

Earliest fossil nematode (Mermithidae) in cretaceous Lebanese amber

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Summary – A mermithid nematode (Nematoda : Mermithidae) from Lebanese amber represent the oldest definite fossil nematode. The specimen is assigned to a new species, *H. libani* sp. n. in the extant genus, *Heleidomermis* Rubstov. This specimen is still coiled inside the abdomen of its insect host, an adult biting midge (Diptera : Ceratopogonidae). This association represents the oldest known example of animal-animal internal parasitism in a terrestrial environment. The find demonstrates the antiquity of mermithid nematodes and establishes mermithid parasitism of the lower Diptera some 120-135 million years ago.

Résumé – *Le plus ancien nématode fossile (Mermithidae) trouvé dans un ambre du Crétacé, au Liban* – Un nématode Mermithidae inclus dans de l'ambre provenant du Liban représente le plus ancien nématode fossile connu. Ce spécimen est assigné à l'espèce nouvelle *H. libani* sp. n., appartenant au genre, encore actuel, *Heleidomermis* Rubstov. Ce nématode est enroulé à l'intérieur de l'abdomen de l'insecte hôte, une similie adulte (Diptère : Ceratopogonidae). Cette association représente, en ce qui concerne l'environnement terrestre, le plus ancien exemple connu de parasitisme interne d'un animal envers un autre animal. Cette trouvaille démontre l'ancienneté des nématodes Mermithides et fait remonter leur parasitisme envers les Diptères inférieurs à quelque 120-135 millions d'années.

Key-words : Fossil nematode, Mermithidae, fossil parasitism, biting midge, Ceratopogonidae.

Up until the present, the earliest known definite fossil nematodes have been reported from Eocene Baltic amber (40 million years) or Rhine lignite from the same Epoch (Taylor, 1935; Dollfus, 1950; Poinar, 1977, 1984). Reports of earlier nematodes from the Paleozoic are doubtful since the fossils do not compare morphologically with any known extant groups of nematodes (Stormer, 1963; Schram, 1973; Arduini *et al.*, 1983).

A fossil mermithid nematode is described here from Lebanese amber dating from the early Cretaceous. This specimen represents not only the oldest known nematode, but also provides the earliest record of terrestrial animal-animal internal parasitism.

Because of its scientific importance, this nematode will be described below, on the basis of morphological characteristics and host type, in the extant genus *Heleidomermis* Rubstov. The size, shape and location of the specimen clearly place it in the family Mermithidae.

Materials and methods

The amber containing the fossil nematode originated from beds located between Jezzine and Dar-al-Baidhar in the southern portion of Lebanon. At those sites, the amber occurs in primary deposits of the Neocomian division of the Early Cretaceous as well as in secondary deposits of the Neocomian and Aptian stages. These

deposits are dated from 120 to 135 million years (Schlee & Dietrich, 1970; Schlee & Glöckner, 1978).

The amber was washed in water and the piece was hand polished by rubbing it against wet emory paper and then on a clean towel containing caesium oxide. The piece of amber containing the fossil nematode is designated as JS 404 and is deposited in the Acra collection of Lebanese amber maintained by Fadi Acra.

Heleidomermis libani sp. n.

(Figs 1, 2)

There can be no doubt of the parasitic nature of this specimen since it is coiled up in the abdominal cavity of an adult female biting midge (Ceratopogonidae : Diptera). The abdomen of the midge is partly missing (probably from the host struggling to free itself from the sticky resin) thus the nematode is clearly seen. The fossil is interpreted as a postparasitic juvenile female in the process of molting since the posterior portion of the shed cuticle clearly is visible. Cuticle smooth, lacking cross fibers. Length = 6.0 mm.; greatest width = 120 μ m. Head broadly pointed; tail bluntly rounded; tail appendage absent. The length suggests that the specimen is a female.

The host family, the characteristic of the final molt occurring in the host, the absence of cross fibers in the



Fig. 1. Postparasitic juvenile of *Heleidomermis libani* sp. n. inside the abdomen of a biting midge (Ceratopogonidae) in Cretaceous Lebanese amber (specimen No. JS 404).

cuticle and the lack of a tail projection on the postparasitic juvenile cuticle are collectively characters that only occur in extant members of the genus *Heleidomermis* Rubstov, 1970. Thus, the fossil specimen is placed in this genus. Of course, it is quite possible that when and if additional material is obtained, the specimen should be transferred into an extinct genus, but at present, there are no morphologically distinct characters which differ from those found in the genus *Heleidomermis*.

The few dimensions obtained from *H. libani* sp. n. fall within the range of *H. vivipara* Rubstov, 1970 females whose length varies from 5.2-6.8 mm (6.0 mm in *H. libani* sp. n.) and width from 113-121 μ m (120 μ m in *H. libani* sp. n.). A comparison of the fossil species with the currently known extant species of *Heleidomermis* is shown in Table 1.

Aside from a more pointed head and tail in *H. vivipara* and *H. ovipara* Rubstov, 1974, there are no distinct morphological differences between the fossil and both of these extant species. However, the fossil is described as a

separate species since it is highly unlikely that, even with a morphologically conservative group like the nematode, a single species could survive for over 100 million years.

