Associations Between Nematodes (Nematoda) and Oligochaetes (Annelida)

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ABSTRACT: The associations between oligochaetes and nematodes are discussed. Oligochaetes can serve as phoretic, paratenic, intermediate or sole hosts for representatives of 10 families and one superfamily of nematodes.

A list citing all types of natural relationships between oligochaetes and nematodes (with over 150 nematode citations) is included and a brief summary is given of the groups of nematodes found in oligochaetes.

Representatives of the thelastomatids (Oxyurida) probably represent the most ancient group of nematode parasites associated with oligochaetes. Through intermediate forms like *Mesidionema*, the thelastomatids gave rise to the Drilonematoidea, unusual parasites of the coelomic cavity of earthworms. Associations involving oligochaetes as intermediate or paratenic hosts of nematodes were probably secondarily acquired to enhance the chances of locating definitive hosts.

The Associations between nematodes and oligochaetes are more extensive than one might suspect. The present work discusses these relationships and presents a host list of oligochaetes known to be associated with specific nematodes.

Perhaps the simplest type of association between these two groups of animals is phoresis, where the nematode is simply carried around in a nonfeeding state (usually as a dauer) somewhere in the oligochaete. In contrast to the phoretic nematodes on insects, which occur mostly on insects, all cases of nematode phoresis in oligochaetes is internal, usually with the nematodes occurring in the excretory system of the host. The nematodes are microbivorous (free-living) forms which return to the environment for development and reproduction or feed on the worm after it dies. Benefits derived by the nematodes are protection during adverse periods and dissemination. There is no obvious damage to the oligochaete, even when the dauer stages sometimes initiate development in the excretory system of the earthworm.

Aside from serving as phoretic hosts, oligochaetes may also serve as paratenic hosts to nematodes. In this case, a juvenile nematode enters the internal tissues of the oligochaete but does not develop until the earthworm is ingested by another (developmental) host. The annelids do not appear to be affected by these nematodes. When the nematode also develops in the initial earthworm host, the oligochaete is known as the intermediate host and the final (second) host the definitive host. Again, there is no evidence of damage to the earthworm.

Finally, some groups of nematodes utilize oligochaetes as the sole host and remain inside the annelid during their entire developmental period. Representatives of this category can cause mortality of the annelid.

Below is a summary of each group of nematodes known to have associations with oligochaetes. The nematode family (or superfamily) is followed by its abbreviation used in the host list, while the nematode order is included in parenthesis.

