First fossil record of nematode parasitism of ants; a 40 million year tale

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SUMMARY

A mermithid nematode emerging from a male ant, *Prenolepis henschei* Mayr, in Baltic amber is the first fossil record demonstrating nematode parasitism of ants. This parasite, described as *Heydenius formicinus* sp. n., is compared to extant mermithid parasites of ants, especially *Allomermis myrmecophila* Baylis 1921. The present fossil, together with earlier reports of braconid and mite parasitism of ants in Baltic amber, indicates that several diverse groups had already evolved parasitic associations with ants by the Eocene.

Key words: fossil Mermithidae, Baltic amber, ant parasitism.

INTRODUCTION

Nematodes of the family Mermithidae (Mermithida: Nematoda) parasitize a wide range of arthropods today, including social insects (Poinar, 1975). Ants are one of the host groups attacked by these parasites and the morphological changes caused by the nematodes have attracted wide attention (Wheeler, 1928). While several mermithids have been described from extant ants (Table 1), no fossil evidence of this association has been reported up to the present.

This study records the first fossil record of ant parasitism by mermithid nematodes and demonstrates a juvenile mermithid emerging from an alate male ant in Baltic amber. The parasite is described in the fossil genus *Heydenius* Taylor 1935 and the association is discussed in relation to extant ant–mermithid relationships.

MATERIALS AND METHODS

The piece of light brown amber containing the parasitized ant originated from the Kaliningrad Region in Russia. Characteristic oak hairs were present in the amber and tests indicated that the specimen was genuine (Poinar, 1982). The amber was re-cut and polished in order to better view the specimen. The final piece of amber weighed 0·8 g, had a greatest length of 24 mm, greatest width of 14 mm and greatest depth of 5 mm. Baltic amber has been dated at approximately 40 million years (Eocene) (for a discussion of the age of these deposits, see Poinar, 1992). Observations and photographs were made with a Nikon Optiphot microscope and a Nikon SMZ-10 stereoscopic microscope.

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RESULTS

The fossil assemblage consists of a mermithid emerging from a male ant of the genus *Prenolepis*. On the basis of size and other characters, the host has been identified as *P. henschei* Mayr 1868. Since the mermithid is obviously a juvenile and lacks adult characters required to place it in an extant genus, it is described below in the fossil mermithid genus *Heydenius* Taylor 1935. This genus was established for fossil mermithids that could not be placed in extant genera due to the lack of, or obstruction of, pertinent characters. It has been proposed that this genus be limited to fossil mermithids from the Tertiary period, and the genus *Cretaciomermis* Poinar (2002) for Cretaceous forms.

Systematics

Mermithidae Braun 1883.
Heydenius Taylor 1935.
Heydenius formicinus n. sp. (Figs 1–2).
Specimen partially emerged from host ant; length of body outside ant host = 8 mm; body colour white in reflected light; greatest body width = 207 μm; width of body at head = 90 μm; head rounded, semi-hemispherical; mouth opening subterminal; cuticle smooth but body surface wrinkled and folded (artifact of preservation).
Comments: While the length of the fossil cannot be established since part of it still resides within the ant, it can be estimated on the basis of body thickness that approximately half of the nematode has emerged. This would provide a value of about 16 mm for the total length of the parasite. A comparison of the length and width dimensions of the fossil with that of the 4 extant ant mermithids (Table 1) places *H. formicinus* n. sp. closest to *Allomermis myrmecophila* Baylis 1921 although the values of the former are

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Table 1. Length/width measurements of Mermithidae described from ants

Mermithid	Hosts	Length (mm)/width (μm)	Reference
Allomermis lasiusi Rub.	*Lasius niger*	53/750	Rubstov (1970)
A. myrmecophila Baylis	*L. alienus*	20–50/300–600	Crawley & Baylis (1921)
	L. flavus, *L. niger*		
Camponotimermis bifidus Ipateva *et al.*	*Camponotus aethiops*	44–61/380–806	Ipateva *et al.* (1990)
Heydenius formicinus sp. n.	*P. henschei* Mayr	16/207	Present study
Pheromermis villosa Kaiser	*L. flavus*, *L. niger*	23–52/430–600	Kaiser (1986)

Fig. 1. *Heydenius formicinus* n. sp. emerging from the ant, *Prenolepis henschei* in Baltic amber. Arrow shows oak trichome adjacent to ant.

