MERMITHIDS (NEMATODA) AND MAYFLIES (EPHEMEROPTERA)

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ABSTRACT

This review is intended to stimulate interest in the presently anecdotal association between mermithids and mayflies. A brief account of the biology of aquatic mermithids is followed by a review of the sparse information available on mermithid parasitism of mayflies. Finally, methods for rearing and preserving mermithids are given, so that the nematodes are in a condition useful for taxonomic purposes.

INTRODUCTION

Nematodes of the superfamily Mermithoidea are obligate parasites of invertebrates, chiefly insects. By our estimation, 650 species in 83 genera have been described, though many species are of doubtful validity. Of these, 424 species in 40 genera were described from aquatic environments where hosts, when they are known, are commonly chironomids, simuliids or culicids. Since these insects frequently coexist with ephemeropterans, it is not surprising that mayflies have also been cited as hosts. What is surprising is the scarcity of these reports. This review will attempt to stimulate interest in the presently anecdotal association between mermithids and mayflies. It is aimed at those workers familiar with ephemeropterans but unfamiliar with mermithids. Therefore, a brief account of the biology of aquatic mermithids is presented. A review follows

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of the little that is known about mermithid parasitism of mayflies. Finally, methods for rearing and preserving mermithids are given so that when mermithids are discovered, they will be in a condition useful for taxonomic purposes. For detailed treatments of the biology and taxonomy of mermithids, the reader is referred to Nickle (1972), Poinar (1975), Rubtzov (1972, 1974, 1977, 1978) and Welch (1965).

BIOLOGY OF AQUATIC MERMITHIDS

Adult aquatic mermithids are slender nematodes, between one and three cm long, that live in or on the bottom substrate, where mating and oviposition occur. After a period of embryonic development and a moult within the egg, the preparasitic juvenile hatches. This non-feeding stage must penetrate a host within a few days if it is to survive. It penetrates directly through the cuticle and undergoes a period of massive growth and development in the haemocoele. For example, *Romanomermis culicivorax* (syn. *Reesimermis nielseni*) increases 18-fold in length during its 6-8 day parasitic existence (Gordon *et al.* 1974). Ultimately, the nematode emerges from late instar larvae or nymphs, from pupae, or from adults and takes up a free-living existence. Most species emerge as postparasitic juveniles and mature for several days to a few weeks. The moult to the adult stage is terminated by the ecdysis of an outer thick cuticle and inner thin membranous one.

During their parasitic existence, mermithids absorb nutrients from the haemolymphs of the host. The intestine, which is modified as a food storage organ, becomes packed with food reserves which, at least in *R. culicivorax*, are predominantly lipids and glycogen (Ittycheriah *et al.* 1977). Postparasitic stages do not feed. The host, in turn, if it survives to adulthood, is sterile due to the depletion of its nutrients. Parasitized mayflies are no exception (Benech 1972a, Murphy 1922, Needham *et al.* 1935). In any case, emergence of the parasite usually signals the death of the host by a combination of a loss of haemolymph through the hole made by the parasite, mechanical injury and reduced nutritional reserves.

Another group of obligate parasites of invertebrates are the hairworms or gordian worms (Nematomorpha), that are sometimes confused with mermithids. Adults are generally found near the edges of lakes, ponds and streams, where eggs are laid. Free-living larvae that hatch are short-lived, though some species extend their survival by encysting. They develop only when ingested by a suitable invertebrate (mainly grasshoppers, crickets, beetles, roaches, mantids, centipedes and millipedes). Larvae penetrate out of the gut and develop in the body cavity. Alternatively, larvae of some species may be eaten be a unsuitable host such as a snail, mayfly, midge, mosquito, fish or amphibian (Inoue 1962, Poinar and

Doelman 1974). Then, the parasite encysts in various tissues and remains viable, but does not develop. If this transport host is eaten by an appropriate host, the parasite resumes development. As the parasitic stages, like those of mermithids, have a non-functional digestive tract, nutrition is probably attained by absorbing materials across the body wall. The parasite emerges from the host as a juvenile, and only when the arthropod is associated with water. It matures in water or damp soil, while the host is sterilized and dies when the parasite emerges.

