BRILL

Nematology 15 (2013) 567-574

Nematology
brill.com/nemy

Traces of marine nematodes from 470 million years old Early Ordovician rocks in China

Andrzej BALIŃSKI [1], Yuanlin SUN [2] and Jerzy DZIK [1,3,*]

[1] *Instytut Paleobiologii PAN, Twarda 51/55, PL-00-818 Warszawa, Poland*
[2] *Key Laboratory of Orogenic Belts and Crustal Evolution, School of Earth and Space Sciences, Peking University, Beijing 100871, P.R. China*
[3] *Instytut Zoologii Uniwersytetu Warszawskiego, Banacha 2, PL-02-097 Warszawa, Poland*

Received: 30 May 2012; revised: 19 November 2012
Accepted for publication: 20 November 2012; available online: 16 January 2013

Summary – Cylindrical, mostly horizontal, burrows of 20-60 μm diam. and sinusoidal course, found in the middle part of the Early Ordovician (early Floian) Fenxiang Formation in the Hubei Province of China, represent the oldest record of activity by marine nematodes, preceding known nematode body fossils by 70 million years. The burrows are filled with secondarily oxidised pyrite framboids and clay mineral flakes, indicating low oxygen content in the mud and proving that the animals lined their burrows with organic matter, being bacteriovores and mud-eaters. The marine bottom environment enabling such a mode of life originated no earlier than the mid Early Cambrian (approximately 535 million years ago) owing to peristaltic bioturbation, mostly by nemathelminthans of priapulid affinities. Before the so-called 'Agricultural Revolution', the bottoms of shallow seas were covered with microbial mats preventing within-sediment animal life. This event imposes the lower time limit on the possible date of origin of nematodes.

Keywords – bioturbation, evolution, Fenxiang Formation, nematode tracks, trace fossils.

Nematodes are among the most abundant animals of terrestrial and marine biota. They originated in the sea (Holterman *et al.*, 2006), where they are represented by a great number of species. The free-living marine nematodes are small or very small, down to 100 μm adult size, which makes them difficult to study (Heip *et al.*, 1985). Although molecular phylogenetic studies have resulted in clarification of the general picture of nematode evolution, it is difficult to calibrate their phylogenetic tree and test it with fossil evidence because of the scarcity of taxonomically determinable fossils. Even if fossilised, ancient nematodes are difficult to determine with reasonable confidence because of their simple anatomy. The palaeontological alternative to morphological evidence is their fossilised behaviour – traces of life activity preserved in rocks. These at least provide insight into the mode of locomotion, size of the organism, environment and mode of feeding. This is not much, but in some cases such trace fossils can be more informative phylogenetically than poorly preserved body fossils.

In this work we present a discovery of the oldest known traces of nematode-within-sediment activity from the Ordovician strata of China. These trace fossils are about 70 million years older than the oldest known nematode body fossil (Poinar *et al.*, 2008; Poinar, 2011). Although of low taxonomical resolution, this record allows us to determine the last possible date of origination of the nematode clade, shows how large nematode individuals were at this stage of their evolution and what environment they inhabited. We also discuss the evolutionary events leading to the origination of the Nematoda in context of the Precambrian-Cambrian transformations of the marine bottom environment.

Materials and methods

GEOLOGICAL SETTING

The specimens under study were collected from the middle part of the Ordovician Fenxiang (transcribed also Fenhsiang) Formation near the village of Tianjialing (Fig. 1A), about 8 km southeast of Xingshan County in the Yichang area (also known as Three Gorge area) of Hubei Province, southern China (Zhan & Jin, 2007).

