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ECOLOGICAL ADAPTATIONS OF PLANT-PARASITIC NEMATODES

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Abstract

Ecological adaptations of Tylenchida, Aphelenchida, Dorylaimida and Triplonchida (= Diphtherophorina Coomans & Loof, 1970, new synonymy) are discussed. The ectoparasites are categorised as (a) passive feeders, (b) migratory root surface feeders, (c) migratory deep root tissue feeders, (d) sedentary root ectoparasites and (e) migratory ectoparasites of aerial parts. The endoparasites are grouped under (a) migratory endoparasites of aerial parts, (b) migratory endoparasites of subterranean parts and (c) sedentary endoparasites.

At least four orders of nematodes-Tylenchida Thorne, 1949; Aphelenchida Siddiqi, 1980 (Subclass Secernentea); Dorylaimida Pearse, 1942 (= Axonchida* Cobb, 1920, senior synonym) and Triplonchida* Cobb, 1920 (= Diphtherophorina Coomans & Loof, 1970) (Subclass Adenophorea), contain known plant parasites and each of these has an independent origin and evolutionary history.

Two broad ecological categories of plant parasitic nematodes can be recognized: the ectoparasites, with most of the body remaining exposed to the environment while feeding, and the endoparasites which lie totally buried in the plant tissue, although some forms may exhibit intergrades between the two categories and others may have stages belonging to both.

The majority of ectoparasites live in a thin film of water in soil and are constantly at the mercy of variations in the soil environment, often having to face moisture, pH and temperature fluctuations. They have, in

*Cobb (1920) proposed these orders as Axonchia and Triplonchia. He stated "In each order, a genus has been selected and given a name philologically connected with that of the order, in fact, the singular of the order name, and in most cases, these genera may be considered as typical of the orders, – for instance, *Axonchium* may be taken as typical of the order Axonchia." By citing this example, Cobb (1920) has in fact made *Axonchium* the type-genus for his order Axonchia. Similarly, *Triplonchium* may be considered as having been made the type-genus of Triplonchia. The order names are here emended as Axonchida and Triplonchida following the Pearse (1942) System. Axonchida is a senior synonym of Dorylaimida Pearse, 1942, but the name Dorylaimida should be retained because of its wide and long usage in literature. Triplonchida is here recognized as a valid order and the suborder Diphtherophorina Coomans & Loof, 1970 is considered its synonym. It should be noted that the International Code of Zoological Nomenclature does not cover taxa above the rank of superfamily.

consequence, a high degree of motility and well developed chemo- and mechanoreceptors. By contrast, the endoparasites enjoy a greater saftey from environmental hazards and have access to a continuous supply of food and water. Also as a result of interaction with host tissues, they show extraordinary parasitic adaptations and even some degree of host specificity and selection of feeding sites.

Yeates (1971) applies modern concepts of parasitism to plant nematodes and suggests that, strictly speaking, only sedentary endoparasites, such as Heteroderidae and Tylenchulidae, are to be regarded as parasites while other plant parasites are to be looked upon as merely plant feeders. The nematodes that live in soil and feed superficially upon roots have been considered by Jones (1965) as free-living.

Yeates (1971) recognizes 7 modes of feeding in soil nematodes bacterial feeding, fungal (hyphae) feeding, yeast feeding, algal feeding, deposit feeding, higher plant feeding and predation. Fungal, yeast and algal feeding nematodes are referred to by him as microherbivores.

Paramonov (1962) considers nematodes associated with plants as *Eusaprobes* (saprophagous nematodes), *Dyssaprobes* (found largely in rhizosphere but may enter healthy root tissues), *Pararhizobionts* (rhizospheric plant nematodes) and *Phytohelminths* (plant-parasitic forms with pathogenic effects).

Most of the Dorylaimida are pararhizobionts or microherbivores following the terminology used by Paramonov (1962) and Yeates (1971), respectively. The plant-parasitic Dorylaimida are similar to predatory dorylaims as regards the feeding apparatus and feeding habit. They anchor themselves to the root surface with the lips while the stylet perforates the cell wall with a twisting action. Soon afterwards, the oesophageal bulb performs rhythmical contractions (1-3 per second) and feeding starts. At each contraction, the bulb stretches and its lumen dilates, then contracts so that the lumen narrows from front to back, forcing the food backwards to the intestine.