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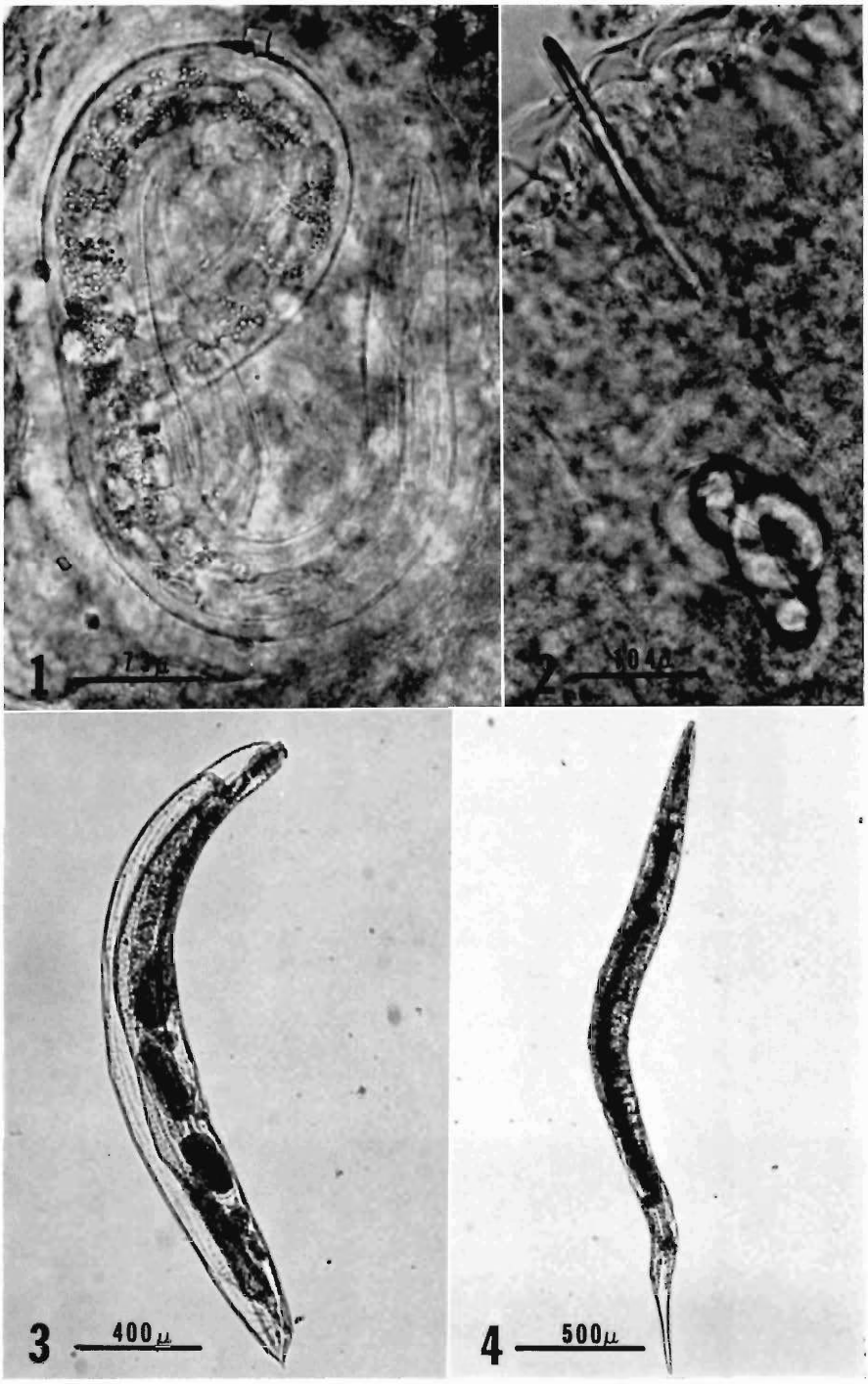
Figures 1–4. 1. A juvenile of *Rhabditis pellio* Schneider in the excretory system of *Aporrectodea trapezoides* (Duges). 2. Infective stage of an unknown mermithid nematode utilizing the oligochaete *Limnodrilus silvani* Eisen as a paratenic host. 3. Adult female drilonematoidid, *Mesidionema praecomasculatis* Poinar, removed from the coelom of *Eudrilus eugeniae* Kinberg. 4. Adult female thelastomatid, *Thelastoma endoscolicum* Poinar, removed from the gut lumen of *Eudrilus eugeniae* Kinberg.



Ascarididae (A) (Ascaridida). Some members of the genus *Porrocaecum* deposit eggs that hatch when ingested by earthworms. These newly hatched juveniles then penetrate the gut wall and enter the blood vessels of the worms where they develop and molt to the infective stage. The earthworm serves as a true intermediate host with birds serving as the final hosts.

Dioctophymatidae (Dio) (Enoplida). Both *Dioctophyme renale* and *Hystrichis tricolor*, parasites of mammals and birds, respectively, utilize earthworms as intermediate hosts. The eggs hatch in the gut of the oligochaete and develop to the infective stage in the blood vessels. They continue their development when ingested by a vertebrate host.

Diplogasteridae (Di) (Rhabditida). All members of this family have phoretic associations with earthworms and apparently occur (mostly as dauer forms) in the excretory system or coelom of their host. The adult stages are free-living.

Drilonematoidea (D) (Rhabditida). All members of this superfamily live in the coelom (some may occasionally enter the lumen of the intestine) of earthworms where they are considered as true parasites, utilizing the oligochaete as the sole host. They may occur free in the coelom, in sperm sacs or embedded in various tissues (especially muscle) of the earthworm (Fig. 3).

Heterakidae (H) (Ascaridida). There is some question whether members of the genus *Heterakis* actually develop in the earthworm before reaching the vertebrate (bird) host. Thus, the oligochaete may simply serve as a paratenic host.

Mermithidae (M) (Enoplida). Members of this family can use earthworms as paratenic hosts (where they lie coiled up in various tissues) (Fig. 2) or as sole developmental hosts. In case of the latter, the earthworms are probably killed after the nematodes make their exit.

Metastrongylidae (Me) (Strongylida). Eggs of some species of both *Metastrongylus* and *Choerostrongylus* hatch when ingested by earthworms. The juveniles penetrate the gut wall and develop to a stage infective to pigs. While in the oligochaetes, the nematodes may occur in the calciferous glands, esophageal wall, heart, crop, intestine, dorsal blood vessel, or gizzard. In these cases, the earthworm serves as an intermediate host.