In the present context, differentiating between mermithids and nematomorphs is not difficult. Mermithids can develop in mayflies, while nematomorphs apparently utilize mayflies only as transport hosts, so they remain as small larvae, encysted within host tissues. Poinar and Doelman (1974) presented excellent photographs and drawings of nematomorph larvae with the characteristic 'head' or presoma, evaginable proboscis, stylets and spines. By contrast, early stages of mermithid parasites are elongated, without hardened structures and usually lie free in the haemocoele. Gordon *et al.* (1974) gave photographs and drawings of a developing mermithid.

MERMITHID PARASITISM OF MAYFLIES

Table 1 lists authors who cited mayflies as hosts for mermithids, together with some notes on the ecology of the host genus. With the exception of Poinar *et al.* (1976), the authors assigned the nematodes to the family Mermithidae or to the genus *Mermis*. *Mermis* is frequently used incorrectly by inexperienced workers as a collective genus rather than as a defined taxon for certain terrestrial mermithids. Therefore, to our knowledge, no mermithid that develops in mayflies has been described though some of the many whose hosts are unknown may be parasites of mayflies. *Pheromermis pachysoma*, which Poinar *et al.* (1976) described, is a parasite of wasps that utilizes aquatic insects as transport hosts.

Although data in Table 1 are limited, they show that mermithids are not restricted to mayflies with particular habitats or habits. Mermithid literature shows that while a few terrestrial species are able to parasitize unrelated insects that occur in the same habitat, most species are more restricted and parasitize members of a single family, genus or even species. Many environmental factors affect host specificity. For example, Galloway and Brust (1976) added 50,000 *R. culicivorax* preparasites/m^2 to a snow-melt pool in Manitoba, Canada, and obtained parasitism of 8-20% of *Aedes vexans* larvae, while six other *Aedes* species and nymphs of a mayfly (probably *Paraleptophlebia* sp.) were not parasitized. It is doubtful that the unparasitized culicids escaped parasitism because of host specificity of this parasite, for it has a wide host range amongst culicids (Petersen 1976). As the authors suggested, mosquitoes

Table 1. Ephemeroptera cited as hosts for mermithid nematodes, with notes on the ecology of the host genus.

Host	Cited by	Ecology of Host Genus[1]		
		Habitat	Habit	Trophic Relationships
BAETIDAE				
Baetis rhodani	Degrange 1960 Benech 1972 a, b Sukop 1973	Lotic (erosional & deposional) and Lentic (vascular hydrophytes)	Swimmers Climbers Clingers	Sediment feeders (detritus, diatoms) or scrapers
Baetis vagans	Murphy 1922			
Callibaetis pretiosus *Callibaetis pictus*	Pescador[2] Poinar *et al.* 1976 (lab. infection)	Lentic (vascular hydrophytes)	Swimmers Climbers	Not Known
CAENIDAE				
Caenis sp.	Pescador[2]	Lotic (depositional) Lentic (littoral: sediments	Sprawlers	Sediment feeders (scrapers)
EPHEMERIDAE				
Ephemera vulgata	von Linstow 1878[2]	Lotic & Lentic (deposit-ional: sand-gravel)	Burrowers	Sediment feeders (engulfers)
Hexagenia limbata *Hexagenia* sp.	Neeve 1932 Needham 1920	Lentic & Lotic (deposit-ional: sand-silt)	Burrowers	Sediment feeders
HEPTAGENIIDAE				
Heptagenia sp.	Muttkowski 1929 Muttkowski & Smith 1929	Lotic (running water riffles)	Clingers	Scrapers Sediment feeders (engulfers)
HOST UNDETERMINED	Needham *et al.* 1935 Zakhidov 1973 Poinar *et al.* 1976			

