

# Parasitism of Molluscs by Nematodes: Types of Associations and Evolutionary Trends<sup>1</sup>

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**Abstract:** Although there are no confirmed fossil records of mollusc parasitic nematodes, diverse associations of more than 108 described nematode species with slugs and snails provide a fertile ground for speculation of how mollusc parasitism evolved in nematodes. Current phylogenetic resolution suggests that molluscs have been independently acquired as hosts on a number of occasions. However, molluscs are significant as hosts for only two major groups of nematodes: as intermediate hosts for metastrongyloids and as definitive hosts for a number of rhabditids. Of the 61 species of nematodes known to use molluscs as intermediate hosts, 49 belong to Metastrongyloidea (Order Strongylida); of the 47 species of nematodes that use molluscs as definitive hosts, 33 belong to the Order Rhabditida. Recent phylogenetic hypotheses have been unable to resolve whether metastrongyloids are sister taxa to those rhabditids that use molluscs as definitive hosts. Although most rhabditid nematodes have been reported not to kill their mollusc hosts prior to their reproduction, some species are pathogenic. In fact, infective juveniles of *Phasmarhabditis hermaphrodita* vector a lethal bacterium into the slug host in which they reproduce. This life cycle is remarkably similar to the entomopathogenic nematodes in the families Steinernematidae and Heterorhabditidae. Also, the discoveries of *Alloionema* and *Pellioiditis* in slugs are interesting, as these species have been speculated to represent the ancestral forms of the entomopathogenic nematodes. Development of the infective stage appears to be an important step toward the acquisition of molluscs as definitive hosts, and the association with specific bacteria may have arisen in conjunction with the evolution of necromeny.

**Key words:** Aracelamida, Ascaridida, Diplogastrida, evolution, Mermithida, Mollusca, nematodes, parasitism, Rhabditida, Spirurida, Strongylida.

Nematodes form diverse associations with slugs and snails that range from paratenic relationships to parasitic or pathogenic relationships. A majority of the Metastrongyloidea (Order: Strongylida) use molluscs as intermediate hosts for which vertebrates serve as final hosts. In contrast, a majority of Rhabditoidea (Order: Rhabditida) use molluscs as definitive hosts in which the entire nematode life cycle is completed. This paper briefly describes the various types of associations between nematodes and molluscs, lists the known species of nematodes associated with molluscs along with their specific hosts, and discusses evolutionary trends in mollusc parasitism.

## TYPES OF ASSOCIATIONS OF NEMATODES WITH MOLLUSCS

**Molluscs as paratenic hosts for nematode parasites of vertebrates:** A paratenic host is an organism that serves to transfer a larval stage or stages of a parasite from one host to another but in which little or no development takes place (Anderson, 2000). The juveniles of many nematode species infect mollusc hosts but do not develop further, while the adult nematodes are parasitic in vertebrate hosts. Such slug and snail hosts of nematodes are called paratenic hosts. This serves as an effective survival-and-transmission strategy for vertebrate parasitic nematodes. For example, aquatic snails *Galba*

*corvus* serve as paratenic hosts for the third-stage juveniles of the nematode *Anguillicola crassus*, a pathogenic swimbladder parasite of the eel *Anguilla anguilla* (Moravec, 1996).

**Molluscs as intermediate hosts for nematode parasites of vertebrates:** Juveniles of many nematode species enter slug and snail hosts for completion of only a part of their life cycles. Such mollusc hosts are called intermediate hosts. Interestingly, a majority of Metastrongyloidea (Order: Strongylida) form this type of association with molluscs (Table 1). Usually the first-stage juvenile enters the mollusc host and develops into an infective stage that is then acquired by the final vertebrate host by either accidentally or intentionally swallowing the infected mollusc. While this is an effective survival-and-transmission strategy for most vertebrate parasitic nematodes, in some cases the third-stage nematodes have been observed to emerge from the intermediate hosts, which are subsequently ingested by the final host (Kutz et al., 2001). The ruminant lungworm *Mullerius capillaris*, a parasite of sheep, uses the slugs *Limax cinereus* and *Arion hortensis* and the snail *Monacha umbrosa* as intermediate hosts. Egorov (1960) indicates that *M. capillaris* could grow and develop in *Deroceras reticulatum* (= *Arion reticulatum*) and *D. laeve* (= *A. laevis*). The free-living juveniles of the lungworm *Protostrongylus tauricus* enter the intermediate snail host *Helicella derbentina* where the infective stage is reached in 25 to 30 days in the foot muscle (Rodonaya, 1977). The nematodes reach maturity 40 days after having been swallowed with the snail by the final host, the European hare (Rodonaya, 1977).

Some nematode species use slugs and snails as intermediate hosts in which some part of the nematode life cycle is completed and the host is killed. The nematodes that form this kind of association with the slugs and snails occur in the orders Strongylida, Oxyurida, and Rhabditida. Members of Angiostomidae (Order,

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TABLE 1. Nematode species and their mollusk intermediate hosts.

