Fine Structure of Cephalic Sense Organs in Meloidogyne incognita Males[1]

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Abstract: Amphids, and the cephalic and labial papillae of *Meloidogyne incognita* males were examined in detail by electron microscopy. Each amphid basically consists of an amphidial gland, a nerve bundle and an amphidial duct. The gland is a broad microvillous organ with a narrow anterior process, which is closely associated with the amphidial duct. A posterior process of the gland contains secretory organelles and proceeds along the esophagus with the lateral cephalic nerve bundle. The nerve bundle penetrates the broad portion of the gland and, subsequently, individual nerve processes (dendrites) separate from one another, thus forming the sensilla pouch which is enveloped by the gland. Anterior to the pouch, the dendrites converge as they enter and eventually terminate in the amphidial duct. The external opening of the duct is a broad slit which separates the cheek, the outermost part of the lateral lip, from the remainder of the lip region. *M. incognita* males have six inner labial papillae and four outer cephalic papillae which are each innervated by two and one cilia, respectively. In labial papillae, the cilia appear to terminate at the base of a pore opening, whereas in cephalic papillae each cilium terminates beneath the labial cuticle. *Key Words*: amphid, labial papillae, cephalic papillae, ultrastructure, amphidial gland, cilium, dendrite, receptor, microvillus, root-knot nematode.

Electron microscope techniques have been used to describe the anterior region of a number of nematode species, and several of these studies refer to labial and cephalic papillae as well as to amphids (12-15, 17-19, 22-24, 26-30, 32, 33, 36, 38, 39). Modified cilia have been described in most of these investigations, and nerves innervating cephalic sense organs have been shown. More recently, Bird (3) illustrated the amphids of *Meloidogyne javanica* (Treub) Chitwood, and McLaren (24) showed that in the animal parasite, *Dipetalonema viteae* (Krepkogorskaya) Bain, the amphid consists of a supporting cell which surrounds several dendrites. However, more detailed information about the fine structure of these sense organs is needed before their function becomes understood. The male of a plant parasite, *Meloidogyne incognita* (Kofoid and White) Chitwood, was chosen for this study because of the large size of the amphids, as seen in the light microscope. Special attention was given to the "amphidial cheek" which was first noted by Cobb (9), and has been recognized as a distinguishing morphological character of this genus (7, 35).

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MATERIALS AND METHODS

A North Carolina population of *M. incognita* was propagated in the greenhouse on tomato (*Lycopersicon esculentum* Mill. 'Rutgers'). Males were obtained from washed roots that had been incubated in a moist chamber at room temperature. Specimens were selected individually and killed and fixed for 1.5 hr in cold (4 C) 5% glutaraldehyde solution buffered with sodium-cacodylate at pH 7.4. The nematodes then were severed through the procorpus region of the esophagus and fixed for an additional 3 hr in fresh glutaraldehyde solution. Post-fixation was with cold 1% osmium tetroxide solution buffered with veronal acetate at pH 7.3 for 3 hr (25). The material was embedded in 1.5% agar (37) and dehydrated through a cold, graded ethanol series over a 3-hr period, using a fritted glass filter and separatory funnel assembly (31). Infiltration was with Epon 812 – Araldite 6005 mixture during 72 hr in a desiccator. The blocks were polymerized at 45 C, then 60 C, and serially sectioned with a diamond knife using a Reichert Om U-2 ultramicrotome. Sections were stained, using the apparatus designed by Fisher (10), in uranyl acetate and lead citrate (34), and were subsequently examined with a Hitachi HS-8 electron microscope operated at 50 kv.

OBSERVATIONS

Amphids: The amphid of the male of *M. incognita* includes a terminal duct (amphidial duct) which contains the distal ends of several nerve processes (dendrites) (Fig. 1-A, B). These dendrites are components of the lateral cephalic nerve bundle which extends anteriorly from ganglia associated with the nerve ring and proceeds along the side of the esophagus. A certain region of the dendrites is enveloped by a large gland (amphidial gland), which has an anterior and a posterior process (Fig. 1-A, 2). Throughout most of the procorpus region of the esophagus, the lateral nerve bundle consists of a number of dendrites which are only about 0.3μm in diam and contain few organelles (Fig. 3). The dendrites are closely associated with the posterior gland process which extends most of the length of the procorpus and contains golgi-like complexes, vesicles, endoplasmic reticulum, ribosomes and mitochondria, which are especially numerous as the process approaches the amphid proper (Fig. 4). Near the level of the dorsal esophageal gland ampulla, the gland process contains several microvilli (Fig. 5). The nerve bundle, consisting of 13-15 dendrites, assumes a dorso-lateral position as individual dendrites enlarge (Fig. 2, 5). In cross sections slightly below the stylet knobs, the amphidial gland broadens to about 8 X 4μm, and as many as 350 microvilli may be present (Fig. 2, 6). Each microvillus is approximately 0.1 X 8μm, and may branch secondarily (Fig. 2, 8). Figure 7 shows the cytoplasm, limiting plasma membrane and microfilaments of the microvilli. The microvilli are grouped in clusters of up to 20 within membranous chambers which are filled with granular material (Fig. 6). The chamber walls support a cytoplasmic region located near the gland's center from which the microvilli originate (Fig. 8). In this same region, the nerve bundle begins to penetrate the gland and again assumes a more lateral position (Fig. 1-A, 2, 9). Individual dendrites, which contain mitochondria and microtubules, are broad (about 1.5μm in diam) and irregularly shaped in cross section, and remain in close proximity to one another (Fig. 1-B, 9). However, in the region where the gland encloses the nerve bundle completely, a series of changes occur in individual dendrites (Fig. 1-A, B). They first become small (0.7μm) in cross section (Fig. 1-B, 11), then enlarge to 1.0μm and contain only a few microtubules and rootlets, but no mitochondria (Fig. 1-B, 10, 12). Simultaneously, individual dendrites become

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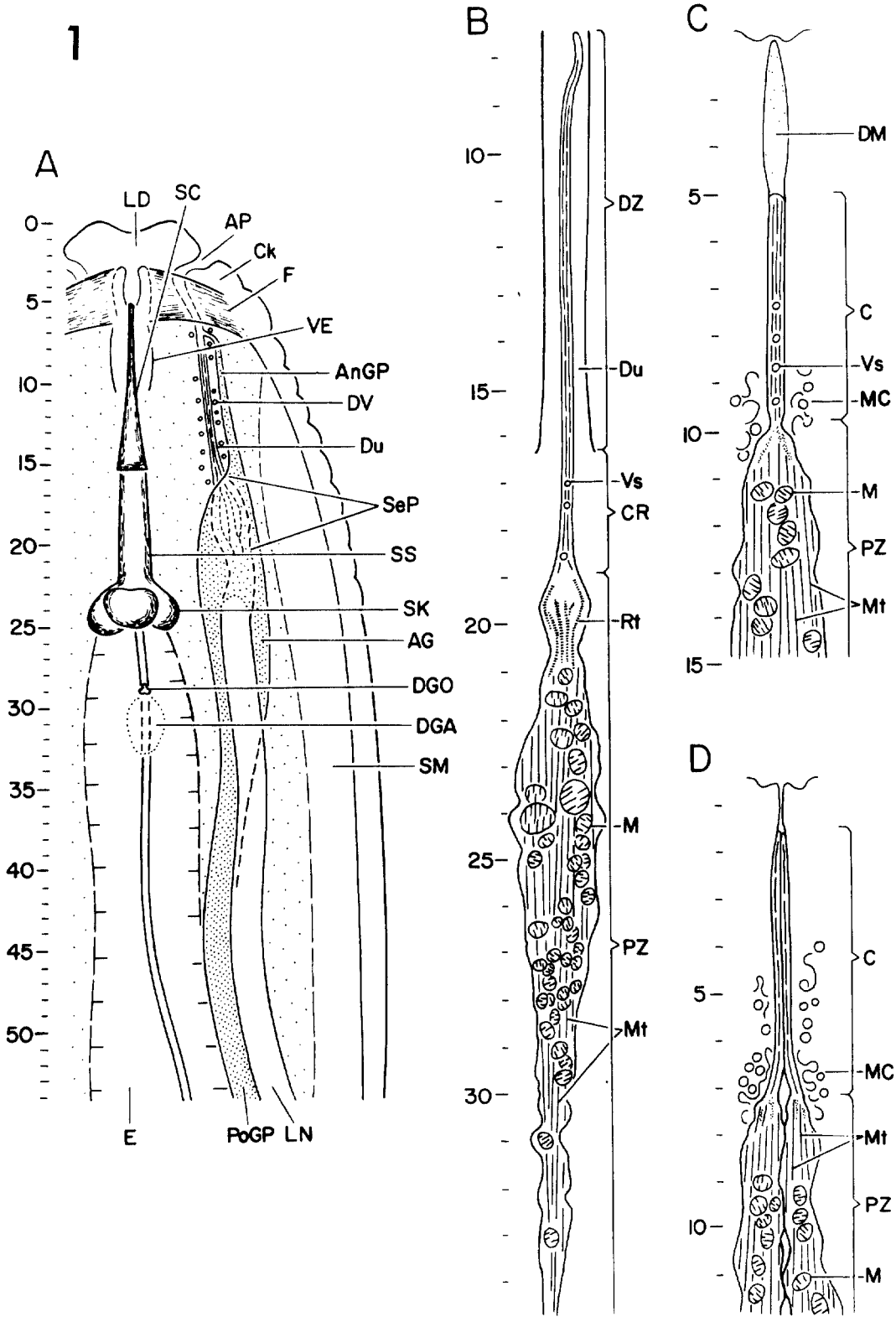
FIG. 1-A, B, C, D. Diagram illustrating relative size of individual sensory receptors in the anterior region of a *Meloidogyne incognita* male. **A.** Dorsal view of anterior portion of male, illustrating the amphid viewed from its narrow side. **B.** Amphidial dendrite (longitudinal section). **C.** Cephalic papillary dendrite (longitudinal section). **D.** Two labial papillary dendrites of a single papilla (longitudinal section). Scale units are in micrometers and indicate distance from anterior extreme of the nematode. They represent levels of sections illustrated in Fig. 3-32. *Key*: AG, amphidial gland; AP, amphidial pouch; AnGP, anterior gland process; C, cilium; Ck, cheek; CR, ciliary region; DGA, dorsal gland ampulla; DGO, dorsal esophageal gland orifice; DM, dense material; Du, duct; DV, dense vesicle; DZ, distal zone; E, esophagus; F, cephalic framework; LD, labial disc; LN, lateral cephalic nerve bundle; M, mitochondrion; MT, microtubules; MC, membranous chambers; PoGP, posterior gland process; PZ, proximal zone; Rt, rootlets; SC, stylet cone; SK, stylet knobs; SM, somatic muscles; SeP, sensilla pouch; SS, stylet shaft; VE, vestibule extension; Vs, vesicle.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separated from one another by layers of granular material which is present throughout the gland. As they separate, the dendrites decrease in diameter, and dense peripheral regions (rootlets), from which double microtubules (doublets) originate, are apparent (Fig. 13). The exact arrangement of these ciliary microtubules is difficult to determine at their proximal origin, because they converge inward (and are thus sectioned obliquely) as the dendrite decreases in size from 0.5 to 0.3μm (Fig. 1-B, 14). Further distally, most dendrites have eight conspicuous doublets, and several scattered single microtubules as well as vesicles in some instances (Fig. 15). This relatively short portion of the dendrite is the only part with doublets and is thus distinguished as the ciliary region (Fig. 1-B). As the preceding changes occur in individual dendrites, seven or eight of them orient into a radial pattern in the matrix of granular material. The region in which the dendrites are separated from one another is the sensilla pouch (Fig. 1-A, 2, 16). Those dendrites which are not constituents of the sensilla pouch become scattered in the amphidial gland as they branch off at various levels. Some terminate as cilia in the gland (Fig. 6), whereas others leave the gland and eventually innervate other areas of the head, including certain papillae. Microvilli of the gland often do not extend as far anterior as the sensilla pouch, so that most of the gland chambers contain only granular material.

