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# Feeding Habits in Soil Nematode Families and Genera—An Outline for Soil Ecologists

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*Abstract:* Because research on nematode involvement in trophic interactions, foodweb structure, and biodiversity is constrained by lack of an overview of nematode feeding habits, this outline presents a consensus of current thought on nematode feeding habits. The source of food is fundamental to trophic interactions and provides the basis for our definitions of the essential feeding types: 1) plant feeder, 2) hyphal feeder, 3) bacterial feeder, 4) substrate ingester, 5) predator of animals, 6) unicellular eucaryote feeder, 7) dispersal or infective stage of parasites, and 8) omnivore. Lists of families and genera with their presumed feeding types are given. Major gaps in knowledge of feeding in the smaller tylenchids and many dorylaims are noted.

*Key words:* bacterial feeding, feeding habit, foodweb, fungal feeding, nematode, omnivore, predator, soil ecology, trophic interaction.

With the increasing interest of soil ecologists in the role of nematodes in ecosystem processes (roles such as nutrient cycling, biological control and economic crop loss), there is an unmet need for a concise summary of current knowledge of nematode feeding habits. The analysis of available information is made increasingly difficult by changes in nematode systematics and recent contributions to nematode ecology. When all species of nematodes can be confidently assigned to feeding groups, there will follow a better understanding of the role of nematodes in soil and how changes in environmental factors influence the composition of the nematode fauna.

The first comprehensive review of nematode feeding habits was given by Neilsen (77). In an attempt to produce functional groups based on feeding habits, Paramonov (84) applied to nematodes terms such as "pararhizobes" (occur in the rhizosphere and sometimes damage plants) and "dyssaprobes" (feed in decomposing material but may enter healthy tissue). Both Wasilewska (121) and Yeates (127) grouped plant and soil nematodes by feeding habits. The classification of Tylenchida advocated by Siddiqi (99) has a strong "feeding habit" component. Recent ecological studies have revealed that feeding-habit groupings may not be sharply delimited. For example, abundant populations of *Aphelenchoides, Tylenchus, Tylencholaimus,* and *Ditylenchus* were discovered that could only be classified as "root/fungal feeding nematodes" (105), as well as "predacious" mononchids that multiplied using bacteria as a food source (130). These examples demonstrate the apparently arbitrary nature of traditional nematode feed-

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ing groups. Moreover, feeding habits of many nematodes have been inferred rather than confirmed by maintenance over many generations under biologically defined conditions.

Following Petersen and Luxton (86), we use "grazing foodweb" and "detritus foodweb" as terms for communities based on living green plants and dead organic matter, respectively. Their comments on the merging of the two webs are particularly relevant for nematodes, which are so often abundant at interfaces between living and dead material (as in the rhizosphere).

This paper is not a literature review and does not present new results; rather we present a basis for advancing understanding of the role of nematodes in soil ecology. The paper originated in discussions at the Second International Nematology Congress and lists nematode families and genera with our assessment of current understanding of their feeding habits. We hope that this paper will serve as a framework for ecologists to use independently of taxonomic philosophies. Andrássy (2,3), Lörenzen (58), Maggenti (62), and Siddiqi (99) all have differing approaches to the general classification of nematodes. The most recent taxonomic overview is contained in the Manual of Agricultural Nematology (76). The generic makeup of the families we use is compatible with these recent works; because they often assign differing taxonomic ranks to these groups, we do not list authorities.

## Conflicting Results and Observations

Soil ecologists are primarily concerned with relationships between biological populations and the soil environment, whether it be a high-input agroecosystem, natural ecosystem, or an area managed for sustained production. When these populations are cultured singly or together in the laboratory, many possible interactions and their consequences are reduced (52); thus, results are difficult to extrapolate to field conditions. The following are examples of such difficult extrapolations.

*1.* Although normally regarded as bacterial feeders, *Chiloplacus* (Acrobelidae) and *Rhabditis* (Rhabditidae) have been cultured on the fungi *Phoma* sp. and *Pythium middletonii,* respectively (39,92). In both cases, the "primary" food source is bacterial; the fact that the apparent secondary food belongs to the same trophic level of the "detritus foodweb" as the primary food shows the value of acknowledging such broad foodwebs. However, our interpretation of this dual feeding habit is i) bacterial contamination of the nematode cultures or ii) direct uptake of nutrients by nematodes, as occurs in axenic culture of *Caenorhabditis elegans* (21,70,132).

*2.* Hooper and Cowland (45) cultured the foliar nematode *Aphelenchoides ritzemabosi,* which normally feeds in the "grazing foodweb," on fungi ("detritus foodweb"), reinforcing observations that fungal feeding is the normal situation in Aphelenchida. Just as plant root cells are fed on in a variety of ways (see "plant feeding"), so are fungi (1).

*3.* It is difficult to extrapolate data from closely controlled monoxenic cultures of *Pratylenchus* and *Radopholus* on carrot discs to the heterogenous environment of field populations.

*4.* Although certain mononchids successfully cultured on bacteria contain living bacteria within the intestines (6), we question whether sufficient aggregations of bacteria exist under field conditions for bacterial ingestion to be of significant nutritional importance to the large mononchids.

*5.* The intestine of mononchids, rhabditids, dorylaims, etc., often appear pigmented, but such pigmentation has not been observed in Tylenchida or plant-feeding *Trichodorus* and *Longidorus* (76). There has been no attempt to relate this pigmentation to feeding habits.

