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# Virus-Transmitting Nematodes: Feeding Behavior and Effect on Root Cells

Experimental evidence for the transmission of soilborne plant viruses by soil-inhabiting vectors was first provided 23 years ago. Both nematodes and fungi were found to be involved in the transmission process, and since then much research has been devoted to these vector groups, particularly to nematodes. Several recent review articles clearly demonstrate the rapid gain in information on the ecology and biology of the nematode vectors and their relationship to plant and virus.

## The Vectors

A PLANT DISEASE feature article (4) dealt with controlling nematode-transmitted viruses and also provided information about types of vectors and the viruses transmitted. Of the 17 nematode orders, only two, Tylenchida and Dorylaimida, include plant parasites, and only members of Dorylaimida have been proved to transmit viruses. Vector species within this order are to be found in the suborders Diphtherophorina (trichodorid nematodes) and Dorylaimina (longidorid nematodes). After 23 years of intensive search for vector species it would now be most surprising if members of the other order, which contains most plant-parasitic nematodes, should ever reveal vector abilities. The incapability of the Tylenchida to function as vectors is probably due to a lack of appropriate retention sites for ingested virus particles. In dorylaimid nematodes these sites are provided by the cuticular lining of the alimentary tract, where, depending on the vector genus involved, the particles are retained at different sites between the mouth opening and the transition of the food canal into the intestine (8).

It is generally assumed that virus particles become selectively and specifically adsorbed to the retention sites of their vectors when virus-containing plant contents are ingested and that they become dissociated by salivary secretions passing from the nematode into the plant cell. As emphasized by Taylor and Robertson (9), a successful virus transmission depends on a successful interaction among plant, virus, and nematode. This article deals with plant/nematode interactions and concentrates on the feeding behavior of the vectors as observed under the microscope and on associated plant cell responses. It will thus help to provide some idea of how virus particles are acquired and inoculated by their vectors and of conditions they may encounter after inoculation.

## Trichodorid Nematodes, Vectors of Tobraviruses

These nematodes are assigned to the suborder Diphtherophorina within the order Dorylaimida. Recently, however, it has been proposed that Diphtherophorina be considered a suborder of the order Enoplida (7). All trichodorids are members of the family Trichodoridae, which until 1973 contained only the genus *Trichodorus*. Four genera—*Trichodorus* (with at present five vector species), *Paratrichodorus* (seven vector species), *Monotrichodorus,* and *Allotrichodorus*—are now included in this family.

In all trichodorid nematodes the stylet, used for plant cell perforation, develops within the stoma. It is a ventrally curved mural tooth called the onchiostyle. The tip is completely solid so that food cannot be ingested through a stylet lumen. Food does, however, pass unimpeded through the pharyngeal lumen, ventrally adjacent to the stylet. The pharyngeal wall lining the lumen has strengthening rods a few microns behind the mouth opening and later becomes dorsally fused to the middle region of the stylet. There it forms a so-called guide ring. The pharynx is followed by the esophagus, at first a narrow tube that gradually enlarges into a pear-shaped basal bulb which contains gland cells and also muscles that assist feeding (Fig. 1).

**Feeding behavior.** Several trichodorid species have been observed feeding on roots of seedlings in agar culture. The first report published in 1957 was followed by many others. From these it can be summarized that trichodorids most commonly attack epidermal cells (including root hairs), moving from cell to cell and staying only a few minutes at each cell (16). They tend to aggregate at or just behind the elongating zone of growing roots (Fig. 2A), avoiding the apical meristem. Only when root growth has slowed down as a result of this gregarious feeding behavior is the apical region also attacked (Fig. 2B), but usually by only a few individuals; most of the

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others have moved away in search of other feeding sites. Epidermal cells within the feeding area collapse and turn brown under aseptic conditions, and root hairs do not form. Trichodorids have been observed to behave in a similar way in soil (5).

Feeding studies on individual trichodorids (mainly *T. similis*) with the aid of special observation chambers and cinematography (11) showed that a complete feeding cycle is composed of the following phases: cell wall exploration, wall perforation, salivation, ingestion, and departure from the feeding site. Cell wall exploration is performed by a side-to-side rubbing of the lips (which have receptors for tactile stimuli) over a short distance of the wall (Fig. 1B) and is terminated by bringing the strengthening rods of the pharyngeal wall into close contact with the cell wall. Immediately thereafter the stylet is rapidly thrust (several times per second) at the same spot, and the wall is usually perforated within a minute. After the perforation hole has been made, stylet thrusting is continued, though at a slower rate. This phase, termed salivation, is the longest of a complete feeding cycle. Although salivary fluids are not visible within the attacked cell, there is strong evidence from the cell's response and other indications that the nematode is injecting saliva. During stylet thrusting, the tip of the stylet is repeatedly inserted 2–3 $\mu$m into the cytoplasm, which starts to aggregate into a large mass at the site of stylet penetration (Fig. 3A). With each thrust the pharyngeal wall is drawn forward as a fold where it is fused to the stylet (Figs. 1A and 1C) and concurrently the esophageal lumen toward the base of the bulb is dilated by the contraction of radial bulb muscles (Figs. 1A and 1D).

