Body Wall Fine Structure of the Anterior Region of Meloidogyne incognita and Heterodera glycines Males[1]

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Abstract: The body wall fine structure including the cuticle, hypodermis, and somatic muscles is similar in males of *Meloidogyne incognita* and *Heterodera glycines*. The cuticle can be regarded as basically three-layered in both species, but is much thicker in *M. incognita* than in *H. glycines*, and differences occur in surface markings. The chordal and interchordal hypodermis is syncytial. Hypodermal tissue pervades the lip region, and lines the stomatal cavity and stylet shaft. Various organelles and structures, some previously undescribed, are concentrated in the chords. Their possible role in lipid metabolism is considered, as well as the probable function of the hypodermis in formation of the cephalic framework and stylet. The interchordal hypodermis which encloses peripheral nerves, is periodically transversed by bundles of fibrils which are homologous with the subcuticular striation previously observed in the light microscope. The somatic musculature is meromyarian, and the muscle cells are of the platymyarian type with I, A, and H bands, but without Z bands or T tubules. Thin dense bands are present in the H bands, and appear to be associated with sarcoplasmic reticulum. *Key Words:* cuticle, hypodermis, somatic musculature, root-knot nematode, cyst nematode.

The body wall, which includes cuticle, hypodermis, and somatic muscles, is structurally variable throughout the Nematoda. The cuticle of the Tylenchida is relatively simple and, with few exceptions (16), consists basically of three strata: cortical, medial, and basal layers (5). Although the cuticles of nonsedentary forms of the Heteroderidae have been described (4, 7, 36, 39), no attempt has been made to compare genera, and many cuticular structures are not yet sufficiently explained. Considerable information is available regarding the development of body wall cuticle, and the role of the hypodermis in this process (7, 19, 20, 21, 27). However, whether or not the hypodermis participates in the formation of other cuticular structures, such as the cephalic framework and stylet, has not yet been investigated. Further investigations are also needed to identify hypodermal organelles and, perhaps, through their presence, suggest additional roles of the hypodermis. Hypodermal structures such as subcuticular striations, cephalids, and hemizonids are clearly observed in the Heteroderidae in the light microscope (23) but are not yet homologized with structures observed in the electron microscope.

The somatic musculature is composed of platymyarian cells in those plant-parasitic Tylenchida which have been examined (8, 12, 15, 39, 41). However, further work is needed to elucidate the detailed structure of these muscles and to clarify inconsistencies with respect to terminology.

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MATERIALS AND METHODS

Meloidogyne incognita (Kofoid and White) Chitwood and *Heterodera glycines* Ichinohe were each isolated from North Carolina populations, and propagated in a greenhouse on tomato (*Lycopersicon esculentum* Mill. 'Rutgers') and soybean [*Glycine max* (L.) Merr. 'Lee'], respectively. Several hundred active males were selected at different times from washed roots that had been incubated in a moist chamber at room temperature or from screened soil. Procedures for killing, fixing, dehydrating, embedding, sectioning and staining were as described previously (2, 3). Most sections examined were from the anterior fifth of the nematode.

OBSERVATIONS

Cuticle: The cuticle surface of *H. glycines* and *M. incognita* is transversely annulated at a periodicity of about 1.7 μm and 2.5 μm, respectively (Fig. 1), and the lateral fields of both species have four longitudinal incisures (Fig. 2). The two outer incisures commence anteriorly, in the region of the stylet shaft (Fig. 3), and the two inner ones arise together near the stylet knobs in *H. glycines* (Fig. 4), but begin near the level of the base of the esophageal procorpus in *M. incognita*. Longitudinal striations occur in the lip region of *H. glycines* as deep clefts which extend from near the stoma opening (Fig. 5) to the

basal plate of the cephalic framework (Fig. 6), where they end at the constriction of the lip region.

The cuticle of *M. incognita* is about 1.5 μm thick, whereas, that of *H. glycines* is about 0.8 μm (Fig. 7, 9). Cuticle layering is generally similar in both nematodes and consists of a cortical, medial, and basal layer. The external cortex can be resolved into at least five layers totalling about 0.1 μm in thickness (Fig. 8): (i) a moderately dense outer layer, (ii) a thin electron-lucent layer, (iii) a thin electron-dense layer, (iv) a thick moderately dense layer, and (v) a dense inner layer. The internal cortex is relatively homogeneous, although externally it may be of slightly greater density. It is about 0.5 μm thick in *M. incognita* and 0.2 μm in *H. glycines*.

The medial layer varies greatly in thickness, although it is usually 0.4 μm in *M. incognita* and 0.1 μm in *H. glycines*. It consists of irregular patches of electron-dense material interspersed by less dense substance which, in some cases, seems to be continuous with the internal cortex. Often the dense material of the medial layer forms large masses or spheres beneath each transverse annulation (Fig. 1). Beneath the lateral field, the dense material tends to be more solid anteriorly (Fig. 3) than posteriorly (Fig. 2).

The basal layer is about 0.5 μm thick in *M. incognita*, and 0.3 μm in *H. glycines*. It is striated transversely and longitudinally (Fig. 1, 7, 9), and tangentially appears cross-hatched (Fig. 10); thus, it is composed of rows of interconnected rods. The periodicity of the striae is about 0.025 μm, although it may appear to vary, if sections are not exactly perpendicular to the plane of the rows. With few exceptions, a disjunction, or convergence of three or more rods, occurs beneath each superficial transverse annulation, and at each midpoint between two such annulations (Fig. 1). Another type of discontinuity of the rods occurs randomly throughout the basal layer in which a layer of rods becomes progressively shorter and overlaps a complementary tapering layer (Fig. 11). In transverse sections of *H. glycines*, the basal layer appears to be divided into three-to-five bands perpendicular to the rods (Fig. 9). Rods of the basal layer are distinct in *H. glycines* (Fig. 1, 9), but only occasionally could be resolved in *M. incognita* (Fig. 7). The striated basal layer does not occur anteriorly to the basal plate of the cephalic framework in both genera (Fig. 5, 6). Similarly, the striation of the basal layer does not extend beneath the lateral field which is occupied by homogeneous layers (Fig. 2, 3). Instead, it forks at the edges of the lateral field and the homogeneous layers form a wedge between the tongues of the striated basal layer. A thin electron-lucent zone separates the striated basal layer of the cuticle from the underlying hypodermis (Fig. 1, 7, 9, 11).

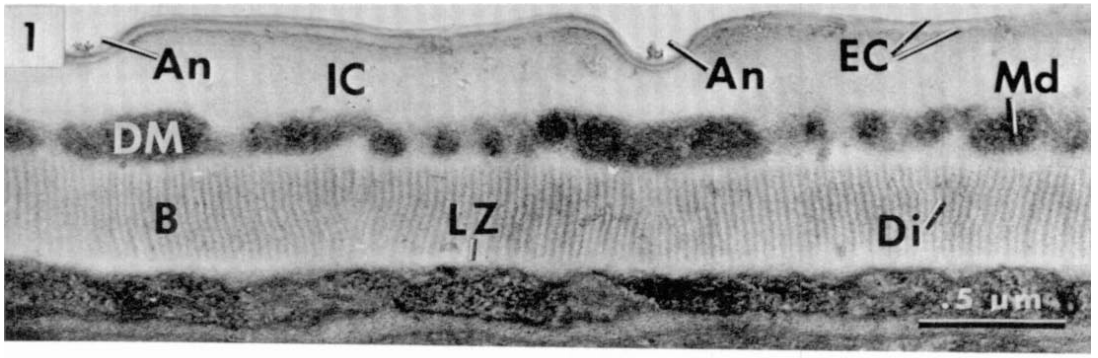
Hypodermis: The hypodermis of *M. incognita* and *H. glycines* is a thin plasmalemma-bound layer (Fig. 12, 13)

FIG. 1-6. **1)** Longitudinal section through cuticle of *Heterodera glycines* with periodic superficial annulations (An). B, basal layer; Di, disjunction; DM, dense material; EC, external cortex; IC, internal cortex; LZ, electron-lucent zone; Md, medial layer. **2)** Cross section through lateral field of *H. glycines* with four incisures (In). B, basal layer. **3)** Cross section near anterior origin of lateral field of *Meloidogyne incognita* with two incisures (In). B, basal layer. **4)** Cross section through lateral field of *H. glycines* showing anterior origin of inner incisures (In). **5)** Cross section through lip region of *H. glycines* with longitudinal striations (St). **6)** Cross section at base of cephalic framework of *H. glycines* with longitudinal striations (St).

FIG. 7-11. **7)** Cross section through cuticle of *Meloidogyne incognita* showing layering: B, basal layer; EC, external cortex; IC, internal cortex; LZ, electron-lucent zone; Md, medial layer. Rectangle indicates area enlarged in Fig. 8. **8)** Enlargement of rectangle in Fig. 7, showing five layers composing external cortex. **9)** Cross section through cuticle of *Heterodera glycines* showing layering: B, basal layer; Bd, bands; EC, external cortex; IC, internal cortex; LZ, electron-lucent zone; Md, medial layer. **10)** Tangential section through striated basal layer of cuticle of *M. incognita* revealing cross hatching. **11)** Cross section through basal layer (B) of *M. incognita* showing overlapping tapering layers (arrows). LZ, electron-lucent zone; Md, medial layer.

FIG. 12-(A-E). Diagram illustrating relationship of hypodermis to other structures in anterior portion of *Heterodera glycines* (also generally applies to *Meloidogyne incognita*). **A)** Ventral view. **B)** Cross section through region of stylet cone. **C)** Cross section through region of anterior procorpus. **D)** Cross section through region of middle procorpus. **E)** Cross section through region of isthmus.