The amphidial duct commences immediately above the sensilla pouch (Fig. 1-B, 2) and is distinguished by a thin lining which is continuous with the external cuticle (Fig. 17). Adjacent and laterally to the duct is the anterior process of the amphidial gland (Fig. 17). The radially arranged dendrites enter the amphidial duct as processes about 0.3μm in diam and are no longer separated by granular material. In this region, the distal zone, they contain only scattered single microtubules (Fig. 17). Thus, the ciliary region which has doublets is limited to the sensilla pouch (Fig. 1-B). Highly electron-dense vesicles and membranes surround the amphidial duct (Fig. 17, 18, 19). Some of the membranes form a continuum between the chambers of the anterior amphidial gland process and the dense vesicles. The vesicles, in turn, appear to be closely associated with the lining of the duct (Fig. 17).

Slightly beneath the basal plate of the cephalic framework, the dendrites terminate as flattened or lobed tips ranging from 0.1 to 0.5μm in diam, and the number of microtubules decreases (Fig. 18). At the tips of the dendrites, an electron-dense substance is often present within the duct (Fig. 19). Anteriorly to the dendrite tips, the duct becomes flattened and slitlike, and the anterior gland process ends (Fig. 20). However, channels extend anteriorly from the gland process and turn inward to connect with the duct (Fig. 21).

At the basal plate of the framework, the amphidial duct broadens to an "I-shaped" slit (Fig. 22) which eventually separates the outer part of each lateral lip or "cheek" from the remainder of the lip region (Fig. 23). This distal broad portion of the duct seems to represent the "amphidial pouch". The cheeks terminate in the framework region and cannot be seen in the anteriormost part of the nematode head, the labial disc (Fig. 24).

Papillae: Meloidogyne incognita males have a complement of six inner labial papillae and four cephalic papillae; outer labial papillae are not present (Fig. 22, 24). The inner papillae are located one in each of the six lip sectors on the labial disc, less than 0.5μm from the slitlike stomatal opening (Fig. 24). Cephalic papillae are located in each of the subdorsal and subventral sectors and are found on the surface about 1.5μm below the labial disc and approximately 2μm from the stylet.

Cephalic papillae are each innervated by a single dendrite included in subdorsal and subventral bundles that apparently originate in ganglia associated with the nerve ring. On the other hand, two dendrites extend to each labial papilla which appear to originate with the lateral nerve bundles that also innervate the amphids. Although these dendrites are difficult to trace, it appears that the labial papillary nerve of the subdorsal and subventral sectors branch into their respective regions about 7μm from the labial disc (Fig. 19).

Fine-structural changes similar to those described for the sensilla of amphids, occur in both types of papillary receptors. However, doublets extend to the distal tip of each dendrite, thus identifying this region as cilium (Fig. 1-C, D). The diameter of the proximal zone of the dendrite may be 1-2μm, and microtubules as well as small mitochondria are present (Fig. 1-C, D). Microtubules of the cilium originate proximally in dense peripheral regions (Fig. 25, 29). The cilium of cephalic papillary dendrites generally has seven peripheral doublets (Fig. 26, 27); whereas, labial papillary cilia have five or less doublets

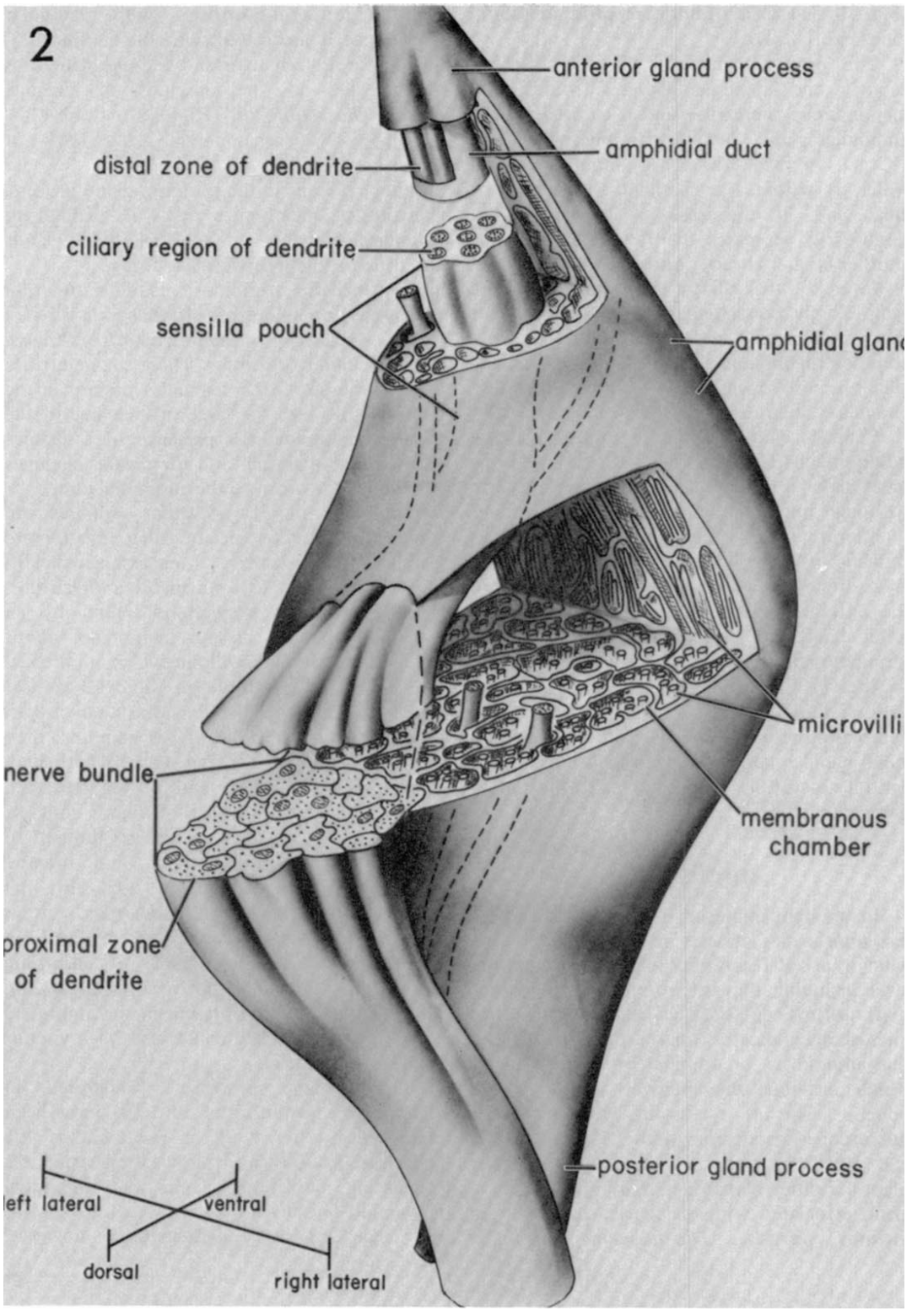


FIG. 2. Three-dimensional diagram of amphid of *Meloidogyne incognita* male; showing relationships among amphidial gland, nerve bundle, sensilla pouch and amphidial duct.

