, which can be integrated without difficulties with the terminology for the ultrastructure (Coomans, 1979). The ciliary differentiations of the dendritic processes are situated in what is called the *fusus amphidialis*. This part distally narrows down to a *canalis amphidialis*, which opens through a *porus canalis amphidialis* into the *fovea amphidialis*. The latter is a depression in the body cuticle that is often filled with a mucous plug, the *corpus gelatum*.

Material and methods

G. disjuncta was isolated from the " Sluice Dock " of Ostend, a man-made marine lagoon near the Belgian coast. In the laboratory, the nematodes were grown in small vented Petri-dishes filled with bacto-agar, using a monoxenic bacterial culture, belonging to the *Alteromonas haloplanktis* rRNA branch, as a source of food (Vranken *et al.*, 1984).

Young adults were picked from the Petri-dishes, cooled in an ice-bath to stretch and then killed and fixed in ice-cooled fixative. The fixative was made up of 1.5 % acrolein, 3 % glutaraldehyde and 1.5 % paraformaldehyde in 0.2 M sodium cacodylate buffer. The fixation was carried out in an ice-bath for 2 h, and followed by 2 h rinsing in 0.2 M buffer at room temperature. Buffer-rinsed nematodes were cut posterior to the pharynx to facilitate fixation and then postfixed in 2 % osmium tetroxide in 0.2 M buffer for 13-15 h, followed by an *en bloc* staining in 2 % uranyl acetate for 1 h. Finally, they were dehydrated in a graded ethanol series and impregnated with Spurr's resin (Spurr, 1969). About fifty specimens in total were handled as described. Some twenty specimens destined for scanning electron-microscopic observations were removed from the liquid Spurr's resin, briefly sprinkled with ethanol to remove the external resin and polymerized in an oven. The polymerized specimens were gold coated in a PS-2 coating unit (ISI) and examined with a Jeol JSM-840 scanning electron-microscope. For transmission electron-microscopy the remainder specimens were embedded in Spurr's resin and polymerized at 60 °C. Transverse and longitudinal serial sections of about ten specimens were cut on a Reichert OMU-2 ultramicrotome and picked up on Formvar film-supported slotted grids. The sections were stained in 2 % uranyl acetate for 35-45 min, and in lead citrate for 10-15 min, prepared according to Reynolds (1963). The micrographs were taken with a Siemens Elmiskop 1 A electron-microscope.

Results

POST-FOVEAL SOMATIC SENSILLA (Fig. 6 A)

A dozen somatic setae are distributed in the pharyngeal region, which all have a similar and relatively simple structure. A particular group of two or three somatic setae is situated posteriorly to the *fovea amphidialis*, and are termed the post-foveal setae. The distance between their implantation and the posterior edge of the *fovea amphidialis* varies considerably, between 4.5 µm (Fig. 1 B), 5 µm (Fig. 1 A) and 8 µm (Fig. 1 C). Their arrangement among themselves is hardly constant : they can be implanted relatively close to each other (Fig. 1 A, respectively 1 C), or they can be arranged as three successive setae with an intermediate space of at least 1 µm (Fig. 1 B).

The internal ultrastructure of the post-foveal setae consists of a neuronal and a non-neuronal part. The neuronal part is made up of two dendrites, each with a well developed modified ciliary structure in its dendritic process. Proximal to this ciliary differentiation, the dendritic processes are only about 0.2 µm wide, and contain two to seven microtubuli shown in cross section (Fig. 1 E). Four dendrites lie embedded in the lateral epidermal chord, isolated from the larger group of dendrites which make up the " lateral nerve ". In a proximal to distal direction, five consecutive regions can be distinguished in the modified ciliary structure :

(1) At the root-region (Fig. 1 D) the dendritic process widens to about 0.6 µm over a length of about 1.25 µm. The outer membrane of this part is undulated. The root region is electron-transparent, contains some electron-transparent vesicles, and centrally has a short electron-dense root which shows a few transverse striation bands.

(2) At the basal region (Fig. 1 D, F), the dendritic process narrows down to about 250 nm, and is circular in cross section. It contains nine doublets of microtubuli arranged in an electron-dense circle. A Y-shaped structure connects each of the doublets with the outer membrane. A small electron-dense spot (probably the continuation of the root) is situated in