---

* Corresponding author, e-mail: dzik@twarda.pan.pl

DOI:10.1163/15685411-00002702

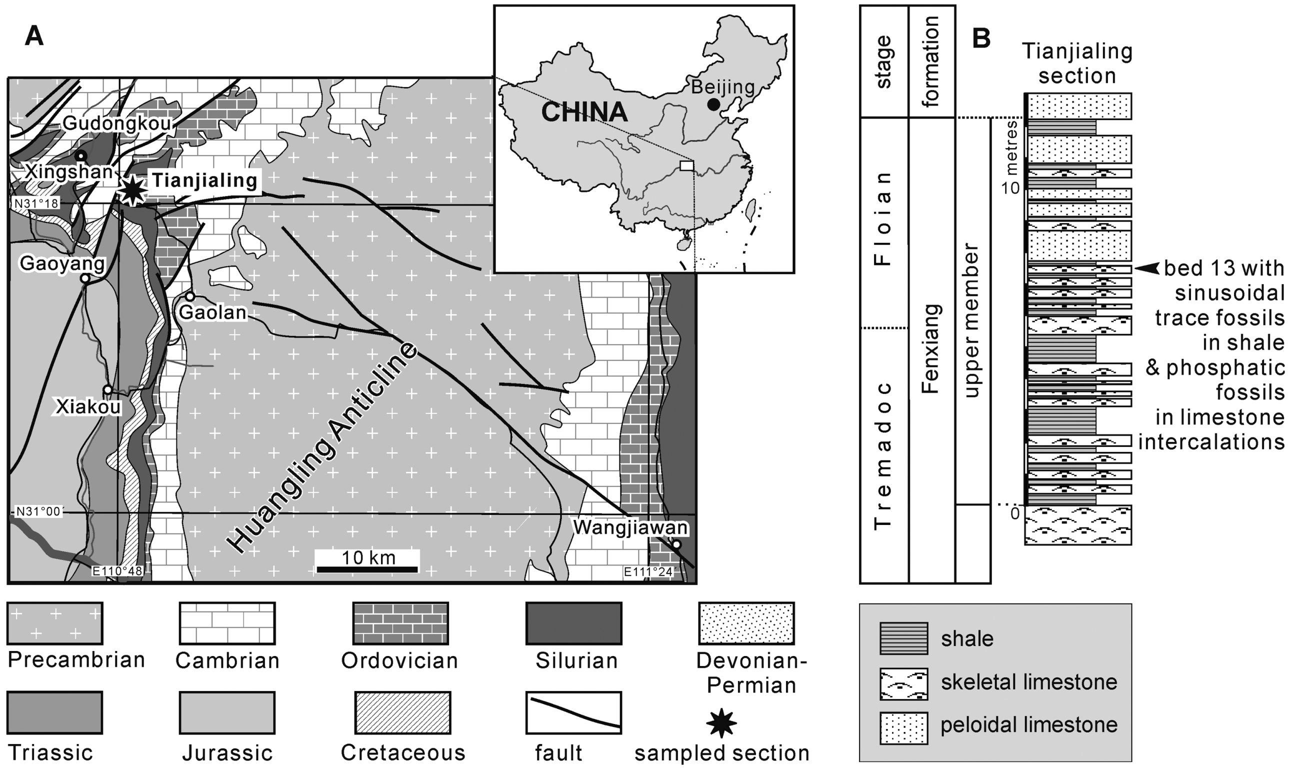

Fig. 1. Location of the Tianjialing section in the Three Gorge area of Hubei Province, southern China. A: Geological map; B: Rock column of the Fenxiang Formation with the source level of the sinusoidal traces indicated (modified after Baliński *et al.*, 2012).

The Formation is built of dark grey to grey skeletal and peloidal limestone intercalating with greenish-grey shale.

In the Tianjialing section, the Formation is about 10 m thick (Fig. 1B). The rather sparse fossils are trepostome and rhabdomesonate bryozoans, trilobites and benthic graptolites. In acid-resistant residues of the limy intercalations, phosphatised antipatharian corals are abundant (Baliński *et al.*, 2012) but brachiopods, conodonts and the phosphatised remnants of arthropods also occur.

The age of the strata can be precisely determined owing to the conodonts they have yielded. Their low-diversity assemblage is dominated by an unidentified generalised species of the protopanderodontid conodont *Drepanodus*, a species of the distacodontid *Drepanoistodus*, and the prioniodontid *Acodus triangularis*. The finely denticulate processes of the latter indicate the early Arenigian stage in the evolution of the lineage. No denticulation occurs in its predecessor, *A. deltatus*, (a chronospecies representing the same lineage) in a sample from the base of the graptolite *Tetragraptus approximatus* Zone at Hunneberg in Sweden, the standard (stratotype) for the boundary between the Tremadocian and Floian, the second global stage of the Ordovician, corresponding to the British Arenigian (for more detailed discussion, see Baliński *et al.*, 2012).

Although the exposure has yielded mostly fragmented fossils, a few specimens preserving mineralised soft body structures of linguloid brachiopods and a hydroid colony are among them. They were all found in a bed of greenish-grey shale a few cm thick. In the same shale, intercalation microscopic size traces occur that are the subject of the present work.

