

# Mermithid Parasitism of Black Flies (Diptera: Simuliidae)<sup>1</sup>

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**Abstract:** Mermithid nematodes are common parasites of black flies and play a significant role in the natural regulation of these medically important insects. Infection levels tend to be moderate and perennial, with epizootics rare and highly localized. Mermithid parasitism almost invariably results in the death of the black fly, and thus considerable attention has focused on the potential of these nematodes as biocontrol agents. Early instar black fly larvae appear most susceptible to infection, and integumental penetration by mermithid preparasites is the only known mode of entry. Postparasitic nematodes typically emerge before host pupation. However, carryover of parasitism into adult simuliids is an important mechanism for local dispersal and recolonization of upstream areas. Following emergence, the mermithids molt to the adult stage. Copulation ensues, the females then laying eggs which eventually give rise to the next generation of infective preparasites. The number of described species is conservatively estimated at 35–40, with most species within the genera *Mesomermis*, *Gastromermis*, and *Isomermis*. The taxonomy of this group of mermithids is a challenging and little explored area. Host-specificity statements, therefore, must be made cautiously because of these systematic problems and others within the Simuliidae. In most instances, temporal and spatial factors limit the host range of these mermithids among simuliid species. Differential susceptibilities among larvae concurrently present within the same microhabitat probably reflect varying degrees of host attractiveness and behavioral-physiological resistance. Effects of parasitism on the host may include prevention of metamorphosis, sterility, intersexual development, and behavior modification. Evaluation of the technical feasibility of mermithid control of black flies has been stymied by the limitations of current inoculum-production technology. Continued advances in *in vivo* and *in vitro* culture methods are required to accelerate the research process. **Key words:** Mermithidae, bionomics, systematics, host specificity, host-parasite relationship, biological control, *Mesomermis*, *Gastromermis*, *Isomermis*.

“On coming downstairs on Aug. 16th, I saw a small Dipteron (*Simulium ornatum*) on the windowpane, and this insect seemed to enjoy its usual activity until a drop of benzene proved fatal. I then mounted it on a slip of cardboard, when what seemed a huge cabbage-green snake-like creature suddenly crept forth from its abdomen.” (55).

The above is one of the earliest and most colorful descriptions of mermithid parasitism of black flies. The Mermithidae parasitize a wide variety of invertebrates. In the class Insecta at least 17 orders, including more than 100 families, have been recorded as hosts (39). Welch (59) cited at least 153 reports of mermithid parasitism of black flies; at least another 50 have appeared since his 1964 review.

Mermithids are common parasites of simuliids and play a significant role in their

natural regulation (4,38,59). Infection levels tend to be moderate (3–15%) and perennial, with epizootics rare and highly localized (12,26,28,53,56). Nevertheless, mermithids have occasionally been reported to cause drastic population reductions (38,60).

Although recorded from black fly populations throughout the world, mermithid parasites appear to have sporadic local distributions—a condition due in part to their limited dispersal capabilities. For example, surveys conducted in Newfoundland (15) and Wisconsin (3) found that only 30 and 23% of the streams, respectively, contained mermithid-parasitized black flies.

Because infection almost invariably results in host death, considerable attention has been focused on these parasites as potential black fly biocontrol agents (23,48). In Central America and Africa, black flies are intermediate hosts and vectors of *Onchocerca volvulus*, a filarioid nematode which causes human onchocerciasis—a vision impairing disease estimated to afflict more than 20 million people. Since present control efforts rely solely on chemical larvicides, the development of biological agents for incorporation into an integrated control program is needed. Mermithids are leading candidates for such a role.

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## BIONOMICS

The infective stage is the newly hatched, preparasitic nematode, and all evidence indicates that early instar black flies are most susceptible to invasion (9,17,31,60). Mermithid life cycles are synchronized with those of their hosts, preparasite hatch occurring during periods when susceptible larval instars are present (12,16,60).