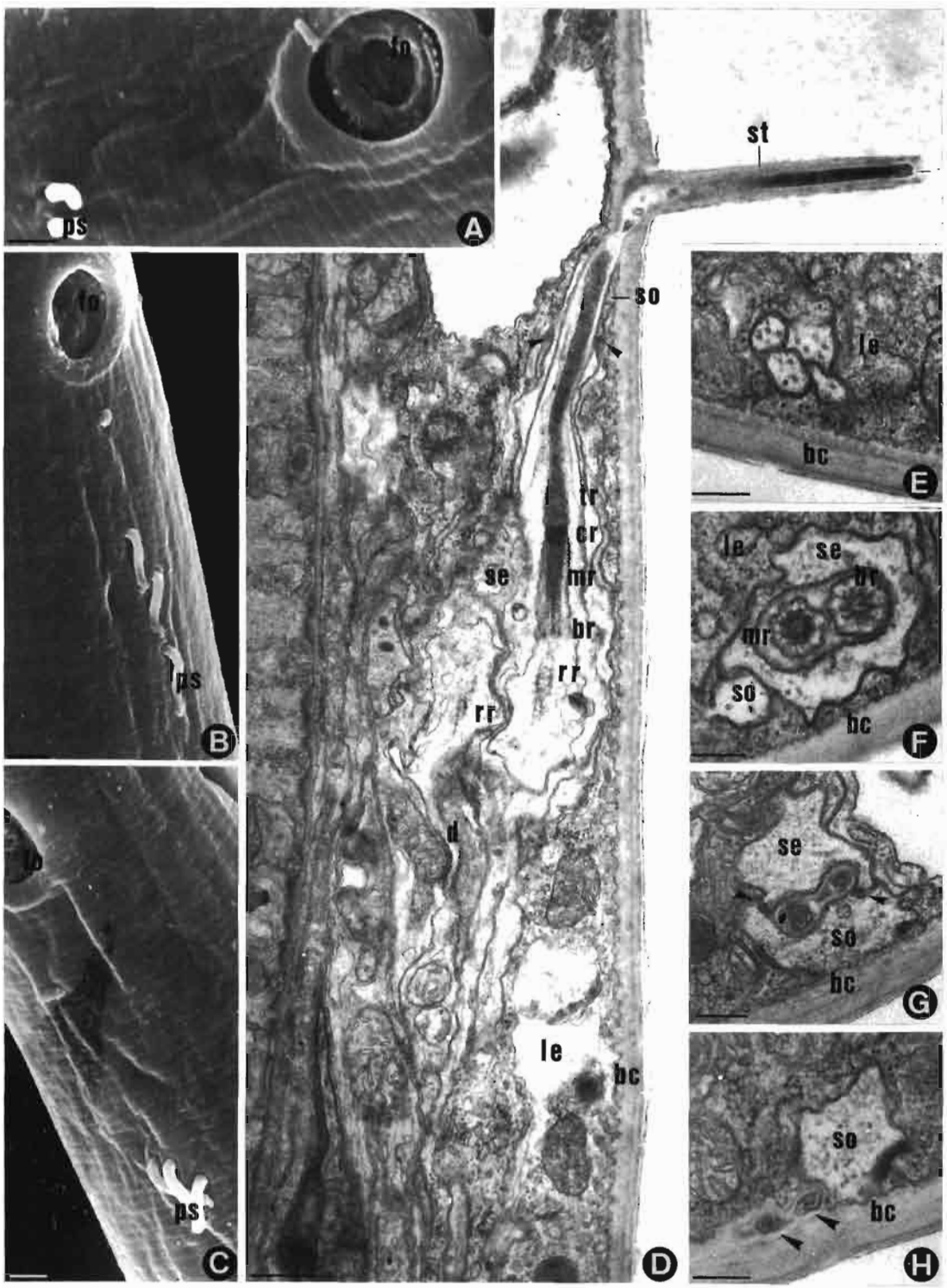

Fig. 1. — A-C : Scanning electron micrographs showing the *fovea amphidialis* and the relative positions of the post-foveal somatic setae (bar = 1 μm); D : Transmission electron micrograph of a longitudinal section through a post-foveal somatic sensillum, with indication of the five regions in the modified ciliary structure. The arrowheads indicate the membrane junction between the socket cell process and the sheath cell process (bar = 0.5 μm) — E-H : Transverse sections through a post-foveal sensillum (bar = 0.25 μm); E : Proximal level : four dendrites whose distal parts form a post-foveal sensillum; F : At the level of a basal region in the one dendritic process and at the level of a median region in the other; G : The terminal region of the two dendritic processes, in between the sheath and the socket cell processes. The arrowheads point to the membrane junctions between the sheath and the socket cell processes; H : At the level where the two terminal regions (arrowheads) are embedded in the cuticle.

Abbreviations to the figures : bc : body cuticle; br : basal region; ca : *canalis amphidialis;* cg : *corpus gelatum;* cr : constriction region; cs : cephalic sensillum; d : dendrite; D : indicates the dorsal direction; el : external labial sensillum; fo : *fovea amphidialis;* fu : *fusus amphidialis;* il : internal labial sensillum; l : lamellar protrusion; le : lateral epidermal chord; mr : median region; p : papilla; ps : post-foveal setae; rr : root region; se : sheath cell process; so : socket cell process; sp : setiform papilla; st : seta; tr : terminal region; V : indicates the ventral direction; (1) (2) (3) (15) : numbered dendritic processes, as refered to in the text.

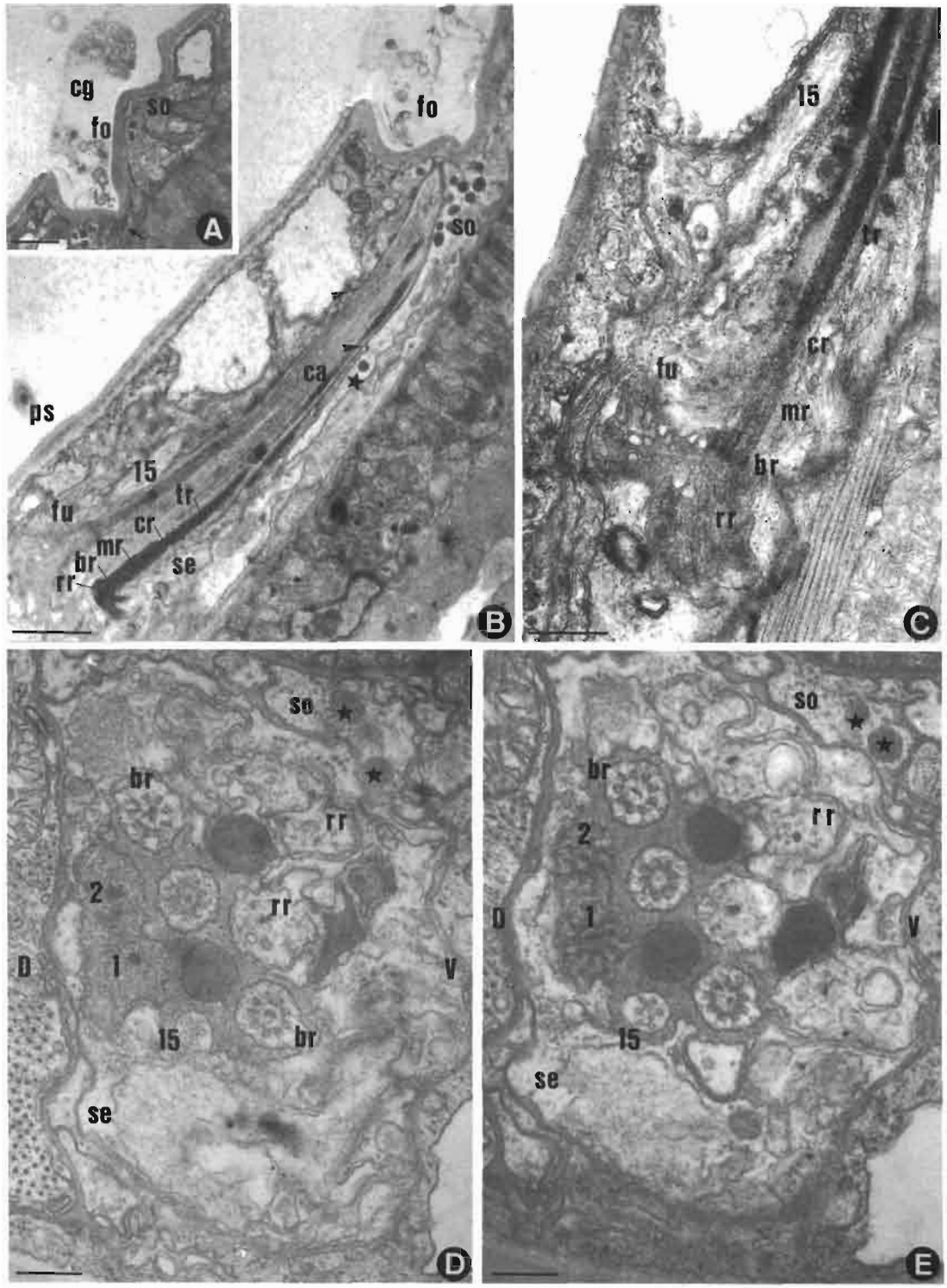

Fig. 2. — A : Longitudinal section through the *fovea amphidialis*, showing the central elevation in the fovea. The arrow points to packets of electron-dense fibers in the socket cell process (bar = 1 µm); B : Low magnification of a longitudinal section through the amphid, with indication of the regions in one of the electron-dense dendritic processes. The arrowheads indicate the membrane junction between the sheath cell process and the socket cell process. An * is put underneath an electron-dense granule in the socket cell process (bar = 1 µm); C : Higher magnification of a longitudinal section through the *fusus amphidialis*, with indication of the regions in a dendritic process (bar = 0.5 µm); D, E : Transverse sections through a posterior (D) and an intermediate (E) level of the *fusus amphidialis*, with indication of two dendritic processes (1) and (2) originating from one dendritic process, and the position of the dendritic process (15). * indicate electron-dense granules in the socket cell process (bar = 0.25 µm). *For abbreviations see Fig. 1.*