[1] from Edmunds 1978

[2] cited by Arvy and Peters 1976

probably escaped parasitism because of factors such as low temperatures that prevented infection by preparasites and death of the preparasites before hatching of several of the *Aedes* species. Indeed, the life cycles of mermithids should be expected to be synchronized with those of their hosts (e.g. Hominick and Welch 1971). Chances of successful penetration and development generally decrease as the host instar increases (e.g. Bailey and Gordon 1977, Petersen and Willis 1970). Consequently, parasitism of any species except the 'natural' or 'usual' one in a particular locality will be a relatively rare occurrence. The limited data of Muttkowski and Smith (1929) support such an hypothesis. They recorded 2 of 12 *Heptagenia* sp. nymphs parasitized, while 5 *Ameletus* sp., 2 *Emphemerela* sp. and 11 *Drunella* sp. nymphs taken from the same site on the same day were not parasitized. This, and the data in Table 1, argues for a mermithid fauna (i.e. more than one species) that is unique to ephemeropterans.

The trophic relationships of 38 genera of Ephemeroptera are listed by Edmunds (1978). Assuming that the method of feeding listed first is the most common, then 22 (58%) of the genera consist primarily of sediment-feeding species. By comparison, four of the five genera (80%) in Table 1 whose trophic relationships are given by Edmunds (1978), have mainly sediment-feeders. Thus, mermithids may be more likely to occur in sediment-feeders than in predators, filterers or scrapers, with the parasite eggs or preparasites ingested by the host. Such a notion is supported by the data in Table 2, which show that the genera parasitized by nematomorphs contain mainly sediment-feeders. These parasites infect their hosts via the mouth (Dorier 1930, Inoue 1962, Poinar and Doelman 1974). Up to now, studies on aquatic mermithids show that infection occurs by penetration of the host cuticle. Thus, even if mermithids do infect sediment-feeding ephemeropterans more often than other types, this may simply reflect the fact that sediment-feeders spend a larger proportion of their time closely associated with substrates where parasites occur.

Some solid facts exist in addition to the preceding speculations. Thus, Muttkowski and Smith (1929) recorded 2 of 12 (16%) *Heptagenia* sp. nymphs parasitized, while Neeve (1932) recorded 7 of 131 (5%) *Hexagenia limbata* nymphs parasitized in Gull Bay, Lake Winnipeg. Furthermore, other collections either at different times at the same site (Muttkowski and Smith 1929), or at different times and sites (Neeve 1932), did not yield parasitized individuals. These data illustrate a basic characteristic of mermithids: they are focal in distribution and usually parasitize a small proportion of the host population, though they may cause high mortality in localized areas (Rubtzov 1977). They show sharp fluctuations in numbers which sometimes are more apparent than real, for mermithids usually delay development of their hosts. Thus, unparasitized insects emerge first, leaving the parasitized ones in seemingly large numbers

Table 2. Ephemeroptera cited as hosts for Nematomorpha, with notes on the ecology of the host genus.

Host	Parasite	Cited by	Ecology of host genus[1]		
			Habitat	Habit	Trophic Relationships
BAETIDAE					
Baetis sp.	*Paragordius varius*	White 1966	Lotic (erosional & deposional) and Lentic (vascular hydrophytes)	Swimmers Climbers Clingers	Sediment feeders (detritus, diatoms) or scrapers
	Paragordius sp.	White 1969			
B. muticus	Gordiidae	Arvy & Sowa 1976			
Cloeon dipterum	*Parachordodes tolosanus*	von Linstow 1892[2] von Linstow 1889[3]	Lotic (erosional)	Swimmers Clingers	Sediment feeders
	Chordodes japonensis	Inoue 1960, 1962 (lab. infection)			
EPHEMERELLIDAE					
Ephemerella spp.	*Paragordius* sp.	White 1969	Lotic (erosional & depositional) and Lentic (vascular hydrophytes)	Clingers Sprawlers Swimmers	Sediment feeders (detritus, diatoms) Scrapers, some shredders
EPHEMERIDAE					
Ephemera vulgata	*Parachordoes tolosanus*	Meissner 1856[2] von Linstow 1891[3]	Lotic & Lentic (depositional: sand-gravel)	Burrowers	Sediment feeders (engulfers)
LEPTOPHLEBIIDAE					
Leptophlebia sp.	*Paragordius* sp.	White 1969	Lotic (erosional: sediments & detritus)	Swimmers Clingers Sprawlers	Sediment feeders
HOST UNDETERMINED	Gordiidae	Hartmeyer 1909			
	Neochordodes occidentalis	Poinar & Doelman 1974			

