Fine Structure of Cephalic Sense Organs in Heterodera glycines Males[1]

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Abstract: Cephalic sense organs of *Heterodera glycines* males were examined in detail by electron microscopy. Each amphid basically consists of an amphidial gland, a nerve bundle, and an amphidial duct. The amphidial gland consists of a microvillous region, and laterally is closely associated with a large secretory cell. The nerve bundle penetrates the microvillous region, and further anteriorly individual nerve processes (dendrites) separate from one another, thus forming a sensilla pouch which is enveloped by the microvillous region of the gland. Anterior to the pouch, the cilia-like dendrites converge as they enter and eventually terminate in the amphidial duct. *Heterodera glycines* males have the innervation basis for a full complement of sixteen papillae, although surface manifestations are present for only six minute inner labial papillae. In addition, four outer labial and four cephalic receptors terminate beneath the surface, and another two dendrite pairs end further posteriorly beneath the basal plate of the cephalic framework. Papillary receptors which terminate beneath the surface are probably mechanoreceptive, whereas inner labial papillae have pore-like openings to the exterior and may be chemoreceptive. Amphids and papillae of *H. glycines* are fundamentally similar to those of *Meloidogyne incognita*, although certain striking differences exist. *Key Words:* amphid, papillae, ultrastructure, cilium, cyst nematode.

Recent fine structure investigations of the anterior region of males of *Meloidogyne incognita* (Kofoid and White) Chitwood indicated that the amphid consists of a gland, a nerve bundle, and an amphidial duct (1). Furthermore, two types of cilia-innervated papillae were present in this nematode. As suggested in these earlier studies (1), there is little information available on the detailed structure of cephalic sense organs of genera closely related to *Meloidogyne*. Yet, variability in structure of amphids and papillae among Tylenchida may be taxonomically important, and additional investigations may also elucidate the function of these organs.

Heterodera glycines Ichinohe males are similar to *M. incognita* males in gross morphology, and until recently (5) both genera were included in the family Heteroderidae (3, 4). In the present study, we examined the fine structure of the anterior region of the *H. glycines* male and compared its amphids and papillae to those of *M. incognita*.

MATERIALS AND METHODS

Heterodera glycines was isolated from a North Carolina population and propagated in a greenhouse on soybean [*Glycine max* (L.) Merr. 'Lee']. Active males were selected from

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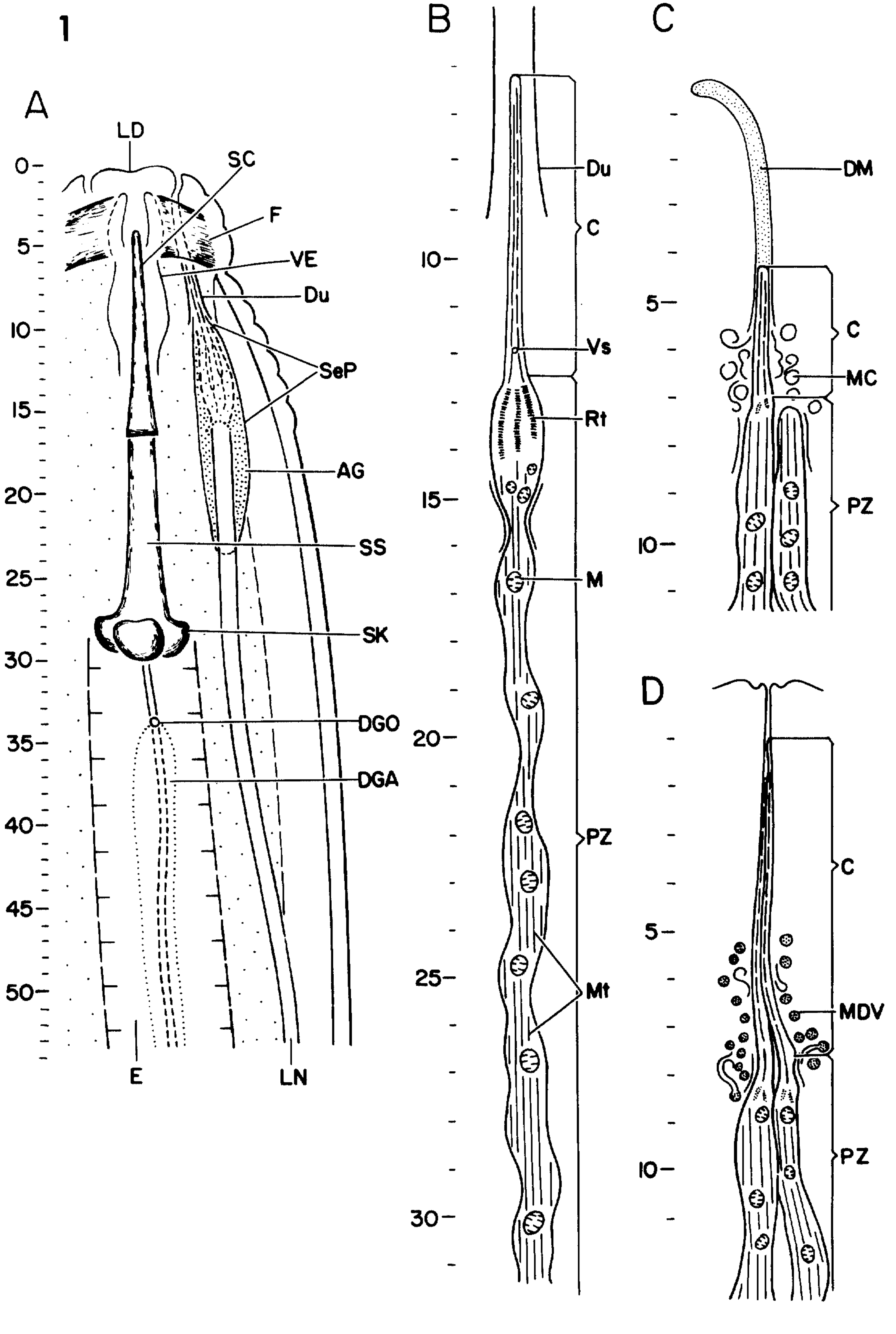
washed roots that had been incubated in a moist chamber at room temperature. Procedures for killing, fixation, dehydration, embedding, sectioning, and staining generally were as described previously (1). However, for good preservation, *H. glycines* males required 4-8 h longer fixation in glutaraldehyde solution than did *M. incognita*. Serial sections were examined with a Hitachi HS-8 electron microscope operated at 50 Kv.

