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Fine Structure of the Head and Cervical Region of *Ceramonema carinatum* (Chromadorida: Ceramonematidae)

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Abstract: Structure of the head and cervical region of *Ceramonema carinatum* (Chromadorida: Ceramonematidae) was described from transmission electron microscopy of serial transverse and longitudinal sections of two females. An unbroken massive cortical layer encompasses the head, except where three thin liplets surround the mouth. A large flask-shaped buccal cavity, with simpler less dense cuticle identical with that of the pharynx, abuts the body cuticle just within the mouth. Myoepithelial cells constituting the buccal and pharyngeal regions were described. Sixteen head sensilla, the amphids, and dorsal and ventral internal sensilla were identified and described, each with associated sheath and socket cells. Ultrasturcture of the head was compared with that of other nematodes. Arrangement of sensilla resembled that of Monhysterida and Rhabditida with some significant variations, such as prominent longitudinally arranged intracellular organelles containing many microtubules associated with the amphids. The buccal cavity was almost entirely pharyngeal in character. A well-developed system of structural fibrils and abundant hemidesmosomes were notable features.
Key words: buccal cavity, *Ceramonema*, cuticle, muscles, Nematoda, pharynx, sensilla, ultrastructure.

Transmission and scanning electron microscope studies have been made of many nematodes, mostly of plant pathogens and animal parasites. The ultrastructure of free-living *Caenorhabditis elegans* is known in greatest detail (13). However, the structure of free-living Adenophorea, apart from some plant pathogenic Dorylaimida, is much less well known, and there appear to be significant physiological and anatomical differences between Adenophorea and Secernentea (1). We have already described the body cuticle of *Ceramonema carinatum*, a heavily armoured minute marine nematode (9) and now turn our attention to the head and cervical region. Cephalic ultrastructure of Chromadoria, to which *Ceramonema* belongs, has not previously been studied. So far as possible we have followed the nomenclature of Van de Velde and Coomans (10,11). In particular, we have followed their descriptions of the head sensilla, a further development of Coomans' (5) analysis of nematode sensilla. The structure of nematode sensilla and sensory nervous system has been reviewed by Coomans and De Grisse (6).

MATERIAL AND METHODS

Ceramonema carinatum was collected from sandy beaches near the low tide mark in the vicinity of Moruya, New South Wales, on the southeast coast of Australia. Specimens were washed from sand, picked up with a fine pipette in sea water, using a low power binocular microscope, and transferred to cold fixative. Specimens were cut after fixing overnight in 2.5% glutaraldehyde in phosphate buffer, pH 7.2, containing 3% sucrose, the postfixed in 1% osmium tetroxide. For scanning electron microscopy (SEM), specimens were washed in distilled water, sonicated, freeze-dried, mounted on metal stubs using nail varnish as glue, and coated with gold palladium under vacuum. For transmission electron microscopy (TEM), postfixed specimens were progressively transferred through graded ethanols and epoxypropane to Spurr epoxy resin. After hardening of the resin at 60 C for 48 hours, serial thin sections were cut, mounted on formvar coated slot grids, and stained with 6% uranyl acetate and Reynolds lead citrate. Serial longitudinal sections were cut through the head of one female and transverse sections through the head of another female.

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Abbreviations: AC = arcade cells; AM = amphidial fovea; AMc = amphidial canal; AMd = amphidial dendrite; AMd′ = external amphidial dendrite; AMN = amphidial nerve; AMn = amphidial nucleus; AMp = amphidial pore; AMSh = amphidial sheath cell; AMSoc = amphidial socket cell; AMSon = amphidial socket cell nucleus; BC = buccal cavity; BL = basal layer of cuticle; CeS = cephalic seta; CeSc = cephalic setae sheath canal; CeSd = cephalic dendrite; CeSd(mr) = cephalic dendrite median region; CeSh = cephalic sheath cell; CeSh = cephalic sensilla sheath cell; Cp = cuticular cortical plate; CP = cortical plate of cuticle; Cu = cuticle; Dgl = dorsal pharyngeal gland; DN = dorsal neuron; DSd = dorsal dendrite; DSh = dorsal sheath cell; EP = epicuticle; ER = endoplasmic reticulum; Hd = hemidesmosome; Hdn = hypodermal nucleus; ILd = inner labial dendrite; ILd(dr) = inner labial dendrite dense region; ILS = inner labial papilla; ILSh = inner labial sheath cell; LC = lacunae; LP = liplet; LSh = inner labial sheath cell; M1, M2, M3 = first, second, and third tiers of buccal muscle cells; MC = marginal cell; MCf = marginal cell fibre; MCn = marginal cell nucleus; MI = mitochondria; MO = microtubule organelle; n = nucleus; N = nerve; NeS = neurosecretory vesicle; NR = nerve ring; OLd = outer labial dendrite; OLd(dr) = outer labial dendrite dense region; OLd(mr) = outer labial dendrite median region; OLd(rr) = outer labial dendrite root region; OLd(tr) = outer labial dendrite terminal region; OLN = outer labial neuron; OLS = outer labial seta; OLSc = outer labial sheath cell canal; OLSh = outer labial sheath cell; OLSo = outer labial socket cell; PBL = pharyngeal basement lamina; Ph = pharyngeal lumen; PM = pharyngeal muscle; PN = pharyngeal nerve; Pn = pharyngeal muscle cell nucleus; R = cuticular ridge; RF = radial connective fibre; SM = somatic muscle cell; SV pore = opening of duct of subventral gland; SVdt = duct of subventral gland; SVgl = subventral gland; Syn = synapse; Tj = tight cell junction; UN = unknown organ; V = ventral side; VN = ventral neuron; VSd = ventral dendrite; VSh = ventral sheath cell; br = basal region; dr = dense region; mr = median region; rr = root region; tr = terminal regions of dendrites.

Results

Scanning electron microscopy: General appearance of the nematode by SEM with enlargements of male and female heads is illustrated in Figure 1. The head, a slightly tapered cylinder slightly longer than wide, is distinguished from the body by the absence of deeply incised annulation. Anteriorly, the cylindrical cephalic region terminates in a circumoral ridge, within which lie three triangular liplets, one dorsal and two subventral, forming an almost flat anterior end. Eight equally spaced longitudinal ridges that extend along the length of the body continue on to the head cylinder about two thirds of the way to the circumoral ridge. Amphidial foveae, deep horseshoe shaped grooves larger in males than females, are located between the lateral pairs of ridges. Six short inner labial papillae arise from the tips of three triangular liplets, six short outer labial setae insert just outside the circumoral ridge, and four cephalic setae insert farther back.

Transmission electron microscopy: A progressive series of transverse sections taken through the head are shown in Figures 2–8; longitudinal sections are shown in Figures 9–11. The buccal cavity is flask-shaped and strongly muscular, its lumen being an equilateral triangle in cross section (Figs. 2,3). The pharyngeal lumen forms a three-pointed star in cross section with rounded apices (Figs. 4A,7,8). In transverse sections both the buccal and the pharyngeal musculature are triangular, enclosed by a uniformly thick basement lamina (50-70 nm, Figs. 5,6). The triradiate alimentary canal imparts a strong triradiate symmetry on the head, with one dorsal and two ventrolateral sectors, but the sensilla and nervous system display bilateral symmetry.

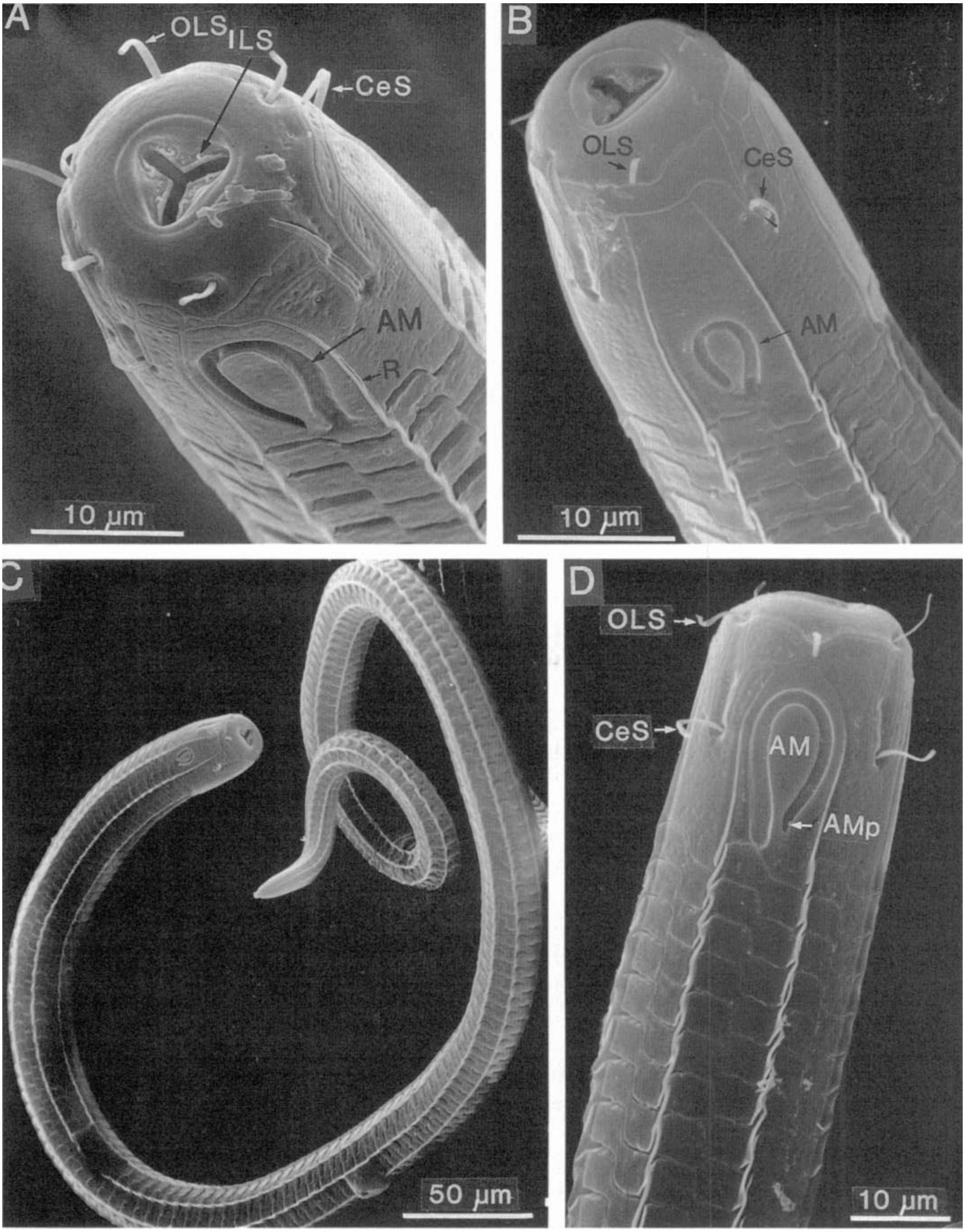

FIG. 1. Scanning electron micrographs of *C. carinatum*. A) Male head. B) Female head. C) Entire female. D) Male head.