[1] from Edmunds 1978

[2] cited by Arvy and Peters 1976

[3] cited by Van Zwaluwenburg 1928

(Welch 1965).

While mermithids may delay development of their hosts, they usually do not affect the number of instars. Thus, Benech (1972b) reported that two parasitized *Baetis rhodani* adult females moulted the same number of times as unparasitized ones. Both the host age at the time of infection and the number of parasites per host are probably important. Craig and Webster (1974) showed experimentally that the older *Schistocerca gregaria* was at the time of infection, the greater the number of *Mermis nigrescens* required to inhibit the next-but-one moult.

In aquatic insects, the time of infection may determine not the number of instars, but whether the parasite is carried into the adult stage of the host. Alternatively, some mermithid species, such as *Perutilimermis culicis* (Nickle 1972), may be adapted to complete their development only when the host becomes adult. In either case, mermithids were recorded from adult mayflies (Benech 1972b, Murphy 1922, Muttkowski 1929, Needham et al. 1935) and this would be an important factor in disseminating the parasites. Presumably, they would emerge when the host alights on water as occurs for some mermithids from chironomids (Hominick and Welch 1971) and simuliids (Mokry and Finney 1977).

The effect of mermithids on the behavior of infected adult mayflies remains to be determined. Murphy (1922) reported that four infected female *Baetis vagans* appeared natural in flight while Muttkowski (1929) captured an adult that was "fluttering weakly" and the "the weight of the parasite held it from rising". These apparently contradictory observations may be equally applicable. Wülker (1961) observed that some infected adult chironomids swarm apart from uninfected ones, some fly near the water surface or settle in the water in sheltered places (Wülker 1963), while others are strong enough to participate in swarms with uninfected individual (Wülker 1963).

One other effect of mermithid parasitism is noteworthy; namely, the formation of intersexes in parasitized adult chironomids, simuliids and heleidids (=Ceratopogonidae) and of intercastes in ants (Welch 1965, Wülker 1964). It is interesting that gynandromorphs, which have erroneously been called 'intersexes', have been reported in the mayfly families Baetidae, Ephemeridae, Heptageniidae, Leptophlebiidae and Potamanthidae (Agnew 1977). Gynandromorphs are individuals with a mixture of male and female tissues composed of cells that differ genetically, while intersexes have all tissues composed of genetically identical cells. As gynandromorphs and intersexes may appear similar, for example, the colour pattern of ephemeropteran gynanders is sometimes described as being atypical, neither female nor male (Agnew 1977), special attention should be given to the secondary sexual characters of mayflies found parasitized by mermithids.

REARING AND PRESERVING MERMITHIDS

To identify mermithids, it is necessary to obtain adult specimens. The Russian worker, Prof. I.A. Rubtzov, classified mermithids using juvenile characters, but his system has not been accepted by other workers. Therefore, it is necessary to detect parasitized hosts, rear them until their parasites emerge, and then rear the parasites until they moult to the adult stage.

Examination of insects for mermithids is best done with a dissecting microscope and transmitted light. Observation is facilitated by placing the nymphs in the inverted cover of a 5 cm diameter glass petri dish with a small amount of water. The bottom is then carefully placed on the specimen, which is slightly flattened between the two layers of glass. The depth of the layer of water is critical - too little and the specimen may be damaged; too much and the specimen is not immobilized.