FIG. 13-15. **13)** Cross section through interchordal hypodermis (H) of *Heterodera glycines* with nerve processes (NP). **14)** Cross section through lateral hypodermal chord of *H. glycines*. Arrows indicate boundary of chord. ER, endoplasmic reticulum; Li, lipid; LN, lateral nerve; Ly, lysosome; My, myelin-like whorl; Sm, somatic muscle. **15)** Cross section of *Meloidogyne incognita* with hypodermal radii (H) connecting interchordal hypodermis with hypodermis surrounding vestibule extension (VE) (see Fig. 12-B). SP, stylet protractor muscles.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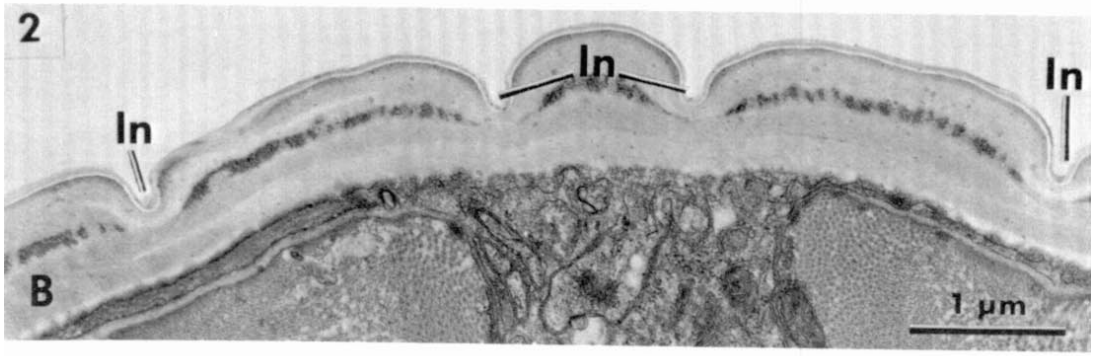
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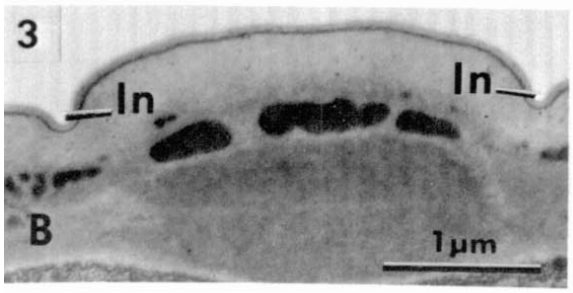
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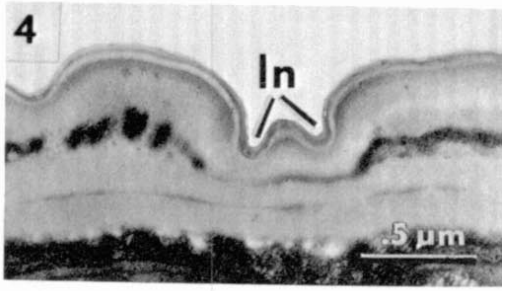
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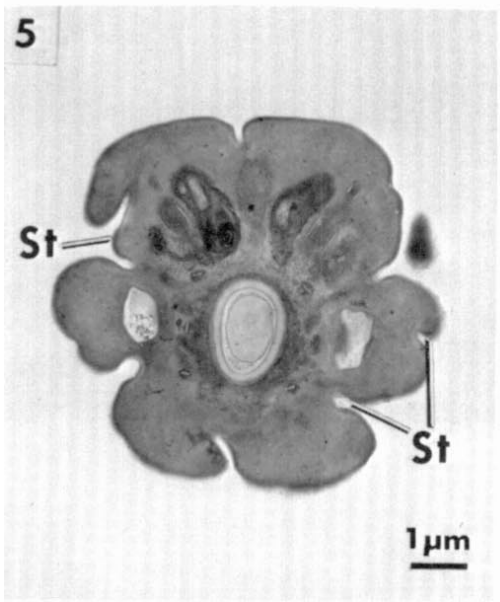
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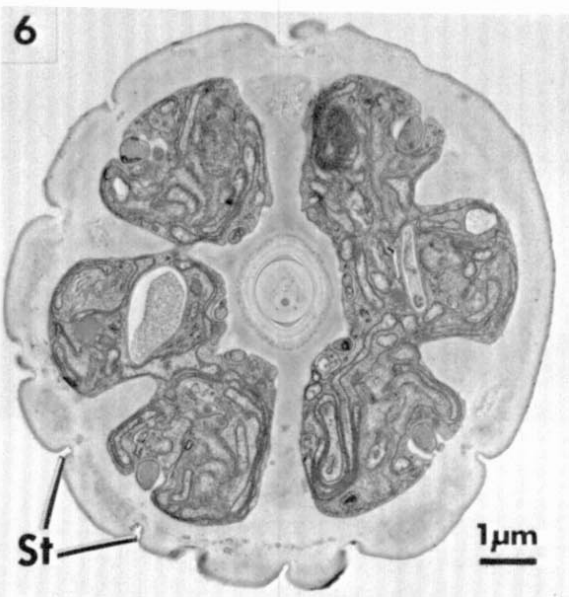
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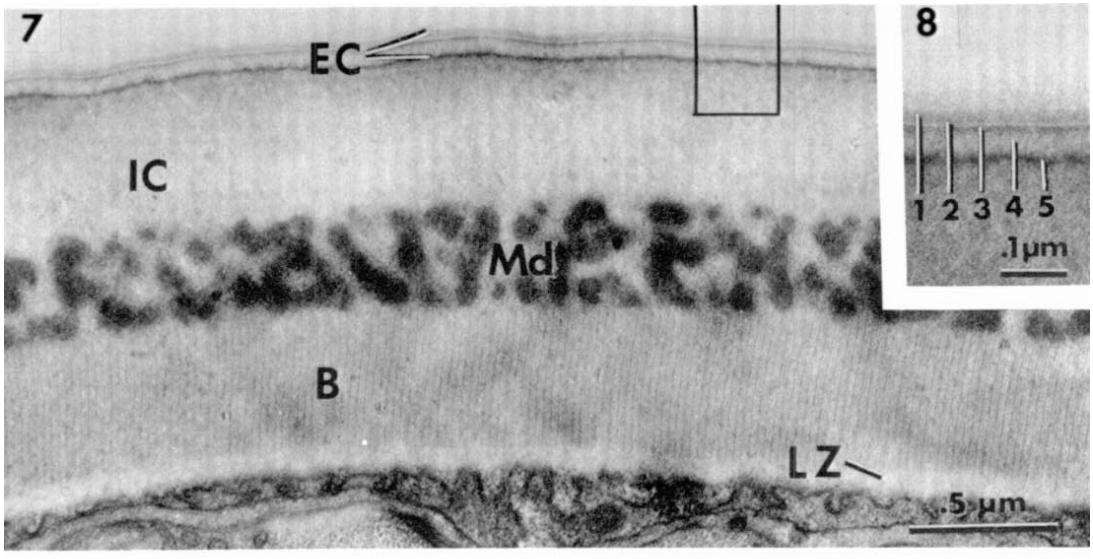
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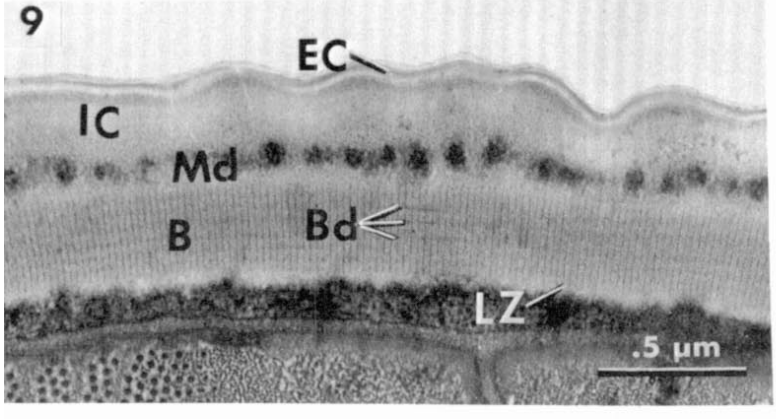
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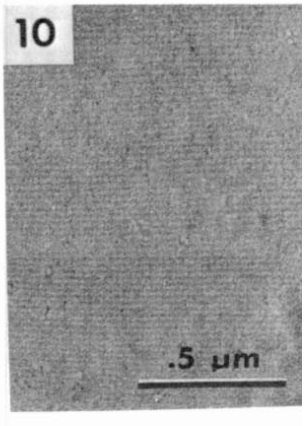
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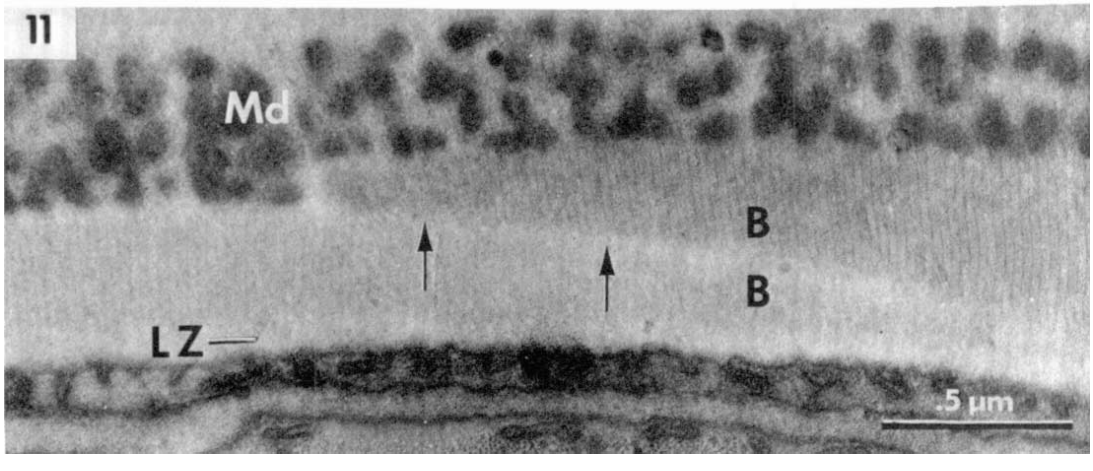
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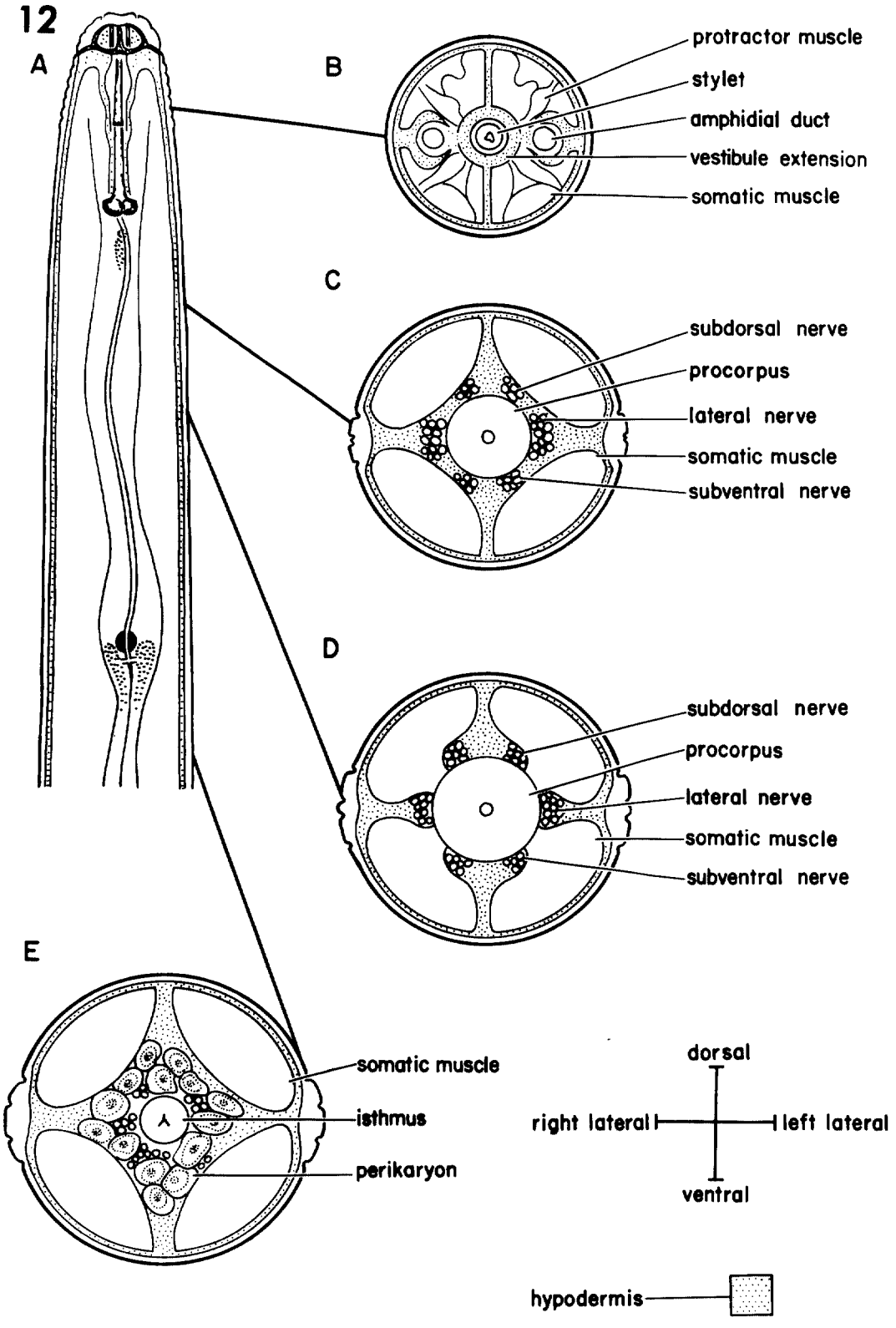
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B
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stylet
amphidial duct
vestibule extension
somatic muscle
C
subdorsal nerve
procorpus
lateral nerve
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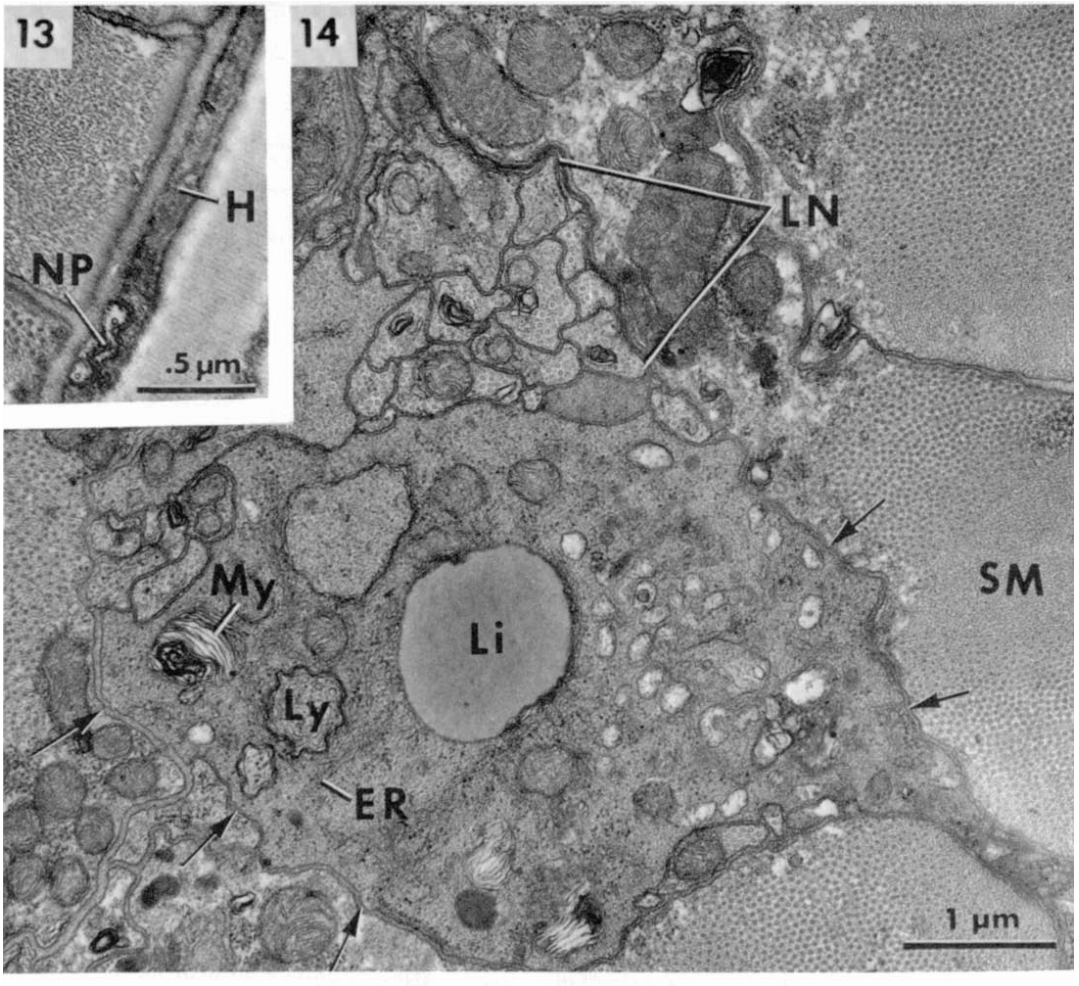
subventral nerve
D
subdorsal nerve
procorpus
