Palaeonema phyticum gen. n., sp. n. (Nematoda: Palaeonematidae fam. n.), a Devonian nematode associated with early land plants

Article *in* Nematology · January 2008

DOI: 10.1163/156854108783360159

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Nematology, 2008, Vol. 10(1), 9-14

Palaeonema phyticum gen. n., sp. n. (Nematoda: Palaeonematidae fam. n.), a Devonian nematode associated with early land plants

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Received: 30 May 2007; revised: 25 July 2007
Accepted for publication: 27 July 2007

Summary – Nematodes are one of the most abundant groups of invertebrates on the face of the earth. Their extremely poor fossil record hinders our ability to assess just when members of this group invaded land and first became associated with plants. This study reports fossil nematodes from the stomatal chambers of the Early Devonian (396 mya) land plant, *Aglaophyton major*. These nematodes, which are tentatively assigned to the order Enoplia, are described as *Palaeonema phyticum* gen. n., sp. n. in the new family Palaeonematidae fam. n. Diagnostic characters of the family are: *i*) cuticular striations; *ii*) uniform, cylindrical pharynx with the terminal portion only slightly set off from the remainder; and *iii*) a two-portioned buccal cavity with the upper portion bearing protuberances. The presence of eggs, juveniles and adults in family clusters within the plant tissues provide the earliest evidence of an association between terrestrial plants and animals and may represent an early stage in the evolution of plant parasitism by nematodes.

Keywords – *Aglaophyton major*, fossil nematode, morphology, morphometrics, Rhynie chert.

Nematodes form one of the most abundant groups of invertebrates on the face of the earth and have probably maintained this position since they first appeared sometime in the Cambrian, even Precambrian, period. Estimates for numbers of individuals range from 1.5 billion in the upper 20 mm of an acre of marine beach sand to 3 billion in a single acre of soil (Chitwood & Chitwood, 1950). These figures do not reflect those that live in the sea, or the multitudes that parasitise plants and animals. Whilst some 20 000 species have been described, estimates for their diversity vary from 500 000 to 10 million (Poinar, 1983; Malakhov, 1994). The extremely poor fossil record of nematodes hinders our ability to assess just when members of this group invaded land and first became associated with plants. The present study describes an Early Devonian (396 mya) nematode from the stomatal chambers of the early land plant, *Aglaophyton major* (Kidson & Lang). The presence of eggs, juveniles and adults in family clusters within the plant tissues provides the earliest evidence of an association between animals and terrestrial plants.

Preservation in the Rhynie chert is so exquisite that very delicate structures and very short-lived developmental stages, such as germinating spores, freshly released sperm cells (Kerp *et al*., 2004) and developing arbuscules of vesicular arbuscular mycorrhiza (Remy *et al*., 1994), are preserved. These indicate that preservation must have occurred very quickly, within hours or even less. Recent radiometric dating of these deposits provide an age of 396 ± 12 million years (Pragian), which is well in accordance with palynological datings of intercalated shale horizons (Rice *et al*., 2002).

Materials and methods

Fossil material was obtained from sectioning loose pieces of Rhynie chert rock containing upright standing plant axes. The fossil nematodes were discovered in thin sections (200-300 μm) of chert within aerial axes (stems) of the early land plant *A. major*. Photos of the plant axes with nematodes were made with a Leitz Ortholux microscope imaging system using 10×, 20× and 40× lenses. The data were saved in bitmap image file formats. Images were scanned and examined under various settings in Adobe Photoshop to detect morphological features.

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Results

Up to 500 nematodes and eggs occurred in the substomatal chambers and intercellular spaces of the plants. Due to their orientation, most nematodes were represented by cross and tangential sections with estimated lengths ranging from 100 μm to slightly over 1000 μm. Analysis of the sections indicated that the nematodes belonged to a single species. The following description relies mainly on a well preserved female whose entire body was exposed in a longitudinal section. The classification system used here follows that presented by De Ley *et al.* (2006). All nematode fossils are deposited in the Forschungsstelle für Paläobotanik, Westfälische Wilhelms-Universität, Münster, Germany.

Palaeonematidae fam. n.

DIAGNOSIS

Nematoda Potts, 1932; Enoplia Inglis, 1983. Medium-sized, slender nematodes; cuticle with transverse striations; cephalic setae present, six lips, amphidial apertures spiral-shaped; buccal cavity tubular, with anterior sclerotised and posterior non-sclerotised portions; anterior portion of buccal cavity bearing protuberances; pharynx cylindrical, uniform, isthmus and median bulb absent, terminal portion slightly expanded; pharyngeal gland nuclei located at extreme base of pharynx; ovaries didelphic, reflexed; vulva located near midbody; tail elongate with swollen tip.

TYPE GENUS

Palaeonema gen. n.

Palaeonema[*] gen. n.