Nematode species	Intermediate host	Reference
<b>Order Strongylida</b>		
<i>Aelurostrongylus abstrusus</i>	<i>Angiolumax agrestis</i> , <i>A. columbianus</i> , <i>A. laevis</i> , <i>Chondrula septemdentata</i> , <i>Helminthoglypta arosa</i> , <i>H. californiensis</i> , <i>H. nickleana</i> , <i>Helicella barbesiana</i> , <i>H. vestalis</i> , <i>Helix aspersa</i> , <i>H. cauvata</i> , <i>Lavantina hierosolyma</i> , <i>L. sesaeana</i> , <i>Limax flavus</i> , <i>Minocha syriaca</i> , <i>Retinella nitellina</i> , and <i>Theba pisana</i>	Hobmaier and Hobmaier (1935a); Gerichter (1949); Mackerras (1957)
<i>A. falciformis</i>	<i>Arion hortensis</i> , <i>Cepaea hortensis</i> , <i>C. nemoralis</i> , <i>Deroceras agrestis</i> , <i>Euomphalia strigella</i> , <i>Fruiticola hispida</i> , and <i>Succinea putris</i>	Wetzel (1937, 1938)
<i>A. pridhami</i>	<i>Ampullaria cuprina</i> , <i>Anguispirina alternata</i> , <i>Armiger crista</i> , <i>Deroceras laeve</i> , <i>Discus cronkhitei</i> , <i>Gyraulus deflexus</i> , <i>Mesodon thyroides</i> , <i>Physa integra</i> , <i>Succinea ovalis</i> , <i>Triodopsis albolabris</i> , and <i>Zonitoides arboreus</i>	Anderson (1962); Stockdale (1970a, b)
<i>Angiostrongylus andersoni</i>	<i>Arion hortensis</i> , <i>Deroceras reticulatum</i> , <i>Helix aspersa</i> , <i>Lymnaea stagnalis</i> , and <i>Planorbrius corneus</i>	Petter (1974)
<i>A. cantonensis</i>	<i>Achatina fulica</i> , <i>Bellamyia ingallsiana</i> , <i>Bradybaena similaris</i> , <i>Cipangopaludina chinensis</i> , <i>Deroceras laeve</i> , <i>Euglandina rosea</i> , <i>Girasia peguensis</i> , <i>Indoplanorbis exustus</i> , <i>Laevicaulus alte</i> , <i>Macrochlamys resplendens</i> , <i>Microparmarion malayanus</i> , <i>Opeas javanicum</i> , <i>Pupina complanata</i> , <i>Pila ampullacea</i> , <i>P. scutata</i> , <i>Quantula striata</i> , <i>Subulina octona</i> , <i>Vaginalus plebeius</i> , and <i>Veronicella alte</i>	Ash (1976); Anderson (2000)
<i>A. costaricensis</i>	<i>Bradybaena similis</i> , <i>Belocaulus angustipes</i> , <i>Limax maximus</i> , <i>L. flavus</i> , <i>Phyllocaulus variegatus</i> , <i>P. soleformis</i> , and <i>Vaginulus plebeius</i>	Morera (1973); Graeff-Teixeira et al. (1989, 1993); Rambo et al. (1997)
<i>A. dujardini</i>	<i>Angiolumax laevis</i> , <i>A. reticulatus</i> , <i>Biomphalaria glabrata</i> , <i>Cepaea nemoralis</i> , <i>Helix aspersa</i> , <i>Hygromia limbata</i> , <i>Lymnaea corvus</i> , <i>L. stagnalis</i> , <i>L. peregra</i> , <i>Planorbis planorbis</i> , <i>P. coreneus</i> , and <i>Retinella incerta</i>	Drozd et al. (1971)
<i>A. malaysiensis</i>	<i>Bradybaena similaris</i> , <i>Laevicaudatus alte</i> , and <i>Microparmarion malayanus</i>	Bhaibulaya and Cross (1971)
<i>A. siamensis</i>	<i>Biomphalaria glabrata</i>	Katakura et al. (1981)
<i>A. vasorum</i>	<i>Arionater</i> , <i>A. rufus</i> , <i>Biomphalaria glabrata</i> , <i>Bradybaena similaris</i> , <i>Deroceras laeve</i> , <i>Laevicaulus alte</i> , <i>Prosoples javanicum</i> , and <i>Subulina octona</i>	Guilhon (1960, 1963); Rosen et al. (1970); Prestwood et al. (1981); Hobmaier (1941a); Criag (1972)
<i>Cresonema mephitidis</i>	<i>Agriolumax sp.</i> , <i>Anguispirina alternata</i> , <i>Ephipharmorpha sp.</i> , <i>Helix sp.</i> , <i>Limax sp.</i> , <i>Mesodon thyroides</i> , <i>Milax sp.</i> , <i>Triodopsis albolabris</i> , and <i>T. tridentata</i>	Addison and Fraser (1994)