lateral nerve
somatic muscle
subventral nerve
E
somatic muscle
isthmus
perikaryon
dorsal
right lateral
left lateral
ventral
hypodermis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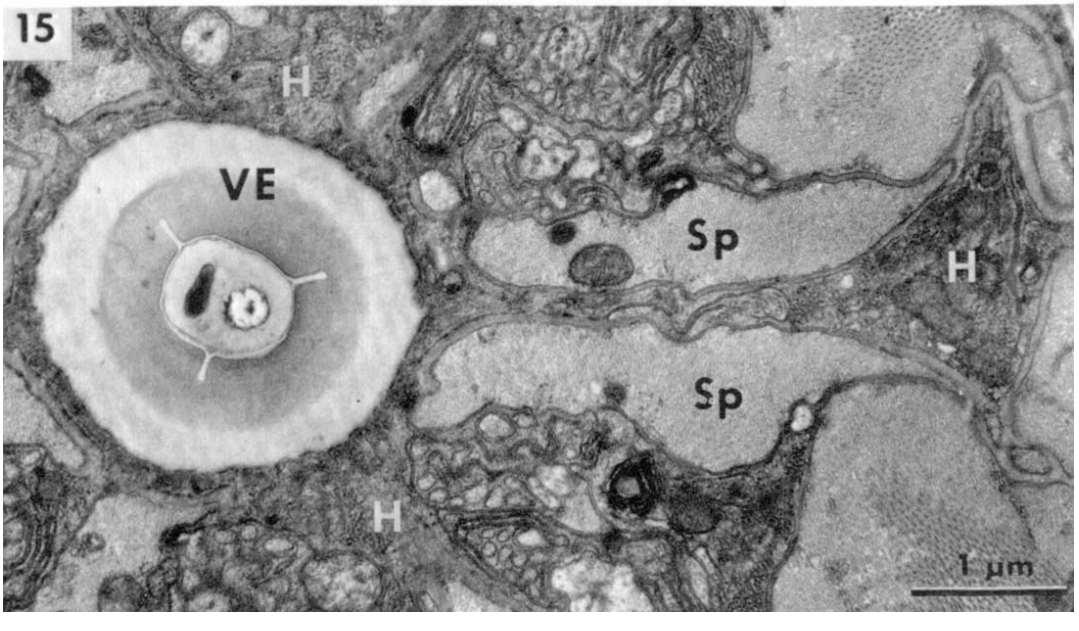
15
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between the cuticle and somatic muscles, which enlarges to varying degrees on the lateral, dorsal and ventral sides forming chords which project into the pseudocoelom (Fig. 12, 14). Anteriorly, the hypodermis pervades the cephalic framework region, and slightly posteriorly, it lines the stomatal cavity and stylet shaft (Fig. 12-A, B; 15). Longitudinal radii of hypodermal tissue extend from the hypodermis surrounding the stoma, between the anterior portion of the stylet protractor muscles, and are continuous with the hypodermis of the body wall (Fig. 12-B, 15). Posteriorly, the chords are generally reduced to accommodate the large amphids (Fig. 16), but immediately beneath the amphids the chords enlarge, partially enclosing the lateral nerve bundles, and contacting the subdorsal and subventral bundles (Fig. 12-C, 17). Thus, in this region, a ring of tissue is present around the esophagus, which is predominantly hypodermis (Fig. 12-C), although, in the case of *M. incognita* the posterior amphidial gland processes occupy the subventral portions of the ring (Fig. 17). Posteriorly, the size of the chords varies throughout the esophageal region (Fig. 12-C-E) and among individuals; starved males tend to have smaller chords. In a ganglionic region which starts at the posterior procorpus and extends beyond the nerve ring, the hypodermal chords are greatly expanded, and enclose many perikaryons (nerve cell bodies) (Fig. 12-E) of six cephalic nerve bundles. The interchordal hypodermis varies little in thickness throughout a given individual (Fig. 12).