DIAGNOSIS

With characters of the family. Anterior end somewhat narrowed; amphidial apertures located in neck region; lower portion of buccal cavity unarmed; nerve ring positioned approximately at mid-pharynx level.

TYPE SPECIES

Palaeonema phyticum gen. n., sp. n.

[*] Generic epithet derived from the Greek *palaios* = ancient, and *nema* = a thread.

Palaeonema phyticum[**] sp. n.
(Figs 1, 2)

DESCRIPTION

Female (holotype)

Medium-sized, slender nematode, 890 μm long; maximum diam. 28 μm; cuticle with transverse striations; cephalic setae present, six lips, each bearing a seta (one seta obscured); lip region slightly offset; amphidial apertures spiral-shaped; buccal cavity tubular, with sides slightly diverging toward apex, 10 μm long $\times$ 5 μm diam.; buccal cavity composed of two portions: anterior portion strongly sclerotised, posterior portion non-sclerotised; upper portion of buccal cavity bearing rounded protuberances (teeth) at base; lower portion unarmed; pharynx cylindrical, uniform, isthmus and median bulb absent, terminal portion slightly expanded, 189 μm long; pharyngeal gland nuclei located at extreme base of pharynx; nerve ring positioned *ca* mid-pharynx level, 99 μm from head. Ovaries didelphic, reflexed; developing ova 18-22$\times$11-15 μm in size; vulva located at *ca* 40% of body length; tail 73 μm long, elongate, with swollen tip.

REMARKS

While only two buccal teeth could be seen, it is probable that a third exists. Also, it is almost certain that at least six setae are present, even if only five can be seen. Although ascertaining relationships is difficult, the fossil shares some features with members of the Tripyloididae, such as inconspicuous lips, a buccal cavity divided into two sections, presence of teeth in the buccal cavity, didelphic and reflexed ovaries, spiral amphidial apertures and a cylindrical pharynx (see Smol and Coomans, 2006). However, as some details were obscured during the fossilisation process (including number and arrangement of head papillae, presence of caudal glands, spinneret, *etc.*) and morphological features of the males have not been observed, it is not possible to assign *Palaeonema* gen. n. to an extant family at this time. In view of the importance of this discovery and the difficulty in establishing its systematic position, the genus is placed in its own family based on the presence of transverse cuticular striations (Figs 1; 2C) and the structure of the pharynx and buccal cavity (Figs 1; 2B).

[**] Specific epithet derived from the Greek *phytos* = plant, and *-icum*, = pertaining to.