PRESERVATION AND TAPHONOMY

Pyrite frequently mineralises soft organic material to reproduce it as fossils (*e.g.*, Gabbott *et al.*, 2004; Moore & Lieberman, 2009). The soft tissue bacterial decay promotes precipitation of poorly crystalline iron sulphides within a bacterial biofilm. They may be subsequently transformed into well-crystallised mackinawite (Fe_9S_8). In present-day seas, the full transformation takes up to 2 years at 25°C (Herbert *et al.*, 1998). In the following succession of mineral transformations ferromagnetic greigite (Fe_3S_4) is a precursor to pyrite (FeS_2), which is a stable component of the rock. In normal sedimentary conditions of low temperature, framboidal pyrite forms within the biofilm (MacLean *et al.*, 2008).

Although the concentrations of framboids in the Fenxiang sinusoidal fossils are arranged in the same way as in associated organic soft-bodied organisms (linguloid brachiopods preserving pedicle and a hydroid colony), these are barely body fossils. Fortunately, a close analogue of the preservation of Ordovician fossils is offered by results of the life activity of infaunal organisms in present-day aquatic environments.

Results

The structures within the shale are cylindrical. Their diam. ranges from 42 to 55 μm in the most complete track. The narrowest trace fossil is 22-24 μm in diam., the largest, in dense assemblages, reaching 63 μm. The course of the cylindrical fossils is almost regularly sinusoidal in the horizontal plane. The sinusoids are more or less asymmetrical with a slope of variable inclination. The shale is deformed by compaction together with skeletal fossils but the cylindrical structures, apparently pyritised during early diagenesis of the sediment prior to its compaction, are weakly deformed. In places they wave in the vertical plane and the sinusoid is strongly flattened by compaction, a fact which makes the burrow almost straight (Fig. 2B, lower burrow; Fig. 2C, additional sediment laminae). The wave is still recognisable because of the preservation of additional sediment laminae in concave parts of the burrow. The degree of compaction as a result of dehydration of the clay and tectonic compaction of claystone is hard to determine, but the original sediment thickness was definitely many times greater than present. In rare cases, burrows with the round pyritised interior transversely sectioned at the shale bedding plane may cross several laminae (Fig. 2C), which means that such burrows were almost vertical prior to compaction.

The general course of the sinusoids may be almost linear for more than 3 mm, which roughly corresponds to eight waves (Fig. 2). They may cross each other and crowd densely in some areas. The fossils are filled with

