

Mermithid Nematode Parasitism of *Solenopsis* Ants (Hymenoptera: Formicidae) of Northern Florida

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ABSTRACT Sexualls collected from nests of the fire ant, *Solenopsis geminata* (F.), the red imported fire ant, *S. invicta* Buren, and *S. pergandei* Forel in the Apalachicola National Forest were parasitized occasionally by a large mermithid nematode. Summer infection rates (1991–1993) varied by species and sex: 0% for *S. invicta* gynes, between 1 and 7% for *S. pergandei* gynes and males of all 3 species, and 16% for *S. geminata* gynes. The seasonality of infection coincided with the summer reproductive period of *S. geminata* and suggests the mermithid has an annual life cycle. The parasites, up to 15.5 cm in length, distend the abdomen of the host, but have little anatomical effect other than detracting from sex organ development. Mermithidized ants do not participate in mating flights and die when the parasites emerge. The mermithids emerge as sexually immature larvae, precluding their identification or taxonomic description. A mermithid this large has not been reported previously in *Solenopsis*. Currently, there is no record of mermithid parasitism in *S. invicta* and *S. pergandei* nor have mermithidized sexuals been reported in the genus.

KEYWORDS *Solenopsis*, fire ants, ants, mermithid nematodes, parasitism

SINCE ITS INTRODUCTION into the United States more than half a century ago, the red imported fire ant, *Solenopsis invicta* Buren, has spread throughout the Southeast and has gained notoriety as an economic, agricultural, medical, and household pest (Lofgren and Adams 1982, Apperson and Adams 1983, Adams 1986). When concern grew over the efficacy and environmental effects of chemical efforts to eradicate fire ants, attention turned to biological control, with investigations to catalog natural enemies launched in both North and South America (Jouvenaz et al. 1977, 1980; Jouvenaz 1983; Wojcik et al. 1987). Although biological control of fire ants is still in an exploratory phase, comparative studies have shown that *S. invicta* is plagued by substantially fewer parasites, pathogens, and predators in North America than in its South American homeland (Jouvenaz et al. 1980, Wojcik 1983, Jouvenaz 1986, Wojcik et al. 1987). The suite of natural enemies in South America is thought to reduce *S. invicta*'s ecological dominance and lessen its effects on humans (Wojcik 1986, Porter et al. 1992). Establishing or promoting a complex of natural enemies in the North American population of *S. invicta* may effect control, even if none of the parasites or pathogens alone is devastating to the host. Multiple natural enemies may act synergistically, because the effects of one may make the host more susceptible

to infection by others (Dogiel 1964, Jouvenaz 1990).

A strategy to find potential biological control agents for *S. invicta* that has not been widely used is the screening of related and ecologically similar ant species. In North America, an obvious source of potential control agents is the native fire ant *S. geminata* (F.). Natural enemies of *S. geminata* are of interest not only because they represent potential control agents of *S. invicta*, but also because *S. geminata* has achieved pest status in many parts of the world (Delabie 1990, Reimer et al. 1990, Veeresh 1990, Williams and Whelan 1991).

In 1991, we serendipitously discovered a mermithid parasite in a gyne (female reproductive) of *S. geminata*. This article reports our efforts to investigate the extent of mermithid parasitism in this species and to determine if the 2 other common species of *Solenopsis* sympatric with *S. geminata* in northern Florida, *S. invicta* and *S. (Diplorhoptum) pergandei* Forel, were also host to the same parasite.

Parasitism of ants by mermithid nematodes has received much attention for its sometimes profound anatomical effects on infected hosts. Such effects have provided clues to the developmental pathways of ant caste determination (Wheeler 1928, Vandel 1930, Passera 1976). Despite this attention, our knowledge of the general biology of ant-infecting mermithids is limited. The life cycle of the nematode has been completely determined in few cases (Bedding 1984), and there are no reports of population level effects on host ants.

