Review Article
Nematode Parasites and Associates of Ants: Past and Present

George Poinar Jr.

Department of Zoology, Oregon State University, Corvallis, OR 97331, USA

Correspondence should be addressed to George Poinar Jr., poinarg@science.oregonstate.edu

Received 14 August 2011; Accepted 9 October 2011

Academic Editor: Jean Paul Lachaud

Copyright © 2012 George Poinar Jr. This is an open access article distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Ants can serve as developmental, definitive, intermediate, or carrier hosts of a variety of nematodes. Parasitic ant nematodes include members of the families Mermithidae, Tetradonematidae, Allantonematidae, Seuratidae, Physalopteridae, Steinernematidae, and Heterorhabditidae. Those nematodes that are phoretically associated with ants, internally or externally, are represented by the Rhabditidae, Diplogastridae, and Panagrolaimidae. Fossils of mermithids, tetradonematids, allantonematids, and diplogastrids associated with ants show the evolutionary history of these relationships, some of which date back to the Eocene (40 mya).

1. Introduction

Nematodes are one of the most abundant groups of animals known. Studies on their evolutionary history suggest that they probably arose in the Precambrian, which explains their wide abundance today in the terrestrial and marine environments. While only some 20,000 have been described, their species diversity has been estimated to be as high as 10 million [1].

One would assume that with their strict housekeeping habits, ants would not tolerate nematodes in or around their nests and would quickly dispose of any nest mates that might have become infected. However nematodes have been able to use some astonishingly sophisticated tactics to successfully parasitize these social insects. The present work covers the systematics, life history, pathology, and records of all described extant and fossil nematodes associated with forminicids. This includes representatives of the nematode families Mermithidae, Tetradonematidae, Allantonematidae, Seuratidae, Physalopteridae, Steinernematidae, Heterorhabditidae, Rhabditidae, Diplogastridae, and Panagrolaimidae. Fossil records of mermithids, tetradonematids, allantonematids, and diplogastrids associated with ants reveal the evolutionary history of these associations, some of which date back 40 million years.

2. Mermithidae

The family Mermithidae includes parasites of invertebrates, especially insects. Because of their large size, mermithids are easily detected in ants upon dissection (Figure 1) or as they leave their hosts (Figure 2). Most mermithid species, including those that attack ants, parasitize only a specific host species, genus, or family while others can infect representatives of several insect orders. Mermithids that attack aquatic insects, such as midges (Chironomidae, Ceratopogonidae) and mosquitoes (Culicidae), have a direct life cycle. Direct life cycles occur when, after growth and development is completed in the host, the mermithid emerges, molts to the adult stage, mates, and oviposits in the host’s environment. The infective stage mermithid emerges from the egg, actively locates and enters a host, and initiates development in the hemocoel.

Some mermithids have an indirect life cycle, which is more complicated but allows hosts to be parasitized in environments hostile to nematodes. In an indirect cycle, the mermithid emerges from the host, molts, mates, and oviposits in the environment. But instead of emerging from the egg to search for a developmental host, the infective stage remains in the egg, waiting to be ingested by an invertebrate that serves as a paratenic host. When mermithid eggs are ingested by a paratenic host, the hatching infective stage penetrates the gut wall and enters the body cavity. But instead of developing, the mermithid encysts and enters a diapause. The encysted nematode can be carried through the different stages of host metamorphosis, but for its cycle to be completed, the paratenic host must be captured and fed to the brood of the developmental host. At the completion of the mermithids growth phase in the development host (like an ant), the latter is attracted to an aquatic or semiaquatic habitat favorable
to the nematode. This is when the mermithid exits, leaving the dying host behind. The developmental host is usually not only larger, but usually in a completely different taxonomic category and environment from the paratenic host. While the developmental host can live in a relatively dry habitat, the paratenic host usually inhabits an aquatic, semiaquatic, or damp biome. Also, both hosts can be widely separated taxonomically and may not even belong to the same phylum.

The first written account of a nematode parasite of ants was made by the Reverend William Gould in his 1747 book *An account of English Ants* (Table 1) [2].

The “white and long kind of worm, which is often met within their bodies” certainly refers to mermithid nematodes. For a number of years, mermithids were listed under “Filaria,” “Gordius,” or “Mermis,” and that is why mermithid systematics can be confusing and why early names for Gould’s ant mermithid included *Gordius formicarum* Diesing [3] and *Filaria formicarum* von Siebold [4].