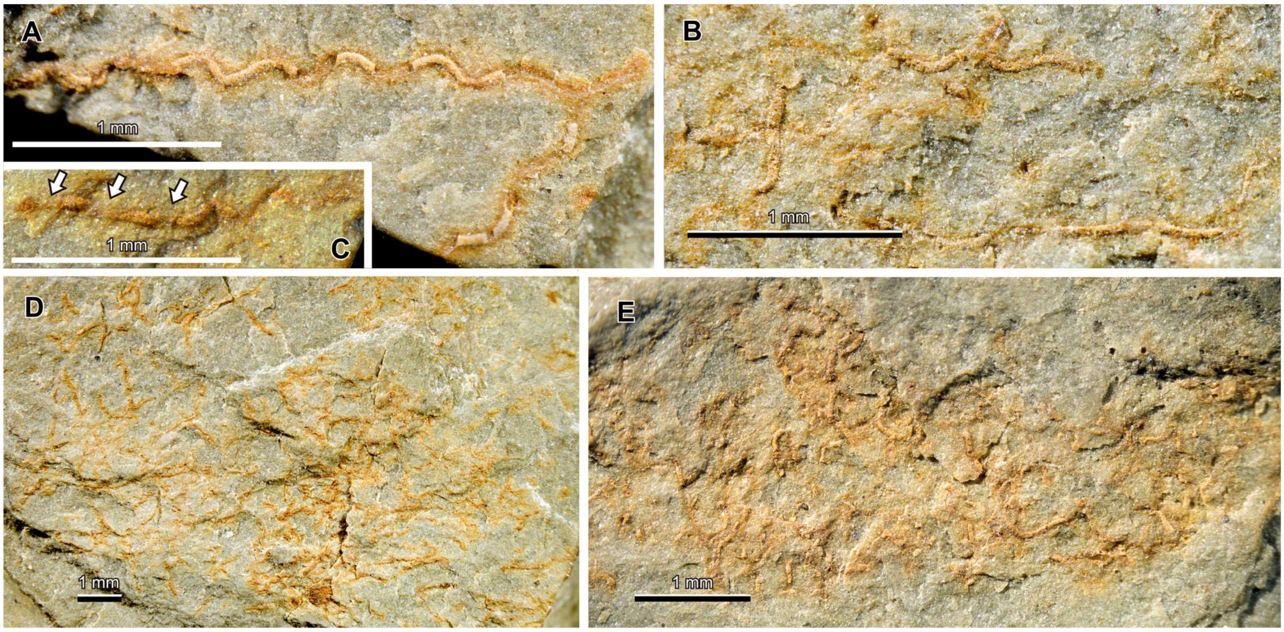

Fig. 2. Sinusoidal tracks in the shale intercalation within the Fenxiang Formation collected at the Tianjialing section. A: The longest linear track crossing with another one under angle. Note that the pyritised (secondarily oxidised) infill of the burrows is preserved three-dimensionally. The rusty coloration of the rock nearby is a result of weathering; B: More typical arrangement of tracks; C: Burrow crossing sediment laminae and with vertical plane of sinusoidal undulation (arrows point to parts of the burrow covered with sediment; see also the seemingly straight burrow in B); D, E: Intensely bioturbated portion of the shale. This figure is published in colour in the online edition of this journal, which can be accessed *via* http://booksandjournals.brillonline.com/content/15685411.

tightly packed spherical framboids, which implies that the original mineral was pyrite (FeS_2). The elemental analysis of the framboids shows a concentration of iron. However, despite the morphology of the framboids, there is no significant sulphur component (Fig. 3D, E). Apparently, the pyrite was altered to iron oxide due to diagenetic and weathering processes. A rusty coloration extends outside the cylindrical core, apparently as a result of weathering. Other mapped elements (silica, aluminium, potassium and magnesium) are mostly associated with the rock matrix and are characteristic for clay minerals. Clay mineral flakes also seem to be originally present between the framboid aggregates and in the central part of the tube (Fig. 3C).

Discussion

INTERPRETATION OF TRACES

The Fenxiang fossils closely resemble the burrows of free-living nematodes (Jensen, 1996). These bacteriovores penetrate the substrate leaving sinusoidal tracks. Their diameter, depending on body size of the trace maker, is similar to those in the Fenxiang Formation. The burrow is a "liquid-filled space surrounded by a bacteria-enriched wall" (Jensen, 1996, p. 323). The nematode burrowing activity induces bacterial growth and colonisation by eukaryotic microbes within a few hours. As a result, the interior of the burrow is filled with an opaque material (Jensen, 1996). The relatively smooth surface of cylindrical walls of the Fenxiang burrows suggests that they were formed by nematodes and lined with mucus. Free-living marine nematodes, such as *Ptycholaimellus*, are known to impregnate the walls of their vertical sinuous burrows with mucus produced by special gland cells (Nehring *et al.*, 1990) but no nematodes are known to construct tubes, although they may inhabit sand tubes made by foraminifera (Hope & Murphy, 1969). Tubes of agglutinating foraminifers are of less regular shape than true nematode burrows (*e.g.*, Gooday *et al.*, 2007).

One may suggest that such burrows, filled or lined with a protein-rich organic matter, were the subjects of pyrite framboids precipitation in the Ordovician Fenxiang environment. The width of the burrows corresponds to the diameter of the trace maker. The Ordovician species was thus within the usual size range of the present-day free-living marine nematodes.

The sinusoidal pattern of the Ordovician burrows in turn suggests that their makers moved by a waving of the body, presumably in the same manner as extant nematodes, *i.e.*, in the dorso-ventral plane of an animal on its side (Robinson & Perry, 2006). Rarely, waving occurred in the vertical plane and the burrows crossed the sediment lamination obliquely. Sinusoidal locomotion ensues from alternate waves of contraction and relaxation of longitudinal body wall muscles. To be efficient this mode of locomotion requires some external resistance afforded by the substrate and stiffness of the body along its axis. In nematodes the body is turgid owing to the high internal pressure of the pseudocoelomic body fluids and a cuticle that does not expand. Nematodes do not have any circular muscles in their body wall and only have four sets of longitudinal muscles that contract in groups according to neuronal stimulation. Although the main body movement is governed by a dorso-ventral wave (Wallace, 1968), the anterior end has complex innervations (Haspel *et al.*, 2010) that permit movements in other planes (Lee & Biggs, 1990). Marine nematodes may penetrate deep into the sediment in search of a food source (Moodley *et al.*, 2000), as was apparently the case with the Chinese Ordovician animals. In certain conditions, nematode burrows of about 50 μm diam. may remain open in a fossil sediment (Pike *et al.*, 2001).

The Fenxiang trace maker was apparently a bacteriovore, as suggested by the organic-rich original contents of the burrows. It could have been a mud-eater, as suggested by the presence of clay mineral particles within the pyritic fill of the burrow. In present-day marine nematode communities, those of a size comparable to the Fenxiang traces are mostly non-selective deposit feeders, the dominant member of the community being *Sabatieria* (Sharma & Bluhm, 2011).