OBSERVATIONS

Amphids: The amphid of the male of *H. glycines* includes a terminal duct which contains the distal ends (cilia) of several of the dendrites which constitute the lateral nerve bundle (Fig. 1-A, 2). Posterior to the duct, the dendrites are enclosed by a sensilla pouch which, in turn, is enveloped by the anterior portion of an amphidial gland (Fig. 1-A, 2). Further posteriorly, the nerve bundle takes a dorsal position in relation to the gland and becomes closely associated with the lateral hypodermal chord in the region of the esophagus. Perikaryons of the dendrites are concentrated in ganglia which ensheath the esophagus anterior to the nerve ring, and which contain large distinct nuclei with dense peripheral chromatin (Fig. 3).

Adjacent to the anterior portion of the procorpus of the esophagus, the enlarged lateral chord partially encompasses the lateral nerve (Fig. 4), but at the level of the stylet shaft, this chord region is occupied by a large nucleated cell filled with ribosomes and rough endoplasmic reticulum (Fig. 2, 5). This cell partially surrounds the lateral nerve bundle as well as the base of the amphidial gland and it extends anteriorly along the lateral surface of the gland to the region of the sensilla pouch (Fig. 5-7).

At the base, near the posterior region of the stylet shaft, the amphidial gland measures about 1 × 1.5 μm and contains several microvilli and rough endoplasmic reticulum. The lateral nerve, which is dorsal to the gland, consists of 13-15 dendrites about 0.3 μm diam which contain microtubules and small mitochondria (Fig. 2, 5). Anteriorly, but still in the region of the stylet shaft, the gland broadens to 2.5 × 3 μm and about 75 microvilli are present (Fig. 2, 6). These microvilli, which are about 0.13 μm diam, are partitioned singly or in groups of a few by walls of chambers. The narrow space between the microvilli and the wall of a given chamber (about 0.004 μm) is filled with granular material (Fig. 6, 7). Further anteriorly in the gland, a cytoplasmic region with degenerating mitochondria is present (Fig. 7), and extending from this region is a spherical structure composed of concentric membranes (Fig. 2, 7, 8). The trilaminate plasmalemmas, which form the sphere, are continuous with those of the membranous chambers and thus, the chambers may extend from this structure (Fig. 8). The microvilli are also formed from the membranes of the sphere. Anteriorly and adjacent to the sphere, the nerve bundle penetrates the gland as it assumes a more lateral position and undergoes various changes (Fig. 1-A, B, 9-15). Individual dendrites contain mitochondria and are broad, 0.6 μm diam, but, as they enter the gland, they may become slightly constricted (0.3 μm diam) for a short region (Fig. 9, 11), and the number of mitochondria is diminished (Fig. 10, 11). Plasmalemmas of adjacent dendrites form junctional complexes, whereas gland-dendrite boundaries generally lack such complexes (Fig. 10, 11). Surrounding the dendrites, the gland consists predominantly of moderately dense vesicles and lamellae of membranes, as well as a few microvilli which extend anteriad (Fig. 10, 11). As the dendrites again enlarge (0.5 μm diam), they become separated from one another by granular material and exhibit irregular profiles (Fig. 9, 12). Only a few microtubules are present at this level and rootlets may also occur (Fig. 1, 9, 12). Slightly anteriorly, the dendrites contain a dense material from which many microtubules generate (Fig. 1-B, 13). As dendrites are further separated by granular material, they are reduced in diameter and give rise to cilia in a well-defined sensilla pouch (Fig. 1, 2, 14, 16). Proximally, cilia contain eight peripheral microtubule doublets attached to a central sheath, generally four (two-to-five) central microtubules, and sometimes bridges which connect the peripheral doublets to the outer surface (Fig. 14). Only seven of the dendrites included in the lateral nerve bundle are radially arranged in the anterior part of the sensilla pouch (Fig. 17), where the cilia occasionally contain vesicles (Fig. 15). Other dendrites branch into the gland or body cavity at various levels (Fig. 2, 16, 17), including two such nerves which terminate as cilia in the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cytoplasmic region of the gland (Fig. 2, 6).

The amphidial duct commences anteriorly to the sensilla pouch, where the amphidial gland terminates. The duct contains seven radially arranged cilia at its base. As in the case of the dendrites in the sensilla pouch, the cilia in the duct contain peripheral doublets (Fig. 18), some of which persist near the tip (Fig. 20). Thus, there is no demarcation between a ciliary region and distal zone in *H. glycines*. The length of the cilia within the duct is highly variable. Some terminate near the base of the duct, whereas others extend to near the basal plate of the framework. Although membranes, which may include junctional complexes, surround the duct (Fig. 18, 19), no distinct electron-dense vesicles are present. The membranes are often in close apposition to the amphidial duct, and may form channels with it (Fig. 19). However, since there is no anterior gland process, the relationship of the membranes to the amphidial gland is not clear.

Varying amounts of a moderately electron-dense substance are present within the duct. Generally the duct is distended posteriorly, and thus is rounded (Fig. 18), but anteriorly it may be collapsed and somewhat flattened (Fig. 20). Near its anterior terminus, the oval duct is generally about 0.6×0.4 μm diam and opens beneath the labial disc about 2 μm from the stoma opening (Fig. 24).

Papillae: Heterodera glycines males have a complement of fourteen papillary receptors which terminate below the cuticle. These receptors exhibit very little external structure and, therefore, cannot be considered as papillae in the true sense. For reasons of uniformity in terminology regarding earlier literature, however, they will be referred to as papillae in this description.

Six inner labial papillae, one on each of the lip sectors, are located less than 0.5 μm from the stomatal openings, where they open out through small pores (Fig. 21, 24, 25). Slightly exteriorly from each of the subdorsal and subventral inner labial papillae are four large outer labial papillae which are embedded in the cuticle and have no surface manifestation (Fig. 21, 24). Four small cephalic papillae terminate just posterior to the large outer labial papillae (Fig. 21, 24).

The six inner labial papillae include two dendrites each, which apparently originate from the lateral nerve bundles and terminate in two cilia (Fig. 1D, 22). Paired dendrites also extend toward each of the outer labial and cephalic papillae. However, one dendrite of each pair terminates beneath the basal plate of the cephalic framework without giving rise to a cilium (Fig. 1-C, 23), whereas the other extends anteriorly terminating in a single cilium (Fig. 1-C, 22). Proximally, dendrites of the four outer labial papillae are closely associated with those of the four cephalic papillae (Fig. 23), and both types of papillae apparently originate from subdorsal and subventral nerve bundles.