Although members of the genus *Heleidomermis* normally parasitize biting midge larvae, Poinar and Mullens (1987) reported adult *Culicoides variipennis* (Coquillett) containing developing stages of *Heleidomermis magnapapula* Poinar & Mullens, 1987 in California. This explains the presence of the mermithid fossil inside an adult biting midge.

Discussion

The present find represents the oldest, definite record of a fossil nematode and the oldest example of animal-animal internal parasitism in a terrestrial environment. Previously, the oldest known example of this phenomenon was parasitic mites attacking adult biting midges (Ceratopogonidae) in Canadian amber (Poinar *et al.*, 1993).

Poinar (1983) speculated that the Mermithidae arose in the Triassic from microbotrophic members of the Dorylaimida. By showing that mermithid parasitism was well established in lower Diptera by the Early Cretaceous, this find does not invalidate this earlier supposition. Although the earliest known lower Diptera occur in Triassic deposits, the Ceratopogonidae, as we define them today, first appear as fossils in Lebanese amber (Poinar, 1992). Clearly both biting midges and mermithids are older than these deposits. The present study shows that biting midges, themselves blood parasites of vertebrates, have been plagued by mermithid nematodes for over 100 million years, demonstrating a remarkable example of co-evolution in a host-parasite association.

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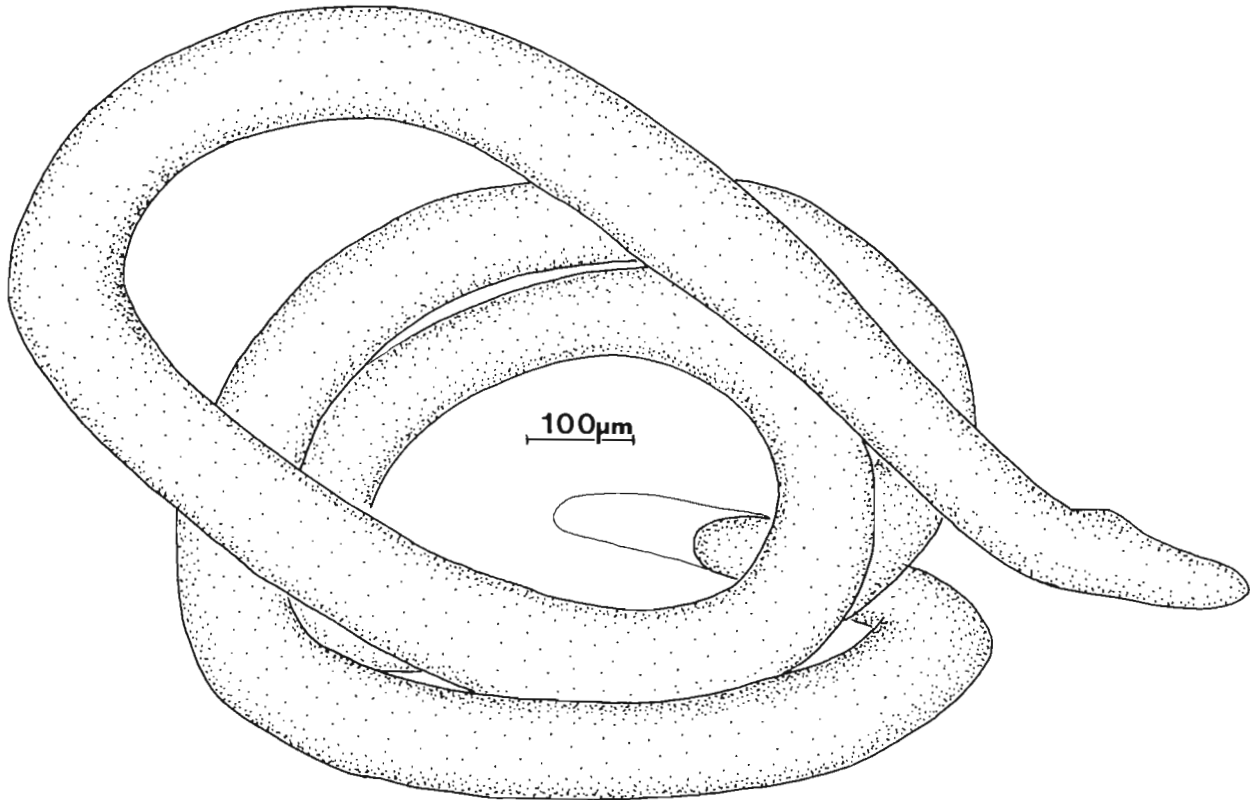


Fig. 2. Lateral view of *Heleidomermis libani* sp. n. in the abdomen of a biting midge (*Ceratopogonidae*) in Cretaceous Lebanese amber (specimen No. JS 404).

Table 1. A comparison of characters of the Cretaceous fossil mermithid *Heleidomermis libani* sp. n. with extant species in the genus.

Species	Length female (mm)	Width female (μm)	Postparasitic tail appendage	final molt in host	Host
<i>H. magnapapula</i> Poinar & Mullens, 1987	9.0-14.0	107-164	absent	+	biting midge
<i>H. ovipara</i> Rubstov, 1974	5.0-12	120-130	absent	+	biting midge
<i>H. libani</i> sp. n.	6.0	120	absent	+	biting midge
<i>H. vivipara</i> Rubstov, 1970	5.2-6.8	113-121	absent	+	biting midge

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