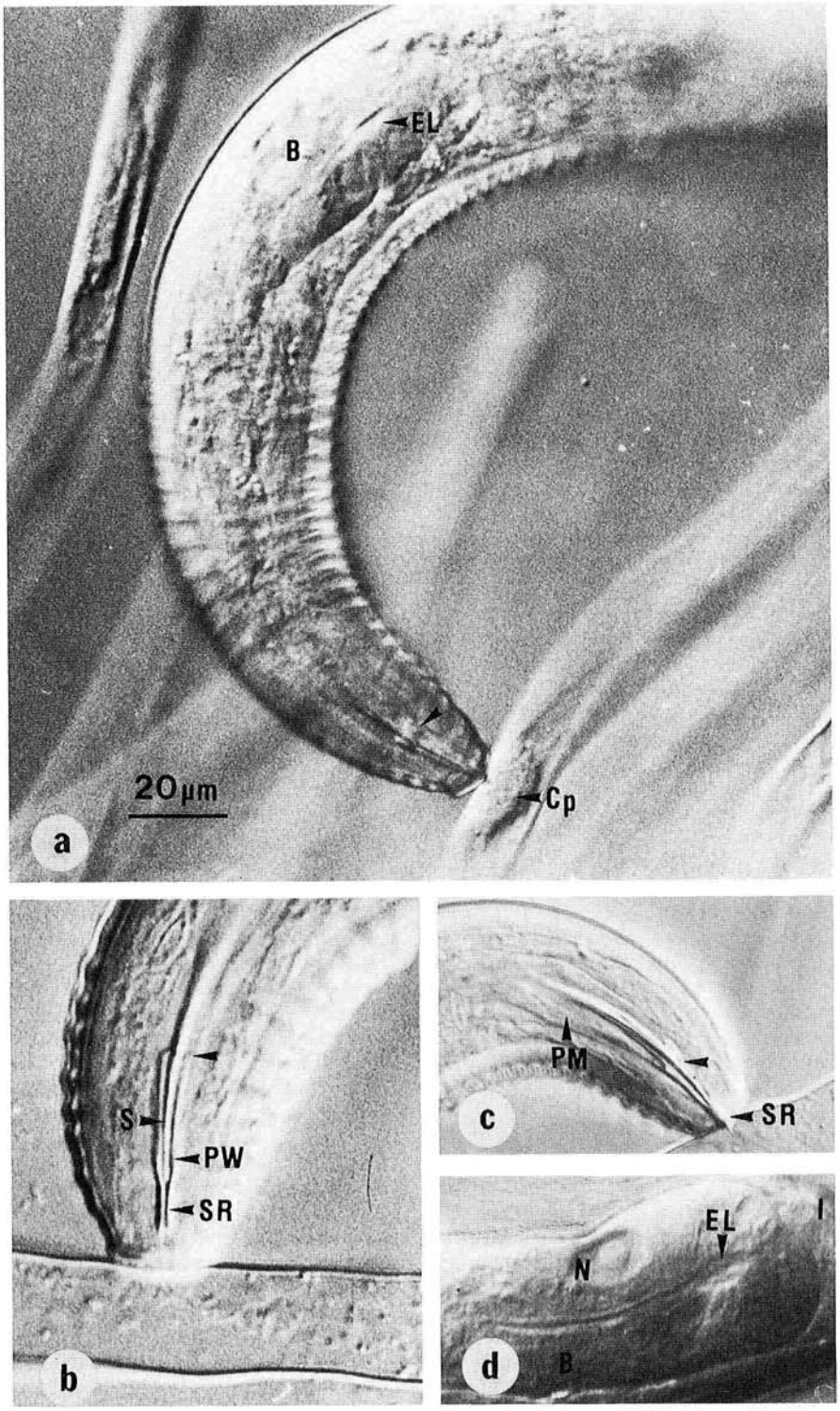


**Fig. 1. *Trichodorus similis* feeding on root hairs of tobacco: (A) During salivation; aggregation of cytoplasm (Cp) at feeding site. (B) Exploration; strengthening rods (SR) of pharyngeal wall (PW) still behind mouth opening. (C) Just after cell wall perforation. (D) Basal esophageal bulb (B) during salivation; esophageal lumen (EL) dilated but still closed in front of intestine (I). Nucleus of dorsal gland cell (N), stylet protractor muscles (PM), stylet (S), fusion of pharyngeal wall to stylet (arrows).**