Cuticle: Externally, a deep electron-dense amorphous cortical layer, about 2–3 µm thick, encompasses the head identical with that forming annulation plates behind the head (Figs. 9–11). On its outer surface lies a thin electron-dense epicuticle of variable thickness (30-250 nm, e.g., Figs. 5,12,13). A very thin uniform electron-lucent basal layer underlies the cortical layer (70-90 nm, Figs. 5,12,13,14). Irregu-

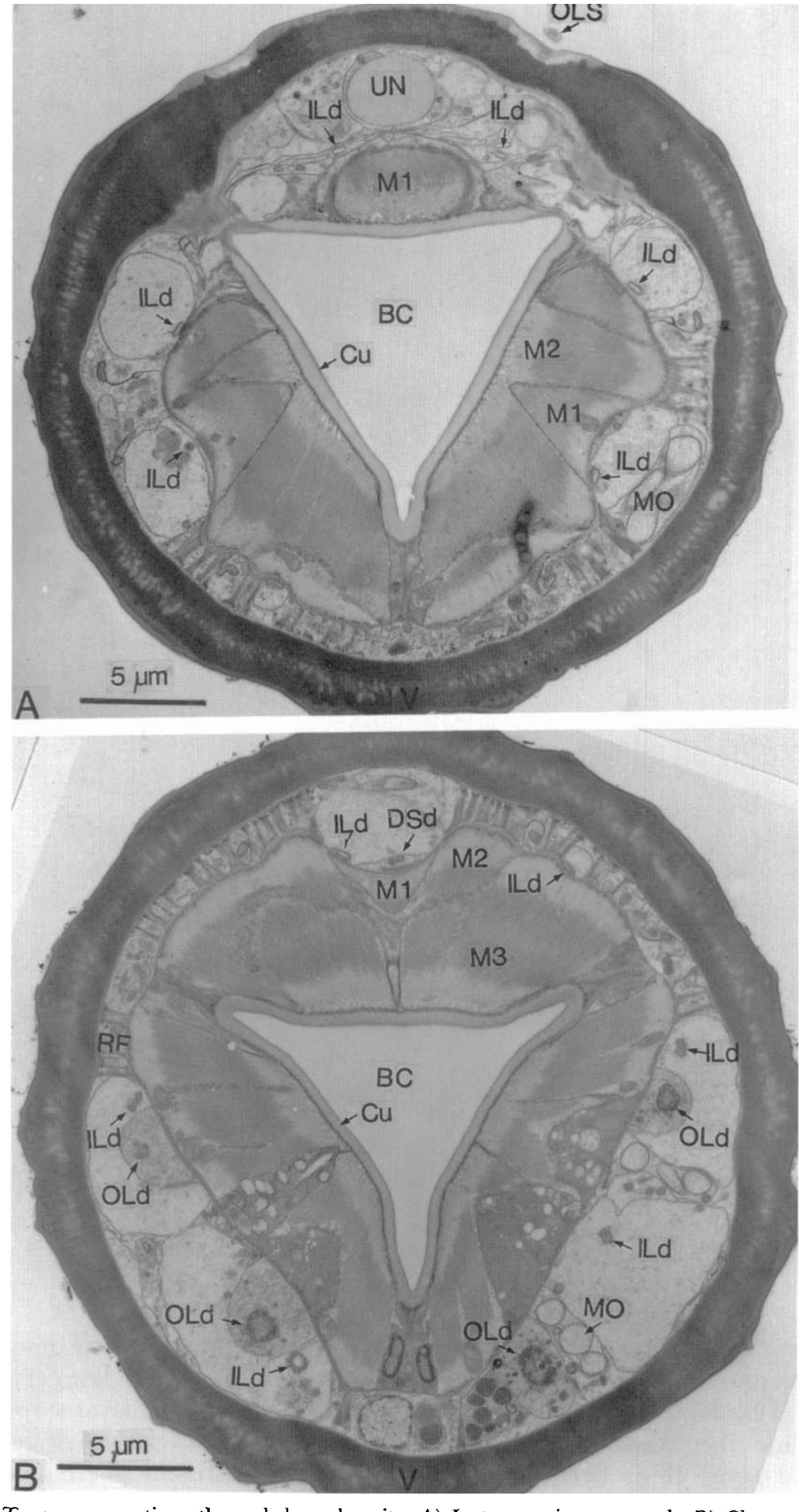

FIG. 2. Transverse sections through buccal cavity. A) Just posterior to mouth. B) Close to posterior of buccal cavity.

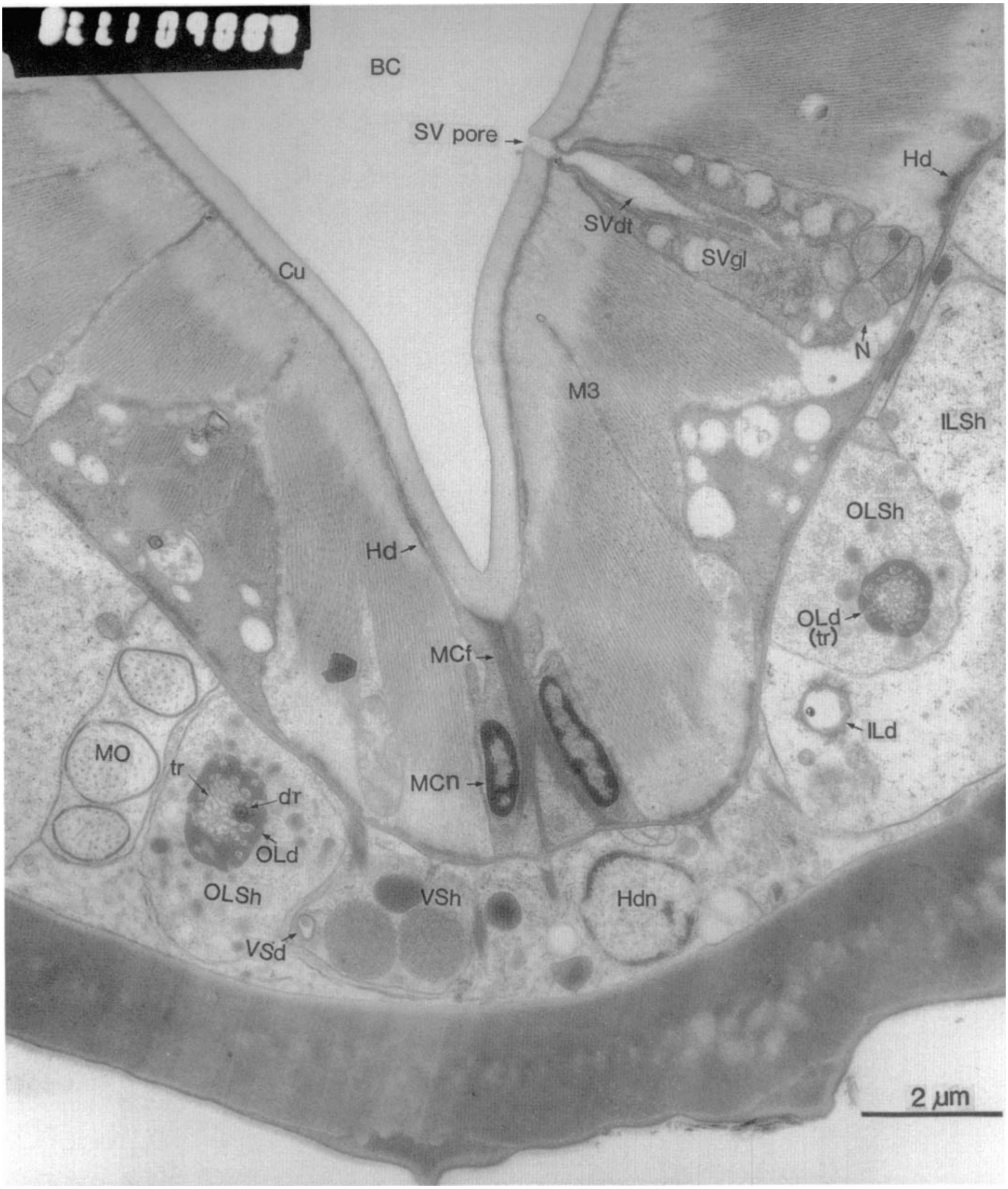

FIG. 3. Ventral part of transverse section of buccal region just posterior to section shown in Fig. 2B to show opening of subventral gland.

lar amorphous electron-dense material of varying thickness occurs beneath the basal layer (Fig. 12). Bands of lacunae, filled with very fine fibrillar material, lie within the cortical layer (Fig. 12). Amphidial foveae form deep horseshoe-shaped grooves in the cortical layer (Fig. 14). Outer labial setae and cephalic setae insert at sockets where less dense amorphous cuticle breaks the cortical layer (Figs. 10A,B).

The dense cortical layer stops at the circumoral ridge; within the ridge the cuticle is less dense, thinner where it forms liplets extending over the buccal cavity, turning under to fuse with the basal layer (Figs. 9,10D,11). Cuticle of this type extends a

