Host Response to *Meloidodera* spp. (Heteroderidae)

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Abstract: Host responses to *Meloidodera floridensis* Chitwood et al., 1956, *M. charis* Hooper, 1960, and *M. belli* Wouts, 1973 were examined on loblolly pine, peony, and sage, respectively, with light, scanning, and transmission electron microscopy. In each case the nematodes induce a single uninucleate giant cell. The giant cell is initiated in the pericycle and expands as it matures. The mature giant cell induced by *M. floridensis* is surrounded by vascular parenchyma, whereas that caused by *M. charis* and *M. belli* contacts xylem and phloem. The cell wall of giant cells induced by all three *Meloidodera* spp. is generally thicker than that of surrounding cells, with the thickest part adjacent to the lip region of the nematode. The thinner portion of the wall includes numerous pit fields with plasmodesmata, but wall ingrowths were not detected in a thorough examination of the entire wall. The nucleus of a giant cell induced by *M. floridensis* is highly irregular in shape with deep invaginations, whereas those caused by *M. charis* and *M. belli* include a cluster of apparently interconnected nuclear units. Organelles, including mitochondria, endoplasmic reticulum, and plastids of giant cells caused by *Meloidodera*, are typical of those reported in host responses of other Heteroderidae. The formation of a single uninucleate giant cell by *Meloidodera, Cryphodera, Hylonema,* and *Sarisodera,* but a syncytium by *Atalodera* and *Heterodera sensu lato,* might be considered in conjunction with additional characters to determine the most parsimonious pattern of phylogeny of Heteroderidae. *Key words:* callose, giant cell, Heteroderoidae, histopathology, plasmodesmata, wall ingrowths.
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Heteroderidae differ among genera in the type of host responses they induce. For example, species of *Heterodera sensu lato* and *Atalodera* induce syncytia (4,14, 15,16,19,20), whereas *Sarisodera hydrophila* Wouts and Sher, 1971 and *Hylonema ivorense* Taylor et al., 1978 induce a single uninucleate giant cell (21,24). Host responses of some genera of the Heteroderidae, including some species of *Meloidodera,* have not been described.

Meloidodera spp. have been associated with several species of cultivated and noncultivated plants (6,12). Comparable detailed studies of host responses, including transmission (TEM) and scanning (SEM) electron microscopy have not been reported, although limited light microscopy (LM) of a few hosts is available (12,23). The need for further work on *Meloidodera*

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host responses has been emphasized previously (10,14,21).

The present study gives a more complete description of the host response induced by *Meloidodera floridensis* Chitwood et al., 1956 and compares it to that induced by *M. charis* Hopper, 1960 and *M. belli* Wouts, 1973.

MATERIALS AND METHODS

A culture of *M. floridensis* on loblolly pine (*Pinus taeda* L.) was obtained from North Carolina. Roots of peony (*Paeonia californica* Nutt.) infected with *M. charis* were collected at Badger Canyon, San Bernardino, California. Limited material of sage (*Artemisia tridentata* Nutt.) infected with *M. belli* was collected at the type locality, German Flats, near Salina, Utah.

Root pieces were processed for histological examination, and examination was with bright field and Nomarski interference LM as well as SEM and TEM. Generally, specimens were prepared as previously reported (21).

LM: Infected roots were fixed in glutaraldehyde, embedded in Paraplast Plus, sectioned at 8 μm, and stained with safranin and fast green (21). For Nomarski interference LM, roots were embedded in Spurr's resin and sectioned at 2 μm. Some resin embedded sections were slightly stained with toluidine blue; others were stained with methylene blue and azure II, specifically for detection of wall ingrowths with bright field LM (8).

SEM: Root segments (about 3 mm long) infected with *M. charis* and *M. belli* were fixed in glutaraldehyde. Some segments were cut to expose infected tissue, and the cytoplasm digested (21); all were postfixed in osmium tetroxide (OsO_4), critical point dried, and examined as previously reported (21). However, root segments of pine, the host of *M. floridensis*, contained resins which interfered with observation of the cell wall surface when prepared as above. The technique was modified as follows: Samples were cut in 50% ethanol, transferred to 95% ethanol for 10 min, and cleaned with a small brush prior to fixation. Fixation, cytoplasm digestion, and critical point drying were completed as above.

TEM: Root segments infected with *M. floridensis* and *M. charis* were fixed in glutaraldehyde, postfixed in osmium tetroxide, embedded in Spurr's resin, sectioned, stained, and examined as previously reported (21). Since only limited material infected by *M. belli* was available, tissue was not processed for TEM.