The irregularly-shaped proximal zones of innervating dendrites of all papillae contain microtubules and a few mitochondria (Fig. 1-C, D, 26). The two dendrites of each papilla are separated by membranous lamellae slightly posterior to the base of the ciliary portion (Fig. 1-C, D, 27, 31). In inner labial papillae, the membranous lamellae are associated with moderately dense vesicles (Fig. 30), which diminish in number in the region of the origin of doublets (Fig. 1-D, 31). Anteriorly, the vesicles are no longer present, and the cilia of inner labial papillae, which are now adjacent, are surrounded by a common membrane (Fig. 32), which is continuous with the cuticle at a small (0.04 μm diam) opening on the lips (Fig. 1-D). Proximally in the channel, the cilia contain microtubule doublets (Fig. 32), but distally only single microtubules are present (Fig. 33) which extend to the terminus, about 1.0 μm beneath the surface (Fig. 1-D).

Although the outer labial and the cephalic papillae are slightly different in size and

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FIG. 1. Diagram illustrating individual sensory receptors in the anterior region of *Heterodera glycines* male. **A**. Dorsal view of anterior portion of male illustrating the amphid. **B**. Amphidial dendrite (longitudinal section). **C**. Dendrite of outer labial papilla (generally applies also to cephalic papilla) (longitudinal section). **D**. Two papillary dendrites of single inner labial papilla (longitudinal section). Scale units are in micrometer and indicate distance from anterior extreme of nematode. They represent levels of sections illustrated in Figs. 1-33. AG, amphidial gland; C, cilium; DGA, dorsal esophageal gland ampulla; DGO, dorsal esophageal gland orifice; DM, dense material; Du, amphidial duct; E, esophagus; F, cephalic framework; LD, labial disc; LN, lateral nerve; M, mitochondrion; MC, membranous chambers; MDV, moderately dense vesicle; Mt, microtubules; PZ, proximal zone; Rt, rootlets; SC, stylet cone; SK, stylet knobs; SeP, sensilla pouch; SS, stylet shaft; VE, vestibule extension; Vs, vesicle.

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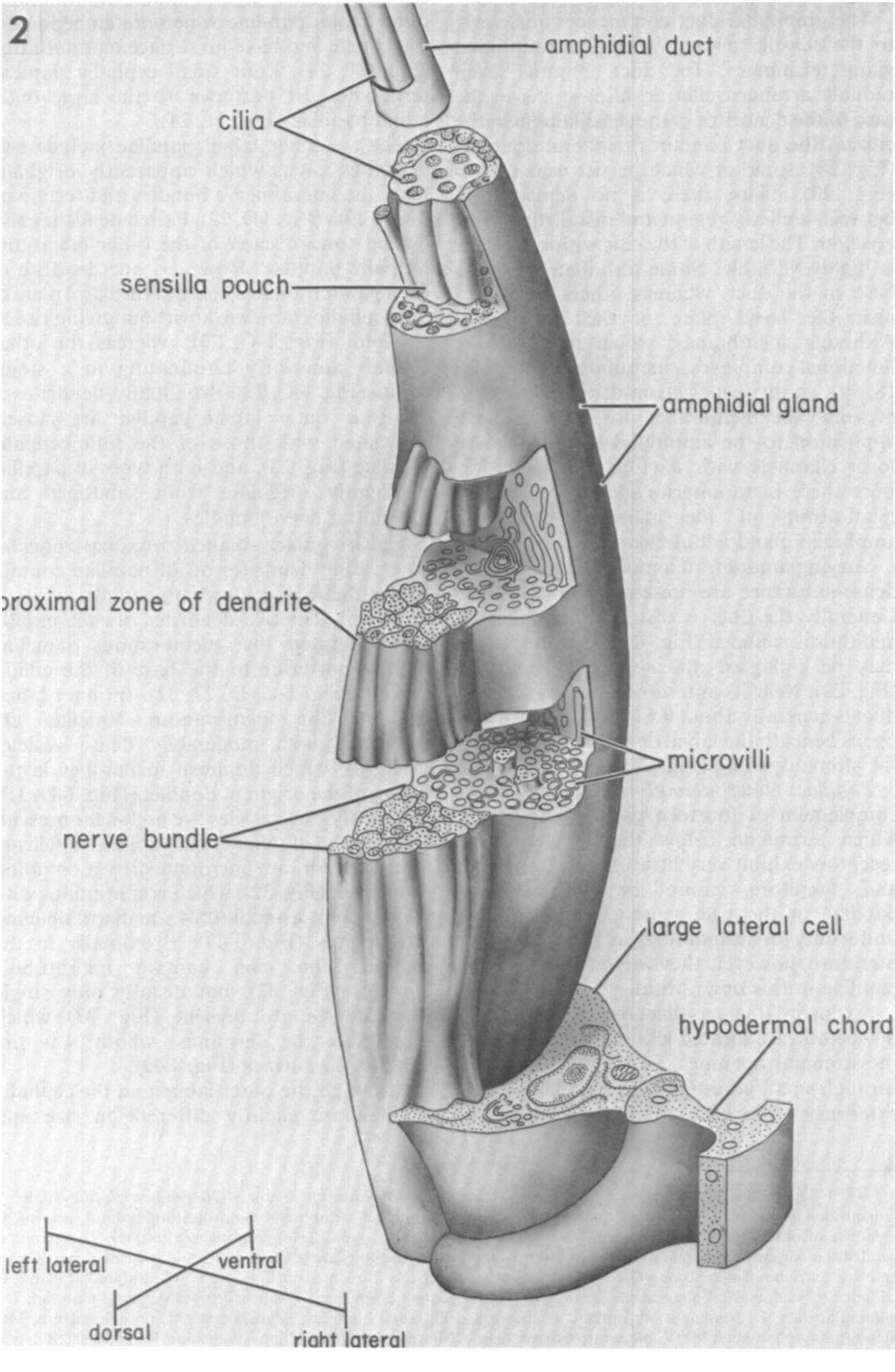

amphidial duct
cilia
sensilla pouch
amphidial gland
proximal zone of dendrite
microvilli
nerve bundle
large lateral cell
hypodermal chord
left lateral
ventral
dorsal
right lateral

location at their distal terminus, their innervating dendrites undergo similar changes in general. Proximally, the outer labial papillary cilia are surrounded by a grainy substance and a few membranous chambers (Fig. 1-C, 28), and anteriorly, the single cilium is also enclosed by a membrane (Fig. 29). Although a distinct pattern of eight microtubule doublets is present proximally in the cilium (Fig. 28), anteriorly only a few doublets, but no single microtubules, have been noted (Fig. 29). Cilia of both the outer labial and the cephalic papillae terminate in an area of dense homogeneous material near the basal plate of the cephalic framework (Fig. 1-C). This material forms a cylinder which, in the case of the cephalic papillae, follows an irregular path. The cephalic papillae are at first inward to the large outer labial papillae (Fig. 22), but eventually turn outward in the cuticle in the anterior-most part of the framework region (Fig. 21). The outer labial papillae, on the other hand, follow the body wall in the framework region externally to the cephalic papillae (Fig. 22), but anteriorly turn sharply inward and terminate in the cuticle, approximately 0.2 μm from the inner labial papillae (Fig. 1-C, 21).