(Fig. 30, 31). Cilia of both receptors are 4-5μm long (Fig. 1-C, D).

The proximal part of the cilia of both cephalic and labial papillae is surrounded by membranous chambers, similar to those of the amphidial gland, but lacking microvilli (Fig. 1-C, D, 26, 30). The same granular material which is within the chambers surrounds the cilia, and in the case of labial papillae, temporarily separates the two cilia from one another (Fig. 1-D, 30). Anterior to this region, however, the two cilia of the labial papillae are again closely associated, and are surrounded for the duration of their length by one or more common membranes (Fig. 1-D, 31). Cephalic cilia are also enclosed by a membrane that extends to their distal ends (Fig. 27).

Cephalic cilia terminate in an area of dense homogeneous material (Fig. 1-C, 28) near the basal plate of the cephalic framework (Fig. 22). Although micrographs of papillae are difficult to interpret in this region, it appears that this cephalic papillary material extends to a thin layer of surface cuticle, and that no opening to the external environment is present. On the other hand, labial papillary cilia appear to terminate about 1.0μm beneath a pore opening 0.04μm in diam (Fig 1-D, 24), and their distal tips are flattened (Fig. 32). There is very little external structure associated with cephalic and labial papillae, although there may be a minute central elevation within a slightly larger depression (Fig. 1-C, D).

DISCUSSION

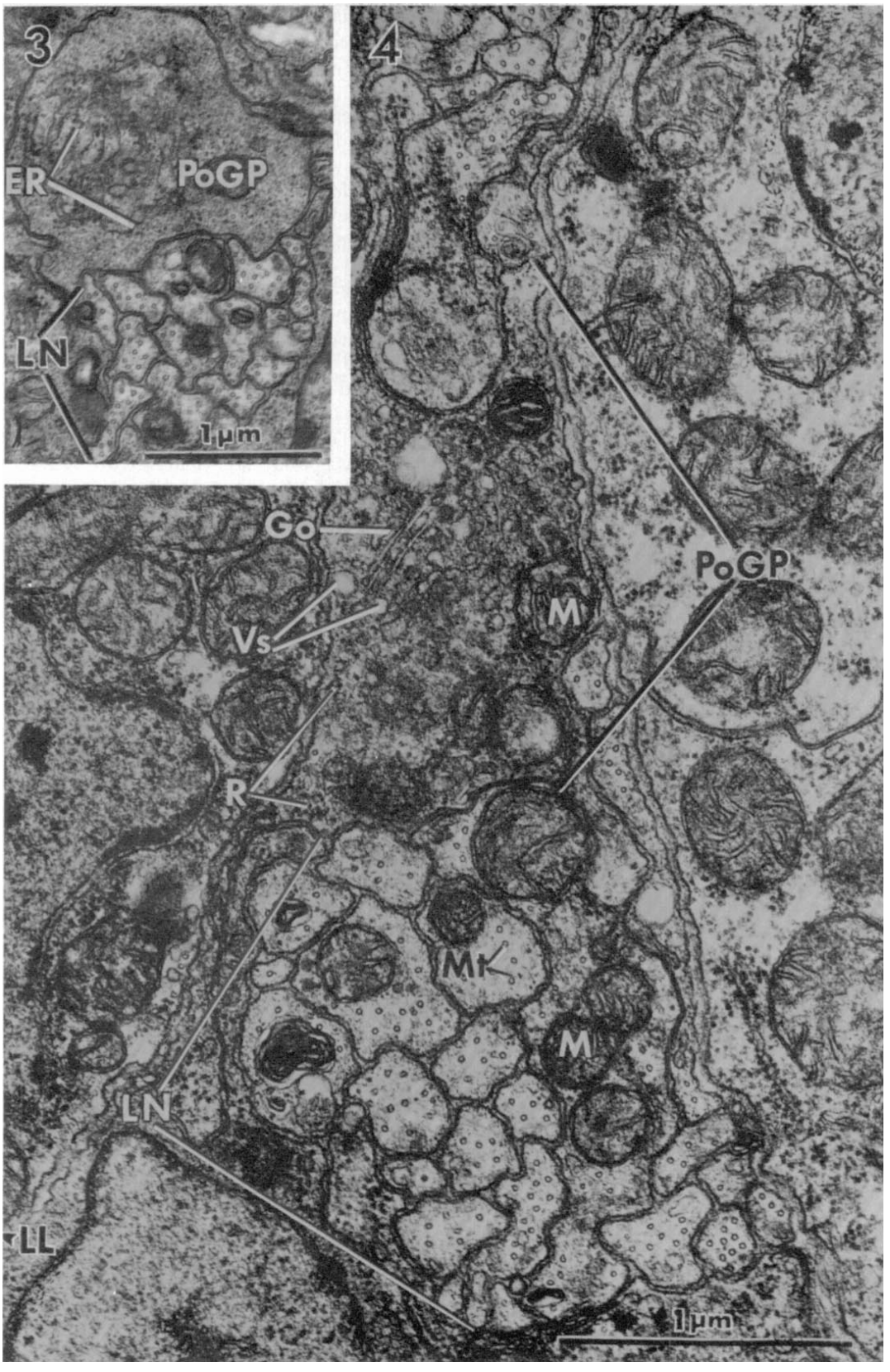
In the light microscope, each amphid of *M. incognita* males appears to be a large pouch which is about 16μm long and extends from the level including the anterior part of the stylet shaft to the dorsal gland ampulla. Electron microscopy indicates, on the other hand, that the amphid is predominately a large gland which envelops the relatively small sensilla pouch. This is consistent with the light microscope description of the *Ascaris* amphid (8). However, electron microscopy of other plant-parasitic nematodes has not shown a gland associated with the sensilla pouch. In an animal parasite, *Dipetalonema viteae*, a multivesicular complex with glandular appearance is associated with the amphid (23, 24), and a few vacuoles and villi-like structures were noted in the amphids of juvenile *Haemonchus contortus* (Rudolphi) Cobb (30). Although nuclei of amphidial glands have not yet been described in *M. incognita*, they are probably present in the posterior gland process. Convoluting membranes make it difficult to distinguish between nuclei of amphidial glands and those of the hypodermal chords.

Evidence for ascribing a glandular function to this enveloping organ in *M. incognita* is based on its similarity to characteristics of known glands in other organisms. These characteristics include the secretory organelles present in the posterior process, the large surface area of the plasma membrane, the presence of a distinct extracellular material and the several channels which link the organ to the amphidial duct.

Microvilli of *M. incognita* amphids are similar to those of certain other invertebrate glands, and particularly those associated with sensory receptors (5). As in other organisms, they are cellular projections bound by an extension of the plasma membrane, about 0.1μm in diam, and contain two or more axial filaments in their cytoplasm. Microvilli of most invertebrates are projections less than 1.0μm long. However, in *M. incognita* amphids, they are often much longer and may be branched. Similarly, the venom gland of the scorpion, *Centruroides sculpturatus* Ewing, contains long-branched microvilli, which are thought to reabsorb water from venom, and thereby increase its concentration (4). In the monogenean trematode *Gyrodactylus*, certain microvillous glands could be involved in production of mucus capable of adsorbing molecules to a chemoreceptive surface (20, 21). The granular material present in the amphidial gland of *M. incognita* could also be a viscous fluid such as mucus.

The "nerve processes" illustrated in *Meloidogyne javanica* by Bird (3) have been identified by our work as microvilli of the amphidial gland. Bird (3) shows these structures originating posteriorly from the amphidial nerve, and terminating anteriorly in the base of the cilia. Our study demonstrates, however,

FIG. 3-4. 3. Cross section through posterior gland process (PoGP) and lateral nerve bundle (LN) (level 50, Fig. 1). ER, endoplasmic reticulum. 4. Montage of cross section through the posterior gland process (PoGP) and the lateral nerve bundle (LN) (level 38, Fig. 1). Go, golgi-like cisternae; LL, left lateral side; M, mitochondria; Mt, microtubules; R, ribosomes; Vs, vesicles.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that the microvilli are physically distinct from the amphidial nerve bundle, and that the ciliary region arises directly from nonbranched dendrites.