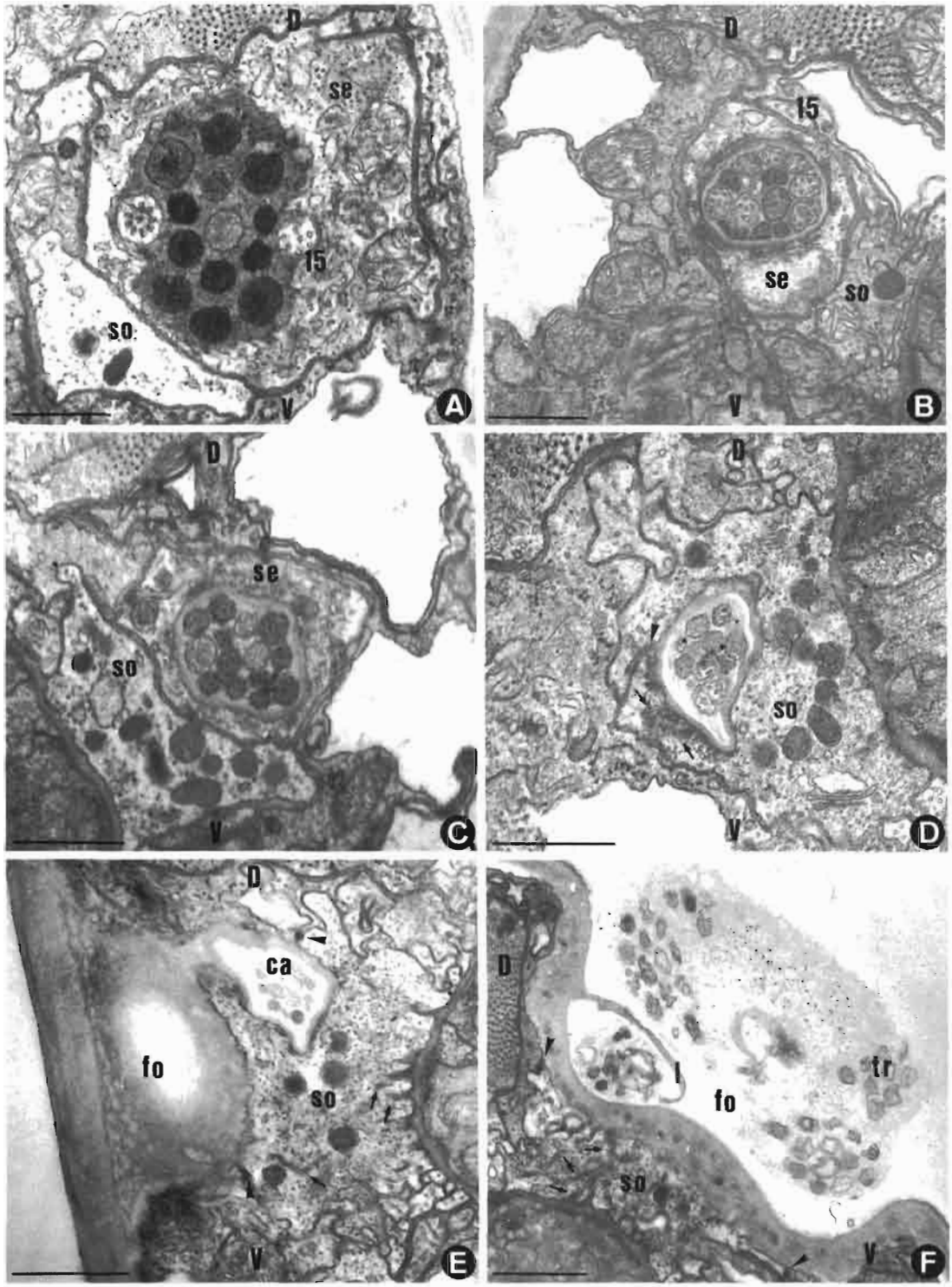

Fig. 3. Transverse sections through successive levels (in forward direction) of the *fusus amphidialis* (A), the *canalis amphidialis* (B-E) and the *fovea amphidialis* (F). The arrowheads indicate the membrane junctions between the sheath cell and the socket cell processes. The arrows point to packets of electron-dense fibers in the socket cell process (bar = 0.5 μm). *For abbreviations see Fig. 1.*