Innervation, possibly for two additional papillae, is present between the amphidial ducts and lateral inner labial papillae (Fig. 23). The two pairs of dendrites originate in the lateral nerve bundle, and undergo a sequence of changes similar to those which occur for inner labial dendrites, except that the cilia terminate less than 1.0 μm from their base, several micrometers beneath the labial surface.

DISCUSSION

The amphid of *H. glycines* males, while considerably smaller than that of *M. incognita* (1), also consists of a microvillous gland which envelops a sensilla pouch. Furthermore, the sequence of changes that occur in amphidial dendrites of the two species is similar, although the proximal dendritic zone is smaller in diameter in *H. glycines,* and the ciliary region extends into the amphidial duct. In spite of basic similarities, the differences between the amphids of the two species are striking.

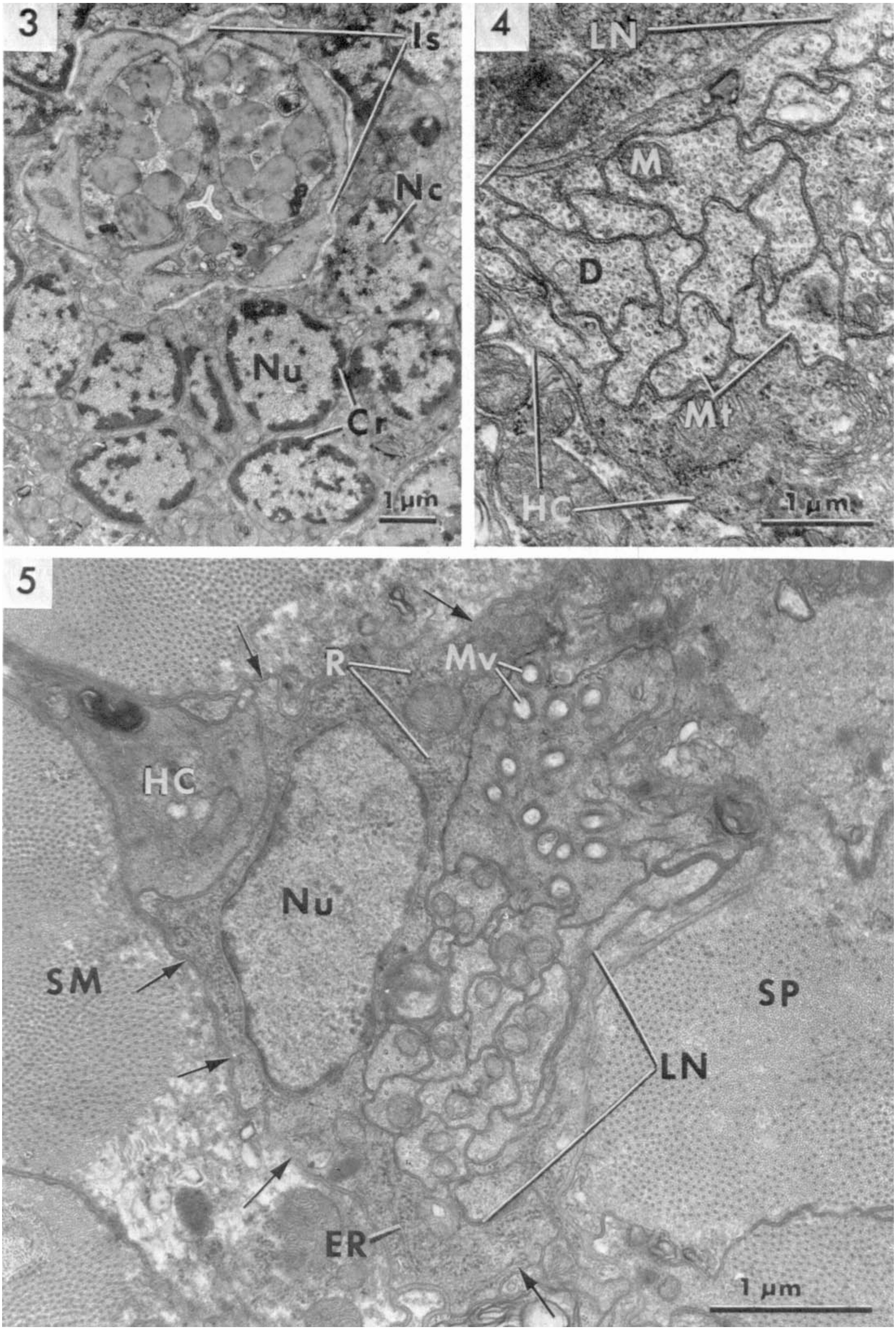
The smaller amphidial gland of *H. glycines* males does not have a posterior gland process as in *M. incognita* (1), but instead is closely associated with the hypodermis posteriorly, and a large secretory cell laterally. We were not able to demonstrate conclusively that this cell is continuous with the microvillous portion of the gland, although some micrographs suggest continuity both anteriorly, near the sensilla pouch, and posteriorly at the base. Regardless of whether or not the lateral cell and the microvillous portion of the gland are separated by plasmalemmas, they probably should be considered as a single functional entity, with the former providing nuclear control as well as secretory materials.

The microvilli of *H. glycines* are more irregularly shaped and of slightly larger diameter than those of *M. incognita* (1). Only one to three microvilli are present in a given chamber in *H. glycines,* and the cytoplasmic space between chambers is broader than in *M. incognita.* This arrangement might provide a more efficient mechanism of absorption or secretion in *H. glycines.* As in *M. incognita,* the large central cytoplasmic region corresponds to the level where the lateral nerve bundle begins to penetrate the gland, and in both species two dendrites, which enter the gland near its base, terminate in this cytoplasmic region. The microvilli do not originate directly from the cytoplasmic region as in *M. incognita,* but instead arise from a whorl of membranes which occurs slightly anteriorly. This whorl may function to collect or concentrate certain materials.