Ingestion is initiated by a few rather slow thrusts during which the tip of the stylet is deeply inserted into the accumulated cytoplasm (Fig. 3B). Then, concurrent with each stylet retraction, the aggregated mass is quickly removed as the rate of thrusting increases again. Ingestion is usually completed within less than half a minute. When the nematode moves away, a short tube can be seen anchored at the feeding site (Fig. 3C). This so-called feeding tube probably serves as a suction tool (remembering that food cannot be ingested through the stylet) and thus assists ingestion. The tube, formed between the strengthening rods of the nematode's pharyngeal wall and passing in a thin layer through the perforated cell wall (Fig. 4), is composed of nematode secretions that harden rapidly. The secretions are most probably produced by one of the gland cells within the esophageal bulb, but as yet little is known about the structure and function of these cells.

The feeding behavior of trichodorids represents a very primitive form of parasitism. Trichodorids are the only nematodes so far observed to thrust their stylet continuously during feeding, an activity that obviously assists salivation and ingestion (14). Despite their primitive nature they have nevertheless evolved a feeding mechanism that allows them to distinguish between living and dead cells. When feeding on living cells, the tip of the stylet is thrust only 2–3 $\mu$m into the cytoplasm until enough has accumulated. In dead cells, however, the stylet is immediately thrust deeper and deeper until it may perforate the wall of an underlying cell to allow food ingestion from this cell (17).

**Cell responses.** In a stimulating review about cellular responses of plants to

nematode infection, Dropkin (3) stated that virus-vector nematodes produced only a mild effect on host cells. This is to be expected, as rapid death of the cell into which virus particles are injected would most probably prevent a successful virus replication. However, collapse and darkening of epidermal cells that had been fed on by trichodorids under aseptic conditions indicate a more drastic effect.

A cinematographic study (12) on the response of root hairs of *Nicotiana tabacum* 'Samsun' seedling roots to *T. similis* feeding provided a detailed analysis, which can be summarized as follows: Cytoplasmic streaming inside attacked root hairs is affected a few seconds after the nematode's stylet has perforated the cell wall. Cytoplasm is drawn from all directions to the site of stylet penetration, where it rapidly accumulates into a large mass (Fig. 3A). The nucleus, if lying nearby, is drawn together with the cytoplasm to the feeding site. It swells and quickly loses its finely granulated appearance, becoming optically empty (Fig. 3B), and it remains irreversibly disorganized after the nematode's departure (Fig. 3C). After the ingestion of the accumulated cytoplasm and occasionally of the nucleus (this happens whenever its envelope is pierced by the deep stylet thrusts that initiate ingestion), the remaining cytoplasm soon coagulates.

The rapid death of attacked cells probably results from the destruction of the cell's tonoplast at the beginning of ingestion (16). Normal cytoplasmic streaming is resumed only when the nematodes suddenly abandon feeding sites without having ingested any of the accumulated cytoplasm. It is thought that a successful virus inoculation by *T. similis* and other trichodorids (U. Wyss, *unpublished*) may occur only under the relatively rare conditions of interrupted feeding. Epidermal cells are affected in the same way as root hairs.

## Longidorid Nematodes, Vectors of Nepoviruses

These nematodes are included in the suborder Dorylaimina within the order Dorylaimida and belong to the family Longidoridae. *Xiphinema* (with at present eight vector species) and *Longidorus* (five vector species) are the only genera that have been shown to be virus vectors. Longidorids are large nematodes (2–12 mm long) equipped with a hollow axial stylet that has a slitlike aperture throughout its 100–300 $\mu$m length. It is attached to the odontophore, a supporting and ejecting structure, that is followed by the esophagus. This is at first a narrow flexible tube with a circular lumen that later turns into a wide cylindrical basal bulb (Fig. 5), which now has a triradiate lumen with a thickened cuticle to form three pairs of platelets. Radial muscles, attached to these platelets, exert a pumping action by which food is ingested and forced through a one-way esophagointestinal valve. The basal bulb also contains saliva-producing gland cells. In *Xiphinema* the dorsal gland cell has a prominent nucleus at the front of the bulb (Figs. 5A and 5B).