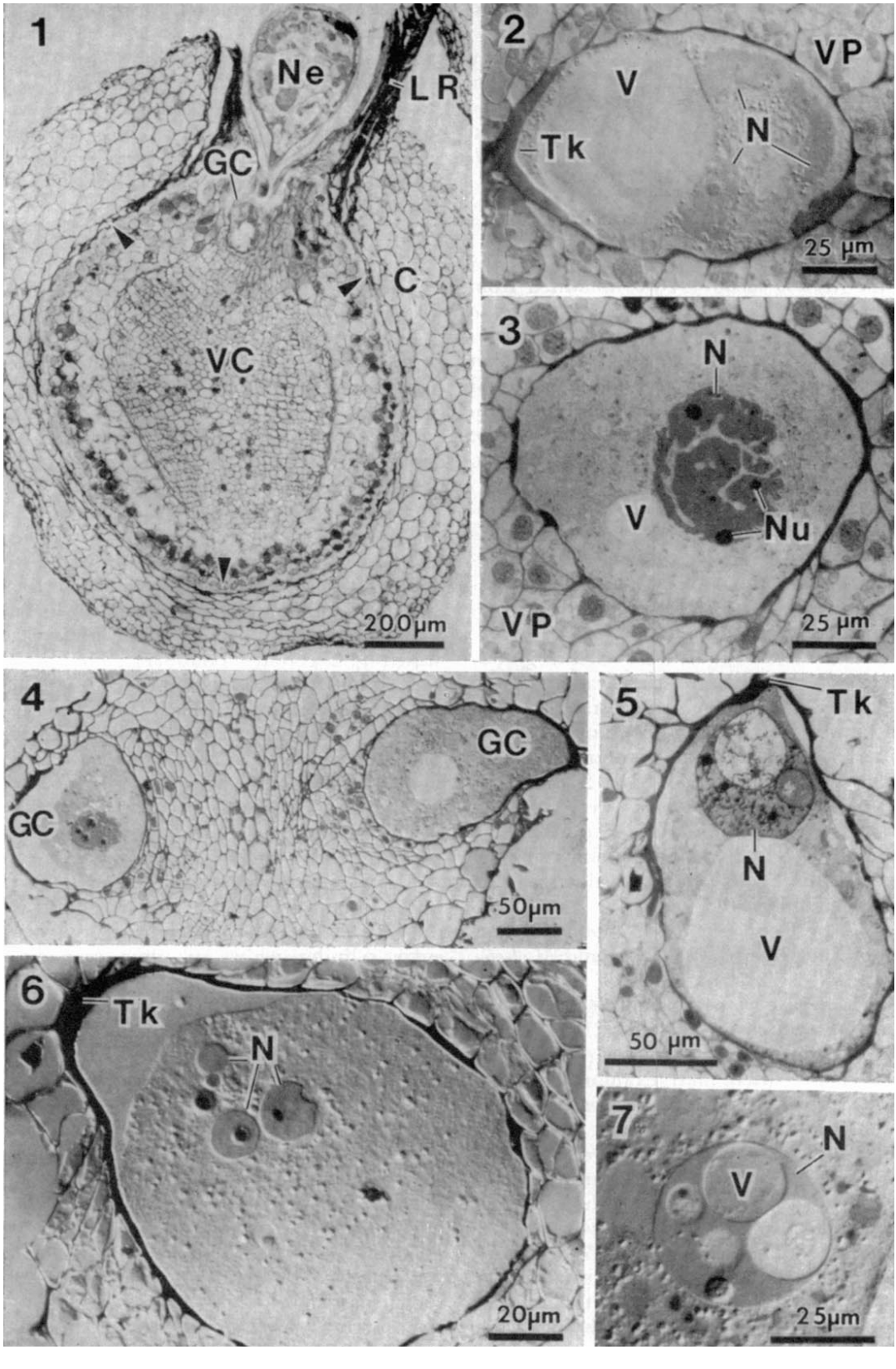
RESULTS

Meloidodera floridensis, M. charis, and *M. belli* induce a single giant cell in loblolly pine, peony, and sage, respectively. Although giant cells induced by the three species resemble each other in many respects, morphological variations occur.

No external symptoms such as galls or lesions were visible on infected roots, but females were partially or totally embedded in root tissues (Figs. 1,13,15,17). *Meloidodera floridensis* initiates the giant cell in the pericycle of pine, and it is restricted to the inner periphery of the vascular cylinder (Fig. 1). The vascular cylinder can be identified by the position of the pericycle, which is the outer boundary. The pericycle is located by its relationship to lateral roots which originate from it (Fig. 1). The giant cell remains surrounded by vascular parenchyma cells, which are continuous with those of the pericycle (Figs. 2,3). Hyperplasia commonly occurs in cells adjacent to the giant cells; however, no hypertrophy or necrosis was observed.

Meloidodera charis and *M. belli* also initiate giant cells in the pericycle, but as the cells enlarge they extend into the vascular cylinder which in some cases becomes greatly distorted (Figs. 13,17). The mature giant cell directly contacts xylem and phloem which are the major components of the vascular cylinder (Figs. 12,13, 17). We observed one exception in which the giant cell partially extended from the pericycle into the cortex. Both hyperplasia and hypertrophy of the adjacent tissues may occur (Figs. 4,17) Secondary invasion by fungi sometimes occurs in giant cells and surrounding tissues.

Giant cells induced by *Meloidodera* spp. vary in shape and size depending on the nematode and host species as well as stage of root development at the time of infection. Generally, giant cells vary from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5
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7
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70 to 180 μm wide and 135 to 520 μm long, but those caused by *M. belli* may be as long as 650 μm (Fig. 12). Apparently only one female is associated with a single giant cell, although several adjacent females may induce several giant cells in close proximity (Fig. 4).

Giant cells induced by the three *Meloidodera* spp. are similar in cell wall morphology but differ in the structure of nuclei. The cell wall is generally thicker than that of surrounding cells, with the thickest region adjacent to the lip region of the nematode (Figs. 2,5,6). The thinner part of the cell wall has a high frequency of pit fields with numerous plasmodesmata, particularly in regions where the giant cell is adjacent to vascular tissue in roots infected by *M. charis* and *M. belli* (Figs. 16,18,19,20,29,30). Pit fields with plasmodesmata also occur in giant cells caused by *M. floridensis* (Figs. 19,20,23), and a callose-like material frequently occurs in conjunction with pit fields (Fig. 22). Detailed examination of cell walls of giant cells induced by *Meloidodera* spp. indicated no wall ingrowths or protuberances adjacent to vascular elements.