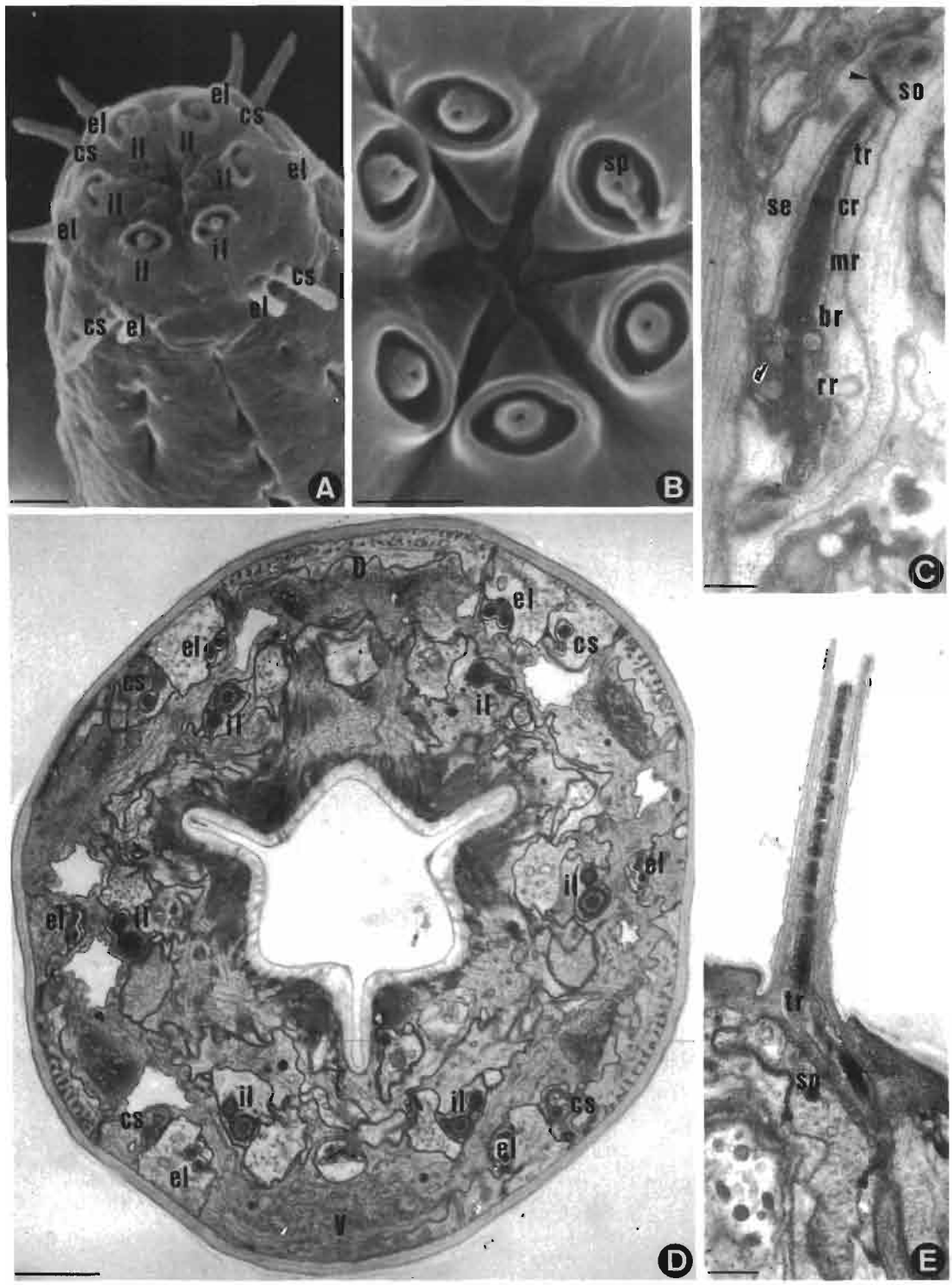

Fig. 4. A, B : Scanning electron micrographs showing form and position of the four cephalic and the six external labial setae, and the six internal labial setiform papillae, with in (B) a higher magnification of the circumvallate internal labial setiform papillae, clearly showing the pore at their tips (bar = 1 μm); C : Longitudinal section through an electron-dense dendritic process of an external labial sensilla, with indication of the regions in the modified ciliary structure. The arrowhead points to the membrane junction between the sheath cell process and the socket cell process (bar = 0.25 μm); D : Low magnification of a transverse section at the level ot the mesostome, showing the relative internal positions of the cephalic sensilla and the external and internal labial sensilla (bar = 1 μm); E : Higher magnification of a longitudinal section through a cephalic seta (bar = 0.25 μm). *For abbreviations see Fig. 1.*

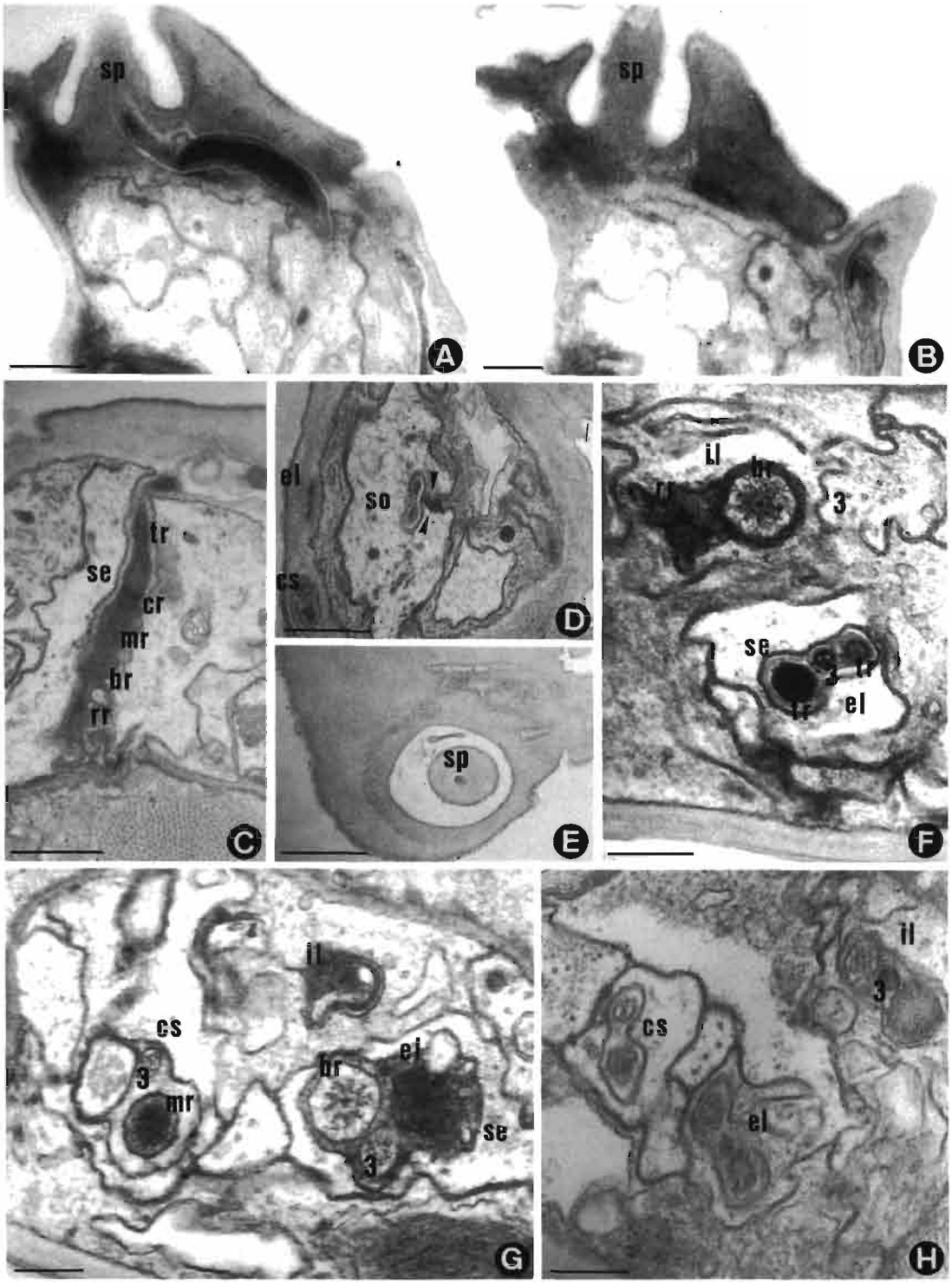

Fig. 5. A, B : Longitudinal sections through the distal part of an internal labial sensillum (bar = 0.25 µm); C : Longitudinal section through the electron-dense dendritic process of an internal labial sensillum, with indication of the different regions in the modified ciliary structure (bar = 0.5 µm); D-E : Transverse sections through the distal parts of the internal labial sensilla. The arrowhead points to the membrane junction of the socket cell (bar = 0.5 µm); F-H : Higher magnification of transverse sections through the cephalic and labial sensilla, showing cross sections of several regions of the modified ciliary structure (bar = 0.25 µm). *For abbreviations see Fig. 1.*

the centre of the doublet circle. The total length of the basal region is about 250 nm. The basal regions of the two dendritic processes are not situated at exactly the same level, as a consequence most cross sections show the basal region of one of the dendritic processes, and the root- or median region of the other (see Fig. 1 F).