In a study based on cinematography, Doncaster & Seymour (1973) found that the feeding of some ectoparasitic Tylenchida and Aphelenchida, both on fungi and on higher plants, showed the same basic pattern of behaviour, in the exploration and selection of penetration sites. The pattern includes (i) *widespread exploration* or searching behaviour, stimulated chemically by a host, leading to locomotion, head movement and surface probing by the stylet; (ii) *local exploration* in which the surface is explored by lip rubbing and stylet probing, and, if found favourable, (iii) *stylet thrusting* begins and penetration is achieved, lips remaining pressed against the surface giving a firm attachement.

The ecological characteristics based mainly on the occurrence in soil or in plant tissues and the behaviour especially the mode of feeding have been used in the ecological classification of plant parasitic nematodes by several workers (Hooper, 1969; Jones, 1965, '80; Mai & Lyon, 1975 and Williams, 1968). But as pointed out by Williams (1968) such classifications are arbitrary being based on phenetic resemblances which are prone to convergence and because species of even a single genus may show a good deal of variability in motility and degree of penetration into the plant tissues. Some typical migratory ectoparasites may be found totally buried in plant tissues and the root parasites may also occur in shoots especially in aquatic plants. Nevertheless, the ecological categories of plant nematodes proposed here do reflect the ecological adaptations and general behavioural patterns that should help in better understanding of these animals.

The nematodes which are intimately associated with plants and are host specific must have evolved alongside their hosts. Co-evolution of parasite and host has been discussed for *Heterodera* spp. by Krall & Krall (1970). According to Krall & Krall (1970), Angiosperms parasitized by *Heterodera* show three groups: (i) the ancient group, Protanthophyta (Mangoliales, Ranunculales, etc.) are not parasitized by *Heterodera;* (ii) the most recent group, Hypsanthophyta (Cyperales, Graminales, Umbellales, Asterales, etc.) are parasitized with limited host range, and (iii) the middle group, Mesanthophyta (Caryophyllales, Leguminales, Solanales, etc.) are extensively parasitized. Stone (1979) considers the evolution of *Punctodera, Globodera* and *Heterodera* to be independent lines and concludes that there is a broad pattern of co-evolution of these heteroderid nematodes with their host plants.

1. The ectoparasites.

All the known plant feeding Dorylaimida and Triplonchida and most members of the Tylenchida are ectoparasites of roots; only the Aphelenchida and some species of Anguinoidea (Tylenchida) are ectoparasites of the aerial parts of plants. To overcome environmental hazards, the ectoparasites have undergone several ethological and morphological adaptations. Of prime importance are the development of a high degree of locomotory ability and stylet modifications. Those which are less motile avoid environmental rigours in other ways: (i) the exposed body surface becomes reduced by being small (Paratylenchidae), (ii) the cuticle becomes thick (Criconematidae, Trichodoridae), (iii) the body is coiled on or around the roots so that it remains close to roots where both physical and chemical conditions are more favourable than in the soil, under stress, at some distance (Hoplolaimidae, Longidoridae) and (iv) they feed on growth zones of roots where there is a greater concentration of moisture and nutrients and where they may initiate galls which become favourable feeding sites (Trichodoridae, Hemicycliophoridae). Five subcategories of ectoparasites are recognized here as follows:

(a) *Passive feeders.* The passively feeding nematodes lack a pumping median oesophageal bulb, have a low turgor pressure in the gut and are force-fed by the pressure in a fungal hypha or plant cell. *Hexatylus viviparus* (Hexatylina) feeds on fungus in this way, as shown by Doncaster & Seymour (1975). The low body pressure is maintained by rectal pumping and the nematode is force-fed by the high pressure in the food cell so that, in a way, the nematode has a rectal feeding apparatus (Seymour, 1975). Some species of *Ditylenchus* (Tylenchina) also show passive feeding, followed by active feeding using the muscular median bulb (Doncaster, 1966). It could be a normal mode of feeding for Tylenchida lacking a muscular median oesophageal bulb and is thought to be an ancient trait of the Tylenchida (Siddiqi, 1980).