Rhabditidae (R) (Rhabditida). Nematodes of this family utilize earthworms as phoretic hosts. Usually the dauer, but also developing juveniles and even the adult, may occur in the excretory system or tissues of oligochaetes (Fig. 1). The adults are free-living or may develop after the host dies and consume the cadaver.

Syngamidae (Sy) (Strongylida). Representatives of both *Syngamus* and *Stephanurus* utilize earthworms to reach the final vertebrate host. With *Syngamus* it is not clear if the earthworm serves as a paratenic or intermediate host. The infective stages of *S. trachea* occur in the oligochaete muscles. With *Stephanurus dentatus*, there is apparently some development and the infective-stage juveniles can be found throughout the earthworm's digestive tract or in the brown bodies.

Thelastomatidae (Th) (Oxyurida). Recently, a representative of this family was recovered from the gut of an African earthworm. This is the first case of a thelastomatid (generally found in arthropods) from an annelid. The nematodes develop and mate in the intestinal lumen of the earthworm and it is assumed that the egg is the infective unit after it passes out of the host into the soil. There is only a single host in the life cycle of these nematodes (Fig. 4).

Trichuridae (T) (Enoplida). Certain representatives of the genus *Capillaria* utilize earthworms as paratenic or intermediate hosts. The eggs hatch in the oligochaete gut and the nematode juveniles enter the intestine and encyst in muscles of the body wall. With *C. plica*, only the first-stage juvenile occurs in the worm and it is doubtful whether any development occurs. However some growth supposedly occurs in other species of *Capillaria* utilizing earthworms as initial hosts.

The purpose of the following host list is to cite all types of relationships between oligochaetes and nematodes. At least the worm and nematode genus (with one exception) had to be known for inclusion in the host list. Attempts were made to include all natural occurrences. Experimental results were also cited when it was probable that the association occurred in nature. Only the earliest most complete reference to specific nematode–oligo-