*6.* Axenic culture of *Caenorhabditis elegans* and other "bacterial feeding" nematodes (21,70,73,132) highlights problems of interpretation, but there is evidence that development may be slower under axenic conditions (20). Bacterial feeding is re-

garded here as the principal source of nutrition for such nematodes under field conditions. Physical crushing of bacteria has been demonstrated in the pharyngeal bulb of *Acrobeloides nanus,* but bacterial feeding nematodes may defecate living bacteria and there is no general knowledge as to whether some nematodes actually kill, rupture, or lyse bacteria or merely remove adhering organic compounds (126). In several situations, there may be a degree of direct nutrient uptake through the cuticle or epidermis (33,50,79,132).

7. Although identification to family level is usually adequate, identification to species is sometimes necessary to accurately assign nematodes to trophic groups. For example, *Ditylenchus dipsaci is* an economically important plant feeding species, but most *Ditylenchus* spp. are hyphal feeding.

8. The delicate-speared Tylenchidae and Psilenchidae remain problematic. Although Sohlenius et al. (105) regarded several groups of them as "root/fungal feeding nematodes," the literature is conflicting and we have been unable to form a consensus about the classification of these two families. We have generally listed them as feeding on root epidermal cells and root hairs. Specific studies of their feeding in the rhizoplane would provide valuable information.

## Feeding Types of Nematodes in Plant and Soil Systems

Ideally the feeding habits of each nematode species should be determined in each particular ecological setting. Because this task is impractical, we offer the following outline for general use. Regardless of the trophic group, we strongly advocate appending species lists and depositing voucher specimens to make reinterpretation possible.

1. *Plant feeding:* This involves feeding on vascular plants; a tylenchoid stomatostyle or dorylaimoid odontostyle is always present. The posthatching life stages of most species are migratory. In sedentary species, the feeding site of the female may be undifferentiated, uninucleate, or polynucleate. Males of sedentary species sometimes have a degenerate stylet or reduced oesophagus, but data on the nutrition of such males is inadequate. Plant feeders may be polyphagous or show host specificity. Migratory species may generally be classified as ecto- or endoparasites. Feeding sites may be root-hair, epidermal, cortical, or vascular.

Although apparently not actively feeding, the migratory phases of *Pratylenchus,* infective second-stage *Heterodera,* and resistant stages of *Paratylenchus* are each an essential part of the life-cycle of these obligate plant feeders and are thus included in this category. This group includes algal feeders that have a narrow stylet and do not ingest chloroplasts, in contrast to types that swallow unicellular algae more or less intact.

The group may be subdivided into the following six groups: 1a) sedentary parasites (e.g., females of *Heterodera, Globodera, Meloidogyne, Verutus, Sphaeronema*); 1b) migratory endoparasites (e.g., Pratylenchidae, some Anguinidae); 1c) semiendoparasites (e.g., Hoplolaimidae, *Telotylenchus*); 1d) ectoparasites (e.g., Dolichodoridae, *Cephalenchus,* Criconematidae, Hemicycliophoridae, Paratylenchidae, Trichodoridae, *Pungentus,* Longidoridae); 1e) epidermal cell and root hair feeders (e.g., Tylenchidae, Psilenchidae, Atylenchidae); and 1f) algal, lichen (algal or fungal component), or moss feeders that feed by piercing (e.g., *Tylenchus, Laimaphelenchus,* Anguinidae).

2. *Hyphal feeding:* This involves penetration of fungal hyphae by a stomatostyle or odontostyle (stylet or spear). In addition to obligate hyphal feeders, this group includes the alternate life cycle of some invertebrate parasites (e.g., *Deladenus*) (75). Yeasts may be included as a food source under this heading, except when ingested whole (see "unicellular eucaryote feeding"). Feeding on hyphae of saprophytic fungi has ecological implications quite different from feeding on mycorrhizal fungi.

There is need for research on such interactions to determine whether the same nematode can feed on both saprophytic and mycorrhizal fungi.

*3. Bacterial feeding:* This category includes species that feed on any procaryote food source, whether through a narrow (*Rhabditis, Alaimus*) or broad (*Diplogaster*) mouth; axenic culture indicates that there may be an element of absorption of nutrients (33,50,79,132). Species with a broad mouth may ingest other types of food. The soil stages of certain nematode parasites of vertebrates and invertebrates that feed on bacteria should be included. Although morphological data (75) suggest that infective stages of *Steinernema* may be nonfeeding, they may be mass produced on artificial media, providing their bacterial symbionts are present (76). Some Rhabditidae and Diplogasteridae may use a phoretic (transport) host, especially insects.

*4. Substrate ingestion:* This type of feeding occurs in at least diplogasterids and *Daptonema* sp. Substrate ingestion may be incidental to bacterial feeding, predation, and unicellular eucaryote feeding in many groups, because more than a pure food source is ingested. Although soil nematodes may ingest and lyse bacteria, there is no available evidence that digestion of complex organic substrates occurs in the gut of soil nematodes (a fact that may reflect technical difficulty). Consequently, no genera have been given primary classification under this type. The expression "nonselective deposit feeding" used for aquatic nematodes covers a similar situation.

*5. Animal predation:* Some species of nematodes feed on invertebrates such as protozoa, nematodes, rotifers, and enchytraeids, either as "ingesters" (type 5a; e.g., *Diplogaster, Mononchus, Nygolaimus*) or as "piercers" (type 5b), sucking body fluids through a narrow stylet (e.g., *Seinura, Labronema, Laimaphelenchus*). The intestine of piercers never contains distinct prey remnants.

*6. Unicellular eucaryote feeding:* A wide range of nematodes reportedly feed on diatoms or other algae, but lack of marker structures in the nematode food and the presence of globules, pigmentation, or inclusions in nematode intestines make determination difficult. This feeding type includes ingestion of fungal spores and whole yeast cells.