(b) *Migratory root surface feeders.* The nematodes have a small stylet and move quickly from one site to another, feeding lasting for a short time. They can be regarded as surface browsers that feed mostly on root hairs and epidermal cells, and show no obvious parastic adaptations to their habitat, morphology or life-history. They can survive away from their host for a long time, the so-called 'free-living' stage depends only on the reserve food material in the intestine or on the possible feeding on fungi and algae and, in the case of Dorylaimida only, on micro-organisms (examples are found in Aphelenchidae, Aphelenchoididae, Tylenchidae and small-stylet-bearing Dorylaimida).

Several Tylenchorhychinae and Merliniinae are also migratory root surface feeders. *Tylenchorhynchus* spp. cause stunting and reduced root system due largely to the cessation of growth. Small stylet forms i.e. *Merlinius brevidens, M. nothus* and *Tylenchorhynchus dubius,* feed on epidermal cells for a short period (a few seconds to 27 min.) and move quickly to other feeding sites, but the long stylet forms move sluggishly and feed on root cell at one site for a long period (13 hrs. 30 min. for *Amplimerlinius macrurus* and 31 hrs. 45 min. for *A. icarus*). The latter may make a hole in the subepidermal tissue and feed on cortical cells, thus approaching the habit of deep root feeders (Bridge & Hague, 1974). *Merlinius joctus* was observed to feed on epidermal cells usually near the root tips of cranberry for 30 seconds to 7 min. (Zuckerman, 1960). The aquatic nematode *Tylenchorhynchus annulatus* is a swimmer and may become a swarmer when there is a rapid growth of roots of its host rice plants (see review on swarming by Siddiqi, 1976); swarmers are more pathogenic to rice than non-swarmers (Joshi & Hollis, 1976).

All root and fungus feeding Aphelenchida come within this category. *Aphelenchoides bicaudatus* is a typical fungal feeder that completes its life-cycle within 5-6 days (Siddiqui, 1976). *A. composticola* is a serious pest of mushrooms. In the U.S.A., it is known to be transmitted by sphaerocerid flies (Haglund & Milne, 1973) (cf. insect vectors of Aphelechida parasitizing aerial parts of plants in 2,a ii).

Most of the short odontostyle bearing Dorylaimida (Tylencholaimoidea, Dorylaimoidea, Belondiroidea) are presumably migratory surface root ectoparasites and all of the plant-parasitic Triplonchida come under this category. The root parasitism has evolved differently in Triplonchida whose stylet, feeding muscles, oesophagus and oesophageal glands are structurally dissimilar to those of Dorylaimida. Long stylet bearing Triplonchida (*Trichodorus* spp.) feed ectoparasitically on root hairs, epidermal cells and, less frequently, on outer cortical cells (Wyss *et al,* 1979). They aggregate at a feeding site, usually at root tips, and their feeding lasts for a few minutes (Wyss, 1971) and causes stubby roots. Since the stylet is solid, the poured out saliva solidifies to form a tube through which food is sucked. The saliva initiates a host reaction causing food to gather at the tip of this feeding tube. Ruehle (1969) reported a balanced parasitism of pine seedlings and *Nanidorus christiei* (= *Trichodorus christiei*) in which no pathogenic effects were noted on roots, parasitized seedlings showing only a reduction in top and root growth and mycorrhizae developing on roots. On cotton, low populations of *N. minor* actually stimulated growth (Schilt & Cohn, 1975). Similar stimulating effects result by the feeding of a few *N. christiei* on sugarcane (Apt & Koike, 1962). Parasitic stimulation of the host plant to produce more roots and increased growth have also been noticed in experiments with small numbers of other nematode species.

(c) Migratory deep root tissue feeders. They feed onthe deeper root

tissues using a relatively long and robust stylet and may or may not have considerable locomotory ability. When feeding, they remain at one feeding site for longer periods (see above for *Amplimerlinius* spp.) and remain in close proximity to roots, especially around the growth zones where physical and chemical conditions are more favourable.

Hemicycliophora arenaria (Criconematina) feeds usually on root tips and produces galls. During feeding, the stylet is inserted 2-3 cells deep; oesophageal gland secretions are poured out; an adhesive plug is formed surrounding the stylet which fixes the nematode to the roots; the median bulb starts pumping and the cell contents are sucked in. Feeding at one site will last for 2 to 6 days (McElroy & Van Gundy, 1968). A continuous supply of new food cells is insured by the dividing meristematic cells.