(3) The median region (Fig. 1 D, F) is about 200 nm in cross section, slightly narrower than the basal region. The nine doublets are arranged in a somewhat smaller and much more electron-dense circle. The Y-shaped connections between the doublets and the outer wall are still present. The median region is about 400 nm long.

(4) A short " constriction " region (Fig. 1 D) separates the median from the terminal region. At the constriction, the dendritic process is only about 160 nm in diameter. This region is usually more electron-dense, and is about 1.25 nm long.

(5) The terminal region (Fig. 1 D, G, H) immediately follows the constriction. At first, it is somewhat broader than the constriction, but soon it narrows down to about 100 nm in diameter. It is rather electron-dense, in which only a few microtubuli are recognizable (Fig. 1 G). Over a length of more than 2 µm, the terminal regions of the dendritic processes are situated in the lateral epidermal chord, becoming situated in the body cuticle over a short distance (Fig. 1 D, H). The shorter of the two dendritic processes ends in the body cuticle, near the base of the seta. The terminal region of the longer dendritic process enters the seta, and ends shortly before the pore at the tip of the seta (Fig. 1 D).

The non-neuronal parts that surround the dendritic processes are consecutively the sheath cell process, the socket cell process and most distally, cuticular material :

(i) The distal process of the sheath cell surrounds the two dendritic processes at the level of the root region, the basal, the median and part of the terminal region (Fig. 1 D, F). This part of the sheath cell measures approximately 3 µm in length. It is about 1.5 µm wide at the root region and narrows proximally down to ± 0.4 µm. The outer cell membrane is undulated, and completely surrounded by cell membranes of the lateral epidermal chord. The cytoplasm of the sheath cell is electron-transparent and contains some microtubuli. The process of the sheath cell has an internal cavity centrally, in which the dendritic processes are situated. The cavity is limited by a single cell membrane and filled with a moderately electron-dense substance.

(ii) The cell process that gives rise to the socket-shaped structure runs along the sheath cell process (Fig. 1 F, G). As the terminal regions of the dendritic processes alter their position from being surrounded by the sheath cell process to being surrounded by the socket cell process, they are at first situated in between both cell processes. At this level, the socket cell process has membrane junction bands with the sheath cell process and the lateral epidermal chord (see arrowheads in Fig. 1 D, G). The distal process of the socket cell then forms a thin, socket-shaped structure around a part of the terminal region of the dendritic processes. The socket-shaped structure surrounds the dendritic processes over a length of only 0.6 µm (Fig. 1 D). As the dendritic processes pass from the socket cell into the body cuticle, the socket cell process widens and forms membrane junctions with membranes of the lateral epidermal chord's cells, and ends shortly anterior to this (Fig. 1 H). The cytoplasm of the socket cell process is electron-transparent and contains some microtubuli (Fig. 1 G, H).

(iii) As previously mentioned, both terminal regions of the dendritic processes are surrounded by cuticle. Near the base of the seta, the dendritic processes are situated just underneath the basal layer of the body cuticle and surrounded by a thin layer of cuticular material (Fig. 1 H). The seta itself is almost cylindrical, about 2 µm long and 0.25 µm in diameter (Fig. 1 D). It is composed of a 75 nm thick, weakly electron-dense cuticle layer (Fig. 1 D), which is surrounded externally by a thin electron-dense layer (most likely a continuation of the epicuticle).

AMPHIDS (Fig. 7)

The amphids are paired, laterally situated sensorial organs. The externally distinct, and hence scanning electron-microscopically visible, part of an amphid is the *fovea amphidialis.* It is a circular depression in the body cuticle with a diameter of about 2.4 µm (Fig. 1 A-C). The scanning electron-microscopical image of the material inside the depression is rather variable (Fig. 1 A-C) The circular depression is surrounded by a ring-shaped cuticular elevation, about 0.6 µm wide (Fig. 1 A-C). The striation of the body cuticle annulation continues at this elevation (Fig. 1 A-C).

The internal structures of the amphids are situated in the lateral epidermal chord, and are situated between 10 and 20 µm behind the anteriormost tip of the head. We will first consider the differentiations that build up the neuronal component, and describe them in proximal to distal direction.

A dozen dendrites of the " lateral nerve " widen as they extend anteriad. Some of these have an exceptionally electron-dense cytoplasm. Distally the dendrites acquire a modified ciliary structure, in which the five regions, already described in the post-foveal sensillum, can be observed.

The root regions are situated at the level of the implantation of the post-foveal setae. The root region is the widest region of the dendritic process, and is surrounded by an undulated membrane (Fig. 2 C-E). The root region is then followed by a short basal region, a median region, a constriction and a terminal region

(Fig. 2 B-C). All of these regions, except for the distal part of the terminal region, are situated in the *fusus amphidialis*. In the *fusus amphidialis*, the modified ciliary structures of the dendrites are not situated at one and the same level; and, hence transverse sections through the *fusus amphidialis* show sections through different regions (Fig. 2 D, E). At least one dendrite is seen to give rise to two dendritic processes with modified ciliary structure. The root region and the basal region of these are situated within one limiting membrane (indicated as (1) and (2) in Fig. 2 D, E). Distally, from the median region on, the dendrite bifurcates dichotomously.

In total fourteen dendritic processes with a modified ciliary structure are situated in the *fusus amphidialis* (see successive transverse sections : Fig. 2 D, at a proximal level; Fig. 2 E at an intermediate level; and Fig. 3 A, at a distal level). Some of these processes have such an electron-dense cytoplasm that it obscures any microtubular arrangement, but the morphology of their outlines suggests that they can be subdivided in five regions (Fig. 2 B).

A fifteenth dendritic process (indicated as (15) in Figs 2 B-E; 3 A-E) lacks a modified ciliary structure. It is characterized by the presence of seven to eight distinct longitudinal microtubuli embedded in an electron-transparent cytoplasm (Figs 2 D, E; 3 A, B). This particular process is always situated at the periphery of the *fusus amphidialis*, towards the side of the body cuticle (Figs 2 B, C; 3 A). Anteriorly, this process leaves the *fusus amphidialis*, to become situated laterally alongside the *canalis amphidialis* (Figs 2 B, 3 B). This process then ends bluntly, having reached a total length of about 2.5 µm (Fig. 2 B, C).