Function and structure of the dorsal gland cell in *X. index* were recently analyzed (6). The cell extends almost the entire length of the bulb on the dorsal side and halfway on the ventral side. It has six ducts, formed by deep infolds of the cell membrane, that are closely surrounded by electron-dense granules. The ducts join into a main duct that opens into the still circular lumen of the bulb (Fig. 5A). During definite feeding phases the ducts

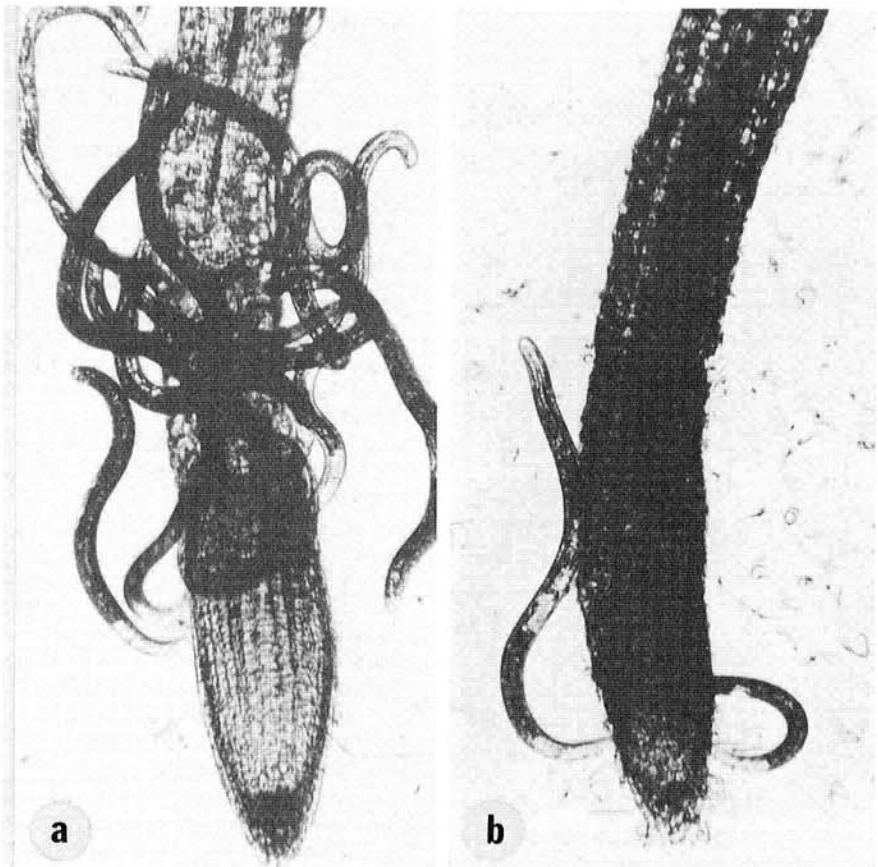


**Fig. 2. *Trichodorus similis* feeding on roots of tobacco seedlings in aseptic agar culture: (A) Nematodes aggregating near elongating zone. (B) Root growth stopped; a few nematodes now attacking meristematic cells.**

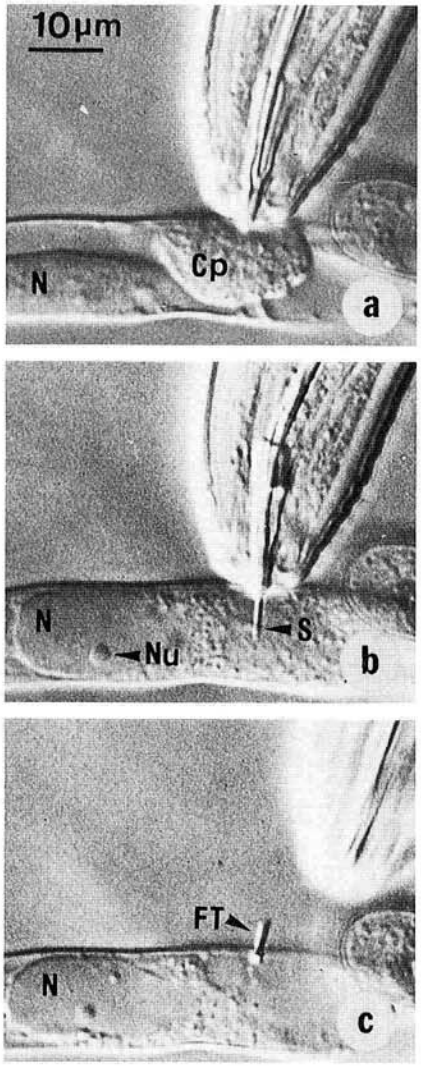


**Fig. 3. *Trichodorus similis* feeding on root hair of tobacco: (A) Aggregation of cytoplasm (Cp) at feeding site, 35 seconds after cell wall perforation. (B) Initiation of ingestion by deep stylet (S) thrusts, 75 seconds after A; nucleolus (Nu) now clearly visible within disorganized swollen nucleus (N). (C) Nematode departs, 95 seconds after A, leaving feeding tube (FT) anchored in cell wall.**

become considerably dilated. Depletion is by a sophisticated mechanism under the control of special muscles. When it happens, fluids can occasionally be seen being flushed forward through the duct system at great speed. It appears that only these fluids will be injected into perforated root cells.