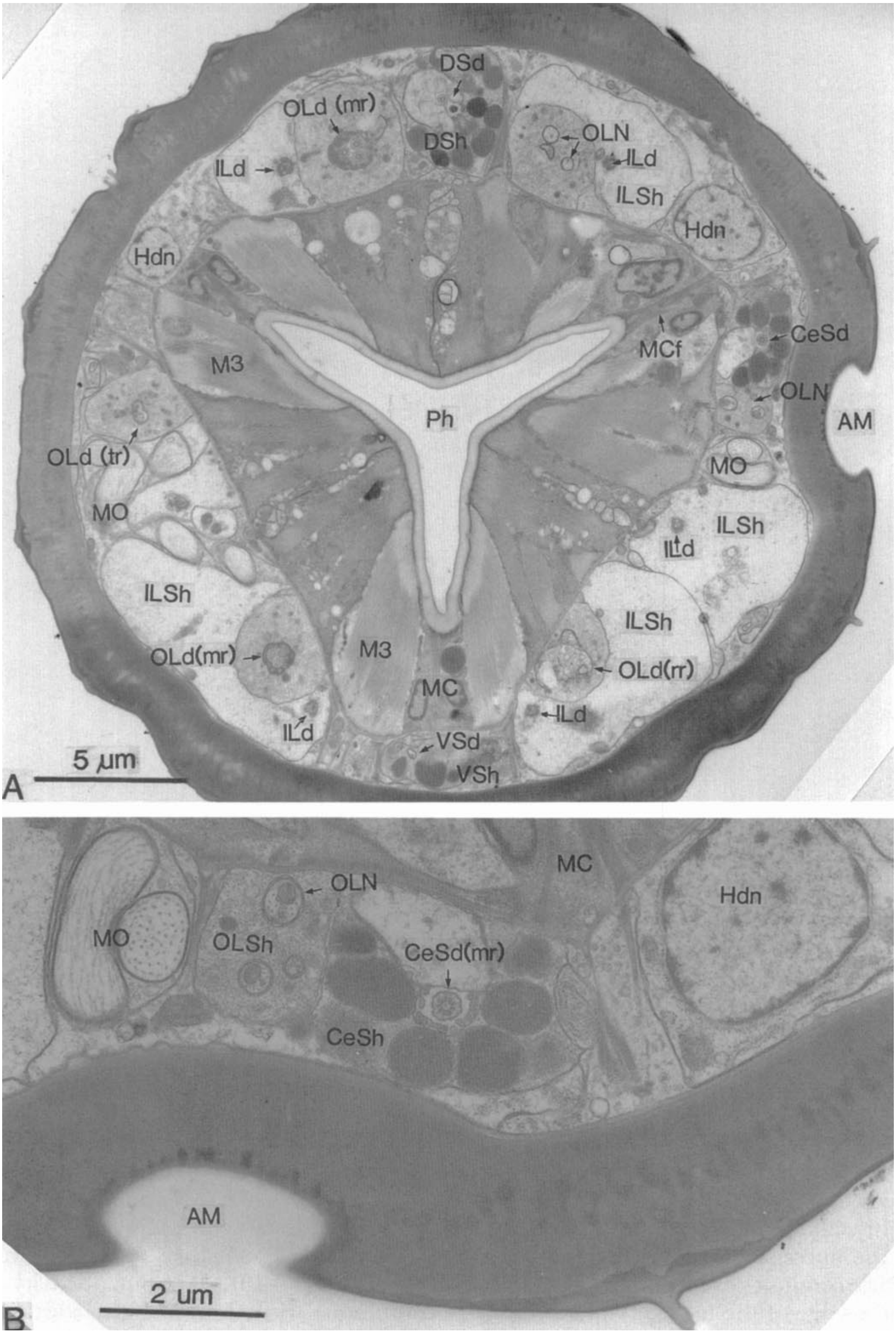

FIG. 4. Transverse sections in pharyngeal region. A) At anterior border of amphid. B) Part of same at higher magnification.

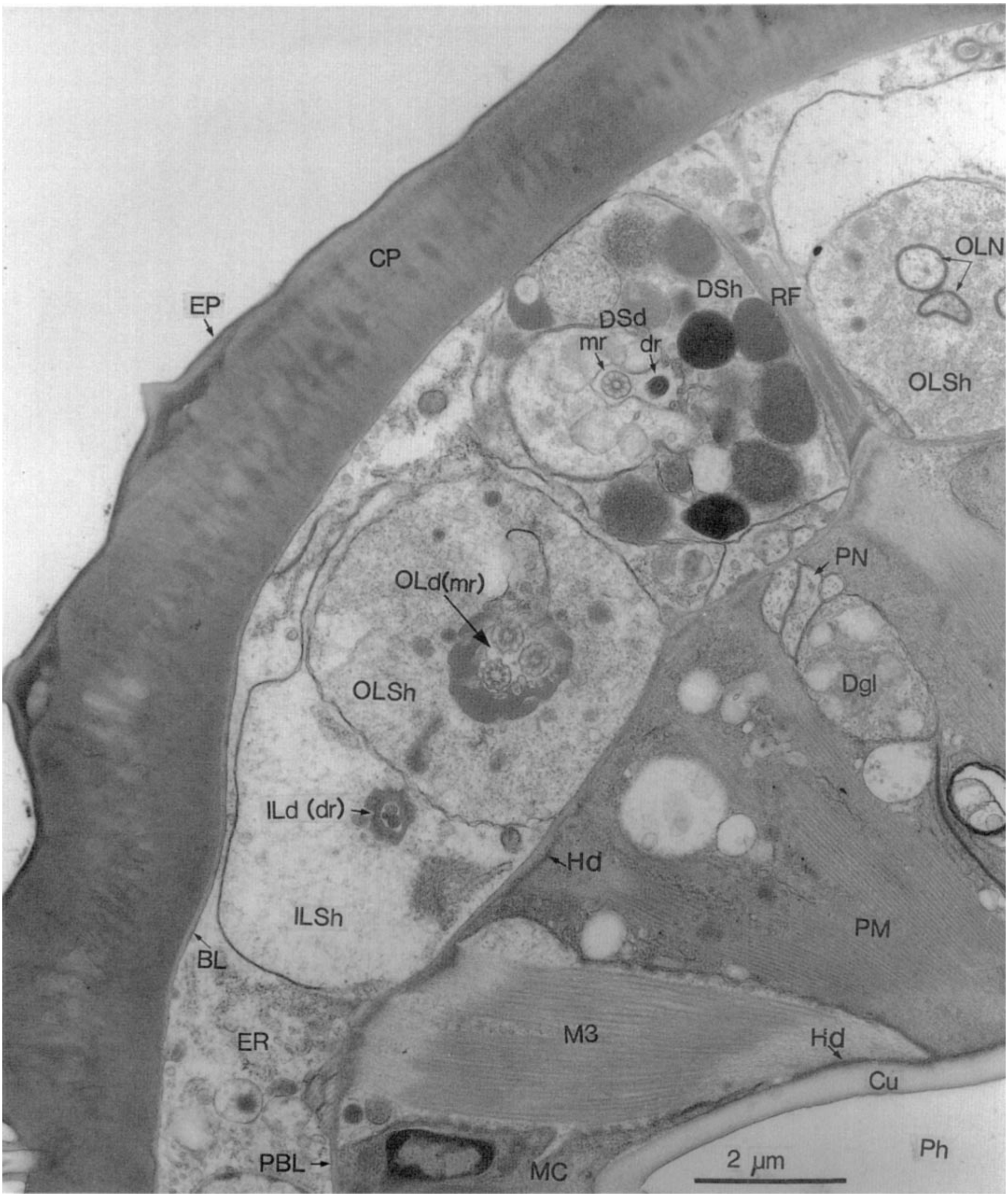

FIG. 5. Enlargement of the dorsal part of Figure 4A.

short distance, where it abuts cuticle of the pharyngeal type, supported by muscle cells, without any discontinuity in contour of the buccal cavity (Figs. 9,10D,11). Epicuticle continues over the external surfaces to the edge of the mouth.

The capacious buccal cavity and pharynx are lined by an apparently structureless electron-lucent cuticle about 370 nm thick, with an electron-denser outer surface (Figs. 3,5,9,11). A continuous band of dense hemidesmosomes binds the buccal and pharyngeal cuticle to the myoepithelium (Figs. 11–13). The buccal cavity is continuous with the pharynx, which in cross section is triradiate, with rounded apices (Figs. 4A,7,8).

Musculature: Two laterodorsal and two

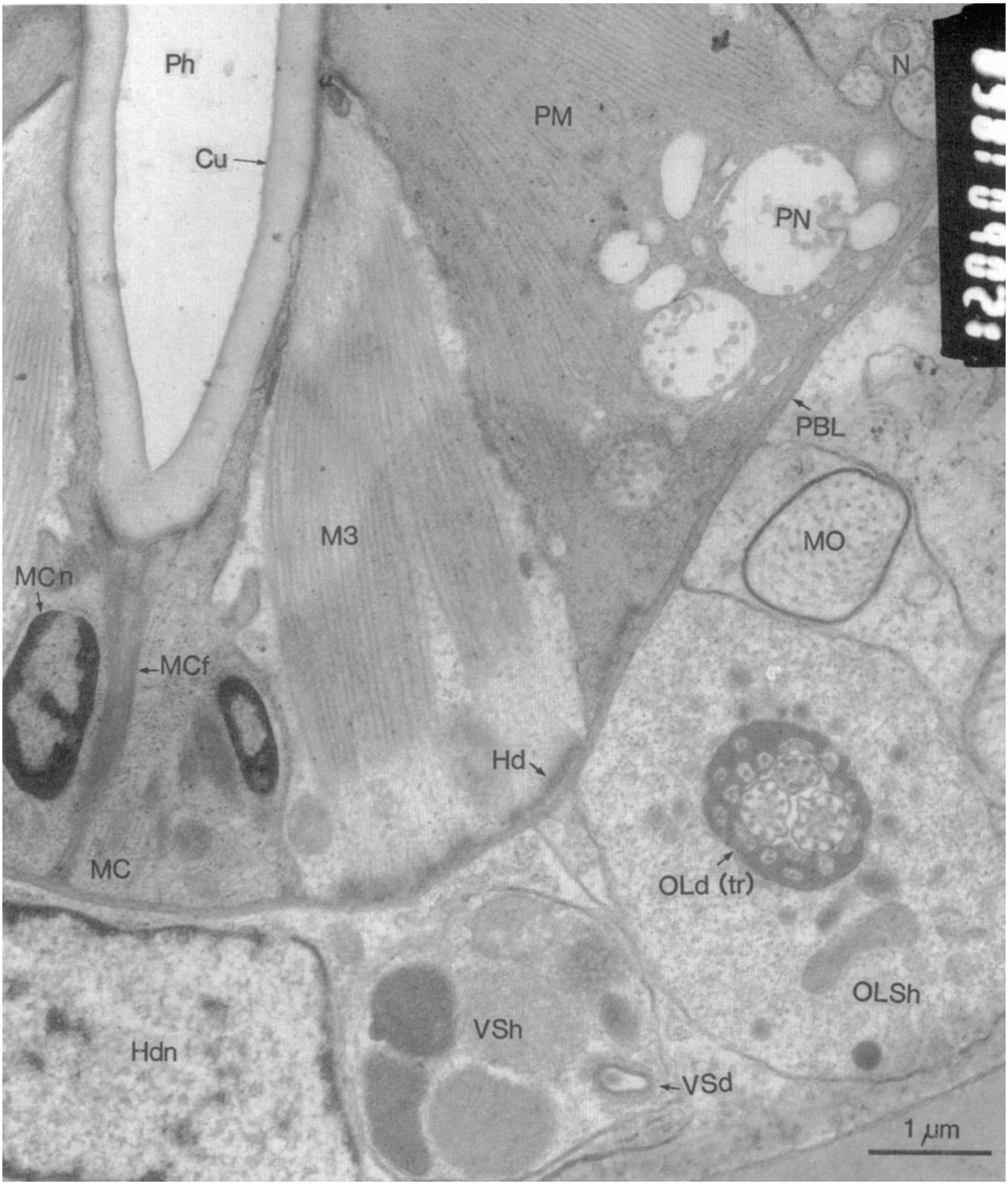

FIG. 6. Transverse section showing sensilla neurons and pharynx at higher magnification.

lateroventral bands of somatic muscles extend from the cervical region into the head to a short distance behind the insertions of the cephalic setae (Figs. 9,10B). In transverse section there are two muscle cells in each quadrant, occupying in total about 14% of the circumference of the head (Fig. 8A) and 20% of the circumference of the cervical region (Fig. 8B). There are no intrinsic liplet muscles.