The terminal regions of the fourteen dendritic processes start in the anteriormost part of the *fusus amphidialis*. All fourteen terminal regions enter the *canalis amphidialis* (Fig. 3 B, C). At this level, the terminal regions contain five to eight microtubuli (Fig. 3 B). The difference in electron-dense and electron-transparent terminal regions is still apparent, but the microtubuli are recognizable in both types (Fig. 3 B, C). The number of electron-dense dendritic processes varies among specimens between five and ten, but within a single specimen, the number of electron-dense processes appears to be identical in the left and the right amphid.

As the terminal regions run along the *canalis amphidialis*, they become thinner and thread-like, and contain only a few microtubuli (Fig. 3 D). Some dendritic processes end in the *canalis amphidialis*, but ten to thirteen of them reach the *porus canalis amphidialis* (Fig. 3 E, F). This pore is situated dorsally in the *fovea amphidialis* (Fig. 3 E, F). The terminal regions of the dendritic processes thus enter the *fovea amphidialis* dorsally, and then make a double helicoidal winding in the depression of the fovea, in a ventral direction. Some of the terminal regions of the dendritic processes end during the course of the double winding, so only about five terminal regions stretch out over the full length of the double winding. In transverse sections the double winding of the terminal regions of the dendritic processes in the *fovea amphidialis* results in four more or less clear packets of sectioned dendritic processes (Fig. 3 F). Here, the dendritic processes are thin and have wrinkled membranes, with microtubuli extending up to the end (Fig. 3 F). The dendritic processes are embedded in a rather electron-transparent, finely granular substance, the *corpus gelatum* (Figs 2 A, 3 F). The *corpus gelatum* is partly situated inside the depression of the *fovea amphidialis*, with about half of it bulging out to the exterior (Figs 2 A, 3 F).

We will now describe the non-neuronal parts of the amphids : the sheath cell, the socket cell and the cuticular differentiation forming the *fovea amphidialis*.

(i) The most proximal non-neuronal component is the sheath cell differentiation. It completely surrounds the *fusus amphidialis*. It is widest (about 1.5 µm in diameter) at the posterior part of the fusus where the root regions of the dendritic processes are situated (Fig. 2 B-E). This cell process has a central cavity, limited by a single cell membrane, in which the ciliary differentiations of the dendrites are located (Fig. 2 D, E). The cavity is filled with a finely granular, moderately electron-dense substance (Fig. 2 D, E). As the *fusus amphidialis* narrows anteriorly, the sheath cell process also becomes narrower (Figs 2 B, C; 3 A). It still has an inner cavity filled with a moderately electron-dense substance (Fig. 3 A). The most distal part of the sheath cell process further narrows down to about 1 µm in diameter and surrounds the proximal part of the *canalis amphidialis* (Fig. 3 B, C). The central cavity now represents the *canalis amphidialis*. It is about 0.6 µm in diameter, and delimited by a single cell membrane, which is covered by a thin (only 30 nm thick) amorphous, moderately electron-dense layer, presumably cuticular in nature (Fig. 3 B, C).

(ii) The cell process of the socket cell runs along the sheath cell process. This cell process contains characteristic rounded electron-dense granules of about 150 nm in size (Fig. 2 A, B, D, E) and widens as the sheath cell process narrows down (Fig. 3 A-C). Distally, the process forms a socket-shaped structure that surrounds the 1.5 µm long distal part of the *canalis amphidialis* (Fig. 2 B) and underlies the *fovea amphidialis* internally (Fig. 2 A). The outer cell membrane of the socket forms membrane junctions with the anterior end of the sheath cell process (Fig. 2 B), and a T-shaped membrane junction with itself (Fig. 3 D). The inner cell membrane is covered internally with a thin moderately electron-dense cuticle (Fig. 3 D, E). Anteriorly, the *canalis amphidialis* occupies a dorsal position within the socket cell process, and reaches a dorso-caudal margin of the

fovea amphidialis (Fig. 3 E). The cytoplasm of the socket cell also contains, apart from its characteristic electron-dense granules, some packets of electron-dense fibers (Figs 2 A, 3 D-F).

(iii) The *fovea amphidialis* is a circular depression in the body cuticle of about 2.4 µm in diameter and about 1 µm in depth. The bottom of the fovea has a centrally located irregular to cone shaped elevation (Figs 2 A, 3 F). The *porus canalis amphidialis* is situated in the dorso-posterior quadrant of the depression. The median part of the *canalis amphidialis* wall connects to the bottom of the depression, while the more lateral part of the wall remains present as a thin cuticular lamellar protrusion on the edge of the *porus canalis amphidialis* (Fig. 3 F). This lamellar protrusion is connected to the dorsal side-wall of the foveal depression (Fig. 3 F). The cuticular lining of the *fovea amphidialis* is continuous with the body cuticle (Figs 2 A, B; 3 F). The epicuticle that covers the body cuticle stops at the point where the cuticle bends inwards to form the depression (Figs 2 A, 3 F). The distinction between the other layers of the body cuticle is no longer possible beyond this point (Fig. 2 A, 3 F). The depression is limited by an amorphous, moderately electron-dense cuticle of about 200 to 300 nm thick, containing several small electron-dense granules (Fig. 3 F).

A schematic representation of the amphid as a whole, is presented in Fig. 7 A, B.

Cephalic and labial sensilla (Fig. 6 B)

Scanning electron-microscopical pictures show the general arrangement of the head setae (Fig. 4 A). The four cephalic setae are situated in an outer circlet, in the middle of each body quadrant. They are rather cylindrical, about 1.5 µm long and 0.25 µm wide (Fig. 4 A). The six external labial setae are situated in a circlet closely adjacent to this outer circlet, but slightly more towards the anterior tip of the head (Fig. 4 A). Two external labial setae are situated subdorsally, two laterally and two subventrally (Fig. 4 A). They have an elongated cone-shape and are about 1 µm long (Fig. 4 A). The outer differentiations of the six internal labial sensilla can be designated as setiform papillae (see discussion), and are positioned on the inner parts of the lips, forming an inner circlet (Fig. 4 A, B). The pore on their apex is clearly visible (Fig. 4 B). Each of the setiform papillae is surrounded by a crater-shaped differentiation of the lip cuticle (Fig. 4 B).

Transmission electron-microscope images of transverse sections through the head at e.g. the level of the mesostome, show that the external arrangement of the sensilla is closely reflected by their relative internal position, and as a consequence all sensilla can be identified (as indicated on Fig. 4 D). The internal structure of the head sensilla is essentially similar for the three types.

