George O. Poinar, Jr.

6 Palaeontology of nematodes

6.1 Introduction

Despite their biodiversity and large numbers, fossil nematodes are quite rare, mainly because the great majority of nematode life stages are small and delicate and not prone to fossilization or detection. In addition, the preservation potential of animal and plant parasites is quite problematic, and even if they were preserved, they normally would not be recognized.

Some types of fossilization, especially amberization, preserve soft-bodied organisms such as nematodes, especially those parasitizing or associated with insects. Tertiary and Cretaceous amber contains a modest selection of nematode fossils, and nematode body and trace fossils also occur in various sedimentary deposits. A brief account of the various types of fossilization is presented below.

6.2 Types of nematode fossils

6.2.1 Amber

Amber is a fossilized resin that preserves a wide range of organisms, from microbes to vertebrates. As amber is fossilized tree resin, the range of organisms it traps is largely composed of forms that live in, on, under or around the resin-producing source tree. The preservative qualities of resin are well known, even to the ancient Greeks and Egyptians, who used them to prevent wine from fermenting and to preserve corpses. Through a combination of inert dehydration and chemical fixatives in the resin, a range of biota can be preserved in life-like form (Poinar 1992, Poinar & Milki 2001). Another advantage of amber is that it can be easily trimmed with a saw and further sanded and polished to obtain a clear view of small objects like nematodes. Amber has captured a number of parasitic nematodes emerging from arthropods freshly caught in the resin, as well as free-living nematodes associated with the bark. Ages of the various amber deposits are listed in Tab. 6.1.

6.2.2 Sedimentary or rock fossils

An example of this type of fossilization, which resulted in the superb preservation of soft-bodied microorganisms including nematodes, is the Early Devonian Rhynie Cherts in Scotland. These 400 million year-old deposits were produced from hot springs and geysers that deposited silica in an opaline form called sinter around the fault zones. Silica molecules enter cells of organisms by permineralization and can provide excellent preservation of the internal tissues of small organisms such as nematodes.

6.2.3 Trace fossils

Trace fossils are defined as any fossils showing the activity or growth of an organism. Those attributed to nematodes consist of trails or tracks left when movement occurs on a high viscosity surface. Sinuous, sinusoidal or traveling wave trails attributed to nematodes have been recorded in Mesozoic deposits, and it is possible (but not certain) that some of those attributed to the form genus *Cochlichnus* Hitchcock (Hantzschel 1975) were made by nematodes.

Other possible nematode trace fossils are holes in foraminifera that resemble borings made by extant nematodes (Sliter 1971).

6.2.4 Coprolites

Eggs and other parasite stages of nematodes can occur in petrified coprolites. Care should be taken to make certain that the nematode stages recovered are not attributable to free-living, coprophagous nematodes that entered the dung after it was deposited. Human coprolites may contain a range of nematode stages, however, nematodes associated with human and animal remains during historic times are not covered here.

Tab. 6.1: Age of amber deposits containing fossil nematodes.

Deposit	Location	Approximate age (million years)
Lebanese, Jordanian	Middle East	130–135
Burmese	Burma (Myanmar)	97–105
Baltic	Northern Europe	40–50
Dominican	Hispaniola	15–40
Mexican	Chiapas	22–26

6.3 Systematics of fossil nematodes

Due to its state of preservation, it is often impossible to assign a fossil nematode to an extant group. To cope with this problem, collective form genera have been proposed. For instance, the genus *Heydenius* Taylor (1935) was proposed for fossil members of the family Mermithidae that could not be assigned to extant genera. This genus was later restricted to Tertiary records and the collective form genus *Cretacimermis* Poinar (2001a, 2003a) was proposed for Cretaceous fossil mermithids not assignable to extant genera. The collective genus *Oligoplectus* Taylor (1935) was erected for undetermined members of the family Plectidae, and the collective genus *Vetus* Taylor (1935) was proposed for free-living nematodes not assignable to a family. Authors describing nematodes in deposits other than amber have proposed their own generic names. Systematic arrangement of the higher nematode categories follows that of Eyualem-Abele et al. (2006).