In longitudinal section (Figs. 9,11,13), three tiers of radial muscle cells (M1, M2, and M3) surround the buccal cavity. In the first and second tiers, one muscle cell lies in each sector, although in the second tier each muscle is partially divided into two parts by an intrusion of M1 cells. In the third tier there are two M3 cells in each sector, so that 12 radial muscles surround the buccal cavity. Because cells overlap,

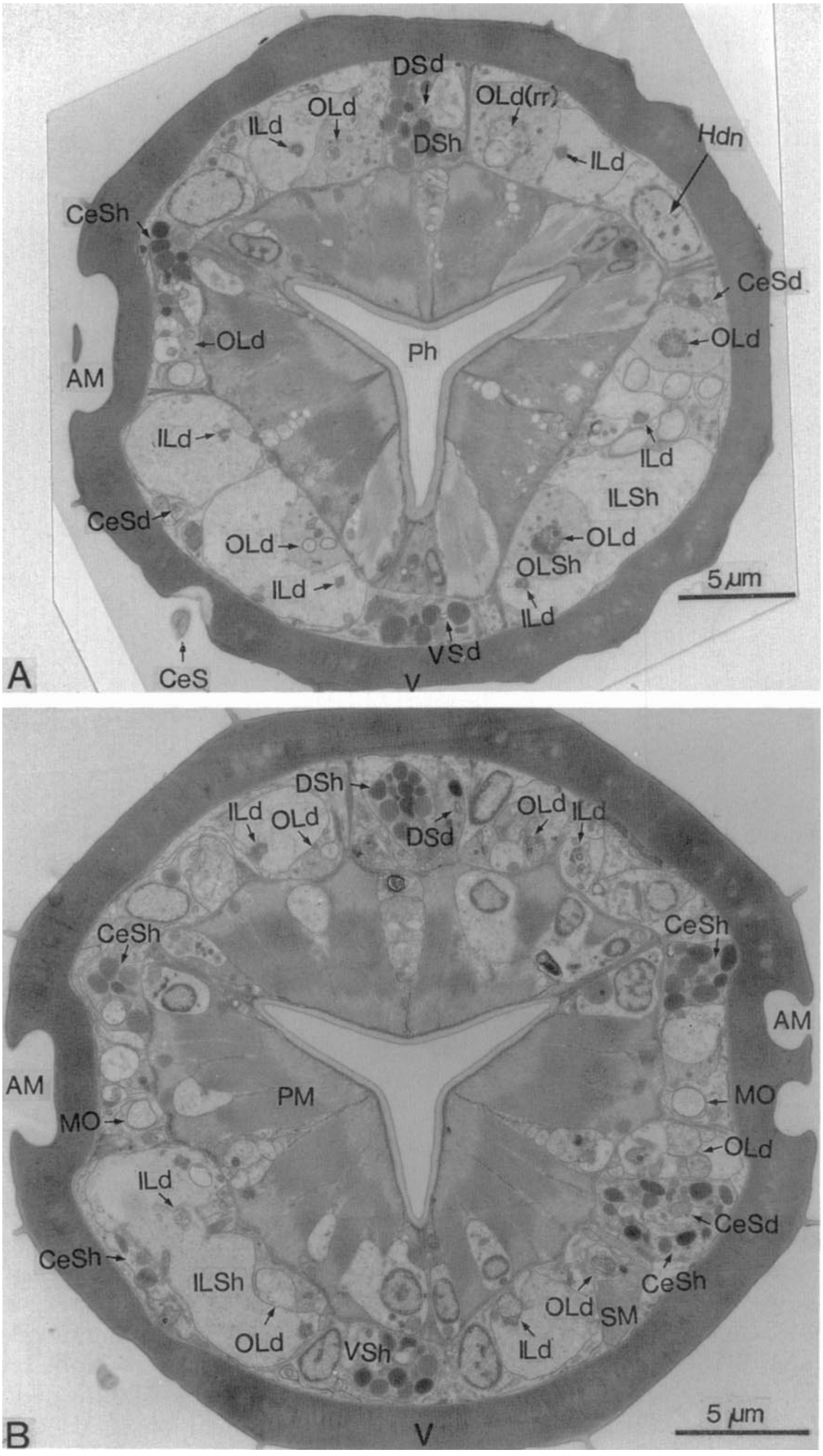

FIG. 7. Transverse sections through pharyngeal region. A) At level of one amphid. B) At level of both amphids.

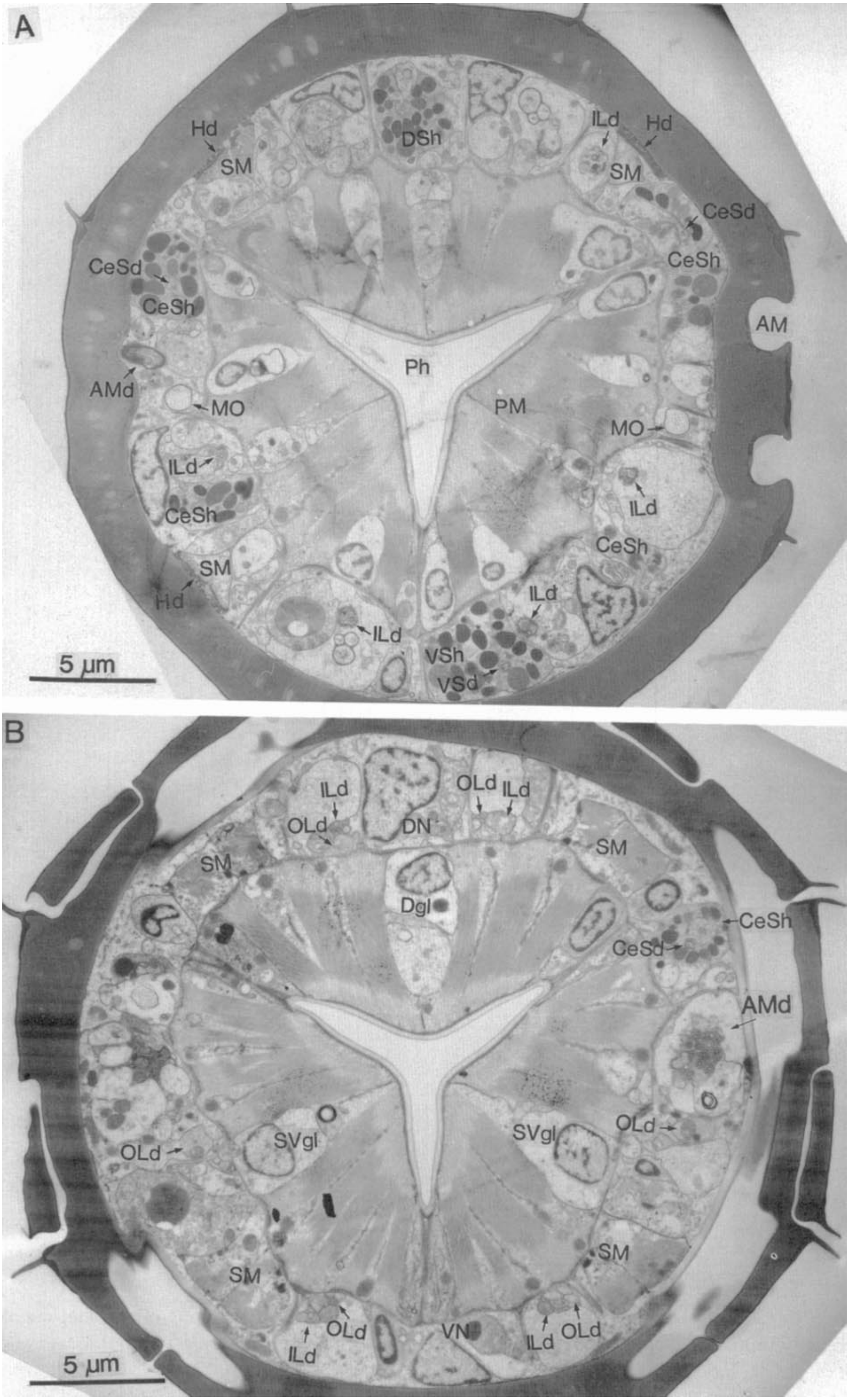

FIG. 8. Transverse sections. A) At base of head on one side, and at amphid level on the other. B) Through cervical region behind head.

FIG. 9. Longitudinal section through buccal region showing relative positions of sensilla, microtubule organelles, mouth muscle, pharyngeal muscle, and long double marginal cell nuclei.

parts of more than one cell can be seen in each sector in transverse sections (Fig. 2). The muscle cells contain a single sarcomere. Because the muscle cells apparently secrete the cuticle, they are myoepithelial cells. A continuous band of hemidesmo-

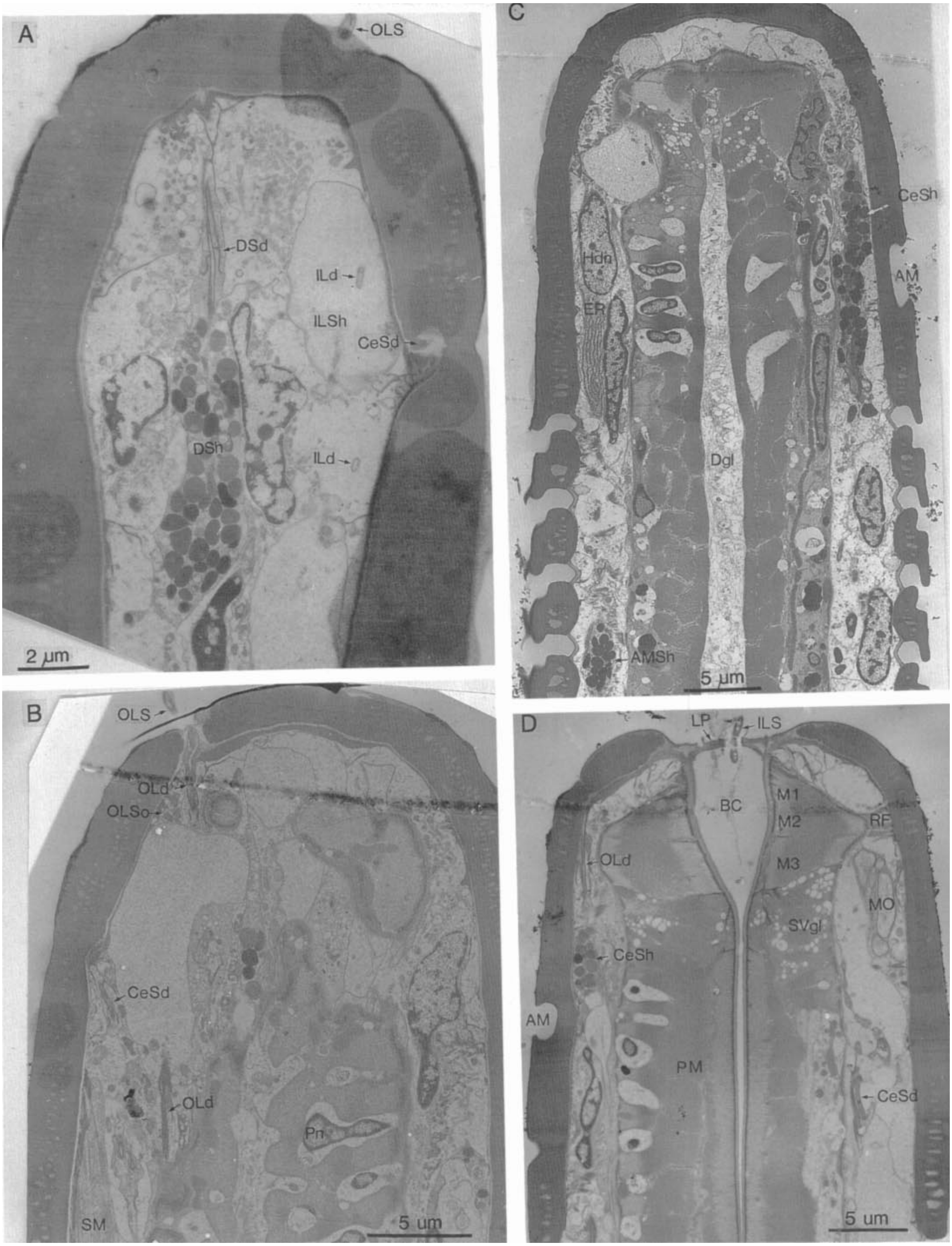

FIG. 10. Longitudinal sections of head. A) Close to dorsal surface. B,C) progressively more ventral. D) Midway through head.