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The ant-mermithid association best studied ecologically is that of *Pheromermis villosa* Kaiser and its hosts, the ants *Lasius flavus* Mayr and *L. niger* Mayr (see Kaiser 1986a, b, 1991). *P. villosa* emerges from its host in late summer, molts to the adult stage after 2 or 3 mo, and reproduces. Each female produces thousands of eggs. An intermediate host, an earthworm, is initially infected. The ants become infected when, as larvae, they consume earthworm muscle tissue containing the infective stage of the nematode. Life cycles of the parasite and its hosts are closely synchronized, and most infections occur when *Lasius* colonies are beginning to produce sexuals in late spring. *P. villosa* starts to grow when the host ant pupates. Infected *Lasius* reproductives are brachypterous and possess incompletely developed flight musculature, as well as distended abdomens. Infection alters the behavior of the host ants; infected individuals seek out moist locations when the parasites are ready to emerge. Infected *L. flavus* females may even submerge themselves in water if it is accessible.

Among ants of the genus *Solenopsis*, mermithid parasites have been reported 3 times. Gösswald (1930) found workers of the thief ant *S. (Diplo-rhoptum) fugax* Mayr parasitized by larval *Mermis* sp. Mitchell and Jouvenaz (1985) discovered 3 mm long larval mermithids in workers of the fire ant *S. geminata* in Alachua County, Florida. Jouvenaz and Wojcik (1990) reported that workers of 2 colonies of the black imported fire ant, *S. richteri* Forel, in Argentina were hosts to a 15 mm long mermithid, which also emerged from the host as a juvenile. Generally, only sexually mature, postparasitic mermithids can be identified. Neither of the mermithids previously found in fire ants has been cultured nor found again (D. Jouvenaz, USDA-ARS, Gainesville, FL, personal communication).

Materials and Methods

Colonies of *S. geminata*, *S. invicta*, and *S. pergandei* were assayed for the presence of mermithids. Ants were collected by spreading a thin layer of soil from the nest mound on the ground and aspirating a sample of sexuals. All males and gynes seen in the first 10–15 min were collected. In nests with many alates, collection was discontinued after obtaining ≈ 100 ants. Initially, workers were also collected. However, none of the 1st several hundred (407 of which were from *S. geminata* nests containing infected sexuals) were parasitized, so routine collection of workers was discontinued after July 1991. Because of the disruption caused by the sampling technique, colonies were not sampled repeatedly. In a few cases, alates were collected from the surface of their nest mounds during mating flight activities. Unless noted, only those ants collected from within nests are included in the analyses.

The thief ant, *S. pergandei* Forel, does not make nest mounds, but in the summer its nests can be

located by the crenelated soil formations created at the time of nuptial flights. *S. pergandei* males and gynes were collected during the summers of 1992 and 1993.

Most of the collecting was done in the northeastern part of the Apalachicola National Forest, 3–20 km south of Tallahassee, FL, a region known as the Munson Sandhills. Samples were taken on 29 July 1992 from *S. geminata* nests in a pasture at the Suwannee River near Mayo in Lafayette County, Florida. Reproductives were collected from *S. geminata* and *S. invicta* nests at the Archbold Biological Station, Highlands County, Florida, in mid-May 1993.

Vials of collected ants were placed in a thermos with ice and taken to the laboratory. The presence of mermithid parasites was determined by dissection or by allowing them to emerge while the host ants were confined in isolation in the laboratory. Often the mermithids could be seen through the cuticle of the ants where the sclerites were separated by the distension of the gaster. If a mermithid was visible, the ant was placed in a small petri dish or a test tube with 1–2 ml of water. The worms usually emerged within a day and were taken from the water and placed in a culture dish. If the ant died or no worm emerged after a few days, the ant was dissected in a dish of water or Ringer's solution under a dissection microscope. With fine forceps, the ant was held by the petiole and the gaster was torn open by pulling away one of the sclerites. The mermithids, which generally occupied most of the interior of the gaster, then uncoiled and moved about in the dish. Except in a few cases where the nematodes were either broken in the process of opening the gaster or less advanced in development (see below), dissection did not seem to adversely affect the parasites. Their survival was similar to that of worms which emerged from hosts on their own.

The lengths of 41 of the worms that emerged on their own from *S. geminata* hosts were measured to the nearest 0.5 cm while alive. The mermithids were straightened gently with forceps while in water in a clear plastic box over a scale.