The morphology of nuclei differs among giant cells induced by the three *Meloidodera* spp. Nuclei in giant cells caused by *M. floridensis* are highly irregular in shape and include deep invaginations (Figs. 3,20,21) which are best elucidated by serial sections. Thus, isolated sections sometimes give the impression of a multinucleate condition because, in a given plane, some lobes appear to be separated (Fig. 2). In addition, in some planes of sectioning, portions of cytoplasm are completely surrounded by nuclear material (Fig. 21). The nucleus includes a variable number of nucleoli (Figs. 3,20). Generally the nucleus of a giant cell is about five times larger than nuclei in adjacent cells (Fig. 20); no mitotic activity was observed in the giant cell.

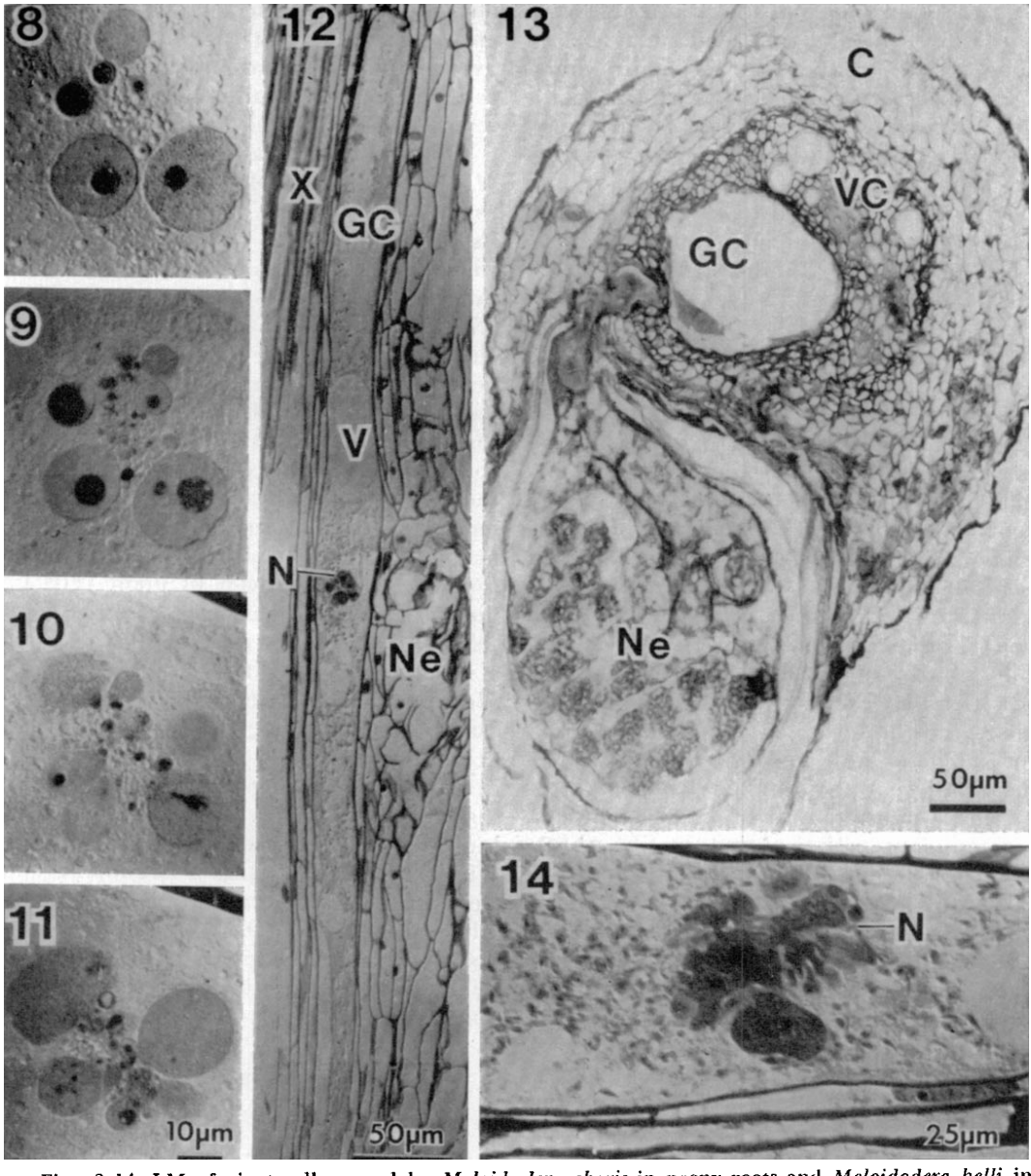
The nucleus of a giant cell caused by *M. charis* is morphologically distinct from that induced by *M. floridensis*. Early in its development, the nucleus enlarges; it is roughly spherical and includes a variable number of vacuoles and nucleoli (Figs. 5,7,26). However, a mature giant cell includes a cluster of apparently interconnected nuclear units, as viewed in serial sections (Figs. 8,9,10,11), and occasionally the nuclear membrane appears to be discontinuous. In some cases invaginations of the nuclear membrane occur which resemble invaginations observed in plasmalemmas associated with pinocytosis (Figs.27,28). The nuclei of giant cells induced by *M. belli* resemble those of giant cells caused by *M. charis* (Fig. 14).