The mode of penetration is unknown for almost all mermithid species parasitic in black flies. The two exceptions are *Iso-mermis lairdi* (33) and *Mesomerms* (= *Neomesomerms*) *flumenalis sensu lato* (2, 31). Preparasites of *I. lairdi* are captured by the cephalic fans of feeding black flies and penetrate the larval cuticle in the cephalic region. Preparasites of *M. flumenalis s. l.* crawl on the streambed in search of hosts (31). In a successful attack, a *M. flumenalis* preparasite typically attaches itself to the thoracic region of the black fly larva, out of reach of the larva's mandibles, and coils tightly around the larva. The black fly moves in quick jerking motions, opening and closing its mandibles in a vain attempt to grasp the nematode. The integument is soon pierced by the stylet, and within a few minutes the preparasite uncoils and passes into the larva's hemocoel. During this period and for several minutes thereafter, the black fly appears to be paralyzed, with its body often in a contorted position. Although normal movement and feeding gradually resume within an hour after penetration, this temporary paralysis eliminates further defensive tactics by a larva and ensures successful penetration by the preparasite. In laboratory trials (Molloy, unpublished data) such defenseless, paralyzed larvae were observed to be easily attacked and penetrated by other preparasites in the vicinity. Wülker (63) reported a similar "paralysis" in chironomid larvae attacked by *Gastromermis rosea* and suggested that the paralysis was induced by injection of a substance into the host's hemocoel by the preparasite. Wülker's hypothesis is plausible, and it is here suggested that the preparasite's penetration glands might be the source of such a muscle-paralyzing fluid.

It is likely that preparasite penetration of the integument is a common mode of entry for mermithids parasitic in black flies.

However, per os entry (ingestion of either an egg or juvenile) should not be ruled out, since it has been reported for mermithids parasitic in other insects (11,41). Others (38,54,60) have suggested that some black fly mermithids enter their hosts by penetration of the gut wall, but conclusive evidence of this mode of entry has not been offered.

The juvenile derives its nourishment from the host's hemolymph. Transcuticular nutrient uptake through the nematode's body wall has been demonstrated for mermithid parasites of grasshoppers (49,50), and a recent ultrastructural study of the black fly parasite *Gastromermis boophthorae* has provided evidence that transcuticular uptake also occurs in this mermithid (7).

When the nematode has completed its development within the abdomen of the black fly, it emerges to resume a free-living existence. Postparasitic emergence typically occurs during the larval stage of the black fly, usually at the time uninfected flies in the population are pupating. The peak emergence of male mermithids often precedes that of the females (5). Emergence generally occurs through the intersegmental areas of the larval abdomen, but penetration of the gut wall and exit through natural openings have also been observed. The length of a postparasite is 1-4 times that of its host, the length varying inversely with the number of mermithids per host.

Although development of some mermithids appears to occur solely within larval simuliids (30), pupation and emergence of infected black flies has frequently been reported (12,29,37,47,51). Parasitism of adult simuliids is advantageous to mermithid populations, since it provides a mechanism for dispersal of these nematodes to neighboring streams and allows recolonization of upstream areas (black flies migrate upstream to oviposit) (59).

After host emergence, the postparasites molt to adults, mate, and lay eggs to produce a new generation of preparasites; these free-living stages in the life cycle occur within the streambed. Immediately after emergence, many postparasites lose their hold on substrates and are carried downstream. Infection foci, however, are likely maintained in upstream areas by those postparasites which are capable of crawling di-

rectly down into the streambed.

Data on the periodicity of molt, mating, oviposition, and egg hatch are available for *Gastromermis viridis*, *I. wisconsinensis* (38), *M. fluminalis* s. l. (14), and *I. lairdi* (33). Although multivoltine mermithids are known from black flies in England (Curran, personal communication) all five species described from North American black flies (30,40,58) are thought to be univoltine. Tropical species (e.g., *I. lairdi*) appear multivoltine.

### SYSTEMATICS

*Mesomermis*, *Gastromermis*, and *Iso-mermis* spp. are the most common mermithids parasitic in black flies. Other genera that have been observed to infect simuliids include *Limnomermis*, *Hydromermis*, and *Spiculimermis*. There are approximately 35-40 widely recognized species including the recently described *M. camdenensis* (30), *M. paradisus* (41), *M. guatemalae* (44), *M. travisi* (57), *M. japonicus* (42), *I. benevolus* (43), *I. vulvachila* (44), and *G. cloacachilus* (44).