FOSSIL RECORD OF NEMATODE EVOLUTION

Nematode anatomy is usually rather simple and its taxonomically diagnostic aspects are unlikely to be preserved in normal conditions of fossilisation. Because of this limitation, virtually all fossil nematodes that are taxonomically identifiable have been found in amber (Poinar, 2011). Transparent amber does not occur in pre-Cretaceous strata and this imposes a geological age limit on the reliable fossil record of their evolution. The Early Jurassic nematode, *Eophasma jurasicum*, from Osteno, Lombardy (Arduini *et al.*, 1983), preserved as pyritised remains in shale, is the only Mesozoic marine nematode known. The famous Early Carboniferous Bear Gulch Limestone of Montana and the Late Carboniferous Mazon Creek sideritic concretions of Illinois yielded another

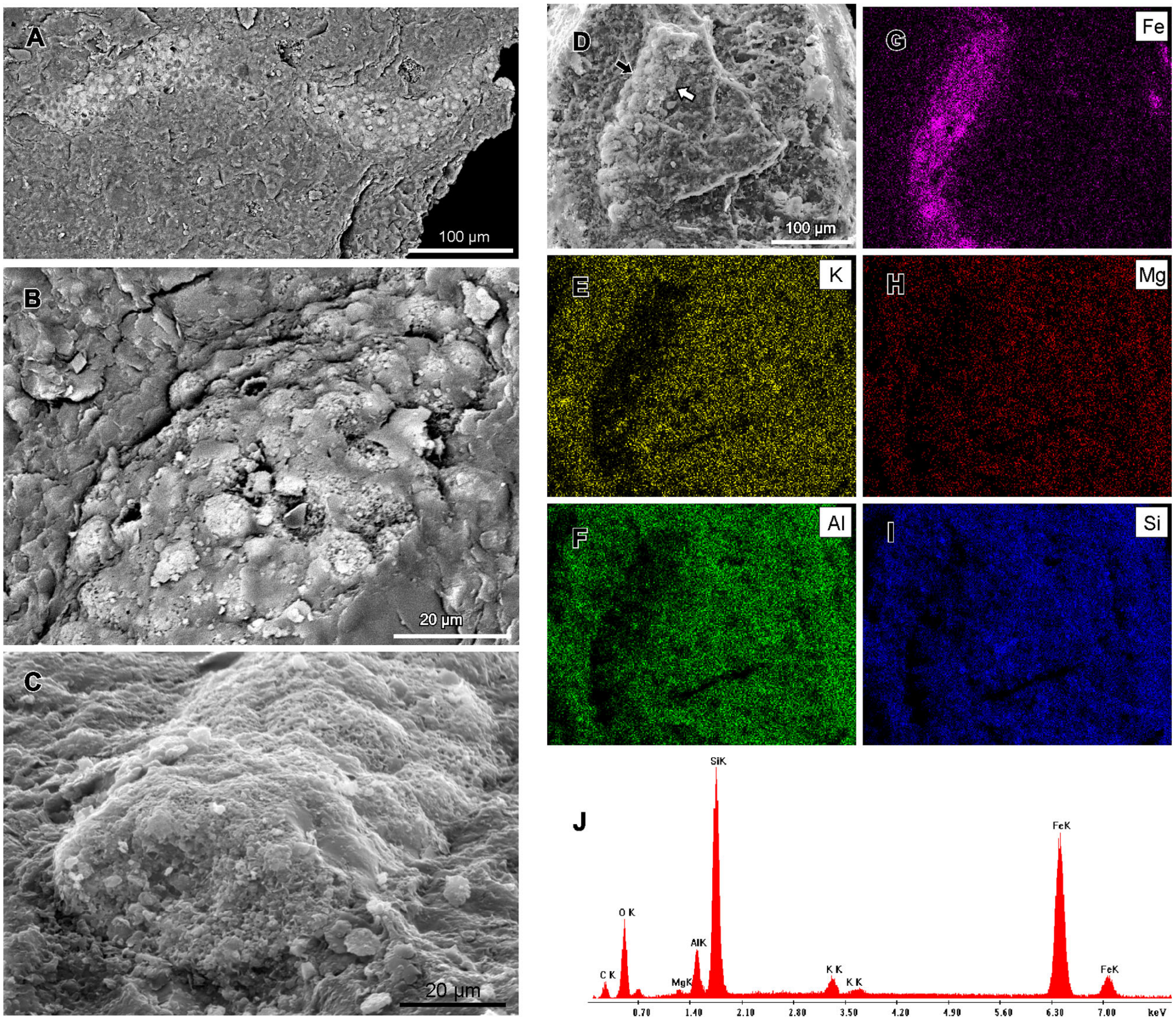

Fig. 3. SEM images and EDS analysis of burrows from the Early Ordovician Fenxiang Formation, China. A: Images with Back-scatter Electron Detector of a portion of rock slab with sinusoidal burrow; B: Enlarged infill of the burrow with pyritic framboids; C: Oblique view of transverse fracture of the burrow showing its three-dimensional aspect and low degree of compaction; D-I: SEM picture and element maps of a piece of burrow; width of the burrow marked with arrows; I: EDS spot analysis spectrum revealing relative contents of elements in a framboid. Note the Fe peak, total absence of S, and presence of Si, Al, Mg, and K connected with the matrix clay minerals; specimen coated with carbon. This figure is published in colour in the online edition of this journal, which can be accessed *via* http://booksandjournals.brillonline.com/content/15685411.

marine nematode, *Nemavermes mackeei* (Schram, 1973, 1979). The "nematodes" described by Størmer (1963) as *Scorpiophagus baculiformis* and *S. latus* are cylindrical structures of 15-22 μm diam. They occur between the dorsal and ventral cuticles of the Early Carboniferous scorpion *Gigantoscorpio willsi* from the Calciferous sandstone of Scotland. Their 'bodies' are invariably straight and were apparently covered with a stiff 'cuticle' which makes the nematode nature of these fossils rather doubtful (Boucot & Poinar, 2010).

Fortunately, a fossilisation medium comparable to amber does occur in the Palaeozoic. This is the famous

Rhynie chert deposited by Early Devonian hot springs near Aberdeen, Scotland. It contains three-dimensionally preserved fossil plants and arthropods giving an insight into the oldest well-preserved terrestrial ecosystem on Earth. The oldest known nematode fossil is the herbivore *Palaeonema phyticum* which comes from these cherts (Poinar *et al.*, 2008).