The moderately dense vesicles and associated membranes which surround the sensilla pouch in the anterior part of the gland may be similar to those encompassing the amphidial duct in *M. incognita* (1), although they do not stain as intensely in *H. glycines.* Since no anterior gland process is present in *H. glycines,* lamellae of membranes surrounding the amphidial duct may originate posteriorly with the gland.

The ciliary doublets of *H. glycines* extend beyond the sensilla pouch and in some cases

FIG. 2. Three-dimensional diagram of the amphid of *H. glycines* male showing relationships among the amphidial gland, nerve bundle, sensilla pouch, and amphidial duct.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even reach the distal tip of the cilium, whereas doublets were never found beyond the sensilla pouch in *M. incognita* (1). Fewer microtubules are present in a given cilium of *H. glycines* than in *M. incognita*.

The relatively small distal portion of the amphidial duct in *H. glycines* does not form an I-shaped pouch which separates the outer part of the lateral lip sectors as observed in *M. incognita*, and, therefore, no "cheeks" are present (1).

The papillary receptors and related dendrites of *H. glycines* are basically similar to their corresponding structures in *M. incognita*, although there are several differences. The vesicles surrounding the inner labial dendrites just posterior to the ciliary region do not occur in *M. incognita* (1). The separation of a given pair of inner labial cilia is not as great, and the region in which the cilia contact one another within a common membrane is somewhat longer in *H. glycines*. The membranous chambers surrounding the outer labial and cephalic cilia are reduced in *H. glycines*, and in the four outer labial papillae, the channel with dense material is more curved so that they terminate much closer to the labial papillae.

The basis for a full complement of sixteen papillae as it occurs in primitive nematodes [viz. *Enoplus* spp. (2)], although not reaching full expression, is present in *H. glycines*. We have noted the presence of six inner labial papillae surrounding the stoma opening, and four large outer labial papillae which terminate only slightly anterior to the inner labial papillae. The basis for two additional outer labial papillae is present as two lateral pairs of dendrites which terminate slightly below the cephalic framework. Thus, there is a basis for two circles of six labial papillae each, giving a complement of twelve. The four cephalic papillae that terminate further posteriad in the lip region and considerably exterior from the labial papillae complete the basic number of sixteen papillary receptors.

The terms "inner, outer and cephalic papillae", as they have been used in describing these sensory receptors in the labial region of other nematodes, refer only to the relative location of the external manifestations of these sensory organs without considering their internal structure and function. We have found in the present study that, based on their internal structure, we can distinguish between two morphological types. The first type includes the inner labial papillae, and probably the reduced form of outer labial papillae. These papillary receptors are innervated by a pair of dendrites terminating in two cilia, which, in the case of the inner labial papillae, end at approximately the same level in a channel with an external opening. The dendrites are associated with moderately dense vesicles, and seem to arise from the lateral nerve bundle. They may be chemoreceptive. The second type includes the outer labial and the cephalic papillae. Each of these is also innervated by two dendrites, one of which, however, terminates proximally, whereas the other extends further anteriorly to form a single cilium. The distal terminus of these papillae includes dense material which terminates under the labial surface without an opening. The dendrites and cilia are associated with membranous chambers, and seem to arise from subdorsal and subventral nerve bundles. These structures may be mechanoreceptive.

From this interpretation, it is evident that the terms inner, outer, and cephalic papillae are not very meaningful in these highly developed plant parasites. Originally, all papillae might have had the same type of innervation and function but upon further development, changes in structure and specialization in function have occurred.

CONCLUSIONS

The much smaller amphid of *H. glycines*, its larger microvilli, the origin of the microvilli with their distribution in smaller chambers, only remotely resembles that of *M. incognita* (1). The secretory cell, lateral to the

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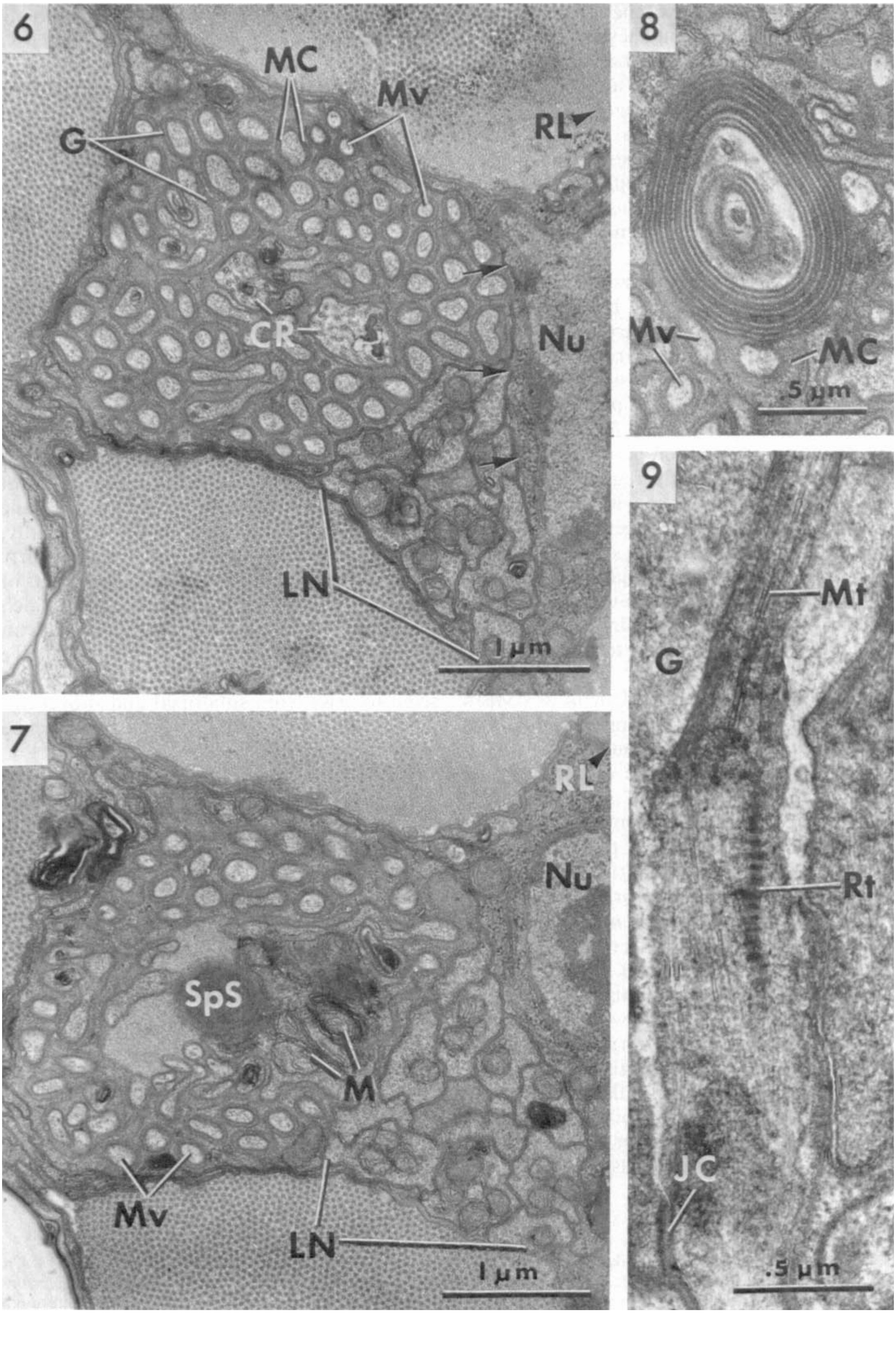
FIG. 3-5. **3.** Cross section of perikaryons of ganglia surrounding the esophageal isthmus (Is) of *H. glycines*. Cr, chromatin material; Nu, nucleus; Nc, nucleolus. **4.** Cross section through a lateral nerve bundle (LN) of *H. glycines* (level 32, Fig. 1). D, dendrite; HC, hypodermal chord; M, mitochondrion; Mt, microtubules. **5.** Cross section through the base of amphidial gland and lateral nerve bundle (LN) of *H. glycines* (level 23, Fig. 1). Arrows indicate boundary of cell adjacent to gland. ER, endoplasmic reticulum; HC, hypodermal chord; Mv, microvilli; Nu, nucleus; R, ribosomes; SM, somatic muscles; SP, stylet protractor muscle.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microvillous portion of the amphidial gland, is an important variation from the long posterior gland process of *M. incognita*. Such extensive morphological differences may reflect a degree of functional diversity between the genera. The reduced number of papillary nerves in *M. incognita* is generally considered more specialized with respect to parasitism than the elaborate receptor arrangement in *H. glycines*.