The hypodermis of *M. incognita* and *H. glycines* males is syncytial (Fig. 14, 17), although occasionally other cells are enclosed within it (viz., nerves and glands). Adjacent membranes which occur through the tissue frequently give the impression of plasmalemmas, although they generally end blindly, and do not completely enclose a given nucleus (Fig. 14, 17). Most nuclei occur in lateral (Fig. 17) and ventral chords, although they may also occur anteriorly in the dorsal chord.

In addition to nuclei, the hypodermis generally includes large numbers of organelles and other structures. The chords are filled with large lipid globules (Fig. 14, 19-21), mitochondria (Fig. 17), lysosomes and their myelin-like products (Fig. 14), as well as smooth and rough endoplasmic reticulum (Fig. 14, 17, 20, 24), free ribosomes (Fig. 24), golgi (Fig. 18), β-glycogen (Fig. 21, 22), and spindle-shaped structures (Fig. 20, 23, 24).

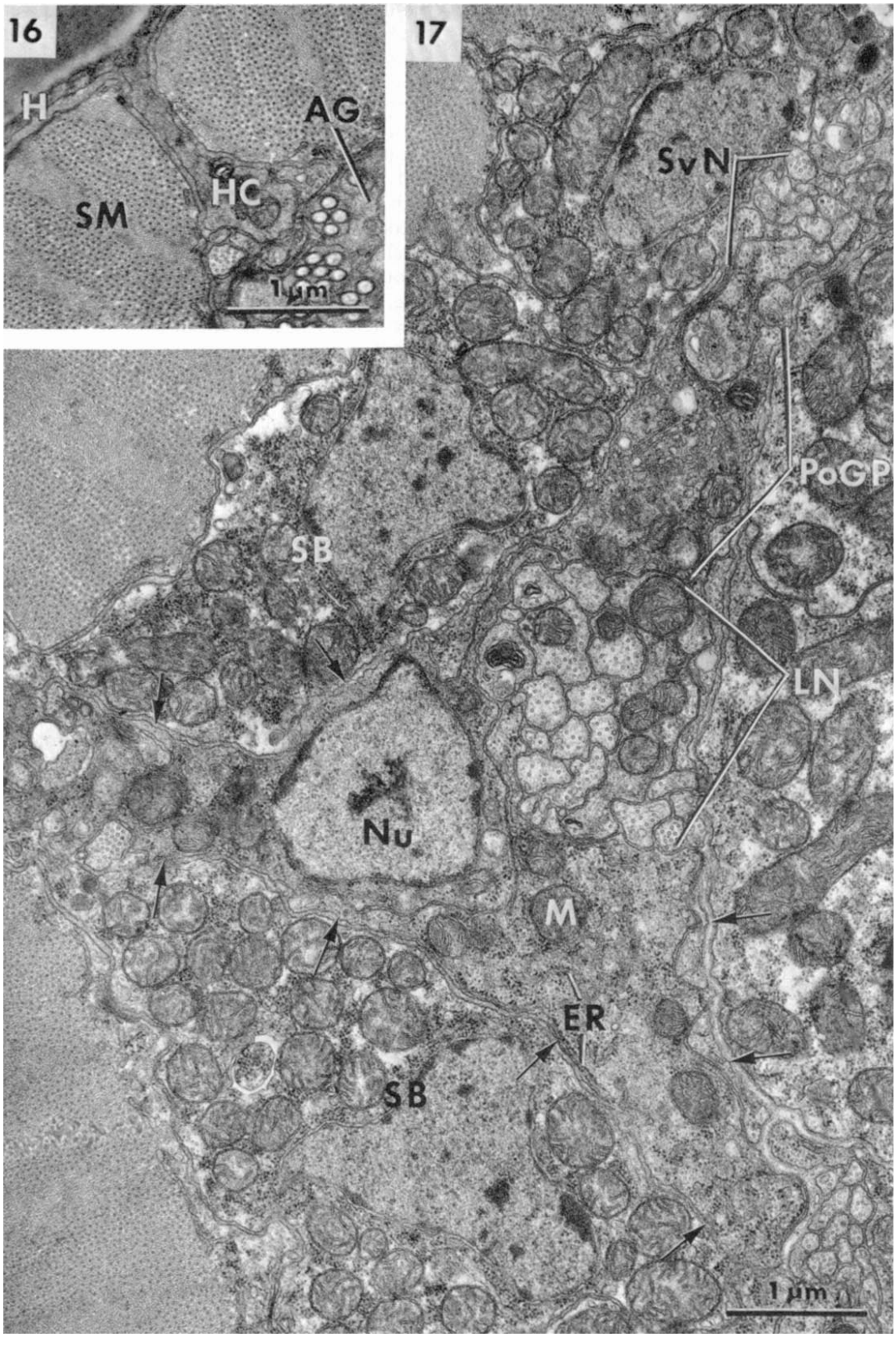
Perhaps the most striking features of the hypodermis is the large lipid globules, which, in the fixed state, are homogeneous, of intermediate electron density, and generally spherical (Fig. 19, 20). The globules often seem to merge with one another (Fig. 19), since they are not membrane-bound (Fig. 19, 20). However, the surface is frequently surrounded by ribosomes and rough endoplasmic reticulum (Fig. 19, 20). Golgi and mitochondria may also be associated with the surface (Fig. 19, 20).

Frequently, a large spherical (or perhaps irregular) space will be only partially filled by a lipid globule and the remaining area is occupied by myelin-like whorls continuous with membranes, which in this case, bind the globule (Fig. 21). Sometimes, what may be membranes of degenerate spindle-shaped structures may also be present in similar "cavities" (Fig. 22), which may or may not contain lipid globules.

Spindle-shaped structures, which are very common in the hypodermis, consist of sheets of roughly parallel membranes, and are most frequently found in the close vicinity of lipids (Fig. 20, 23). They are generally about 1 μm by 0.5 μm, and do not appear to be bound by a continuous outer membrane (Fig. 23). Their

FIG. 16, 17. **16)** Cross section through lateral hypodermal chord (HC) adjacent to amphidial gland (AG) in *Meloidogyne incognita*. H, hypodermis; SM, somatic muscle. **17)** Cross section through lateral hypodermal chord of *M. incognita* showing relationship to lateral nerve bundle (LN), posterior gland process (PoGP) of amphid, and subventral nerve bundle (SvN) (see Fig. 12-C). Arrows indicate boundary of chord. ER, endoplasmic reticulum; M, mitochondrion; Nu, nucleus; SB, sarcoplasmic body of somatic muscle.