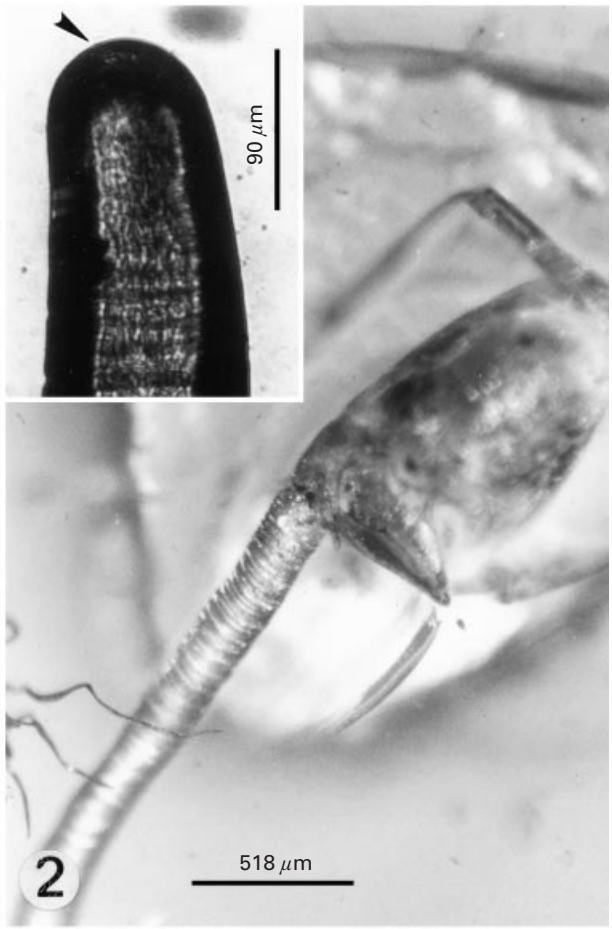

Fig. 2. Detail of exit area of *Heydenius formicinus* n. sp. through the anus of the ant, *Prenolepis henschei*, in Baltic amber. Insert shows anterior portion of mermithid with fleche denoting mouth opening.

somewhat less than the minimum values of the latter. Of course, size has little to do with systematic position and *H. formicinus* n. sp. could belong to a completely separate clade. Two characters that separate the fossil from the extant mermithids listed in Table 1 are the semi-hemispherical head (the others have a more pointed head) and a subterminal mouth opening (the others have the mouth opening shifted considerably further ventrad). All of the extant mermithids in Table 1 are represented only by females that develop fertile eggs in the absence of males. This suggests that *H. formicinus* n. sp. may also be a female if autotoky had developed that early in mermithid clades parasitizing ants.

Type specimen: Deposited in the Poinar amber collection (N-3-52) maintained at Oregon State University, Corvallis, OR.
Host: Alate male of *Prenolepis henschei* Mayr 1868.
Etymology: The specific name 'formicinus' is Latin for 'of ants'.

DISCUSSION

According to Wheeler (1915), *P. henschei* is one of the commonest ants in Baltic amber and is considered to be closely related to the present day *P. nitens* of Southern Europe and *P. imparis* of North

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America. Wheeler (1915) commented that *P. imparis* makes small colonies with nests in damp soil and shady areas but is arboreal in habit, preferring oak trees. The workers feed on sweet liquids from plant sources or honeydew from homopterous insects (Creighton, 1950). It is interesting that adjacent to the parasitized fossil ant is an oak trichome, suggesting a similar ecotype in the amber forest.

While there are no extant records of mermithid parasites of *Prenolepis* species, mermithids do occur in the closely related genus *Lasius* (Poinar, 1975; Wheeler, 1928). Crawley & Baylis (1921) describe the behaviour of *A. myrmecophila* from *Lasius* spp. in Great Britain and noted that upon emergence, the parasite always exited through the anus or pierced the integument just below the anus. The fossil mermithid exhibits a similar behaviour. Only mature or nearly mature extant mermithids exit their host, so it is assumed that *H. formicinus* n. sp. was probably fully or nearly fully developed. An early emergence may have occurred when the host became immersed in the resin, but a certain degree of maturity would have been necessary for this to occur.

Crawley & Baylis (1921) supposed that *A. myrmecophila* emerged after the host ants left the nest, since they observed that worker ants would attack newly emerged nematodes in the colony. The male of *P. henschei* in amber obviously had left the nest. Crawley & Baylis (1921) also noted that reduced wings and an enlarged abdomen were obvious external symptoms of mermithid parasitism while the thorax was devoid of flight muscles and parasitized alates could not fly. A comparison of the ratio of the wing length with the distance from the wing insertion to the tip of the abdomen between the male *P. henschei* illustrated by Mayr (1868) and the male fossil gave a value of 0·66 for the former and 0·84 for the latter. The greater wing/body ratio in *H. formicinus* n. sp. could be the result of parasitism. Unfortunately, without opening the thorax of the fossil ant, there is no way to determine if the parasitized *P. henschei* had the power of flight.

Crawley & Baylis (1921) observed that after emergence of the nematode from the ant, the host's abdomen was essentially empty. In the fossil ant, the anterior part of the abdomen is collapsed as a result of the parasite having partially emerged, while the posterior portion is distended from the body of the nematode still remaining in the host.

The present find is the third report of fossil parasitism in ants, all in Baltic amber. The first, made by Wheeler (1915), involved a parasitic mite attached to the leg of a worker *Lasius schiefferdeckeri* Mayr. The second was a neoneurine braconid larvae emerging from a worker of the same ant species (Poinar & Miller, 2002). It is obvious that by the Eocene, diverse groups had evolved parasitic associations with ants, which have persisted, without much apparent change, to the present.

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