<i>C. petrowi</i>	<i>Mesodon thyroideus</i>	Petrov (1941); Lammler and Saupe (1968); Barus and Blazek (1971)
<i>C. striatum</i>	<i>Agriolumax agrestis</i> , <i>Arianta arbustorum</i> , <i>Arion circumscriptus</i> , <i>Australorbis glabratus</i> , <i>Bithynia leachi</i> , <i>Cepaea hortensis</i> , <i>Limax tenellus</i> , <i>Lymnaea peregra</i> , <i>Milax rusticus</i> , <i>Monachoides umbrosa</i> , <i>Oxychilus glaber</i> , <i>Planorbis spp.</i> , and <i>Succinea putris</i>	Wetzel and Muller (1935a, b); Petrov and Gagarin (1938); Wetzel (1940); Petrov (1941); Stockdale and Hulland (1970)
<i>C. vulpis</i>	<i>Agriolumax agrestis</i> , <i>Arianta arbustorum</i> , <i>Arion circumscriptus</i> , <i>A. hortensis</i> , <i>A. intermedius</i> , <i>Cepaea hortensis</i> , <i>C. nemoralis</i> , <i>Fruiticola fructiculum</i> , <i>Helix pomatia</i> , <i>Mesodon thyroides</i> , <i>Succinea putris</i> , <i>Triodopsis albolabris</i> , <i>Zonitoides excavata</i> , and <i>Z. nitida</i>	Boev (1975); Manga-Gonzalez and Morrondo-Pelayo (1999)
<i>Cystocaulus ocreatus</i>	<i>Abida frumentum</i> , <i>Agriolumax agrestis</i> , <i>A. schulzi</i> , <i>Cathaica semenovi</i> , <i>Cermuella cespitum arigonis</i> , <i>Cepaea hortensis</i> , <i>C. vindobonensis</i> , <i>Chondrula septemdentata</i> , <i>Cochlicella acuta</i> , <i>Ena asiatica</i> , <i>E. eleonorae</i> , <i>Euparypha pisana</i> , <i>Fruiticola rubens</i> , <i>Helicella barbesiana</i> , <i>H. canadicans</i> , <i>H. itala</i> , <i>H. joppensis</i> , <i>H. obvia</i> , <i>H. vestalis</i> , <i>Helix cavata</i> , <i>H. pomatia</i> , <i>Jamimia potaniniana</i> , <i>Levantina caecariana</i> , <i>L. hierosolima</i> , <i>Limax flavus</i> , <i>L. maximus</i> , <i>Monacha syriaca</i> , <i>Monachoides umbrosa</i> , <i>Parachondrula aptycha</i> , <i>Retinella nitellina</i> , <i>Theba carthusiana</i> , <i>T. pisana</i> , and <i>Zebrina detrita</i>	Prestwood (1976)
<i>Didelphostrongylus hayesi</i>	<i>Mesodon perigraptus</i> and <i>Triodopsis albolabris</i>	Lankester and Fong (1989); Lankester et al. (1998);
<i>Elaphostrongylus alces</i>	<i>Arianta arbustorum</i>	Panin (1964a, b), Rezac et al. (1994)
<i>E. cervi</i>	<i>Agriolumax agrestis</i> , <i>Arimata arbustorum</i> , <i>Bradybaena fructicum</i> , <i>Cochlicopa lubrica</i> , <i>C. lubricella</i> , <i>C. pseudonitens</i> , <i>Discus ruderatus</i> , <i>Euconulus fulvus</i> , <i>Helix pomatia</i> , <i>Perforatella bicalliosa</i> , <i>Perpolita petronella</i> , <i>Succinea altaica</i> , <i>S. granulosa</i> , <i>Vitrina rugulosa</i> , <i>Zenobiella acuteata</i> , <i>Z. nordenskioldi</i> , and <i>Zonitoides nitidus</i>	Mitskevich (1957, 1958); Lankester and Fong (1996)
<i>E. rangiferi</i>	<i>Trichida hispida</i> , <i>Succinea putris</i> , <i>Deroceras laeve</i>	Dubnitski (1955); Anderson (1962); Stockdale and Anderson (1999)
<i>Filaroides martis</i> (=F. <i>branchialis</i> )	<i>Angiolumax reticulatus</i> , <i>Anguispirina alternata</i> , <i>Arion intermedius</i> , <i>A. agrestis</i> , <i>Deroceras laeve</i> (D. <i>gracile</i> ), <i>Discus cronkhitei</i> , <i>Eulota fruticicola</i> , <i>Succinea ovalis</i> , <i>S. putris</i> , <i>Zonitoides arboreus</i> , <i>Z. excavata</i> , and <i>Z. nida</i>	