Because of the scarcity of anatomical evidence, traces of life activity specific to nematodes remain the main source of information on the earliest stages of their evolution. Any animal using undulatory propulsion can leave sinusoidal traces, and many such traces from continental deposits (*e.g.*, Moussa, 1970; Uchman *et al.*, 2009) are more likely to be the product of insect larvae rather than nematodes (Metz, 1987). Geologists classify various sinusoidal traces in the parataxonomic (ichnotaxonomic) genus *Cochlichnus*. Its type species, the Middle Triassic *Cochlichnus anguineus*, is a horizontal trace on the limestone bedding surface about 1 mm wide. It may or may not be a nematode track. However, pyritised sinusoidal traces about 10 μm wide (see Knaust, 2010, Fig. 11C), their dimension suggestive of nematode affinity, do occur in these strata. Some other 'species' of *Cochlichnus* of macroscopic size bear transverse wrinkles indicating peristaltic movement of the trace maker (*e.g.*, Orłowski, 1990; Głuszek, 1995), or longitudinal marks left by parapodia or appendages (*e.g.*, Crimes & Anderson, 1985). Clearly, sinusoidal tracks left by nematodes cannot be diagnostic for particular species, although nematodes of different taxonomic position leave different traces on a standardised substrate (Jensen, 1996). However, before the Fenxiang finding reported here, the oldest trace fossil evidence of nematodes was of Middle Triassic age.

The small size of the Fenxiang traces contrasts with that of fossil marine nematodes known from their body fossils. Clearly, large specimens are the easiest to notice as fossils. The Early Jurassic nematode *Eophasma* is approximately 2 mm wide (Arduini *et al.*, 1983), thus an order of magnitude larger than the Ordovician trace. The Early Carboniferous specimens of *Nemavermes* from the Bear Gulch Limestone of Montana reach 3.5 mm in width (Schram, 1979), its Late Carboniferous type material from the Mazon Creek fauna of Illinois includes specimens more than 6 mm wide (Schram, 1973). If these truly were nematodes, the upper size range of ancient free-living nematodes is different than that of their extant relatives. In fact, this may be an indication of proximity to the closest relatives of nematodes, the Nematomorpha. They also have only longitudinal muscles and move by lateral waving of the body, being unable to penetrate the substrate peristaltically. Their probable ancestors, palaeoscolecids, are diverse and common fossils in the early Palaeozoic strata, including the Ordovician (*e.g.*, Whittard, 1953; Conway Morris, 1997; Botting *et al.*, 2012). This may mean that some large-size sinusoidal traces may truly represent nematodes or forms transitional to the palaeoscolecids and they should be re-examined more closely.