FIG. 18-22. **18)** Cross section through golgi apparatus (Go) in lateral hypodermal chord of *Heterodera glycines*. **19)** Lipid globules (Li) in lateral hypodermal chord of *H. glycines* merging with one another. **20)** Cross section through lateral hypodermal chord of *H. glycines* showing lipid globule (Li) and spindle-shaped structures (SpS). ER, endoplasmic reticulum; Go, Golgi apparatus. **21)** Large space in lateral hypodermal chord of *H. glycines* partially filled with lipid globule (Li) and myelin-like whorls (My). Gl, β-glycogen. **22)** Large space in lateral hypodermal chord of *H. glycines* filled with various materials including membranes (Me) similar to those found in spindle-shaped structures. Gl, β-glycogen; My, myelin-like whorl.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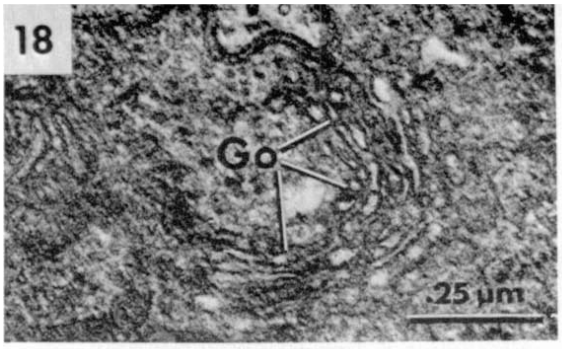
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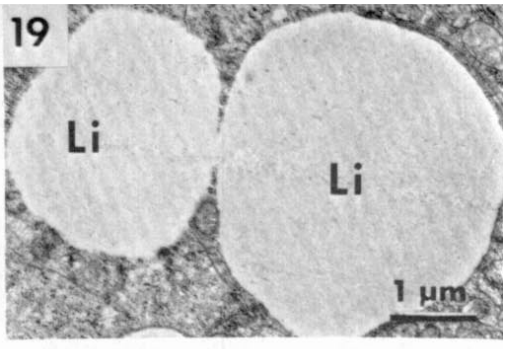
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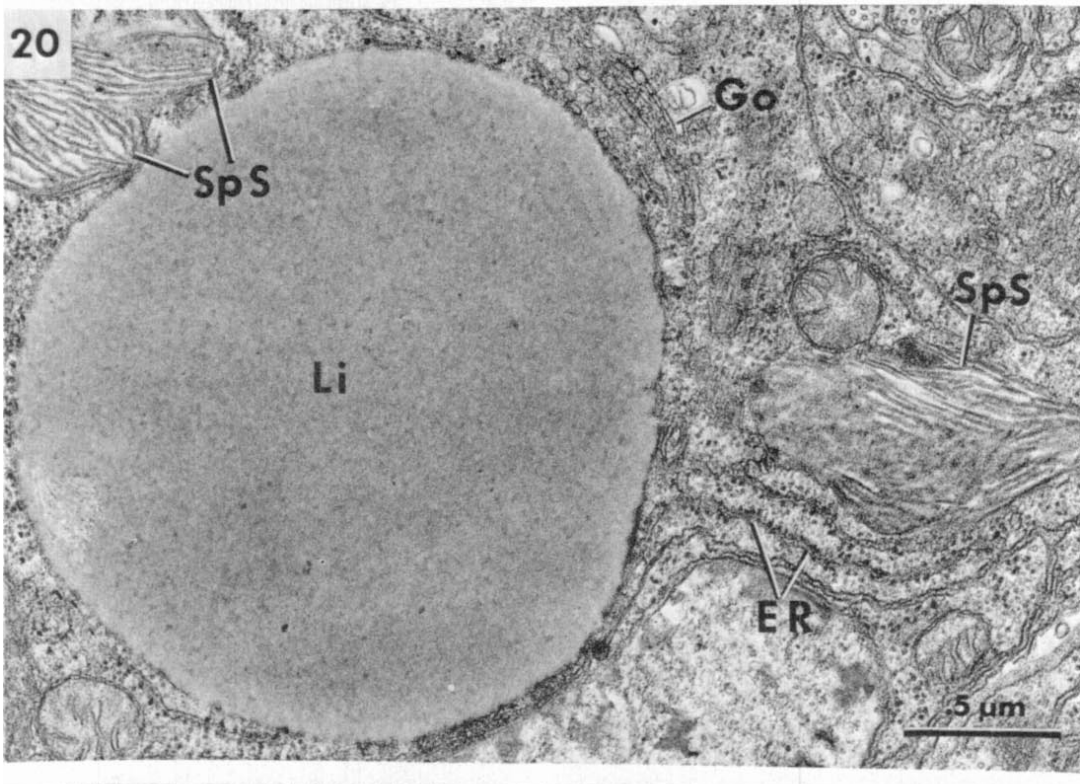
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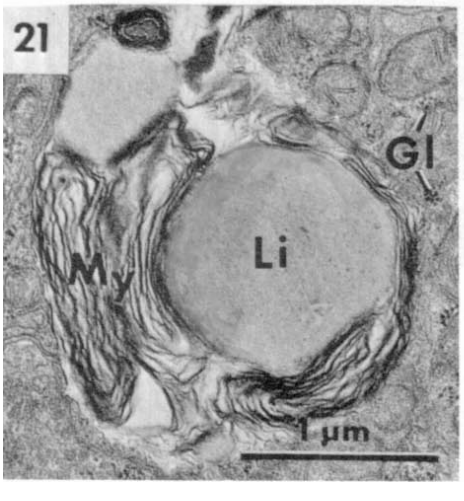
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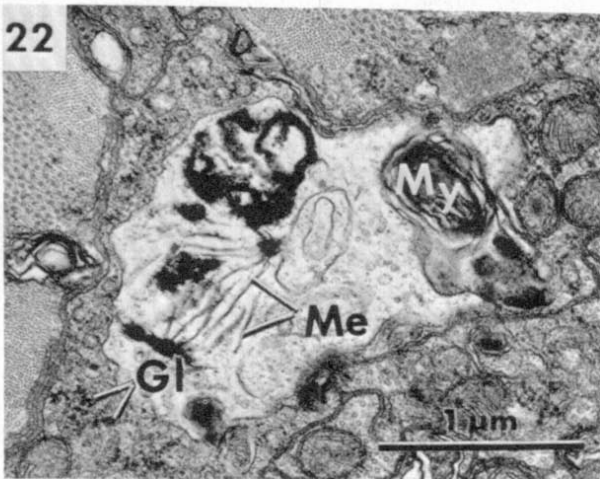
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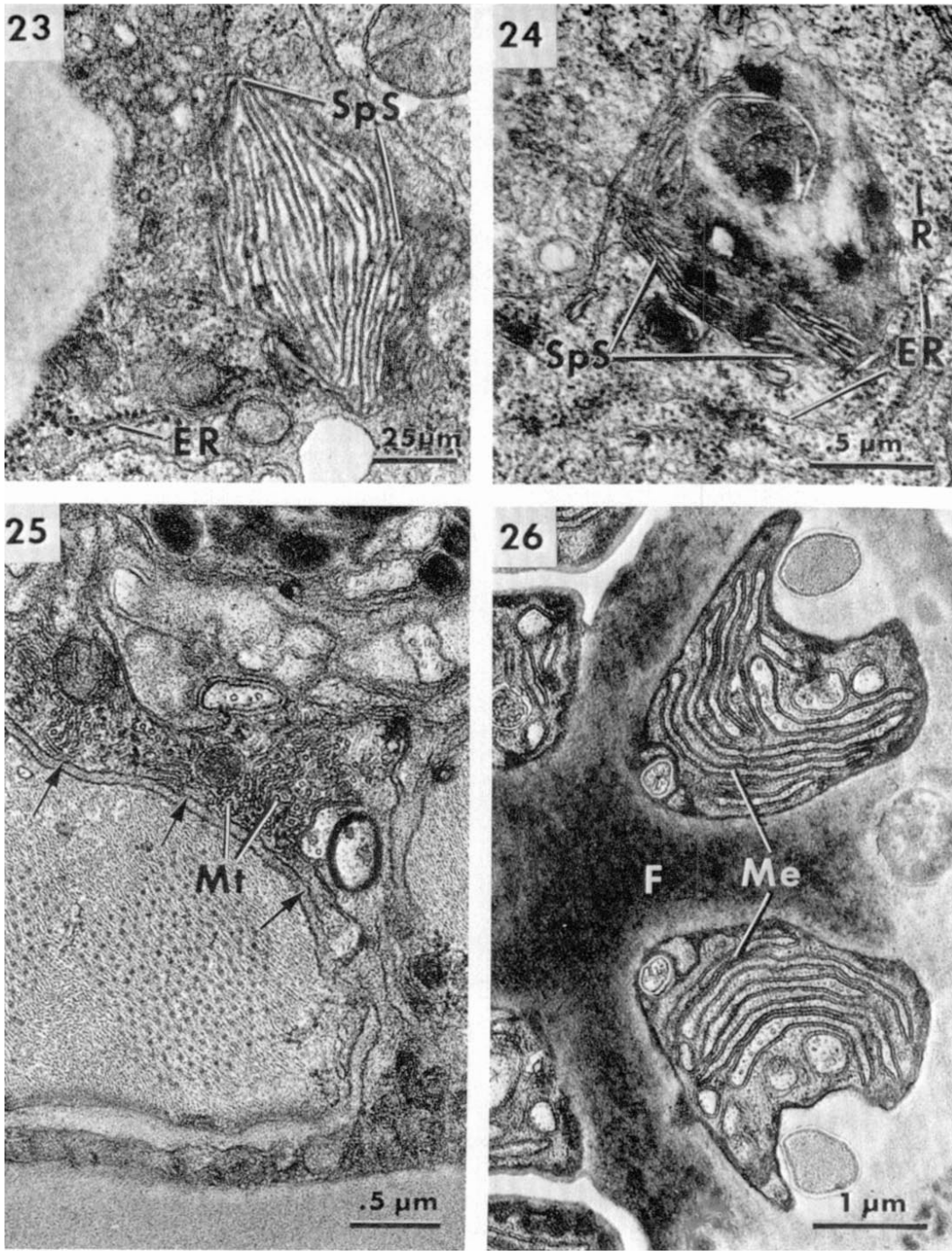


FIG. 23-26. **23)** Spindle-shaped structure (SpS) and closely associated endoplasmic reticulum (ER) in lateral hypodermal chord of *Meloidogyne incognita*. **24)** Degenerating spindle-shaped structure (SpS) in lateral hypodermal chord of *M. incognita*. ER, endoplasmic reticulum; R, ribosomes. **25)** Lateral hypodermal chord (arrows) slightly posterior to basal plate of cephalic framework in *M. incognita* showing numerous microtubules (Mt). **26)** Hypodermal tissue filling the lip region of *M. incognita* with lamellae of parallel membranes (Me). F, framework.

inner matrix is generally electron-lucent, although grainy material sometimes adheres to the membranes (Fig. 23). Endoplasmic reticulum adjacent to spindle-shaped structures may extend to nearby lipid globules (Fig. 20, 23). Spindle-shaped structures occur in various degrees of disarray in which membranes cease to be parallel, and the matrix becomes dense and grainy (Fig. 20, 24).

Microtubules of the hypodermis, which are especially numerous in *M. incognita,* are concentrated in the region slightly posterior to the basal plate of the cephalic framework (Fig. 25). Similarly, lamellae of parallel membranes are unique to the hypodermis of the anterior framework and lip region (Fig. 26).

The interchordal hypodermis, while generally devoid of organelles, encloses fine peripheral nerve processes (Fig. 13), and provides points of attachment of cuticle and somatic muscles, through modifications of its plasmalemma into regularly spaced hemidesmosomes (Fig. 27, 28). Fine fibrils extend across the hypodermis from hemidesmosomes underlying the cuticle, to corresponding structures on the basal lamina of the somatic muscles (Fig. 28). Between hemidesmosomes, the hypodermis is frequently invaginated by projections of the cuticle (Fig. 29).

Somatic muscles: The somatic musculature of *M. incognita* and *H. glycines* males is similar. Both are meromyarian, having from two-to-five muscle cells between each of the four chords. Two muscle cells per interchordal region are present in the cephalic region, at least three in the region of the stylet shaft, and four or five throughout most of the esophageal region. The spindle-shaped cells, which are arranged in alternate rows, are platymyarian with the contractile portion

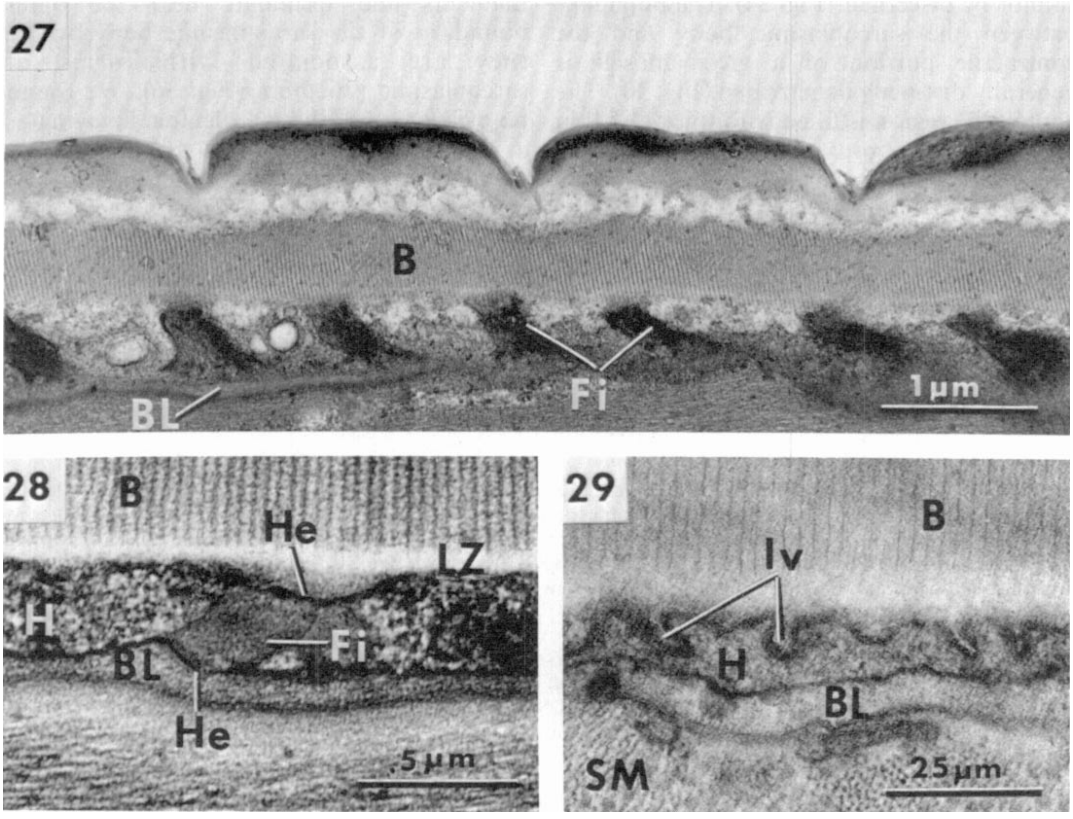


FIG. 27-29. **27)** Longitudinal section of body wall cuticle and hypodermis in *Heterodera glycines* showing fibrils (Fi) transversing hypodermis from hemidesmosomes on the basal lamina (BL) of muscles, to those underlying the cuticle. B, basal layer of cuticle. **28)** Enlargement of fibrils (Fi) crossing interchordal hypodermis (H) of *H. glycines*. B, basal layer of cuticle; BL, basal lamina; LZ, electron-lucent zone; He, hemidesmosomes. **29)** Cross section of interchordal hypodermis (H) of *H. glycines* showing invaginations (Iv). B, basal layer of cuticle; BL, basal lamina; SM, somatic muscles.