The first described ant mermithid was *Pheromermis myrmecophila* from *Lasius* spp. [5]. However it was originally described in the genus “Mermis,” then assigned to the genus *Pheromermis* [6], then moved to the genus *Allomermis* [7] and lastly to the genus *Camponotimermis* [8]. Its position in the genus *Pheromermis* was recently confirmed by Kaiser, who showed its similarity with the European ant mermithid, *Pheromermis villosa* [9]. Over the years, a large number of ant species have been reported parasitized by mermithids. A list of Holarctic parasitized ants was presented by Passera [10] and Neotropical parasitized ants by Poinar et al. [11]. A compilation of all described mermithids from ants is presented in Table 2.

Fossils, such as the postparasitic juvenile of *Heydenius formicinus* emerging from a male *Prenolepis henscheii* (Figure 3) [15], as well as from a worker ant (Figure 4) in Baltic amber [1] show that ants have been parasitized by mermithids for at least 40 million years and probably much longer. The fossil record of Neotropical mermithid parasites of ants is represented by a parasitic juvenile of *Heydenius myrmecophila* adjacent to its ant host, *Linepithema* sp. in 20–30-million-year-old Dominican amber (Figure 5) [11]. It is assumed that the traumatic events of the ant host entering the resin caused the mermithid to emerge prematurely from an opening in the gaster of the ant.

**Table 1**: Section from Gould [2] referring to the first reported instance of mermithid parasitism of ants.

Amongst other Incidents that tend to lessen and destroy Ant-Flies, it is observable that abund- dance of them are demolished by a white and long Kind of Worm, which is often met with in their Bodies. You may frequently take three from the Insides of the large, but seldom more than one from a small Ant-Fly. These Worms lie in a spiral Form, and some of them may be extended Half an Inch.

**Table 2**: Mermithid nematodes described from ants.

<table>
<thead>
<tr>
<th>Mermithid</th>
<th>Host</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Agamomermis cephaloti</em></td>
<td><em>Cephalotes minutus</em></td>
<td>[11]</td>
</tr>
<tr>
<td><em>Agamomermis costaricensis</em></td>
<td><em>Odontomachus hastatus</em></td>
<td>[11]</td>
</tr>
<tr>
<td><em>Agamomermis ecitonii</em></td>
<td><em>Ecton burchelli</em></td>
<td>[11]</td>
</tr>
<tr>
<td><em>Allomermis solenopsi</em></td>
<td><em>Solenopsis invicta</em></td>
<td>[12]</td>
</tr>
<tr>
<td><em>Camponotimermis bifidus</em></td>
<td><em>Camponotus aethiops</em></td>
<td>[13]</td>
</tr>
<tr>
<td><em>Comanimermis clujensis</em></td>
<td><em>Formica fusca</em></td>
<td>[14]</td>
</tr>
<tr>
<td><em>Heydenius formicinus</em></td>
<td><em>Prenolepis henscheii</em></td>
<td>[15]</td>
</tr>
<tr>
<td><em>Heydenius myrmecophila</em></td>
<td><em>Linepithema</em> sp.</td>
<td>[11]</td>
</tr>
<tr>
<td><em>Meximermis ectatommi</em></td>
<td><em>Ectatomma raidum</em></td>
<td>[11]</td>
</tr>
<tr>
<td><em>Pheromermis lasiusi</em></td>
<td><em>Lasius niger</em></td>
<td>[16]</td>
</tr>
<tr>
<td><em>Pheromermis myrmecophila</em></td>
<td><em>Lasius</em> spp.</td>
<td>[5]</td>
</tr>
<tr>
<td><em>Pheromermis villosa</em></td>
<td><em>Lasius flavus, L. niger</em></td>
<td>[17]</td>
</tr>
</tbody>
</table>

* fossil.
Depending on the caste and length of time the mermithid is associated with its host, various degrees of host intercastes and abnormalities appear. Wheeler [18] was the first to provide an explanation for these phenomena by correlating the unusual morphological conditions with mermithid infections (Figure 6). Parasitized queen ants (mermithogynes) are shorter, have a smaller thorax (stenothoracy), reduced wings (brachyptery), enlarged abdomen (physogastry), and smaller head (microcephaly) than their uninfected counterparts. Parasitized worker ants (mermithergates or macroergates) often develop morphological features characteristic of queens and soldiers. Attacked male ants (mermithaners) have shorter wings but enlarged heads, eyes, and gasters. Infected soldiers (mermithostratiotes) have reduced heads, an ocellus, and changes in pilosity (Figure 7) [19–24].