*7. Dispersal or infective stages of animal parasites:* Other stages of animal parasitic nematodes outside their alternate or definitive hosts may occur in the soil (e.g., *Deladenus, Heterorhabditis*) or vertebrates (e.g., *Strongyloides*); we include here entomogenous species. If they feed and contribute to soil processes, these species should be included in other appropriate categories; if they invade a host they leave the soil system (in the narrow sense); if they die in the soil they contribute to nutrient pools. We do not include in this category forms (especially Rhabditidae and Diplogasteridae) that merely use animals as phoretic (transport) hosts.

*8. Omnivorous:* Although some nematodes appear normally to feed on a wide range of foods (particularly combining feeding types 2–6), it is best to restrict use of this term to (a few) dorylaims (31,95); when possible, nematodes should be classified in types 1–7. A similar procedure was used for soil fauna by Petersen et al. (87).

## Feeding Types in Nominal Orders and Families

In the following systematic list of nematode families and feeding type, we give indicative genera for each family; the numbers refer to the eight feeding types. Numbers in parentheses refer to tentative assignments or situations with alternative food sources. For a given family or genus, if two or more types are indicated, they are presented in strictly numerical order. For some groups, detailed information is given (e.g., algal feeding may be a specialization of unicellular eucaryote feeding). Table 1 contains an alphabetical list of nematode genera and their feeding types.

TABLE 1. Feeding types in nematode genera. Numbers refer to the eight feeding types outlined in the text; numbers in parenthesis indicate a tentative assignment. The main food source is given first. For genera maintained for several generations under defined conditions, unqualified reference is made to that publication by number; for genera where the publication number is preceded by "see," a more general (or less specific) support for allocation to the feeding type is indicated; for genera where we have not obtained a direct reference to feeding activity, the family name is given.

| Genus | Feeding type | Family or literature citation |
|---|---|---|
| *Ablechroiulus* | 3 | Rhabditidae |
| *Achromadora* | (6) | Achromodoridae |
| *Acontylus* | 1b | (66) |
| *Acrobeles* | 3 | (111,126) |
| *Acrobeloides* | 3 | (71,104,126) |
| *Acrobelophis* | 3 | Cephalobidae |
| *Acrolobus* | 3 | Cephalobidae |
| *Acromoldavicus* | 3 | Cephalobidae |
| *Acrostichus* | 3 | Diplogasteridae; (88) |
| *Actinca* | 5, 8 | Actinolaimidae |
| *Actinolaimus* | 5, 8 | (56); (see 31,100) |
| *Aetholaimus* | 5 | Nygolaimidae |
| *Aglenchus* | 1e | Tylenchidae; (122) |
| *Alaimus* | 3 | (see 77) |
| *Allantonema* | 7 or 2 | (119) |
| *Allodorylaimus* | 8 | Dorylaimidae |
| *Allotrichodorus* | 1d | Trichodoridae; (see Decraemer in 76) |
| *Amphidelus* | 3 | Alaimidae |
| *Amplimerlinius* | 1d | (14,36); (see Anderson & Potter in 76) |
| *Anaplectus* | 3 | (122) |
| *Anatonchus* | 5a | (18); (see 100) |
| *Anguina* | 1a or b | (22); (see Krall in 76) |
| *Anomyctus* | 2? | (see Nickle & Hooper in 76) |
| *Antarctylus* | 1c | Hoplolaiminae |
| *Aorolaimus* | 1c | Hoplolaiminae |
| *Aphanolaimus* | 3 | Halaphanolaimidae |
| *Aphasmatylenchus* | 1c | (34); (see Fortuner in 76) |
| *Aphelenchoides* | 2 or 1b, 1e or 1f | (68); (see 122) |
| *Aphelenchus* | 2 or 1e | (17,23,40,65); (see 122) |
| *Aporcelaimellus* | 5, 8 | (117,122); (see 31) |
| *Aporcelaimium* | 8 | Aporcelaimidae |
| *Aporcelaimus* | 5, 8 | (114,122); (see 31,100) |
| *Apratylenchoides* | 1b | Pratylenchidae |
| *Aprutides* | 2 | Aphlenchoididae |
| *Aquatides* | 5 | (10); (see 100) |
| *Atylenchus* | 1d | Tylenchidae |
| *Aulolaimus* | 3 | Cryptonchidae |
| *Axonchium* | 1, 8? | (see 100) |
| *Basiria* | 1e | Tylenchidae |
| *Bastiania* | 3 | Bastianiidae |
| *Bathyodontus* | 3 | Bathyodontidae; (see 12) |
| *Belonolaimus* | 1d | (15) |
| *Bicirronema* | 3 | Chambersiellidae |
| *Bitylenchus* | 1d | Tylenchorhynchidae; (see Anderson & Potter in 76) |
| *Boleodorus* | 1e or 2(?) | Tylenchidae |
| *Brevibucca* | 3 | Brevibuccidae |
| *Brittonema* | 5, 8 | Actinolaimidae |
| *Bunonema* | 3 | (77,128) |
| *Bursaphelenchus* | 2 | (32,63); (see Nickle & Hooper in 76) |
| *Bursilla* | 3 | Rhabditidae |
| *Butlerius* | 3, 5 | (28,89,101); (see 100) |
| *Cacopaurus* | 1a | Paratylenchidae; (112); (see Raski in 76) |
| *Cactodera* | 1a | (19,98); (see Baldwin & Mundo-Ocampo in 76) |
| *Caenorhabditis* | 3 | (25,78,97); (see 107) |