Organelles of giant cells caused by *Meloidodera* spp. are typical of those induced by other Heteroderidae. Mitochondria are numerous, hypertrophied, and hetermorphic varying from elongate to cup shaped (Figs. 24,31). Endoplasmic reticulum (Fig. 25) and vacuoles of variable size (Fig. 20) are particularly abundant, and free membranes in the cytoplasm are usually present (Fig. 29). Plastids and lipid bodies were observed in giant cells induced by *M. charis* but not in those caused by *M. floridensis* (Fig. 32).

DISCUSSION

Meloidodera spp. induce cells in host tissue which resemble the single uninucleate giant cells caused by *H. ivorense* (24),

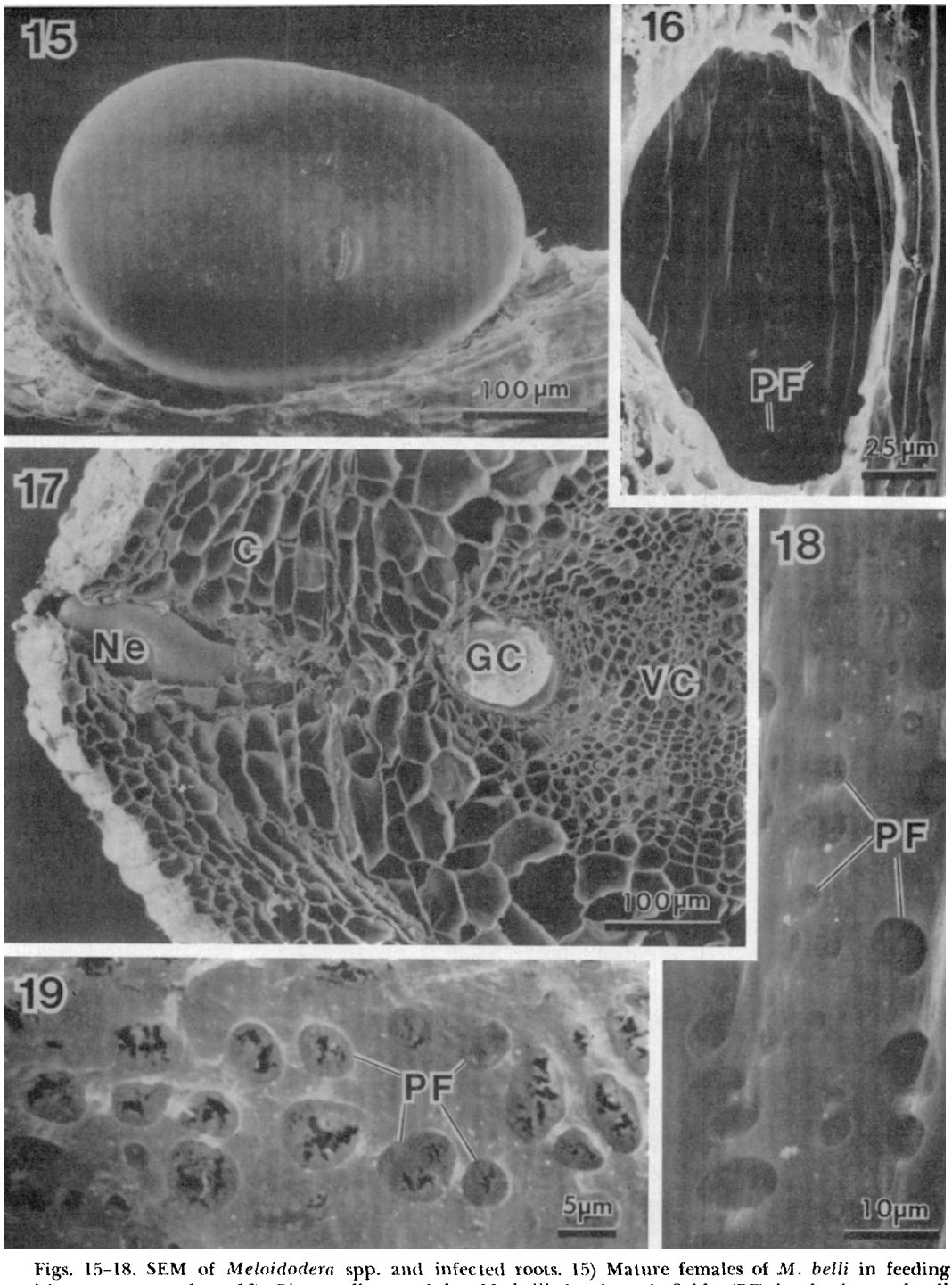
Figs. 1–7. LM cross sections of giant cells caused by *Meloidodera floridensis* and *Meloidodera charis* (Nomarski optics unless indicated). 1) *M. floridensis* embedded in root of pine (bright field). Arrows indicate position of pericycle. C = cortex, GC = giant cell, LR = lateral root, Ne = nematodes, VC = vascular cylinder. 2) Giant cell induced by *M. floridensis* surrounded by vascular parenchyma (VP). The thick cell wall (Tk) is adjacent to the feeding position of the nematode. N = nucleus, V = vacuole. 3) Giant cell caused by *M. floridensis* showing the invaginated nucleus (N), in contrast to nuclei of adjacent vascular parenchyma cells (VP). Nu = nucleoli, V = vacuole. 4) Adjacent giant cells (GC) induced by two individuals of *M. charis*. Note cell hyperplasia in surrounding protoxylem and protophloem. 5) Giant cell of *M. charis* in an intermediate stage of development with thick cell wall (Tk) adjacent to nematode lip region. N = nucleus, V = vacuole. 6) Giant cell induced by *M. charis* in advanced stage of development. Thick cell wall (Tk) occurs adjacent to nematode lip region. Nucleus (N) composed of cluster of nuclear units. 7) Nucleus of a giant cell induced by *M. charis* in an early stage of development showing vacuoles (V).