The life cycle of most ant mermithids remains a mystery. Crawley and Baylis [5] assumed that *P. myrmecophila* has a direct cycle, where infection is brought about by the eclosing preparasitic mermithid entering the ant host. When development is completed, the postparasitic juvenile emerges, molts to the adult stage in the ant’s habitat, mates, oviposits and the cycle continues. However, no one has demonstrated a direct cycle for any mermithid parasite of ants. In 1934, Vandel [25] studied a mermithid parasite of *Pheidole pallidula* and realized that the infection must be initiated in the ant larva. He assumed that the nematodes were in the soil surrounding the ant colony so the infective stages could penetrate directly into

---

**Figure 3:** The fossil nematode, *Heydenius formicinus*, emerging from a male *Prenolepis henschei* in Baltic amber.

**Figure 4:** *Heydenius formicinus* adjacent to its worker ant host in Baltic amber.

**Figure 5:** *Heydenius myrmecophila* adjacent to its *Linepithema* ant host in Dominican amber.

**Figure 6:** Plate (modified) of *Pheidole dentata* (referred to as *P. commutata*) from [18] showing the first evidence that mermithid nematodes could cause intercastes of ants. (a) Normal soldier; (b) normal worker; (c) parasitized worker (mermithergate).
the leaf cutting ants), and this behavior suggests they have an indirect life cycle involving a paratenic host. The two genera, Agamomermis and Heydenius, are collective group genera for immature extant and fossil mermithids, respectively [1].

There are some morphological and behavioral patterns that characterize mermithids with indirect cycles. They normally have smaller eggs with thicker shells than the eggs of direct development soil or freshwater mermithids. Also, their eggs are completely embryonated when laid. Finally, the deposited eggs will not hatch in the environment even though the enclosed parasitic juvenile is fully developed. Hatching only occurs when a potential invertebrate paratenic host ingests the eggs. The eggs of Pheromermis spp. are small, numerous, fully embryonated when laid and do not hatch in the environment. Fully embryonated eggs ensure that the infective stages are ready to enter paratenic hosts as soon as they are ingested [6, 17].

The ant mermithid, Allomermis solenopsi [12], possess an unusual morphological feature on the mature eggs that could play a crucial role in its life cycle. The surface of the eggs is covered with elongate, erect, spiny adhesive processes. How these function in the life cycle is unknown, but the related species, A. trichotopson, possesses similar structures [28]. Since A. solenopsi parasitizes the fire ant, Solenopsis invicta in Brazil (Figure 2), the related A. trichotopson, whose host is unknown, may infect Solenopsis gmininata in Jamaica. Could these egg processes somehow be connected with parasitism of Solenopsis spp.?

Can mermithids be manipulated to control ants? Aside from killing the ant host upon emergence, mermithids drain the host of food, reduce the flight muscles and fat body, and cause morphological modifications as mentioned above [9, 17, 24, 26]. Since mermithid-infected Solenopsis has reduced reproductive organs and die shortly after the nematodes emerge [11, 12, 29], it has potential as a biological control agent. However, if the cycle is always indirect as shown for P. villosa, it would be very difficult to artificially infect the ant brood. It would be necessary to first infect the paratenic host and then supply large numbers of these infected invertebrates to worker ants for transport back to the nest. Working with a mermithid that has a direct cycle would be easier; however there is still the problem of raising and disseminating the nematodes.

3. Tetradonematidae

The tetradonematids are a diverse group of nematodes that have traditionally been aligned with the Mermithidae. However, aside from some distinctive morphological characters, female tetradonematids normally mature, mate, and produce eggs within the host, which does not occur with mermithids. Two tetradonematids have been described from extant ants. Tetradonema solenopsi is a parasite of the red imported fire ant, Solenopsis invicta, in Brazil [30, 31]. Very little is known about this nematode aside from the scant description showing that females contained eggs and worker infection levels reached 12.5%. Parasitized ants that succumbed to the infections could be recognized by their slightly enlarged gaster with scallop‐appearing dorsal sclerites.
The second tetradonematid from extant ants is *Myrmeconema neotropicum* from *Cephalotes atratus* in Peru and Panama [32]. *Myrmeconema* is the only nematode that causes its ant host to radically change color (from black to red), which is crucial for completion of its life cycle [33]. This color change was a mystery for early taxonomists and the variety *Cephalotes atratus* var. *rufiventris* was erected solely on the basis of its red abdomen, which was later shown to be the result of *Myrmeconema* infections [32].

Developing females of *M. neotropicum* occur in ant pupae (Figure 9) but do not produce masses of eggs until they are carried into the adult ant (Figure 10). As the females deteriorate, eggs are released into the ant’s hemocoel (Figure 11). At this stage of development, the gasters of the infected worker ants turn from black to red and are held high in the air (Figure 12) [33]. Birds mistake the red gasters for fruits and the nematode eggs are passed through the birds’ digestive system and end up in the droppings, which are deposited on leaves and branches. *Cephalotes* workers collect and feed the infested excreta to their brood, which is how the larvae become infected [33].