TABLE 1. *Continued*

| Genus | Feeding type | Family or literature citation |
|---|---|---|
| *Caloosia* | 1d | Hemicycliophoridídae |
| *Campydora* | 8? | Campydoridae |
| *Carcharolaimus* | 5 | (28); (see 100) |
| *Cephalenchus* | 1d | (37,109); (see 122) |
| *Cephalobus* | 3 | (81,88); (see 72,122) |
| *Ceratoplectus* | 3 | Plectididae |
| *Cervidellus* | 3 | (122) |
| *Chambersiella* | 3 | Chambersiellidae |
| *Cheilorhabditis* | 3 | Rhabditidae |
| *Chiloplacus* | 3 | (118,122) |
| *Choanolaimus* | 5a | Choanolaimidae |
| *Chondronema* | 7, 2? | (16) |
| *Chromadorina* | 3, 6? | Chromadoridae; (116) |
| *Chromadorita* | 6 | (49) |
| *Chronogaster* | 3 | Leptolaimidae |
| *Chrysonemoides* | ? | Chrysonematidae |
| *Clarkus* | 5a | (67,106); (see 101,130) |
| *Coarctadera* | 3 | Rhabditidae; (see 107) |
| *Cobbonchus* | 5a | (see 100) |
| *Coomansus* | 5a | (31) |
| *Coslenchus* | 1e | (as *Aglenchus*); (122) |
| *Craspedonema* | 3 | Butonematidae |
| *Criconema* | 1d | (see 26,93) |
| *Criconemoides* | 1d | (see 26,93) |
| *Crossonema* | 1d | (see 26,93) |
| *Cruznema* | 3 | (108) |
| *Cryphodera* | 1a | (see 8,60) |
| *Cryptonchus* | 3 | Cryptonchidae |
| *Curviditis* | 3 | Rhabditidae |
| *Cuticonema* | 3 | Breviibuccidae |
| *Cuticularia* | 3 | Rhabditidae |
| *Cylindrolaimus* | 3 | Diplopeltidae |
| *Daptonema* | 3, 4, 5 or 6 | (13) |
| *Deladenus* | 2 | (9,129); (see 62) |
| *Demaniella* | 3 | (88) |
| *Deontolaimus* | 3 | Leptolaimidae |
| *Desmodora* | 3, 6 | Desmodoridae; (74) |
| *Desmolaimus* | 3 | Linhomoeidae |
| *Desmoscolex* | 3 | Desmoscolecidae |
| *Dichromadora* | 3, 6? | (13,120) |
| *Diphtherophora* | 2 | Diphtherophoridae; (see 4) |
| *Diplenteron* | 3? | (64,125); (see 100) |
| *Diplogaster* | 3, 5a, 6 or 8 | (see 72,100) |
| *Diplogasteritus* | 3 | (124) |
| *Diplogasteroides* | 3 | Diplogasteroididae |
| *Diploscapter* | 3 | (42,88) |
| *Discolaimium* | 5? | (see 100) |
| *Discolaimus* | 5 | (28,56); (see 31,100) |
| *Ditylenchus* | 2, or 1b | (55,122); (see Sturhan & Brezeski in 76) |
| *Dolichodorus* | 1d | (82,83,85); (see Smart & Nguyen in 76) |
| *Dolichorhabditis* | 3 | Rhabditidae |
| *Dolichorhynchus* | 1d | Dolichodoridae |
| *Domorganus* | 3 | Diplopeltidae |
| *Dorydorella* | 8 | Dorylaimidae |
| *Dorylaimellus* | 1, 2? | Belondiridae; (see 131) |
| *Dorylaimoides* | 8? | Leptonchidae |
| *Dorylaimus* | 8 | (56); (see 77,100) |
| *Doryllium* | 2? | Leptonchidae |
| *Drilocephalobus* | 3 | Osstellidae |

TABLE 1. *Continued*

| Genus | Feeding type | Family or literature citation |
|---|---|---|
| *Durinema* | 5 | (see 77,100) |
| *Ecphyadophora* | 1d or 2(?) | Ecphyadophoridae |
| *Ecumenicus* | 8 | Dorylaimidae |
| *Elaphonema* | 3 | Elaphonematidae |
| *Enchodelus* | 8 or 6? | Nordiidae |
| *Epidorylaimus* | 8 | Dorylaimidae |
| *Ereptonema* | 3 | Ereptonemidae |
| *Ethmolaimus* | 3, 6? | Ethmolaimidae |
| *Eucephalobus* | 3 | (122) |
| *Eudorylaimus* | 5, 8 | (29,44,117); (see 31,100) |
| *Eurystomina* | (5) | Eurystominidae |
| *Eumonhystera* | 3, 4 | Monhysteridae |
| *Euteratocephalus* | 3 | Teratocephalidae |
| *Fictor* | 3, 5, 6 | (88,103); (see 100) |
| *Filenchus* | 1e | Tylenchidae |
| *Funaria* | 2? | Leptonchidae |
| *Fungiotonchium* | 2 | Iontonchiidae (see 99) |
| *Geocenamus* | 1d | Dolichodoridae |
| *Geomonhystera* | 3, 4 | Monhysteridae |
| *Glauxinema* | 6 | Neodiplogasteridae |
| *Globodera* | 1a | (53); (see Baldwin & Mundo-Ocampo in 76) |
| *Goffartia* | 3 | Diplogasterididae |
| *Goodeyus* | 3 | Cylindrocorporidae |
| *Gracilacus* | 1d | Paratylenchidae; (see Raski in 76) |
| *Granonchulus* | 5a | Mononchidae; (35) |
| *Haliplectus* | 3 | Haliplectidae |
| *Helicotylenchus* | 1c | (51); (see Fortuner in 76) |
| *Hemicriconemoides* | 1d | Criconematidae; (see 93) |
| *Hemicycliophora* | 1d | Criconematidae; (see 93) |
| *Heterocephalobellus* | 3 | Cephalobidae |
| *Heterocephalobus* | 3 | Cephalobidae |
| *Heterodera* | 1a | (see Baldwin & Mundo-Ocampo in 76) |
| *Heterorhabditis* | 7, 3 | (90); (see Wouts in 76) |
| *Hexatylus* | 2 | (24); (see 72) |
| *Hirschmanniella* | 1b | (7); (see Loof in 76) |
| *Hoplolaimus* | 1c | Hoplolaimidae |
| *Hoplotylus* | 1b | Pratylenchidae |
| *Howardula* | 7 or 2 | Allantonematidae |
| *Huntaphelenchoides* | 2 | Aphelenchoididae |
| *Iotonchus* | 5a | (67,100,101) |
| *Ironus* | 5a or 6 | (47); (see 100) |
| *Isolaimium* | (3) | Isolaimidae |
| *Kirjanovia* | 3 | Cephalobidae |
| *Kochinema* | 8 | Nordiidae |
| *Labronema* | 5, 8 | (28,30,88,122); (see 31,100) |
| *Laimaphelenchus* | 5b, 1f, 2 | (see 100) |
| *Laimydorus* | 8 | (see 100) |
| *Lelenchus* | 1e | Tylenchidae |
| *Leptolaimus* | 3 | (13) |
| *Leptonchus* | 2 | (see 31) |
| *Longidorella* | 1d | Nordiidae |
| *Longidorus* | 1d | Longidoridae |
| *Loofia* | 1d | Hemicycliophoridae |
| *Macrotrophurus* | 1d | Dolichodoridae |
| *Malenchus* | 1e | Tylenchidae |
| *Meloidodera* | 1a | (see Baldwin & Mundo-Ocampo in 76) |
| *Meloidoderita* | 1a | (see 76) |
| *Meloidogyne* | 1a | (see 27,96) |
| *Merlinius* | 1d | (see Anderson & Potter in 76) |