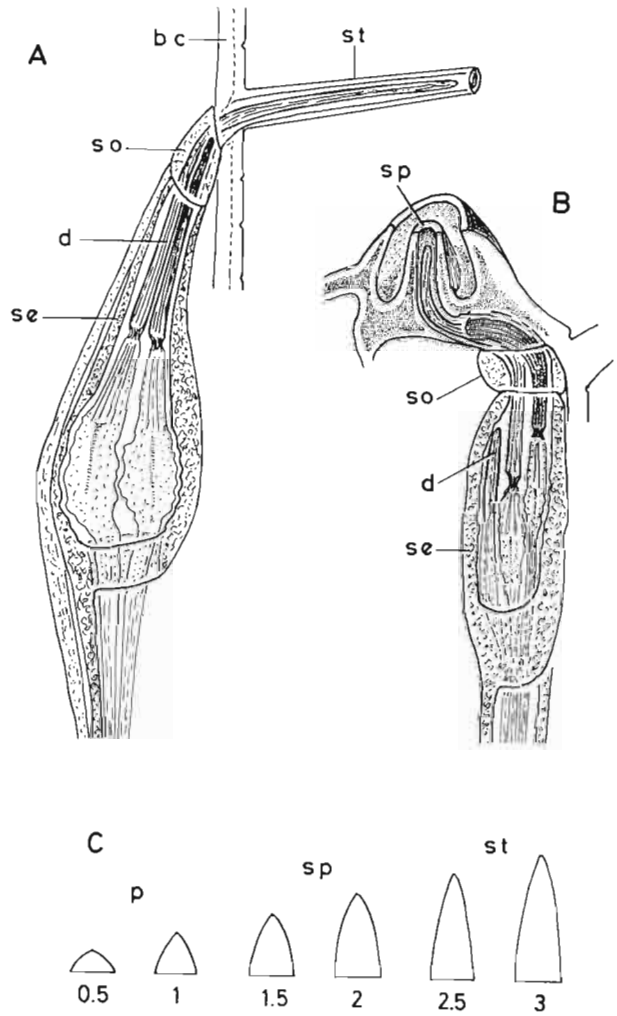

Fig. 6. A : Schematic representation of a post-foveal somatic sensillum; B : Schematic representation of an internal labial sensillum; C : Diagram showing some ratios for papillae, setiform papillae and setae. *For abbreviations see Fig. 1.*

The internal structure of the cephalic and the external labial setae only differs marginally regarding form and size, and will not be described separately here.

The neuronal component of either a cephalic or an external labial sensillum is composed of three dendritic processes (Fig. 5 F). One of these dendritic processes (indicated (3) in Fig. 5 F-H) is short (especially in the cephalic sensilla), thin and contains only a few (3 to 7) microtubuli (Fig. 5 F-H). The other two dendritic processes each develop a modified ciliary structure (Figs 4 C, 5 F, G). Each sensillum has an electron-dense and an electron-transparent dendritic process (Fig. 5 F-G). The arrangement of the microtubuli is more easily recognizable in the electron-transparent

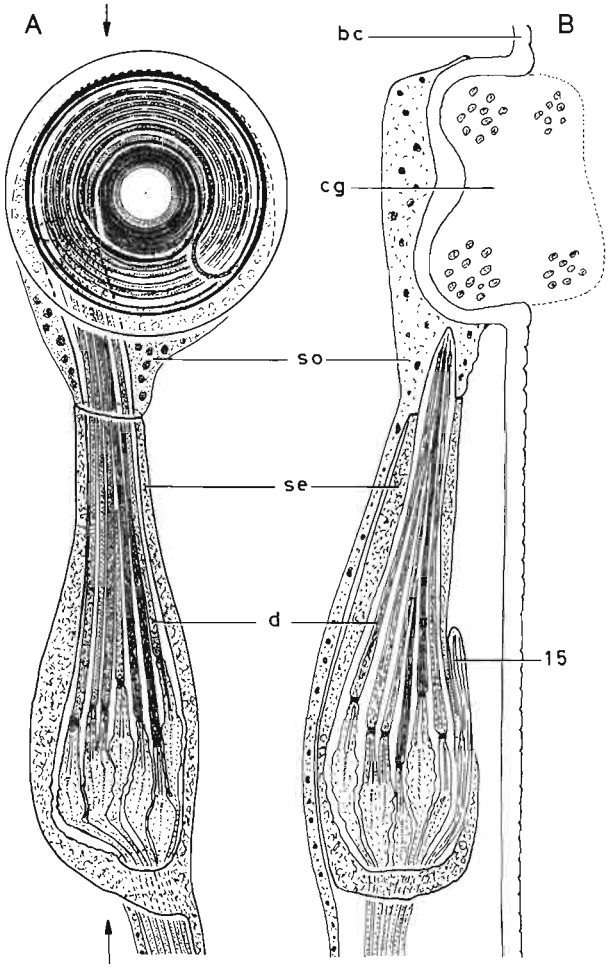

Fig. 7. A : Schematic representation of an *en face* view on the amphid; B : Schematic representation of a longitudinal section through the amphid, at the height of a plane indicated by the arrows in A. *For abbreviations see Fig. 1.*

dendritic process (Fig. 5 F-G), but the overall morphology suggests that the five regions typical of the modified ciliary structure (see post-foveal sensilla) are also discernable in the electron-dense dendritic process (Fig. 4 C). The terminal region of both these dendritic processes reaches the head cuticle near the base of the seta (Fig. 4 E). The terminal region of the electron-dense dendrite, which is usually the thickest of the two, ends at the base of the seta. The terminal region of the electron-transparent dendritic process enters the seta and then continues onwards until it almost reaches the tip of the seta (Fig. 4 E).

The non-neuronal components surrounding either cephalic or external labial sensilla are :

(i) The process of the sheath cell, which surrounds the dendritic processes, starts from the point at which two of these processes develop into a root region, and runs up to the posterior part of their terminal region (total length of about 2 µm) (Fig. 4 C). The cytoplasm of the sheath cell process contains only a few inclusions, apart from some microtubuli. The inner cavity of the sheath cell process is again delimited by a single cell membrane, and contains a finely granular, moderately electron-dense substance (Fig. 5 F, G).

(ii) The socket cell process distally takes over the position of the sheath cell process. It forms a membrane junction band with the anterior edge of the sheath cell process (Fig. 4 C), and within itself forms a characteristic T-shaped membrane junction that extends to the cavity in which the dendritic processes are situated.

(iii) The cuticular differentiation of the setae is either cylindrical (cephalic setae) or elongated conical (external labial setae) in shape. Externally, the seta is covered with a trilamellar layer which overlays an amorphous cuticular layer of about 50 nm thick (Fig. 4 E). The central canal in the seta is about 100 nm in diameter, and is limited by a single electron-dense layer (Fig. 4 E). Each of the setae clearly has a pore at its tip (Fig. 4 E). The head cuticle has a small invagination at the base of the seta (Fig. 4 E).

The neuronal component of the internal labial sensilla (Fig. 6 B) has, similar to the cephalic or external labial sensilla, three dendritic processes : a thin, poorly developed, short process, and two processes with a modified ciliary structure, of which one is electron-dense and the other one is electron-transparent (Fig. 5 C, F). The terminal regions of both the long dendritic processes reach the head cuticle at the outer margin of the lips. In the lip cuticle, the terminal region of the electron-dense dendritic process widens and has an extremely electron-dense cytoplasm (Fig. 5 A). This terminal region is situated underneath the exterior part of the crater shaped cuticular elevation, and ends there (Fig. 5 A, 6 B). The other terminal region enters the cylindrical cuticular differentiation and runs towards its tip (Fig. 5 A, E).