Aside from their red gasters, parasitized ants are smaller with reduced head widths. They are sluggish, clumsy, generally less aggressive, and about 40% heavier than nonparasitized workers. They do not bite when handled, and their alarm/defense pheromone supply is significantly reduced or absent.

*Myrmeconema* is probably widely distributed throughout the Neotropics since this association has been in existence for some 20–30 million years. The fossil worker ant, *Cephalotes serratus* in Dominican amber, is surrounded by the eggs of *Myrmeconema antiqua* (Figure 13) [1]. The ant has a hole in its abdomen that quite possibly was made by a bird. Many of the eggs, which closely resemble those of *M. neotropicum* in size and shape, contain fully developed juveniles (Figure 14). All indications suggest that *M. antiqua* had a similar life history to the extant *M. neotropicum* and involved bird carriers.
4. Allantonematidae

It is curious why so few cases of allantonematid infections have been reported in ants. Since ants are probably one of the most investigated insect groups, is the absence of tylenchid parasitism due to a lack of observations or its rarity? The first and only described allantonematid parasite of extant ants is *Formicitylenchus oregonensis* that was parasitizing a queen *Camponotus* ant in Western Oregon, USA [34]. The queen had already chewed off her wings and appeared to be searching for a nesting site. There was a single large parasitic female (Figure 15) and 120 third-stage juvenile nematodes in the ant’s gaster. The third-stage juveniles exited through the ants reproductive and digestive tracts and molted twice to reach the adult stage. The enlarged pharyngeal glands in the free-living females suggest that they penetrate the cuticle to enter the body cavity of the host, probably ant larvae. Although the complete life cycle is unknown, the nematodes are clearly distributed by infected queen ants. The gonads of the infected ant were greatly reduced, and her eggs were abnormal. Since carpenter ants can be damaging to structures, *F. oregonensis* can be considered as a potential biological control agent.

Since the original report of this parasite, the present author recovered a worker carpenter ant also infected with *F. oregonensis*, thus indicating that *Formicitylenchus* is probably restricted to ant hosts, especially members of the genus *Camponotus*. *Formicitylenchus* shows a close relationship with the allantonematid beetle parasite, *Metaparasitylenchus* [34]. It is possible that their last common ancestor parasitized beetles and the host shift from arboreal beetles to arboreal ants occurred during the anagenesis of *Formicitylenchus*. The close physical association between wood-boring beetles and *Camponotus* ants may be significant. Rogers [35] commented that “…the potential parasite would be expected to find its hosts in organisms which occupy the same niche largely independent of their phylogenetic position. In fact the specificity of many parasites is based on the ecological relationship of the hosts, especially in groups which have only recently become parasitic.”

Another reason that allantonematid parasitism of ants may be more widespread than presumed is the discovery of juveniles of a fossil allantonematid, *Palaeoallantonema cephalotae*, in the ant, *Cephalotes serratus*, in Dominican amber [1] (Figure 16). Just before this fossil was discovered, Steven Yanoviak submitted an extant worker of *Cephalotes christopherseni* from Peru that was also infected with an allantonematid. The parasitic female (Figure 17) of this still undescribed species and the developing juveniles inside her body (Figure 18) show features typical of the family.

5. Seuratidae

The discovery of adults of *Rabbium paradoxus* [36] inside the gaster of worker *Camponotus castaneus* in Florida (Figure 19) was a surprise since all known nematodes of the Seuratidae are heteroxenous and develop to the adult stage in the digestive tract of vertebrates [37]. However, in *R. paradoxus*, the
vertebrate host is obviously not required for adult development. The females of *R. paradoxus* have an anteriorly placed vulva (Figure 20), and the eggs embryonate inside the uterus (Figure 21). Since the other member of the genus, *R. caballeroi*, occurs in the gut of lizards in the Bahamas [38], it is likely that *R. paradoxus* originally had (or still has) a lizard definitive host. If the complete life cycle occurs just in ants, then *C. castaneus* would serve as both intermediate and definitive hosts. *C. castaneus* is a generalist feeder and will ingest vertebrate feces so it could acquire nematode eggs from lizard droppings. Parasitized worker ants had swollen gasters and showed unusual behavior by foraging during the day instead at night. This would make them easily captured by vertebrate predators.
The original life cycle of *R. paradoxus* may have been similar to that of the seuratoid *Skrjabinelaia galliardi*, a parasite of sphaerodactyline lizards in Brazil [37]. The female nematodes living in the gut of the lizard produce eggs that are passed out and ingested by insects. These eggs hatch in the insect gut and the juveniles enter the body cavity without further development. Growth is resumed when the insect intermediate hosts are eaten by lizards [38]. Unfortunately, the complete life cycle of *R. paradoxus* remains a mystery, but its precocious development is quite interesting.