Oligochaete Hosts of Nematodes

Oligochaete	Nematode	Reference
Acanthodrilidae		
Diplocardia sp.	M-unknown	Timm, 1969
Parachilota sp.	D-*Ungella sucofera* Timm, 1962	Timm, 1962a
Plutellus sp.	D-*Plutellonema clitellatum* T. & M., 1966	Timm & Maggenti, 1966
Plutellus sp.	D-*Siconema ovimammillatum* Timm, 1966	Timm, 1966b
Criodrilidae		
Criodrilus lacuum Hoffmeister	Dio-*Hystrichis tricolor* Duj., 1845	Karmanova, 1959
Eudrilidae		
Eudrilus eugeniae Kinberg	D-*Mesidionema praecomasculatis* Poinar, 1978	Poinar, 1978a
Eudrilus eugeniae Kinberg	Th-*Thelastoma endoscolicum* Poinar, 1978	Poinar, 1978b
Glossoscolecidae		
Aptodrilus festae Cognetti	D-*Opistonema minutum* Pier., 1916	Pierantoni, 11916
Thamnodriloides yunkeri Gates	D-*Diceloides mirabilis* Timm, 1967	Timm, 1967c
Lumbricidae		
Allolobophora chlorotica Savigny	Di-*Anchidiplogaster eurycephalus* (Völk, 1950)	Völk, 1950
Allolobophora chlorotica Savigny	R-*Caenorhabditis dolichura* (Schneider, 1866)	Völk, 1950
Allolobophora chlorotica Savigny	Di-*Diplogasteritus stoeckherti* (Völk, 1950)	Völk, 1950
Allolobophora chlorotica Savigny	R-*Diploscapter lycostoma* Völk, 1950	Völk, 1950
Allolobophora chlorotica Savigny	R-*Pelodera cylindrica* (Cobb, 1898)	Völk, 1950
Allolobophora chlorotica Savigny	R-*Pelodera strongyloides* (Schneider, 1860)	Völk, 1950
Allolobophora chlorotica Savigny	R-*Pelodera teres* Schneider, 1866	Völk, 1950
Allolobophora chlorotica Savigny	R-*Rhabditis aspera* Bütschli, 1873	Völk, 1950
Allolobophora chlorotica Savigny	R-*Rhabditis elongata* (Schneider, 1866)	Völk, 1950
Allolobophora chlorotica Savigny	R-*Rhabditis maupasi* Seurat, 1919	Völk, 1950
Allolobophora chlorotica Savigny	R-*Rhabditis oxycerca* de Man, 1895	Völk, 1950
Allolobophora chlorotica Savigny	R-*Rhabditis pellio* (Schneider, 1866)	Völk, 1950
Allolobophora chlorotica Savigny	R-*Rhabditis verneti* Maupas, 1900	Völk, 1950
Allolobophora chlorotica Savigny	Di-*Rhabditolaimus stigmatus* Steiner, 1930	Völk, 1950
Allolobophora dubiosa var. *pontica* Pop.	Dio-*Hystrichis tricolor* Duj., 1845	Karmanova, 1959
Alllobophora tenuis Eisen	Me-*Metastrongylus elongatus* (Duj., 1845)	Alicata, 1936
Aporrectodea giardi Ribar. (=*Allolobophora terrestris* Savigny)	R-*Rhabditis pellio* (Schneider, 1866)	Cuénot, 1898
Aporrectodea longa (Ude)	T-*Capillaria annulata* (Molin, 1859)	Allen, 1950
Aporrectodea longa (Ude)	T-*Capillaria caudinflata* Molin, 1858	Savvateeva, 1966
Aporrectodea longa (Ude)	Me-*Choerostrongylus pudendotectus* (Wost., 1905)	Shope, 1941
Aporrectodea longa (Ude)	R-*Rhabditis maupasi* Seurat, 1919	Johnson, 1913
Aporrectodea longa (Ude)	Sy-*Syngamus trachea* (Montagu, 1811)	Taylor, 1935
Aporrectodea rosea (Savigny)	R-*Rhabditis craspedocerca* Völk, 1950	Völk, 1950
Aporrectodea rosea (Savigny)	R-*Rhabditis maupasi* Seurat, 1919	Völk, 1950
Aporrectodea rosea (Savigny)	R-*Rhabditis pellio* (Schneider, 1866)	Völk, 1950
Aporrectodea trapezoides (Duges)	Me-*Choerostrongylus pudendotectus* (Wost., 1905)	Schwartz & Alicata, 1935
Aporrectodea trapezoides (Duges)	Me-*Metastrongylus elongatus* Duj., 1845	Schwartz & Alicata, 1935
Aporrectodea trapezoides (Duges)	Me-*Metastrongylus salmi* Gedoelst, 1923	Alicata, 1936
Aporrectodea trapezoides (Duges)	R-*Rhabditis pellio* (Schneider, 1866)	Poinar & Thomas, 1975
Bimastos parvus (Eisen)	H-*Heterakis perspicillus* Rud., 1803	Scott, 1913
Dendrobaena kurashvilii K. & K., 1974	D-*Dicelis kurashvilii* K., 1974	Kakulia & Kvavadze, 1974
Dendrobaena octaedra Savigny	R-*Rhabditis pellio* (Schneider, 1866)	Völk, 1950
Dendrodrilus rubidus (Savigny)	T-*Capillaria caudinflata* Molin, 1858	Savvateeva, 1966
Dendrodrilus rubidus (Savigny)	T-*Capillaria plica* (Rud., 1819)	Enigk, 1950
Dendrodrilus rubidus (Savigny)	D-*Dicelis dendrobaena* Timm, 1967	Timm, 1967c
Dendrodrilus rubidus (Savigny)	R-*Rhabditis maupasi* Seurat, 1919	Johnson, 1913
Eisenia foetida Savigny	T-*Capillaria annulata* (Molin, 1859)	Wehr, 1936
Eisenia foetida Savigny	Me-*Choerostrongylus pudendotectus* (Wost., 1905)	Schwartz & Alicata, 1935
Eisenia foetida Savigny	D-*Dicelis filaria* Duj., 1845	Keilin, 1915
Eisenia foetida Savigny	H-*Heterakis gallinarum* (Schrank, 1788)	Lund et al., 1966
Eisenia foetida Savigny	Me-*Metastrongylus elongatus* (Duj., 1845)	Schwartz & Alicata, 1935
Eisenia foetida Savigny	A-*Porrocaecum ensicaudatum*(Zeder, 1800)	Jogis, 1967
Eisenia foetida Savigny	R-*Rhabditis maupasi* Seurat, 1919	Johnson, 1913
Eisenia foetida Savigny	Sy-*Stephanurus dentatus* Diesing, 1839	Tromba, 1955
Eisenia foetida Savigny	Sy-*Syngamus merulae* Baylis, 1927	Clapham, 1934
Eisenia foetida Savigny	Sy-*Syngamus trachea* (Montagu, 1811)	Clapham, 1934
Eisenia kucenkoi Michaelsen	D-*Dicelis rossica* Timm, 1962	Timm, 1962b
Eiseniella tetraedra (Savigny)	R-*Rhabditis pellio* (Schneider, 1866)	Völk, 1950
Eisenoides carolinensis (Michaelsen)	D-*Dicelis ciseniae* Timm, 1967	Timm, 1967
Eisenoides lonnbergi (Michaelsen)	Me-*Choerostrongylus pudendotectus* (Wost., 1905)	Dayton, 1957
Eisenoides lonnbergi (Michaelsen)	Me-*Metastrongylus elongatus* (Duj., 1845)	Dayton, 1957
Helodrilus caliginosus Savigny	T-*Capillaria aerophila* (Creplin, 1839)	Borovkova, 1941 (In Rysavy 1969)
Helodrilus caliginosus Savigny	T-*Capillaria annulata* (Molin, 1859)	Wehr, 1936