Be that as it may, the Fenxiang fossil suggests that, in the Early Ordovician, marine nematodes of size similar to extant species were already present. Their small size may be connected with adaptation to life in low oxygen conditions within the marine mud. As shown by their abundance in the Fenxiang shale, they were locally important bioturbators, penetrating and distorting much of the sediment volume. Such a mode of life was barely possible before the advent of macroscopic bioturbators, which homogenised the bottom sediments in the early Cambrian (the "Agricultural Revolution" of Seilacher, 1999). These were nemathelminthans with the ability for peristaltic penetration of the sediment owing to the transverse musculature in their body walls, and were ancestors of the present-day priapulids (Dzik, 2003). Even less likely is the origin of nematodes in the conditions prevailing at the sea bottom in the earliest Cambrian and Ediacaran, when its surface was covered with microbial mats. The fossil evidence seems to be more or less consistent with this scenario. Presumably, the main anatomical and ecological transformations that resulted in developing the nematode body plan took place during the Cambrian.

Acknowledgements

SEM pictures and EDS measurements were taken at the Institute of Paleobiology (Warsaw, Poland). Anna Kozłowska (Institute of Palaeobiology) determined graptolites co-occurring in the sample. The research was founded by the Polish Ministry of Science and Higher Education, project No. N307 130537 to A.B.

References

Arduini, P., Pinna, G. & Teruzzi, G. (1983). *Eophasma jurassicum* n. g. n. sp., a new fossil nematode of the Sinemurian of Osteno in Lombardy. *Atti della Società Italiana di Scienze Naturali a del Museo Civico di Storia Naturale, Milano* 124, 61-64.

Baliński, A., Sun, Y. & Dzik, J. (2012). 470-Million-years-old black corals from China. *Naturwissenschaften* 99, 645-653.

Botting, J.P., Muir, L.A., Van Roy, P., Bates, D. & Upton, C. (2012). Diverse middle Ordovician palaeoscolecidan worms from the Builth-Llandrindod inlier of central Wales. *Palaeontology* 55, 501-528.

Boucot, A.J. & Poinar Jr, G.O. (2010). Predation and feeding behaviors. In: Boucot, A.J. & Poinar Jr, G.O. *Fossil behavior compendium*. Boca Raton, FL, USA, CRC Press, pp. 79-118.

Conway Morris, S. (1997). The cuticular structure of the 495-Myr-old type species of the fossil worm *Palaeoscolex*, *P. piscatorum* (?Priapulida). *Zoological Journal of the Linnaean Society* 119, 69-82.

Crimes, T.P. & Anderson, M.M. (1985). Trace fossils from late Precambrian-Early Cambrian strata of southeastern Newfoundland (Canada): temporal and environmental implications. *Journal of Paleontology* 59, 310-343.

Dzik, J. (2005). Behavioral and anatomical unity of the earliest burrowing animals and the cause of the 'Cambrian explosion'. *Paleobiology* 31, 507-525.

Gabbott, S.E., Xiang-Guang, H., Norry, M.J. & Siveter, D.J. (2004). Preservation of Early Cambrian animals of the Chengjiang biota. *Geology* 32, 901-904.

Głuszek, A. (1995). Invertebrate trace fossils in the continental deposits of an Upper Carboniferous coal-bearing succession, Upper Silesia, Poland. *Studia Geologica Polonica* 108, 171-202.

Gooday, A.J., Cedhagen, T., Kamenskaya, O.E. & Cornelius, N. (2007). The biodiversity and biogeography of komokiaceans and other enigmatic foraminiferan-like protists in the deep Southern Ocean. *Deep-Sea Research Part II* 54, 1691-1719.

Haspel, G., O'Donovan, M.J. & Hart, A.C. (2010). Motoneurons dedicated to either forward or backward locomotion in the nematode *Caenorhabditis elegans*. *The Journal of Neuroscience* 30, 11151-11156.

Heip, C., Vincx, M. & Vranken, G. (1985). The ecology of marine nematodes. *Oceanography and Marine Biology Annual Reviews* 23, 399-489.

Herbert, R.B., Benner, S.G., Pratt, A.R. & Blowes, D.W. (1998). Surface chemistry and morphology of poorly crystalline iron sulfides precipitated in media containing sulfate-reducing bacteria. *Chemical Geology* 144, 87-97.

Holterman, M., van der Wurff, A., van den Elsen, S., van Megen, H., Bongers, T., Holovachov, O., Bakker, J. & Helder, J. (2006). Phylum-wide analysis of SSU rDNA reveals deep phylogenetic relationships among nematodes and accelerated evolution toward crown clade. *Molecular Biology and Evolution* 23, 1792-1800.