TABLE 1. Continued

Nematode species	Intermediate host	Reference
<i>Meullerius capillaris</i>	<i>Agriolimax agrestis</i> , <i>A. reiculatum</i> , <i>A. laevis</i> , <i>Anguispira alternata</i> , <i>Anisus centortus</i> , <i>A. leucostoma</i> , <i>Arinata arbustorum</i> , <i>Arion circumscriptus</i> , <i>A. hortensis</i> , <i>A. subfuscus</i> , <i>A. empiricorum</i> , <i>Bradybaena fruticum</i> , <i>Cepaea hortensis</i> , <i>C. nemoralis</i> , <i>C. vindobonensis</i> , <i>Cernuella cespitum</i> , <i>C. virgata</i> , <i>Cingulifera planospira</i> , <i>Chondrula septemdentata</i> , <i>Coclicella acuta</i> , <i>Cochlicopa lubrica</i> , <i>Deroceras reticulatum</i> , <i>Euparypha pisana</i> , <i>Fruticola hispida</i> , <i>Galba corvus</i> , <i>Goniodiscus rotundatus</i> , <i>Gyraulus albus</i> , <i>G. laevis</i> , <i>Helicella acuta</i> , <i>H. barbesiana</i> , <i>H. candaharica</i> , <i>H. candicus</i> , <i>H. diecta</i> , <i>H. obvia</i> , <i>H. vestalis</i> , <i>H. virgata</i> , <i>Helicolimax pellucidus</i> , <i>Helicigona arbustratum</i> , <i>Helix cavata</i> , <i>Helix pomatia</i> , <i>Hyalina cellaria</i> , <i>Levantina caesareana</i> , <i>L. hierosolima</i> , <i>Limax flavus</i> , <i>Lymnaea stagnalis</i> , <i>Monacha syriaca</i> , <i>Monachoides umbrosa</i> , <i>Milax sowerbyi</i> , <i>Planorbis planorbis</i> , <i>P. coreneus</i> , <i>Perforatella bidentata</i> , <i>Physa fontinalis</i> , <i>Praticollella griesola</i> , <i>Pseudotrichia rubigibosa</i> , <i>Radix peregra</i> , <i>Retinella nitellina</i> , <i>R. petronella</i> , <i>Succinae putris</i> , <i>S. pfeiffei</i> , <i>Theba pisana</i> , <i>Trichia hispida</i> , <i>Zebrina cylindrica</i> , <i>Z. detrita</i> , <i>Zonitoides arboreus</i> , and <i>Zonitoides nitidus</i>	Anderson (2000)
<i>Neostromylus linearis</i>	<i>Arianta arbustorum</i> , <i>Arion hortensis</i> , <i>A. subfuscus</i> , <i>Cepaea hortensis</i> , <i>C. nemoralis</i> , <i>C. vindobonensis</i> , <i>Cernuella cespitum</i> , <i>C. virgata</i> , <i>Cochlicella ventricosa</i> , <i>Deroceras agrestis</i> , <i>Fruticola strioleta</i> , <i>Helicella apicina</i> , <i>H. aspera</i> , <i>H. candicans</i> , <i>H. neglecta</i> , <i>H. variabilis</i> , <i>H. pomatia</i> , and <i>Zebrina detrita</i>	Muller (1934); Rojo-Vazquez and Cordero del Campillo (1974); Marcos Martinez (1977); Boev (1975); Manga-Gonzalez and Morrondo-Pelayo (1994)
<i>Oslerus ostratus</i> (= <i>Anafilaroides rostratus</i> )	<i>Achatina fulica</i> , <i>Helix aspersa</i> , <i>Laevicaulus alte</i> , <i>Limax maximus</i> , <i>Mariella dussumieri</i> , <i>Monacha syriaca</i> , and <i>Theba pisana</i>	Gerichter (1949); Klewer (1958); Seneviratna (1959)
<i>Parelaphostromylus andersoni</i>	<i>Deroceras laevae</i> , <i>Mesodon perigraptus</i> , <i>M. thyroides</i> , <i>Triodopsis albolabris</i> , <i>T. multilineata</i> , and <i>T. vannostrandii</i>	Prestwood (1972); Nettles and Prestwood (1976); Anderson and Prestwood (1981)
<i>P. odocoilei</i>	<i>Agriolimax agrestis</i> , <i>A. campetris</i> , <i>Deroceras laeve</i> , <i>Epigramphora arrosa</i> , <i>Euconulus fulvus</i> , <i>Helix aspera</i> , <i>Planorbis sp.</i> , <i>Triodopsis multilineata</i> , <i>Vitrina limpida</i> , and <i>Zonitoides arboreus</i>	Hobmaier and Hobmaier (1934); Brunetti (1969); Platt and Samuel (1978, 1984)
<i>P. tenuis</i>	<i>Anguispira alternata</i> , <i>A. circumscriptus</i> , <i>Deroceras laeve</i> , <i>D. reticulatum</i> , <i>Discus cronkhitei</i> , <i>Haplotrema concavum</i> , <i>Mesodon thyroides</i> , <i>Strenotrema fracternum</i> , <i>Triodopsis albolabris</i> , <i>T. notata</i> , and <i>Zonitoides arboreus</i> , and <i>Z. nitidus</i>	Anderson (1963b); Lankester and Anderson (1968); Kearney and Gilbert (1978)
<i>Pneumostromylus calcaratus</i>	<i>Urocyclus (Elisolimax) flavescens</i>	Anderson (1974, 1976, 1982)
<i>Protostrongylus boughtoni</i>	<i>Vallonia pulchella</i>	Kralka and Samuel (1984)
<i>P. cunicularum</i>	<i>Helicella rugosiuscula</i>	Joyeux and Gaud (1946)
<i>P. davtianii</i>	<i>Subzebrinus sogdianus</i> and <i>Xeropicta candahrica</i>	Boev (1975)
<i>P. hobmaieri</i>	<i>Euconulus fulvus</i> , <i>Pupilla muscorum</i> , <i>P. sterri</i> , <i>P. triplicata</i> , <i>Vallonia costata</i> , <i>V. pulchella</i> , <i>Vertigo alpestris</i> , <i>V. antivertigo</i> , <i>V. pygmea</i> , <i>V. ronneybyansis</i> , and <i>Zonitoides nitidus</i>	Boev (1975)
<i>P. kamenskii</i>	<i>Pupilla muscorum</i> , <i>Succinea elegans</i> , <i>Vallonia tenuilaris</i> , and <i>Vertigo alpestris</i>	Ryzhikov et al. (1956); Kralka and Samuel (1990)
<i>P. pulmonalis</i>	<i>Pupilla muscorum</i> , <i>Succinea elegans</i> , <i>Vallonia tenuilaris</i> , and <i>Vertigo alpestris</i>	Ryzhikov et al. (1956); Kralka and Samuel (1990)
<i>P. rufescens</i>	<i>Agriolimax kervillei</i> , <i>Albrida frentum</i> , <i>Cepaea vindobonensis</i> , <i>Cochlicopa contermina</i> , <i>C. lubrica</i> , <i>Enomphalia strigella</i> , <i>Euconulus fulvus</i> , <i>Eutola fruticum</i> , <i>Goniodiscus ruderatus</i> , <i>Helicella candaharica</i> , <i>H. candicanus</i> , <i>H. obvia</i> , <i>Helix aspersa</i> , <i>H. promatia</i> , <i>Monachodes incarnata</i> , <i>Pupilla muscorum</i> , <i>Succinea putris</i> , <i>Theba corthusiana</i> , <i>Vallonia costata</i> , <i>V. pulchella</i> , <i>Zenbrina detrita</i> , <i>Zenobiella rubignosa</i>	Boev (1975)
<i>P. skrjabini</i>	<i>Helicella candaharica</i> and <i>Subzebrinus albipicatus</i>	Azimov et al. (1976)
<i>P. stilesi</i>	<i>Euconulus fulvus</i> , <i>Pupilla blandi</i> , <i>P. muscorum</i> , <i>Pupoides sp.</i> , <i>Vallonia cyclophorella</i> , <i>Vertigo gouldi</i> , and <i>V. modesta</i>	Forrester (1971); Hibler et al. (1982)
<i>P. rushi</i>	<i>Euconulus fulvus</i> , <i>Pupilla blandi</i> , <i>P. muscorum</i> , <i>Pupoides sp.</i> , <i>Vallonia cyclophorella</i> , <i>Vertigo gouldi</i> , and <i>V. modesta</i>	Forrester (1971); Hibler et al. (1982)
<i>P. tauricus</i>	<i>Helicella derbentina</i> , <i>H. krynickii</i> , <i>H. obvia</i> , <i>Pupilla muscorum</i> , <i>Vallonia costatus</i> , and <i>V. emmiensis</i>	Boev (1975); Rodonaya (1977)
<i>Skrjabingylus chitwoodorum</i>	<i>Agriolimax agrestis</i> , <i>Limax maximus</i> , <i>L. cinereus</i> , <i>L. flavus</i> , <i>L. niger</i> , <i>Mesodon thyroides</i> , <i>Milax sp.</i> , and <i>Triodopsis albolabris</i>	Lankester and Anderson (1971); Lankester (1983)
<i>S. lutrae</i>	<i>Mesodon roemori</i>	Lankester and Crichton (1972)

