

## FOSSIL EVIDENCE OF NEMATODE PARASITISM

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Fossil remains of nematodes are quite rare. This is due to the nematode's lack of hard parts and subsequent rapid deterioration before preservation can be initiated. Nevertheless, fossil remains of microbotrophic, plant parasitic and animal parasitic

nematodes do exist. The following discussion reviews the occurrence of fossil parasitic nematodes. A distinction is made here between historic and pre-historic finds (less than 1 million years of age) and fossil specimens (greater than 1 million years).

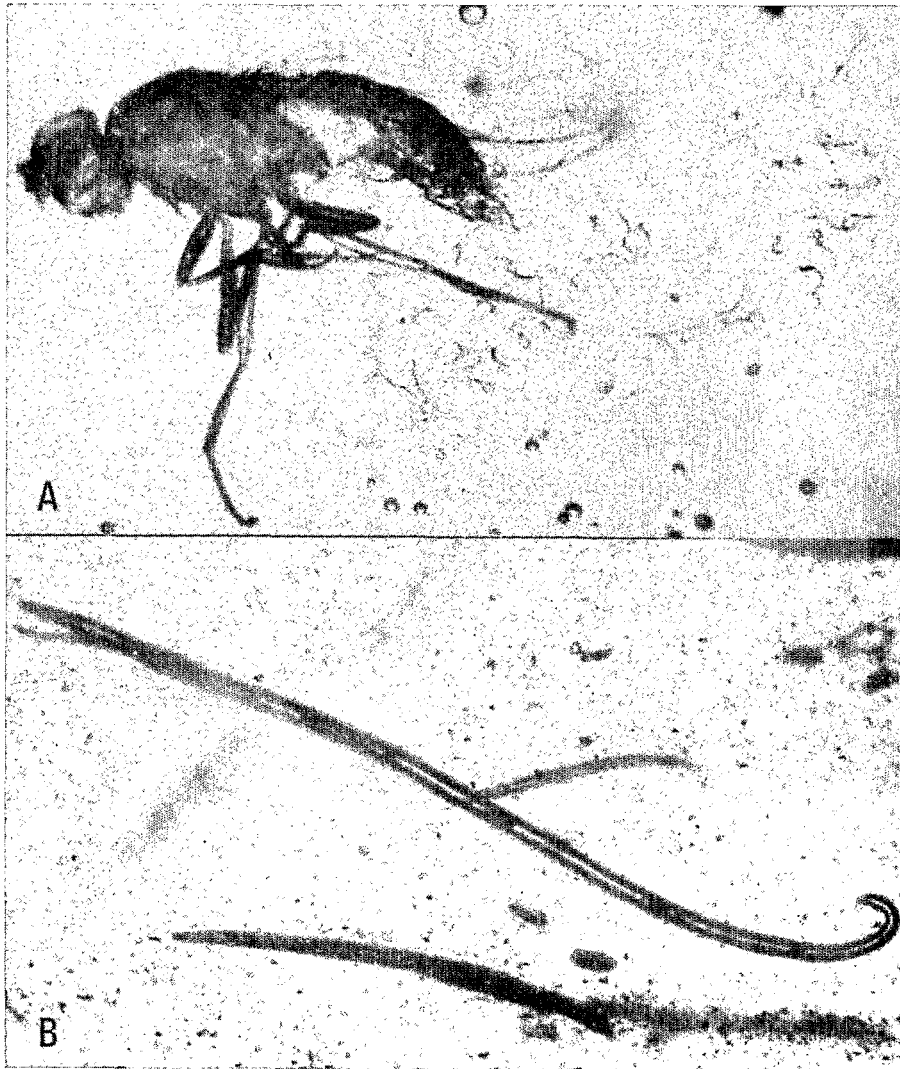


Fig. 1. A : Adult fruit fly (*Drosophila* sp., Diptera) and associated third and fourth stage juvenile allantonematids in a piece of Dominican amber ( $\times 80$ ) ; B : Male and other stages of *Oligaphelenchoides atrebora* Poinar, a mycetophagous aphelenchoidid from Mexican amber ( $\times 180$ ).

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True fossils of parasitic nematodes exceeding a million years in age have for the most part been recovered from amber. This fossilized resin varies in age and composition depending on its source and geographical location. All amber sources that contain parasitic nematodes are roughly either 25 million years old (Dominican and Mexican amber) or 40 million years of age (Baltic amber).

There are no records of vertebrate parasites in this age category. Several records include insect parasitism by Mermithidae. The first of such reports is attributed to von Heyden (1860, 1862) who described the mermithid, *Mermis antiqua* projecting from the anus of the cerambycid beetle, *Hesthesis immortua* Heyden. The species was transferred to the collective fossil mermithid genus *Heydenius* Taylor, 1935 (see also Dollfus, 1950). This specimen was collected in Rhine lignite of the Eocene.

There are two pieces of Baltic amber, each with a midge parasitized by a mermithid nematode, in the Copenhagen amber collection (Larsson, 1978). Neither of these specimens has been described in detail and due to their degree of preservation, the present author could only identify them as members of the family Mermithidae.