6.3.1 Fossil nematode groups

6.3.1.2 Phylum Nematoda

Order Enoplida

Family Palaeoenoploididae

Palaeoenoploides alessandrellianus Mattavelli & Bracchi, 2008 (Upper Cretaceous)

Family Palaeonematidae

Palaeonema phyticum Poinar, Kerp & Hass, 2008 (Upper Devonian) (Fig. 6.1)

Comment: *Palaeonema* was found in the stomatal chambers of the Early Devonian land plant, *Aglaophyton major* (Kidson & Lang 1920).

Order Desmoscolecida

Family Eophasmidae

Eophasma jurasicum Arduini, Pinna & Teruzzi, 1983 (Jurassic)

Order Plectida

Family Captivonemidae

Captivonema cretacea Manum, Bose, Sayer & Boström, 1994 (Lower Cretaceous)

Comment: *Captivonema cretacea* was found in the wall of a clitellate cocoon.

Order Chromadorida

Family Nemavermidae

Nemavermes mackeei Schram, 1973 (Carboniferous)

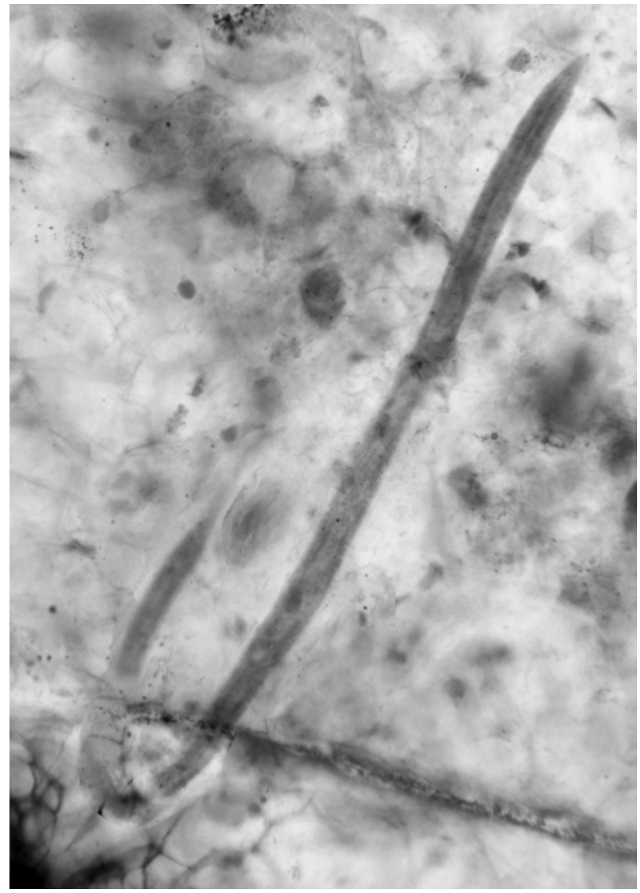

Fig. 6.1: *Palaeonema phyticum* Poinar, Kerp & Hass, 2008 in the stomatal chamber of the Early Devonian land plant, *Aglaophyton major* (Kidson & Lang) preserved in Rhynie Chert, Scotland. Specimen deposited in the Forschungsstelle für Paläobotanik, Westfälische Wilhelms-Universität, Münster, Germany.

Order Plectida

Family Plectidae

Oligoplectus succini (von Duisburg), 1862 (Baltic amber)

Comments: Members of this family are microbotrophic and occur in a wide range of habitats, including soil, fresh water and decaying vegetation.

Order Mermithida

Family Mermithidae

Cretacimermis protus Poinar & Buckley, 2006 (Burmese amber)

Cretacimermis libani Poinar, Acra & Acra, 1994 (Lebanese amber) (Fig. 6.2)

Heydenius antiqua von Heyden, 1860 (Eocene Brown coal)

Heydenius araneus Poinar, 2000 (Baltic amber)

Heydenius brownii Poinar, 2001b (Baltic amber)

Heydenius dominicus Poinar, 1984a (Dominican amber)

Heydenius formicinus Poinar, 2002 (Baltic amber)

Heydenius matutina (Menge, 1863) (Baltic amber)

Fig. 6.2: *Cretacimermis libani* Poinar, Acra & Acra, 1994 inside the abdomen of a midge (Diptera: Chironomidae) in Lebanese amber. Specimen deposited in the Acra amber collection, Lebanon.