6. **Physalopteridae**

There are few reports of heteroxenous nematodes utilizing ants as intermediate hosts, that is, hosts where the nematodes develop only to the third-stage infective juveniles. Maturity to the adult stages occurs when the intermediate host is eaten by a vertebrate definitive host. One such nematode is the physalopterid, *Skrabinoptera phrynosoma* that lives in the stomach of the Texas horned lizard, *Phrynosoma cornutum*, and uses the harvester ant, *Pogonomyrmex barbatus*, as an intermediate host [39]. However instead of depositing isolated eggs that would pass from the lizard, the gravid nematodes die with the retained eggs enclosed in thick walled capsules. The females with their enclosed eggs pass out of the insect and are collected by worker ants that feed them to their brood. The nematode eggs hatch in the gut of the ant larvae and the juveniles enter the fat body, where they develop only to the third stage. These juveniles are carried through the pupal and into the adult stage of the ant, where they eventually reside in membranous capsules. The nematodes complete their development to the adult stage when infected ants are eaten by the lizards. Worker ants with more than 10 nematodes were still active but had enlarged, lighter colored gasters. The interesting, pivotal stage in this life cycle is the attractiveness of the dead, egg-laden female nematodes to worker ants.

7. **Rhabditidae, Diplogastridae, and Panagrolaimidae**

This category includes juvenile nematodes living in the postpharyngeal glands of ants (internal phoresis) or being carried on the outside surface of ants (external phoresis) (Table 3). While these might not be considered parasites, in some instances where the association has been examined critically [40] damage has been inflicted on the ant’s postpharyngeal glands and some of the nematodes increased in size during their stay in this location. Thus at most, they could be considered weak parasites. If they break through the glands and introduce microbes into the body cavity of the ant, they could even be regarded as pathogenic. However the latter scenario has not been documented.

Most of the nematodes in the postpharyngeal glands are dauer juveniles of free-living microbotrophs living in the ant’s environment. The dauers enter the glands when environmental conditions become unsuitable (low humidity or diminishing food supply). These resistant dauer juveniles can survive for relatively long periods. The nematodes may leave the glands when the environment is more suitable (moist with associated microbes), if the ant dies and the dauer initiates development within the decomposing ant, or when the nematodes are transferred from ant to ant during trophallaxis.

Janet [43] was the first to discover postpharyngeal rhabditids (*Oscheius dolichurus*) in *Lasius flavus* and *Formica ru-fa* in France. Wahab [42] was the first to systematically study these associations in the ant genera *Lasius*, *Formica*, *Tetramorbitum*, and *Myrmica* in Germany (Table 3). More recently Köhler [41] examined nematodes in the heads of ants collected from sap fluxes and rotten wood on trees in Germany. The most common ant that visited these fluxes was *Lasius brunneus* and, from a total of 262 workers collected, 43.5% carried nematodes, with *Koerneria histophora* being the most common associate. While most ants carried a single nematode, numbers occasionally reached up to 85 dauers per ant. Köhler [41] also found diplogastrid dauers in 4 males and a queen of *L. brunneus*. The infection rate of ants associated with *L. brunneus* workers varied depending on the weather cycle. There were more nematodes in ants during the dry period in August than during the rainy months of April and May. Also important in determining the rate of nematodes being carried by the ants was the location of the nests. Rates of infestation by nematodes in *L. brunneus* were much higher when the ants were collected from sap fluxes and rotten wood [41], than were collected from under stones and leaf litter [42].

Köhler [41] was able to infest ants by placing them in a Petri dish with rotten wood containing waving dauer stages. Both Wahab [42] and Köhler [41] provided evidence that the dauers can be transmitted from ant to ant via trophallaxis, which was supported in part by the experiments of Naarman [53] showing that *Formica* ants mix food with secretions from the postpharyngeal gland before regurgitating it to nest mates. These ant-dauer associations probably occur worldwide since Markin and McCoy [40] reported *Diploscapter lyctosoma* in the postpharyngeal glands of the Argentine Ant, *Linepithema humile* in California and Nickle & Ayre...
Table 3: Juvenile nematodes of Rhabditida and Tylenchina associated with ants.