TABLE 1. *Continued*

| Genus | Feeding type | Family or literature citation |
|---|---|---|
| *Mesocriconema* | 1d | (see 93) |
| *Mesodiplogaster* | 3, 5 | (102,103); (see 100) |
| *Mesodorylaimus* | 8 | (29); (see 31,95,100) |
| *Mesorhabditis* | 3 | (107,122,126) |
| *Metacrobeles* | 3 | Cephalobidae |
| *Metadiplogaster* | 3 | Diplogasteridae |
| *Metateratocephalus* | 3 | Teratocephalidae |
| *Miconchus* | 5a | (see 100) |
| *Microdorylaimus* | 8 | Nordiidae |
| *Microlaimus* | 3 | Microlaimidae |
| *Monhystera* | 3, (4) | (122); (see 77,115) |
| *Monhystrella* | 3, 4 | (13) |
| *Monobutlerius* | 3 | Diplogasteridae |
| *Mononchoides* | 3, 5a | (89); (see 100) |
| *Mononchulus* | 3 | (see 31) |
| *Mononchus* | 5a | (38,88); (see 31,100) |
| *Monotrichodorus* | 1d | Trichodoridae; (see Decraemer in 76) |
| *Morulaimus* | 1d | Belonolaimidae; (see Smart & Nyguen in 76) |
| *Mylonchulus* | 5a | (48,67); (see 31,100) |
| *Myolaimus* | 3 | Myolaimidae |
| *Nacobbus* | 1a | (see Jatala in 76) |
| *Nagelus* | 1d | Dolichodoridae |
| *Namibinema* | 3 | Cephalobidae |
| *Neoactinolaimus* | 5, 8 | (101); (see 100) |
| *Neoaplectana* | 7, 3 | (see 76) |
| *Neodiplogaster* | 3, 4 or 5 | Neodiplogasteridae |
| *Neopsilenchus* | 1e | Tylenchidae |
| *Neothada* | 1e or 2(?) | Tylenchidae |
| *Nothacrobeles* | 3 | Cephalobidae |
| *Nothotylenchus* | 2 | Anguinidae |
| *Nullonchus* | 5a | (see 100) |
| *Nygolaimium* | 5 | (see 100) |
| *Nygolaimoides* | 5 | Nygolaimidae |
| *Nygolaimus* | 5 | (113,122); (see 31,100) |
| *Odontolaimus* | 3 or 6? | Odontolaimidae |
| *Odontopharynx* | 3, 5a | Odontopharyngidae |
| *Odontorhabditis* | 3 | Odontorhabditidae |
| *Ogma* | 1d | (see 93) |
| *Oionchus* | 3 | Mononchulidae |
| *Onchulus* | 5a or 6 | Onchulidae |
| *Opisthodorylaimus* | 8 | Dorylaimidae |
| *Orrina* | 1a or b | (see Krall in 76) |
| *Osstella* | 3 | Osstellidae |
| *Oxydirus* | 1, 8? | Belondiridae |
| *Panagrellus* | 3 | (21) |
| *Panagrobelium* | 3 | Panagrolaimidae |
| *Panagrobelus* | 3 | Panagrolaimidae |
| *Panagrocephalus* | 3 | Cephalobidae |
| *Panagrolaimus* | 3 | (88,126) |
| *Paracrobeles* | 3 | Cephalobidae |
| *Paractinolaimus* | 5 | (46) (see 100) |
| *Paracyatholaimus* | 6? | (13) |
| *Parahadronchus* | 5a | (see 100) |
| *Paralongidorus* | 1d | (see 11,54) |
| *Paramphidelus* | 3 | Alaimidae |
| *Paraphanolaimus* | 3 | Halaphanolaimidae |
| *Paraphelenchus* | 2 | (110); (see Nickle & Hooper in 76) |
| *Paraplectonema* | 3 | Leptolaimidae |
| *Pararotylenchus* | 1c | (see Fortuner in 76) |