Oligochaete Hosts of Nematodes (*Continued*)

Oligochaete	Nematode	Reference
Lumbricidae (Continued)		
Helodrilus caliginosus Savigny	T-*Capillaria caudinflata* (Molin, 1858)	Morehouse, 1944
Helodrilus caliginosus Savigny	D-*Dicelis nira* Chit. & Luck., 1934	Chitwood & Lucker, 1934
Helodrilus caliginosus Savigny	H-*Heterakis gallinarum* (Schrank, 1788)	Lund et al., 1966
Helodrilus caliginosus Savigny	A-*Porrocaecum ensicaudatum* (Zeder, 1800)	Atlavinyte, 1963
Helodrilus caliginosus Savigny	Me-*Metastrongylus apri* Gmelin, 1790	Dunn, 1955
Helodrilus caliginosus Savigny	Sy-*Syngamus trachea* (Montagu, 1811)	Taylor, 1935
Helodrilus rhodensis Cogn.	D-*Mesonema rhodense* Pier., 1916	Pierantoni, 1916
Lumbricus rubellus Hoff.	T-*Capillaria aerophila* (Crelpin, 1839)	Borovkova, 1941 (In Rysavy 1969)
Lumbricus rubellus Hoff.	T-*Capillaria caudinflata* (Molin, 1858)	Savvateeva, 1966
Lumbricus rubellus Hoff.	T-*Capillaria mucronata* Molin, 1858	Skarbilovic, 1950
Lumbricus rubellus Hoff.	T-*Capillaria plica* (Rud., 1819)	Petrov & Borovkova, 1942
Lumbricus rubellus Hoff.	Me-*Choerostrongylus pudendotectus* (Wost., 1905)	Alicata, 1936
Lumbricus rubellus Hoff.	D-*Dicelis filaria* Duj., 1845	Wulker, 1926
Lumbricus rubellus Hoff.	Me-*Metastrongylus elongatus* (Duj., 1845)	Alicata, 1936
Lumbricus rubellus Hoff.	A-*Porrocaecum ensicaudatum* (Zeder, 1800)	Joges, 1967
Lumbricus rubellus Hoff.	R-*Rhabditis anomala* Hertwig, 1922	Goodchild & Irwin, 1971
Lumbricus rubellus Hoff.	R-*Rhabditis maupasi* Seurat, 1919	Johnson, 1913
Lumbricus rubellus Hoff.	R-*Rhabditis pellio* (Schneider, 1866)	Goodchild & Irwin, 1971
Lumbricus terrestris L.	T-*Capillaria aerophila* (Creplin, 1839)	Borovkova, 1941 (In Rysavy 1969)
Lumbricus terrestris L.	T-*Capillaria plica* (Rud., 1819)	Enigk, 1950
Lumbricus terrestris L.	Me-*Choerostrongylus pudendotectus* (Wost., 1905)	Alicata, 1936
Lumbricus terrestris L.	D-*Dicelis filaria* Duj., 1845	Dujardin, 1845
Lumbricus terrestris L.	H-*Heterakis gallinarum* (Schrank, 1788)	Lund et al., 1966
Lumbricus terrestris L.	Me-*Metastronglus elongatus* (Duj., 1845)	Alicata, 1936
Lumbricus terrestris L.	Me-*Metastrongylus salmi* Gedoelst, 1923	Alicata, 1936
Lumbricus terrestris L.	R-*Pelodera strongyloides* (Schneider, 1860)	Völk, 1950
Lumbricus terrestris L.	R-*Pelodera teres* Schneider, 1866	Völk, 1950
Lumbricus terrestris L.	A-*Porrocaecum ensicaudatum* (Zeder, 1800)	Cori, 1898
Lumbricus terrestris L.	R-*Rhabditis anomala* Hertwig, 1922	Goodchild & Irwin, 1971
Lumbricus terrestris L.	R-*Rhabditis maupasi* Seurat, 1919	Johnson, 1913
Lumbricus terrestris L.	R-*Rhabditis pellio* (Schneider, 1866)	Goodchild & Irwin, 1971
Lumbricus terrestris L.	R-*Rhabditis verneti* Maupas, 1900	Völk, 1950
Lumbricus terrestris L.	Sy-*Stephanurus dentatus* Diesing, 1839	Tromba, 1955
Lumbricus terrestris L.	Sy-*Syngamus trachea* (Montagu, 1811)	Clapham, 1934
