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Nemerteans as hosts for symbionts: a review

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Abstract

Nemerteans utilize other animals as hosts in a variety of well-studied, symbiotic relationships, but relatively little is known concerning nemerteans as hosts for other organisms. Only three haplosporidians, one microsporidian, two gregarines, three ciliates, five mesozoans, one mite and one copepod have been identified to species from nemerteans, whereas 34 nemertean species (one Archinemertea, 17 Heteronemertea, 15 Hoplonemertea, one Bdellonemertea) have been recorded as hosts. The majority of recorded nemertean symbionts are endoparasitic protozoans and orthonectids. Among the Haplosporidia, there are three species of *Haplosporidium*. The hyperparasite, *Nosemoides vivieri*, from an unidentified gregarine, is the only known microsporidian associated with a nemertean. Within the phylum Apicomplexa, besides the two species of gregarines from three species of nemerteans, there are 11 other species of nemerteans with unidentified gregarines. One species of nemertean has been found with an unidentified coccidian parasite. ‘Sporozoan-like’ parasites, however, are known from three other species of nemerteans, two of which are pelagic polystiliferans. Two endosymbiotic and one ectosymbiotic species of ciliates have been identified from three species of nemerteans. At least five species of mesozoans (Orthonectida) infect nine species of nemerteans. Unidentified cestode, trematode and nematode juveniles, using nemerteans as intermediate hosts, have been recorded rarely and have not been linked to any life cycles. An ectosymbiotic mite and a copepod from two species of nemerteans are likely incidental associates. The nature of the host–symbiont relationships has been rarely reported. Castration of hosts by haplosporidians and orthonectids, and tissue damage by an unidentified coccidian and some gregarines, are known to occur. The suitability of nemerteans as hosts for parasites, hypersymbioses and approaches for future studies of parasite prevalence and host–parasite relationships are discussed.

Keywords: *Apicomplexa*, *Ciliophora*, *Haplosporidia*, *Microsporida*, *Orthonectida*, *parasites*

Introduction

Nemerteans are well-known symbionts on other organisms. For example, carcinonemertids are semiparasitic on brachyuran crabs and other crustaceans (Kuris 1993); bdellonemerteans, such as *Malacobdella* spp. live in the mantle chambers of bivalve molluscs (Gibson 1967, 1968; Kozloff 1991), and several worms associate with ascidians (Gibson 1974; Egan and Anderson 1979; Egan 1984) and sea anemones (Gibson 1986). On the other hand, we

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have scant knowledge of symbionts that use nemerteans as hosts. Gibson (1972) and Varndell (1980) provided brief summaries of known parasites and Lauckner (1980b) contributed an expanded review with illustrations of several species. Such symbionts are predominantly internal parasites, usually discovered in the process of examining histological sections used for specific taxonomic identifications. Major taxa to which known symbionts belong are the phyla Apicomplexa (coccidians and gregarines), Microsporida (microsporidians and haplosporidians), Ciliophora, Orthonectida, Platyhelminthes (cestodes and trematodes) and Nematoda. Nemerteans are either definitive or intermediate hosts in the life cycles of these taxa. The arthropods are also represented by a single species of ectosymbiotic arachnid (mite) and an ectosymbiotic crustacean (copepod). Very few experimental studies have been done on most of these relationships (Varndell 1980, 1981a, b; Langlet and Bierne 1989; Vernet and Fargette 1990; Haloti and Vernet 1994; Vernet and Haloti 1997), and many of the protozoan parasites have yet to be identified to species or higher taxa; most are known only incidentally from histological specimens of hosts.

I review species of nemerteans that harbour symbionts, the suitability of nemerteans as hosts, the roles of nemerteans as definitive or intermediate hosts and the effects of symbionts on their hosts. Future studies are suggested to develop a better understanding of these relationships.