TABLE 1. *Continued*

| Genus | Feeding type | Family or literature citation |
|---|---|---|
| *Paratrichodorus* | 1d | Trichodoridae; (see Decraemer in 76) |
| *Paratripyla* | 5a | Tripylidae |
| *Paratrophurus* | 1d | Dolichodoridae |
| *Paratylenchus* | 1d | (94,122); (see Raski in 76) |
| *Paravulvus* | 5? | Nygolaimidae |
| *Paraxonchium* | 5, 8 | Aporcelaimidae |
| *Pareudiplogaster* | 6, 3 | (13) |
| *Paroigolaimella* | 3 | (88) |
| *Paurodontus* | 2, 7 | (as *Neotylenchus*); (40) |
| *Pellioditis* | 3 | (107) |
| *Pelodera* | 3 | (88,107,122) |
| *Peltamigratus* | 1c | (see 76) |
| *Phasmarhabditis* | 3 | (107) |
| *Placodira* | 3 | Cephalobidae |
| *Plectonchus* | 3 | Brevibuccidae |
| *Plectus* | 3 | (77,88,122) |
| *Pleurotylenchus* | 1d | Tylodoridae |
| *Pratylenchoides* | 1b | (see Loof in 76) |
| *Pratylenchus* | 1b | (see Loof in 76) |
| *Prionchulus* | 5a | (5,61,69); (see 100) |
| *Prismatolaimus* | 3? | (see 77) |
| *Pristionchus* | 3, 5a | Neodiplogasteridae |
| *Prochromadora* | 3, 6? | Chromadoridae |
| *Prodesmodora* | 3 | Desmodoridae |
| *Prodorylaimium* | 8 | Dorylaimidae |
| *Prodorylaimus* | 8 | Dorylaimidae |
| *Proleptonchus* | 8? | Leptonchidae |
| *Protocylindrocorpus* | 3 | Cylindrocorporidae (88) |
| *Protorhabditis* | 3 | Rhabditidae |
| *Pseudacrobeles* | 3 | Cephalobidae |
| *Pseudhalenchus* | 2 | Anguinidae |
| *Pseudoaulolaimus* | 3 | Cryptonchidae |
| *Psilenchus* | 1e | Psilenchidae |
| *Pterotylenchus* | 1a or b | Anguinidae |
| *Pterygorhabditis* | 3 | Pterygorhabditidae |
| *Punctodera* | 1a | (see Baldwin & Mundo-Ocampo in 76) |
| *Punctodora* | 3, 6? | Chromadoridae |
| *Pungentus* | 1d, 5, 8 | (see 31,100) |
| *Quinisulcius* | 1d | (see 76) |
| *Radopholus* | 1b | (see Loof in 76) |
| *Rhabditis* | 3 | (88,102,107,122) |
| *Rhabditoides* | 3 | Rhabditidae |
| *Rhabditophanes* | 3 | Alloionematidae |
| *Rhabdolaimus* | 3 | (see 77) |
| *Rhabdontolaimus* | 3 | (88) |
| *Rhadinaphelenchus* | 1b | (see Nickle & Hooper in 76) |
| *Rhodolaimus* | 3 | Bunonematidae |
| *Rotylenchulus* | 1a | (57) |
| *Rotylenchus* | 1c | Hoplolaiminae; (see Fortuner in 76) |
| *Scottnema* | 3 | Cephalobidae; (80) |
| *Scutellonema* | 1c | Hoplolaiminae; (see Fortuner in 76) |
| *Scutylenchus* | 1d | Dolichodoridae |
| *Sectonema* | 5, 8 | (see 100) |
| *Seinura* | 5b | (28,41,43,101,123); (see 100) |
| *Seleborca* | 3 | Acrobelidae |
| *Sphaerolaimus* | 5a | Sphaerolaimidae |
| *Sphaeronema* | 1a | (see Raski in 76) |
| *Sphaerularia* | 7, 2 | (91) |
| *Sporonchulus* | 5a | (see 100) |

TABLE 1. *Continued*

| Genus | Feeding type | Family or literature citation |
|---|---|---|
| *Stegelleta* | 3 | Cephalobidae |
| *Stegelletina* | 3 | Cephalobidae |
| *Steinernema* | 7, 3 | (see 76) |
| *Stomachoglossa* | (5) | (see 100) |
| *Subanguina* | 1a or b | (see 76) |
| *Sulphuretylenchus* | 7 or 2 | (see 76) |
| *Synonchium* | 5 | (see 100) |
| *Telotylenchus* | 1c | Dolichodoridae |
| *Tenunemellus* | 1d or 2(?) | Ecphyadorphoridae |
| *Teratocephalus* | 3 | (see 77) |
| *Teratolobus* | 3 | Cephalobidae |
| *Teratorhabditis* | 3 | Rhabditidae |
| *Theristus* | 3, 4 or 6 | (see 77) |
| *Thonus* | 5, 8 | (31) |
| *Thornenema* | 8 | Dorylaimidae |
| *Thornia* | 8? | (see 100) |
| *Tobrilus* | 5a or 6 | (see 100) |
| *Torumanawa* | 8 | Aporcelaimidae |
| *Tricephalobus* | 3 | Panagrolaimidae |
| *Trichodorus* | 1d | Trichodoridae; (see Decraemer in 76) |
| *Tripius* | 7, 2 | (see 76) |
| *Tripyla* | 5a | (77,100) |
| *Trischistoma* | 5a | Tripylidae; (see 100) |
| *Trophonema* | 1a | Tylenchulidae; (see Raski in 76) |
| *Trophotylenchus* | 1a | Tylenchulidae |
| *Trophurus* | 1d | Dolichodoridae |
| *Turbatrix* | 3 | (70,89) |
| *Tylencholaimellus* | 2 | (122) |
| *Tylencholaimus* | 2 | (29,105,122); (see 31) |
| *Tylenchorhynchus* | 1d | (see Anderson & Potter in 76) |
| *Tylenchulus* | 1a | (see Raski in 76) |
| *Tylenchus* | 1f, 2? | Tylenchidae; (122) |
| *Tylocephalus* | 3 | (see 77) |
| *Tylodorus* | 1d | Tylodoridae |
| *Tylolaimophorus* | 2 | Diphtherophoridae |
| *Tylopharynx* | 3 | Tylopharyngidae |
| *Verutus* | 1a | (see Baldwin & Mundo-Ocampo in 76) |
| *Westindicus* | (5) | (see 100) |
| *Wilsonema* | 3 | (77,122) |
| *Xiphinema* | 1d | Longidoridae |
| *Ypsylonellus* | 3 | Acrobelidae |
| *Zeldia* | 3 | (126) |
| *Zygotylenchus* | 1b | (see Loof in 76) |