Detailed examination of additional species of Tylenchida will facilitate a better understanding as to which fine-structural traits are characteristic of the order, as opposed to traits unique to lower taxonomic categories. This will place the differences between sense organs of *M. incognita* and *H. glycines* in perspective, relative to other Tylenchida.

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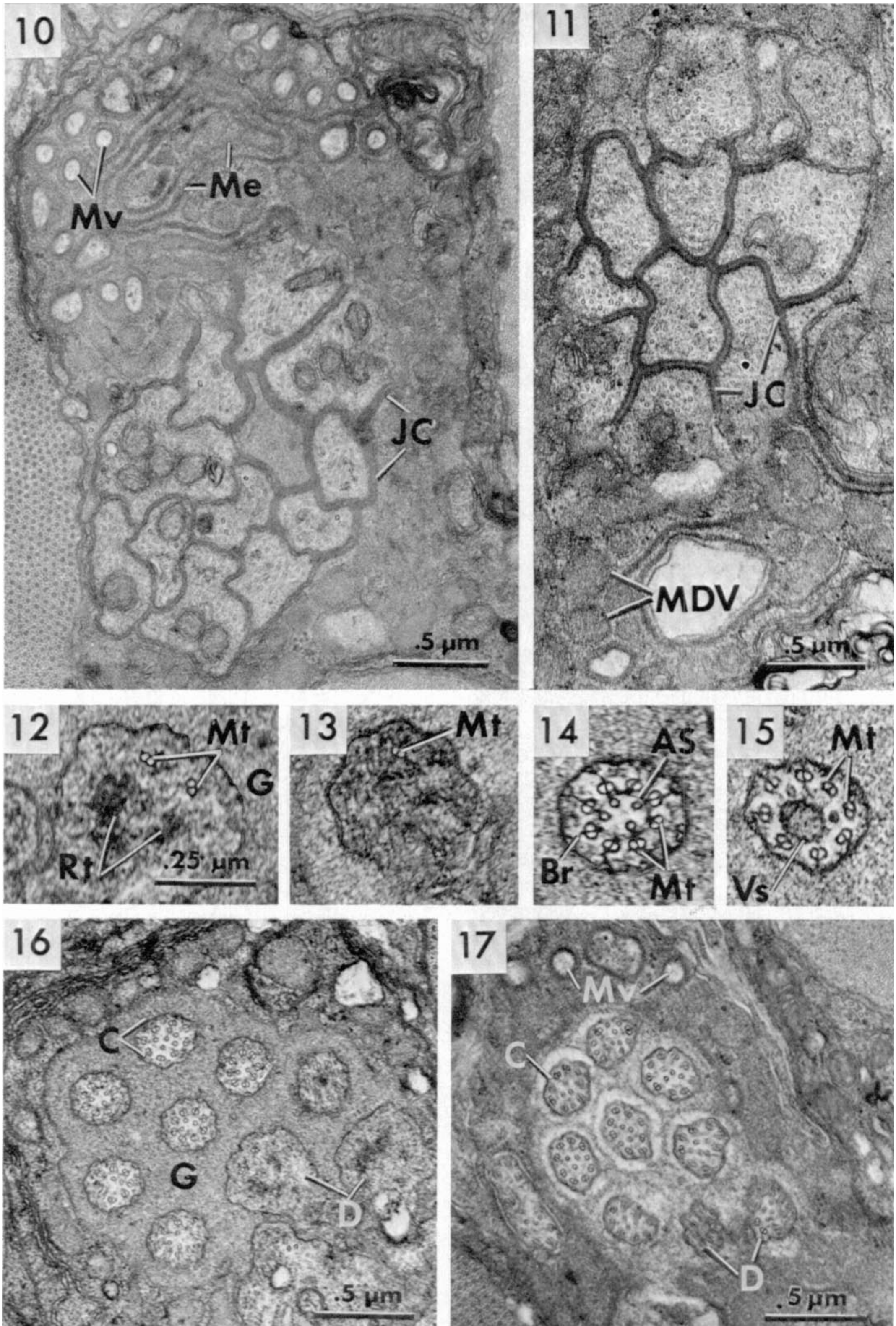
FIG. 6-9. **6.** Cross section through the broadest region of an amphidial gland of *H. glycines* (level 20, Fig. 1). Arrows indicate boundary of cell adjacent to microvillous portion of gland. CR, ciliary region of dendrites penetrating gland; G, granular material; LN, lateral nerve bundle; MC, membranous chamber; Mv, microvilli; Nu, nucleus; RL, right lateral. **7.** Cross section through an amphidial gland of *H. glycines* (level 18, Fig. 1). Spherical structure (SpS) arises from central cytoplasmic region. LN, lateral nerve; M, degenerating mitochondria; Mv, microvilli; Nu, nucleus; RL, right lateral. **8.** Cross section through spherical structure in *H. glycines* (level 17, Fig. 1). Trilaminate membranes are continuous with microvilli (Mv) and membranous chambers (MC). **9.** Longitudinal section through an amphidial dendrite in the proximal portion of the sensilla pouch of *H. glycines*. G, granular material; JC, junctional complex; Mt, microtubule; Rt, rootlet.