TABLE 1. Continued

Nematode species	Intermediate host	Reference
<i>S. nasicola</i>	<i>Angiulimax reticulatus</i> , <i>Cochlicopa lubrica</i> , <i>Euparypha pisana</i> , <i>Helicella arenosa</i> , <i>Mesodon thyroidus</i> , and <i>Zenobiella rubiginosa</i>	Dubnitski (1956); Theron (1975); Lankester (1983)
<i>S. petrovi</i>	<i>Succinea ovalis</i>	Gagarin (1938) in Anderson (2000)
<i>Syngamus trachea</i>	<i>Lymnaea stagnalis</i>	Rizhikov (1941)
<i>Troglostrongylus brevior</i>	<i>Chondrula septemdentata</i> , <i>Helicella barbesiana</i> , <i>H. ustalis</i> , <i>Limax flavus</i> , <i>Monaca syriaca</i> , <i>Retinella nitellina</i> , and <i>Theba pisana</i>	Gerichter (1949)
<i>Trilobostongylus bioccai</i>	<i>Deroceras laeve</i> , <i>Discus cronkhitei</i> , <i>Physa integra</i> , and <i>Zontoides arboreus</i>	Anderson (1963a)
<i>Umingmastrongylus pallikuukensis</i>	<i>Deroceras reticulatum</i> , <i>D. laeve</i> , <i>Euconulus fulvus</i> , <i>Columella alticola</i> , <i>Aplexa hypnorum</i>	Hoberg et al. (1995)
<i>Varestrongylus capreoli</i>	<i>Angiulimax sp.</i> , <i>Arion rufus</i> , <i>A. subfuscus</i> , <i>Deroceras reticulatum</i> , <i>Cepaea hortensis</i> , <i>Clausilia pila</i> , <i>Cochlicopa lubrica</i> , <i>Discus rotundatus</i> , <i>Monachoides inamata</i> , <i>M. umbrosa</i> , <i>Succinea putris</i> , <i>Trichia unidentata</i> , and <i>Vitrina sellucida</i>	Stroh and Schmid (1938); Boev (1975)
<i>V. pneumonicus</i>	<i>Agriolimax agrestis</i> , <i>A. schulzi</i> , <i>Cochlicopa lubrica</i> , <i>Ena eleonorae</i> , <i>Euconulus fulvus</i> , <i>Fruiticola lantzi</i> , <i>Macrochlamys cassida</i> , <i>M. kazachstani</i> , <i>M. schmidtii</i> , <i>M. turanica</i> , <i>Phenacolimax rugulosa</i> , <i>Subzebrinus labiellus</i> , <i>Succinea evoluta</i> , <i>S. martensiana</i> , <i>Vallonia pulchella</i> , and <i>Zonitoides nitidus</i>	Boev (1940, 1952); Boev and Vol'f (1940); Bhalerao (1945)
<i>V. sagittatus</i>	<i>Bradybaena fructicum</i> , <i>Succinea altaica</i> , <i>Zenobiella acuteata</i> , and <i>Z. nordenskoldi</i>	Panin (1967)
Order: Ascaridia		
<i>Falcaustra wardi</i>	<i>Lymnaea stagnalis</i>	Bartlett and Anderson (1985)
<i>Sulcascaris sulcata</i>	<i>Polinices sordidus</i>	Lichtenfels et al. (1978)
Order: Spirurida		
<i>Anguillicola crassus</i>	<i>Galba corvus</i> (a paratenic host)	Moravec (1996)
Order: Rhabditida		
<i>Angiostoma asamati</i>	<i>Gigantomilax ferganus</i>	Spiridinov (1985)
<i>A. aspersae</i>	<i>Helix aspersa</i>	Morand (1986)
<i>A. dentifera</i> (= <i>Limaconema dentifera</i> )	<i>Arion subfuscus</i> , <i>Limax cinerioniger</i>	Mengert (1953)
<i>A. helicis</i>	<i>Helix hortensis</i>	Mengert (1953)
<i>A. kimmeriensis</i>	<i>Zonitoides arboreus</i>	Korol and Spiridinov (1991)
<i>A. limacis</i> (= <i>Limaconema limacis</i> )	<i>Arion ater</i> , <i>A. circumscriptus</i> , <i>A. empiricorum</i> , <i>A. slivaticus</i> , <i>A. subfuscus</i>	Mengert (1953); Campana-Rouget and Théodoridès (1956); Morand and Spiridinov (1989); Spiridinov (1989)
<i>A. scizoglossae</i>	<i>Schizoglossa novaseelandica</i>	Morand and Barker (1995b)
<i>A. spiridonovi</i>	<i>Limax flavus</i>	Morand (1992)
<i>A. stammeri</i> (= <i>Limaconema stammeri</i> )	<i>Limax cinerioniger</i> , <i>L. maximus</i>	Mengert (1953)

Rhabditida) are parasites of amphibians and reptiles but use snails and slugs as obligatory intermediate hosts (Table 1). For example, *Angiostoma limacis*, a parasite of salamanders, has been isolated from the digestive tract of *Arion ater* (= *Limax rufus*) (Morand and Spiridinov, 1989). The nematode *Parelaphostongylus tenuis* (Order, Strongylida), a parasite of white-tailed deer, uses snails including *Mesodon sayanus* as intermediate hosts for transmission to the definitive vertebrate host (McCoy and Nudds, 2000).

*Molluscs as definitive hosts:* Many species of slugs and snails serve as final definitive hosts for nematodes, and these associations differ (Table 2). In some cases only juvenile nematode stages develop inside the body cavity or foot muscle, while the adult nematodes are free-living. In other cases the entire nematode life cycle is completed inside the host. In the latter case, the nematodes may or may not kill their definitive host. At least

three types of associations of nematodes with definitive mollusc hosts can be identified. In the first type of association, the nematodes live as juveniles (agamic forms) in the body cavity, but the adult nematodes are free-living. For example, juveniles of *Mermis nigrescens* living in the slug *Deroceras agrestis* (= *Limax agrestis*) and of *Mermis albicans* living in the snails *Succinea putris* and *Lymnaea sp.* leave the mollusc host after reaching maturity (Chitwood and Chitwood, 1937), and the mature nematodes then mate and reproduce in the soil. In another example of this type of association, *Alloionema appendiculata* juveniles live in the foot muscle of *Arion ater* and adults are free-living (Mengert, 1953).