Heydenius myrmicophila Poinar, Lauchaud, Castillo & Infante, 2006 (Dominican amber)

Heydenius quadristriata (Menge, 1872) (Baltic amber)

Comments: Mermithids occur either as developmental or resting stages in the body cavity of a wide range of invertebrates, such as insects, arachnids, mollusks, myriapods, crustaceans and even annelids. All growth occurs in the host and those seen emerging from fossil insects represent the beginning of the free-living stages (unless they emerged prematurely). After molting twice to the adult stage, mating and oviposition occurs in the immediate environment. There is usually only a single specimen per host, but several specimens can occur in the same host. If they are within the body cavity of the insect, fossilized forms can be only be detected if the resin clears the host's cuticle.

There are numerous accounts of mermithids associated with fossil insects in amber, especially parasitizing chironomids in Baltic amber, and only those that were described are covered here. Two reports of mermithids in sedimentary deposits also exist. The first was made by von Heyden (1860, 1862) who described *Heydenius antiqua* projecting from the anus of the cerambycid beetle, *Hesthesis immortua* Heyden in Eocene Rhine lignite. The other is a mermithid emerging from a tabanid larva (Diptera: Tabanidae) from the Pliocene of Willershausen, Germany (Grabenhorst 1985). As this group was already established by the Early Cretaceous (Fig. 6.2), it probably extends back to the Permian at least. While most fossil mermithids are associated with insects, *H. araneus* Poinar (2000) in Baltic amber and *H. arachnius* Poinar (2012) in Dominican amber parasitized spiders.

Order Rhabditida

Family Rhabditidae

Vetus duisburgi Taylor, 1935 (Baltic amber)

Vetus capillacea Menge, 1863 (Baltic amber)

Vetus pristina Menge, 1863 (Baltic amber)

Vetus robustus Poinar, 1977 (Mexican amber)

Comments: Most extant species of Rhabditidae are cosmopolitan, free-living microbotrophic nematodes inhabiting a variety of terrestrial (and rarely aquatic) habitats. They have been found in various amber deposits but are difficult to identify to family level due to the poor preservation of their taxonomic characters. Fossil representatives have been described from Mexican (Poinar 1977) Baltic (Menge 1863, Taylor 1935), Dominican (Poinar, 2011) and Lebanese (Poinar 2011) amber. Many members of this group form a third-stage resistant juvenile, or "dauer larva". This stage attaches to various arthropods in a phoretic relationship. A fossil record of such an association was reported in Dominican amber with several dauer juveniles adjacent to an ant (Poinar 1982).

Infraorder Diplogastromorpha

Family Diplogastridae

Oligodiplogaster antiqua Poinar, 1977 (Mexican amber)

Comments: Members of this group have a similar biology to those of the Rhabditidae and also occur in a variety of terrestrial environments. A few species have become parasitic or phoretic on insects. The free-living *Oligodiplogaster antiqua* Poinar (1977) was described from Mexican amber, and *Syconema dominicana* Poinar (2011) was described from a fossil fig wasp in Dominican amber (Poinar & Poinar 1999, Poinar 2011).

Infraorder Tylenchomorpha

Family Aphelenchoididae

Oligaphelenchoides atrebora Poinar, 1977 (Mexican amber) (Fig. 6.3)

Comments: Members of this family possess a stylet and feed on fungal hyphae as well as higher plant tissues. They are cosmopolitan and occur in a variety of habitats. A population of *Oligaphelenchoides atrebora* Poinar (1977) consisting of eggs, juveniles and adults, together with

Fig. 6.3: Various stages of *Oligaphelenchoides atrebora* Poinar 1977 in Mexican amber. Specimen deposited in the UC Berkeley Museum of Paleontology.

hyphae of the fungus upon which they were probably feeding was preserved in Mexican amber.