FIG. 10-17. **10.** Cross section through the region of the amphidial gland of *H. glycines* where the lateral nerve further penetrates the gland, and some dendrites are separated by junctional complexes (JC) (level 16, Fig. 1). Me, membranes; Mv, microvilli. **11.** Cross section of a lateral nerve of *H. glycines* completely enclosed by the amphidial gland with junctional complexes (JC) between dendrites (level 15, Fig. 1). MDV, moderately dense vesicles. **12.** Cross section of an amphidial dendrite in *H. glycines* separated by granular material (G) from other dendrites in the posterior part of the sensilla pouch (level 14, Fig. 1). Mt, microtubules; Rt, rootlets. **13.** Cross section of an amphidial dendrite in *H. glycines* showing the dense region from which many of the microtubules (Mt) form (level 13.5, Fig. 1). **14.** Cross section through the posterior portion of an amphidial cilium in *H. glycines* (level 13, Fig. 1). AS, axial sheath; Br, bridges; Mt, microtubules. **15.** Cross section through a cilium in the anterior portion of the sensilla pouch in *H. glycines* (level 11, Fig. 1). Mt, microtubules; Vs, vesicle. Scale for Fig. 13-15 as in Fig. 12. **16.** Cross section through the posterior portion of a sensilla pouch in *H. glycines* (level 13, Fig. 1). C, cilium; D, dendrites; G, granular material. **17.** Cross section through the anterior portion of a sensilla pouch in *H. glycines* with cilia (C) arranged in a radial pattern (level 10, Fig. 1). D, dendrites; Mv, microvilli.

FIG. 18-23. **18.** Cross section of an amphidial duct in *H. glycines* containing several cilia (C) separated by a moderately dense substance (MDS) (level 8, Fig. 1). Me, membranes. **19.** Enlargement of membranes (Me) forming channels (Ch) close to the amphidial duct. **20.** Cross section through a collapsed amphidial duct near the anterior terminus of the cilia in *H. glycines* (level 7, Fig. 1). **21, 22, 23.** Diagrams illustrating the arrangement of papillary receptors in the anterior region of *H. glycines* male. **21.** Cross section at level 1.8 of Fig. 1A. **22.** Cross section at level 4.5 of Fig. 1A. **23.** Cross section at level 7.5 of Fig. 1A. AD, amphidial duct; CP, dendrites of cephalic papillae; ILP, dendrites of inner labial papillae; LOLP, dendrites of lateral outer labial papillae; OLP, dendrites of outer labial papillae; x, dendrites that do not terminate in cephalic papillae.