adjacent to the basal lamina which separates it from the interchordal hypodermis, and the sarcoplasmic body with nucleus extending into the pseudocoelom (Fig. 17, 30). The basal lamina also extends between muscles (Fig. 30, 33), and, just below the basal plate of the cephalic framework, surrounds the muscle tip (Fig. 31, 32). In *M. incognita,* it forms a relatively smooth surface around the muscle (Fig. 31), whereas in *H. glycines* it penetrates by deep invaginations (Fig. 32). The sarcoplasmic body contains a large nucleus with a distinct spherical nucleolus and dense peripheral chromatin (Fig. 30), as well as mitochondria, β-glycogen, and some smooth endoplasmic (sarcoplasmic) reticulum. Innervation processes extend from muscles above or below the broadest part of the sarcoplasmic body, to nerve processes included in the six major cephalic bundles (Fig. 33, 34). The innervation processes merge with nerves so that boundaries between them cannot be discerned (Fig. 34). The boundary between the sarcoplasmic body and the contractile portion of a given muscle is generally distinctly demarcated (Fig. 30). The contractile region is filled with thick and thin myofilaments approximately 0.024 μm and 0.006 μm in diam (Fig. 36), and arranged parallel to the longitudinal axis in oblique bands. In a given cross section (Fig. 35), each cycle of bands includes band I, with only fine filaments, band A, with thick filaments each surrounded by a hexagonal pattern of about 10-15 fine filaments, and a narrow H band of only thick filaments, followed again by band A. No Z band or T system is present. About five to six cycles occur in the broadest portion of a given muscle (Fig. 35), whereas, the narrow tips contain only fine filaments of the I band (Fig. 31, 32). Individual bands vary in thickness: for example, frequently every other I band is greatly reduced so that A bands of adjacent cycles partially fuse toward the inside of the contractile portion (Fig. 35).

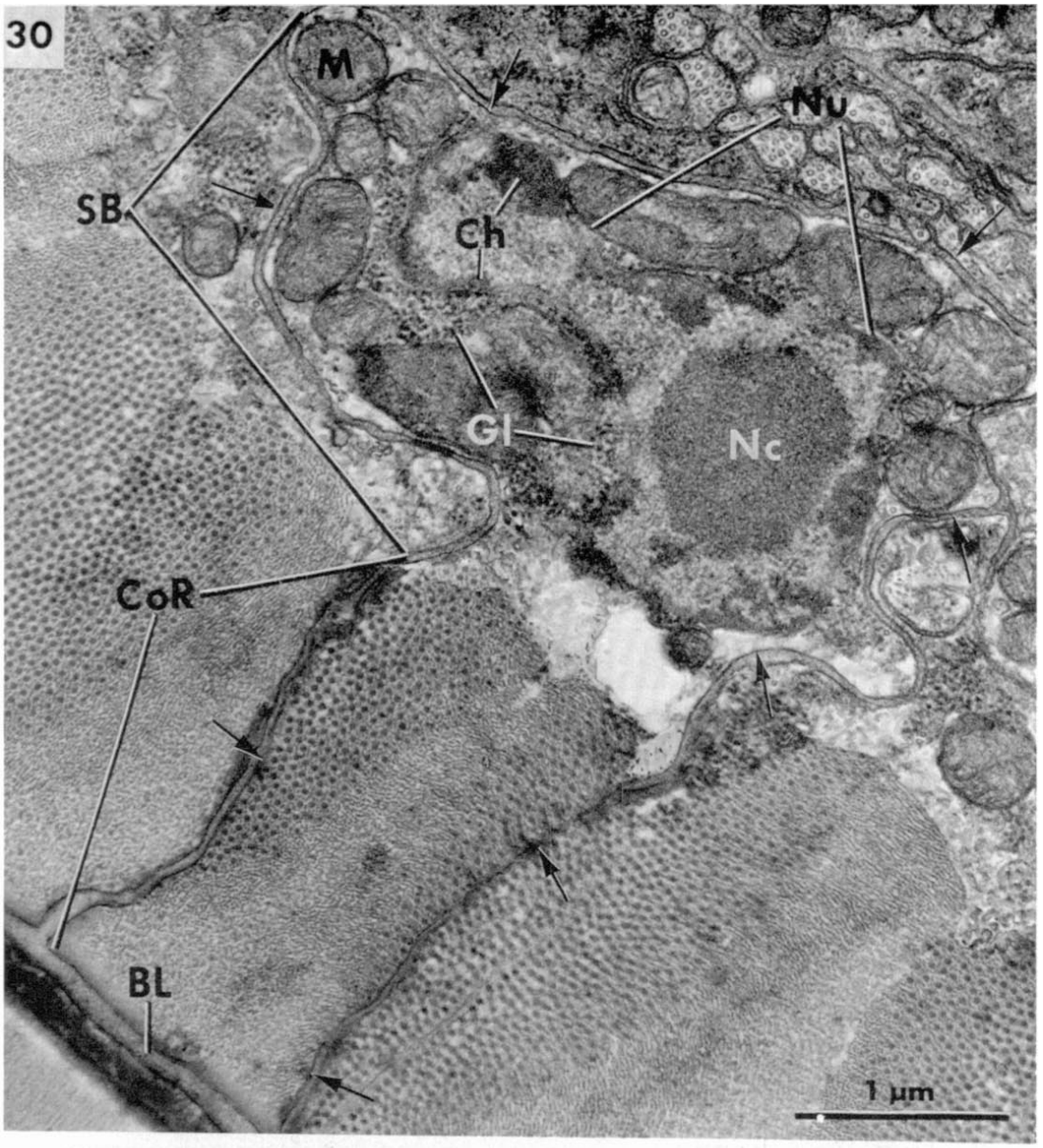
The sarcolemma adjacent to the I band is bound to the basal lamina by hemidesmosomes, which generally span the width of the band (Fig. 35, 38). In contrast, the sarcolemma underlying the A band is generally associated with cisternae of the sarcoplasmic reticulum (Fig. 36, 39) which, in many cases, resemble the dyads described by Rosenbluth (34). These structures are physically related to thin, dense bands which extend from a broad base on the sarcolemma, between rows of large filaments in the H band (Fig. 35-37). The bands are continuous with material forming cross bridges with these filaments and terminate near the outer boundary of the sarcoplasmic body, where they are associated with forms of sarcoplasmic reticulum (Fig. 36). We found no evidence that the sarcolemma invaginates at the base of the dense band; possibly membranes lining this structure appear, instead, to be part of the sarcoplasmic reticulum. In some instances, where the H band is broad, it is associated with more than one dense band (Fig. 37).

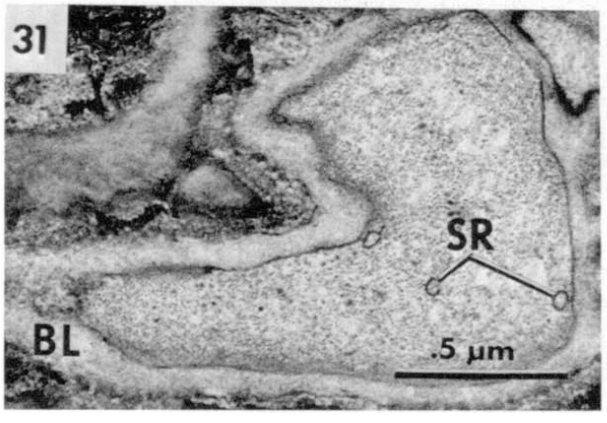
The sarcoplasmic reticulum is not limited to association with A and H bands, but is present in various forms in the I bands at the tips of muscles (Fig. 31), as well as in flattened

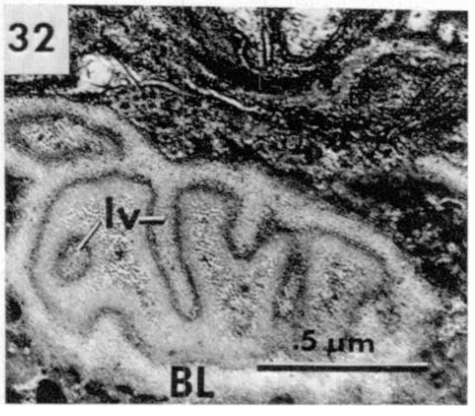
FIG. 30-32. **30)** Montage of cross section of muscle cell of *Heterodera glycines* with contractile region (CoR) and sarcoplasmic body (SB). Arrows indicate sarcolemma boundary. BL, basal lamina; Ch, chromatin; Gl, β-glycogen; M, mitochondrion; Nu, nucleus; Nc, nucleolus. **31)** Cross section slightly posterior to basal plate of cephalic framework in *Meloidogyne incognita* showing basal lamina (BL) surrounding muscle tip. SR, sarcoplasmic reticulum. **32)** Cross section slightly posterior to basal plate of cephalic framework in *H. glycines* showing invaginations (Iv) penetrated by basal lamina (BL).

FIG. 33-35. **33)** Cross section of contractile regions of several somatic muscles in *Meloidogyne incognita*. Rectangle enlarged in Fig. 34. BL, basal lamina; H, hypodermis. **34)** Enlargement of rectangle in Fig. 33 showing relationship of sarcoplasm to one of several nerve processes (NP). LN, lateral nerve; M, mitochondrion. **35)** Cross section of contractile region of somatic muscle in *M. incognita* showing H, A, I bands. BL, basal lamina; H, hypodermis; He, hemidesmosomes; TD, thin, dense bands.