In the second type of association with the definitive mollusc host, the entire nematode life cycle is completed inside the host, but the nematodes are not pathogenic and do not kill the host. *Agfa flexilis* nematodes live as adults in the genital organs of *Limax ci-*

TABLE 2. Nematode species and their mollusk definitive hosts.

Nematode species	Host	Reference
Order: Ascaridia		
<i>Ascaris cylindrica</i>	<i>Helix alternata</i>	Leidy (1849)
<i>Cosmocercoides dukae</i>	<i>Agriolimax</i> sp., <i>Deroceras laeve</i> (= <i>D. gracile</i> ), <i>Cepaea nemoralis</i> , <i>C. hortensis</i>	Ogren (1953, 1959a,b); Anderson (1960); McGraw (1968); Morand (1989); Vanderburgh and Anderson (1986, 1987)
<i>Nemhelix bakeri</i>	<i>Helix aspersa</i>	Morand and Petter (1986); Morand and Faliex (1994)
Order: Mermithida		
<i>Mermis nigrescens</i>	<i>Limax agrestis</i>	Chitwood and Chitwood (1937)
<i>M. albicans</i>	<i>Succinea putris</i>	Chitwood and Chitwood (1937)
Order: Araeolamida		
<i>Plectus cirratus</i>	<i>Limax tenellus</i>	Mengert (1953)
<i>P. rhizophilus</i>	<i>Helix pomatia</i>	Mengert (1953)
Order: Rhabditida		
<i>Agfa flexilis</i>	<i>Limax cinereoniger</i>	Morand and Homay (1990)
<i>A. tauricus</i>	<i>Limax cinereoniger</i>	Korol and Spridinov (1991)
<i>Alloionema appendiculata</i>	<i>Arion ater</i> , <i>A. agrestis</i> , <i>A. circumscriptus</i> , <i>A. empiricum</i> , <i>A. intermedius</i> , <i>A. subfuscus</i> , <i>Succinea avara</i>	Pelseneer (1928); Mengert (1953)
<i>Bunonema reticulatum</i>	<i>Arion circumscriptus</i> , <i>Limax tenellus</i>	Mengert (1953)
<i>Caenorhabditis formosana</i>	<i>Oncomelania formosana</i>	
<i>Cephalobus butschlii</i>	<i>Polygyra albolabrus</i>	Mengert (1953)
<i>C. persegnis</i>	<i>Helix hortensis</i>	Mengert (1953)
<i>Chielobus schneideri</i>	<i>Arion circumscriptus</i> , <i>A. empiricum</i> , <i>Limax tenellus</i>	Mengert (1953)
<i>Cruzanema lambdiensis</i>	<i>Deroceras reticulatum</i> , <i>Agriolimax reticulatus</i>	Arias and Crowell (1963)
<i>Daubaylia capillaris</i>		
<i>D. helicophilus</i>	<i>Gyraulus spirillus</i>	Poinar and Richards (1979)
<i>D. malayanum</i>	<i>Gyraulus convexisculus</i>	
<i>D. potomaca</i>	<i>Biomphalaria glabrata</i> , <i>Planorbis trivolvis</i>	Mengert (1953)
<i>D. seistamensis</i>	<i>Gyraulus convexisculus</i>	Mengert (1953)
<i>Panagrolamus detritiphagus</i>	<i>Arion circumscriptus</i> , <i>A. empiricum</i> , <i>Limax tenellus</i>	Mengert (1953)
<i>P. superbis</i>	<i>Arion circumscriptus</i> , <i>Deroceras reticulatum</i>	Mengert (1953)
<i>Pellioditis pellioditis</i> (= <i>Rhabditis oncomelaniae</i> )	<i>Oncomelania nosophora</i>	Yokoo and Okabe (1968)
<i>Phasmarhabditis hermaphrodita</i>	<i>Deroceras reticulatum</i>	Schneider (1859); Mengert (1953); Wilson et al. (1993); Tan and Grewal (2001 a,b)
<i>P. neopapillosa</i>	<i>Deroceras reticulatum</i>	Mengert (1953)
<i>P. papillosa</i>	<i>Arion circumscriptus</i> , <i>A. empiricum</i> , <i>Deroceras laeve</i> , <i>Limax cinero-niger</i> , <i>L. maximus</i> , <i>L. tenellus</i>	Mengert (1953)
<i>Pelodera terres</i> ( <i>Rhabditis terres</i> )	<i>Arion empiricum</i> , <i>Limax cinero-niger</i> , <i>Helix pomatia</i>	Mengert (1953)
<i>Rhabditis aspera</i>	<i>Arion empiricum</i> , <i>Deroceras reticulatum</i>	Mengert (1953)
<i>R. axei</i>	<i>Archachatina marginata ovum</i> , <i>A. marginata saturalis</i> , <i>Achatina achatina</i>	Odaibo et al. (2000)
<i>R. caussaneli</i>	<i>Arion empiricum</i>	Mengert (1953)
<i>R. coarctata</i>	<i>Arion empiricum</i>	Mengert (1953)
<i>R. conica</i>	<i>Arion empiricum</i>	Mengert (1953)
<i>R. ecosiensis</i>	<i>Arion empiricum</i>	Mengert (1953)
<i>R. elegans</i>	<i>Limax tenellus</i>	Mengert (1953)
<i>R. elongata</i>	<i>Deroceras reticulatum</i>	Mengert (1953)
<i>R. cylindrica</i>	<i>Oncomelania nosophora</i>	Mengert (1953)
<i>R. dolichura</i>	<i>Arion circumscriptus</i> , <i>Limax maximus</i> , <i>Succinea oblonga</i>	Mengert (1953)
<i>R. gongyloides</i>	<i>Helix pomatia</i>	Mengert (1953)
<i>R. maupasi</i>	<i>Arion empiricum</i>	Mengert (1953); Brokelman and Jackson (1974)
Order: Diplogastrida		
<i>Diplogaster austriacus</i>	<i>Arion empiricum</i>	Mengert (1953)
<i>D. gracilis</i>	<i>Deroceras reticulatum</i>	Mengert (1953)
<i>D. maupasi</i>	<i>Helix aspersa</i>	Arias and Crowell (1963)