General survey of relationships

Table I lists known relationships of the Nemertea with the Microsporida through the Arthropoda. While most nemertean hosts have been identified, the identities of many symbionts have not been determined. Only three haplosporidians, one microsporidian, two gregarines, three ciliates, five orthonectids, one arachnid and one copepod have been specifically identified, whereas 33 nemertean hosts have been recorded (one Archinemertea, 17 Heteronemertea, 15 Hoplonemertea, one Bdelonemertea). Twelve of the hoplonemerteans belong to the suborder Monostilifera and two to the pelagic Polystilifera (Table II). Parasitic protozoans, previously referred to the phylum Sporozoa, are now within the Apicomplexa and are the most often recorded nemertean parasites. Members of this phylum are characterized by the presence of an apical complex, with complex life cycles alternating between sexual and asexual phases, some requiring intermediate hosts; constituents of most groups are intracellular while some (e.g. gregarines) are both intracellular and extracellular. Members of the class Sporozoa, such as malarial parasites, coccidians and gregarines, are probably the most well-known.

Systematic discussion of relationships (Table I)

Haplosporidia

Haplosporidians are intracellular protozoan parasites found in a variety of fresh water and marine invertebrates; some are hyperparasitic in trematodes and nematodes that use marine molluscs and decapod crustaceans as hosts (Lee et al. 2000). Their life cycles are poorly understood and their identification relies chiefly on electron microscopical analysis of the morphological characteristics of mature spores. Three species of haplosporidians have been described from nemerteans, all belonging to the genus *Haplosporidium*.

Haplosporidium malacobdellae parasitizes *Malacobdella grossa*, itself a symbiont from the mantle cavity of bivalve molluscs, and the free-living monostiliferan, *Amphiporus lactifloreus*. Jennings and Gibson (1968) examined 1218 specimens of *M. grossa* of which 36 (2.9%)

Table I. Summary of known symbionts of the Nemertea.

Symbionts (Classification)	Host nemerteans ¹	References
Phylum Haplosporidia ²		
Class Haplosporea		
<i>Haplosporidium malacobdellae</i> Jennings & Gibson, 1968	<i>Malacobdella grossa</i> Müller, 1776	Jennings and Gibson (1968)
<i>Haplosporidium malacobdellae</i> Jennings & Gibson, 1968	<i>Amphiporus lactifloreus</i> (Johnston, 1928)	Varndell (1980)
<i>Haplosporidium nemertis</i> Debaisieux, 1920	<i>Lineus bilineatus</i> (Renier, 1804)	Debaisieux (1920)
<i>Haplosporidium prostomae</i> Gibson & Moore, 1979	<i>Prostoma eilhardi</i> (Montgomery, 1894)	Gibson and Moore (1979)
Phylum Microsporidia		
<i>Nosemoides vivieri</i> Vinckier, Devauchelle & Prensier 1970 ³	Microsporidian in unidentified monocystid gregarine from gut of unspecified worm	Vinckier et al. (1970, 1971); Vinckier (1975)
Phylum Apicomplexa		
Class Conoidasida		
Subclass Gregarinasina		
<i>Lecudina linei</i> Vinckier 1973 ⁴	<i>Lineus viridis</i> (Müller, 1774)	Vinckier (1972, 1973); Arnoult and Vernet (2000)
<i>Lecudina</i> sp.	<i>Ramphogordius bicolor</i> (Vernet, 1997)	Arnoult and Vernet (2000)
<i>Urospora nemertes</i> Kölliker, 1845	<i>Baseodiscus delineatus</i> (Delle Chiaje, 1825)	Kölliker (1848); Lee et al. (2000)
<i>Urospora nemertes</i> Kölliker, 1845)	<i>Lineus ruber</i> (Müller, 1774)	Jennings (1960)
Unidentified	<i>Amphiporus lactifloreus</i> (Johnston, 1928)	McIntosh (1873–1874)
Unidentified	<i>Antiponemertes pantini</i> (Southgate, 1954)	Moore et al. (2001)
Unidentified (suspected)	<i>Baseodiscus hemprichii</i> (Ehrenberg, 1831)	Punnett (1900); Gibson (1979)
Unidentified	<i>Craticulineus novaezealandiae</i> Gibson, 1984	Gibson (1984)
Unidentified	<i>Cyanophthalma obscura</i> (Schultz, 1851)	Norenburg (1986)
Unidentified (suspected)	<i>Diopsonemertes acanthocephala</i> Kajihara, Gibson & Mawatari, 2001	Kajihara et al. (2001)
Unidentified	<i>Ovicides julieae</i> Shields, 2001	Shields (2001)
Unidentified (suspected)	<i>Paranemertes peregrina</i> Coe, 1901	Roe (1971, 1976), pers. comm. (2004)
Unidentified	<i>Potamonemertes percivali</i> Moore & Gibson, 1973	Moore and Gibson (1973)
Unidentified	<i>Ramphogordius sanguineus</i> Rathke, 1799	Gontcharoff (1950)
Subclass Coccidiasina		
Unidentified	<i>Quasilineus lucidoculatus</i> Gibson, 1990	Gibson (1990); Canning and Gibson (1990)
Sporozoon-like		
Unidentified	<i>Nectonemertes primitiva</i> Brinkmann, 1917	Brinkmann (1917)
Unidentified	<i>Parabalaenanemertes fusca</i> Brinkmann, 1917	Brinkmann (1917)