During an examination of the Copenhagen collection, the present author noted a third piece of amber containing a mermithid still coiled up in the abdomen of an adult midge (Fig. 2 A). This specimen was collected in Samland in 1900.

An interesting photograph of a mermithid leaving its adult chironomid host in Baltic amber was presented by Schlee and Glöchner (1978). An unusual aspect of this association is that the midge is an intersex, a condition known to be brought about by mermithid parasitism.

Recently a piece of amber from the Dominican Republic was found by the present author to contain the first fossil evidence of insect parasitism by members of the Tylenchida. This piece of amber contained an adult drosophilid fly (Drosophilidae: Diptera) which had been parasitized by nematodes of the family Allantonematidae. Around the parasitized fly were 120 nematodes that had obviously left the host soon after it had become entrapped in the sticky resin (Fig. 1 A). Some nematodes were in the process of emerging from the fly's abdomen and others were adjacent to the body and wings of the host (Fig. 2 B).

The entrapped insect apparently dragged itself through the resin for several millimeters before expiring. This is revealed by a wide trail of nematodes behind it (Fig. 1 A).

In the life cycle of a typical allantonematid, infection is initiated by a fertilized free-living female. After penetrating into the body cavity of the juvenile

stage of the host, the parasite matures and egg development is initiated. Development of the nematodes continue through the various host stages (larva, pupa, adult) and by the time the imago emerges, most of the nematodes are in the third and fourth juvenile stages.

Fourth stage juvenile exit via the alimentary or reproductive tract and enter the environment where they mature to the adult stage and mate.

In the present fossil specimen, the abdomen of the struggling fly had ruptured and both third and fourth stage juveniles had emerged.

There is no indication in any of the above examples that the parasite or the parasitic relationship differs from present day associations. Thus the mermithids and allantonematids were well established as groups in the mid-tertiary and their origin obviously extends well before that period.

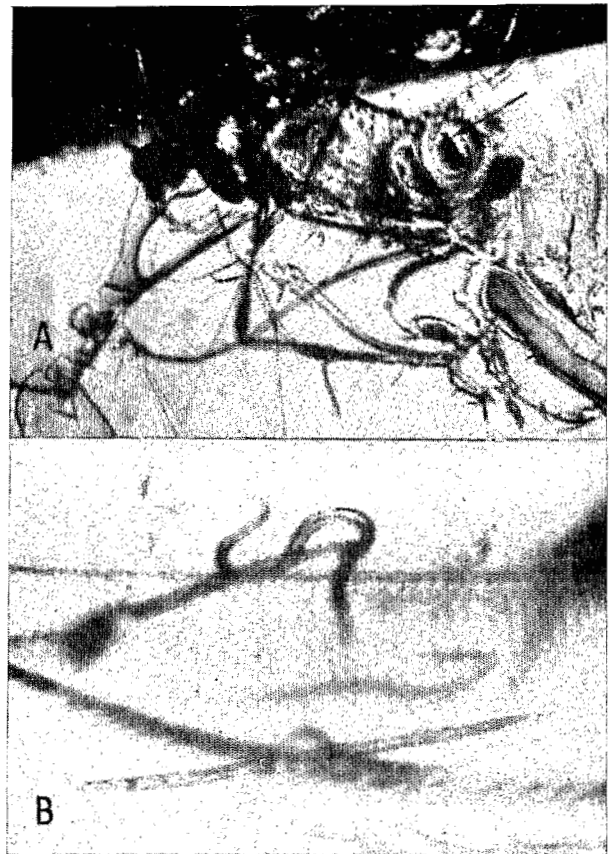


Fig. 2. A : Adult midge with a coiled mermithid nematode (arrow) in its abdomen. (From the Copenhagen collection of Baltic amber at the Zoological Museum. Courtesy of S. L. Tuxen. Photo by G. Brovad,  $\times 60$ ); B : Detail of two fourth stage juvenile allantonematids that crawled out of the body cavity of a drosophilid fly in Dominican amber ( $\times 450$ ).

These third and fourth stage juveniles ranged in length from 140 to 240  $\mu\text{m}$  and were 6-8  $\mu\text{m}$  in width. These dimensions overlap with those of the third and fourth stage juveniles of *Parasitylenchus diplogenus* Welch, 1959, which have been described from recent drosophilid flies in Great Britain.

The only fossil plant parasitic nematode described is *Oligaphelenchoides atrebora* Poinar, 1977, from Mexican amber (Fig. 1 B). This form resembles a modern day *Aphelenchoides* or *Bursaphelenchus* and was considered to be mycetophagous in habit (Poinar, 1977).

In conclusion, fossil remains of parasitic nematodes, are limited to invertebrate and fungal parasites. Mermithid nematodes constitute the largest single group of fossil parasites, with single examples of an allantonematid, a mycetophagous aphelenchoidid and an unknown nematode encysted in the muscles of a beetle (Voigt, 1957).

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Accepté pour publication le 13 juillet 1983.