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Ultrastructure of root cortical cells parasitized by the ring nematode *Criconemella xenoplax*

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Summary. Individuals of the plant-parasitic nematode *Criconemella xenoplax*, monoxenically cultured on root explants of clover, carnation, and tomato, fed continuously for up to 8 days from single cells in the outer root cortex. Individual cortical cells parasitized by nematodes were modified into discrete "food cells" in all hosts examined. The nematode's stylet penetrated between epidermal cells and frequently through a subepidermal cortical cell. Electron-transparent callose-like material continuous with the cell wall enveloped the portion of the stylet that traversed subepidermal cortical cells. Food cells were typically located in the first or second cell layers of the cortex. The stylet penetrated 5–6 μm through the wall of the food cell without penetrating the plasma membrane. Electron-transparent callose-like deposits formed between the invaginated plasma membrane and stylet, except at its aperture. The plasma membrane of the food cell was appressed tightly to the wall of the stylet aperture creating a 130–160 nm hole in the membrane. This opening provided continuity between the lumen of the stylet and the food cell cytosol for ingestion of nutrients by the nematode. Ribosomes were dissociated from the cisternae of the endoplasmic reticulum in food cells and accumulated with other cell organelles in a zone of modified cytoplasm around the stylet. A fibrillar material appeared to form a barrier in the cytosol around the stylet aperture that limited movement of cell organelles toward the aperture. Electron-dense secretory components were secreted into the food cell by the nematode. Clusters of putative nematode secretory components consisting of 20–40 nm diameter, electron-dense particles were dispersed in the densely particulate zone of cytoplasm around the stylet tip. The cytosol immediately around the stylet aperture in the center of the modified cytoplasm was finely granular.

Plasmodesmata connecting the cytoplasm of the food cell with the cytoplasm of neighboring cells were greatly modified in a way that could facilitate solute transport into the food cell. The plasma membrane-lined canals of the modified plasmodesmata appeared to be increased in diameter and lacked desmotubules. Additionally, they frequently were lengthened by electron-transparent callose-like deposits projecting from the wall into the cytoplasm of the food cell. An electron-dense "cap" that formed an apparent tight seal with the plasma membrane developed over the entrance of each modified plasmodesma in the neighboring cells. These caps excluded all cell organelles from the cytosol contained within them. The nucleus of the food cell was usually enlarged and atypically shaped with dense peripheral clumps of condensed chromatin. Our results show that *C. xenoplax* induces elaborate cellular modifications in host tissue to support sustained ingestion of nutrients from a single food cell.

Keywords: Ectoparasite; Feeding site; Host–parasite interface; Monoxenic culture; Plant-parasitic nematode; Plasmodesmata; Symplastic transport; Transmission electron microscopy.

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Introduction

Plant cells parasitized by different nematode species are modified in diverse ways. Cellular changes due to nematode parasitism have been categorized as either destructive or adaptive cell modifications (Dropkin 1969). Destructive cellular changes range from limited removal of cell contents by feeding nematodes to complete destruction of cells. In contrast, adaptive cellular changes result in the formation of discrete feeding sites. These feeding sites result from nematode secretions modifying and regulating cell function and metabolism (Hussey 1989). The type of plant cellular modification elicited by nematodes is not specific to an ecto- or endoparasitic feeding habit.

Ring nematodes belonging to the genus *Criconemella* feed on roots primarily as ectoparasites, although the anterior ends of these nematodes have been observed embedded in ruptured cortical tissue (Streu et al. 1961). These nematodes are considered to induce destructive cellular changes by completely removing contents of

roots cells (Dropkin 1979). In the only histopathology study of roots parasitized by *Criconemella* species, Streu et al. (1961) showed with light microscopy that deeply stained granular cytoplasm aggregated around the nematode's stylet in parasitized cortical cells. In another study, individuals of *C. xenoplax* were observed to feed at one site for up to 18 h (Thomas 1959). Root explant cultures of plant-parasitic nematodes are particularly useful for studying the changes in plant cells parasitized by nematodes. Recently, *C. xenoplax* was established on root explants of several plant species (Westcott 1990). In these cultures, individuals of *C. xenoplax* were observed to feed continuously with uninterrupted pumping of the metacorpus for several days from a single cell in the outer root cortex. Since detailed information on the ultrastructure of cells parasitized by *C. xenoplax* is unavailable, the present study was undertaken to determine whether the cellular changes are destructive or adaptive and what modifications, if any, occurred in cells parasitized by this nematode.

Materials and methods

Criconemella xenoplax (Raski) Luc & Raski was monoxenically cultured on root explants of *Trifolium incarnatum* L. Dixie, *Lycopersicon esculentum* Miller Rutgers, and *Dianthus caryophyllus* L. Double Grenadin (Westcott 1990). Root explants were maintained on 1% Bacto agar containing Gamborg's B-5 salts and 20 g/l sucrose (Gamborg et al. 1976).

Adult nematodes feeding on roots were fixed for electron microscopy by flooding the agar of established cultures with 20 ml of a fixative consisting of 2% paraformaldehyde and 2.5% glutaraldehyde in 0.05 M phosphate buffer (pH 7.2). Following incubation in fixative for 20–72 h, cultures were rinsed in the same buffer and root sections with feeding nematodes embedded in the agar were excised. Agar blocks containing the root sections with attached nematodes were transferred to vials containing the phosphate buffer. After three rinses with buffer, specimens were post-fixed 2 h at 4 °C in similarly buffered 1% OsO_4. Specimens were then washed in distilled water, bulk-stained overnight in 0.5% aqueous uranyl acetate, washed in distilled water, dehydrated in an ethanol series to acetone, and infiltrated with Spurr's resin. Specimens were embedded in resin using 60 × 15 mm Lux Contur Permanox disposable tissue culture dishes (Nunc, Inc., Naperville, IL) as embedding molds (Mims et al. 1988). Following polymerization of the plastic, specimens were excised and glued onto specimen stubs so as to yield transverse sections of the root. Serial ultrathin (70–80 nm) sections were cut with a diamond knife, collected on Formvar-coated copper slot grids, stained with aqueous uranyl acetate and lead citrate, and examined using a Zeiss EM 10 A transmission electron microscope.