The lack of clear-cut, distinguishing morphological features at the species level makes the taxonomy of the Mermithidae challenging. The systematic position of *M. fluminalis* is a prime example. Although this species was originally described from a *Simulium* sp. (58), a mermithid of similar morphology parasitizing *Prosimulium* spp. has also been widely referred to as "*M. fluminalis*." Only recently have sufficient biological-ecological data (6,12) been available to indicate a lack of conspecificity between these *Simulium*- and *Prosimulium*-emerging mermithids.

### HOST SPECIFICITY

Black fly mermithids are not known as parasites of any other stream fauna. Moreover, mermithids which are naturally parasitic in other insects have not been found in field-collected black flies. The mosquito mermithid, *Romanomermis culicivora*x, which had been demonstrated in the laboratory to infect black flies (20), was proposed as a black fly biocontrol agent (27). However, after it was demonstrated that this mermithid had markedly little invasive-

ness in moving water and that it did not develop normally in those few black fly larvae that it did successfully invade (21), interest in its biocontrol potential quickly faded.

It is difficult to accurately assess the specificity of black fly mermithids because of systematic problems within the parasite and the host groups. Host-list tables give the impression that black fly mermithids have a broad host range and that individual black fly species serve as hosts for a wide range of mermithids. Both impressions are misleading. For example, although *M. fluminalis* is listed as a parasite of 13 black fly species (28,53), it is likely that at least three mermithid species (*M. fluminalis sensu strictu*, *M. camdenensis*, and an undescribed *Mesomermis* sp. infecting *Prosimulium* spp.) were involved in these records. The identification of the host species in many records likewise may be inaccurate, since it has been demonstrated that a large number of species complexes exist in the Simuliidae. Thus, considering these systematic problems, host specificity statements have to be made cautiously. We do know, however, from field observations and laboratory tests that black fly species are differentially susceptible to mermithid infection. For example, a complete lack of infection in *S. tuberosum* was noted in streams where high levels of mermithid infection were present in *S. vittatum* (38). Colbo and Porter (12) reported 19% and 0% mermithid infection in *P. mixtum* and *Stegopterna mutata* larvae, respectively, even though early instars of both species were present in the same microhabitats in Newfoundland. Similarly, significantly higher rates of infection were achieved in *S. verecundum* than in *S. vittatum* larvae in a New York field trial with *M. fluminalis* s. l. (32). This trial also demonstrated that cross-generic infection by a mermithid species was possible, since the mermithids used in the test had been field-collected from *Prosimulium* larvae.

In most instances, temporal and spatial factors (e.g., asynchronous life cycles, differing geographical and habitat preferences) limit the host range of mermithid parasites. However, when larvae of two or more black fly species are present together,

differential host attraction or behavioral and physiological resistance may account for differential rates of parasitism (36). Behavioral resistance occurs when black fly larvae put up an active defense to attacking preparasites. In moving water, *S. vittatum* larvae are capable of grasping and mortally wounding host-searching *M. fluminalis* s. l. preparasites (Molloy, unpublished observations). Resistance based on the physiological response of the host does not appear to play a significant role in the differential susceptibility of mermithid infection in black flies. Nothing is presently known about host attraction and the kinds of stimuli that may be involved.

#### HOST-PARASITE RELATIONSHIPS

Mermithid parasitism causes serious morphological and physiological disturbances in the larval fly, as shown by the host's abdominal distortion, discolored integument, and depleted fat body (38,54,59). Arrested development of pupal and adult histoblasts is common in parasitized larvae and can prevent metamorphosis. Condon and Gordon (13) suggested that inhibition of pupation associated with parasitism is probably a consequence of severe nutrient depletion rather than an active manipulation of the black fly's hormonal system by the parasite. However, parasitized flies that do pupate and emerge are usually sterile due to incomplete development of their gonads (3,37,38,51). Moreover, Hocking and Pickering (25) reported degeneration of the nervous and digestive systems in parasitized adult *S. venustum*. Ovarian development was inhibited in 99% of infected adult *Simulium damnosum*, and these flies lived only half as long as nonparasitized females (34).

Intersexual adult black flies can result from mermithid parasitism, and Rubtsov (46) suggests that a disturbance to the fly's endocrine system is responsible. Intersexual development in chironomids and mosquitoes only occurs in genetically male individuals (10), and nematode parasitism of these flies is a known cause of this condition (22). Genetically male *Chironomus anthracinus* and *C. rempelli* larvae parasitized by mermithids uniformly develop into phenotypically female adults possessing

male genitalia; parasitism of genetically female individuals, while it induces alterations in their internal and external adult morphology, does not result in major intersexual traits (45,61,62).