Family Iotonchidae

Comments: Members of this family also possess a stylet and some species have two separate life cycles, one mycophagous, with the individuals feeding on fungal hyphae, and the other entomophagous, developing inside insects that are also associated with the host of the mycophagous stages. *Paleoiotonchium dominicanum* Poinar (2011) parasitizing a fungus gnat in Dominican amber is the only known fossil of this family (Poinar 1991, Poinar 2011).

Family Allantonematidae

Howardula helenoschini Poinar, 2003b (Baltic amber) (Fig. 6.4)

Comments: Members of this family are parasites of arthropods, especially insects. The fertilized female is the infective stage and enters the host through the cuticle, then swells up into a reproductive parasitic female that produces eggs and young within the hosts' body. Mature juveniles or young adults leave the host and mature in the immediate environment. Members of the orders Coleoptera and Diptera are the most common

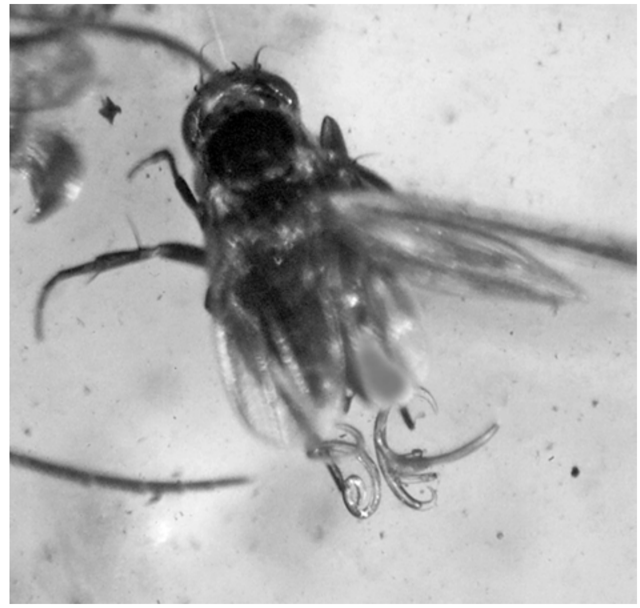

Fig. 6.4: The allantonematid *Howardula helenoschini* Poinar emerging from its dipteran host (Diptera: Phoridae) in Baltic amber. Specimen deposited in the Poinar amber collection, Oregon State University, accession # N-3–64.

hosts for nematodes of this family. *Palaeoparasitylenchus dominicanus* Poinar (2011) parasitizing a fruit fly (Diptera: Drosophilidae) (Poinar 1984b, c) and *Palaeoallantonema dominicana* Poinar (2011) parasitizing a rove beetle (Coleoptera: Staphylinidae) (Poinar & Brodzinsky 1986), both in Dominican amber, are other examples of fossil allantonematids (Poinar 2011).

Infraorder Ascaridomorpha

Family Ascaridae

Ascarites gerus Poinar & Boucot, 2006 (Early Cretaceous)

Ascarites priscus Poinar & Boucot, 2006 (Early Cretaceous) (Fig. 6.5)

Comments: Members of this family are vertebrate parasites that reproduce in the digestive tract of their hosts. The eggs, which pass out of the body with fecal material, are very resistant and can survive for months in the environment. Infection is normally established through the ingestion, either directly or indirectly, of eggs. Many species have a migratory phase where, after hatching, the juveniles enter the blood or lymph system and are then carried to the lungs, coughed up, swallowed and finally establish themselves in the digestive tract to reproduce. The eggs of *Ascaris* and related genera have diagnostic characteristics that can be used for identification. The fossil ascarids, *Ascarites gerus* and *Ascarites priscus*, were recovered from an Early Cretaceous dinosaur coprolite (Poinar & Boucot 2006, Poinar & Poinar 2008) (Fig. 6.5).