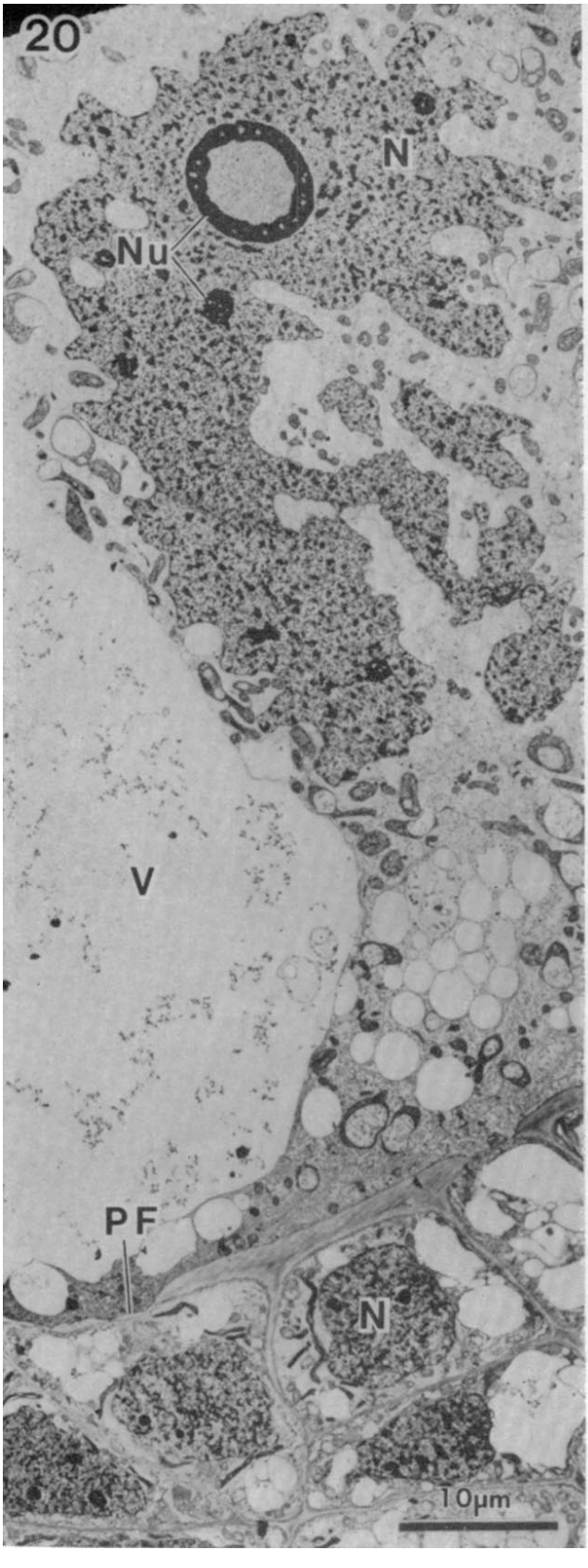
Figs. 8–14. LM of giant cells caused by *Meloidodera charis* in peony roots and *Meloidodera belli* in sage roots (Nomarski optics unless indicated). 8–11) Sequential sections through nucleus of a mature giant cell induced by *M. charis* showing cluster of apparently interconnected nuclear units. 12) Longitudinal section of a giant cell (GC) caused by *M. belli* (bright field) showing original position of head of nematode (Ne) (dislocated in preparation) and adjacent xylem (X). N = nucleus, V = vacuole. 13) Cross section of a root with partially embedded *M. charis* female (Ne) in a feeding position (bright field). Giant cell (GC) is located adjacent to xylem and phloem within the vascular cylinder (VC). C = cortex. 14) Longitudinal section of a giant cell induced by *M. belli;* giant cell includes nucleus (N) composed of interconnected nuclear units.

S. hydrophila (21), and the nonheteroderid, *Rotylenchulus macrodoratus* (3). Furthermore, preliminary observations indicate a similar host response to *Cryphodera utahensis* Baldwin et al., 1983 (Mundo-Ocampo and Baldwin, unpublished observations). A single uninucleate giant cell previously was considered to be unusual (3,24), but more recently it has been shown to be commonly induced by Heteroderoidea (21).

The basic host response to infection



Figs. 15–18. SEM of *Meloidodera* spp. and infected roots. 15) Mature females of *M. belli* in feeding position at root surface. 16) Giant cell caused by *M. belli* showing pit fields (PF) in the internal cell wall surface (cytoplasm digested). 17) Young female of *M. charis* (Ne) fully embedded in root. Giant cell (GC) occurs adjacent to xylem and phloem within vascular cylinder (VC). Note hyperplasia and hypertrophy of adjacent tissues. C = cortex. 18) Enlargement from Fig. 16 showing numerous pit fields (PF) in the internal cell wall. 19) Pit fields (PF) on the internal cell wall of a giant cell induced by *M. floridensis*.