somes binds the buccal and epithelial muscle cells to the buccal and pharyngeal cuticles (Figs. 3,5,6,9,11–14); a discontinuous band of hemidesmosomes also binds them to the basal lamina (Figs. 9,11–13). Dense bundles of fine radial fibres bind the buccal muscle cells through hemidesmosomes to the external cuticle (Figs. 2,11,13) and

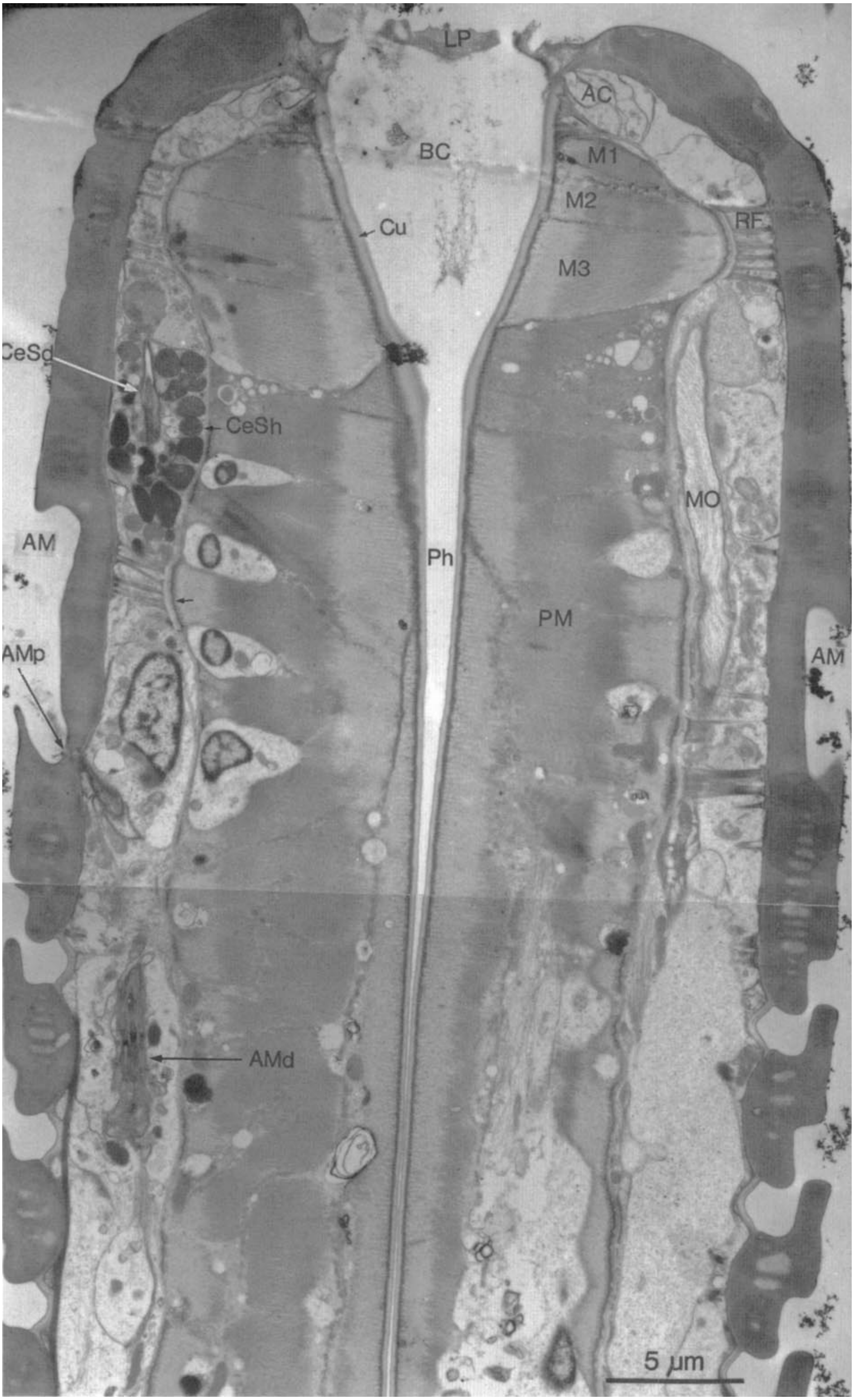

FIG. 11. Longitudinal section showing relative positions of cephalic and amphidial sensilla.

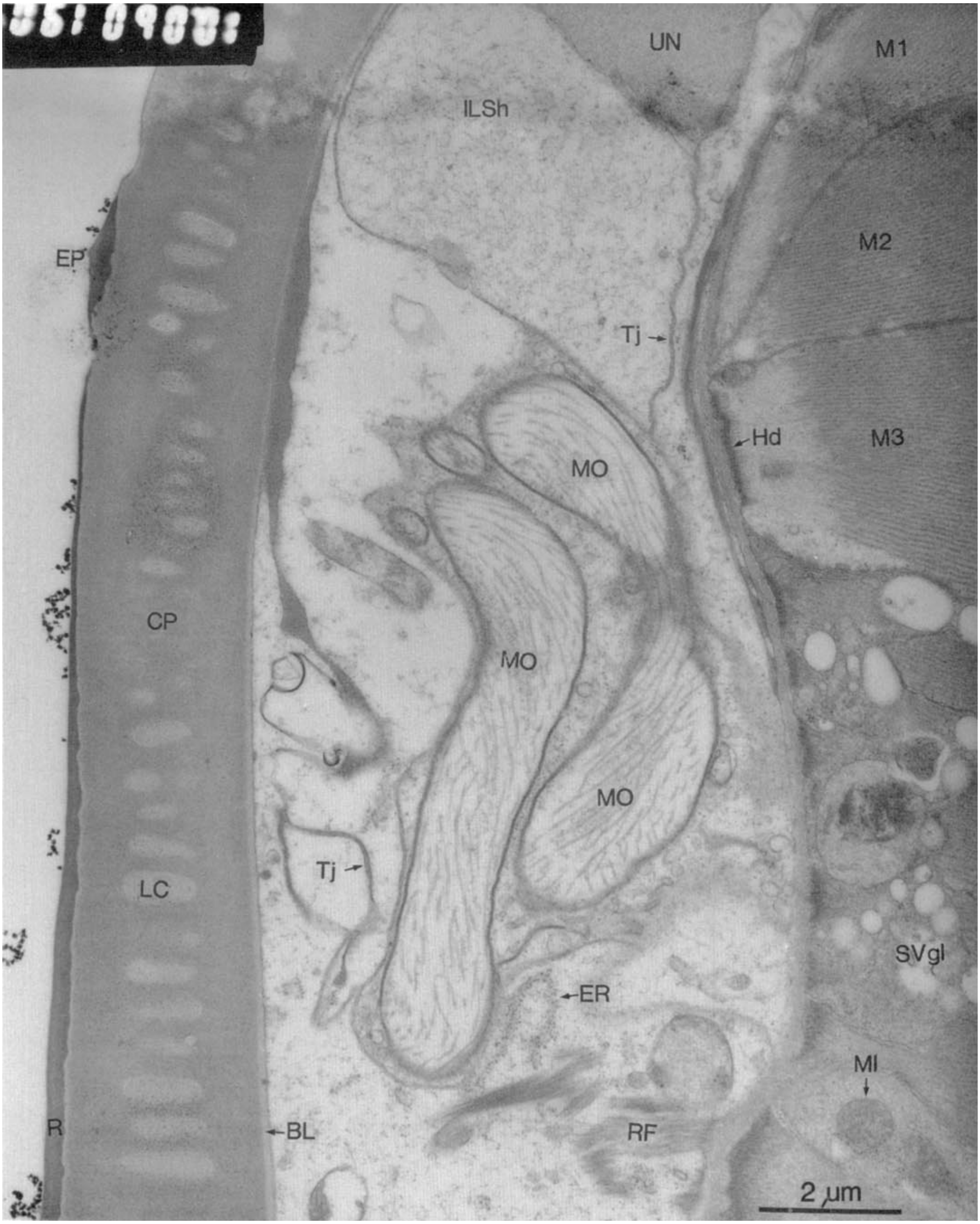

FIG. 12. Longitudinal section through buccal region to show microtubule organelle.

in smaller bundles irregularly along the length of the pharynx (Figs. 5,11). These are particularly prominent between cells of the second and third tiers of buccal muscles and the cuticle (Figs. 2,11), but occur at intervals along the whole length of the pharynx.

In transverse sections of the pharynx, there are two adradial myoepithelial cells in each sector, six in a cross section (Figs. 4A,7,8). Each adradial muscle possesses a single sarcomere, broken up into bands of myofibrils by intracellular organelles; the cell nuclei are on the outer part of the cell