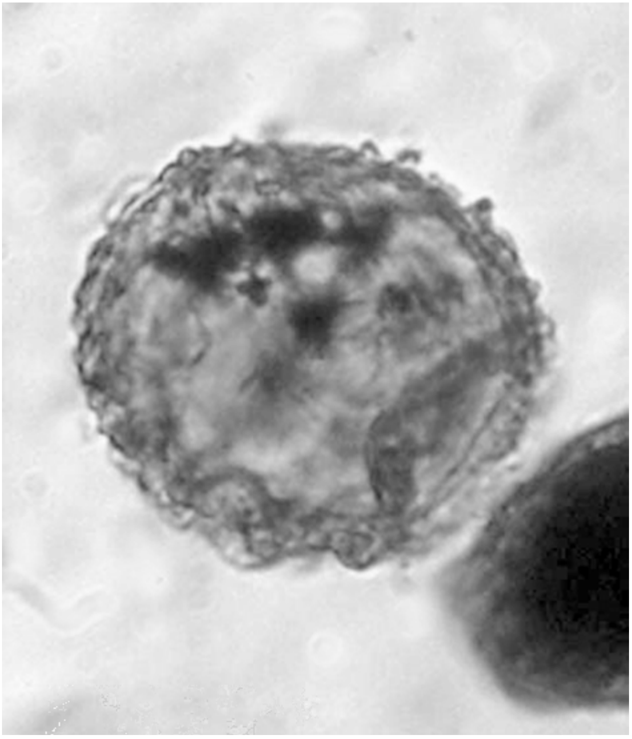

Fig. 6.5: Egg of the dinosaur parasite, *Ascarites priscus* Poinar & Boucot, 2006 in a coprolite from the Early Cretaceous Bernissart Iguanodon shaft, Belgium. Specimen deposited in the Department of Zoology, Oregon State University; slide # Y2 852 (2).

6.4 Questionable fossil nematodes

Some fossils previously described as nematodes are questionable. Examples are the specimens described by Størmer (1963) as *Scorpiophagus baculiformis* and *S. latus* from the decomposed remains of the Lower Carboniferous scorpion *Gigantoscorpio willsi* Størmer. Although numerous linear objects were illustrated, all had the posterior portions of their bodies missing or partly disintegrated. Although many contained a short, narrow, darkened invagination thought to represent a buccal cavity at the "anterior" end, there was no evidence of an associated alimentary tract or any other structure that suggests these objects are nematodes.

Another questionable fossil nematode is the specimen described by Voigt (1957) as a vertebrate parasitic nematode in the muscles of a fossil buprestid beetle, *Chlorodema primordialis* Pongraz, 1935 (Coleoptera: Buprestidae) from the Eocene brown coal deposits by Halle, Germany. The object in question is partially coiled up in a cyst-like compartment within the musculature of the beetle. Voigt felt the beetle served as an intermediate host for a vertebrate parasitic nematode and compared the specimen with the encysted juvenile of the parasitic lungworm nematode, *Metastrongylus* (= *Choerostrongylus*) *pudendotectus*, which encysts in the body cavity of earthworms. However, vertebrate parasitic nematodes that utilize members of the families Buprestidae or Cerambycidae as intermediate or paratenic hosts are unknown.

Sedimentary deposits from the Eocene Green River Formation in Utah, USA commonly contain sinusoidal trails that have been attributed to free-living microbotrophic nematodes (Moussa 1969). Whether these tracks were made by nematodes or legless insect larvae, such as the elongate larvae of the dipterous family Ceratopogonidae, is unresolved.

6.5 Summary

The first appearance of higher nematode groups in the fossil record is summarized in Tab. 6.2.

It should be noted that although the list of fossil nematodes will never be complete, as new forms will be continuously found and described, the types of fossilization that preserve nematodes are quite selective. Thus, animal and plant parasites within their respective hosts will rarely become fossilized, whereas nematodes associated with invertebrates or plant debris in close association with amber-forming trees have a better chance of becoming fossilized. It is quite likely

Tab. 6.2: First appearance of Nematode groups in the fossil record.

Order/Indraorder	Family	Age (mya)	Fossilization-locality
Enoplida	Palaeonematidae	395	Rhynie Chert-Scotland
Mermithida	Mermithidae	130–135	Lebanese amber
Rhabditida	Rhabditidae	130–135	Lebanese amber
Ascaridomorpha	Ascaridae	110	Coprolite-Belgium
Enoplida	Enoplidae	95	Sedimentary-Lebanon
Tylenchomorpha	Allantonematidae	40–50	Baltic amber
Plectida	Plectidae	40–50	Baltic amber
Rhabditida	Diplogastridae	22–26	Mexican amber
Tylenchomorpha	Aphelenchoididae	22–26	Mexican amber
Tylenchomorpha	Iotonchidae	15–40	Dominican amber

that the Nematoda extends back to the Cambrian and even the Precambrian, yet obtaining fossil remains with morphological characters assigning them to the Phylum are problematical. Additional fossil nematodes have recently been described (Poinar 2011, 2012).