**Feeding behavior of *Xiphinema*.** Of the several *Xiphinema* spp. proved to be virus vectors, *X. index* has been studied most intensively, probably mainly because it can be kept without great difficulty on roots of seedlings growing in agar culture. Its feeding behavior under such conditions was first observed in 1967, and in subsequent years more and more information became available. The data given here are mainly from a cinematographic study (13) during which *X. index* was kept in observation chambers, where it fed on roots of *Ficus carica* seedlings.

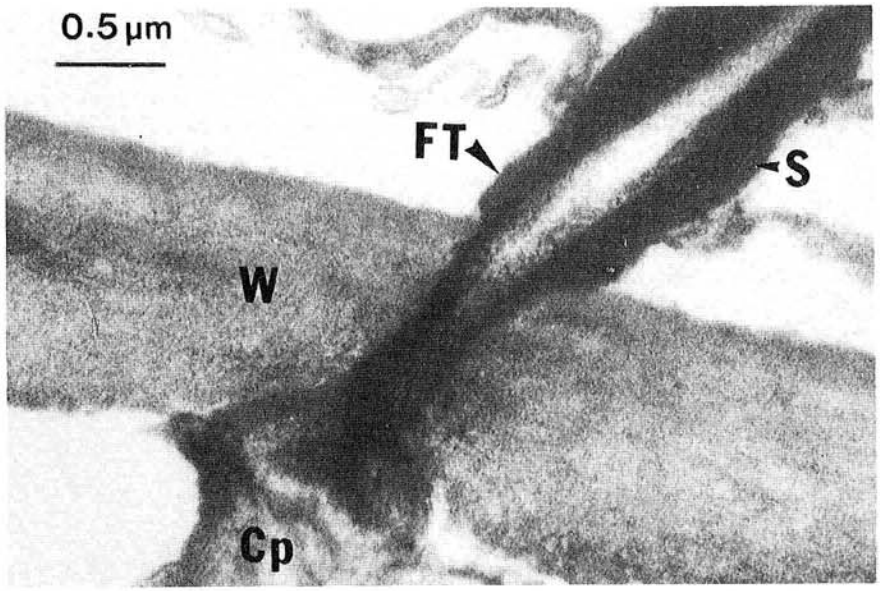


**Fig. 4. Electron micrograph of feeding tube (FT) on passage through wall (W) of epidermal cell parasitized by *Trichodorus similis*. Nematode secretions (S), coagulated cytoplasm (Cp).**