Results

Specimens of *C. xenoplax* were observed feeding singly or in close proximity to each other anywhere along the length of cultured roots, including the tips. Actively feeding nematodes usually assumed a curved shape (Fig. 1) and fed continuously as an ectoparasite from the same cortical cell for up to 8 days. Cytoplasm of the parasitized cortical cell frequently appeared to aggregate around the stylet tip (Fig. 1 inset). The parasitic behaviour, including extended exploration of root surface, prior to selection of a feeding site by *C. xenoplax* precluded determining precisely how long an individual nematode had been feeding prior to fixation for electron microscopy.

Nematodes established feeding sites in individual cells, hereafter called "food cells", in the first or second layer of the root cortex. The stylet of a feeding nematode penetrated between epidermal cells and frequently through one subepidermal cortical cell to establish a food cell in an adjacent cell (Fig. 2). After the stylet had penetrated root tissue to its final depth, it remained stationary through the remainder of the feeding episode. Electron-transparent callose-like deposits continuous with the cell wall enveloped the stylet where it had traversed the subepidermal cortical cell (Fig. 2).

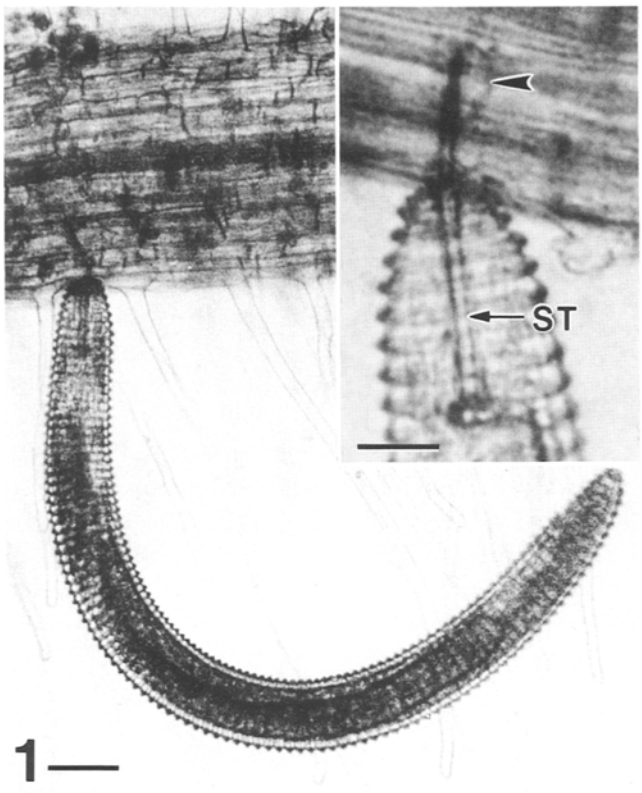
One nematode was fixed while in the process of apparently injecting secretory components through its sty-

Fig. 1. *Criconemella xenoplax* feeding from the cortical tissue of a tomato root explant culture. Bar: 50 µm. **Inset** Higher magnification of a nematode feeding on a carnation root. Cytoplasm (▼) of cortical cell being parasitized is aggregated around the nematode's stylet (*ST*) tip. Bar: 20 µm

Fig. 2. Penetration of a nematode's (*NE*) stylet (*ST*) between two epidermal cells (*EC*) and through a subepidermal cortical cell (*CC*) in a crimson clover root. An adjacent cortical cell formed the food cell at this feeding site. Electron-transparent callose-like (*CA*) material is deposited between the stylet and the plasma membrane (*PM*) of the cortical cell and is continuous (▼) with the cell wall. Bar: 5 µm

Fig. 3. Longitudinal section of a nematode stylet (*ST*) tip penetrating the wall of a cortical cell of a crimson clover root. Electron-dense nematode secretory components (*SC*) apparently are being secreted through the stylet aperture into the cytoplasm adjacent to the central vacuole (*V*) of the cell. Numerous dictyosomes (*D*) are around the stylet tip. Electron-transparent callose-like (*CA*) material continuous with the cell wall (*CW*) is present between the invaginated plasma membrane (▼) and the stylet tip. *M* Mitochondria. Bar: 1 µm