Longidoroidea, *Dolichodorus* and *Belonolaimus* have extremely long stylets and also feed on root tips, causing stubby roots and reduced root systems, and in some cases, necrosis and the formation of terminal galls. *Xiphinema index* and *X. brevicolle* feed along the roots rather than at the root tips and remain at one feeding site for several days, while *Longidorus africanus* feeds on root tips for up to 15 min. and produces stubby, swollen root tips (Cohn, 1970). The galls of *Longidorus* are smaller than those of *Meloidogyne* and are produced as a result of nematode feeding interfering with pyroline metabolism and cell wall biosynthesis of the host plant (Epstein & Cohn, 1971).

(d) Sedentary root ectoparasites. As these nematodes lie partly buried in plant tissue while the free part of the body, which is often obese, lies in close proximity to the roots, fluctuations in soil moisture and temperature have less effect on their activity and development, as compared to the migratory ectoparasites.

Tylenchulus semipenetrans, the citrus root nematode, is an obligate plant parasite that becomes obese and sedentary whilst feeding with head and neck buried deep in citrus root tissues, sometimes reaching the pericycle; the larvae are surface root ectoparasites. In the cortex around the head of the feeding female, some cells become modified as 'nurse cells' or transfer cells; they have thick walls and enlarged nuclei. Several races or biotypes are known to occur and resistance in some citrus plants may develop due to the formation of a wound periderm and the possible toxic effects of plant secretions on nematodes (see details in Siddiqi, 1974). Those related to *Tylenchulus* are *Meloidoderita* and *Sphaeronema* which are also true sedentary root ectoparasites. *Meloidoderita* is known to produce 'cysts' containing eggs with its thickened uterine walls. All of them belong to the suborder Criconematina (see Siddiqi, 1980a).

Among the Tylenchinae, the reniform nematodes, *Rotylenchulus* spp. of the Hoplolaimoidea, feed near the stele and on the pericycle while the major portion of their body swells to become kidney-shaped and hangs outside the root. Their feeding induces syncytia which appear to differ from those produced by *Heterodera* and *Nacobbus* (Endo, 1978; Rebois, 1981). Razak & Evans (1976) observed that the feeding of *R. reniformis* on cowpea roots induces the production of a feeding peg on the cell adjacent to the nematode lips and a hyaline feeding tube coiling helically within the feeding cell. *Acontylus vipriensis* can bury its anterior end up to the excretory pore in the roots of *Eucalyptus* sp., its body swelling posteriorly. It aggregates and forms colonies on the root surface where eggs are laid in a gelatinous matrix to keep them adhering to the roots (Meagher, 1976).

(e) Migratory ectoparasites of aerial parts. They are fast movers in a thin film of water or in the intercellular spaces and parasitize leaves, buds and flowers. At times they may also become embedded in leaf, stem, flower, fruit or seed tissues and feed endoparasitically.

Aphelenchoides ritzemabosi and *A. fragariae*, commonly known as bud and leaf nematodes, are obligate plant parasites that feed ectoparasitically on buds and growing points and parenchymatous cells of the leaf mesophyll and fail to complete the life-cycle in soil. Feeding on buds retards growth and produces distorted tissues; on leaves, feeding spots or blotches are produced. *A. ritzemabosi* is a menace to the growing of chrysanthemums. On strawberries, it occurs usually with *A. fragariae* and produces the disease called strawberry crimp or spring dwarf (Siddiqi, 1974a, 1975). Ectoparasitic feeding of *A. besseyi* on growing points of rice shoots produces 'white tip' disease. On strawberries, *A. besseyi* produces 'summer dwarf' or crimp disease (see Franklin & Siddiqi, 1972).

These Aphelenchida can survive anhydrobiotic conditions for several months and can easily be cultured on fungi. Thus the plant parasitism of the aerial parts in Aphelenchida appears to have evolved through fungal feeding.

Only a few Tylenchida are ectoparasites of the aerial parts of plants. *Ditylenchus angustus* feeds ectoparasitically on rice stems, leaves and inflorescence of rice producing malformation of tissue. It is a pathogenic species and causes 'ufra' disease of rice in Bangladesh and other South East Asian countries.

2. The endoparasites.

Only Tylenchida and Aphelenchida show endoparasitic adaptations. As endoparasites in plant tissues, their rate of activity and development is correlated with that of the host and especially in cooler parts of the world, depends largely on temperature (Jones, 1975a).