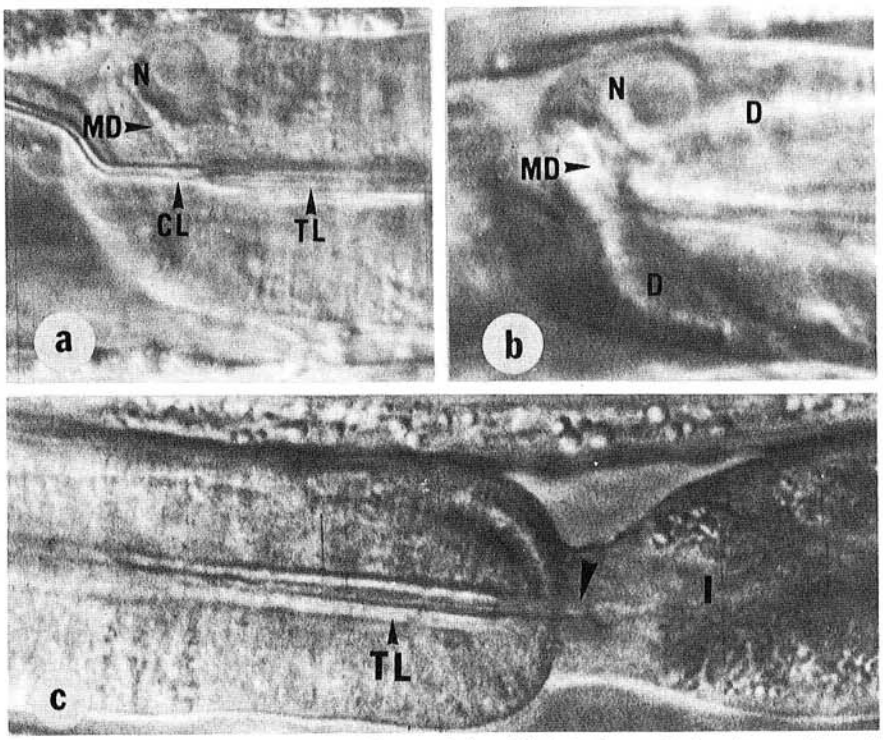


**Fig. 5. Basal esophageal bulb of *Xiphinema index*: (A) Anterior part, showing nucleus of dorsal gland cell (N) and main duct (MD) of this cell opening into circular lumen (CL) in front of triradiate lumen (TL). (B) Anterior part, showing dilated ducts (D) of gland cell during ingestion. (C) Posterior part, showing esophagointestinal valve dilated (arrow) by food forced into intestine (I) as triradiate bulb lumen (TL) narrows from front to back.**

When added to the seedling roots, the nematodes nearly always start to feed in the region of cell elongation. After a suitable site for cell wall perforation has been found by lip rubbing, the stylet is thrust vigorously against the cell wall so that perforation is achieved within a few seconds. During this process the base of the odontophore (onto which the stylet protractor muscles are attached) can be seen rotating, an action that may assist perforation. Having made the perforation hole, the stylet is rapidly thrust through the attacked cell until it hits the wall of the underlying cell. This is then also perforated. *X. index* usually perforates intracellularly a column of three or four cells before it starts ingesting plant cell contents. After the last stylet thrust, ingestion is preceded by a definite sequence of events lasting few seconds, at the end of which dilated ducts of the dorsal gland cell in the basal bulb become depleted. Then ingestion starts by a rapid pumping action of the bulb, forcing contents of the perforated root cell through the esophagointestinal valve into the intestine. At the same time the ducts again become dilated (Fig. 5B); these empty when pumping stops. Food ingestion is typically intermittent, periods of continuous bulb pulsation with duct dilation (on the average about half a minute) being interspersed with short pauses (1–8 seconds) with duct depletion.

*X. index* usually feeds on an individual cell for several minutes only, then it pushes its odontostyle into the next deeper cell, gradually reaching cells far below the epidermis. Occasionally, long rest periods with no sign of activity inside the bulb occur after cell wall perforation. Having fed in such a way on a column of cells, the nematode withdraws its stylet completely and searches for another feeding site within the root's elongation zone. Root growth slows down when this is repeated for several hours, and the root starts to swell, usually behind the region of elongation (Fig. 6A). Continuous feeding at the same tip for several days transforms the swelling into a terminal gall (Fig. 6B), which remains strongly attractive to feeding nematodes, obviously providing the appropriate food for egg production (16).

Not all *Xiphinema* spp. feed invariably on root tips. Feeding on older parts of the root, far behind the tip, and then most probably within the vascular cylinder (depending on the root's diameter) is characterized by feeding periods at one site lasting many hours or even a few days (2). No marked alteration of the root's anatomy as a result of feeding at these sites can be seen.

**Feeding behavior of *Longidorus*.** *Longidorus* spp. appear to be less suitable than *Xiphinema* spp. for feeding studies in agar culture as, until recently, no adequate information was available, in spite of several attempts to observe them

feeding under such conditions. The only detailed report so far is on *L. caespiticola*, feeding on root tips of *Lolium perenne* in water agar (10). Compared to *Xiphinema* spp., this species displays a quite different feeding behavior. The stylet is thrust into root tips without odontophore rotation and does not come to a rest until it is fully protracted. Only indirect evidence of salivation can be obtained. It is thought to occur within 30–60 minutes between final stylet penetration and ingestion proper. Bouts of slow contractions of the anterior bulb wall may assist saliva flow, but neither gland cell ducts nor salivary fluids become visible in the bulb during this phase. As the "salivation phase" is interspersed with short bouts of bulb pumping, the nematode may test the suitability of food cells. It then either withdraws its stylet or proceeds to ingest by prolonged bulb pumping with short, infrequent rests. When undisturbed, the nematode may feed at one site (with the stylet remaining protruded in a single cell) for several hours. It is thought that, in this case, food may also be derived from cells adjacent to the food cell.