Fig. 4. Higher magnification of stylet (*ST*) tip in Fig. 3. Detailed view of the secretory components (*SC*) present in the stylet lumen (*L*) being secreted through the stylet aperture (*SA*) into the host cell cytoplasm. *ER* Endoplasmic reticulum. Bar: 100 nm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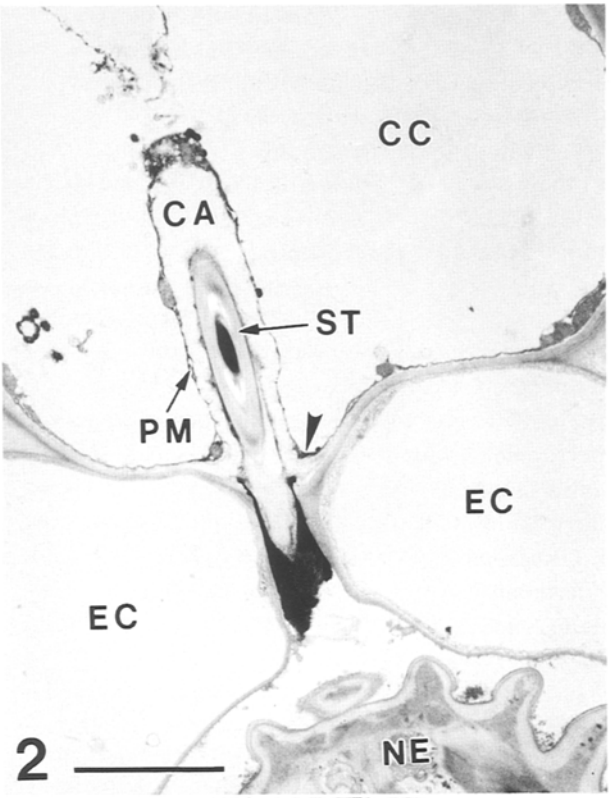
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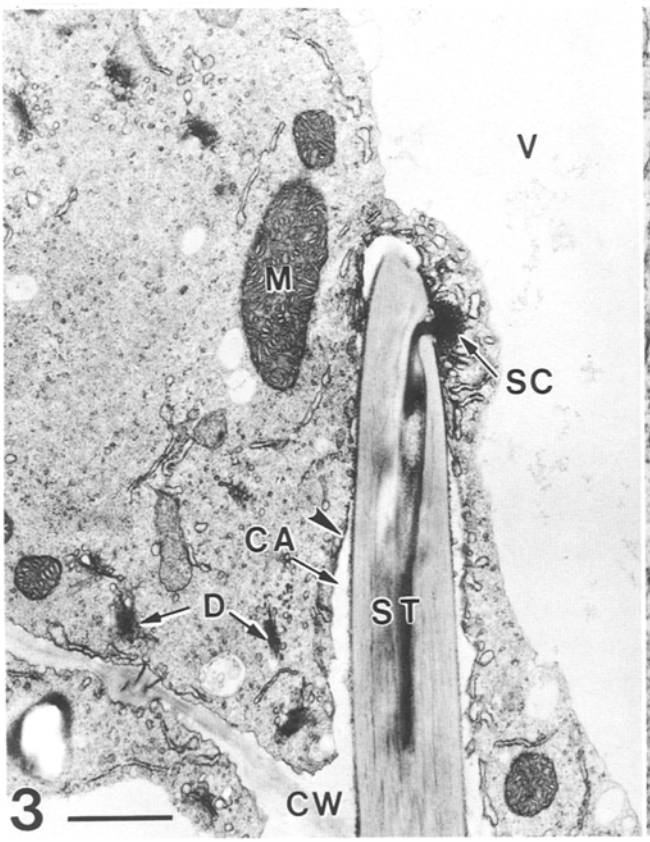
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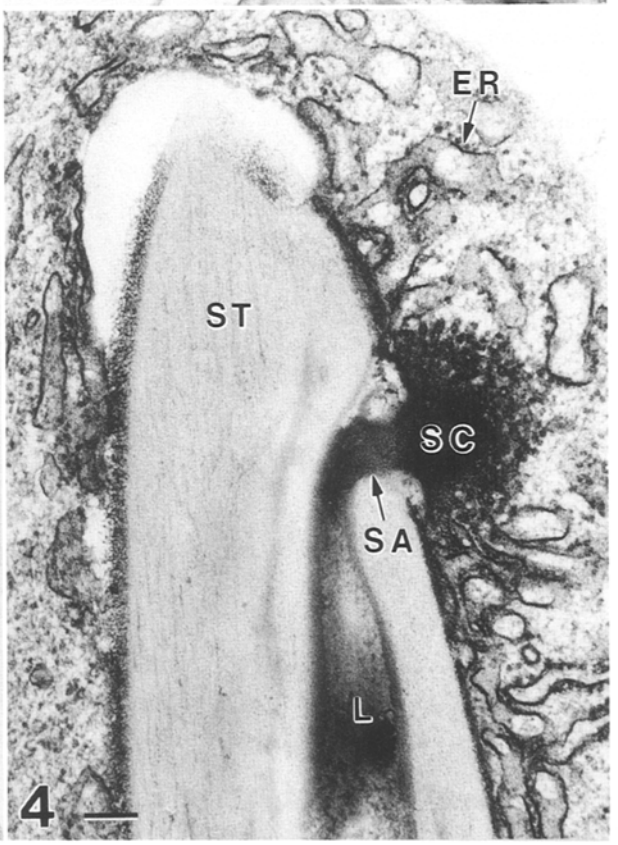
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let into a cortical cell in a clover root. The stylet of this nematode penetrated the wall of the cortical cell and invaginated the plasma membrane a distance of 5.6 μm into the cytoplasmic layer of the cell (Fig. 3). Although the cytoplasm was not greatly modified in this cell, active dictyosomes with hypertrophied cisternae and numerous electron-transparent vesicles associated with the cisternal margins were abundant in the cytoplasm surrounding the stylet. Electron-dense secretory components were apparently being secreted through the stylet aperture directly into the cytosol of the cell (Figs. 3 and 4). The domed shape of the putative secretory material indicates that it was being discharged from the stylet aperture rather than being ingested. Secretory components at the margin of the secreted material and in contact with the cytoplasm of the host cell appeared to separate into discrete particles (Fig. 4). Hypertrophied cisternae of rough endoplasmic reticulum were abundant in the host cell cytoplasm around the secretory components.

Food cells presumably provided nutrients for the nematode and exhibited several characteristic ultrastructural modifications. The stylet tip of a feeding nematode usually was inserted 5–6 μm through the wall of a food cell without penetrating the plasma membrane (Figs. 5 and 6). Analyses of serial sections confirmed that the invaginated plasma membrane was intact completely around the inserted stylet except at its aperture. Electron-transparent callose-like material continuous with the food cell wall was deposited between the invaginated plasma membrane and the stylet, except at the stylet aperture. In mature cortical cells, the cytoplasmic layer around the stylet tip was greatly expanded and modified (Figs. 5 and 6). An outer zone of the cytoplasm around the stylet tip was densely particulate due to the accumulation of free ribosomes and surrounded an inner core of finely granular cytosol (Figs. 6 and 7). Fibrillar material was present at the interface of the outer particulate zone and the less dense inner core (Fig. 7). Several clusters of electron-dense particles (30–40 nm diameter) were dispersed in the modified cytoplasm around the stylet (Figs. 6, 7, and 9). The number of densely stained particles in each cluster was variable. The tonoplast was not visible in some food cells (Fig. 5), but remained intact in others (Fig. 8). Nuclei of food cells were usually enlarged and irregular in shape with peripheral clumps of condensed chromatin (Figs. 5 and 10).

The nematode presumably ingested nutrients from the cytosol of its food cell through the aperture of its stylet. The plasma membrane of the food cell was perforated at the point of its contact with the stylet aperture. In a median section through the aperture, the plasma membrane was tightly appressed to the aperture wall (Fig. 6). This tight association between the plasma membrane and aperture wall created a hole in the membrane that was the width (160 nm) of the stylet aperture (Fig. 6 inset). This opening provided continuity between the lumen of the stylet and the cytosol of the food cell presumably allowing withdrawal of nutrients by the nematode.

In one food cell in a carnation root where the nematode's stylet had been withdrawn, a channel lined with electron-transparent callose-like deposits persisted where the stylet had been inserted (Fig. 8).