Lumbricus terrestris L.	Sy-*Syngamus trachea* (Montagu, 1811)	Walker, 1886
Octolasion cyaneum (Savigny)	R-*Rhabditis maupasi* Seurat, 1919	Johnson, 1913
Octolasion hemiandrum Cogn.	D-*Mesonema acuminatum* Pier., 1916	Pierantoni, 1916
Octolasion transpadanum Rosa	D-*Opistonema acuminatum* Pier., 1916	Pierantoni, 1916
Octolasion tyrtaeum (Savigny)	A-*Porrocaecum ensicaudatum* (Zeder, 1800)	Levin, 1957
Octolasion tyrtaeum (Savigny)	R-*Rhabditis maupasi* Seurat, 1919	Völk, 1950
Lumbriculidae		
Lumbriculus variegatus Müller	Dio-*Diotophyme renale* (Goeze, 1782)	Karmanova, 1960
Lumbriculus variegatus Müller	R-*Rhabditis lumbriculi* v. Linst., 1895	von Linstow, 1895
Megascolecidae		
Perionyx excavatus Perrier	D-*Scolecophilus mus* Timm, 1967	Timm, 1967a
Perionyx macintoshi Beddard	D-*Scolecophilus gatesi* Baylis, 1943	Timm, 1967a
Perionyx macintoshi Beddard	D-*Scolecophilus lumbricicola* B. & D., 1922	Baylis & Daubney, 1922
Perionyx sp.	D-*Scolecophiloides gatesi* Baylis, 1943	Baylis, 1943
Perionyx sp.	D-*Synoecnema perionychis* Baylis, 1943	Baylis, 1943
Pheretima alexandri (Beddard)	D-*Homungella siamense* Timm, 1966	Timm, 1966a
Pheretima alexandri (Beddard)	D-*Siconema siamense* Timm, 1966	Timm, 1966b
Pheretima a. analecta Gates	D-*Adieronema mirabile* Timm, 1967	Timm, 1967c
Pheretima andersoni Michaelsen	D-*Adieronema magnum* Timm, 1967	Timm, 1967c
Pheretima asiatica Michaelsen	D-*Siconema ovicoronatum* Timm, 1966	Timm, 1966b
Pheretima benguetensis Beddard	D-*Filiponema philippinense* T. & M., 1966	Timm & Maggenti, 1966
Pheretima benguetensis Beddard	D-*Siconemella philippensis* Timm, 1967	Timm, 1967b
Pheretima bipora Beddard	D-*Filiponema burmense* Timm, 1967	Timm, 1967c
Pheretima bulmeri Gates	D-*Gatesnema bilobatum* Timm, 1971	Timm, 1971
Pheretima bulmeri Gates	D-*Iponema pheretimae* Timm, 1971	Timm, 1971
Pheretima carinensis (Rosa)	D-*Adungella gatesi* Timm, 1967	Timm, 1967b
Pheretima carinensis (Rosa)	D-*Adungella major* Timm, 1967	Timm, 1967b
Pheretima carinensis (Rosa)	D-*Siconema saccaturum* Timm, 1966	Timm, 1966b
Pheretima compta Gates	D-*Mesonema burmense* Timm, 1967	Timm, 1967c
Pheretima defecta Gates	D-*Siconemoides disarmatus* Timm, 1967	Timm, 1967b
Pheretima doliaria Gates	D-*Siconema micrurum* Timm, 1966	Timm, 1966b
Pheretima doliaria Gates	D-*Sucamphida robustum* Timm, 1966	Timm, 1966c
Pheretima fucosa Gates	D-*Siconema ovicostatum* Timm, 1966	Timm, 1966b
Pheretima grata Cogn.	D-*Dionyx guineensis* Pier., 1916	Pierantoni, 1916
Pheretima longicauliculata Gates	D-*Homungella monodontium* Timm, 1966	Timm, 1966a
Pheretima longicauliculata Gates	D-*Mesonema burmense* Timm, 1967	Timm, 1967c
Pheretima longicauliculata Gates	D-*Siconema limonovatum* Timm, 1966	Timm, 1966b
Pheretima longicauliculata Gates	D-*Siconema micronchium* Timm, 1966	Timm, 1966b
Pheretima manicata decorosa Gates	D-*Adungella manicatae* Timm, 1967	Timm, 1967b