FIG. 36-40. **36)** Cross section of a single cycle of the contractile portion of a *Meloidogyne incognita* muscle with H, A, I bands. BL, basal lamina; Br, bridges; SL, sarcolemma; SR, sarcoplasmic reticulum; TD, thin, dense bands. **37)** Cross section through a portion of the contractile region of a muscle cell in *Heterodera glycines* with more than one thin, dense band (TD) per H band. A, A band; I, I band. **38)** Cross section of hemidesmosome (He) underlying I band in *M. incognita*. BL, basal lamina; H, hypodermis; SR, sarcoplasmic reticulum. **39)** Cross section of flattened sarcoplasmic reticulum (SR) at base of thin, dense band in *M. incognita*. BL, basal lamina; H, hypodermis; SL, sarcolemma. **40)** Cross section of flattened sarcoplasmic reticulum (SR) cisternae between two somatic muscle cells of *M. incognita*. BL, basal lamina; SL, sarcolemma.


30
M
Nu
SB
Ch
Gl
Nc
CoR
BL
1 µm


31
SR
BL
.5 µm


32
lv
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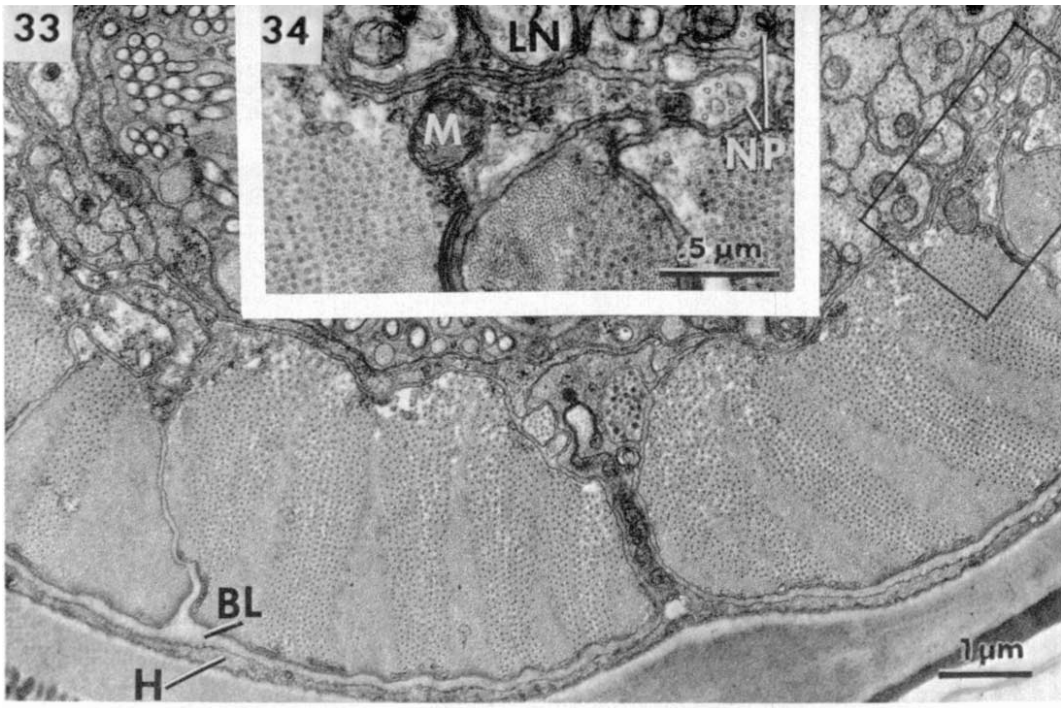
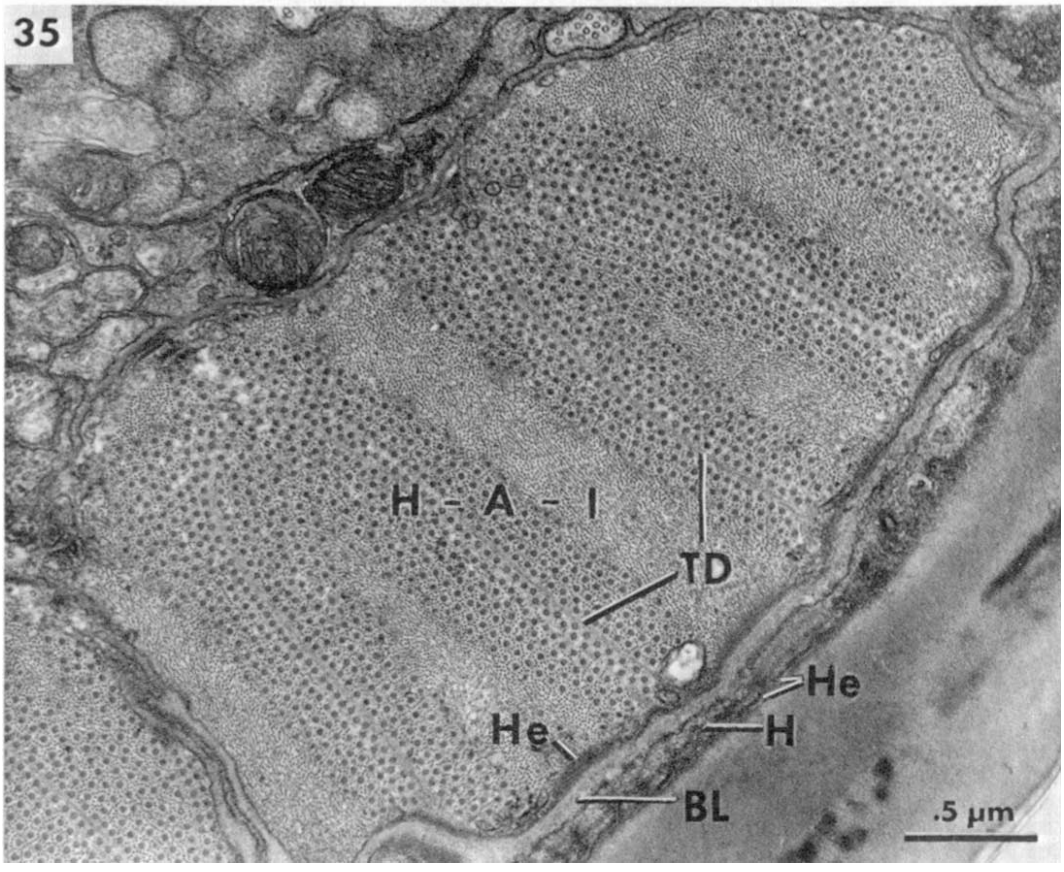
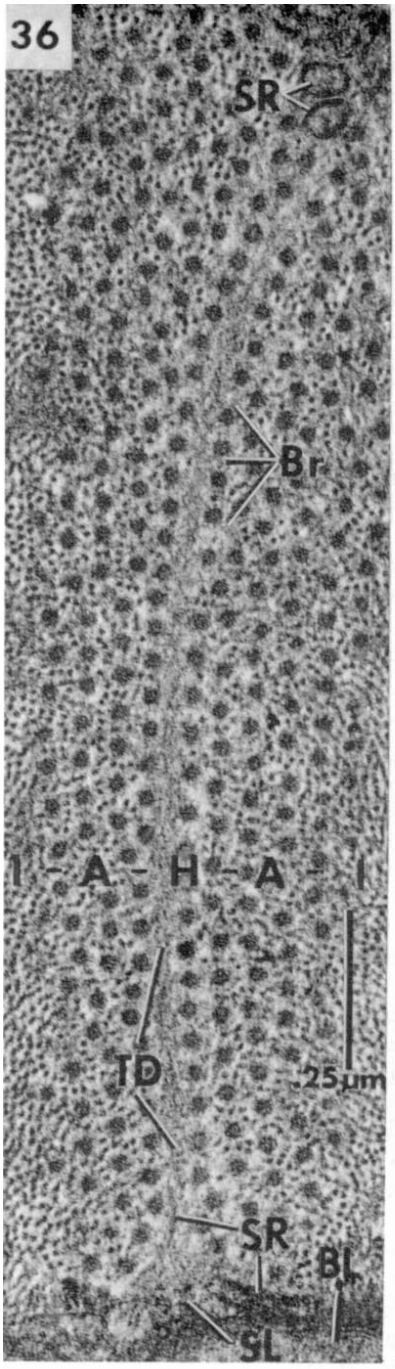
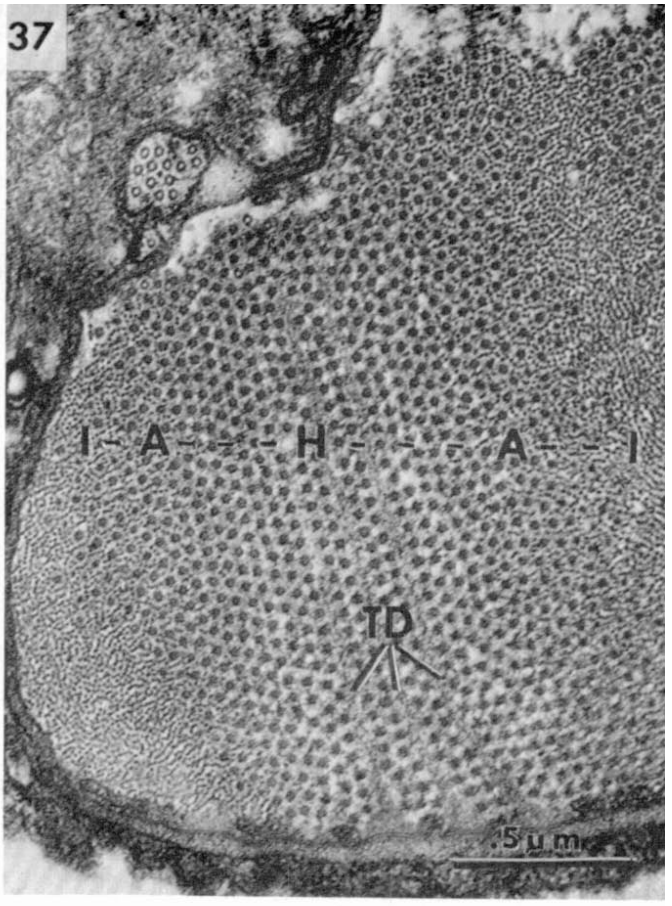
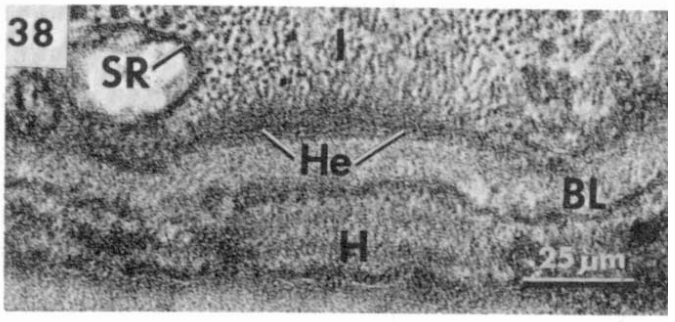
BL