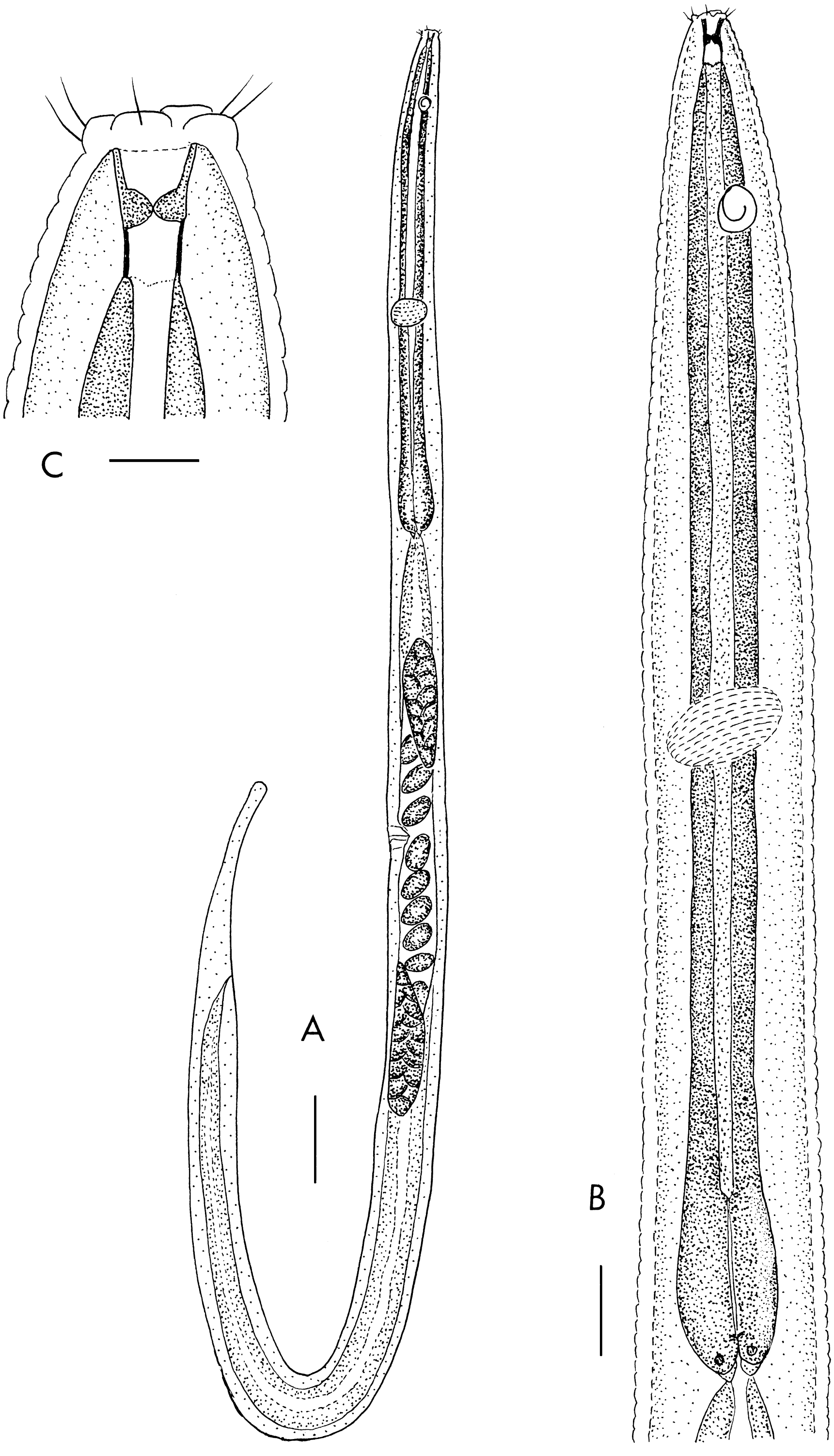

Fig. 1. *Holotype of* Palaeonema phyticum *gen. n., sp. n. A: Entire female; B: Anterior portion; C: Buccal cavity. (Scale bars: A = 39 μm; B = 13 μm; C = 6 μm.)*

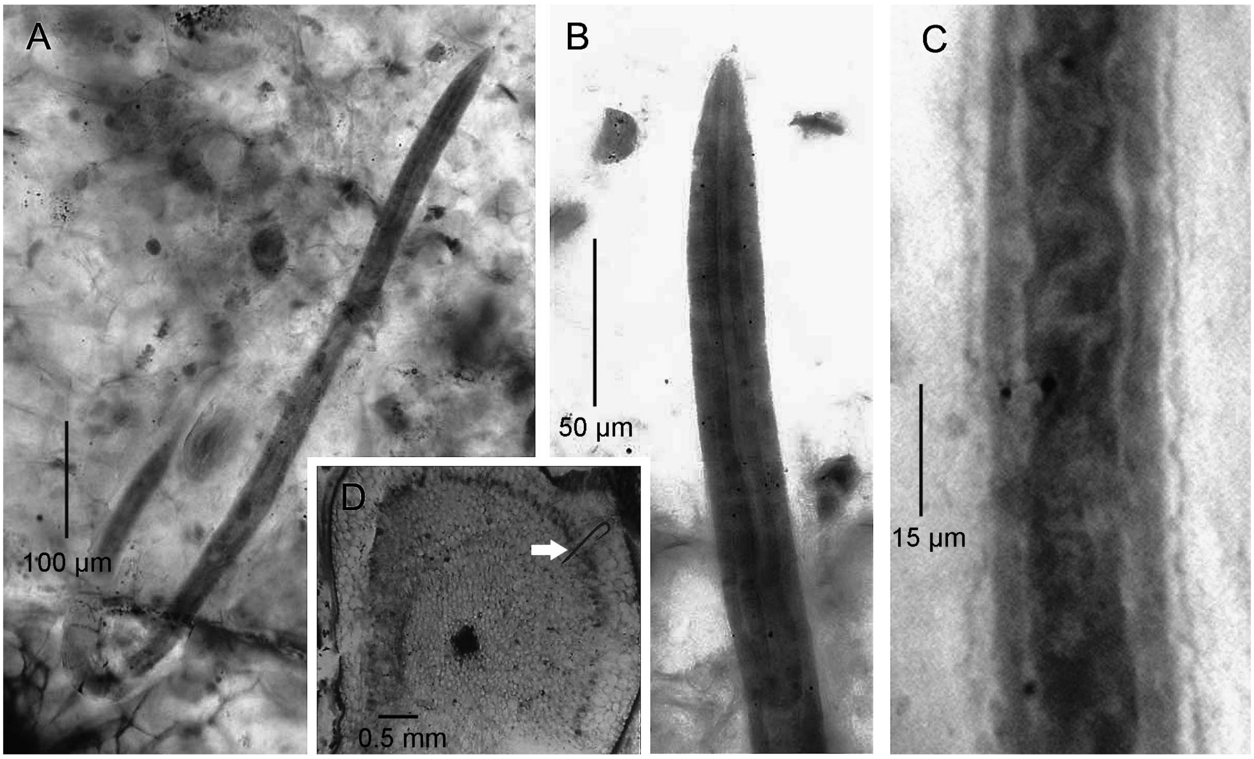

Fig. 2. Palaeonema phyticum *gen. n., sp. n. A: Holotype in a stomatal chamber of* Aglaophyton major*; B: Pharyngeal region of holotype; C: Intestinal region of juvenile in a stomatal chamber of* A. major*; D: Cross section of* A. major *with holotype female in a stomatal chamber (arrowed). The nematode body has been digitally enhanced.*