FIGS. 24-33. **24.** Slightly oblique cross section showing the anterior terminus of amphidial ducts (AD) of *H. glycines*, as well as outer labial (OLP) and cephalic papillae (CP) (level 2, Fig. 1). ILP, inner labial papillae. **25.** Slightly oblique cross section through the labial disc of *H. glycines* with six inner labial papillary openings (ILP) surrounding the stoma opening (SO) (level 1.5, Fig. 1). **26.** Cross section through the proximal zone of dendrites (D) innervating papillary receptors in *H. glycines* (level 10, Fig. 1). Mt, microtubules. **27.** Slightly oblique cross section through the proximal end of a cilium of an outer labial papilla in *H. glycines*, showing the origin of microtubule doublets (Mt) (level 6, Fig. 1). **28.** Cross section through a cilium of an outer labial papilla in *H. glycines* surrounded by granular material (G) and membranous chambers (MC) (level 5.5, Fig. 1). **29.** Cross section through a cilium of an outer labial papilla surrounded by a membrane (Me) (level 4.8, Fig. 1). Mt, microtubules. **30.** Cross section through two dendrites of an inner labial papilla of *H. glycines* in the region slightly posterior to the base of the cilia (level 8, Fig. 1). Me, membranes; Vs, vesicle. **31.** Cross section through the base of two cilia of an inner labial papilla of *H. glycines*, with the proximal origin of doublet microtubules (Mt) (level 5, Fig. 1). Vs, vesicles. **32.** Cross section through two cilia of an inner labial papilla of *H. glycines* in close proximity to one another and surrounded by a common membrane (Me) (level 3, Fig. 1). Mt, microtubules. **33.** Cross section through the distal tips of two cilia of an inner labial papilla in *H. glycines* (level 2, Fig. 1). Mt, microtubules. Scale for Fig. 27-33 as in Fig. 26.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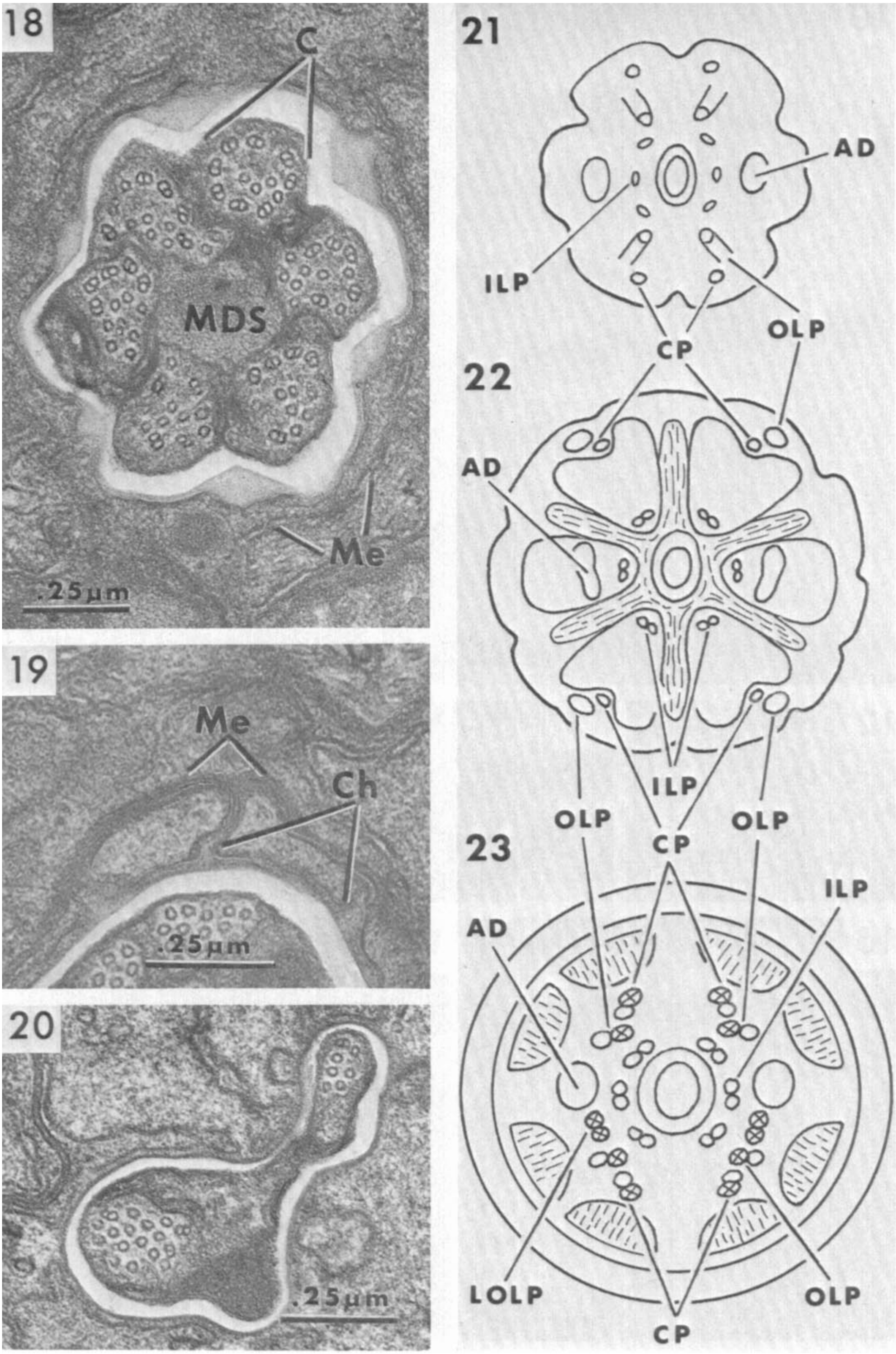
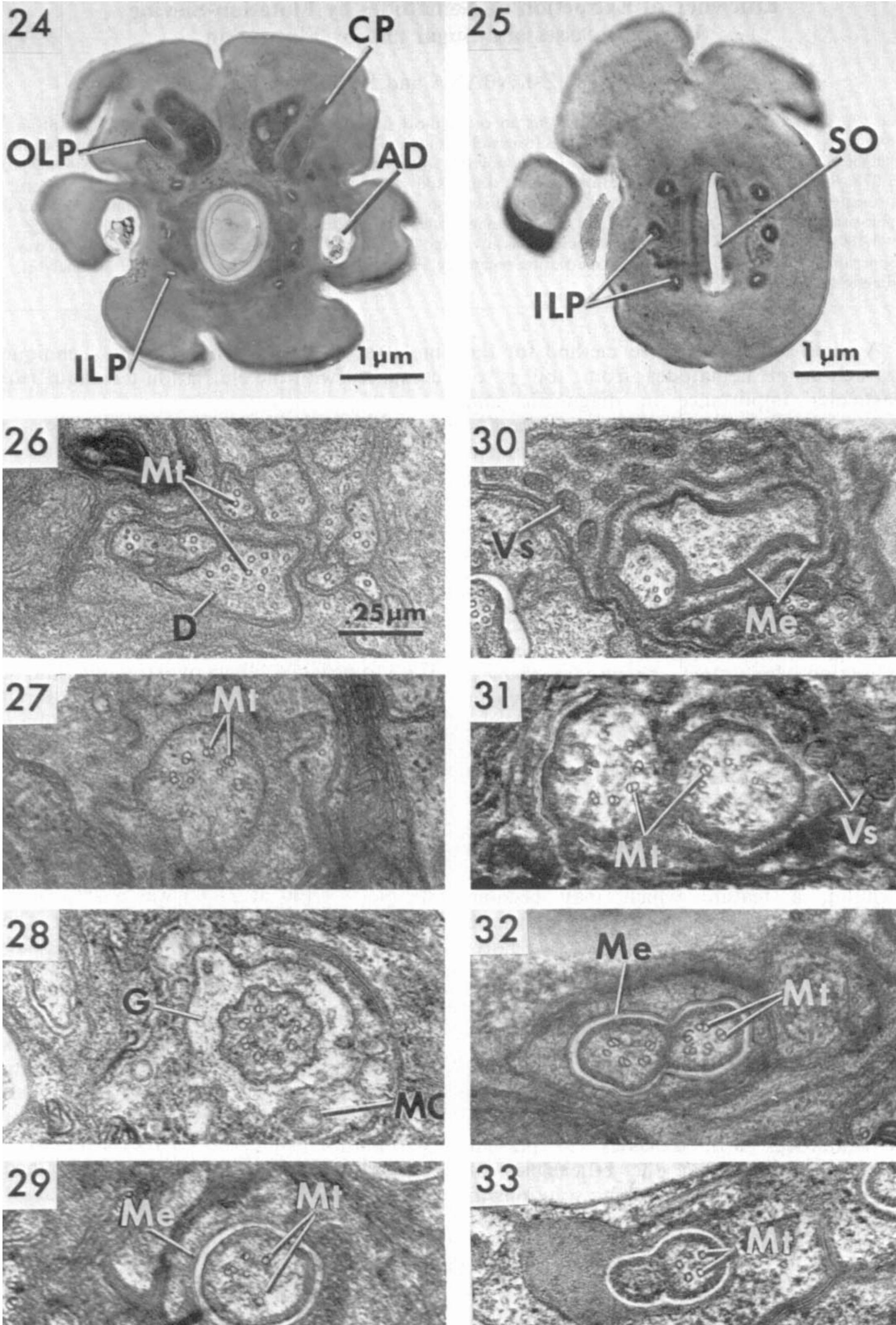
D
.5 µm


18
C
MDS
Me
.25 µm
19
Me
Ch
.25 µm
20
.25 µm
21
AD
ILP
CP
OLP
22
AD
ILP
OLP
CP
OLP
23
ILP
AD
LOLP
OLP
CP


24
CP
OLP
AD
ILP
1 µm
25
SO
ILP
1 µm
26
Mt
D
.25µm
27
Mt
28
G
MC
29
Me
Mt
30
Vs
Me
31
Mt
Vs
32
Me
Mt
33
Mt