Results

Mermithids occur commonly in *S. geminata* nests in the Apalachicola National Forest, and their presence coincides with *S. geminata*'s summer reproductive season. Mature gynes and males of *S. geminata* can be found in low numbers in late May and are numerous by mid-June. The earliest we found reproductives containing mermithids was 10 June (no mermithids were found in 150 gynes and 113 males collected from 12 colonies in late May and early June 1992, 1993). In all 3 yr sampled, 1991–1993, the incidence of parasitism of reproductives in *S. geminata* nests followed the same temporal pattern, increasing over the summer, so that by August, a majority of the col-

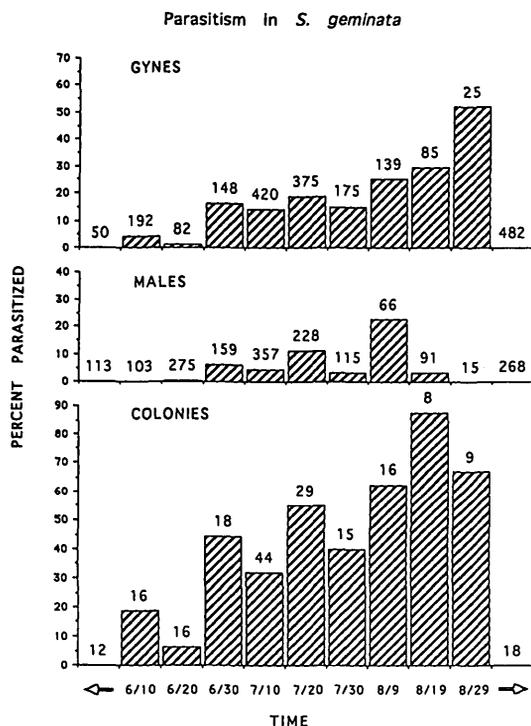


Fig. 1. Incidence of parasites in *S. geminata* gynes, males, and colonies in the Apalachicola National Forest. Data from 1991 to 1993 were combined. Data are grouped into 10-d periods, starting on the date under each bar. Number above each bar is the sample size. No mermithids were found in alates collected before 9 June nor after 8 September. Colony data include only colonies containing reproductives at the time of collection.

onies containing reproductives were host to nematode parasites (Fig. 1). The rate of infection among all *S. geminata* colonies did not increase significantly throughout the summer because fewer colonies contained reproductives as the season progressed (McInnes and Tschinkel 1995). Overall, more than 10% of the *S. geminata* reproductives collected in summer were parasitized (Table 1).

The abrupt decline in mermithid parasitism (Fig. 1) coincides with a major shift in the reproductive biology of *S. geminata*. In northern Florida, *S. geminata* produces 2 female reproductive morphs. Some colonies produce macrogynes in late spring and summer, and some colonies produce microgynes in the fall (McInnes and Tschinkel 1995). All of the colonies from which we collected mermithids were macrogyne-producing colonies. By the time microgynes were present in nests, in mid-September, neither type of *S. geminata* colony hosted mermithids (103 gynes and 61 males from 9 microgyne-producing nests and 379 gynes and 207 males from 9 macrogyne-producing nests collected after the 1st wk of September were examined).

Mermithids were also found in *S. geminata* alates collected near Mayo, FL. Four of the 9 nests

Table 1. Rates of parasitism

Host	Date of collection	% reproductives infected	
		Gynes	Males
<i>S. geminata</i>	1991	6.1% (589)	3.2% (342)
	1992	32.1% (212)	6.8% (352)
	1993	18.8% (840)	5.7% (715)
	Total	16.0% (1,641)	5.5% (1,409)
<i>S. invicta</i>	1991	0% (232)	0% (73)
	1992	0% (40)	2.7% (112)
	1993	0% (492)	6.6% (287)
	Total	0% (764)	4.7% (472)
<i>S. pergandei</i>	1992	2.3% (44)	1.1% (89)
	1993	5.7% (157)	1.8% (170)
	Total	5.0% (201)	1.5% (259)

Percentage of infected reproductives collected between 10 June and 8 September in the Apalachicola National Forest. Outside of this period, *S. pergandei* was not collected, and no mermithids were found in *S. geminata* nor in *S. invicta*. Sample sizes are in parentheses. For *S. invicta*, only data for the site where infected colonies were found is included (see text).

sampled contained parasitized reproductives. In total, 115 gynes and 105 males were examined from the 9 nests, and 4 ants of each sex were found to harbor nematodes. No mermithids were found in fire ants collected at the Archbold Biological Station. Only 4 of the *S. geminata* nests examined contained alates, and most of these alates were callow. None of the 18 *S. geminata* gynes or 44 males collected contained mermithids, nor did any of the 68 gyne or 147 male pupae reared to maturity in the laboratory.