Table I. (continued.)

Symbionts (Classification)	Host nemerteans ¹	References
Unidentified	<i>Ischyronemertes albanyensis</i> Gibson, 1990	Gibson (1990)
Phylum Ciliophora		
Class Phyllopharyngea		
Subclass Suctorina		
<i>Ophryodendron prenanti</i> (Duboscq, 1925)	<i>Cephalothrix linearis</i> (Rathke, 1799)	Duboscq (1925)
Class Heterotrichea		
Order Heterotrichida		
<i>Orchitophrya malacobdellae</i> Jennings, 1968	<i>Malacobdella grossa</i> (Müller, 1776)	Jennings (1968)
<i>Thigmophrya annella</i> , Fenchel 1965	<i>Malacobdella grossa</i> (Müller, 1776)	Fenchel (1965)
Unidentified 'protozoan'	<i>Heteroenopelus enigmaticus</i> Wern, 1998	Wern (1998)
Phylum Orthonectida		
<i>Intoshia linei</i> Giard, 1877 ⁵	<i>Lineus ruber</i> (Müller, 1774) <i>Lineus viridis</i> (Müller, 1774) <i>Ramphogordius sanguineus</i> Rathke, 1799	Giard (1877); Nouvel (1935); Kozloff (1992); Vernet and Haloti (1997); Arnoult and Vernet (2000)
<i>Intoshia linei</i> Giard, 1877 ⁵	<i>Lineus</i> sp.	Aleksandrov (1989); Kozloff (1992)
<i>Intoshia metchnikovi</i> Caullery & Mesnil, 1899	<i>Tetrastemma flavidum</i> Ehrenberg, 1828 ⁶	Caullery and Mesnil (1899); Kozloff (1992)
<i>Rhopalura intoshi</i> Metschnikoff, 1881 ⁷	<i>Ramphogordius lacteus</i> Rathke, 1843	Metschnikoff (1881)
<i>Rhopalura pelseneeri</i> Caullery & Mesnil, 1901 ⁷	<i>Tetrastemma flavidum</i> Eherenberg, 1828	Caullery and Mesnil (1901)
<i>Rhopalura pelseneeri</i> var. <i>vermiculicola</i> Caullery, 1914 ⁷	<i>Tetrastemma verinigrum</i> Iwata, 1954	Caullery (1914)
<i>Rhopalura sanguinea</i> Haloti & Vernet 1996	<i>Ramphogordius sanguineus</i> Rathke, 1799	Haloti and Vernet (1996)
<i>Rhopalura sanguinea</i> Haloti & Vernet 1996	<i>Ramphogordius bicolor</i> (Vernet, 1997)	Arnoult and Vernet (2000)
<i>Rhopalura</i> sp.	<i>Amphiporus ochraceus</i> (Verrill, 1873)	Meinkoth (1956)
Phylum Platyhelminthes		
Class Cestoda		
Subclass Eucestoda		
<i>Echeneibothrium</i> sp.	<i>Cerebratulus lacteus</i> (Leidy, 1851)	Hunter (1950)
Class Trematoda		
Unidentified metacercariae	<i>Amphiporus lactifloreus</i> (Johnston, 1828)	McIntosh (1873/1874)
Phylum Nematoda		
Unidentified larvae	<i>Geonemertes philippinensis</i> Gibson & Moore, 1998	Gibson and Moore (1998)
Phylum Arthropoda		
Subclass Arachnida		
<i>Parhalixodes travei</i> Laubier, 1960	<i>Cerebratulus hepaticus</i> Hubrecht, 1879	Laubier (1960)

Table I. (continued.)