*Order Monhysterida*

Linhomoeidae: *Desmolaimus*
(3) bacterial feeding
Monhysteridae: *Monhystera, Geomonhystera*
3 bacterial feeding
4 substrate ingestion
Sphaerolaimidae: *Sphaerolaimus*
5 predacious
Xyalidae: *Theristus, Daptonema*
3 bacterial feeding
4 substrate ingestion
5 predacious
6 algal feeding

*Order Desmoscolecida*

Desmoscolecidae: *Desmoscolex*
(3) bacterial feeding

*Order Araeolaimida*

All terrestrial forms are apparently type 3.
Diplopeltidae: *Cylindrolaimus, Domorganus*

(3) bacterial feeding
7 *Domorganus* (sometimes associated with earthworms)
Halaphanolaimidae: *Aphanolaimus*
(3) bacterial feeding
Haliplectidae: *Haliplectus*
(3) bacterial feeding
Leptolaimidae: *Leptolaimus, Chronogaster*
3 bacterial feeding
Plectidae: *Plectus, Anaplectus*
3 bacterial feeding (*Plectus*)
Rhabdolaimidae: *Rhabdolaimus*
3 bacterial feeding
Wilsonematidae: *Wilsonema, Tylocephalus, Ereptonema*
3 bacterial feeding

*Order Chromadorida*

Achromadoridae: *Achromadora*
6 algal feeding
Choanolaimidae: *Choanolaimus, Synonchium*
5 predacious
Cyatholaimidae: *Paracyatholaimus*
6 algal feeding
Desmodoridae: *Desmodora*
(3) bacterial feeding
6 algal feeding
Ethmolaimidae: *Ethmolaimus*
3 bacterial feeding
6 algal feeding
Hypodontolaimidae: *Chromadorita*
6 algal feeding
Microlaimidae: *Microlaimus*
3 bacterial feeding
6 algal feeding

*Order Rhabditida*

Members of this order that occur in soil are basically type 3 (bacterial feeding).
Acrobelidae: *Acrobeles, Cervidellus, Acrobeloides*
3 bacterial feeding
Alloionematidae: *Alloionema, Rhabditophanes*
3 bacterial feeding (soil-dwelling stages only)
7 insect parasites
Brevibuccidae: *Brevibucca, Cuticonema*
(3) bacterial feeding; insect associates
Bunonematidae: *Bunonema, Rhodolaimus, Craspedonema*
3 bacterial feeding
Cephalobidae: *Cephalobus, Heterocephalobus, Eucephalobus*
3 bacterial feeding
Chambersiellidae: *Chambersiella, Bicirronema*
3 bacterial feeding
Cylindrocorporidae: *Protocylindrocorpus, Goodeyus*
(3) bacterial feeding
Diploscapteridae: *Diploscapter*
3 bacterial feeding
Elaphonematidae: *Elaphonema*
3 bacterial feeding
Myolaimidae: *Myolaimus*
3 bacterial feeding
Odontopharyngidae: *Odontopharynx*
3 bacterial feeding
5 predatory
Odontorhabditidae: *Odontorhabditis, Cheilorhabditis*
3 bacterial feeding
Osstellidae: *Osstella*
3 bacterial feeding
Panagrolaimidae: *Panagrolaimus, Panagrellus, Turbatrix*
3 bacterial feeding (many are insect associates)
Pterygorhabditidae: *Pterygorhabditis*
3 bacterial feeding
Rhabditidae: *Rhabditis, Mesorhabditis, Pelodera*
3 bacterial feeding (many are associated with earthworms, arthropods, or vertebrates)
Steinernematidae: *Steinernema* (= *Neoaplectana*), *Heterorhabditis*
7 entomogenous
3 bacterial feeding in free-living stages
Teratocephalidae: *Teratocephalus, Euteratocephalus*
3 bacterial feeding

*Order Diplogasterida*

The basic habit of these is apparently type 3 (bacterial feeding).
Diplogasteridae: *Diplogaster, Butlerius*
These may use insects for dispersal.

3 bacterial feeding
5 predacious

Diplogasteroididae: *Diplogasteroides, Goffartia*
3 bacterial feeding

Neodiplogasteridae: *Neodiplogaster, Diplenteron, Fictor, Pristionchus*
These may use insects for dispersal.
3 bacterial feeding
4 substrate ingestion
5 predacious
6 in *Pareudiplogaster*

Tylopharyngidae: *Tylopharynx*
3 bacterial feeding

*Order Tylenchida*
*Suborder Tylenchina:*

Allantonematidae: *Allantonema, Howardula, Sulphuretylenchus*
7 insect parasites
? alternate generation possibly feeds in soil

Anguinidae: *Anguina, Ditylenchus, Nothotylenchus*
1 parasites of aerial parts of plants
2 fungal feeders

Atylenchidae: *Atylenchus, Eutylenchus*
(1) root feeding

Caloosiidae: *Caloosia*
1 ectoparasites of roots

Chondronematidae: *Chondronema*
7 juveniles parasitic in insects
? adults free-living, possible nonfeeding

Criconematidae: *Criconema, Ogma, Criconemella, Hemicriconemoides*
1 ectoparasites of roots; males often without stylets