A significant fraction of the infected *S. geminata* reproductives contained >1 mermithid (Table 2). More than 20% of the infected gynes and nearly 8% of the infected males contained 2 or more parasites. None of the males contained >2 worms; however, gynes were found to contain as many as 5. Uncoiled, the parasite is much longer than its host, up to 15 times as long. Worms that emerged from *S. geminata* gynes were larger than those from males. Those from gynes averaged 11.4 cm (0.4 cm SE, $n = 23$). The mean length of those from males was 7.9 cm (0.6 cm SE, $n = 18$; ANOVA: $F = 27.4$; $df = 1, 39$; $P = 0.0001$).

In June and July (1993), 11 dissected *S. geminata* ants contained smaller (0.5–4 cm) and nearly

Table 2. Numbers of parasites in *S. geminata* reproductives

No. mermithids per host	No. (%) of host ants	
	Gynes	Males
1	209 (79.8%)	71 (92.2%)
2	42 (16.0%)	6 (7.8%)
3	8 (3.1%)	0
4	2 (0.7%)	0
5	1 (0.4%)	0

Shown is the number of *S. geminata* reproductives of each sex containing ≥ 1 mermithid parasites. Data from 1991 to 1993 were combined. Dates of collection and number of reproductives examined are the same as in Table 1.

transparent mermithids. These were probably less developed individuals of the same mermithid species. Apparently their cuticles were quite permeable, because these worms quickly ruptured upon contact with water. Water had no detrimental effects on the parasites which emerged from their hosts naturally. The smaller and more transparent mermithids were found in adult ants and advanced pupae, indicating that the main period of growth of this parasite comes after eclosion of the host ant. Microscopic examination of squashes of 40 large *S. geminata* sexual larvae from infected colonies yielded no nematodes.

Mermithids were also found in males of the exotic fire ant *S. invicta* and in males and gynes of the thief ant, *S. pergandei* (Table 1). The seasonal pattern of parasitism in *S. invicta* appears to be the same as in *S. geminata*. Dissections were performed on 100 *S. invicta* alates of each sex collected from 15 colonies before 10 June and 183 gynes and 40 males collected from 12 colonies in late September and October 1992. These ants were collected from the same area in which infected *S. invicta* colonies were found in the summer, but all were free of mermithids. Reproductives of *S. pergandei* were collected only during early and mid-summer.

All of the parasitized *S. invicta* ants were collected from colonies located within a few hundred meters of one another. *S. invicta* colonies from other areas of the Apalachicola National Forest were apparently free of mermithids, including colonies in other areas of the Munson Sandhills region found as close as 10 m to parasitized *S. geminata* colonies. The *S. pergandei* hosts were collected at several sites in the Apalachicola National Forest, all within 40 m of parasitized *S. geminata* colonies. For both *S. geminata* and *S. pergandei*, nematode parasitism was found at every Munson Sandhills site sampled. None of the *S. invicta* reproductives (120 gynes and 180 males from 10 nests) collected at the Archbold Biological Station contained nematodes.

Aside from distension of the gaster, there were no outward signs of parasitism in the host ants. This is probably because the nematode has few strong effects until after eclosion of the ant. Internally, the parasites occupied most of the space within the gaster. The reproductive structures of the host individuals were almost always underdeveloped and usually only vestigial. In gynes, the contents of the crop appeared watery, whereas normally they are oily. The flight musculature, wings, and ocelli, which are sometimes affected by mermithid parasitism (Wheeler 1928, Vandel 1930, Passera 1976), appeared normal in host individuals of all 3 ant species. In 2 *S. geminata* males, the worms were not contained entirely in the gaster; they extended through the petiole and into the thorax. In 1 *S. invicta* male, the worm extended from the abdomen, through the thorax, and into the head.