Non-neuronal components :

(i) The broad sheath cell process surrounds the dendritic processes for almost their entire length (Fig. 5 C).

(ii) The socket cell process, which itself can be recognized by its T-shaped tight junction surrounds the terminal regions of the dendritic processes anteriorly from the buccal ring (Fig. 5 D).

(iii) The external cuticular differentiation, associated with the internal labial sensilla is a rather conical, setiform papilla, surrounded by a crater-shaped differentiation. The setiform papilla is about 0.5 µm long and 0.3 µm in diameter. It is externally surrounded by an electron-dense layer, and its inner canal is limited by a single thin electron-dense layer (Fig. 5 E). The crater-shaped protrusion around the setiform papilla is about 0.4 µm deep and has an internal diameter of

about 0.5 µm (Fig. 4 A, B, 5 E). The inner and the outer surface of the crater is covered with an electron-dense layer (Fig. 5 A, B, E).

Discussion

The cephalic and labial sensilla of *G. disjuncta* all contain three dendritic processes, while the somatic sensilla contain only two dendritic processes. This means that the number of dendritic processes in simple sensilla lies well within the range of two to five processes per sensillum as reported for other adenophorean nematodes (Coomans, 1979).

In *G. disjuncta* all these simple sensilla have an external cuticular protrusion. The protrusions of the post-foveal, the cephalic and the external labial sensilla are relatively long and cylindrical, and are therefore generally referred to as setae. The protrusion of the internal labial sensilla is however a much shorter setiform papilla. Each setiform papilla is surrounded by a crater-shaped elevation of the lip cuticle.

As mentioned in the introduction, the terms " seta " and " papilla " only have a descriptive significance (Coomans & De Waele, 1979; Malakhov & Ovchinnikov, 1980), and a precise distinction between both terms has not yet been made. Generally, sensilla with a small, hardly protruding outer differentiation are called papillae (sometimes even peg- or cone-shaped papilla), while the longer rod- or spine-shaped differentiations are called setae, and for the intermediate forms the term setiform papilla is in use. Both scanning and transmission electron-microscopes have a much higher resolution than light microscopes, which implies a necessity for an arbitrarily defined distinction between these terms. We propose to take the ratio length : width at the base as the distinctive characteristic. A papilla would then be defined as having a ratio smaller than or equal to 1; and a seta would be defined as having a ratio higher than 2; while a structure with an intermediate ratio would be designated as a setiform papilla (Fig. 6 C).

The cuticular projection of the internal labial sensilla of *G. disjuncta* is about 0.5 µm long, and about 0.3 µm in diameter at the base. The ratio as defined above is less than 2 and higher than 1, hence the projection can be called a setiform papilla. The whole outer cuticular differentiation could then be described as a circumvallate setiform papilla.

All somatic and anterior sensilla show much resemblance in structural composition (Fig. 6). They might have a bimodal function, i.e. both mechanoreceptive and chemoreceptive. This hypothesis is supported by the presence of differently shaped structures in each sensillum. The long and thin electron-transparent dendritic process situated in the seta or setiform papilla with a pore at the tip is in direct contact with the environment, and this implies chemoreceptive capacities. The wider, electron-dense dendritic process that ends in the body cuticle would be mechanoreceptive.

According to Thurm *et al.* (1983), well established ciliary arrangement of microtubuli is an essential requirement to indicate mechanoreceptive capacities in insect cilia. Since both the electron-transparent and the electron-dense processes in the setae of *G. disjuncta* have well developed ciliary structures, they could both have the potential for a mechanoreceptive function.

Since De Coninck (1965) and Lorenzen (1981), the taxonomic significance of the shape of the *fovea amphidialis* is well established. According to these authors a " ventrally wound " fovea is dominant in Chromadoria. The Monhysterida are characterized by a circular *fovea amphidialis*. Based on the fact that the *porus canalis amphidialis* of monhysterids is situated dorsally in the fovea, Lorenzen (1981) concludes that this fovea can also be considered as ventrally wound. According to Lorenzen (1978), the winding results from the ventrally coiled *corpus gelatum*.

Our observations show that it is less the *corpus gelatum*, but essentially the terminal regions of the dendritic processes that make a ventrally wound double coil in *G. disjuncta*. Malakhov and Ovchinnikov (1980) observed that in *Sphaerolaimus balticus*, the terminal regions of the dendritic processes make one single winding in the *fovea amphidialis*. This configuration is basically different from the ultrastructure of the chromadorid *fovea amphidialis*, as e.g. described for *Paracanthonchus macrodon* in Malakhov and Yushin (1984). This fovea is ventrally wound by the fact that a cuticular ridge on the bottom of the fovea shows three concentric spiral windings.

The amphid of *G. disjuncta* is composed of fourteen fully developed dendritic processes, and an additional fifteenth receptor. This receptor is short and shows few morphologic specializations. According to its position it may be considered as a " sheath "-receptor, which in other nematodes often has elaborate morphological specializations (Coomans & De Grisse, 1981).

The functional significance of the amphidial receptors is generally based on comparative morphological interpretations. The assumption of a chemoreceptive function is originally based on the observation that the receptors are in direct contact with the outer environment. The amphidial receptors of *G. disjuncta* have fourteen long, and in the *fovea amphidialis* coiled, dendritic processes. As a consequence, the contact surface with the exterior is rather substantial and implies chemoreceptive capacities for the amphidial receptors. Recently, the role of the amphids in chemotaxis was demonstrated by laser-ablation experiments in *C. elegans* (Davis *et al.*, 1986).

As Inglis (1964) already mentioned, it is difficult to accept that the elaborate foveal differentiations are developed only to improve chemoreceptive capacities. Riemann (1966) proposed that the amphids could also

be used to detect pressure differences in the water. Our observations neither substantiate nor contradict this hypothesis. It is conceivable that movement in the water can result in differences in resistance, which could be transmitted to the double helicoidal wound dendritic processes, and transferred inwardly. All fourteen dendritic processes that reach the *canalis amphidialis* have a well developed ciliary structure. Croll and Smith (1974) assumed that an arrangement of nine microtubular doublets indicates mechanoreceptive potentials (see also Thurm *et al.*, 1983).

A secretory activity has also been put forward as a possible function of the amphids (Coomans, 1979). Recently, Premachandran *et al.* (1988) have demonstrated the secretory activity of the amphids of *Belonolaimus* and *Meloidogyne*. No doubt the formation of the *corpus gelatum* is a result of a secretory activity. The sheath cell has been considered to be a gland cell (McLaren, 1976), but our observations do not show any evidence for a gland function of the sheath cell. Nor does this study show clearly where the *corpus gelatum* would be secreted, only the process of the socket cell contains many electron-dense granules.

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