Symbionts (Classification)	Host nemerteans ¹	References
Subclass Copepoda <i>Nemerthessius nemertophilus</i> Gallien, 1936	<i>Lineus longissimus</i> (Gunnerus, 1770)	Gallien (1936); Stock (1985, new genus)
Major taxa unknown		
Internal parasite	<i>Cephalurichus antarcticus</i> Gibson, 1985	Gibson (1985)
Internal parasite	<i>Paraborlasia fueguina</i> Serna de Esteban & Moretto, 1968	Gibson (1985)
Internal parasite	<i>Lineus bioculatus</i> Sundberg & Gibson 1995	Sundberg and Gibson (1995)

¹Gibson's (1995) world list of species is a major reference to nemertean taxa. ²Lee et al. (2000) is reference for this phylum and other major protozoan taxa. ³Hyperparasite of unidentified gregarine. ⁴In same host with orthonectid *Intoshia linei*. ⁵In same host with gregarine *Lecudina linei*. ⁶The polychaete *Spio martinensis* is also host for this species. ⁷Kozloff (1992) could not assign this parasite with certainty to this genus.

prevalence) were infected. Examination of this large number of nemerteans involved serial histological sections and fresh squashes of worm tissue. *Haplosporidium nemertis* parasitizes the heteronemertean *Lineus bilineatus*, and *Haplosporidium prostomae* lives in the tissues of the freshwater hoplonemertean *Prostoma eilhardi*. All three species of *Haplosporidium* may castrate their hosts (Debaisieux 1920; Jennings and Gibson 1968; Gibson and Moore 1979; Varndell 1980) and, at least in the case of *H. malacobdellae*, causes mortality (Jennings and Gibson 1968). Varndell (1981a, b) further demonstrated a variety of enzymes and metabolites in the life-history stages of *H. malacobdellae*.

Microsporida

Microsporidians are all intracellular protozoan parasites of hosts that include probably all invertebrate phyla and the five classes of vertebrates (Lee et al. 2000). Most life cycles are unknown and, like the haplosporidians, identification relies primarily on the morphology of mature spores, in this phylum, especially their elaborate internal structure. The only microsporidian associate of nemerteans is the hyperparasitic *Nosemoides vivieri* whose host is an unidentified gregarine parasitic in an unidentified nemertean (Vinckier et al. 1970, 1971; Vinckier, 1995) (Table III).

Apicomplexa (formerly Sporozoa)

The gregarines (subclass Gregarinasina) are primarily parasites of invertebrates, but also occur in lower vertebrates. They are generally conspicuous in sections of the digestive tract and body cavities due to their relatively large size. They have simple or complex life cycles. Gregarines are the most common apicomplexans to occur in nemerteans and have been found in 14 species of nemerteans (seven Heteronemertea, seven Hoplonemertea). All nemertean hosts, except the terrestrial *Antiponemertes pantini* and the freshwater *Potamonemertes pericvali*, have been marine. Only two species of gregarines, however, have been specifically identified. Vinckier (1972, 1973) described the new species, *Lecudina linei*, from the intestinal epithelium of the heteronemertean *Lineus viridis* (this description appeared first in 1972 as an abstract without illustrations, and later in 1973 in his doctoral

Table II. Nemertean species known to harbour symbionts (alphabetically listed within four orders).¹