Hope, W.D. & Murphy, D.G. (1969). *Syringonornus typicus* new genus, new species (Enoplida: Leptosomatidae) a marine nematode inhabiting arenaceous tubes. *Proceedings of the Biological Society of Washington* 82, 511-518.

Jensen, P. (1996). Burrows of marine nematodes as centres for microbial growth. *Nematologica* 42, 320-329.

Knaust, D. (2010). Remarkably preserved benthic organisms and their traces from a Middle Triassic (Muschelkalk) mud flat. *Lethaia* 43, 344-356.

Lee, D.L. & Biggs, W.D. (1990). Two- and three-dimensional locomotion of the nematode *Nippostrongylus brasiliensis*. *Parasitology* 101, 301-308.

MacLean, L.C., Tyliszczak, T., Gilbert, P.U., Zhou, D., Pray, T.J., Onstott, T.C. & Southam, G. (2008). A high-resolution chemical and structural study of framboidal pyrite formed within a low-temperature bacterial biofilm. *Geobiology* 6, 471-480.

Metz, R. (1987). Sinusoidal trail formed by a recent biting midge (Family Ceratopogonidae): trace fossil implications. *Journal of Paleontology* 61, 312-314.

Moodley, L., Chen, G., Heip, C.H.R. & Vincx, M. (2000). Vertical distribution of meiofauna in sediments from contrasting sites in the Adriatic Sea: clues to the role of abiotic versus biotic control. *Ophelia* 53, 203-212.

Moore, R.A. & Lieberman, B.S. (2009). Preservation of early and Middle Cambrian soft-bodied arthropods from the Pioche Shale, Nevada, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 277, 57-62.

Moussa, M.T. (1970). Reviewed source: nematode fossil trails from the Green River Formation (Eocene) in the Uinta Basin, Utah. *Journal of Paleontology* 44, 304-307.

Nehring, S., Jensen, P. & Lorenzen, S. (1990). Tube-dwelling nematodes: tube construction and possible ecological effects on sediment-water interfaces. *Marine Ecology Progress Series* 64, 123-128.

Orłowski, S. (1990). Trace fossils in the Lower Cambrian sequence in the Świętokrzyskie Mountains, Central Poland. *Acta Palaeontologica Polonica* 34, 211-231.

Pike, J., Bernhard, J.M., Moreton, S.G. & Butler, I.B. (2001). Microbioirrigation of marine sediments in dysoxic environments: implications for early sediment fabric formation and diagenetic processes. *Geology* 29, 923-926.

Poinar Jr, G.O. (2011). *The evolutionary history of nematodes: as revealed in stone, amber and mummies*. *Nematology Monographs & Perspectives 9* (Series Editors: Hunt, D.J. & Perry, R.N.). Leiden, The Netherlands, Brill.

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

Robinson, A.F. & Perry, R.N. (2006). Behaviour and sensory perception. In: Perry, R.N. & Moens, M. (Eds). *Plant nematology*. Wallingford, UK, CABI Publishing, pp. 210-233.

Schram, F.R. (1973). Pseudocoelomates and a nemertine from the Illinois Pennsylvanian. *Journal of Paleontology* 47, 985-989.

Schram, F.R. (1979). Worms of the Mississippian Bear Gulch Limestone of central Montana, USA. *Transactions of the San Diego Society of Natural History* 19, 107-120.

Seilacher, A. (1999). Biomat-related lifestyles in the Precambrian. *Palaios* 14, 86-93.

Sharma, J. & Bluhm, B.A. (2011). Diversity of larger free-living nematodes from macrobenthos (>250 μm) in the Arctic deep-sea Canada Basin. *Marine Biodiversity* 41, 455-465.

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

Uchman, A., Kazakauskas, V. & Gaigalas, A. (2009). Trace fossils from Late Pleistocene varved lacustrine sediments in eastern Lithuania. *Palaeogeography, Palaeoclimatology, Palaeoecology* 272, 199-211.

Wallace, H.R. (1968). The dynamics of nematode movement. *Annual Review of Phytopathology* 6, 91-114.

Whittard, W.F. (1953). *Palaeoscolex piscatorum* gen. et sp. nov., a worm from the Tremadocian of Shropshire. *Quarterly Journal of the Geological Society of London* 109, 125-135.

Zhan, R. & Jin, J. (2007). *Ordovician-Early Silurian (Llandovery) stratigraphy and palaeontology of the Upper Yangtze Platform, South China*. Beijing, China, Science Press.