Dolichodoridae: *Dolichodorus, Tylenchorhynchus, Merlinius, Belonolaimus*
1 migratory ectoparasites of roots

Ecphyadophoridae: *Ecphyadophora, Tenunemellus*
(1) root feeding

Hemicycliophoridae: *Hemicycliophora*
1 ectoparasites of roots; males often without stylet

Heteroderidae: *Heterodera, Globodera, Cryphodera*
1 obligate endoparasites; female cuticle produces resistant cyst

Hoplolaimidae: *Hoplolaimus, Rotylenchus, Helicotylenchus*
1 ectoparasitic or semi-endoparasitic on roots

Iotonchiidae: *Iotonchium*
2 hyphal feeding in some stages
7 insect parasites

Meloidogynidae: *Meloidogyne*
1 obligate endoparasites; female saccate

Nacobbidae: *Nacobbus*
1 gall-forming root endoparasites; saccate females

Neotylenchidae: *Fergusobia, Deladenus*
7 insect parasites with alternate generation being
2 hyphal-feeding or
1 plant feeding

Paratylenchidae: *Paratylenchus, Gracilacus*
1 ectoparasites of roots; male often without stylet

Paurodontidae: *Paurodontus*
2 hyphal-feeding generation and
7 probable insect-parasitic generation

Pratylenchidae: *Pratylenchus, Radopholus*
1 migratory endoparasites of roots

Psilenchidae: *Psilenchus*
1 associates of lower plants (other than fungi); feed on root hairs and epidermal cells

Rotylenchulidae: *Rotylenchulus*
1 ectoparasitic on roots of higher plants; female saccate

Sphaeronematidae: *Sphaeronema, Meloidoderita*
1 females sedentary ecto- or endoparasites of roots

Sphaerularidae: *Sphaerularia, Tripius*
2 hyphal-feeding generation may occur
7 females parasitic in insect haemocoel

Sychnotylenchidae: *Sychnotylenchus, Neoditylenchus*
7 associates of bark beetles

Tylenchidae: *Tylenchus, Filenchus, Boleodorus*
1 associates of algae, mosses, lichens, and plant roots

Tylenchulidae: *Tylenchulus, Trophonema*
1 ectoparasites of roots; female saccate but usually outside root

Tylodoridae: *Tylodorus, Cephalenchus*
1 root feeding

*Suborder Aphelenchina:*

Aphelenchidae: *Aphelenchus*
2 hyphal feeding; sometimes feed on fungi in diseased plants
Aphelenchoididae: *Aphelenchoides, Bursaphelenchus, Anomyctus, Rhadinaphelenchus*
1 plant feeding in a minority of forms (*Aphelenchoides* may feed on fungi but also on aerial parts of plants including ferns)
2 hyphal feeding in terrestrial species; may be insect associated
5 predacious (*Laimaphelenchus*)
6 algal feeding (*Laimaphelenchus*)
Paraphelenchidae: *Paraphelenchus*
2 hyphal feeders
Seinuridae: *Seinura*
5 predacious

*Order Enoplida*

Alaimidae: *Alaimus, Amphidelus*
3 bacterial feeding
Cryptonchidae: *Cryptonchus, Aulolaimus*
(3) bacterial feeding (*Aulolaimus*)
Ironidae: *Ironus*
5 predacious
Oncholaimidae: *Bastiania*
(3) bacterial feeding
Onchulidae: *Onchulus, Stenonchulus*
(3) bacterial feeding
(5) predacious
(8) omnivorous
Prismatolaimidae: *Prismatolaimus*
3 bacterial feeding
Tobrilidae: *Tobrilus*
(5) predacious
(6) algal feeding
Tripylidae: *Tripyla, Trischistoma*
(5) predacious

*Order Mononchida*

Most common forms are type 5 (predacious) but some are type 3 (bacterial feeding).
Anatonchidae: *Anatonchus*
5 predacious; prey may be ingested whole
Bathyodontidae: *Bathyodontus, Mirolaimus*
(3) bacterial feeding
Mononchidae: *Mononchus*
5 predacious; prey not ingested whole
(3) may also feed on bacteria
Mononchulidae: *Mononchulus, Oionchus*
(3) bacterial feeding

*Order Dorylaimida*

Actinolaimidae: *Actinolaimus, Brittonema, Actinca*
5 predacious
(8) omnivorous
Aporcelaimidae: *Aporcelaimus, Paraxonchium, Sectonema*
5 predacious
(8) omnivorous
Belondiridae: *Axonchium, Dorylaimellus, Oxydirus*
(1) plant feeding
Diphtherophoridae: *Diphtherophora, Tylolaimophorus*
(2) hyphal feeding
Discolaimidae: *Discolaimus, Discolaimium*
(5) predacious
Dorylaimidae: *Dorylaimus, Laimydorus, Mesodorylaimus, Prodorylaimus, Thornenema, Thornus*
(8) omnivorous
5 predacious (*Labronema*)
Leptonchidae: *Leptonchus, Tylencholaimellus, Doryllium*
(2) hyphal feeding
Longidoridae: *Longidorus, Xiphinema*
1 plant feeding; may transmit plant viruses
Nordiidae: *Eudorylaimus*
(8) omnivorous (possibly all genera are plant feeding)
(1) plant feeding
Nygolaimidae: *Nygolaimus*
5 predacious, especially on enchytraeids
Trichodoridae: *Trichodorus, Paratrichodorus*
1 plant feeding; may transmit plant viruses

*Order Isolaimida*

Isolaimidae: *Isolaimium*
(3) bacterial feeding

*Order Stichosomida*

Mermithidae: *Mermis, Agamomermis*
7 parasites of arthropods and other invertebrates; postparasitic stages may occur in soil

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