**Cell responses.** Root tips attacked by *Longidorus* and *Xiphinema* spp. are transformed into swellings, curls, or galls that often contain necrotic spots or even cavities. Feeding in the zone of root elongation inhibits meristematic activity and cell expansion but does not affect cell maturation. As a consequence, the vascular tissue extends close to the root's apex. Root tip swellings become clearly visible within 1 day of root tip feeding, and there is evidence that, once initiated, the swelling process continues for some hours in the absence of the nematode. Meristematic activity in attacked root tips is not always irreversibily blocked, as new growth can emerge from swellings or even galls (15).

Root tip galls of celery fed on by *L. elongatus* contain clusters of hypertrophied cells with single enlarged nuclei and dense cytoplasm. They surround necrotic cells from which the nematodes have most probably fed (16). Galls on the same plant species caused by *L. apulus* reveal so-called lysogeneous cavities with an amorphous mass of cytoplasm in which cell organelles are no longer detectable. These cavities are surrounded by hypertrophied cells with thickened walls and disorganized cell contents (1). It is most likely that these cells represent the actual feeding site of the nematodes.

Galls caused by *Xiphinema* spp. also contain hypertrophied cells, but these have more than one nucleus. Multinucleate cells in *Xiphinema*-induced galls were recorded as early as 1960, but they have only recently been more closely examined. Fig seedlings grown under aseptic conditions in agar and inoculated with surface-sterilized *X. index* offer good possibilities for detailed studies of the root tip/nematode interaction (15,18).

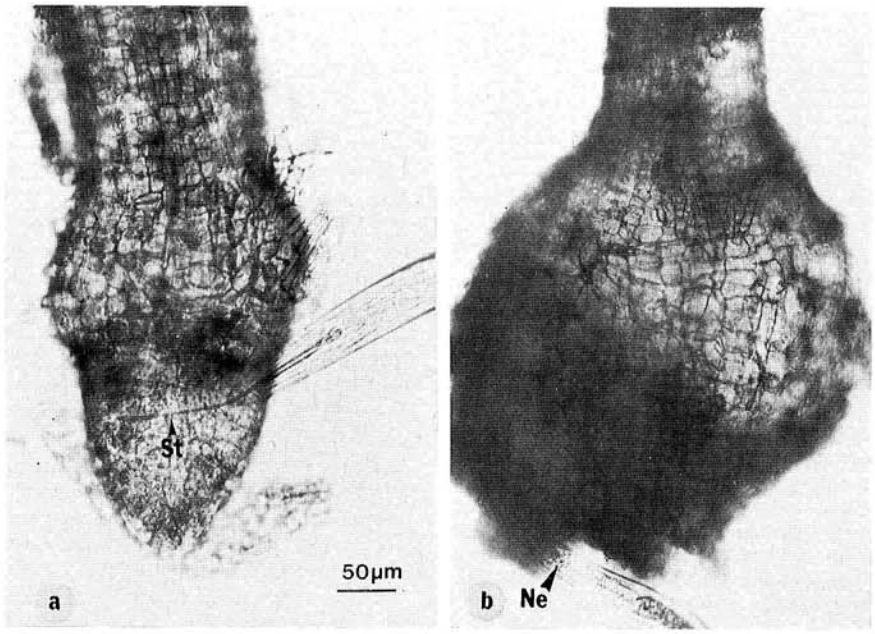


**Fig. 6. *Xiphinema index* feeding on tips of fig roots in aseptic agar culture: (A) Root tip swelling 16 hours after first attack with stylet (St) deeply inserted. (B) Nematode (Ne) feeding on root tip gall 6 days after first attack.**

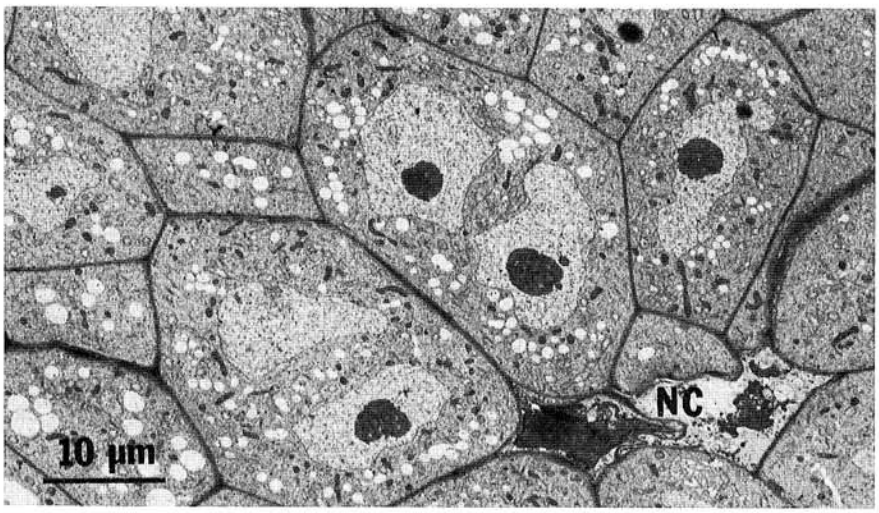


**Fig. 7. Transmission electron micrograph of longitudinal section through part of swollen root tip of fig seedling fed on by *Xiphinema index*. Two necrotic cells (NC) are surrounded by binucleate cells about 1 day after first attack.**