Cellular modifications were accentuated in food cells induced near the root tip (Figs. 9–16). Ribosomes dissociated from the endoplasmic reticulum (Figs. 9, 10, 13) and along, with mitochondria, small vacuoles, and the nucleus, accumulated around the inserted stylet

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Fig. 5. Cross-section of a food cell (*FC*) in the cortex of a tomato root. The stylet (*ST*) penetrated between two epidermal cells (*EC*) and was inserted into the food cell without penetrating the plasma membrane (▼). A zone of the cytoplasm of the food cell is modified around the stylet tip. A profile of the cell's nucleus (*N*) is visible. Bar: 5 μm

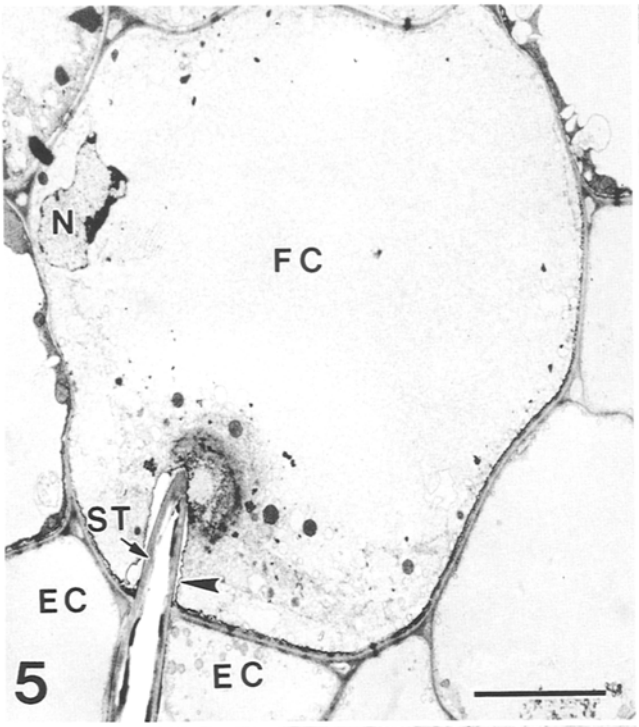
Fig. 6. Detailed view of the modified cytoplasm around the stylet (*ST*) tip. A densely particulate outer zone (*OZ*) of the modified cytoplasm surrounds a finely granular inner core (*IC*). Clusters of electron-dense particles (*EP*) are visible at the periphery of the modified cytoplasm. Electron-transparent callose-like (*CA*) material is deposited between the stylet and the invaginated plasma membrane (*PM*). Bar: 1 μm. **Inset** Higher magnification of the opening created in the plasma membrane when the membrane (arrow) became tightly appressed (▼) to the wall of the stylet aperture. Bar: 200 nm

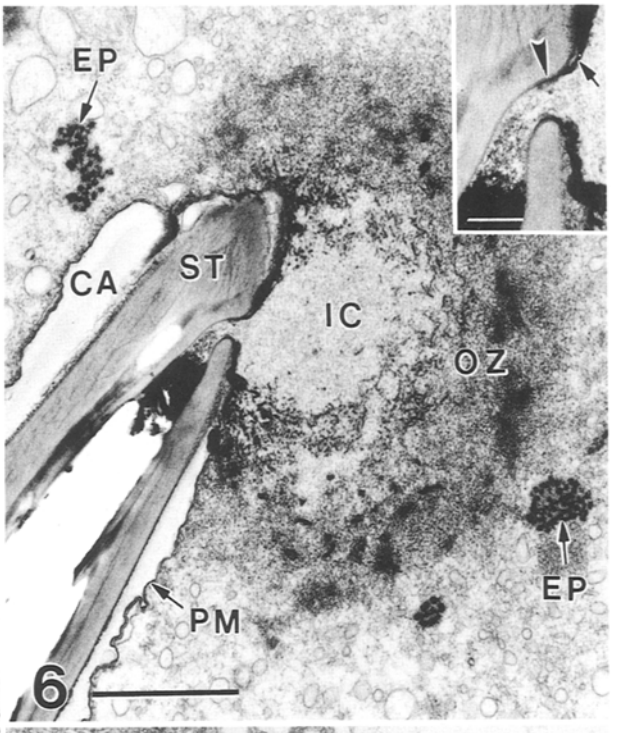
Fig. 7. Higher magnification of the interface of the densely particulate outer zone (*OZ*) and the finely granular inner core (*IC*) of the modified cytoplasm. Fibrillar material (▼) is present at the interface. A section of the electron-transparent callose-like (*CA*) deposits that formed around the stylet tip and a cluster of electron-dense particles (*EP*) are visible. Bar: 0.5 μm

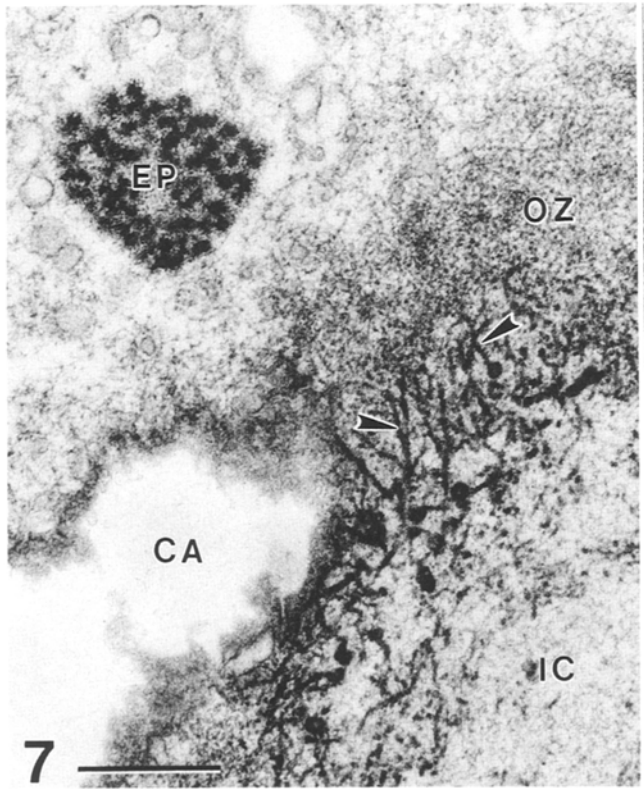
Fig. 8. Electron-transparent callose-like (*CA*) material lines the path where a stylet was withdrawn from a food cell in a carnation root. The cytoplasm is modified (*MC*) where the stylet tip was located. The callose-like material is continuous with the wall (*CW*) of the food cell and projects into the cytoplasm between two vacuoles (*V*). Bar: 1 μm