<table>
<thead>
<tr>
<th>Nematode</th>
<th>Family</th>
<th>Host</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diplogasteroides spengeli</td>
<td>Diplogastridae</td>
<td>Lasius brunneus</td>
<td>[41]</td>
</tr>
<tr>
<td>Diploscapter lycostoma</td>
<td>Rhabditidae</td>
<td>Formica spp., Lasius spp.</td>
<td>[42]</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>Myrmica rugulosa</td>
<td>[42]</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>Linepithema humile</td>
<td>[40]</td>
</tr>
<tr>
<td>*Formicodiplogaster myrmenema</td>
<td>Diplogastridae</td>
<td>Azteca alpha</td>
<td>[1]</td>
</tr>
<tr>
<td>Halicephalobus similigeraster</td>
<td>Panagrolaimididae</td>
<td>Lasius brunneus</td>
<td>[41]</td>
</tr>
<tr>
<td>Koerneria histophora</td>
<td>Diplogastridae</td>
<td>Lasius spp.</td>
<td>[42]</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>Lasius brunneus</td>
<td>[41]</td>
</tr>
<tr>
<td>Oscheius dolichurus</td>
<td>Rhabditidae</td>
<td>Formica rufa, Lasius flavus</td>
<td>[42, 43]</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>Tetratomorium caespitum</td>
<td>[42]</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>Camponotus herculeanus</td>
<td>[44]</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>Lasius claviger</td>
<td>[44]</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>Lasius brunneus</td>
<td>[41]</td>
</tr>
<tr>
<td>Pristionchus lheritieri</td>
<td>Diplogastridae</td>
<td>Formica rufa, Lasius spp.</td>
<td>[42]</td>
</tr>
<tr>
<td>*Unknown</td>
<td>&quot;</td>
<td>Azteca spp.</td>
<td>[1]</td>
</tr>
<tr>
<td>Unknown</td>
<td>&quot;</td>
<td>Formica obscuriventris</td>
<td>Present work (Figure 22)</td>
</tr>
</tbody>
</table>

*Fossil.

Figure 22: Dauer juveniles of a diplogastrid in the postpharyngeal glands of Formica obscuriventris clivia from Oregon.

[44] found Oscheius dolichurus in the head glands of Camponotus herculeanus and Lasius claviger in Ontario, Canada. The author has also found dauer diplogastrids in the postpharyngeal glands of workers of Formica obscuriventris in Oregon (Figure 22).

The association between dauer nematodes and ants is at least 20–30 million years old. Evidence for this is the discovery of dauer juveniles of the fossil diplogastrid, Formicodiplogaster myrmenema, carried by Azteca alpha workers in Dominican amber [1] (Figures 23 and 24). The dauer stages appear to be associated with the abdomen of the ants, suggesting that they were being carried in the segmental membranes of the gaster (external phoresis). None of the fossil stages occurred around the mouthparts of the ants. Also, developing stages of F. myrmenema were associated with nest material adjacent to worker Azteca ants in Dominican amber [1]. This indicates that F. myrmenema was developing in the nests of A. alpha, which is probably the case with extant nematodes in the head glands of ants. Whether the dauers of F. myrmenema were also in the postpharyngeal glands of the fossil ants is unknown.

Figure 23: Three dauer juveniles of Formicodiplogaster myrmenema adjacent to a worker of Azteca alpha in Dominican amber.
8. Steinernematidae and Heterorhabditidae

Included in this section are the so-called entomopathogenic nematodes belonging to the genera *Steinernema* and *Heterorhabditis*. It is quite likely that entomopathogenic nematodes infect ants under natural conditions, but no reports are known. Infection is initiated by a third-stage infective juvenile that enters the host’s body cavity, apparently per os [50]. After reaching the hemocoel, the infective stage initiates development and, in so doing, releases a symbiotic bacterium (*Xenorhabdus* spp. in *Steinernema* nematodes and *Photorhabdus* spp. in *Heterorhabditis* nematodes) that is carried in the infective stage’s gut lumen. The bacterium kills the insect soon after it is released in the body cavity. The nematodes feed on the mixture of bacteria and insect hemolymph and develop to the adult stage in the body cavity. With adequate nourishment, the nematodes undergo a second generation but when nourishment is limited, the juveniles form third-stage infective juveniles. By introducing the bacteria that quickly kill the hosts, these nematodes avoid specific defense responses and have a wide host range, attacking representatives of many insect orders and even other arthropods [54].

Laboratory experiments have shown that these nematodes can infect a number of ant species (Table 4) and they also have been used in the field against pest ants [50, 52, 54–56]. Poole [50] attempted to control field populations of ants (*Solenopsis richteri* and *S. invicta*) with *Steinernema carpocapsae*. Using a dose of 1 million infective stages per mound for *S. invicta*, the nematodes caused 35% mortality in the fall and 80% mortality in the spring. With *S. richteri*, the death rate was 80% in the spring and 36% in the fall. Poole [50] noted that workers were infected less than other stages, possibly because of their greater activity and grooming behavior. However, workers regurgitated infective stages to the alates and larvae. Queen ants were more susceptible and up to 3,000 infective stage juveniles could be produced in some infections (Figure 25).