TABLE 2. Continued

Nematode species	Host	Reference
<i>D. lheritieri</i>	<i>Arion circumscriptus</i> , <i>Deroceras reticulatum</i> , <i>Lehmania marginata</i>	Mengert (1953)
<i>Hugodiplogaster neozelandia</i>	<i>Athoracophorus bitentaculatus</i>	Morand and Barker (1995a)
Order: Nematomorpha		
<i>Gordius aquaticus</i>	<i>Lymnea vulgaris</i> , <i>L. ovata</i>	Chitwood and Chitwood (1937)
<i>G. villoti</i>	<i>Lymnea ovata</i>	Chitwood and Chitwood (1937)

*neruus*. Similarly, *Rhabditis axei* lives in the rectum of African giant snails *Arachchata marginata ovum*, *A. marginata saturalis*, and *A. achatina* (Odaibo et al., 2000). In yet another example, *Hugodiplogaster neozelandia* lives in the genital tract of the slug *Athoracophorus bitentaculatus* (Morand and Barker, 1995a). *Nemhelix bakeri* lives in the genital tract of the snail *Helix aspersa* and is transmitted sexually (Morand and Faliex, 1994). A proteinacious inhibitor of the haemolymph plasma from the snail *Helix aspersa* permits a commensal relationship between the nematode *Rhabditis maupasi* and the host snail. It also helps to regulate the population level of the nematode (Brokelman and Jackson, 1974).

In the third kind of association, the entire nematode life cycle is completed in the definitive mollusc host and the nematodes are pathogenic, causing host mortality. *Daubaylia potomaca*, *Pellioiditis pelloides* (= *Rhabditis oncomellaniae*), *Phasmarhabditis hermaphrodita*, *P. papillosa*, and *P. neopapillosa* form this kind of association with their mollusc hosts. In the case of *P. hermaphrodita*, the third-stage infective juveniles (also called dauers) initiate infection by entering through the shell cavity underneath the mantle (Tan and Grewal, 2001a; Wilson et al., 1993). Following penetration into the shell cavity, the infective juveniles release their associated bacteria, which multiply and produce an endotoxin (Tan and Grewal, 2001b, 2002) that kills the host within 4 to 7 days. The infective juveniles develop into hermaphrodites in the shell cavity and reproduce. The nematodes continue to multiply until the entire slug body is consumed, at which time the next generation of host-seeking infective juveniles is produced.

#### EVOLUTIONARY TRENDS

Based on current phylogenetic resolution of the nematodes (Adamson, 1987; Blaxter et al., 1998, 2000), it appears that molluscs have been acquired as hosts by nematodes independently on a number of occasions. However, it is apparent from this study that molluscs are significant as hosts for only two major groups of nematodes: as intermediate hosts for metastrongyloids and as definitive hosts for a number of rhabditids. Of the 61 species of nematodes known to use molluscs as intermediate hosts, 49 belong to Metastrongyloidea

(Order Strongyloida) (Table 1). Of the 47 species of nematodes that use molluscs as definitive hosts, 33 of these belong to the Order Rhabditida (Table 2). When mapped onto a best estimate of phylogenetic relationships among nematode taxa (Adamson, 1987; Blaxter et al., 2000; DeLey and Blaxter, 2002), it appears that parasitism of molluscs arose frequently and independently (up to four times in the Nematoda and up to three times in the Chromadoria) (Fig. 1). Such a distribution suggests that utilization of molluscan hosts can be lucrative for nematodes, and that nematodes display extreme adaptive plasticity. The hypothesis that parasites first establish paratenic relationships prior to establishing themselves within a definitive host is controversial (Combes, 2001). Although phylogenetic relationships among the Diplogasterida, Rhabditina, and Strongyloida are poorly understood, as a general trend in the Nematoda it appears that an association with a definitive host predates their use of an intermediate host. Improved resolution among the Diplogasterida/

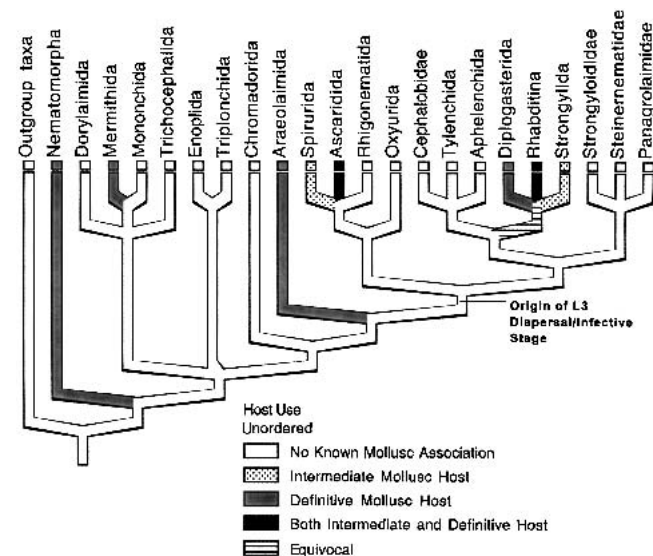


FIG. 1. Phylogenetic distribution of mollusc host utilization among the Nematoda. Phylogenetic tree is modified from Blaxter et al. (2000). The origin of the L3 dispersal/infective stage is indicated at the node shared by the Rhabditina, Tylenchida, and Spirurina of DeLey and Blaxter (2002). Notable exceptions to the L3 dispersal/infective stage occur in the Aphelenchida and Tylenchida (Tylenchomorpha).

Rhabditina/Strongylida and Spirurida/Ascaridida/Rhigonematida by future phylogenetic analyses will facilitate further testing of this hypothesis.