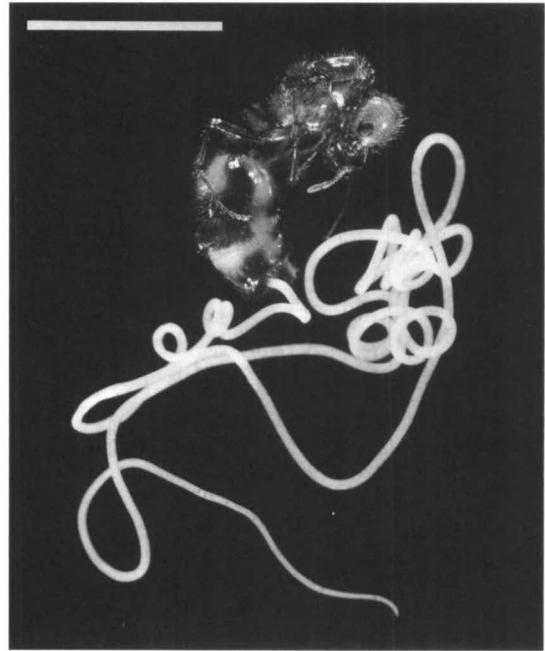


Fig. 2. Mermithid emerging from a *S. geminata* gyne. Scale bar = 5.0 mm.

Five parasitized workers were detected. These were conspicuous within their nests at the time of alate collection because of their swollen gasters. All 5 were *S. geminata* majors. One contained 2 mermithids, whereas the other 4 each contained 1. Like the alate hosts, the parasitized workers appeared normal except for a distended gaster. The mermithids emerging from the workers were indistinguishable from those from gynes and males.

Emergence from the host took nearly 1 h each of the 3 times it was observed from start to finish (with the aid of a video camera). The mermithid exits its host between 2 sclerites (Fig. 2), but the location of the exit hole varied from ant to ant. One worm failed to completely exit its male *S. invicta* host. Dissection revealed that part of this worm was folded and lodged in the post petiole of the ant. The host ant always died within a few hours of mermithid emergence.

Parasitized ants do not participate in mating flights. Of 384 gynes and 307 males collected from the surface of *S. geminata* nest mounds during mating flights, none were parasitized, nor were any parasitized ants detected during extensive alate trapping of *S. geminata* and *S. invicta* nests in the Munson Sandhills (McInnes 1994, McInnes and Tschinkel 1995). Two parasitized *S. geminata* gynes were collected while they were walking on the ground, indicating dispersal may occur on foot. One of these was only 2–3 m from a nest mound. The other was collected at a pond margin, ≈40 m from the nearest *S. geminata* nest. The successful emergence of mermithids while the host ants are still within the nest seems unlikely—those emerg-

ing in laboratory nests ($n = 14$) were quickly destroyed by workers.

Culture of the nematodes was attempted in water and on damp sand. Worms placed in petri dishes containing water usually died in <1 wk. Even on sterilized sand, many of the worms apparently succumbed to fungi. Lower mortality was achieved by using Fungusguard (Tetra, Melle, Germany), a fungicide used to treat aquarium fishes (1.25 ml/liter H_2O), to wet the sand. Molting does not occur until ≥ 3 mo after emergence at $24^\circ C$, and few of the mermithids have survived to maturity (mortality was typically 5–10%/wk). All of the survivors were female (G. Poinar, University of California, Berkeley, personal communication). According to W. Nickle (USDA, Beltsville, MD, personal communication), these mermithids do not belong to the genus *Allomermis*, but male specimens are needed for further identification.

Discussion

Little is known of the life cycle of this mermithid, but the seasonality of its appearance in nests and finding the less developed individuals only in June and July suggest that the life cycle of the parasite is tied closely to that of at least 1 of its hosts, *S. geminata*. Summer mating flights in *S. geminata* typically begin in June, peak in midsummer, and taper off as the season progresses. Most nests lack reproductives by late summer, when the incidence of parasitism drops to zero (Fig. 1). *S. pergandei* nests contained alates from late spring to late summer, but nothing more of their reproductive cycle is known. Alates can be seen in *S. invicta* nests all year round (Morrill 1974, Tschinkel 1993), but mermithid parasitism of this species seems to occur only during the summer reproductive period of *S. geminata*. The discreet seasonality of host infection and the long maturation period of emerged juveniles indicate that this parasite possesses a generation time of 1 yr or possibly longer.