Distinct cellular alterations can be noticed in root tip swellings 12–24 hours after the first nematode attack. Necrotic, collapsed cells with electron-dense contents, most probably the result of a hypersensitive reaction to direct nematode feeding, are surrounded by hypertrophied binucleate cells with dense cytoplasm. Several cell groups, like those shown in Figure 7, can be found in a single root tip swelling. There is always a clear-cut demarcation between necrotic and modified cells, indicating that the hypersensitive response remains confined to parasitized cells, whereas the trigger for cell modification passes into neighboring cells. Two days after the initial nematode attack, the modified cells are more enlarged and now possess four to eight nuclei. They abut empty cells with remnants of more than one nucleus, showing that the nematodes have, most probably, fed from modified cells. At later stages the modified cells can attain large dimensions by crushing surrounding necrotic cells. Because they undergo synchronous mitoses without cytokinesis, they contain numerous nuclei, usually clustered in the center of the cell.

A characteristic feature of *X. index*-induced modified cells is their high metabolic activity, as expressed in nuclear and nucleolar hypertrophy, invagination of the nuclear envelope, and increased cytoplasmic density caused by an increase in rough endoplasmic reticulum, plastids, and mitochondria and the formation of numerous small vacuoles (Fig. 8). Their precise function in the host/parasite relationship is not yet

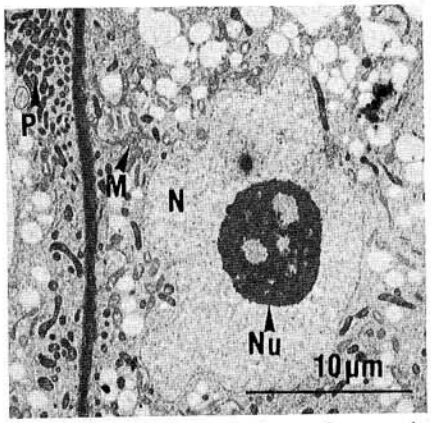


**Fig. 8. Transmission electron micrograph of longitudinal section through part of cell modified by *Xiphinema index* showing signs of high metabolic activity, expressed by lobed nucleus (N), vacuolated nucleolus (Nu), and dense cytoplasm with small vacuoles and abundant mitochondria (M) and plastids (P) near cell wall.**

fully elucidated, but there are several indications that their induction and maintenance may be a prerequisite for the nematode's reproduction (15).

## Summary

It has been found that a number of virus-transmitting nematodes can be kept without difficulty on roots of host-plant seedlings in aseptic agar culture, where they may also reproduce. Special observation chambers and high-power interference contrast cinemicroscopy allow clear observation of living tissues in nematodes and attacked roots and, together with electron microscopy, detailed analysis of changes in these tissues. Although all virus-transmitting dorylaimid nematodes are pure ectoparasites and hence less advanced in their modes of parasitism than many of the nontransmitting tylenchid nematodes, they show a highly sophisticated feeding mechanism. This is, for instance, well documented by the function and structure of the dorsal esophageal gland cell in *X. index*, which plays a vital role in the process of virus transmission and the host/nematode relationship.

Vectors of nepoviruses, feeding near or on meristematic root tip cells of their host plants (where the viruses will also occur), may kill the cells on which they feed and transform neighboring ones into a state of high metabolic activity. This at least appears to be the case for *X. index*. Vectors of tobraviruses have a lethal effect on epidermal cells from which they ingest cytoplasm, and thus, purely theoretically, they are less suited to act as vectors than the nontransmitting tylenchid epidermal feeders, which are not so destructive to their food cells.

The possibility of observing host/nematode vector relationships in agar cultures offers good prospects for well-defined experiments on virus acquisition and inoculation. It will further allow careful studies on the effect of control chemicals, such as the nonphytotoxic systemic oxime carbamates, which affect nematode feeding behavior without necessarily killing the vectors and thus, at least for definite periods, protect crops from nematode-borne viruses.

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