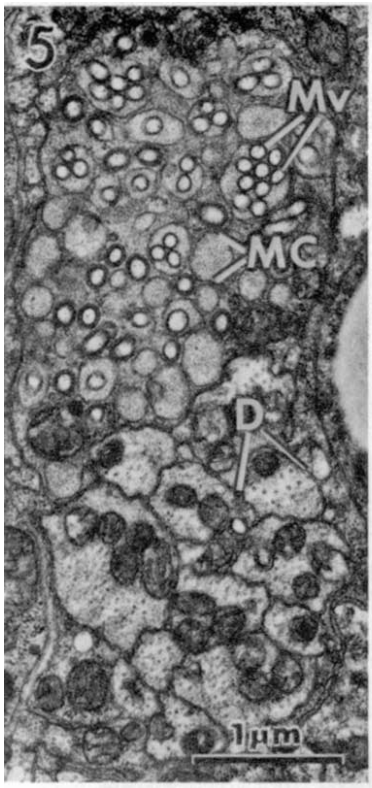
The dense vesicles which surround the amphidial duct are closely associated with the anterior gland process as well as the amphidial duct. It is possible that they contain a modified form of the granular material in the gland, or they may transfer other materials to the duct. Bird (2) identified esterases in *M. incognita* which apparently were confined to the duct, and did not occur in the region corresponding to the amphidial gland. Additional techniques and studies are required to more specifically define these materials.

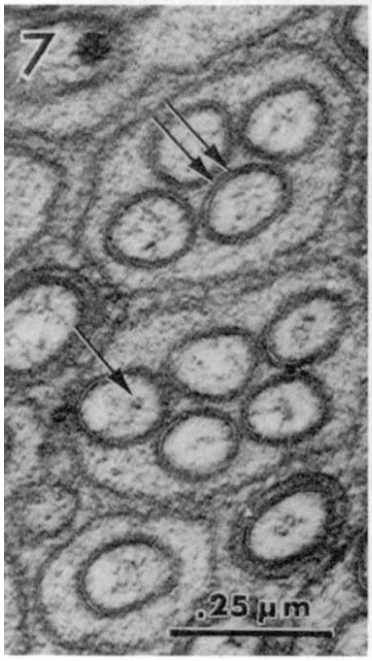
Limited fine structure studies indicate that nematode cilia vary within individuals and among species, with respect to number and arrangement of microtubules, and the number of cilia in the sensilla pouch. In certain Adenophorea, viz. *Trichodorus christiei* Allen, as many as 23 cilia were noted per amphid (12), and *Xiphinema index* Thorne and Allen appears to have about 19 per duct (28, 29). On the other hand, most Secernentea examined have fewer cilia per pouch, viz. *Ditylenchus dipsaci* (Kühn) Filipjev has eight (38), *Pratylenchus penetrans* (Cobb) Filipjev and Schuurmans Stekhoven seven (6), and *M. incognita* seven. In one *M. incognita* specimen that we examined, eight cilia were included in the sensilla pouch and duct.

Cephalic sense organs of *M. incognita* appear to be innervated differently from those of *T. christiei* (13), in which the amphidial nerves are independent of the papillary nerves, and *X. index* (29) which has separate lateral and amphidial nerves. The lateral cephalic nerves of *M. incognita* innervate the amphids as well as certain papillae, which is also the case in *Ditylenchus dipsaci* and *Panagrellus silusiae* (de Man) Goodey (39). In *M. incognita*, apparently all labial papillae are innervated by lateral nerves, whereas cephalic papillae are innervated by sublateral nerve bundles. In *P. silusiae*, a given sublateral nerve innervates both the labial and cephalic papillae of that sector (39).

Cobb (9) correctly described the *Meloidogyne* amphid as having an opening "... leading to amphidial 'sacs' (= amphidial pouch) which narrow considerably opposite to and just behind the labial framework ...", and then lead to a "... definite swollen portion ..." which, in the present study, was found to be predominantly the amphidial gland. Cobb further recognized that the "amphidial cheeks" which he felt "protect" the amphid, distinguish males of *Meloidogyne* from other members of the Heteroderidae. Allen (1) considered the cheeks to be synonymous with the amphid pouches, which he stated were particularly large in *Meloidogyne* sp. On the other hand, Geraert (11) believed that the cheeks were external to the amphid canal, and Whitehead (35) described them as "subspherical areas marked off on the cuticle of the lateral head sectors." However, our work reveals the cheek to be the outer part of the lateral lip sector separated from the rest of the lip region by the broad amphidial opening, the pouch.

There are striking similarities among labial papillae, cephalic papillae and amphids. All three receptors are innervated by nerve processes which undergo a similar sequence of changes throughout their length. We consider each entire nerve process to be a dendrite according to Horridge and Bullock's (16) definition: "... dendrites are those processes of neurons specialized as though to act as receptive regions for the neuron". The dendrites of all the receptors in *M. incognita* males have similar proximal zones with numerous mitochondria and microtubules. The proximal zone terminates distally at the base of a ciliary region. This junction is obscure in dendrites of all the receptors, and serial sections seem to indicate the absence of a distinct basal body. The ciliary region is limited to the distal part of the sensilla pouch in amphidial dendrites, whereas doublets extend almost to the tips of cephalic and labial papillary dendrites. The proximal portion of the ciliary regions of nematode cephalic receptors is enclosed by granular material, and individual dendrites are thus isolated from one another. In each case, the granular material is continuous with that present in membranous chambers which surround the ciliary regions. Both the cephalic and labial papillary cilia terminate one or more micrometers beneath the labial surface. The thin cuticle at the surface and dense material beneath the cephalic papillae doubtlessly limits direct access of the receptor to the external environment, thus suggesting a response to mechanical rather than chemical stimuli. On the other hand, labial papillae apparently have porelike openings which would permit contact with chemicals of the external environment. Thus labial papillae may function as chemoreceptors. Similarly, amphids are most





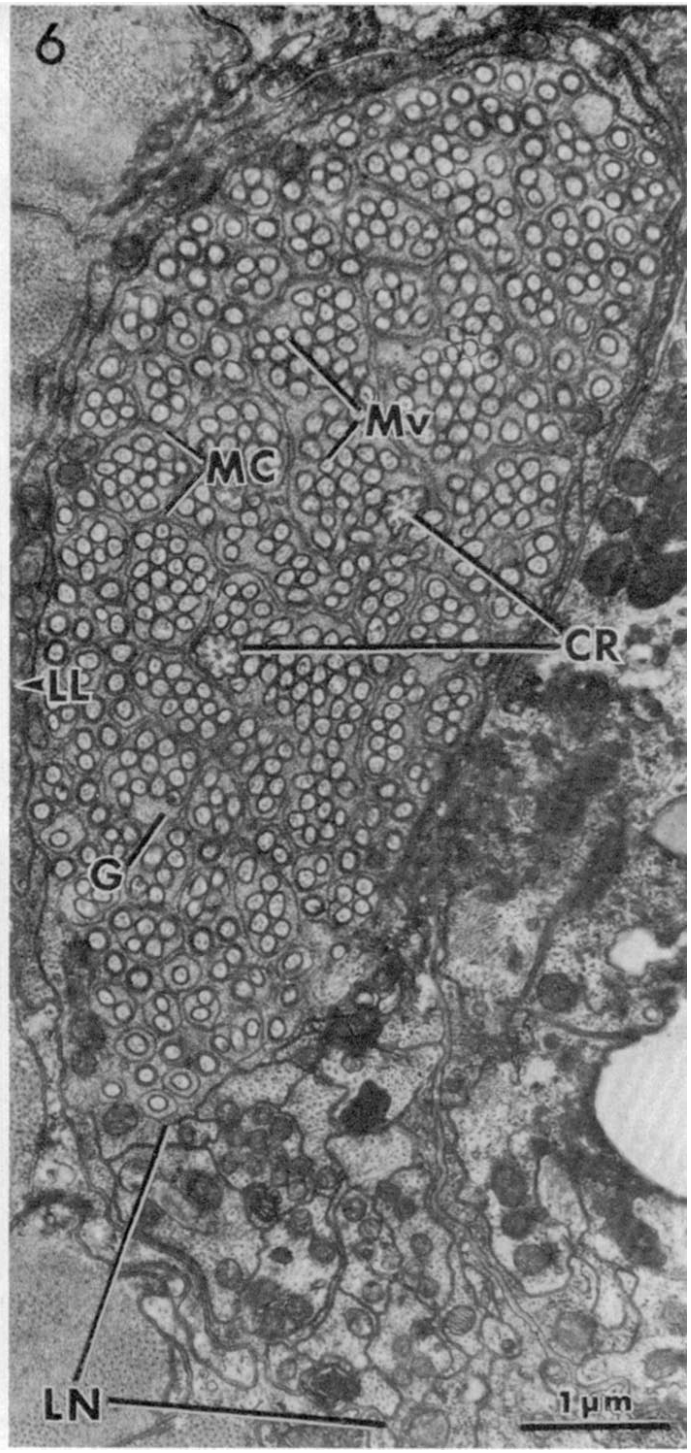


FIG. 5-7. **5.** Cross section through base of amphidial gland and lateral nerve bundle (level 30, Fig. 1). D, dendrite; MC, membranous chamber; Mv, microvilli. **6.** Cross section through broadest region of amphidial gland (level 26, Fig. 1). CR, ciliary region of dendrite penetrating gland; G, granular material; LL, left lateral side; LN, lateral nerve bundle; MC, membranous chamber; Mv, microvilli. **7.** Enlargement of microvilli in cross section; showing microfilaments (single arrow) within their cytoplasm, and limiting plasma membrane (double arrow).