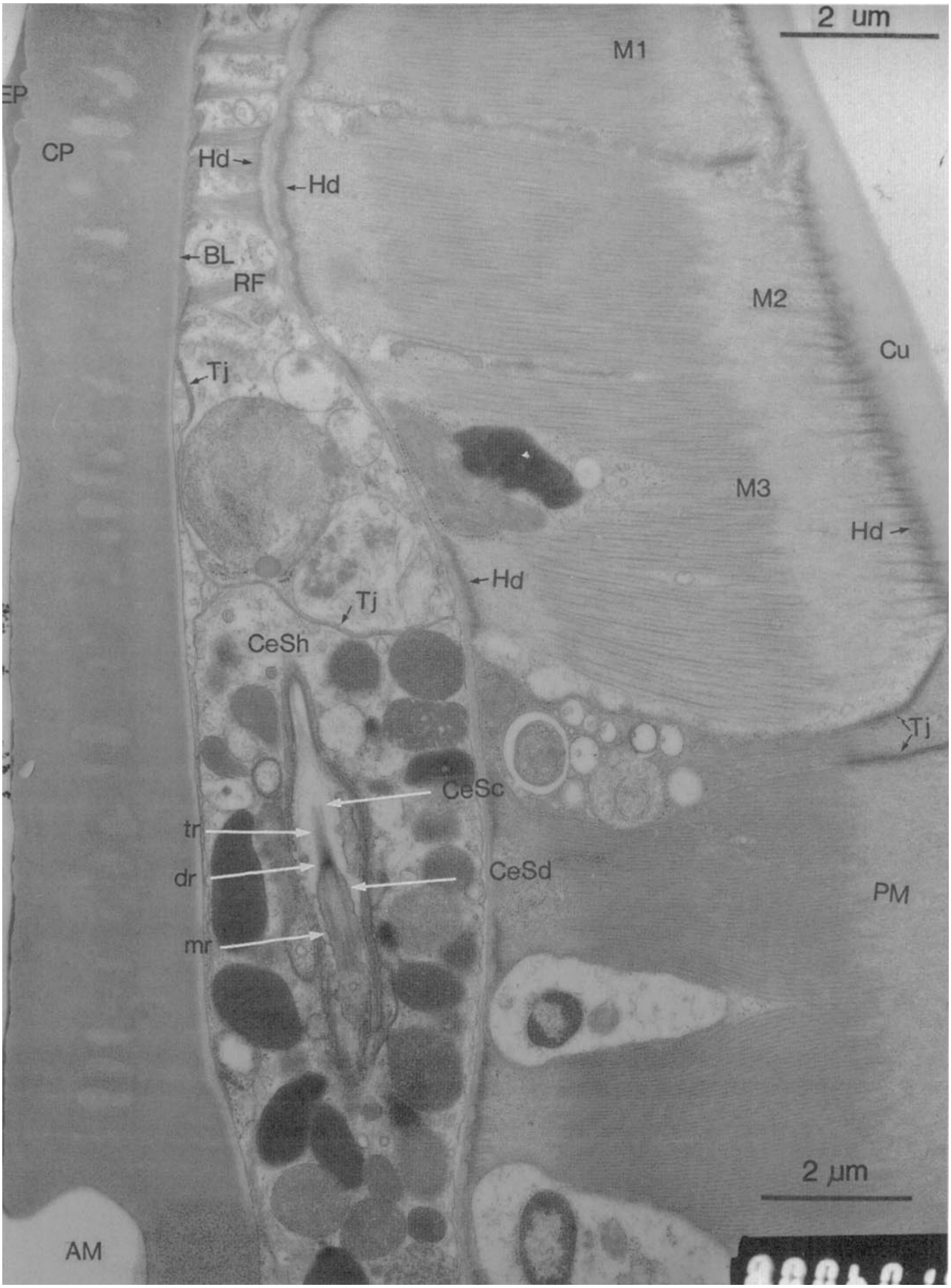

FIG. 13. Longitudinal section through cephalic sensillum.

(Fig. 11). Between each pair of muscles in a sector, a narrow cleft includes neurons, glandular tissue, and other unidentified organelles. The most posterior of the buccal cells have extensions of the third tier of radial muscle cells along both sides of the

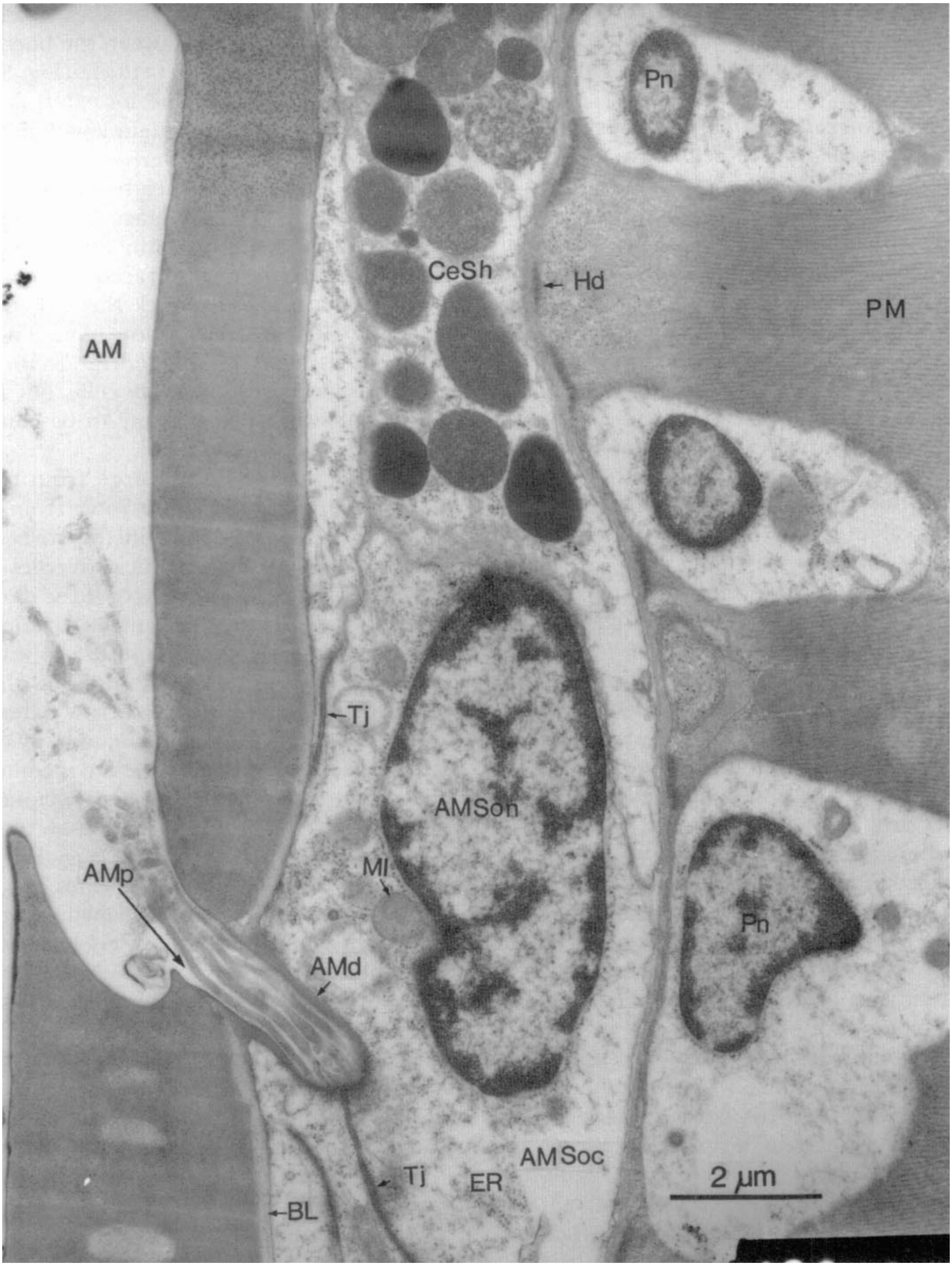

FIG. 14. Longitudinal section through amphidial pore.

marginal cells (Figs. 4–6,9). In consequence, for some distance, cross sections show 12 muscle cells instead of six. The buccal muscles are less dense than the pharyngeal; their myofilaments are more obvious. At the apices of the pharyngeal radii, there are two marginal cells containing fine fibres, their paired elongated nuclei evident in some sections (Figs. 3,4,6,9). These two cells extend forward from the pharyngeal region as far as M3 in the buccal region.

Pharyngeal glands: The most anterior pharyngeal muscle cells have more cytoplasm and numerous pale vesicles than the posterior cells, contain numerous low-density vesicles as well as myofilaments, and are probably also secretory. Two ducts with no cuticle open subventrally into the base of the buccal cavity (Fig. 3). We cannot determine from our sections whether or not there is a corresponding duct in the dorsal sector, but a very long cell, with its nucleus in the cervical region, lies in the cleft between the two myoepithelial cells of the dorsal sector as far as the first tier of buccal muscles (Figs. 5,8,10C), and, despite the absence of secretory vesicles in our specimens, we believe from its location that it is a dorsal pharyngeal gland.

Sensilla: Sixteen sensilla are identifiable, each with two or more dendrites. The terminal dendrites enter the setae, and the basal and medial parts lie within a membrane-lined canal within the sheath cell. The dendrites and sheath cells extend posteriorly to the vicinity of the nerve ring, where their nuclei are located. Socket cells surround the base of each seta, their nuclei like those of other hypodermal nuclei. The lateral amphidial sensilla have a similar structure, though more complex, with dendrites and sheath cells in the cervical region. Additional dorsal and ventral sensilla dendrites also follow the same plan, but have no external manifestation on the head. Each dendrite has a terminal region, with nine pairs of peripheral microtubules, a short dense region, a median region with cartwheel appearance in cross-section, and a root region of simple profile, which continues within the neuron cell to the nerve ring (Figs. 5,15).

Six inner labial sensilla emerge from near the apices of the liplets (Fig. 1A). Each sensillum contains the terminal regions of two dendrites, enclosed in a very thin cuticle (Fig. 10D). Median and basal regions of the inner labial dendrites lie within thin extensions of the sheath cells (Fig. 15B) in the space between the buccal musculature and the liplet cuticle (Fig. 9). Socket cells enclose the anterior extensions of the sheath cells and contain low-density inclusions (Fig. 15A). Dense, tight cell junctions occur where sheath and socket cell membranes are in contact. Dendrites, electron-dense rings within apparently empty sheath cells, can be traced in successive transverse sections back through the head into the cervical region (e.g., Figs. 2–4,7–9). In the two subventral sectors, these are large rather empty cells, but in the dorsal sector they appear to be compressed by lack of space.

Six outer labial setae emerge from behind the circumoral ring, arising from a socket formed by a break in the cortical layer, where less dense cuticle overlies a socket cell. Terminal regions of three dendrites are enclosed by thin cuticle forming the seta (Figs. 3–6,15A). A socket cell with sparse inclusions (Fig. 15A) underlies the socket cuticle and encloses narrow extensions of the sheath cell. The main body of the sheath cell lies just posterior to the buccal region enclosing the sheath canal, within which lie the median, basal, and root regions of three dendrites (Fig. 15A). Cytoplasm of the outer labial sheath cell is denser than that of the inner labial sheath cell, which sometimes partially encloses the outer labial sheath cell. Successive regions of the outer labial dendrite (i.e., terminal, dense, median, basal, and root) are illustrated in Figure 15C–H. There are clearly three dendrites, each with nine pairs of microtubules, in the terminal region (Fig. 3,6,15D).