It has been contemplated for quite some time that parasitic nematodes may have evolved from free-living, terrestrial, ancestral forms (Andrassy, 1976; Anderson, 2000). The soil-dwelling rhabditid nematodes that feed on bacteria were considered to be the most primitive nematodes (Chitwood and Chitwood, 1937), and it has been proposed that rhabditids gave rise to four parasitic orders in vertebrates (the Strongylida, Oxyurida, Ascaridida, and Spirurida) and one parasitic order in diplopods (the Rhigonematida) (Anderson, 2000). However, recent molecular evidence (Blaxter et al., 1998, 2000) concurs with earlier analyses of morphological characters (Adamson, 1987) that imply the Rhabditida, although clearly paraphyletic (Blaxter et al., 1998), are probably not modern representatives of the ancestral lineage that led to the diversification of the aforementioned orders.

Almost all species of rhabditids that use molluscs as definitive hosts feed on bacteria. These rhabditid nematodes can penetrate and complete development in mollusc hosts, but almost all maintain free-living life cycles. It is interesting that even pathogenic nematodes that kill their hosts maintain the ability to complete their life cycle in the absence of mollusc hosts in nature. For example, *Phasmarhabditis hermaphrodita* kills its host *Deroceras reticulatum* and several other *Deroceras* and *Arion* species (Grewal et al., 2003) within 4 to 7 days after penetration and completes its development and reproduction in the mollusc host. This nematode species is also able to initiate and complete its life cycle on feces of its slug hosts (Tan and Grewal, 2001a). This species, however, did not multiply in sterile or non-sterile soil containing a suite of naturally occurring bacteria. Therefore, it is conceivable that the use of molluscs as definitive hosts by the nematodes may have evolved from the free-living Rhabditida in the soil that developed the ability to penetrate and reproduce in molluscs. We have found that the dauer juveniles of *P. hermaphrodita* enter the shell cavity under the mantle of slugs and snails but not through the digestive tract. Thus, it is not a passive intake of *P. hermaphrodita* by slugs and snails during feeding on the dead organic matter in the soil, but rather active penetration of the host by the nematodes.

Development of a durable infective stage appears to be a significant step in the evolution of nematodes toward parasitism of invertebrates. The infective stage in the parasitic nematodes is very similar in its ontogeny and morphology to the dauer stage produced by many rhabditid nematodes for dispersal and survival in the absence of food. This certainly seems to be true for nematodes that use molluscs as definitive hosts and in which detailed studies have been made. In most species, it is the third juvenile stage that is morphologically

distinct from the normal third stage and is the only stage that can infect mollusc hosts. In case of *P. hermaphrodita*, although adults and other juvenile stages could establish and reproduce when injected into the mantle cavity of the slug *D. reticulatum*, only the infective stage was able to invade the live slugs by itself (Tan and Grewal, 2001a). In this respect, the infective stage is very similar to the entomopathogenic nematodes in the genera *Steinernema* and *Heterorhabditis* (Rhabditida: Steinernematidae and Heterorhabditidae), which are lethal insect parasites.

Although the associations between mollusc parasitic nematodes and bacteria have not been studied in any significant detail, the emerging evidence suggests that the association with bacteria is an important step in the evolution of mollusc parasitism and necromeny in nematodes. Wilson et al. (1995) isolated nine species of bacteria from the infective juveniles of *P. hermaphrodita* and the slugs infected by the nematodes. They found that nematodes cultured on only certain bacterial species were pathogenic to the slugs and certain bacteria favored nematode reproduction more than others. Wilson et al. (1995) thus selected *Moraxella osloensis* as a candidate bacterium to mass-produce *P. hermaphrodita*. Tan and Grewal (2001b) discovered that *M. osloensis* is in fact the main slug-killing agent that the nematodes vector into the slug mantle. Tan and Grewal (2002) found that *M. osloensis* produces a potent endotoxin that results in slug death. This kind of bacteria-nematode association is in fact very similar to the association between entomopathogenic nematodes *Steinernema* and *Heterorhabditis* and their symbiotic bacteria *Xenorhabdus* and *Photorhabdus*, respectively. Thus, acquisition of a specific association with bacteria appears to be an important step in the evolution of necromeny in the slug parasitic nematodes.

Reconstructions of metazoan phylogeny (Giribet, 2002; Zrzavy et al., 1998) and molecular clock estimates (Ayala and Rzhetsky, 1998) suggest that the ancestral nematode lineage originated in the mid to late Neoproterozoic, prior to the Cambrian explosion that produced the majority of the major extant phyla, including arthropods and molluscs. The Nematomorpha (sister taxon to the Nematoda) and the Mermithida (a lineage branching near the base of the Nematoda) have both established parasitic relationships with arthropods and molluscs, suggesting that parasitism of both of these phyla could have occurred very early in the post-Cambrian radiation. However, for some nematode lineages it is possible that animal parasitism evolved first in molluscs from free-living ancestors, followed by the parasitism of other invertebrates and vertebrates. For example, several nematode species (e.g. *Diplogaster mauvasi*, *Alloionema*, and *Pellioiditis*) infect both molluscs and insects. Poinar (1993) suggested that the entomopathogenic nematodes Steinernematidae and Heterorhabditidae may have evolved from *Alloionema* and

*Pellioiditis*-like ancestors, respectively, implying an evolutionary trend in two phylogenetically independent lineages that mollusc parasitism arose first, followed by parasitism of arthropods. Furthermore, the parasitic life cycle of the slug-parasitic *P. hermaphrodita* remarkably parallels that of Steinernematidae and Heterorhabditidae.

Mapping host associations on phylogenetic trees reveals the apparent ease at which nematodes have successfully established parasitic relationships with other eucaryotes since Cambrian times. That parasitism in general, and of molluscs in particular, is such a successful strategy among the Nematoda implies an astonishing proclivity for parasitism by the nematode bauplane. Interestingly, it is this diversity of independent acquisitions of hosts that confounds our ability to infer with confidence the direction of evolutionary changes associated with the origins of mollusc parasitism. Thanks to the rapidly improving phylogenetic resolution among the Nematoda, questions surrounding the origin and maintenance of mollusc parasitism by nematodes are eminently tractable.

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