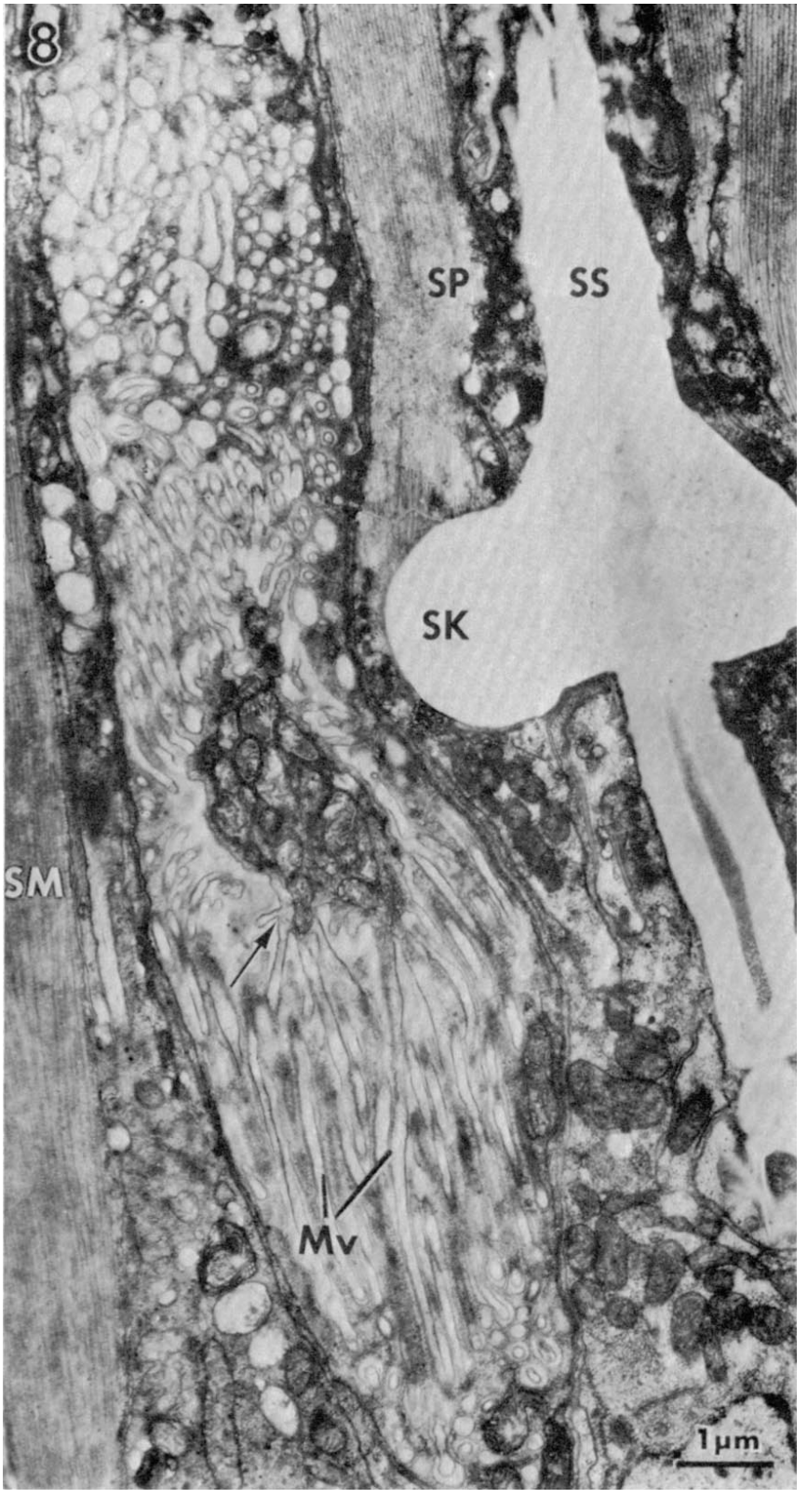

8
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FIG. 8. Montage of longitudinal section through amphidial gland, showing central region from which many microvilli (Mv) originate. Arrow indicates branching microvillus. SK, stylet knobs; SM, somatic muscles; SP, stylet protractor muscle; SS, stylet shaft.

likely chemoreceptors. Their broad slitlike opening would funnel traces of materials to the relatively deep-set receptive dendrites.

From the limited studies on fine structure of cephalic sense organs, it appears that they are diverse among nematode genera with respect to the presence of glands, the source of their innervating nerves, the number of cilia in a given organ, and the number, arrangement and external structure of papillae. Perhaps additional comparative studies on these organs will be useful not only in explaining their structure and function, but also in elucidating phylogenetic relationships among nematodes.

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FIGURE LEGENDS

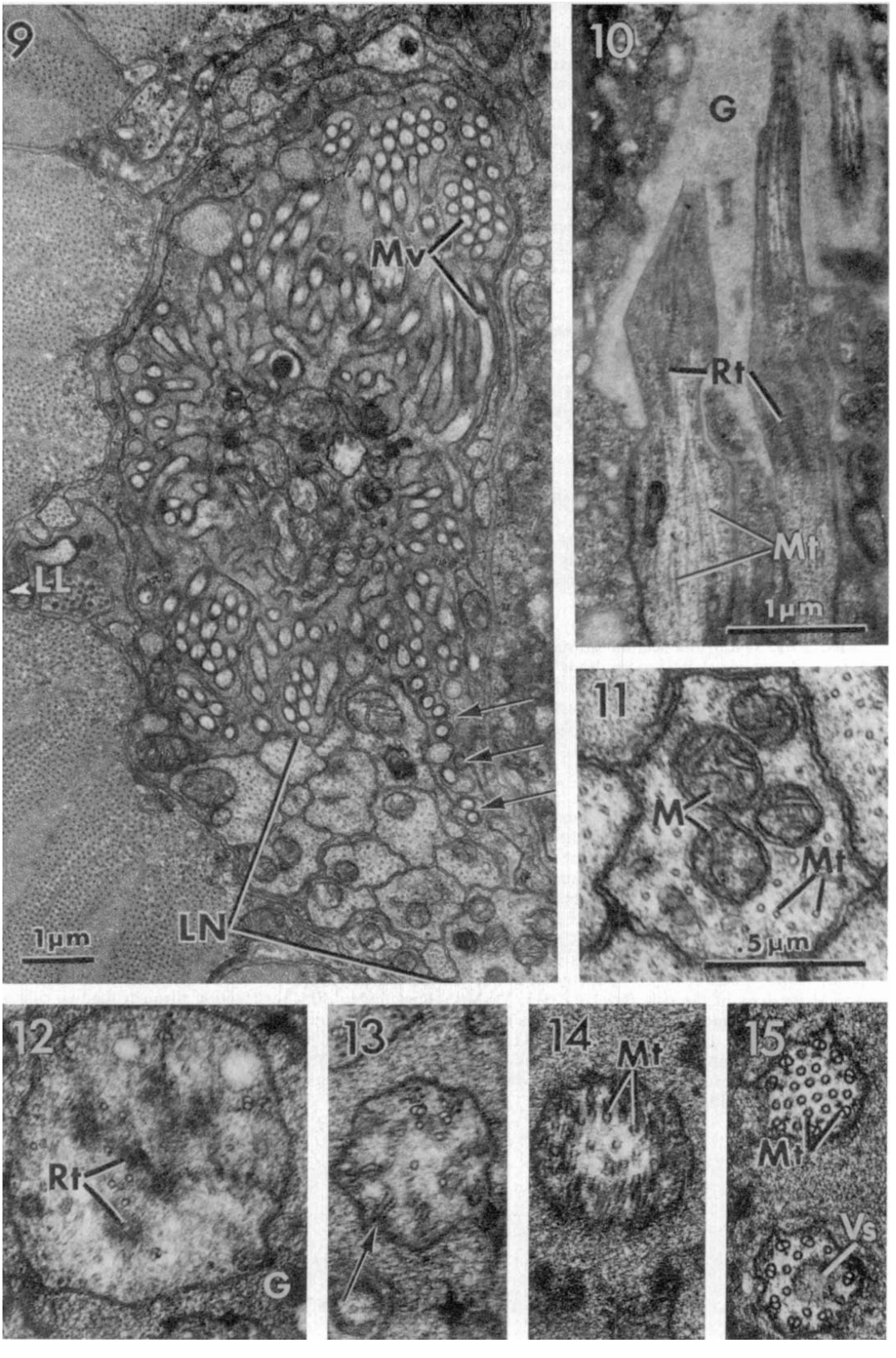
FIG. 9-15. **9.** Cross section through region of amphidial gland where many microvilli (Mv) originate (level 24, Fig. 1). Amphidial gland begins to surround (arrows) nerve bundle (LN) as bundle moves to a more lateral position. LL, left lateral side. **10.** Longitudinal section through amphidial dendrite in proximal portion of sensilla pouch. G, granular material; Mt, microtubules; Rt, rootlets. **11.** Cross section of proximal zone of amphidial dendrite adjacent to other dendrites of bundle (level 21.5, Fig. 1). Dendrites are reduced in size at this level and contain microtubules (Mt) and mitochondria (M). **12.** Cross section of amphidial dendrite separated by granular material (G) from other dendrites in the posterior part of the sensilla pouch (level 19.5, Fig. 1). Rootlets (Rt) tend to be axial. **13.** Slightly oblique cross section of amphidial dendrite showing dense peripheral region (arrow) from which microtubules originate (level 18.9, Fig. 1). **14.** Cross section of amphidial dendrite in proximal part of ciliary region (level 18.7, Fig. 1), where converging microtubules (Mt) are apparent. **15.** Cross section through anterior part of sensilla pouch, showing the ciliary region of two amphidial dendrites (level 17, Fig. 1). Mt, microtubules; Vs, vesicle. Scale for Fig. 12-15 as in Fig. 11.