Further field trials of *S. carpocapsae* and *Heterorhabditis bacteriophora* against the red imported fire ant, *S. invicta*,

---

### Table 4: Ants infected by entomopathogenic nematodes (*Steinernema carpocapsae* and *Heterorhabditis bacteriophora*) under laboratory and/or field conditions.

<table>
<thead>
<tr>
<th>Ant</th>
<th>Nematode</th>
<th>System</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acromyrmex octospinosus</em></td>
<td><em>S. carpocapsae</em></td>
<td>Aqueous</td>
<td>[45]</td>
</tr>
<tr>
<td><em>Camponotus</em> sp.</td>
<td><em>S. carpocapsae</em></td>
<td>Sucrose</td>
<td>[46]</td>
</tr>
<tr>
<td><em>Camponotus</em> sp.</td>
<td><em>S. carpocapsae</em></td>
<td>Aqueous</td>
<td>[47]</td>
</tr>
<tr>
<td><em>Myrmica</em> sp.</td>
<td><em>S. carpocapsae</em></td>
<td>Aqueous</td>
<td>[47]</td>
</tr>
<tr>
<td><em>Pogonomyrmex</em> sp.</td>
<td><em>S. carpocapsae</em></td>
<td>Sucrose</td>
<td>[48]</td>
</tr>
<tr>
<td><em>Solenopsis</em> spp.</td>
<td><em>S. carpocapsae</em></td>
<td>Aqueous</td>
<td>[46]</td>
</tr>
<tr>
<td><em>Solenopsis</em> geminata</td>
<td><em>S. carpocapsae</em></td>
<td>Aqueous</td>
<td>[49]</td>
</tr>
<tr>
<td><em>Solenopsis</em> invicta</td>
<td><em>S. carpocapsae</em></td>
<td>Aqueous</td>
<td>[50, 51]</td>
</tr>
<tr>
<td><em>Solenopsis</em> invicta</td>
<td><em>H. bacteriophora</em></td>
<td>Aqueous</td>
<td>[52]</td>
</tr>
<tr>
<td><em>Solenopsis richteri</em></td>
<td><em>H. bacteriophora</em></td>
<td>Aqueous</td>
<td>[52]</td>
</tr>
<tr>
<td><em>Solenopsis richteri</em></td>
<td><em>S. carpocapsae</em></td>
<td>Aqueous</td>
<td>[50]</td>
</tr>
</tbody>
</table>

---

**Figure 24:** Detail of a dauer juvenile of *Formicodiplogaster myrmenema* adjacent to a worker of *Azteca alpha* in Dominican amber.

**Figure 25:** Developing stages of *Steinernema carpocapsae* removed from the body of an infected queen of *Solenopsis invicta*.
Psyche 11

Table 5

<table>
<thead>
<tr>
<th></th>
<th>Nematodes represented as dauer or postdauer juveniles in the pharyngeal glands of ants</th>
<th>Rhabditidae, Diplogastridae and Panagrolaimidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1)</td>
<td>Nematodes developing in the body cavity of ants</td>
<td></td>
</tr>
<tr>
<td>(2)</td>
<td>Only juvenile nematodes present</td>
<td>Elongate nematodes normally over 15 mm in length at completion of development; not enclosed in membranous capsules</td>
</tr>
<tr>
<td>(3)</td>
<td>Adult nematodes with or without juveniles</td>
<td>Nematodes under 10 mm in length; enclosed in membranous capsules</td>
</tr>
<tr>
<td>(4)</td>
<td>Elongate nematodes normally over 15 mm in length at completion of development; not enclosed in membranous capsules</td>
<td>Nematodes developing in the body cavity of ants (2)</td>
</tr>
<tr>
<td>(5)</td>
<td>Nematodes reproducing in dead ants; infective juveniles produced</td>
<td>Nematode adults, eggs and/or juveniles in living ants; infective juveniles absent (4)</td>
</tr>
<tr>
<td>(6)</td>
<td>Males with a bursa; females with a pointed tail</td>
<td>Males without a bursa; females with a bluntly rounded tail, often bearing a small point at tip</td>
</tr>
<tr>
<td>(7)</td>
<td>Eggs and juveniles present</td>
<td>Allantonematidae</td>
</tr>
<tr>
<td></td>
<td>Eggs, but no juveniles present</td>
<td>Tetrarongematidae</td>
</tr>
<tr>
<td></td>
<td>Vulva positioned at middle or lower half of body</td>
<td>Seuratidae</td>
</tr>
<tr>
<td></td>
<td>Vulva positioned in upper fourth of body</td>
<td></td>
</tr>
</tbody>
</table>

gave control rates of 37.5% with *S. carpocapsae* but less with *H. bacteriophora* [52]. In field trials comparing applications of *Steinernema carpocapsae* and amidinohydrazone against *S. invicta*, Morris et al. [55] estimated that nematode applications at a rate of 2 million per gallon per mound resulted in 47% mortality.