Archinemertea			
<i>Cephalohrix linearis</i> (Rathke, 1799)			
Heteronemertea			
<i>Baseodiscus hemprichii</i> (Ehrenberg, 1831)			
<i>Baseodiscus delineatus</i> (Delle Chiaje, 1825)			
<i>Cephalurichus antarcticus</i> Gibson, 1985			
<i>Cerebratulus hepaticus</i> Hubrecht, 1879			
<i>Cerebratulus lacteus</i> (Leidy, 1851)			
<i>Craticulineus novaezealandiae</i> Gibson, 1984			
<i>Heteroenopelus enigmaticus</i> Wern, 1998			
<i>Lineus bilineatus</i> (Renier, 1804)			
<i>Lineus bioculatus</i> Sundberg & Gibson, 1985			
<i>Lineus longissimus</i> (Gunnerus, 1770)			
<i>Lineus ruber</i> (Müller, 1774)			
<i>Lineus viridis</i> (Müller, 1774)			
<i>Parborlasia fueguina</i> Serna de Esteban & Moretto, 1968			
<i>Quasilineus lucidocolatus</i> Gibson, 1990			
<i>Ramphogordius bicolor</i> (Vernet, 1997)			
<i>Ramphogordius lacteus</i> Rathke, 1843			
<i>Ramphogordius sanguineus</i> Rathke, 1799			
Hoplonemertea			
<i>Amphiporus lactifloreus</i> (Johnston, 1828)			
<i>Amphiporus ochraceus</i> (Verrill, 1873)			
<i>Antiponemertes pantini</i> (Southgate, 1954)			
<i>Cyanophthalma obscura</i> (Schultz, 1851)			
<i>Diopsonemertes acanthocephala</i> Kajihara, Gibson & Mawatari, 2001			
<i>Geonemertes philippinensis</i> Gibson & Moore, 1998			
<i>Ischyronemertes albanyensis</i> Gibson, 1990			
<i>Nectonemertes primitiva</i> Brinkmann, 1917 ²			
<i>Ovicides julieae</i> Shields, 2001			
<i>Parabalaenanemertes fusca</i> Brinkmann, 1917 ²			
<i>Paranemertes peregrina</i> Coe, 1901			
<i>Potamonemertes percivali</i> Moore & Gibson, 1973			
<i>Prostoma eilhardi</i> (Montgomery, 1894)			
<i>Tetrastemma flavidum</i> Ehrenberg, 1828			
<i>Tetrastemma verinigrum</i> Iwata, 1954			
Bdellonemertea			
<i>Malacobdella grossa</i> Müller, 1776			

¹Classification according to Gibson (1995). ²Suborder Polystilifera; all other hoplonemerteans are Monostilifera.

Table III. Hypersymbioses involving nemerteans.

Primary symbiont	Hypersymbiont	Primary host	Reference
Unidentified gregarine	<i>Nosemoides viveri</i>	Unidentified nemertean	Vinckier et al. (1970); Vinckier (1975)
<i>Ovicides julieae</i>	Unidentified gregarine	<i>Chlorodiella nigra</i> , C. <i>xishaensis</i> ¹	Shields (2001)
<i>Malacobdella grossa</i>	<i>Haplosporidium malacobdellae</i>	<i>Zirfaea crispata</i> ²	Jennings and Gibson (1968)
<i>Malacobdella grossa</i>	<i>Orchitophrya malacobdellae</i>	<i>Zirfaea crispata</i> ²	Jennings (1968)
<i>Malacobdella grossa</i>	<i>Thignophrya annella</i>	<i>Arctica islandica</i> ²	Fenchel (1965)

¹Brachyuran crabs (Xanthidae). ²Bivalvia.

dissertation). Arnoult and Vernet (2000) also reported finding this gregarine in the same host. In his study on the nutrition of *Lineus ruber*, Jennings (1960) noted that the intestines of ~75% of the worms examined were infected with the acephaline eugregarine *Urospora nemertes* (trophozoites in the lumen and intracellular stages in columnar cells). Distinct damage was caused to the epithelial cells of the hosts. *Baseodiscus delineatus* is also a host for *U. nemertes*.

Gregarines have been observed in 11 other nemerteans (seven hoplonemerteans and four heteronemerteans), but none of these parasites was identified. In three cases, authors were tentative in their characterization of the parasites as gregarines. Gibson (1979) found what appeared to be gregarines in the blood vessels and rhynchocoel fluid of *Baseodiscus hemprichii*, and noted that Punnett (1900) had misidentified them as nemertean ova. Cysts of an unidentified gregarine were found hyperparasitic in tissues of the egg predator *Ovicides julieae*, symbiotic in xanthid crabs from Australia (Shields 2001) (Table III). Roe (1976) provided prevalence data on what she considered to be (P. Roe, pers. comm. 2004) an unidentified gregarine from the hoplonemertean *Paranemertes peregrina*. Examination of feces for gregarine cysts in three populations of worms from Washington revealed a range in prevalence from 6.3 to 26.0%; examination of gut tissue from 17 worms showed 15 to be infected (88.2%).