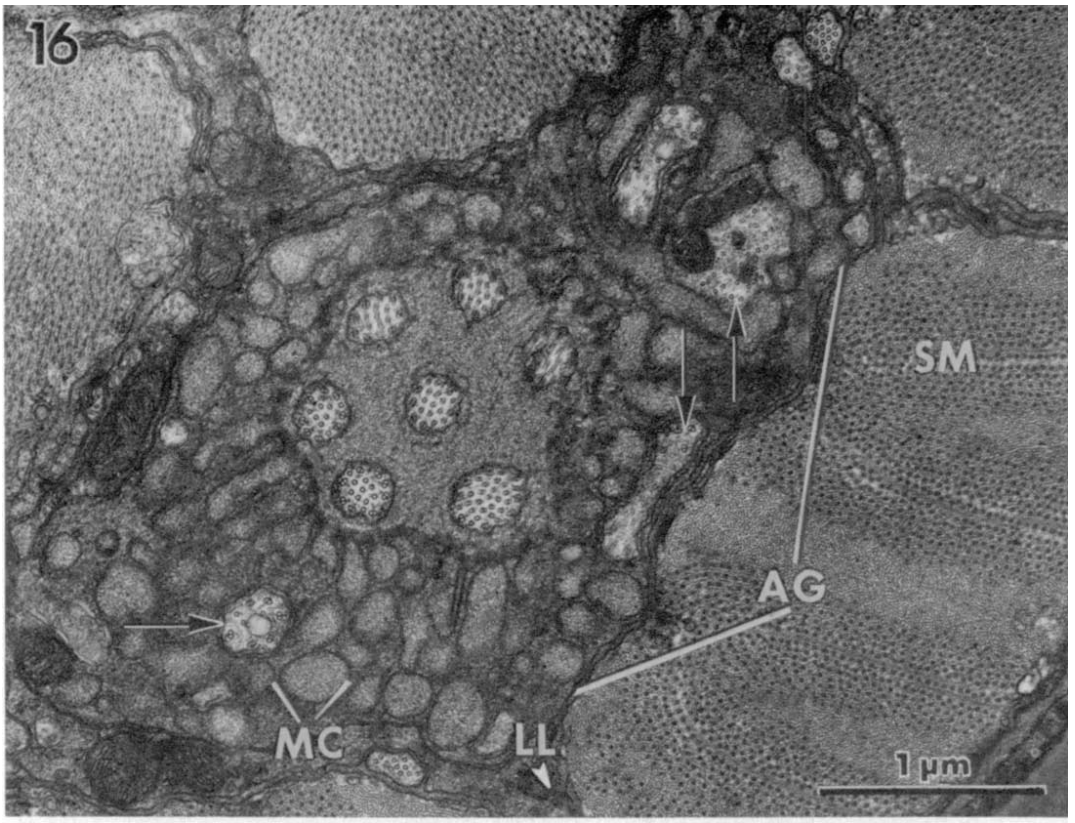
FIG. 16-17. **16.** Cross section through anterior part of sensilla pouch which includes ciliary region of amphidial dendrites (level 17, Fig. 1). Surrounding amphidial gland (AG) contains dendrites (arrows) which do not become included in the pouch. LL, left lateral side; MC, membranous chamber; SM, somatic muscles. **17.** Cross section through proximal end of amphidial duct with distal zone of dendrites (D) (level 15.5, Fig. 1). Membranes (Me) surrounding dense vesicles (DV) are associated with anterior gland process (AnGP) and duct lining (DL). RL, right lateral side.

FIG. 18-19. **18.** Cross section through flattened or lobed tips of dendrites (D) in amphidial duct (level 8, Fig. 1). AnGP, anterior gland process; DV, dense vesicles; LL, left lateral side; Me, membranes. **19.** Cross section through amphidial duct containing dense substance (DS) (level 7, Fig. 1). Labial papillary dendrite (D) sectioned longitudinally as it extends subventrally from lateral sector. AnGP, anterior gland process; DV, dense vesicles; Me, membrane; SL, stylet lumen; SM, somatic muscles: SP, stylet protractor; VE, vestibule extension.

FIG. 20-22. **20.** Cross section through flattened amphidial duct (level 6.5, Fig. 1). Channel (Ch) at distal terminus of anterior gland process leads into duct (Du). RL, right lateral side; DV, dense vesicles. **21.** Same as Fig. 20 but showing particularly broad channels (Ch) extending from anterior gland process. **22.** Slightly oblique cross section through basal plate of cephalic framework (F) with "I-shaped" amphidial pouches (AP) (level 6, Fig. 1). Single arrows, labial papillary dendrites; double arrows, cephalic papillary dendrites; DV, dense vesicles; RL, right lateral side.

FIG. 23-32. **23.** Slightly oblique cross section through distal end of amphidial pouch (AP) (level 4, Fig. 1). The "cheek" (Ck) is separated from the remainder of the lip region. **24.** Slightly oblique cross section through labial disc (level 1.5) showing six labial papillary openings (LP), and the thin cuticular coverings of two of the four cephalic papillae (CP). SO, stomatal opening. **25.** Slightly oblique cross section through proximal extreme of cilium of cephalic papillary dendrite showing the proximal origin of doublet microtubules (Mt) (level 10, Fig. 1). **26.** Cross section through cilium of cephalic papilla surrounded by membranous chambers (MC) (level 9, Fig. 1). Mt, microtubules; Vs, vesicle. **27.** Cross section through cilium of cephalic papilla surrounded by membrane (Me) (level 7, Fig. 1). Mt, microtubules. **28.** Cross section through dense material (DM) lying distal to receptor of cephalic papilla (level 4, Fig. 1). Cu, cuticle. **29.** Cross section through the two dendrites of a labial papilla in the region at the base of the cilia (level 7.2, Fig. 1). Mt, microtubules. **30.** Cross section through the two cilia of a labial papilla surrounded by membranous chambers (MC), and separated from one another by granular material (G) (level 6.7, Fig. 1). Mt, microtubules. **31.** Cross section through the two cilia of a labial papilla in close proximity to one another and surrounded by common membranes (Me) (level 5, Fig. 1). Mt, microtubules; Vs, vesicle. **32.** Cross section through flattened distal tips of the two cilia of a labial papilla (level 1.5, Fig. 1). Scale for Fig. 26-32 as in Fig. 25.