20
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Nu
V
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N
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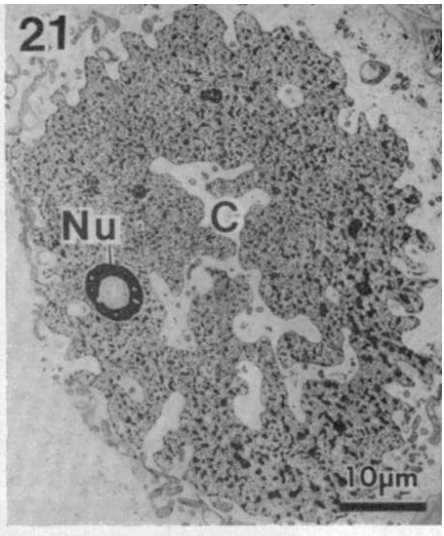
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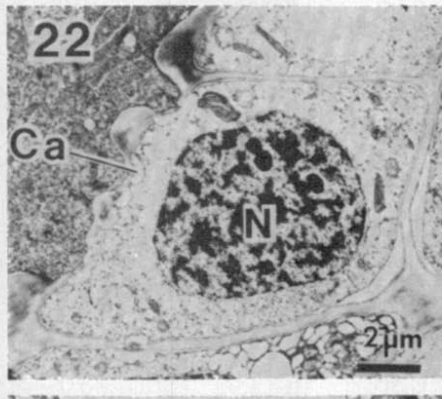
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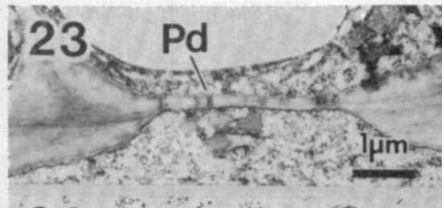
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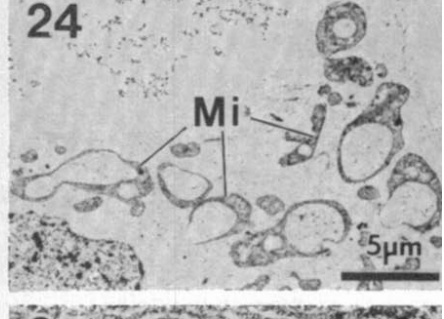
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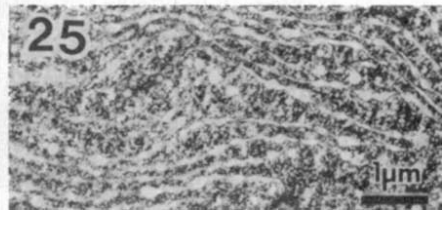
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by *Meloidodera* spp. was consistent among pine, peony, and sage, but the host range of this genus may be large (6,12), indicating a need for analysis of responses in additional plant species. Preliminary reports of *M. charis* on ridgeseed euphorbia and okra describe the response as "uninucleate giant cells" (12), although illustrations have not been published. Information on the number of giant cells caused per nematode and their internal morphology was not previously described for *M. floridensis;* however, photographs suggest a single giant cell (23).

Ruehle (23) reported that giant cells induced by *M. floridensis* ". . . developed in the region of cortex not infected with mycorrhizal fungi, in protophloem and in protoxylem in both slash and loblolly pine roots." In addition, a giant cell was illustrated and surrounding tissue labeled cortex. Different authors have since considered the giant cell induced by this nematode to be distinctive among heteroderids in that it occurs in the "cortex" (10,14,15). However, our observations indicate that the giant cell is initiated in the pericycle as in those formed by other *Meloidodera* spp. The pericycle is identified by its relationship to lateral root initials (5). Parenchyma cells surrounding the giant cell induced by *M. floridensis* are within the vascular cylinder and are thus vascular parenchyma. We suggest that cells surrounding the giant cell as illustrated by Ruehle (23) are mislabled "cortex."

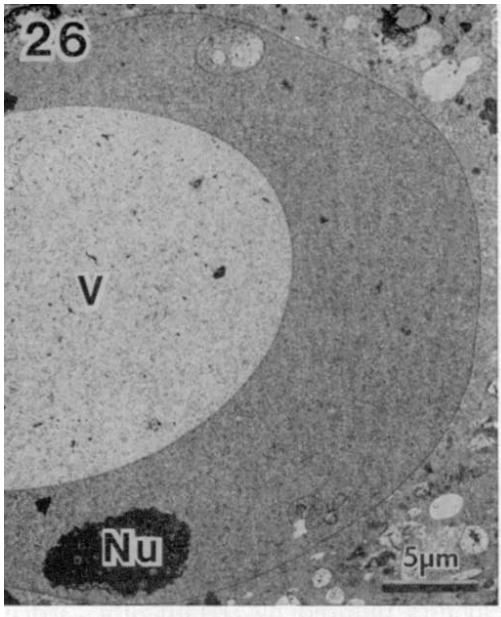
The walls of giant cells induced by *Meloidodera* spp., like those caused by *S. hydrophila* and *Atalodera* spp. (20,21), are thickened in the region adjacent to the nematode lip region, which may be in response to stylet penetration (21). The degree of thickening is greater in giant cells induced by *M. floridensis* than in *M. charis* or *M. belli* and most nearly resembles that associated with *S. hydrophila.*