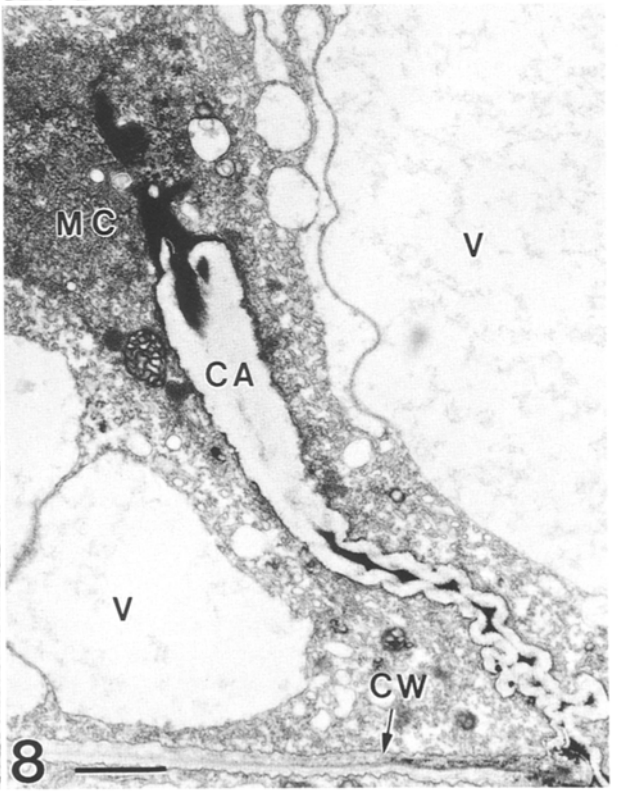
(Fig. 9). The densely particulate nature of the cytoplasm in this modified zone of the cell resulted from the accumulation of free ribosomes, similar to that illustrated in Fig. 7. Cisternae of endoplasmic reticulum outside of this modified zone in food cells lacked ribosomes whereas those in the neighboring cells were studded with ribosomes (Figs. 10 and 13). In a section of a food cell at a different plane than where the stylet was positioned, mitochondria, small vacuoles, and the nucleus were concentrated near the middle of the cell (Fig. 10).

In both tomato and carnation, plasmodesmata con-









necting the cytoplasm of the food cells with the cytoplasm of neighboring cells were greatly modified and differed in ultrastructure from plasmodesmata connecting cells remote from a food cell (Fig. 11). The plasma membrane-lined canals of modified plasmodesmata were enlarged, uniform in diameter throughout, and lacked desmotubules (Fig. 12 and 13). These canals were frequently lengthened by deposition of electron-transparent callose-like material onto the surrounding wall that projected into the cytoplasm of the food cell. Unique, densely stained structures (Figs. 12–15) were present in the cells contacting food cells and were associated with the modified plasmodesmata. These discrete electron-dense structures formed a "cap" over the orifice of each modified plasmodesma in the neighboring cells. These caps seemed to exclude all cell organelles from the finely granular cytosol contained within them and appeared to form tight seals where they contacted the plasma membrane (Fig. 14). At low magnifications, densely stained caps were readily visible along the walls of cells contiguous to food cells (Figs. 9 and 10). In an end-on view of the modified plasmodesmata, the open canals were irregular in shape (Fig. 16).

Discussion

Our ultrastructural study of feeding sites of *C. xenoplax* revealed that this parasitic nematode does not induce destructive cellular changes in host roots as previously thought (Dropkin 1979). By contrast, our results indicate that this ectoparasite has evolved a highly specialized feeding relationship with cells of its hosts. Nematode parasitism leads to elaborate modifications of the symplastic transport pathway between a specialized food cell and neighboring cells. The modified plasmodesmata presumably facilitate movement of solutes into the food cell to support sustained ingestion of nutrients by the nematode. In the absence of these elaborate cellular modifications, prolonged feeding from a single cell by *C. xenoplax* would presumably result in collapse and death of the parasitized cell.

Several of the cytoplasmic modifications of the specialized food cell appear to result from the feeding activity of the nematode. The movement of cell organelles to a zone of the cytoplasm around the stylet tip, particularly in food cells formed near the root tip, may be the consequence of the continuous withdrawal of nutrients from the cell by the uninterrupted feeding of the nematode. The dissociation of ribosomes from cisternae of the endoplasmic reticulum might occur from changes in ionic conditions in the cytosol of the food cell. Elevated salt concentrations are known to release ribosomes from membranes (Adelman et al. 1973). Whether this rearrangement of cell organelles and dissociation of ribosomes from the endoplasmic reticulum adversely affects the metabolism of the food cell and ultimately the cell's capacity to provide nutrients to the nematode is unknown. In contrast, the specialized feeding sites induced by sedentary endoparasitic nematodes are characterized by increased numbers of cytoplasmic components and reduction of the central vacuole to small vacuoles, resulting in protoplasts with high rates of metabolism (Jones 1981).

Invagination of the plant host cell plasma membrane when a nematode's stylet penetrates the cell wall has

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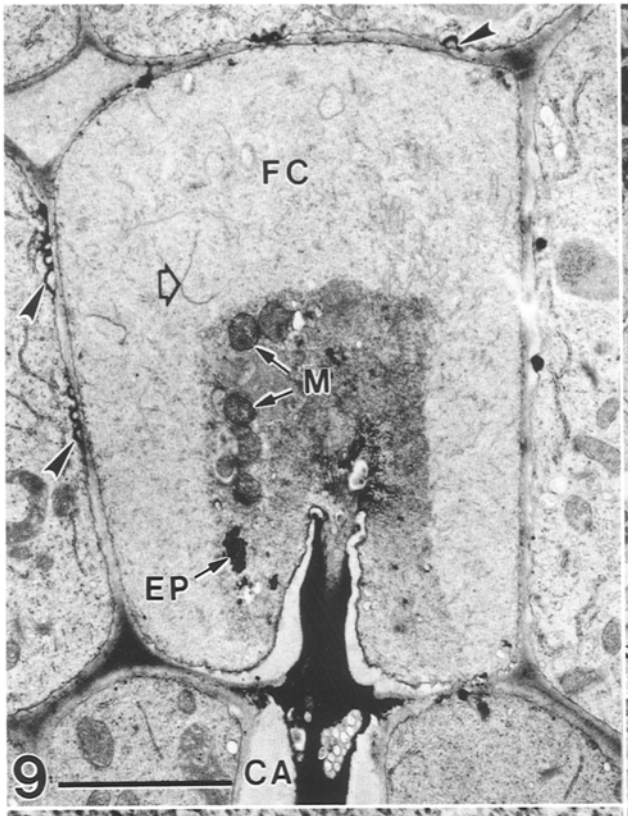
Fig. 9. Low magnification view of a food cell (*FC*) formed in a carnation root tip. All large cell organelles of the FC have assembled in a densely particulate region of the cytoplasm where the stylet tip was located. Electron-transparent callose-like (*CA*) deposits form a channel where the stylet was inserted. The densely particulate appearance of the cytoplasm results from the accumulation of ribosomes dissociated from the endoplasmic reticulum (open arrow). A cluster of electron-dense particles (*EP*) is visible in the modified cytoplasm. Densely stained caps (▼) are visible along the wall of the neighboring cells where modified plasmodesmata are located. *M* Mitochondria. Bar: 3 μm