The above pattern of intersexual development may also occur among black flies which, like mosquitoes and chironomids, are nematocercous Diptera. Mokry and Finney (29) and Colbo and Porter (12) reported finding only "female" adults infected with mermithids. They observed that their results were atypical, since other studies (24,37,38) had reported mermithid infection in both males and females. Colbo and Porter (12) suggested that parasitized male flies may have been killed prior to pupation. However, one might suggest that as with mosquitoes and chironomids, all intersexual black flies are genetically male and that in certain simuliid-mermithid associations (e.g., as present in the Newfoundland studies) mermithid parasitism of male larvae results in their intersexual development. Thus, in the Newfoundland studies, all parasitized male flies would have appeared as female phenotypes. Morphological and cytological determination of the sex of parasitized and nonparasitized flies, following Rempel et al. (45), would test this hypothesis.

Mermithid parasitism also modifies adult behavior. Parasitized males have been observed to attach to oviposition substrates (38) and simulate oviposition (12). Grunin (24) observed mermithids emerging from male *Prosimulium* which were flying over streams. The mock ovipositional behavior of these adults increases the likelihood that an emerging mermithid will be deposited in an upstream area. It would be interesting to examine if intersexual development of genetically male flies further reinforces this oviposition behavior.

The sex of mermithids developing within an insect usually depends upon the intensity of infection, with the proportion of males to females increasing with the number of nematodes per host; mermithids parasitic in black flies are not an exception. A single mermithid in a black fly is almost invariably a female, while superparasitized hosts usually produce males (15,18). Sexual determination in *I. lairdi* may be atypical,

however, since male adult *S. damnosum s. l.* typically contain only male mermithids (35).

### BIOCONTROL POTENTIAL

Mermithids parasitic in black flies have several characteristics that make them ideal biocontrol agents. Their host range appears limited to simuliids; they kill or sterilize their hosts; and, being natural parasites of black flies, they have good potential for permanent establishment, thereby giving long-term control following a single application.

Encouraged by steady progress in the development of the mermithid, *Romanomermis culicivorax*, as a mosquito control agent (36), hope ran high in the early 1970s that the biocontrol potential of black fly mermithids could be systematically exploited (1). Field-oriented research focused on host-parasite interrelationships and provided baseline data on the biology and ecology of host and parasite. However, the technical feasibility of using mermithids in a black fly control program has yet to be adequately addressed. The control potential of these parasites is most readily evaluated through comprehensive laboratory and field trials, in which the effects of mermithid treatments on black flies are carefully quantified. Few such tests have been conducted to date (31,32,33) due to difficulty of obtaining inoculum. Since laboratory colonies of black fly mermithids are not yet available, all inoculum must be produced from nematodes which have emerged from field-collected flies. This is an expensive procedure, and one which is highly dependent on the seasonal and local availability of infected black fly populations.

Only one field trial with mermithid preparasites has thus far been conducted (32). High rates of mortality (> 70%) were achieved in early instar *S. verecundum*, but only after application of large quantities of inoculum. It should be noted, however, that the mermithids used as the inoculum were naturally parasitic in *Prosimulium* larvae, and greater infectivity would probably have been obtained against larvae of this genus.

More laboratory and field trials are obviously required, but the problem of inoculum production must first be resolved.

Recent studies are somewhat encouraging. Significant advances have been made toward the establishment of continuous laboratory colonies of black flies (8,52), thus making *in vivo* production of black fly mermithids potentially feasible. Considerable progress has also occurred in the area of *in vitro* culturing of mermithids (19). In the short term it is more likely that an *in vivo*-produced mermithid colony will be available; the establishment of *in vitro* production is a more challenging research area, but one which may ultimately prove to be a more economical method of inoculum production.

Although emphasis here is placed on the pressing need for comprehensive laboratory and field trials, other aspects of research on mermithid parasitism of black flies should not be neglected. Further taxonomic studies on both host and parasite groups are necessary if species are to be accurately identified. Studies such as host-parasite life cycle synchrony, host specificity, and the environmental parameters affecting the free-living stages of these mermithids are needed to better define the factors influencing the prevalence and intensity of parasitism.

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