One of the most significant features of giant cells induced by *Meloidodera* spp. is the apparent absence of cell wall ingrowths. Wall ingrowths increase surface area of the plasmalemma and characterize "transfer cells" which reportedly play a role in short-distance transport of solutes (11). The ingrowths are usually located in portions of the walls of some nematode-induced syncytia or giant cells which are adjacent to xylem and phloem elements (10,14,15,16). Wall ingrowths are particularly evident in host responses to species of *Heterodera sensu lato, Meloidogyne,* and *Rotylenchulus macrodoratus* (10,14, 16). Their presence together with modified nuclei, distinct vacuoles, and increased numbers of mitochondria and Golgi, led Jones and Dropkin to consider them "exaggerated multinucleate transfer cells" (14, 16).

Wall ingrowths do not occur in host responses induced by certain other sedentary nematodes such as *Rotylenchulus reniformis* (2,16,22) and *Nacobbus* spp. (17), nor were they observed associated with *S. hydrophila* or *Atalodera* spp. (20,21). Despite predictions of their presence in giant cells caused by *Meloidodera* spp. (14), our observations did not support this hypothesis. We conclude that wall ingrowths are absent in giant cells induced by *Meloidodera* spp. Serial sections stained with fast green, methylene blue, azure II, and toluidine blue have been previously used to observe cell wall ingrowths (3,8,11,18). Furthermore, we did not detect ingrowths with SEM or TEM, although walls adjacent to vascular tissue were thoroughly examined.

Although wall ingrowths are absent in giant cells induced by *Meloidodera,* transfer of solutes may occur through abundant plasmodesmata, as proposed for other sedentary Tylenchida (14,15,17,20,21). These plasmodesmata are concentrated in pit fields which occur in the thin part of the giant cell wall adjacent to vascular parenchyma. The plasmodesmata in giant cells caused by *M. floridensis* are frequently associated with an accumulation of an

Figs. 20–25. TEM cross sections of giant cells induced by *Meloidodera floridensis* in pine roots. 20) Large invaginated nucleus (N) of giant cell and smaller nucleus (N) of adjacent vascular parenchyma cell. Cell wall with pit fields (PF). 21) Nucleus enclosing areas of cytoplasm (C) in deep invaginations. Nu = nucleolus. 22) Pit field showing accumulation of callose. N = nucleus of adjacent vascular parenchyma cell. 23) Pit field with faint indication of plasmodesmata (Pd). 24) Distorted mitochondria (Mi). 25) Endoplasmic reticulum.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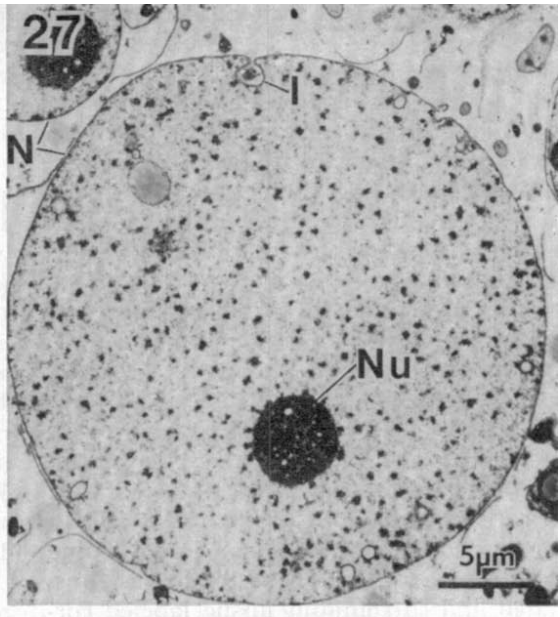
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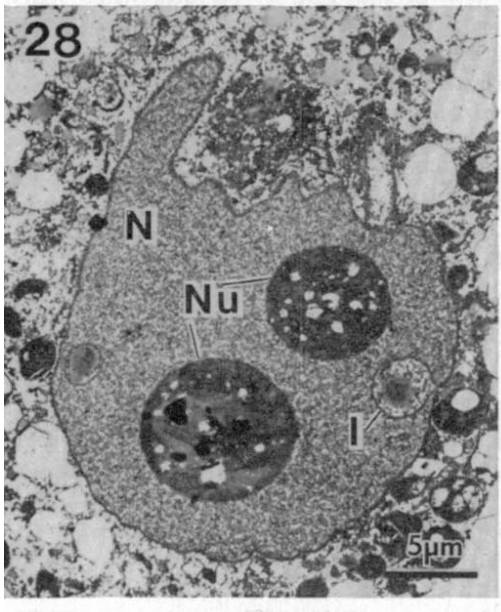
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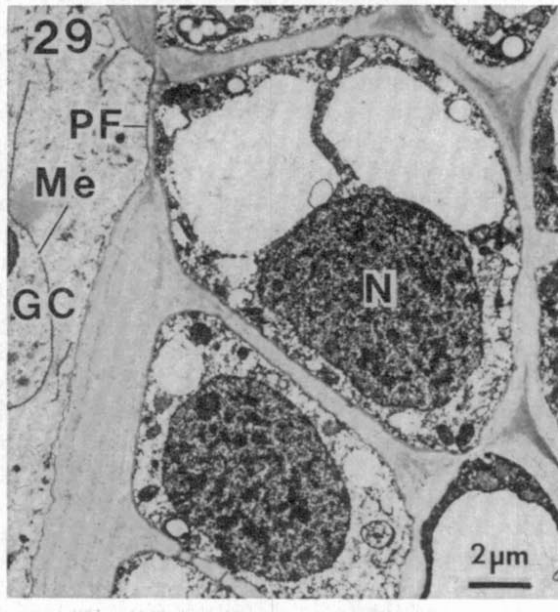
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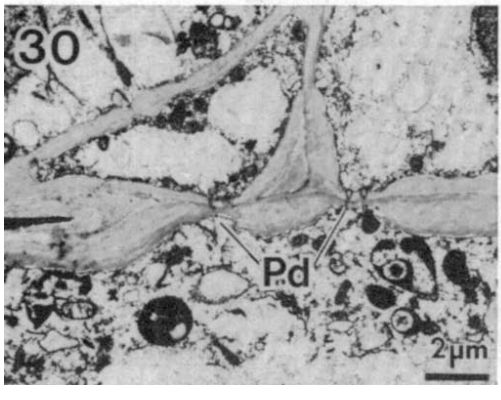
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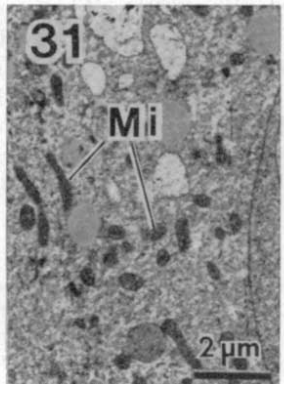
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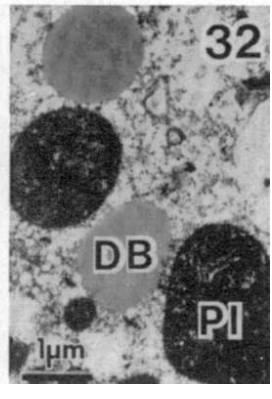
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electron-lucent material, presumed to be callose and similar to that observed in syncytia induced by *Nacobbus aberrans* (17). Jones and Payne (17) suggested that this callose accumulation is a plant defense response which protects plasmodesmata during cell wall dissolution; however, wall dissolution does not occur in giant cells associated with *M. floridensis*. Hughes and Gunning (13) note that aldehyde fixatives may induce a wound reaction in some tissues, including callose accumulation at plasmodesmata. This might explain our observation of callose accumulation in giant cells caused by *M. floridensis*.