Fig. 10. Cross-section of food cell (*FC*) in a carnation root at a different plane than where the stylet was positioned showing mitochondria (*M*), nucleus (*N*), and vacuoles (*V*) assembled in the center of the cell. *ER* Ribosome-denuded endoplasmic reticulum. Bar: 5 μm

Fig. 11. High magnification of plasmodesmata (*PD*) connecting cells remote from a food cell in a carnation root tip. Desmotubules (▼) are visible in the plasmodesmatal canals. Microtubules (*MT*) are visible adjacent to the plasma membrane (open arrow) lining the cell wall (*CW*). Bar: 100 nm

Fig. 12. Detailed view of modified plasmodesmata visible in Fig. 10 connecting the food cell (*FC*) with a neighboring cell. The plasma membrane-lined plasmodesmatal canals (*PD*) have no desmotubules and are lenghtened by electron-transparent callose-like (*CA*) deposits projecting into the cytoplasm of the food cell. A densely stained cap (*CP*) is formed in the neighboring cell over the orifice of each modified plasmodesma. *CW* Cell wall. Bar: 200 nm

Fig. 13. Micrograph of two modified plasmodesmata (*PD*) covered by a densely stained cap (*CP*) in the cell wall (*CW*) between a food cell (*FC*) and a neighboring cell in a carnation root. The endoplasmic reticulum (*ER*) in the neighboring