Detection of early stages of mermithids without dissecting the host is difficult because their small size and lack of distinguishing features cause them to look like host structures such as tracheae, ducts or tubules. Later stages are more easily detected because they occupy most of the haemocoele, are coiled on themselves several times, and having depleted most of the host's nutrient reserves, cause the body wall to be more transparent than normal. These stages will be found in the large (late) instars.

The method for rearing parasitized nymphs will depend on the species and its habitat, which would be simulated as closely as possible. J.F. Flannagan (pers. comm.) routinely rears burrowing nymphs in a layer of mud that has been sterilized and covered with dechlorinated water to a depth of about 10 cm. The water is gently aerated and pulverized Tetramin fish food provides nutrients. With such a system, the water and substrate would have to be gently washed through a series of sieves (smallest aperture approximately 0.1 mm) weekly to monitor the progress of the hosts and to obtain any parasites that had emerged.

Adult hosts are more easily maintained, as they can be kept in a small container with some water in the bottom. When the mayfly rests on the water, the parasites should emerge.

Mermithids that have emerged should always be kept and examined in a layer of water. They can be picked up with pasteur pipettes, but should be handled as little as possible as they are easily damaged. Although the morphology of mermithids from mayflies is unknown, aquatic mermithids have postparasitic juveniles with a posterior tail appendage. As the adult has no such appendage, its absence serves as a simple indication that the final ecdysis has occurred. Also, adult females are characterized by a ventral vulva and muscular vagina in the midregion of the body, while adult males have one or two cuticularized, refractile spicules at the terminus.

If the final ecdysis has not occurred, the parasites should be maintained in a layer of fine sand covered with dechlorinated tap water. During this time, a common problem is infection and rapid destruction of the nematodes by aquatic fungi, Hence, it is prudent to keep the specimens in more than one container. Best survival is usually obtained by using large culture vessels (approximately 500 mL) and xenic rather than axenic methods (see Bailey *et al.* 1977). In our experience with mermithids from blackflies, a layer of autoclaved sand about 0.5 cm deep is covered to a depth of about 5 cm with dechlorinated tap water that is changed every two days. Nematodes are not surface sterilized before addition to the vessel, and strict aseptic techniques are not followed. Flaming instruments is a good precaution against transfer of microorganisms between vessels. A temperature of about 15° is usually satisfactory.

The method by which the specimens are killed and fixed is critical as some methods cause distortions of taxonomic characters. Detailed experiments by a colleague at Imperial College Field Station, J. Curran, show that the nematodes should be killed by plunging them into 65° water for three seconds. Hotter or longer results in distortions The nematodes are immediately fixed in TAF (7 mL formalin, 2 mL triethanolamine, 91 mL distilled water) for at least three days. They can then be processed to glycerol by the Seinhorst method (see Poinar (1975), page 17) and mounted permanently. If they belong to a described genus, two recent keys to genera of mermithids (Poinar 1977, Rubtzov 1978) will be useful. However, mermithid taxonomy is in a state of flux, so the specimens are best sent to an authority for identification. In all likelihood, they will belong to at least one species that is new to science.

RESUME

Cette étude a pour but de stimuler l'intérêt a l'égard de l'association entre les mermithidés et les éphéméroptères présentement au stade anecdotique. Un apercu biologique des mermithidés aquatiques précède l'étude des renseignements fort peu nombreux qui existent sur le parasitisme des éphéméroptères au dépens des mermithidés. Enfin, on suggère des méthods de culture et de préservation des mermithidés propres à rendre les nématodes utiles à des fins taxonomiques.

ZUSSAMENFASSUNG

Dieser Bericht beabsichtigt das Interesse an der gegenwärtig anekdotenhaften Verbindung zwischen Mermithiden und Eintagsfliegen anzuregen. Einem kurzen Rückblick auf die Biologie der aquatischen Mermithiden folgt ein Überblick über die spärliche Information, die wir in Bezug auf das Mermithiden Parasitentum der Eintagsfliegen besitzen. Zum Abschluß werden Methoden für die Zucht und Konservierung von Mermithiden angegeben, damit die Nematoden sich in einem für taxonomische Zwecke brauchbaren Zustand befinden.

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