Four cephalic setae emerge about halfway up the head capsule, located dorsolaterally and ventrolaterally (Figs. 1,7B,10A). As with the outer labial setae, they arise from a socket breaking the cortical layer, supported by a socket cell. A socket cell underlies each seta, enclosing sheath cell extensions with tight cell junctions where their membranes are in contact. The main body of the sheath cell, packed with dense vesicles, lies anterior to the amphidial

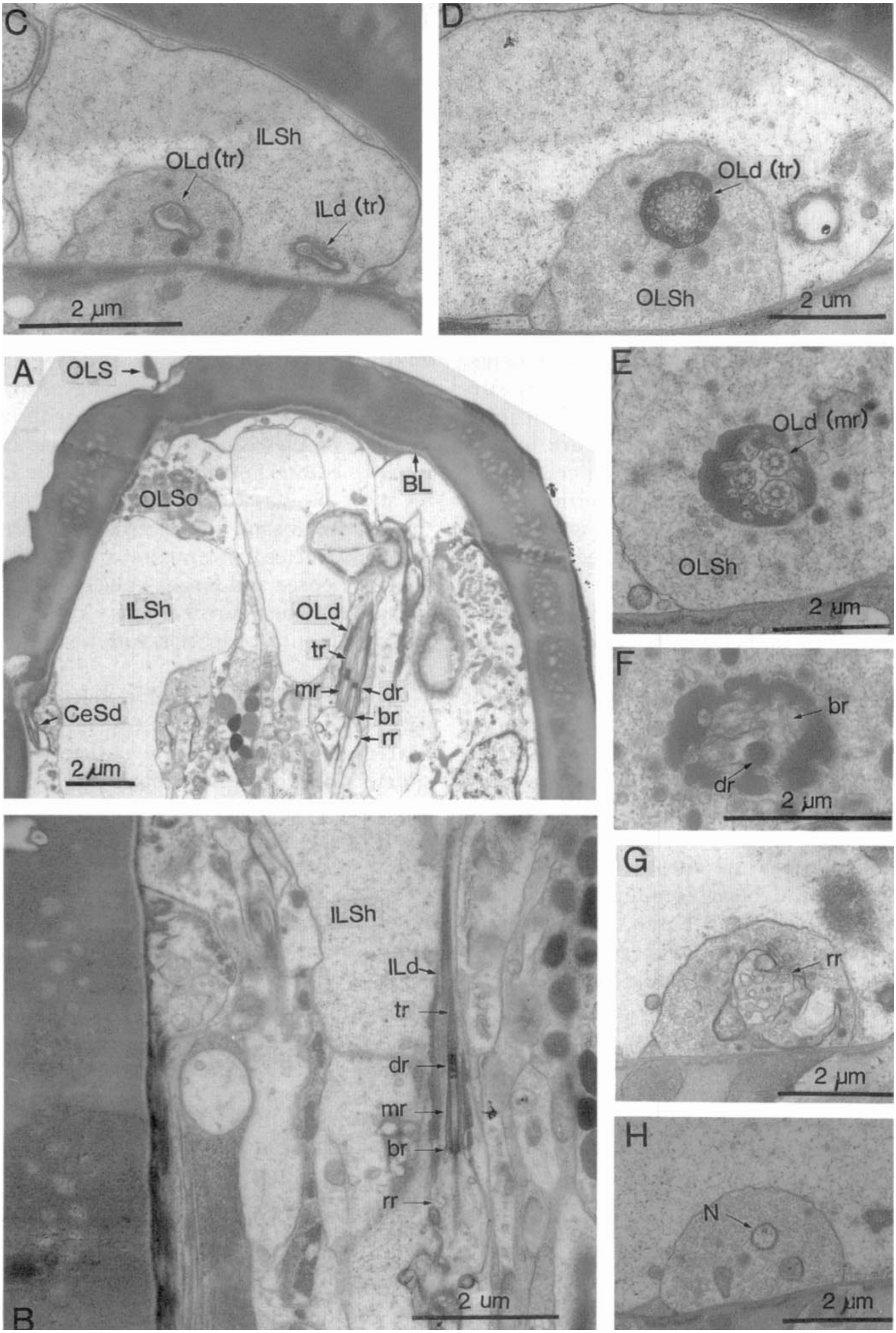

FIG. 15. Longitudinal section of head to show: A) outer labial dendrite and B) inner labial dendrite. C–H) Transverse sections of outer labial dendrite at successive levels.

foveae (Figs. 9,11,13). The sheath cell canal surrounds the dendrites (Figs. 9,13, 15). Posterior extensions of cephalic dendrite and cephalic sheath cells enclosing the dendrites can be traced posteriorly into the cervical regions in successive transverse sections (Figs. 4,7,8,10C). The relative positions of inner labial and outer labial sensilla are clearly shown in Fig. 4A, and outer labial and cephalic setae in Fig. 7B.

Amphidial dendrites emerge through a pore from a narrow canal at the posterior margin of the amphidial fovea (Figs. 1D,11,14,16A). The sheath cell is surrounded by a socket cell with tight junctions where their membranes are in contact. The region of the sheath cell enclosing the sheath canal lies posterior to the head in the cervical region (Figs. 10C,11, 14,16). The amphid can be seen in transverse sections of the cervical region (Fig. 8). Successive sections through the amphid are shown in Figure 16. Transverse sections (in the cervical region just posterior to the head capsule) show 15 closely packed dendrites within the amphidial canal, which itself has relatively dense contents. A separate larger dendrite, with about eight microtubules, lies to one side within the sheath cell (Fig. 16D). Also included within the sheath cell is a membrane-bound body containing numerous microtubules. Dendrites of the amphid can be traced through the cervical region to the nerve ring, where the cell nucleus is located (Fig. 18). Beginning in the cervical region, cellular extensions of the amphid sheath cell extend forward towards the buccal region, within which are large tubular organelles 0.75 nm in diameter, containing 60–70 widely spaced microtubules (Figs. 2–4,6–12,16). The organelles become larger, about 1–2 μm in diameter, and very convoluted, still with numerous microtubules, in the space between the buccal muscles and the external cuticle of the head capsule (Fig. 12).

Dorsal and ventral sensilla dendrites, without external manifestations, are apparent in transverse sections (Figs. 2–8). Two dendrites extend from the level of the cephalic setae to that of the outer labial setae (Fig. 10A). At the level of the amphids, these dendrites are encompassed by large sheath cells containing many dense vesicles. The dendritic roots enclosed in narrower sheath cells can be followed into the cervical region. In Figure 5, inner, outer, and dorsal sensilla lie side by side, showing their distinctive appearance in transverse section.

The nerve ring surrounding the pharynx is shown in Figures 17 and 18. The nerve ring constricts the pharyngeal muscle to a narrow isthmus. Neurons with numerous vesicles can be identified, as can numerous interneuron synapses. The latter show an increase in density adjacent to the cell membrane backed by a concentration of vesicles. Several neuron profiles contain denser and larger vesicles and are presumed to be neurosecretory. The nerve ring is surrounded by cells with prominent nuclei.

Other cellular structures: Hypodermal cells with large nuclei lie between the pharyngeal musculature and the cuticle, interspersed between the sheath and socket cells of the cephalic sensilla, and in the cervical region (Figs. 3,4,6,7,10C). Socket cells can be distinguished from hypodermal cells only by their location beneath setae and by the tight cell junctions with the terminal extensions of the sheath cells. Some hypodermal cells show a prominent endoplasmic reticulum (Fig. 10C). An undetermined number of rather empty arcade cells occupy the narrow space between the most anterior buccal muscle cells and the inner surface of the liplets, and also abut a very short length of the buccal cuticle (Figs. 10,11). Tight junctions occur where these cells are in contact. Dendrites of the inner labial setae pass through these cells to reach the inner labial papillae. A large unidentified cell with uniform finely granular contents lies dorsal to the buccal cavity, external to the inner labial sensilla (Figs. 2A,7).

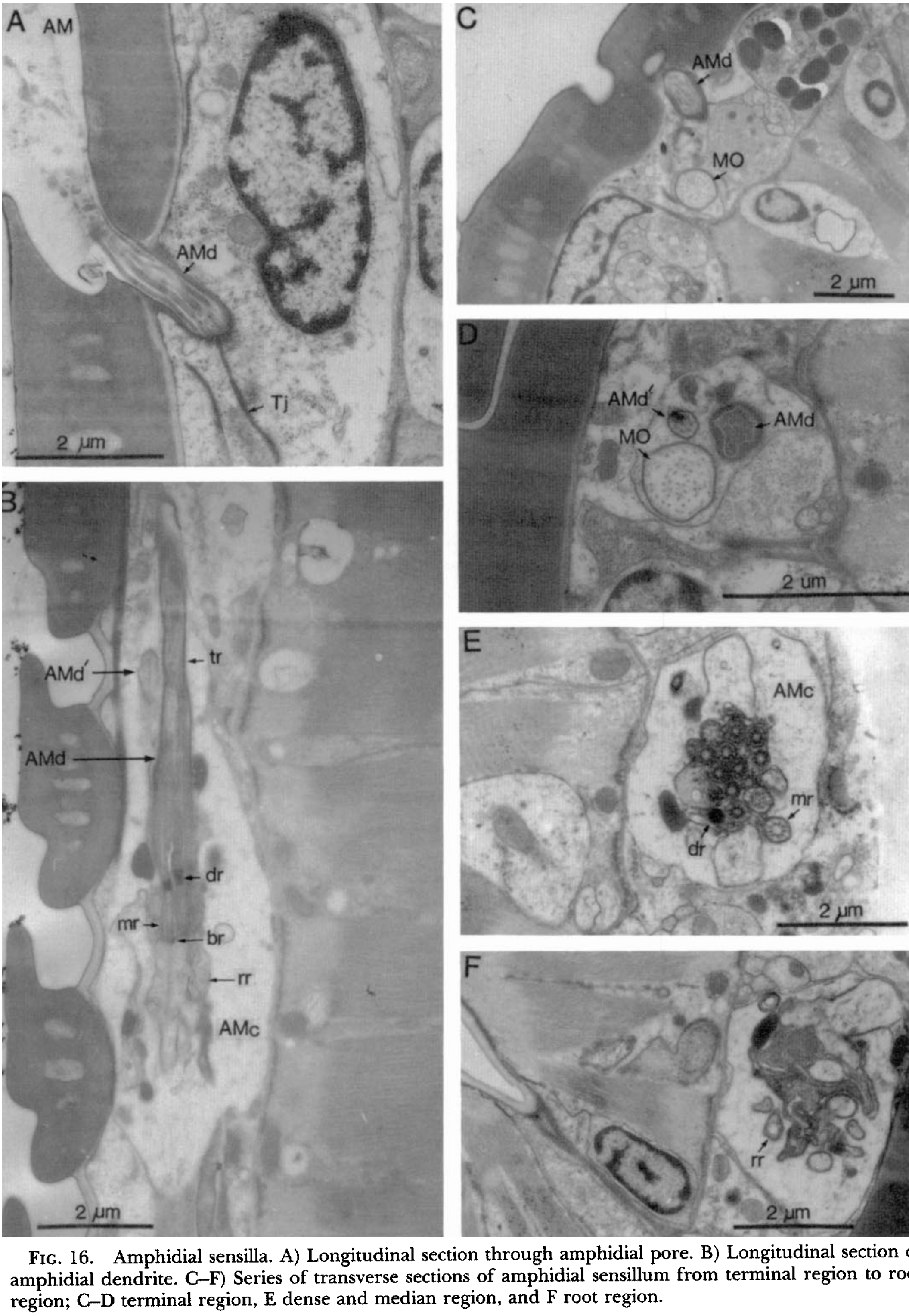

FIG. 16. Amphidial sensilla. A) Longitudinal section through amphidial pore. B) Longitudinal section of amphidial dendrite. C–F) Series of transverse sections of amphidial sensillum from terminal region to root region; C–D terminal region, E dense and median region, and F root region.