Literature

Arduini, P., Pinna, G. & Teruzzi, G. (1983): *Eophasma jurasicum* n.g., n.sp., a new fossil nematode of the Sinemurian of Osteno in Lombardy. *Nat. Mus. Civ. Stor. Nat. Milano* 111: 104–108.

Von Duisburg, H. (1862): Beitrag zur Bernstein-Fauna. *Schriften der Königlichen Physikalisch-Ökonomischen Ges. Königsberg* 3: 31–36.

Eyualem-Abebe, Andrássy, I. & Traunspurger, W. (2006): *Freshwater Nematodes: Ecology and Taxonomy*, pp. 752. CABI publishing, Cambridge.

Grabenhorst, H. (1985): Eine zweite Bremse (Tabanidae) zusammen mit ihrem Parasiten (Nematoda, Mermithoidae) aus dem Oberpliozän von Willershausen Krs. Osterode. *Osterode Aufschluss* 36: 325–328.

Hantzschel, W. (1975): Trace fossils and problematics. In: Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology.* Part W., Supplement 1, pp. 1–269. The Geological Society of America, Boulder.

Heyden, C. von (1860): *Mermis antiqua*, ein fossiler Eigeweidewurm. *Entomol. Zeitschrift Stettin* 21: 38.

Heyden, C. von (1862): Gliederthiere aus der Braunkohle des Niederrheins, der Wetterau und der Röhn. *Palaeontographica* 10: 62–82.

Manum, S. B., Bose, M. N., Sayer, R. T. & Bostrom, S. (1994): A nematode (*Captivonema cretacea* gen. et. sp.n.) preserved in a clitellate cocoon wall from the Early Cretaceous. *Zool. Scripta* 23: 27–31.

Mattavelli, A. & Bracchi, G. (2008): *Palaeoenoploides alessandrellianus* n. gen. n. sp.: a late Cenomanian 'roundworm' from the Upper Cretaceous of Lebanon (Nematoda: Enoplidae). *Atti Soc. Ital. Sci. Nat. Mus. Civ. Storia Nat. Milano* 149: 179–194.

Menge, A. (1863): Ueber ein Rhipidopteron und einige andere im Bernstein eingeschlossene Tiere. *Schr. Naturforsch. Ges. Danzig N. F.* 1: 1–8.

Menge, A. (1872): Ueber eine im Bernstein eingeschlossene *Mermis*. *Schr. Naturforsch. Ges. Danzig N. F.* 3: 1–2.

Moussa, M. T. (1969): Nematode fossil tracks of Eocene age from Utah. *Nematologica* 15: 376–380.

Poinar, Jr., G. O. (1977): Fossil nematodes from Mexican amber. *Nematologica* 23: 232–238.

Poinar, Jr., G. O. (1982): Fossil dauer rhabditid nematodes. *Nematologica* 27: 466–467.

Poinar, Jr., G. O. (1984a): *Heydenius dominicus* sp. n. (Nematoda: Mermithidae), a fossil parasite from the Dominican Republic. *J. Nematol.* 16: 371–375.

Poinar, Jr., G. O. (1984b): Fossil evidence of nematode parasitism. *Revue Nematol.* 7: 201–203.

Poinar, Jr., G. O. (1984c): First fossil record of parasitism by insect parasitic Tylenchida (Allantonematidae: Nematoda). *J. Parasitol.* 70: 306–308.

Poinar, Jr., G. O. (1991): The mycetophagous and entomophagous stages of *Iotonchium californicum* n. sp. (Iotonchidae: Tylenchida). *Revue Nematol.* 14: 565–580.

Poinar, Jr., G. O. (1992): *Life in Amber*, pp. 350. Stanford University Press, Stanford.