The endoparasites are usually specialized for feeding on particular plant tissues, though the parasitic adaptations are not as marked in migratory endoparasites as in sedentary ones. Those that parasitize roots do not attack shoots, and vice versa, although some genera (e.g. *Ditylenchus, Aphelenchoides*) have species that attack both. *Rhadinaphelenchus cocophilus,* the causative agent of the red ring disease of coconut, may seem to be an exception, but this nematode is a typical parasite of stems and in spite of its generic name, is not a root parasite; it occurs in roots only in transit to the stem (R. Griffith, pers. commun.).

(a) Migratory endoparasites of aerial parts. (i) Tylenchida. Only Anguinoidea among the Tylenchina and some Hexatylina *(Fergusobia, Deladenus)* parasitize above-ground parts of plants. Seed gall-forming *Anguina* spp. are parasites of monocotyledonous plants. *A. tritici* grows and reproduces within wheat grains which transform into black irregular galls. The female becomes obese and somewhat sedentary, lays up to 2000 eggs and dies *in situ.* The second-stage juveniles lie dormant in the galls, emerge in favourable conditions and reinfect wheat plants, developing in inflorescence and seeds (rarely in leaves). *A. agrostis* and *A. graminis* form galls in flowers and leaves respectively of *Agrostis* and several other grasses. *Subanguina mobilis* produces galls on leaves and stems of capeweed *(Arctotheca calendula)* and survives during summer in dried galls as third-stage juveniles. Several generations are passed within the galls; juveniles may leave the galls, migrate through leaf or stem tissues and initiate further gall formation (Chit & Fisher, 1975). *Nothanguina cecidoplastes* forms galls on grass leaves, stems and axis of inflorescence. *Orrina phyllobia* is another such example of gall producing Anguinoidea. *Ditylenchus dipsaci* parasitizes stems of lucerne, pea, oats etc. and is pathogenic.

(ii) Aphelenchida. The aphelenchs have successfully parasitized the aerial parts of ferns, plants and trees and are not significant parasites of roots (the soil-inhabiting aphelenchs are mostly fungal feeders). Those dicussed under ectoparasites of aerial parts may at times become endoparasites *(Aphelenchoides ritzemabosi, A. fragariae).*

The endoparasitic Aphelenchida are transmitted by insect vectors as fourth-stage juveniles (called dauerlarvae) and usually enter through wounds in plant/tree caused by insect feeding or oviposition as seen in *Bursaphelenchus* spp., & *Rhadinaphelenchus cocophilus* respectively. *Bursaphelenchus lignicolus* causes a destructive disease of pine in Japan. This species and *B. mucronatus* are transmitted by a caerambycid beetle, *Monochasmus alternatus.* The nematode lives in axial and radial resin canals and causes serious pathological conditions resulting in the death of the trees (Mamiya & Kiyohara, 1972; Mamiya & Enda, 1979). Both these species can be reared on fungi, the life cycle being completed in about 5 days. *B. lignicolus* feeds and reproduces on callus tissues of higher plants and can also feed ectoparasitically on young cells of alfalfa seedling roots (Tamura & Mamiya, 1976). *Rhadinaphelenchus cocophilus* uses palm weevil, *Rhyncophorus palmarum,* as a transporter. The nematodes may enter the body cavity of the insect larvae through the mouth or spiracles and persist during metamorphosis. On the emergence of the female, a large number of nematodes are injected into the soft tissues of coconut when the eggs are laid through the ovijector.

Fern fronds are parasitized by *Aphelenchoides fragariae* with typical leaf-blotch symptoms (see Siddiqi, 1975). In its its natural forest habitat in Oregon, USA, on western sword-fern *(Polystichum. munitum),* this nematode produces typical water-soaked stripes on the fronds which later turn dark brown in the summer (Sandeno & Jensen, 1962).