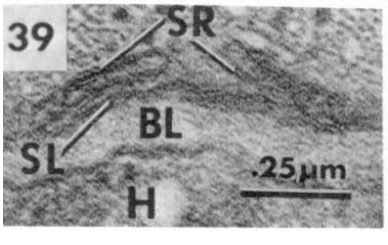

33
34
LN
M
NP
.5 µm
BL
H
1µm


35
H - A - I
TD
He
He
H
BL
.5 µm


36
SR
Br
I - A - H - A - I
TD
.25 µm
SR
BL
SL


37
I - A - - - H - - - A - - I
TD
.5 µm


38
SR
I
He
BL
H
.25 µm


39
SR
BL
SL
H
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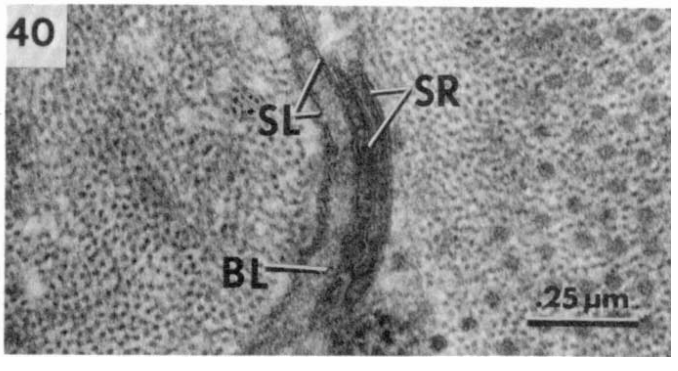
40
SL
SR
BL
.25 µm

cisternae which may occur apposed to the sarcolemma between adjacent cells (Fig. 40).

DISCUSSION

Cuticle: The cuticles of *M. incognita* and *H. glycines* males are basically similar, and with respect to layering of the cuticle, our observations are generally in agreement with those of Bird (5) on *Meloidogyne javanica* (Treub) and Shepherd et al. (36) on *Heterodera rostochiensis* Woll. However, the external cortex, in our preparations, could be resolved into five layers, similar to those observed earlier in second stage larvae of *M. javanica* (4), but not shown in males. Layer 1, of males, is much thicker than the outer unit of the "triple-layered membrane" present in larvae. We could not determine if this outermost layer of the external cortex is an artifact, or if it represents a true modification of the male cuticle, perhaps an outer coating of substance of similar electron density to the surface of the trilaminate layer, or a thickening of the trilaminate surface itself.

The medial layer of nonsedentary Heteroderidae previously was characterized as vacuolated and electron-lucent, with periodically arranged dense balls or globular deposits of electron-dense matter (36, 39). With very few exceptions we found this layer to be filled with a compact network of dense material, and few vacuoles in both species. In longitudinal sections, however, periodically spaced regions of increased size and density were present, which probably correspond to "dense balls." In some preparations, the medial layer apparently becomes depleted of most of its dense contents, and perhaps the remaining material condenses into spheres. The loss of this material might also explain the variability in thickness of the medial layer.

Although striations of the basal layer were readily and consistently resolved in specimens of *H. glycines,* they often could not be seen anteriorly in *M. incognita,* in spite of good preservation of cellular components. The outer cuticular layers may be more permeable in *M. incognita* than *H. glycines,* and thus, leaching would more readily destroy the striated structure of the basal layer in *M. incognita.* Greater permeability of the cuticle of *M. incognita* males might also be deduced from the fact that, regardless of its greater thickness, better preservation of cellular components was achieved, under identical preparation methods, than in *H. glycines.*

The electron-lucent zone underlying the striated basal layer was not observed in previous studies on *Meloidogyne* (5, 7, 36, 39), but may be comparable to the basal lamella (6, 15) or basement membrane (1) reported for other nematode genera.

Hypodermis: The hypodermis of *M. incognita* and *H. glycines,* as in certain other nematodes (5, 42), is described as syncytial. However, in some cases it may be difficult to distinguish between partially cellular and syncytial. For example, the large cell, we found in *H. glycines* internally to the chord and laterally to the amphidial gland (3), may prove to be ontogenetically part of the hypodermis. Thus, in such cases the hypodermis could be considered partially cellular. Similarly, the amphidial gland (2, 3) may constitute a large cell within the hypodermis. Developmental studies are needed to further clarify these points.

The presence of a stomatal hypodermis was described in many large nematodes as an arcade (14), and was also identified in light-microscope studies of females of *M. hapla* Chitwood (17). More recently, connections have been observed between the chordal and stomatal, or arcade hypodermis (40). In the Tylenchida, this layer probably not only is responsible for producing the stoma lining, but may be involved in forming the stylet cone, and perhaps the shaft and knobs. Similarly, the hypodermis which fills the head region is most likely responsible for the formation of the cephalic framework. Parallel folded membranes in the lip region of *M. incognita* and *H. glycines* may be homologous with the clavate cells of larger animal parasites (25), and together with the microtubules posterior to the framework, may function in the transport and orientation of framework precursor material during molting.

The large lipid globules present in the chordal hypodermis of *M. incognita* and *H. glycines* are readily visible in the light microscope, and probably occur throughout the Nematoda. Such globules doubtlessly represent sites of food storage, and apparently play a particularly important role in maintaining nonfeeding nematode stages. Lee (28) demonstrated that certain esterases (lipase ?) are associated with fat globules, which, he proposed, might be involved in catabolizing the globules during starvation.

This would explain the close association of mitochondria, the sites of respiration, with lipid globules.

The spindle-shaped structures may be synonymous with the "membrane-filled vesicles" noted in larvae of *H. rostochiensis* (39). This structure has apparently not been described earlier, and may be unique to nematodes. It is, apparently, associated with lipid globules, perhaps in their formation, or more probably, in their catabolism. It might be proposed that catabolytic enzymes are confined within the parallel membranes, which, when released, may result in digestion of lipids and other cellular components. Myelin-like phospholipid whorls, also associated with lipids, may have lysosomal functions (35). The large numbers of hypodermal ribosomes suggest this as a site of protein synthesis, and additional materials are doubtlessly produced by well-developed golgi.

That nerve bundles are closely associated with the hypodermis is well established, and it is possible that the hypodermis provides a supporting or glial-like role for nerve processes. We have noted occasional peripheral nerves in the interchordal hypodermis, especially anteriorly. Although cephalids and hemizonids were not observed, it appears that peripheral nerves are concentrated in regions corresponding to the expected location of these structures as in certain Ancylostomatoidea (37). However, in the Heteroderidae, they do not result in a thickening of the hypodermis. The concentration of nerves in such regions prevents the formation of hemidesmosomes, between the hypodermis and cuticle, on the one hand, and basal lamina and the muscles, on the other. Thus, even gentle heat, or certain fixatives may result in the cuticle pulling away from the hypodermis in these regions, and structures such as cephalids and hemizonids are thus formed.

Striations are clearly resolved in the subcuticular or hypodermal layer of whole mounts of Heteroderidae in the light microscope. Such striations have not been previously homologized with structures visible in the electron microscope, although it was proposed that a connection of the cuticle to the muscles may be involved (23). Because hemidesmosomes occur at a periodicity corresponding to that of the "subcuticular striae," these structures, with their fibrils, apparently are homologous.

Somatic muscles: The platymyarian somatic muscles of *M. incognita* and *H. glycines* males, are similar to those described in other Tylenchida, and possess typical H, A, I, bands. Although Z bands have been described in some Tylenchida, they may represent misidentified structures, and perhaps do not occur in this group. By definition, Z bands are septa or plates through the I band (9, 10, 11). Thus, the dense lines through the H band of *Criconemoides similis* Cobb (8) cannot be Z bands, but like the "supporting structures" in *H. rostochiensis* larvae (39), probably are synonymous with the "thin, dense lines" of the present study. Furthermore, these dense lines cannot be considered as T tubules, as described in other organisms (11, 30, 34, 38), since careful examination indicates that they do not involve invaginations of the sarcolemma, nor are they present in the I band. Similar dense lines were labeled as T tubules in *Macroposthonia xenoplax* Raski (15), although they occurred in the H band, and invaginations of the sarcolemma, while reported, are not visible in the published micrographs. Similar dense bands are illustrated in micrographs, but not discussed, in *M. javanica* larvae (4), *Pratylenchus penetrans* Cobb (13), *Tylenchorhynchus dubius* Bütschli (12), and *Hemicycliophora arenaria* Raski (26, 27). *Ditylenchus dipsaci* Kühn may also have thin, dense lines, although neither they, nor Z bands, are mentioned (41). The presence of Z bands has been suggested for *T. dubius,* although micrographs showing such bands were not published (12). Since Z bands occur in certain other species outside the Tylenchida that have platymyarian muscles (18, 24), additional investigations may confirm their presence in Tylenchida.

The role of the thin, dense bands, and related sarcoplasmic reticulum is not understood, although a function related to the distribution of materials throughout the contractile region is conceivable. Furthermore, materials may be more easily transported across the sarcolemma underlying the base of the dense line, since unlike the I band it is not separated from the basal lamina by a thick, perhaps impermeable, hemidesmosome. Cross bridges, described in the H band of *H. glycines*

and *M. incognita*, have been noted in animal parasites (29, 32).

The sarcoplasmic portion of the muscle, with its store of β-glycogen and numerous mitochondria, is known to provide a source of energy through respiration for muscular contraction. The amount of organelles and glycogen is variable among muscle cells and individuals; starved nematodes have fewer mitochondria and are depleted of glycogen. The innervation process, which extends from the sarcoplasmic body, is considerably more simple in males of *M. incognita* and *H. glycines* than that of animal parasites (22, 31, 33) in that it appears to directly fuse with the nerve, without complex finger-like process, or a neuromuscular gap. Further investigations are needed to clarify this relationship in the Tylenchida.

Additional comparative work on the body walls of other Tylenchida may also suggest possible trends of cuticle, hypodermal and somatic muscle development, and thus elucidate the phylogeny of the order.

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