9
Mv
LL
LN
1µm
10
G
Rt
Mt
1µm
11
M
Mt
.5µm
12
Rt
G
13
14
Mt
15
Mt
Vs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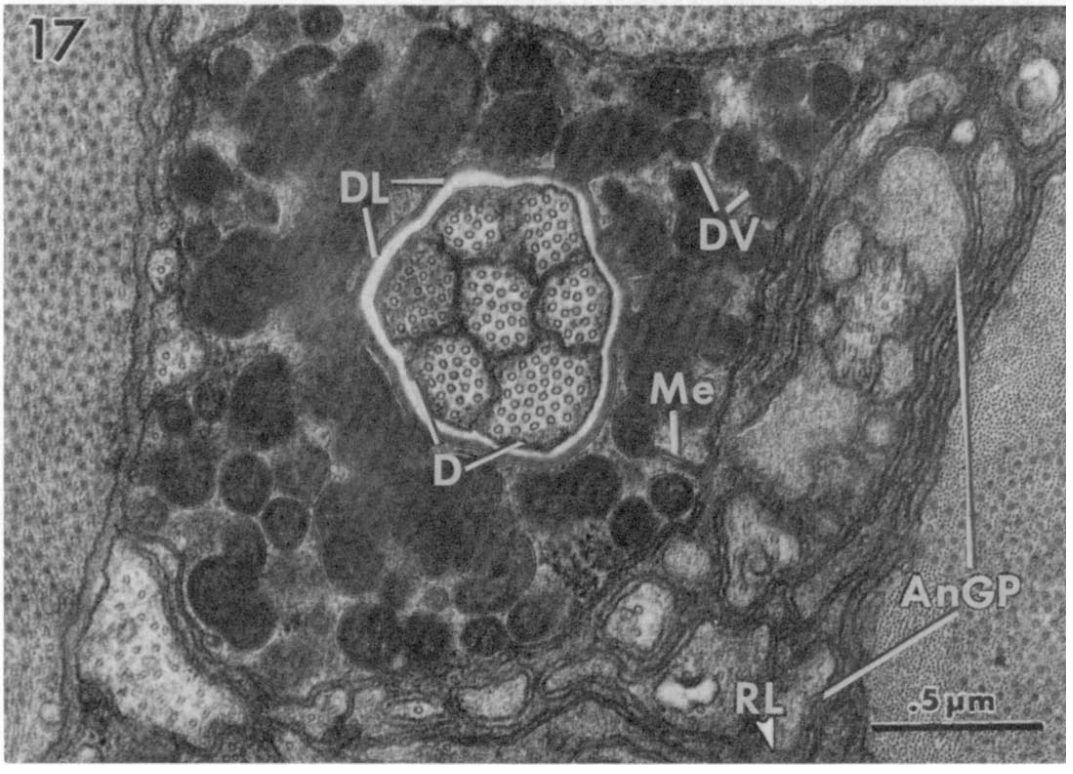
AG
MC
LL
1 µm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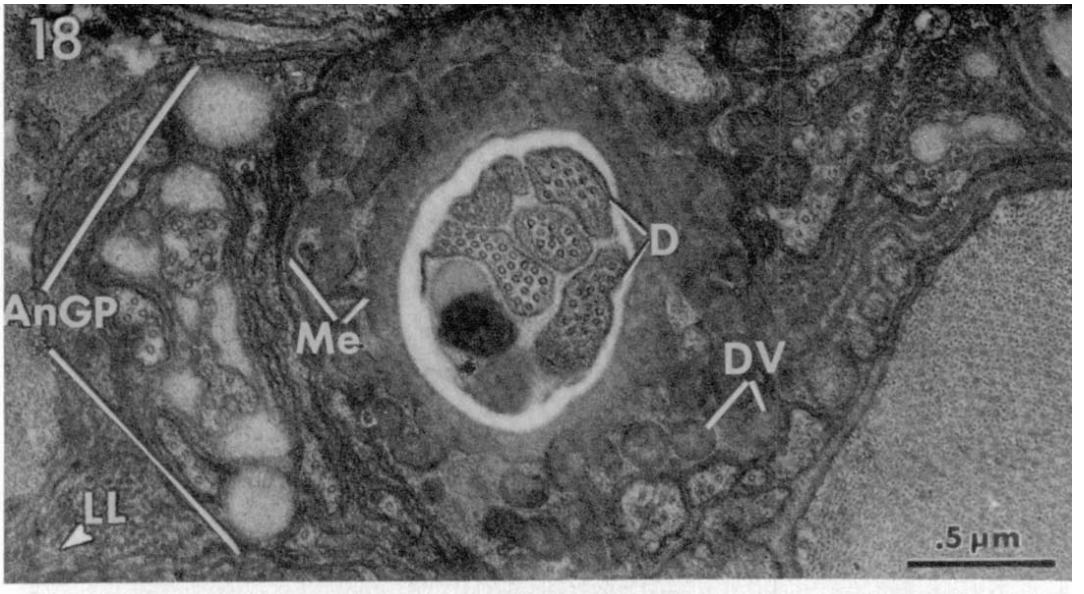
DV
Me
D
AnGP
RL
.5µm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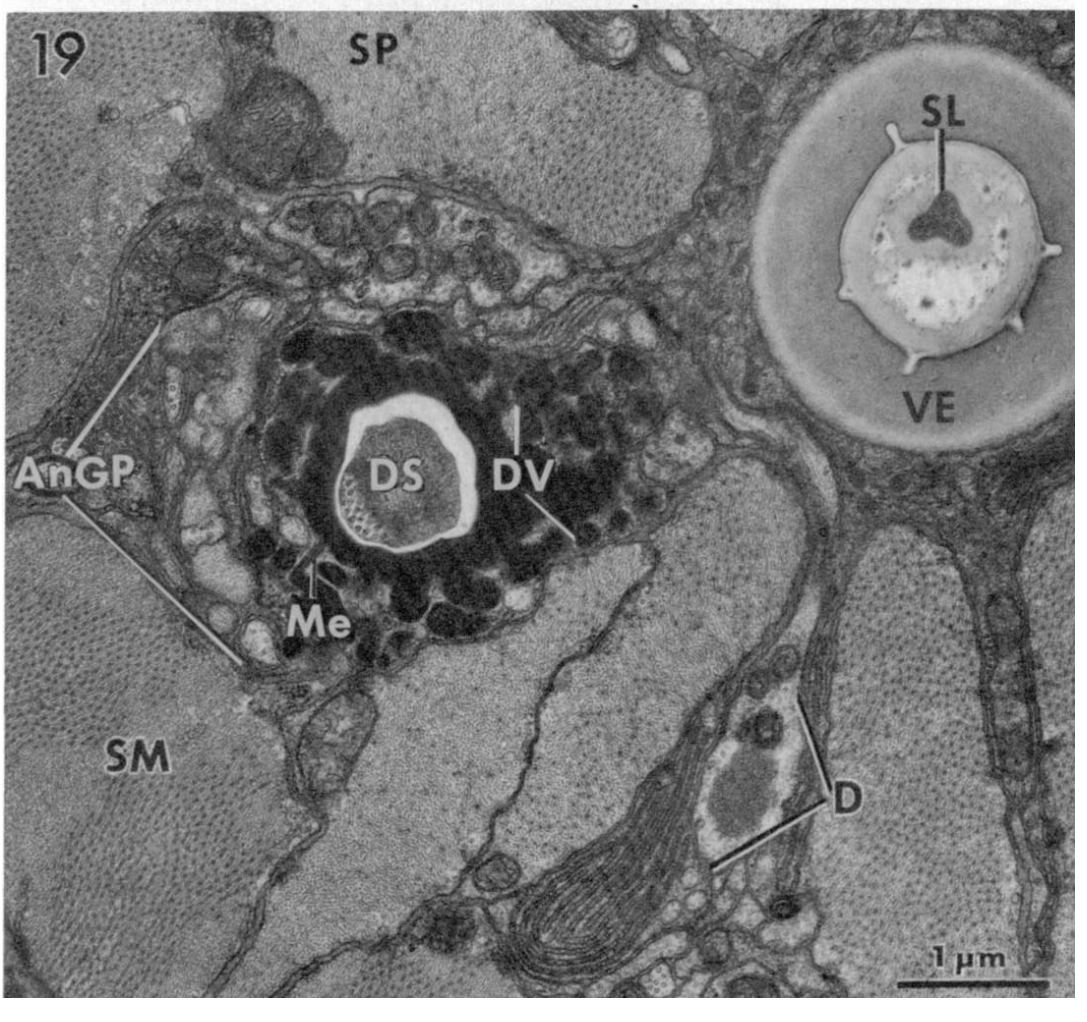
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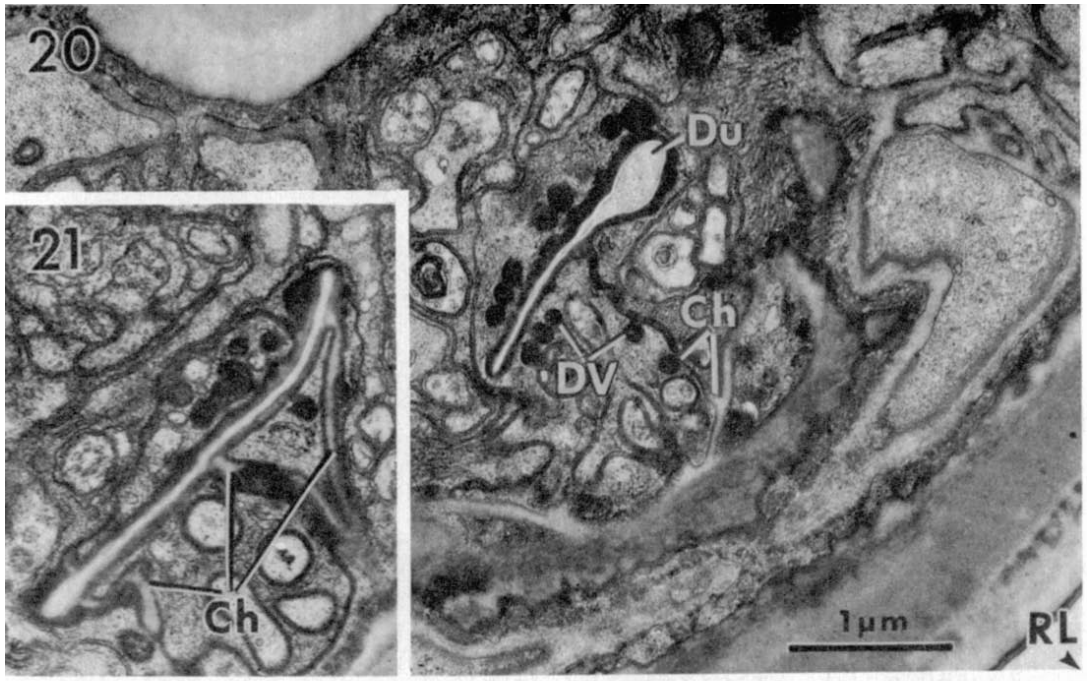
SL
VE
AnGP
DS
DV
Me
SM
D
1 µm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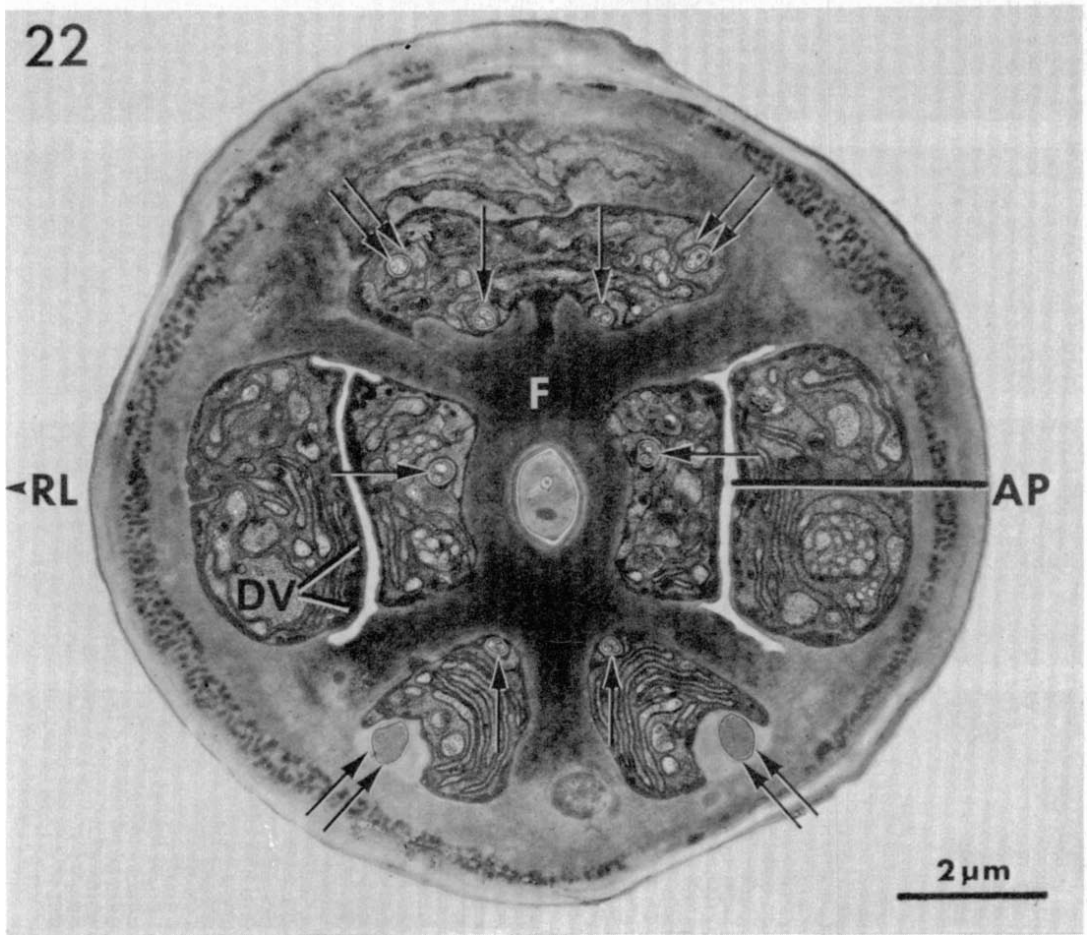
Du
Ch
DV
1µm
R'L
21
Ch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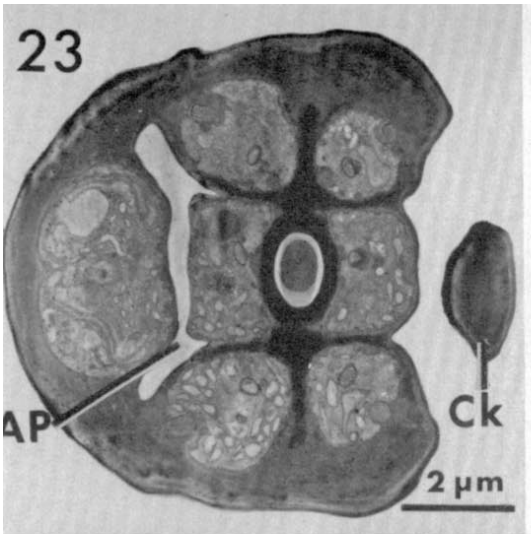
F
RL
AP
DV
2µm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Ck
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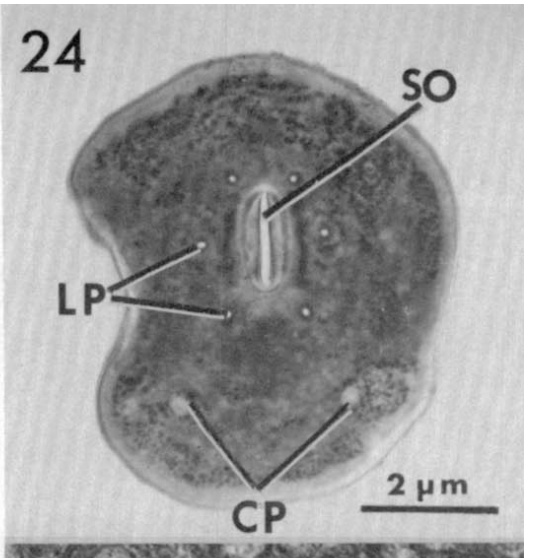
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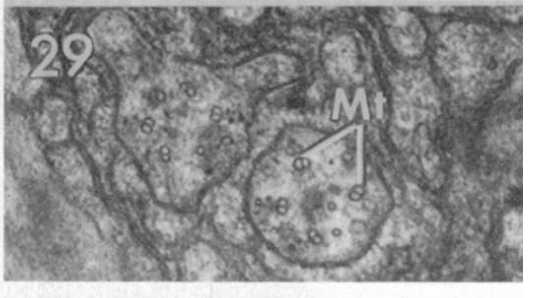
SO
LP
CP
2 µm