Controlling fire ants in the field is difficult because of the small mound opening through which the nematodes are introduced. Also, it is desirable to have recycling of the nematodes in the nests, but healthy ants appear to remove infected individuals before the cycle is completed. Since the number of nematodes needed to overwhelm a colony of ants is quite high using inundative methods, consideration was given to the development of baits or other more efficient delivery systems [46, 48, 52, 55, 56]. These other methods are still under investigation.

### 9. Unknown Nematodes

Gösswald [57] reported the presence of several encysted nematodes in the flight muscles of a queen *Teleutomyrmex schneideri* in Germany. The cysts were quite small, being only 25 µm in diameter. Except for their small size, the cysts are similar in appearance to those of the vespid mermithid, *Pheromermis pachysoma*, formed in the body wall of Trichoptera paratenic hosts [27] and the ant parasite, *P. villosa*, in the body of oligochete paratenic hosts [26]. However, the *Pheromermis* cysts are 60–100 µm and 80 µm in diameter, respectively. It is possible that juvenile nematodes of a mermithid parasite were acquired after the queen was fully formed and the nematodes preferred to encyst rather than initiate development. The other likelihood is that the nematodes were the infective stages of a heteroxenous nematode parasite and were waiting for transfer to a vertebrate definitive host. However, the only cysts of heteroxenous nematodes known from ants are those of the physalopterid, *S. phryn- osoma*, the smallest of which measures 633 µm in diameter [39].

In 1907, Janet [58] found nematodes 7-8 mm in length developing in the head cavities and emerging from the labial region of workers of *Formica fusca*. Just before the nematodes emerged, the infected ants began trembling and eventually died. The head cavities of infected ants were empty upon nematode exit. This behavior of developing in the head of ants is known for some phorid flies but not for nematodes. Whether this was a mermithid with an unusual developmental location or a heteroxenous nematode using the ant as an intermediate host is unknown.

### 10. Identification Key to Nematode Families Associated with Ants

See Table 5.

### 11. Conclusions

Representatives of most invertebrate parasitic nematode families attack ants, with the exception of sphaerulariids, entaphelenchids, and oxyurids. While mermithids are the most commonly encountered nematode parasites of ants, the complete life cycle of only a single species is known. The life cycle of ant mermithids can be quite complicated when it involves paratenic hosts living in completely different habitats. Even less is known about the life cycles of other ant parasitic nematodes, certainly not enough to consider using them as biological control agents. While the inundative application of entomopathogenic nematodes (*Steinernema* and *Heterorhabditis*) can control ants in isolated colonies, establishing nematodes for the sustained control of ant populations has not been achieved.

There are probably many additional nematode parasites of vertebrates utilizing ants as intermediate hosts. Reptiles,
mammals, and amphibians eat ants, and it follows that nematodes other than *Skryabinoptera phrynosoma* would have devised methods of cycling themselves through ants to reach their definitive hosts. In the mysterious case involving *Rabbitsum paradoxus*, the presence of adults of a heteroxenous nematode in an ant raises the question of whether formicids can serve as sole hosts or this is just a case of precocity.

Fossils show that mermithids were infecting ants over 40 million years ago and tetratomematids and allottonematids had established parasitic associations with ants some 20–30 million years ago. Such fossils, which can be used to calibrate molecular clocks, provide minimum dates for the occurrence of nematode lineages and show the antiquity of nematode-ant relationships.

**Acknowledgments**

The author thanks S. D. Porter, Luc Passera and Stephen P. Yanoviak for supplying photos and Brad Vinson for supplying the queen of *Solenopsis invicta* infected with *Steinernema carpocapsae*. Grateful appreciation is extended to Roberta Poinar for commenting on earlier versions of the paper.

**References**


[36] G. Poinar Jr., A. G. Chabaud, and O. Bain, “Rabbium para-
doxus sp. n. (Seuratidae: Skrabinelaziae) maturing in Cam-
ponotus castaneus (Hymenoptera: Formicidae),” Proceedings of
the Helminthological Society of Washington, vol. 56, pp. 120–

ete cycle biologique,” Annales de Parasitologie, vol. 63, no.


[42] A. Wahab, “Untersuchungen über Nematoden in den drüsen des kopfes der Ameisen (Formicidae),” Zeitschrift für Mor-