The large, deep invaginations of the nucleus in giant cells induced by *M. floridensis* result in an immense surface area of the nuclear membrane facilitating exchange between the nucleus and cytoplasm, which may indicate a high rate of metabolism in the giant cell (14). The cluster of apparently interconnected nuclear units in giant cells induced by *M. charis* also results in a larger nucleus-cytoplasm interface than if the nuclear material was concentrated in a single sphere. Presence of nucleoplasm extending free into the cytoplasm with a discontinuous nuclear membrane suggests burst nuclei. It was not determined if this phenomena is part of the morphogenesis of these affected nuclei, or if it was an artifact of material preparation. However, the nuclear membrane of giant cells caused by *M. floridensis* prepared under identical conditions was consistently intact.

Other organelles in giant cells induced by *Meloidodera* spp., including heteromorphic mitochondria, endoplasmic reticulum, and free membranes, are abundant, as previously reported in other host responses (14,15,20,21).

Meloidodera has been considered distinctive among Heteroderidae because of the primitive expression of most of its characters, including the subequatorial vulva, striated cuticle in females, and absence of a cyst (9). It has also been described as a "link" between *Meloidogyne* (root-knot nematodes) and *Heterodera sensu lato* (cyst nematodes) (1). Chitwood et al. (1) and Wouts (26) suggested that other subfamilies of Heteroderidae evolved from Meloidoderinae (i.e., Meloidoderinae in the sense that includes *Meloidodera* and *Cryphodera*). More recently, *Verutus* Esser, 1981, which has primitive characters similar to genera in the Meloidoderinae, has been described (7). However preliminary observations of plant roots infected by *Cryphodera* indicate that it induces a single giant cell similar to that of *Meloidodera*, whereas *Verutus* induces a syncytium-like plant response (Mundo-Ocampo and Baldwin, unpublished observations).

The pattern of responses of plant hosts to infection by *Meloidodera* spp., as well as responses to nematodes of other Heteroderidae (20,21), is a parameter which can be used in interpreting phylogeny of the family. However, the character "host response" cannot be used independently; rather it must be considered in combination with the wide range of additional available characters to determine the most parsimonious (*sensu* Wiley [25]) pattern of phylogeny of Heteroderidae.

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Figs. 26–32. TEM of giant cells caused by *Meloidodera charis* in peony roots. (26) Portion of nucleus in early developmental stage showing vacuole (V) and nucleolus (Nu). 27) Two adjacent nuclear units (N). Note invaginations (I) of the nuclear membrane. Nu = nucleolus. 28) Slightly lobed nucleus (N) with nucleoli (Nu). I = invagination. 29) Pit field (PF) of giant cell (GC) and adjacent vascular parenchyma cells. Note free membranes (Me) fragmented in cytoplasm. N = nucleus. 30) Pit field showing plasmodesmata (Pd). 31) Mitochondria (Mi). 32) Plastids (Pl) and densely stained lipid bodies (DB).

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