Poinar, Jr., G. O. (2000): *Heydenius araneus* n.sp. (Nematoda: Mermithidae), a parasite of a fossil spider, with an examination of helminthes from extant spiders (Arachnida: Araneae). *Invert. Biol.* 119: 388–393.

Poinar, Jr., G. O. (2001a): Nematoda and Nematomorpha. In: Thorp, J. H. & Covich, A. P. (eds) *Ecology and Classification of North American Freshwater Invertebrates, Second edition*, pp. 255–295. Academic Press, New York.

Poinar, Jr., G. O. (2001b): *Heydenius brownii* (Nematoda: Mermithidae) parasitizing a planthopper (Achilidae: Homoptera) in Baltic amber. *Nematology* 3: 753–757.

Poinar, Jr., G. O. (2002): First fossil record of nematode parasitism of ants: a 40 million year tale. *Parasitology* 125: 457–459.

Poinar Jr., G. O. (2003a): Trends in the evolution of insect parasitism by nematodes as inferred from fossil evidence. *J. Nematol.* 35: 129–132.

Poinar, Jr., G. O. (2003b): Fossil evidence of phorid parasitism (Diptera: Phoridae) by allantonematid nematodes (Tylenchida: Allantonematidae). *Parasitology* 127: 589–592.

Poinar, Jr., G. O. (2011): *The Evolutionary History of Nematodes*. Brill, Leiden.

Poinar, Jr., G. O. (2012): New fossil nematodes in Dominican and Baltic amber. *Nematology* 14: 483–488.

Poinar, Jr., G. O., Acra, A. & Acra, F. (1994): Earliest fossil nematode (Mermithidae) in Cretaceous Lebanese amber. *Fund. Appl. Nematology* 17: 475–477.

Poinar, Jr., G. O. & Boucot, A. (2006): Evidence of intestinal parasites of dinosaurs. *Parasitology* 133: 245–249.

Poinar, Jr., G. O. & Brodzinsky, J. (1986): Fossil evidence of nematode (Tylenchida) parasitism in Staphylinidae (Coleoptera). *Nematologica* 31: 353–355.

Poinar, Jr., G. O. & Buckley, R. (2006): Nematode (Nematoda: Mermithidae) and hairworm (Nematomorpha: Chordodidae) parasites in Early Cretaceous amber. *J. Invertebr. Pathol.* 93: 36–41.

Poinar, Jr., G. O., Kerp, H. & Hass, H. (2008): *Palaeonema phyticus* gen. n., sp.n. (Nematoda: Palaeonematidae fam. n.), a Devonian nematode associated with early land plants. *Nematology* 10: 9–14.

Poinar, Jr., G. O., Lachaud, J.-P., Castillo, A. & Infante, F. (2006): Recent and fossil nematode parasites (Nematoda: Mermithidae) of Neotropical ants. *J. Invertebr. Pathol.* 91: 19–26.

Poinar, Jr., G. O. & Milki, R. (2001): *Lebanese Amber*. Oregon State University Press, Corvallis.

Poinar, Jr., G. O. & Poinar, R. (1999): *The Amber Forest.* Princeton University Press, Princeton.

Poinar, Jr., G. O. & Poinar, R. (2008): *What Bugged the Dinosaurs?*. Princeton University Press, Princeton.

Schram, F. R. (1973): Pseudocoelomates and a nemertine from the Illinois Pennsylvanian. *J. Paleontol.* 47: 985–989.

Sliter, W. V. (1971): Predation on benthic Foraminifera. *J. Foraminifera Res.* 1: 20–29.

Størmer, L. (1963): *Gigantoscorpio willsi* a new scorpion from the Lower Carboniferous of Scotland and its associated preying microorganisms. *Skrifter Utgitt av Det Norske Vidénskaps-Akademi I Oslo 1. Mat.-Naturv. Klasse. Ny Serie* 8: 1–171.

Taylor, A. L. (1935): A review of the fossil nematodes. *Proc. Helminth. Soc. Wash.* 2: 47–49.

Voigt, E. (1957): Ein parasitischer Nematode in fossiler Coleopteren-Muskulatur aus der eozänen Braunkohle des Geiseltales bei Halle (Saale). *Paläontol. Zeitschr.* 31: 35–39.