25
Mt
.5µm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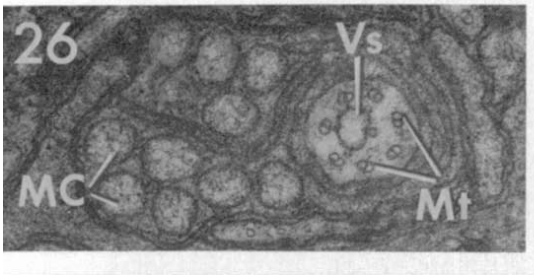
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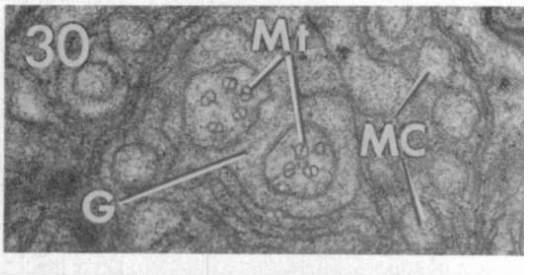
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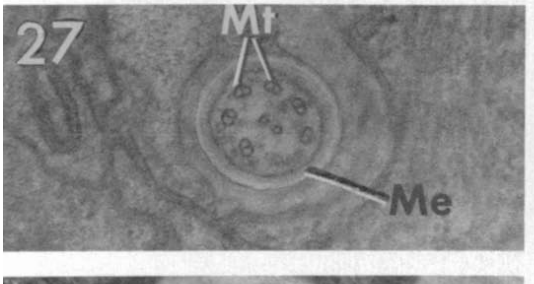
MC
G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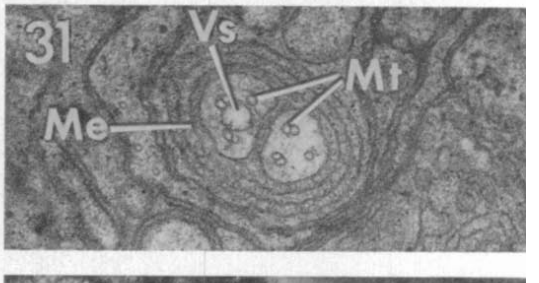
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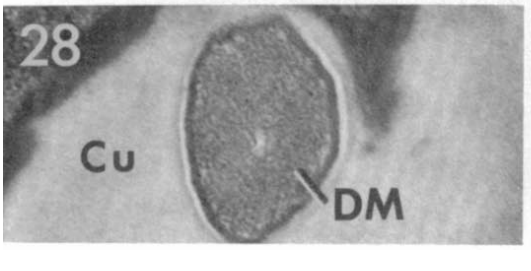
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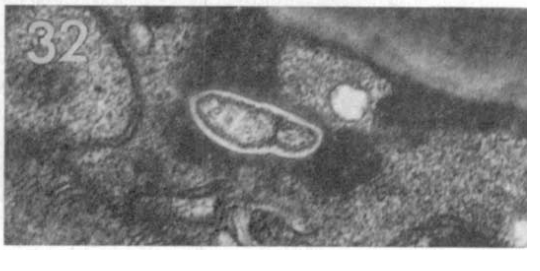
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