Discussion

It is likely that the predecessors of *Palaeonema* gen. n. were aquatic forms; quite possibly marine nematodes that entered brackish or fresh water and then moved to the land. *Aglaophyton* was a small terrestrial plant with repeatedly bifurcating axes up to 4 mm thick that developed rhizoids where the axes touched the substrate. The areas where *A. major* grew were surrounded by hot springs that periodically flooded the region with silica-rich waters. Because the axes of the fossilised plant did not show evidence of decay, the nematodes must have invaded the plants prior to the inundation. The presence of various developmental stages (up to 500 individuals) in substomatal cavities located between the cortex and phloematic tissue is evidence that *Palaeonema* gen. n. was reproducing inside the tissues of *Aglaophyton* and presumably obtaining nourishment from the cortical cells. The nematodes also occurred in intercellular spaces in nearly fresh axes, inside cortical cells and in large cavities containing disrupted cortical tissue. Since a few of the nematode-inhabited stomatal cavities contained microorganisms, *Palaeonema* gen. n. may have been a facultative plant parasite that supplemented its diet with various microorganisms. There was no evidence of any other invertebrates inside the stomatal chambers, which eliminates any possibility that *Palaeonema* gen. n. was predaceous.

Entry of *Palaeonema* gen. n. into the stomatal chambers was probably similar to the pathway used by extant species of *Aphelenchoides* and *Ditylenchus*, which take only a few seconds to glide through the stomata of healthy plants (Christie, 1959; Wallace, 1963).

Based on the structure of its buccal cavity, *Palaeonema* gen. n. would be classified as an epistrate feeder, which employs a tear and swallow feeding strategy (Moens *et al.*, 2006). By everting its buccal teeth, *Palaeonema* gen. n. could have been capable of mechanically disrupting cortical cells and swallowing the contents. Some extant diplogastrids (*Tylopharynx* spp.) have a narrow stoma that is apparently protrusible and could be used to break through plant cell walls (Maggenti, 1981).

It is possible that *Palaeonema* gen. n. possessed a life style similar to some extant free-living, non-stylet bearing, nematodes that are known to enter, develop and reproduce in roots, stems and leaves of healthy plants. Such 'dyssaprobes' (especially members of the families Panagrolaimidae and Cephalobidae) utilise their chitinised stoma to break open plant cells mechanically and ingest the contents (Christie, 1933; Filipjev & Schuurmans Stekhoven, 1959; Paramonov, 1962).

Living in the stomatal chambers of *A. major* would have supplied *Palaeonema* gen. n. not only with nourishment but also could have offered protection from predators recovered from the same fossil deposits. These would have included Collembola (Hirst & Maulik, 1926) and several families of mites (Hirst, 1923), all of which have modern representatives that feed on nematodes (Small, 1988). Even the now-extinct spider-like trigonotarbids would probably have preyed on nematodes (Kevan *et al*., 1975; Fayers *et al*., 2005).

Despite their present day prolific diversity and numbers, fossil nematodes are quite rare and most have been reported from amber. Of these, the oldest was from Lower Cretaceous deposits in Lebanon (Poinar *et al*., 1994). Compression fossils from the Jurassic (Arduini *et al*., 1983) and Carboniferous (Størmer, 1963; Schram, 1973) are too fragmentary for positive identifications. Trace fossil tracks cannot be definitely assigned to nematodes since there could be other invertebrates making the same patterns (Hantzschel, 1975).

Palaeonema gen. n. triples the age of previously undisputed fossil nematodes and provides a crucial link in the evolutionary pathway of plant parasitism by nematodes by providing a minimum date when nematodes established associations with terrestrial plants. It also represents the earliest known parasitic relationship between terrestrial plants and animals. Previously, the oldest definite records of animal-plant parasitism were arthropod galls and signs of foliage feeding on Late Cretaceous tree ferns. While dispersed coprolites, hypertrophied cortical cells, tissue lesions and wounds in sections of Lower Devonian rhyncophytes have been noted, there is no definite evidence of what organisms, if any, caused these conditions (Labandeira, 2002).

Acknowledgements

The authors thank Art Boucot, an anonymous reviewer and Roberta Poinar for comments on earlier drafts of this manuscript, and Duane Hope for providing references on marine nematodes.

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