(b) Migratory endoparasites of subterranean parts. The endoparasites lie totally embedded in the tissues which may rupture secondarily to expose the body of the parasites. Some complete their life-cycles within the plant tissue, but others may have various stages in the soil for various lengths of time. The intimate relationship that exists between these parasites and their hosts has given rise to various shades of parasitic adaptations which are less pronounced in the migratory than in the sedentary forms. Motility and elongate tails characterize the migratory endoparasites. The family Pratylenchidae encompasses migratory root endoparasites. The lesion nematodes, *Pratylenchus* spp., have a strong stylet and heavily sclerotized, flattened, cephalic framework. They are the parasites of the root cortex and feed on or break and destroy, cortical cells causing dark brown, necrotic lesions on the roots; they are recognized by the lesions they cause. Their feeding in the stele region results in extensive necrosis

and occlusion of xylem and phloem tissues (Olowe & Corbett, 1976). *Radopholus similis* is pathogenic to banana and many other tropical and subtropical crops. The nematode feeds and burrows in the cortex producing severe disease conditions. The genus seems to have evolved in the Australian Region and has been spread by man throughout the tropical and subtropical areas. The activity of these endoparasites produces lesions on roots which soon become invaded by fungi and bacteria and decay. Rot sets in and the nematodes then quickly move to attack healthier root tissues. *Hirschmanniella* spp. are aquatic forms which commonly parasitize roots of rice. They enter roots at some distance from the root tips and move freely in the air channels, between the radial lamellae of the parenchymatous cells, causing some necrosis, damage to cortical cells, retarded growth and low yields. However, the parasitized plants often recover due to increased production of roots.

Subterranean parts other than roots can also be attacked by members of the families Pratylenchidae, Anguinidae and Aphelenchoididae. Rhizomes of turmeric and banana are parasitized by *Pratylenchus* spp. *Ditylenchus dipsaci* is a serious pest of the bulbs of onion, narcissus, tulip, etc. in which its activity is continuous throughout the year. *Ditylenchus destructor* is a fungal feeder but it also infests potato tubers in which feeding cavities are formed which later start decaying. The nematode's saliva causes cell disorganization and starch hydrolysis through dehydrogenase activity. *Aphelenchoides arachidis* is endoparasitic on seed coats and pod shells of groundnuts and may also infest the roots and hypocotyl. Nematodes in harvested peanuts from Nigeria revived after one year when soaked in water (pers.obs.).

(c) Sedentary endoparasites. The endoparasitic Heteroderidae enter roots as second-stage larvae and develop to maturity whilst feeding; the female swells, ruptures the plant tissues and protrudes into the soil, its head remaining *in situ;* the male fertilizes the female, leaves the plant tissues and thereafter ceases to feed and eventually dies.

Among the Anguinoidea, only adults of *Anguina* spp. become sedentary in the grass and wheat seed galls and *Subanguina radicicola* is known to produce and inhabit galls on the roots. Among the Hoplolaimoidea, *Nacobbus* spp. produce galls that look similar to those produced by the *Meloidogyne* spp. and hence they are called false root-knot nematodes.

The primary objective of these nematodes is to establish themselves in the tissues, avoid necrosis and prevent the entry of decay-causing microorganisms by the sealing off of their place of entry and creating feeding sites for continuous food supply. The hosts have responded either by providing such amenities for the parasites or by developing defensive physical and chemical mechanisms to ward off or remove parasites, or at least to minimize their impact on general health. Under selection pressures, the parasites acquire the ability to break this resistance. Such resistance-breaking biotypes are known to occur in Heteroderidae. Pathotypes, as they are commonly called, differ in virulence: this has been explained by a gene for gene hypothesis, although it has not yet been proved in the case of nematodes. Several schemes have been put forward for the nomenclature and classification of the pathotypes of *Globodera rostochiensis* and *G. pallida* (Kort *et al.*, 1977; Canto Saenz & de Scurrah, 1977). Stone (1977) reviewed the taxonomy of the Heteroderoidea.

All pathotypes of *Globodera rostochiensis* and *G. pallida* parasitizing potato roots induce syncytial transfer cells (= feeding cells, nurse cells, giant cells) from which the parasites get a continuous supply of food. The ability to induce transfer cells depends on a compatible response from the plant to nematode saliva (Jones, 1975).

The root-knot nematodes (*Meloidogyne* spp.) also produce nectaries in the form of transfer cells around the head on which sedentary females go on feeding for a long time. The galls on the roots are produced by the host's reaction to parasitism involving extensive hypertrophy and hyperplasia. Cases are known where *Meloidogyne* spp. infection results in the eroding of the host's resistance to fungal infections.

The specialized morphological adaptations of the endoparasitic Tylenchida have been discussed by Bird (1971).

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