Most coccidians (subclass Coccidiasina) are parasites of vertebrates. The first and only coccidian reported from a nemertean was found in the gut of two of seven specimens of *Quasilineus lucidoculata* examined by Gibson (1990). Canning and Gibson (1990) subsequently described and illustrated the stages in the life cycle as revealed in histological sections of the worm. Because oocysts were unsporulated, it was not possible to give a generic diagnosis of this parasite. Evidence of widespread epithelial sloughing due to development of the merozoites and sexual stages was documented.

Sporozoan-like, unidentified parasites were reported by Brinkmann (1917) from the tissues of two species of pelagic polystiliferans, *Nectonemertes primitiva* and *Parabalaenanemertes fusca*. Given the relative frequency of gregarines in the tissues of other species of nemerteans, it is likely that these were also gregarines. Recent taxonomic studies on collections of pelagic nemerteans, however, have failed to reveal infections with parasitic protozoans (Norenburg and Roe 1998a, b; Roe and Norenburg 2001; P. Roe pers. comm. 2004).

Ciliophora

Only three species of ciliates are known from the Nemertea; two of these are associated with *Malacobdella grossa*. The stomatous *Thigmophrya annella* lives within the gut of this worm as does the astomatous *Orchitophrya malacobdellae*. Fenchel (1965) speculated that *T. annella* might have evolved from a species of *Thigmophrya* that lived in the mantle chamber of bivalves known to harbour *M. grossa*. Jennings (1968) found *O. malacobdellae* in four of 175 worms (2.3%) examined. Duboscq (1925) described a new suctorian, *Ophryodendron prenanti*, from the integument of the archinemertean *Cephalothrix linearis*. The nature of these symbioses is unknown, but given the fact that these ciliates have not penetrated the body cavity of the host, and given their symbiotic nature in other host taxa, it seems likely that these are relatively benign associations.

Orthonectida

Orthonectids are mesozoans that parasitize the tissues and body cavities of marine invertebrates (e.g. turbellarians, nemerteans, polychaetes, bivalve mollusks, ophiuroids,

etc.). The microscopic, ciliated, dioecious adults reproduce outside of their host and ciliated larvae infect new hosts where they become amoeboid, syncytial plasmodia, reproducing asexually. Kozloff (1992, 1994), however, believes that the “plasmodium” is not a part of this life cycle, but rather hypertrophied, infected, host cells. The life cycles of the orthonectids are poorly known as are those of the other mesozoan phylum, Rhombozoa, parasitic in the excretory organs of Cephalopoda. Infections with orthonectids may cause host sterilization (Stunkard 1982). All of the species from nemerteans apparently belong to the family Rhopaluridae (Stunkard 1982), but there are still uncertainties concerning family designations (Kozloff 1992). *Intoshia linei* lives in the connective tissue and muscle layers of *Lineus ruber*, *L. viridis* and *Ramphogordius sanguineus*. *Rhopalura sanguinea* similarly infects *R. sanguineus*. These orthonectids may coexist with gregarines in the same hosts (Table I). Kozloff (1992) expressed difficulty in confirming the generic characteristics of *Rhopalura intoshi* and *R. pelseeneeri* as well as *R. pelseeneeri* var. *vermiculicola*. The only apparent record of orthonectids from nemerteans in North America is a species of *Rhopalura* from a single specimen of *Amphiporus ochraceus* collected by Meinkoth (1956) near Woods Hole, Massachusetts. These parasites were found inside the worm and swimming in the water of a whole-mount preparation. Additional worms ($n=171$) were without infections. Meinkoth (1956) noted that the parasites were similar to *R. metchnikovi* or *Intoshia linei*.