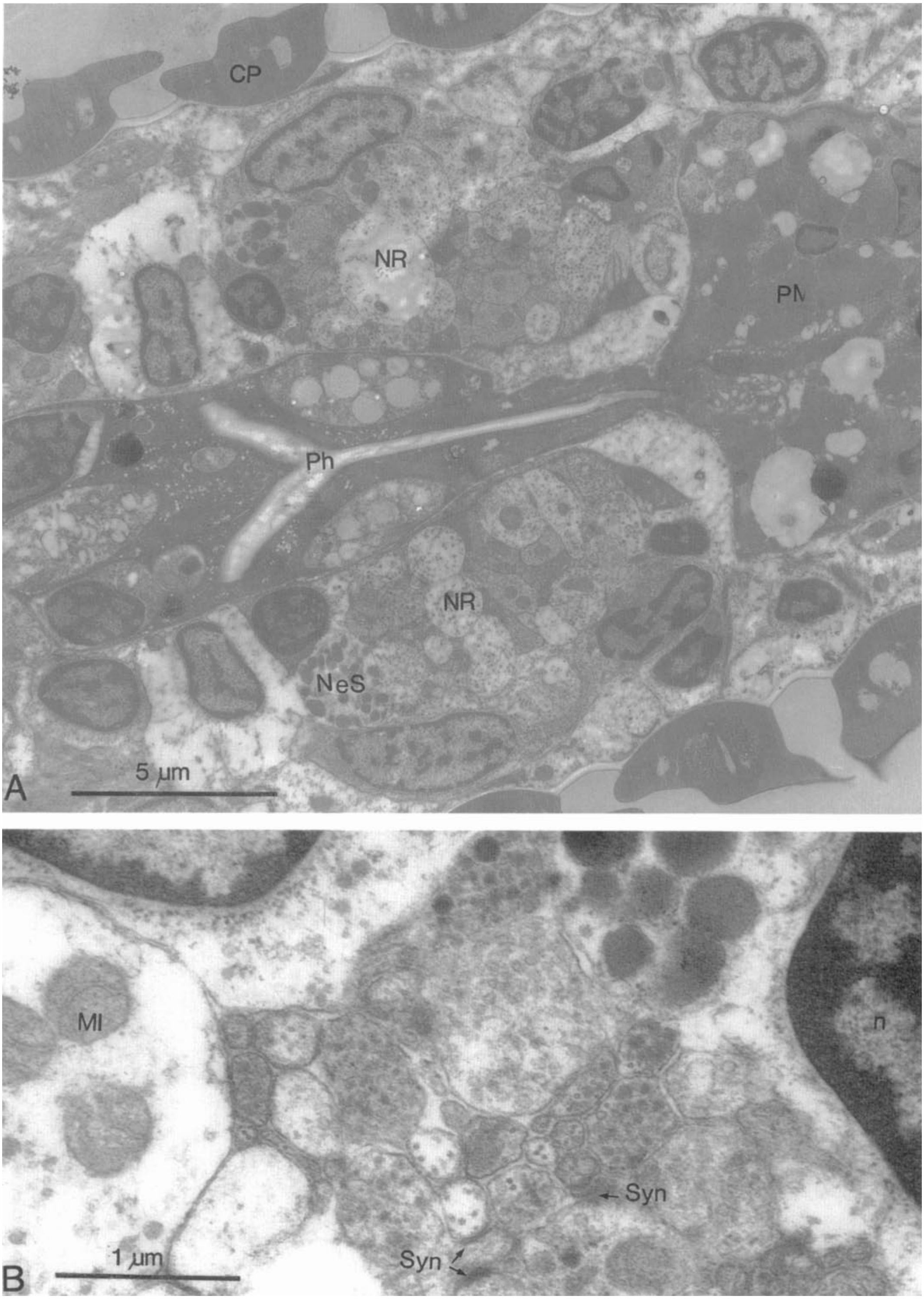

FIG. 17. A) Longitudinal section of nerve ring; B) nerve ring at higher magnification.

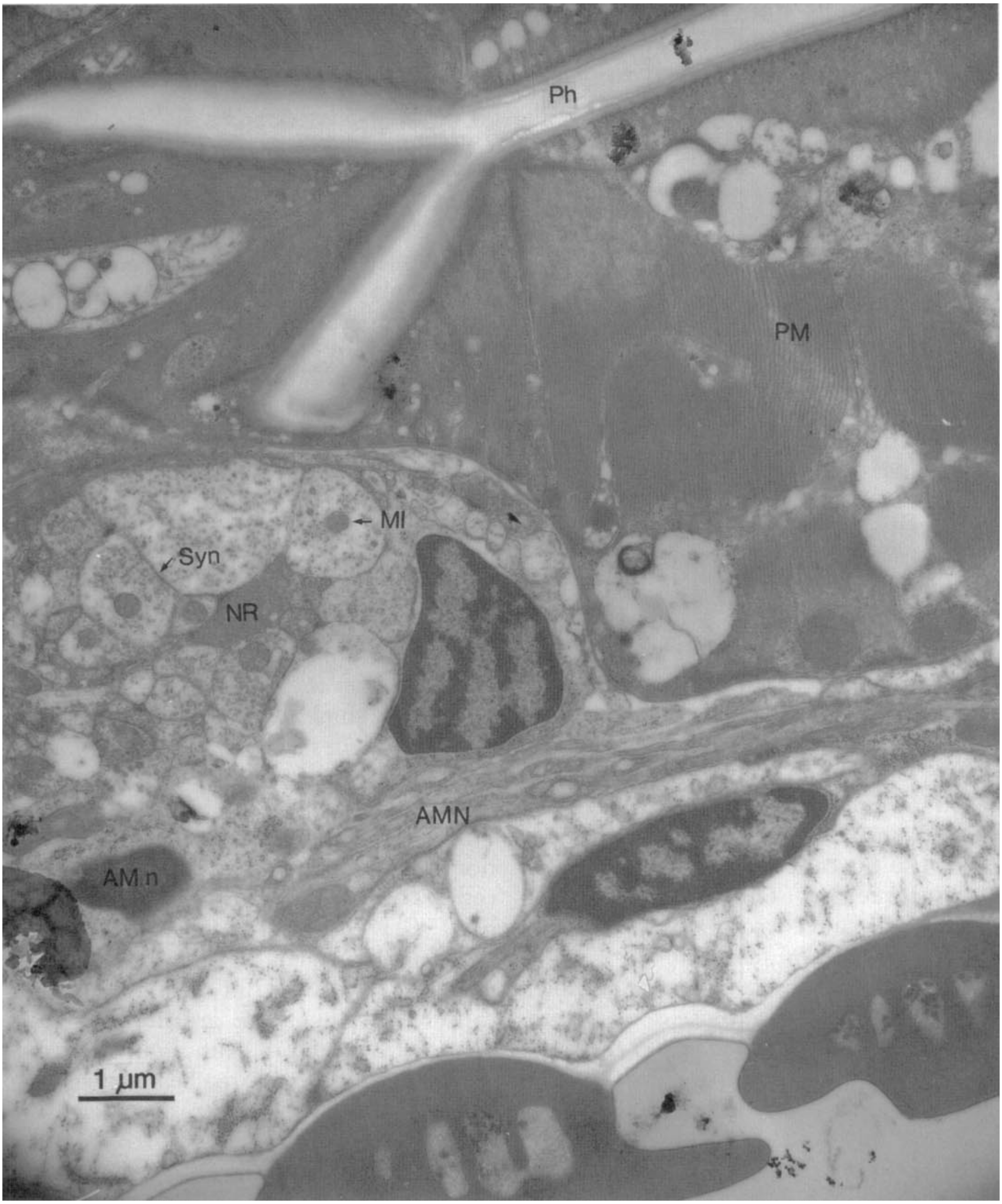

FIG. 18. Relationship between amphid cell and nerve ring.

DISCUSSION

Typically the nematode buccal cavity can be subdivided into five successive regions, namely, cheilostom, prostom, mesostom, metastom, and telostom (1). Ultrastructural studies of *Caenorhabditis* (Rhabditida) (13), *Geomonhystera* and *Diplolaimella* (Monhysterida) (10), and *Rhabdodemania* (Enoplida) (8) have shown that each region is supported by different tissues. In *C. carinatum* (Chromadorida) the cuticle of the capacious buccal cavity is identical with that of the pharynx, supported, except for about 10% of its length just within the mouth, by myoepithelial cells. Here, the external body cuticle that forms the liplets, lacking the cortical layer, borders the mouth. Typically the cheilostom is bordered by external body cuticle, but in *C. carinatum* the narrow rim around the mouth is equivalent to the mouth cuticular ring present in several Linhomoeidae (3,4), but unlike the situation in Linhomoeidae and Xyalidae (Monhysterida) (2), it does not lead to a distinct cheilostom chamber bordered by external body cuticle.

The narrow space between the liplets and the most anterior muscle tier (M1) is filled by cells with low-density cytoplasm. Where they are in contact there are tight junctions. These cells correspond to the arcade tissue of other nematodes, resembling closely the arcade cells found in *Geomonhystera* (10), thereby defining the prostom (Fig. 11). Arcade cells lie directly beneath the liplets so that they probably secrete the liplet cuticle as well as the anterior 10% of buccal cuticle. The dendrites of the inner labial papillae pass through these cells to reach the papillae, so that they also correspond to socket cells. A mesostom, a region of thickened cuticle backed by epidermal tissue between the prostom and metastom, is lacking. The rest of the buccal cuticle is supported by the first three tiers of buccal myoepithelial cells (M1-M3) and corresponds to the combined metastom and telostom.

Sixteen head sensilla are recognizable, resembling in structure those described in *Geomonhystera* and conforming to the typical nematode plan (5,6). In *Geomonhystera* the socket cells contain numerous dense inclusions, but not the sheath cells. In *C. carinatum* the socket cells, within the head, contain some not very dense inclusions, but they are largely empty of organelles. The outer labial and cephalic sheath cells, however, where they surround the sheath canal in the median dendrite region, are filled with electron-dense vesicles. Amphid sheath cells have dense vesicles, which lie in the cervical region. The socket cell nuclei lie close to the setae and not in the vicinity of the nerve ring, consistent with observations on other Adenophorea and unlike Secernentea (6). Dorsal and ventral nerves with two dendrites, with sheath cells, and that do not enter the cuticle or have any external sensory structure have been observed in addition to the 16 sensilla typical of nematodes. Additional neurons without any external expression were also observed in *Caenorhabditis elegans* (12).

The nuclei of the sensory dendrites and sheath cells do not lie in the cephalic region, and from observations on other nematodes are probably located in front of the nerve ring. The structure of the nerve ring has been interpreted in the light of Ware et al.'s (6) observations on *C. elegans*. An amphidial neuron nucleus was identified beside the nerve ring.

Prominent intracellular convoluted tubular organelles, with numerous well-spaced microtubules, occupy a large volume of the head. They originate in the amphidial sheath cells in the cervical region and extend forward beyond the amphids, lying between the pharynx and the hypodermis. In the buccal region the microtubule organelles become larger, and are convoluted and branching. Nothing quite like them has previously been described in other nematodes, although they may be homologous with the lateral amphidial receptors observed in *Aphelenchoides fragariae* by De Grisse et al. (7). Perhaps they act as compensation chambers when the buccal muscles contract within the rigid cephalic capsule, and (or) act as pressure receptors or osmotic receptors. Although the nematode lives in sea water, the beaches where it is found are subject to fresh water from rain from time to time.

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