cell is studded with ribosomes whereas the endoplasmic reticulum in the food cell lacks ribosomes. Bar: 200 nm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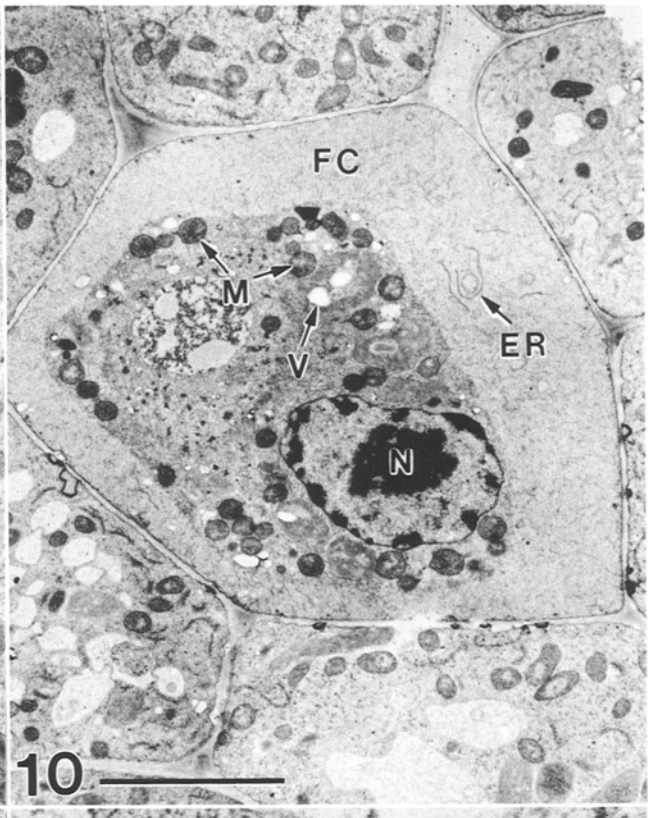
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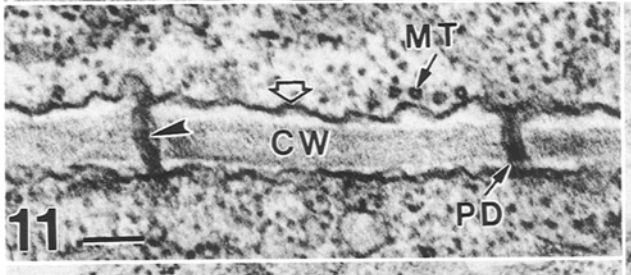
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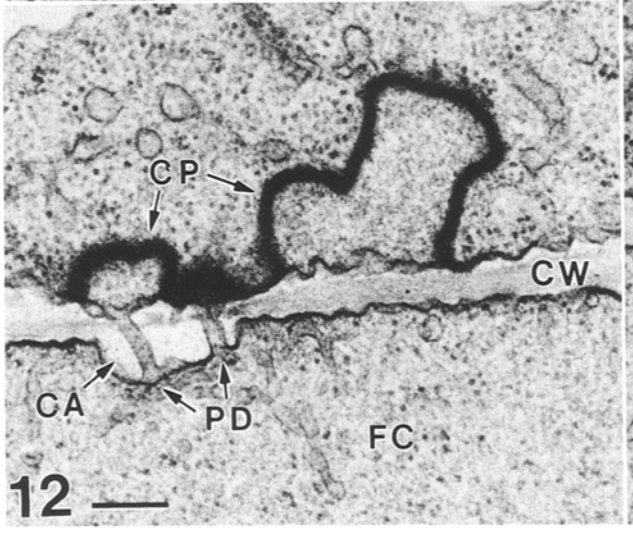
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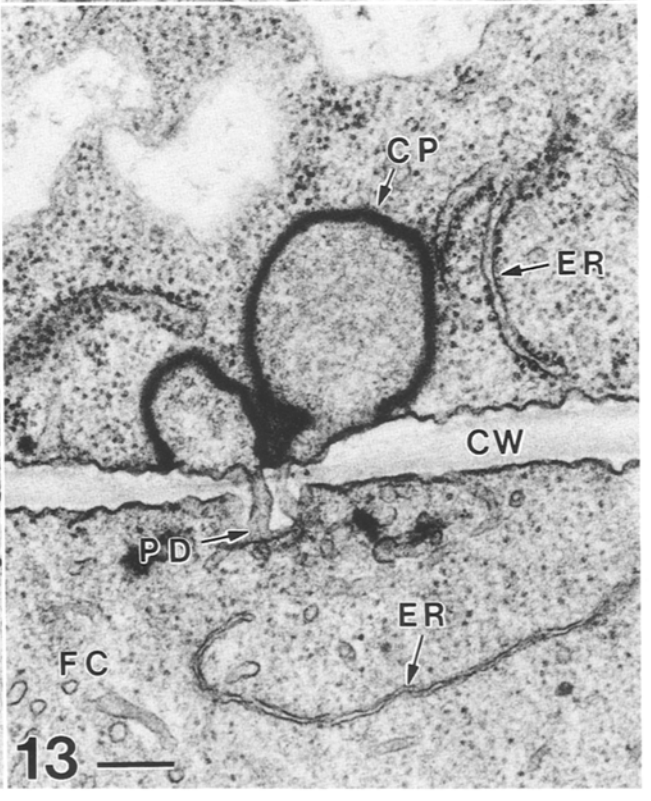
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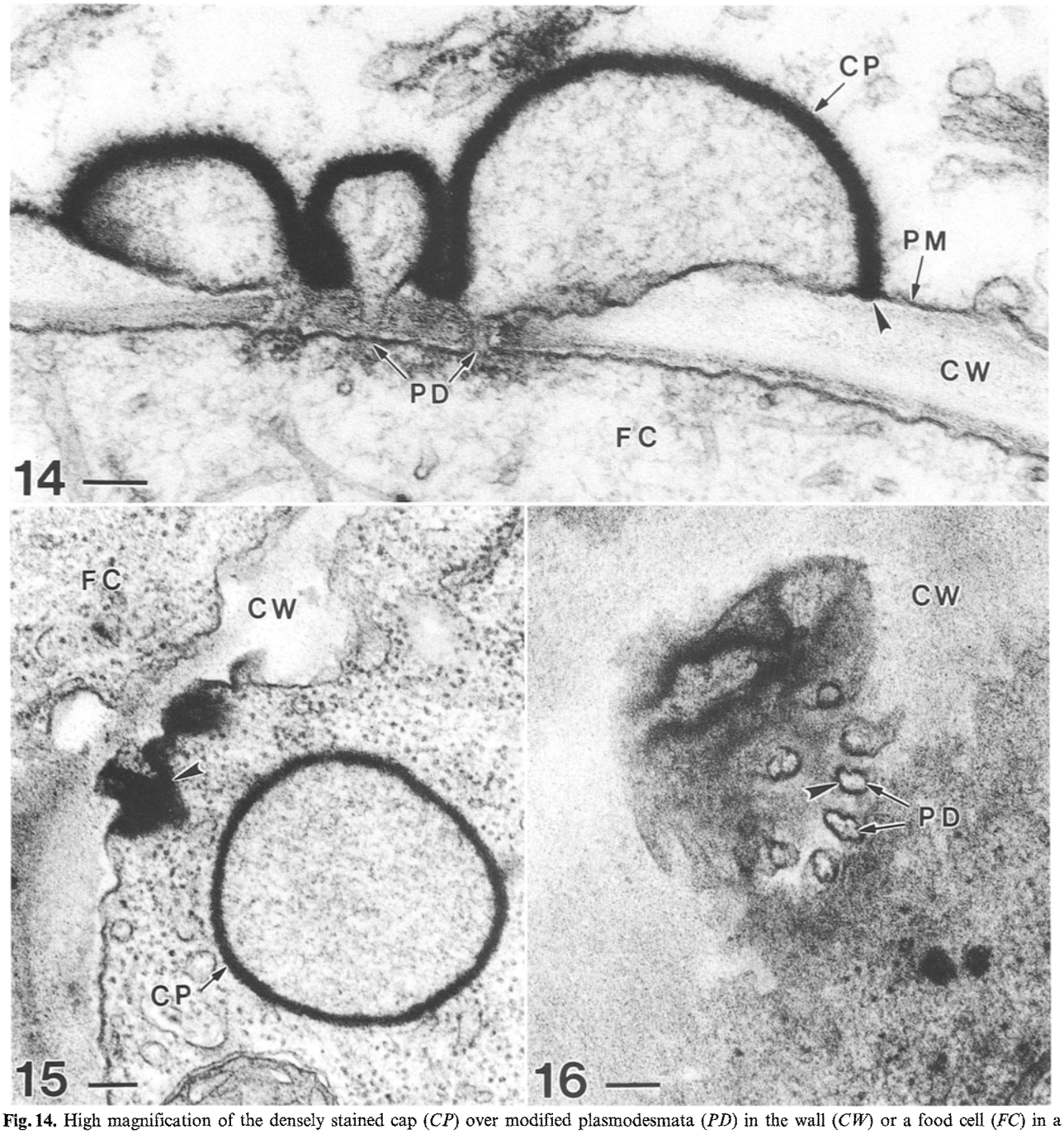

Fig. 14. High magnification of the densely stained cap (*CP*) over modified plasmodesmata (*PD*) in the wall (*CW*) or a food cell (*FC*) in a carnation root. The cap is continuous over adjacent plasmodesmata and forms an apparent tight seal (▼) with the plasma membrane (*PM*) around the orifice of each plasmodesma. Bar: 100 nm

Fig. 15. Cross-section of a densely stained plasmodesmatal cap (*CP*) located in the cytoplasm of cell adjacent to a food cell (*FC*) in a carnation root. The cytosol within the cap is finely granular and free of cell organelles. In adjacent serial sections this cap was connected to the portion of the cap (▼) attached to the cell wall (*CW*). Bar: 100 nm