Oligochaete Hosts of Nematodes (*Continued*)

Oligochaete	Nematode	Reference
Megascolecidae (Continued)		
Pheretima mekongianus (Cognetti)	D-*Pharyngonema mekongianus* Pier., 1923	Pierantoni, 1923
Pheretima mira Gates	D-*Miranema mirae* Timm, 1967	Timm, 1967b
Pheretima montana (Kinberg)	D-*Synoecnema drawidae* Baylis, 1943	Timm, 1962a
Pheretima omtrekensis Cogn.	D-*Dionyx acutifrons* Pier., 1916	Pierantoni, 1916
Pheretima peguana (Rosa)	D-*Synoecnema gatesi* Timm, 1962	Timm, 1962a
Pheretima posthuma (L. Vaillant)	D-*Perodira pheretimae* Timm, 1960	Timm, 1960
Pheretima posthuma (L. Vaillant)	D-*Pharyngonema pheretimae* Timm, 1959	Timm, 1959b
Pheretima posthuma (L. Vaillant)	D-*Synoecnema anseriforme* Timm, 1959	Timm, 1959a
Pheretima posthuma (L. Vaillant)	D-*Synoecnema hirsutum* Timm, 1959	Timm, 1959a
Pheretima procera Gates	D-*Synoecnema pheretimae* Baylis, 1943	Baylis, 1943
Pheretima sermowaiana Cogn.	D-*Opistonema subtile* Pier., 1916	Pierantoni, 1916
Pheretima sp.	D-*Buronanema singulare* Timm, 1967	Timm, 1967c
Pheretima sp.	D-*Synoecnema fragile* Magalhães, 1905	Magalhães, 1905
Pheretima szechuanensis Chen.	D-*Macramphida sinense* Timm, 1966	Timm, 1966c
Pheretima terrigena Gates	D-*Adungella major* Timm, 1967	Timm, 1967b
Pheretima velata Gates	D-*Siconemella burmensis* Timm, 1967	Timm, 1967b
Pheretima virgo (Beddard)	D-*Siconema turgidum* Timm, 1966	Timm, 1966b
Pheretima vittata (Goto & Hatai)	Me-*Metastrongylus elongatus* (Duj., 1845)	Isoda & Kato, 1956
Pheretima vulgaris Chen.	D-*Siconema sinense* Timm, 1966	Timm, 1966b
Pheretima wendessiana Cogn.	D-*Cephalonema macrocephalum* Pier., 1916	Pierantoni, 1916
Pheretima wendessiana Cogn.	D-*Cephalonema microcephalum* Pier., 1916	Pierantoni, 1916
Pheretima wendessiana Cogn.	D-*Drilonema wendessianum* Pier., 1916	Pierantoni, 1916
Pleurochaeta sp. (=*Megascolex*)	D-*Dicelis pleurochaetae* Beddard, 1883	Beddard, 1883
Tonoscolex conversus Gates	D-*Tonoscolecinema setosum* Timm, 1967	Timm, 1967c
Tonoscolex depressus Gates	D-*Tonoscolecinema burnemse* Timm, 1967	Timm, 1967c
Tonoscolex lunatus Gates	D-*Tonoscolecinema parvum* Timm, 1967	Timm, 1967c
Tonoscolex sp.	D-*Tonoscolecinema gatesi* Timm, 1967	Timm, 1967c
Tonoscolex triquetrus Gates	D-*Tonoscolecinema triquetrum* Timm, 1967	Timm, 1967c
Moniligastridae		
Drawida ampullacea Gates	D-*Perodira alata* Baylis, 1943	Baylis, 1943
Drawida dolosa Gates	D-*Synoecnema drawidae* Baylis, 1943	Baylis, 1943
Moniligaster gravelyi Stephenson	D-*Creagrocercus barbatus* Baylis, 1943	Baylis, 1943
Octochaetidae		
Dichogaster duwonica Cognetti	D-*Dionyx minuta* Pier., 1916	Pierantoni, 1916
Dichogaster gestri Cognetti	D-*Dionyx cognettii* Pier., 1916	Pierantoni, 1916
Dichogaster italiensis (Mich.)	unknown	Cognetti de Martiis, 1909
Eutyphoeus bullatus Gates	D-*Iponema minor* T. & M., 1966	Timm & Maggenti, 1966
Eutyphoeus planatus Gates	D-*Iponema major* T. & M., 1966	Timm & Maggenti, 1966
Eutyphoeus rarus Gates	D-*Adieronema eutyphoei* Timm, 1967	Timm, 1967c
Eutyphoeus rarus Gates	D-*Ungella secta* Cobb, 1928	Cobb, 1928
Hoplochaetella anomala Steph.	D-*Perodira alata* Baylis, 1943	Baylis, 1943
Hoplochaetella anomala Steph.	D-*Synoecnema hoplochaetellae* Baylis, 1943	Baylis, 1943
Ramiellona balantina Gates	D-*Dicelis guatemalana* Timm, 1962	Timm, 1962b
Tubificidae		
Limnodrilus silvani Eisen	M-unknown	Poinar, 1976