Intoshia linei is probably the best-studied species of orthonectid parasitizing nemerteans. Anatomical descriptions of adults based on light and scanning electron (SEM) microscopy were done by Kozloff (1992) and Haloti and Vernet (1993). Grafting experiments with parasitized tissues from *Lineus ruber* and *L. viridis* have been used to investigate the nemerteans' immune responses of these hosts to *I. linei* (Langlet and Bierne 1989; Vernet and Fargette 1990; Haloti et al. 1992; Haloti and Vernet 1994). Surprisingly, successful grafts from infected *L. ruber* into nonparasitized hosts resulted in a decrease in the parasites during the first 2 months, but was followed by a rapid increase in the parasite load during the next 2 months. This indicated that the immune response to the orthonectids occurred but was not strong enough to eliminate the parasites (Langlet and Bierne 1989).

Platyhelminthes

From a fragmented specimen of *Cerebratulus lacteus*, collected at Beaufort, North Carolina, Hunter (1950) recovered 120 unencysted, plerocercoid larvae (order Tetraphyllidea). Characteristics of the scolices suggested that these cestodes belonged to the genus *Echeneibothrium* Van Beneden, 1850, species of which are exclusive intestinal parasites of their definitive hosts, elasmobranch fishes. As plerocercoid larvae are usually found in the tissues of teleost, cephalopod or crustacean intermediate hosts, it remains to be determined how nemerteans might be involved in tetraphyllidean life cycles (McDermott 2001).

There are a few records of trematode metacercariae occurring in nemertean tissue, but their specific identity has not been determined (McIntosh 1873/1874; Gibson 1972).

Nematoda

A single specimen of the terrestrial *Geonemertes philippinensis* harboured large numbers of unidentified, coiled, encapsulated nematodes in its muscles, parenchyma and intestinal epithelium (Gibson and Moore 1998). Worms were 15–16 μm in diameter and some were 180–220 μm long. These larval worms were presumably employing *G. philippinensis* as an intermediate host in an unknown life cycle.

Arthropoda

Two species of arthropod ectosymbionts have been recorded from nemerteans. Laubier (1960) described a new species of mite, *Parhalixodes travei*, from a larva and adult male collected from the body of *Cerebratulus hepaticus*. Gallien (1936) described the only known crustacean from a nemertean, the copepod *Pseudanthessius nemertophilus*, living on the body of *Lineus longissimus*. Stock (1985) later created the new genus, *Nemerthessius*, for this species. Nothing is known concerning relationships of these two symbionts with their nemertean hosts, if indeed they are any more than incidental occurrences of free-living organisms.

Major taxa unknown

At least three encysted, unknown, microscopic parasites have been reported in the tissues of heteronemerteans from the southern hemisphere. In all cases, nondescript cysts could not be identified with certainty.

General discussion and conclusions

Several questions arise concerning the meagre literature on symbionts of nemerteans: (1) what are the probabilities of finding parasites in nemerteans compared to other invertebrates? (2) How suitable are nemerteans as host for parasites? (3) What is the status of nemerteans as intermediate hosts in parasitic life cycles? (4) Can we learn more about the parasites of nemerteans?

Probabilities of finding parasites

The heavy mucus covering the external surfaces and the burrowing habit of many species of nemerteans makes them extremely unlikely hosts for ectosymbionts and, to date, this seems to be the case (Lauckner 1980b). In general, the same may be said for turbellarians as hosts for epibionts (Lauckner 1980a). As far as internal parasites are concerned, a few orthonectid infections have been detected from external signs on the surface of some worms (Langlet and Bierne 1989), but the opaque and dense body of most nemerteans obscures the revelation of most internal parasites. However, parasites certainly gain access to the interior of nemerteans. Thus, the time-consuming examination of histological sections for the purpose of locating protozoan and metazoan endoparasites needs to continue, but this process certainly sets a lower limit on the number of worms that can be examined, compared to other types of hosts for which sectioning is not required. Added to this is the burden of fixation for electron microscopy or molecular analysis, and species identifications become insurmountable. However, the chance revelation of plerocercoid larvae in a fragmenting *Cerebratulus lacteus* by Hunter (1950) suggests that such observations, along with whole animal dissections, might be rewarded with the discovery of greater prevalences of encysted larval metazoans. Jennings and Gibson (1968) made squashes of fresh *Malacobdella grossa* for detecting the presence of haplosporidians, and Roe (1976) was able to detect gregarines in *Paranemertes peregrina* by examining the gut tissue. Isolating nemerteans and examining the feces for gregarine cysts (Roe 1976), or looking for emerging stages of orthonectid parasites (Meinkoth 1956), may prove fruitful. The latter is reminiscent of the well-known parasitological technique isolating large numbers of snails in shell vials for determining the prevalence of infections with digenetic trematodes by examining those releasing cercarial larvae.