Fig. 16. End-on view of several irregularly shaped plasma membrane-lined (▼) canals of modified plasmodesmata (*PD*) in the wall (*CW*) of a food cell in a carnation root. Bar: 100 nm

been observed for several nematode species in addition to *C. xenoplax* (Endo 1987, Rebois 1980, Schuerger and McClure 1983, Wyss et al. 1984). In these feeding relationships, electron-transparent callose-like material continuous with the cell wall appears to form (our interpretation of published figures) between the stylet

tip and the invaginated plasma membrane, similar to our observations in the present study. Callose deposition occurs rapidly in fungal-infected or wounded cells (Aist 1976, Conti et al. 1986, Nims et al. 1967, Valluri and Soltes 1990) and possibly a nematode's stylet penetrating a cell wall could similarly elicit callose synthesis. In addition, the plasma membrane is considered to be a site for β-1,3-glucan synthesis (Van der Woude et al. 1974) and possibly could be the site for the synthesis of the material deposited between the stylet and the invaginated plasma membrane in nematode parasitized cells. Callose is also associated with plasmodesmata (Jones and Payne 1977, Northcote et al. 1989) and its formation may be involved in lengthening the canals (Fig. 12) of the modified plasmodesmata in the food cells. Histochemical (Jones and Payne 1977) or immunocytochemical (Northcote et al. 1989) studies should be able to confirm the synthesis of callose in plant cells parasitized by nematodes.

Removal of nutrients from plant cells via the stylet by sedentary endoparasitic nematode species is apparently facilitated by the formation of a feeding tube (Hussey and Mims 1991). However, *C. xenoplax*, which feeds as an ectoparasite, withdraws nutrients directly from the cytosol of a food cell through an opening created in the plasma membrane by the tight association of the membrane with the wall of the stylet aperture. Tight contact between the membrane and the aperture wall would be necessary to maintain an opening in the plasma membrane during feeding by the nematode. When the nematode was ingesting nutrients from the food cells, the tonoplast of the cell pulsated in rhythm with the pumping (about one and a half beats per second) metacorpus in the esophagus of the nematode (Hussey unpubl. obs.). The rhythmic movement of the tonoplast could indicate some backward flow of nutrients through the stylet aperture simultaneously with the closing of the nematode's triradiate pump chamber. The cytosol immediately around the stylet aperture was finely granular and free of cell organelles that potentially could occlude the stylet aperture and block withdrawal of nutrients. Cell organelles may have been excluded from the inner core of the modified cytoplasm by the fibrillar material present around its outer margin.

The clusters of electron-dense particles found in the particulate cytoplasm surrounding the stylet tip (Figs. 6 and 7) were only observed in food cells and do not resemble any known plant cell organelle. We believe these particles are secretory components injected into the food cell through the nematode's stylet. Support for this conclusion is provided by the micrographs (Figs. 3 and 4) of electron-dense secretions being secreted through a stylet aperture into the cytoplasm of a putative food cell. The density and size of these secretions are similar to the electron-dense particles observed in the food cells. The composition and function of these secretions are unknown and they do not resemble any known secretions of other plant-parasitic nematodes (Hussey 1989).

One of the most striking modifications of the food cell was the changes in the ultrastructure of the plasmodesmata connecting the food cell with surrounding cells. The canals of these plasmodesmata were wider than canals of plasmodesmata connecting unmodified cells, were uniform in diameter throughout their length which was frequently increased by electron-transparent callose-like deposits, and lacked the desmotubules that are a normal feature of plasmodesmata in walls of most higher plant cells (Robards and Lucas 1990, Robards 1976). The modified plasmodesmatal canals and the associated callose-like wall projections were reminiscent of modifications of plasmodesmata observed in cells of *Zinnia elegans* infected with dahlia mosaic virus (Kitajima and Lauritis 1969). While the plasmodesmata in virus-infected *Z. elegans* cells are modified to permit cell-to-cell movement of viral particles, plasmodesmata modifications in ring nematode-infected cells presumably are necessary to accommodate fluxes of solute into the food cell created by the uninterrupted feeding of the nematode. These modified plasmodesmata undoubtedly would facilitate solute transport from the neighboring cells into the food cell for consumption by the nematode. Modified plasmodesmata were common in food cells induced at root tips but were less frequent in food cells located in mature cortical tissue.

A truly unique feature of the modified plasmodesmata of the nematode-infected cells was the formation of a cap over the plasmodesmatal orifices in cells adjacent to the food cell in tomato and carnation. As far as we know, this structure has not been reported previously with any plasmodesmata and seems to be unique to this host-nematode relationship. One can postulate several functions for the cap. It might function (1) as a molecular sieve to limit the size of molecules that pass through the plasmodesma into the food cell, and/or (2) as a permeable barrier to prevent cell organelles from occluding the modified plasmodesmatal canal. The fact that cell organelles were excluded from the cytosol within caps supports the notion that the caps at least function as a barrier to ensure the enlarged plasmo-

desmatal canals remain open. Alternatively the cap could be considered a plant-cell defense response to block the modified plasmodesmata to limit the loss of solutes to the food cell. However, we believe cellular changes to enhance movement of solutes into the food cell would be necessary to support the sustained feeding of the nematode and prevent collapsing of the parasitized cell. Formation of the caps on the outside entrance of the modified plasmodesmata and electron-transparent callose-like deposits lengthening the canal in the internal wall of the food cell indicates unidirectional transport of solutes through the plasmodesmata into food cells, especially while the nematode is feeding from the cell. Although feeding activities of other plant-parasitic nematodes are known to increase the frequency of plasmodesmata in walls of parasitized cells (Jones and Pagne 1977, Jones 1976), this is the first report of ultrastructural modification of plasmodesmata in a nematode feeding site.

The minimal root cell disruption associated with the feeding relationship that *C. xenoplax* established with host tissue possibly accounts for the limited amount of crop damage attributed to this plant-parasitic nematode. Plant damage and yield reductions occur primarily in the presence of very high population densities of *C. xenoplax* (Nyczepir et al. 1988). Under high population densities, root damage occurring from mechanical injury to the tissue from penetration of the stylets and consumption of nutrients by the nematodes may contribute to suppressing plant yield.

The food cell induced by *C. xenoplax* is another example of the remarkable manner in which plant cells are modified by plant-parasitic nematodes to function in increased uptake of solutes destined for the parasite (Jones 1981). The highly specialized cellular adaptations induced by this ectoparasitic nematode were unexpected. However, few ultrastructural studies have concerned cellular changes in host tissue parasitized by ectoparasitic tylenchid nematodes (Wyss 1981). Future investigations of host–parasite interactions involving other genera of ectoparasitic nematodes may reveal additional unique cellular modifications.

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