chaete associations was cited. The oligochaete families, genera and species are listed in alphabetical order. When more than one nematode is recorded under the same oligochaete, then the genera and species of nematodes are also arranged in alphabetical order. Abbreviations before the scientific name of the nematode represent the family or superfamily of that particular nematode. These abbreviations and their corresponding families (or superfamilies) and orders are discussed above, along with a brief summary of each family in regards to its association with oligochaetes. The last column of the host list gives the references to the most complete report of the association.

Discussion

It is clear from the above host list that oligochaetes can harbor many types of nematodes in a variety of associations.

From the standpoint of human welfare, perhaps the most important associations are the nematode parasites of domestic animals that utilize earthworms as paratenic or intermediate hosts. This topic has been discussed further by Rysavy (1969). From the standpoint of basic science, nematodes of the superfamily Drilonematoidea represent one of the more interesting groups of oligochaete parasites since they have so many unique morphological characters and show no direct relationship to any of the free-living nematodes.

For those attempting to culture earthworms, mermithid nematodes would be the only group showing potential danger since they usually kill their host. However their occurrence in oligochaetes is rare, insects being the preferred host to most mermithids. It is possible that those representatives of the Rhabditidae and Diplogasteridae which enter the excretory system of earthworms, could rupture the nephridia and cause a general septicemia of the oligochaete.

Since annelids are considered the most primitive coelomate animals known (Raymond, 1950), it is interesting to consider in evolutionary terms when the various groups of nematodes became associated with earthworms.

The Oxyurida are probably the most ancient group of nematodes and Inglis (1965) considers the Thelastomatidae as the most primitive family in this order. Representatives of this family, whose members probably arose from terrestrial Rhabditidae, thus represent one of the earliest known groups of animal parasites, and thus *Thelastoma endoscolicum* might have become associated with earthworms in the Lower Cambrian.

Representatives of the thelastomatids probably gave rise to the Drilonematoidea, another very ancient group of nematode parasites of the coelomic cavity of earthworms (Timm, 1964). An intermediate form sharing characters of the gut-inhabiting thelastomatids and coelom-inhabiting drilonematoidids is *Mesidionema praecomasculatis*.

Aside from rare cases of earthworm parasitism by mermithid nematodes, the two abovementioned groups are the only nematodes that utilize earthworms as sole hosts.

Most of the other nematodes cited in the host list utilize earthworms as intermediate or paratenic hosts. Such associations were probably secondarily acquired and enhanced the possibility of the nematodes finding the definitive hosts.

Those nematode groups which contain representatives that utilize earthworms as phoretic hosts and then lead a free-living existence in the environment may also have a long-standing association with their hosts.

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