Suitability of nemerteans as hosts

Considering the method for finding endoparasites in nemerteans and the limited literature, nemerteans may not be unusual hosts for haplosporidians, microsporidians and gregarines. Three haplosporidians and the hyperparasitic microsporidian *Nosemoides vivieri*, from an unidentified gregarine, have been found in at least four species of nemerteans. Gregarines have been shown to parasitize at least 14 species of nemerteans (seven heteronemerteans and seven hoplonemerteans) (Table I). Hyperparasitism is most likely overlooked by those examining histological sections. Orthonectids, on the other hand, utilize nemerteans for their early development, releasing males and females to the aquatic environment; these and the infective larvae may be collected and identified through the careful culture and handling of potentially infected hosts. At least five species of orthonectids are known from nine species of nemerteans. One of these orthonectids, *Intoshia linei*, lacks host specificity, infecting three species of nemerteans (Table I).

Nemerteans as intermediate hosts

Some helminth parasites (platyhelminths and nematodes) use nemerteans as intermediate hosts. In light of the negligible literature on nemerteans as intermediate hosts for parasites, it is difficult to evaluate their roles in parasite life cycles. A number of conditions might be considered. Copious mucus produced by epidermal glands may present an initial barrier that must be traversed by, for example, cercariae liberated from the snail first intermediate host in trematode life cycles. Furthermore, it has been demonstrated that the mucus of nemerteans has many toxic properties (Kem 1985, 2000) that must be tolerated by potentially invasive larvae. The burrowing nature of many nemerteans presents a further problem for the establishment of infective larval stages. Turbellarians, however, have similar characteristics and are known to harbour a variety of metacercariae linked with described life cycles (Lauckner 1980a). It seems reasonable that nemerteans may eventually be found to harbour these trematodes (Lauckner 1980a). The coracidium larvae of cestodes, however, are generally ingested by arthropod or molluscan intermediate hosts. On the other hand, infective orthonectid larvae (one host cycle) penetrate, not only nemerteans, but also numerous mucus-producing turbellarians, polychaetes and molluscs that are susceptible to parasite invasion (Kozloff 1992).

For the completion of cestode or trematode life cycles, it is expected that the intermediate host falls prey to definitive or paratenic hosts. The palatability of nemerteans as prey for a variety of animals has been reviewed (McDermott 2001). While there is evidence that nemerteans are consumed by some fishes, birds and other invertebrate predators, there is no substantial evidence that they are important prey, and there is experimental evidence that nemerteans are violently rejected by some predators (Sundberg 1979; McDermott 1984, 1993; Heine et al. 1991). It appears that toxic mucus is the distasteful element.

Host resistance

Little is known concerning innate (cellular) or acquired resistance in nemerteans that might limit the establishment, growth and development of invasive larvae, but nemertean grafting studies have shed some light on resistance to orthonectids (Langlet and Bierne 1989; Haloti and Vernet 1994).

Hypersymbiosis

There are five hypersymbiotic relationships involving nemerteans (Table III), three of which involve the commensal of bivalves, *Malacobdella grossa*, host for two endosymbiotic ciliates and a haplosporidian. There is little biological information on the nature of these relationships except for the parasite *Haplosporidium malacobdellae* (Jennings and Gibson 1968).

Future studies

To learn more about the importance of nemerteans as hosts for parasites, it will be necessary to continue searching through histological sections, but we must also employ whole animal dissections to find encysted metazoans. Isolation of worms for fecal examinations and detection of liberated life history stages of parasites may be useful. Experimental exploration of the susceptibility of nemerteans to cercarial invasion or coracidial ingestion could prove enlightening and may be accomplished with relative ease as these parasitic life-history stages are readily manipulated. Experimentation on the life cycles of parasites and susceptibility of nemerteans to infections, however, requires finding populations of nemerteans with high prevalences of infections – and this is a major challenge.

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