The parasite load on macrogyne-producing colonies may have played a significant role in the evolution or maintenance of the reproductive polymorphism exhibited by the Apalachicola National Forest population of *S. geminata*. The majority of alates in this population are males and microgynes released by colonies in the fall (McInnes and Tschinkel 1995). Interestingly, the infection of reproductives by mermithids is limited to macrogyne-producing colonies reproductively active in summer. The lack of parasitism in *S. geminata* fall reproductives cannot be explained by body size—microgynes are larger than *S. geminata* and *S. invicta* males and both sexes of *S. pergandei*, and fall males are the same size as *S. geminata* summer males and larger than both sexes of *S. pergandei*. Delaying their reproductive season allows colonies producing sexuals in the fall to escape the considerable selective pressure of mermithid parasitism.

As an exotic species, *S. invicta* may have escaped many of the parasites and pathogens native to its South American homeland (see Jouvenaz 1986, Porter et al. 1992). The occasional presence of mermithids within *S. invicta* males may be the case of a parasite of the native ants *S. geminata* and *S. pergandei* adapting to a new host. This hypothesis is consistent with the increasing incidence of parasitism in *S. invicta* from 1991 to 1993. Jouvenaz et al. (1977) concluded that a microsporidian, which normally parasitizes *S. geminata*, has also developed the ability to infect *S. invicta*. All of the parasitized *S. invicta* ants were collected at a site near the Public Dove Field in the Apalachicola National Forest (9–10 km southwest of the Tallahassee Regional Airport). This area contains both *S. invicta* and *S. geminata*, but the infected *S. invicta* colonies were isolated from the native fire ants by ≈ 100 m of scrubby forest. Other *S. invicta* colonies closer to infected *S. geminata* colonies in this and other areas, were free of mermithids. Whether this is a case of localized adaptation on the part of the nematodes or whether the interaction is mediated by some historical or environmental factor is unknown.

The difference in the incidence of mermithids in *S. geminata* and *S. invicta* is in the percentage of females infected. Parasitism is absent or very rare in gynes of *S. invicta*, but common in gynes of *S. geminata*. In the summer of 1992, nearly 1 in 3, and in 1993 nearly 1 in 5, *S. geminata* gynes were parasitized. Estimates of infection rates may be biased if parasitism affects the length of tenure of the host ant within the nest. Whether nest tenure in *Solenopsis* is affected by mermithid parasitism is unknown, but such effects might be expected considering infected reproductives do not participate in mating flights. Our observations of mermithid parasitism of *S. geminata* gynes indicate somewhat higher infection rates than Crawley and Baylis (1921) reported for *Lasius* in England; 1 in 12 gynes harbored mermithids in their study.

Solenopsis invicta has displaced *S. geminata* from many sites in the southeastern United States (Hung and Vinson 1978, McInnes 1994, Wojcik 1994). Although many factors could influence the interactions of these ants (McInnes 1994) and the incidence of mermithid parasitism across the former range of *S. geminata* is unknown, the high rate of parasitism and its consequential drain on reproductive output may have played an important role in the displacement of *S. geminata* by giving *S. invicta* an advantage in reproductive potential.

The mermithids collected from all 3 *Solenopsis* species were similar in structure, size, and seasonality and presumably belong to the same species. As is typical of mermithid nematodes, they emerge from their hosts as juveniles and must molt before attaining sexual maturity. Although the mermithid we have discovered in northern Florida is not yet identified, its large size precludes it from belonging to any of the species previously collected in *Sole-*

nopsis. The mermithids observed in *Solenopsis* by Gösswald (1930), Mitchell and Jouvenaz (1985), and Jouvenaz and Wojcik (1990) were all an order of magnitude smaller than what we have found. Given the consistent and high rate of occurrence of this mermithid, the prospects are good for its future identification or description.

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