Paläontologische Zeitschrift	73 (1/2)	187–193	5 Abb.	Stuttgart, Mai 1999

A Lower Cambrian shallow-water occurrence of the branching 'deep-water' type trace fossil *Dendrorhaphe* from the Lontova Formation, eastern Latvia

SÖREN JENSEN, Cambridge & KAISA MENS, Tallinn

With 5 figures

Kurzfassung: Das Vorkommen des verzweigten Spurenfossils *Dendrorhaphe* wird aus der unterkambrischen Lontova Formation von Litauen beschrieben. Im Mesozoikum und Känozoikum tritt dieser Spurentyp ausnahmslos in Flyschablagerungen des Tiefwassers auf. Bei *Dendrorhaphe* handelt es sich deshalb vermutlich um ein weiteres Beispiel eines Flysch-Spurenfossils, das im frühen Paläozoikum im Flachwasser entstand und anschließend in Richtung offenes Meer verdrängt wurde bzw. möglicherweise in diese Richtung expandierte. *Dendrorhaphe* SEILACHER 1977 wurde jüngst mit *Dendrotichnium* FARRÉS 1967 und *Ubinia* GROSSHEIM 1961 synonymisiert. Dies bedarf jedoch noch gründlicherer Untersuchung, bei der vor allem die Beziehung dieser Spurenfossilien zu *Chondrites patulus* FISCHER-OOSTER 1858 geklärt werden muß.

Abstract: We describe a unique Lower Cambrian (Lontova Formation, Latvia) occurrence of a branching trace fossil assigned to *Dendrorhaphe* isp. In the Mesozoic and Cenozoic this type occurs exclusively in deep-water flysch deposits. *Dendrorhaphe* may, therefore, be an additional example of a flysch-type trace fossil with an origin in early Palaeozoic shallow-water environments and subsequent onshore-offshore displacement, or perhaps, expansion. Recently, *Dendrorhaphe* SEILACHER 1977, has been synonymized with *Dendrotichnium* FARRÉS 1967 and *Ubinia* GROSSHEJM 1961. This needs further consideration, especially because of possible relation of these ichnogenera to *Chondrites patulus* FISCHER-OOSTER 1858.

Introduction

Throughout most of the Phanerozoic, trace fossils occur in recurrent assemblages. These assemblages are apparently related to environmental factors such as availability of food and depositional dynamics. This was first formulated by SEILACHER (1967) as several ichnofacies representing increasing water depth with the ichnofacies sequence Skolithos, Cruziana, Zoophycos, and Nereites (following BROMLEY 1996 we do not italize the eponymous ichnogenera). SEILACHER (1967) realised that water depth only indirectly controlled this distribution, and this has been further emphasised by others, notably EKDALE (1988). Mesozoic and Cenozoic deep-water flysch deposits are characterised by the Nereites ichnofacies, which includes regular spirals, networks, and meanders. SEILACHER (1977) interpreted several of these traces as shallow-tier open mud-burrows, that to be preserved were exhumed and cast on the sole of turbidite beds. Several of these traces, broadly referred to as graphoglyptids, show features that do not conform to a deposit-feeding origin. Those include leaving much unused space, multiple exits, and the complex patterns (SEILACHER 1977). SEILACHER (1977) presented the elegant and plausible theory that these traces are galleries for cultivation of micro-organisms. There is, however, no direct evidence for either the nature of the producers of graphoglyptids or their ecological significance (MILLER 1991). Even so, they appear to be structures constructed by ecologic specialists in stable and predictable environments (EKDALE 1985). Graphoglyptids range throughout the Phanerozoic, but by-and-large are restricted to deep-water settings. In the Cambrian, however, things appear to be different. Somewhat surprisingly, there is a growing record of such trace fossils found in Cambrian shallow-water deposits (see CRIMES et al. 1992; CRIMES & FEDONKIN 1994). Their history, of apparent migration into deeper water may, therefore, parallel the onshore-offshore trends documented in many animal groups. CRIMES (1992) interprets this as shallow water origination of the trace producers with a displacement and retreat into deep-sea environments, already underway in the Ordovician. In some forms there appears to have been an initial phase of expansion, lasting at least until the end of the Ordovician (STANLEY & PICKERILL 1993). On-

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Addresses of the authors: Dr. SÖREN JENSEN, Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK; Dr. KAISA MENS, Institute of Geology at Tallinn Technical University, Estonia Blvd. 7, EE-0001 Tallinn, Estonia.

0031-0220/99/0073-0187 $ 1.75

shore-offshore trends in trace fossils have also been documented later in the Phanerozoic, notably for *Ophiomorpha* and *Zoophycos* (BOTTJER et al. 1988). The causes of this offshore trend are poorly understood, but it is probable that in the case of graphoglyptids increased vertical bioturbation during the Phanerozoic would have been detrimental to this type of burrow strategy in shallow waters (GOLDRING & JENSEN 1996).

Here we report a regularly branching trace fossil from the Lontova Formation in eastern Latvia, identified as the probable graphoglyptid *Dendrorhaphe* isp. The specimen is incompletely preserved, but shows that it is a type of trace that has been largely reported from Cretaceous-Paleogene flysch deposits. Our purpose is to document, for the first time, the occurrence of this type of branching trace in the Cambrian, so providing additional documentation of deep-water type trace fossils in early Palaeozoic shallow water sediments. We also briefly discuss the relationships and taxonomy of *Dendrorhaphe*, *Dendrotichnium*, and *Chondrites patulus*.

The described material is deposited in the Institute of Geology at Tallinn Technical University, Tallinn, Estonia.

Stratigraphy and geological setting

The Lontova Formation was deposited on the East-European Platform during pre-trilobite early Cambrian. On palaeontological criteria (shelly fossils and acritarchs) the Baltic Group is subdivided into the Rovno (lower) and Lontova (upper) Regional Stages (MENS et al. 1990). By its later phase, the Lontova sedimentary basin covered a wide area of the Baltic region and was connected to similar sedimentary basins in northern Scandinavia, Poland and the Ukraine (MENS 1987). Biostratigraphically, the Lontova Formation is characterised by an assemblage of acritarchs and shelly fossils, including *Platysolenites antiquissimus* (MENS 1987; MENS et al. 1990). Traditionally, the Lontova Regional Stage has been considered a time equivalent of the Siberian Tommotian Stage, but there is growing evidence that the latter correlates with the somewhat younger trilobite-bearing early Cambrian sequences on Baltica (MOCZYDLOWSKA & VIDAL 1988; VOLKOVA et al. 1990).

In eastern Latvia the thickness of the Lontova Formation increases to the south-east, reaching about 130 m. The most detailed sedimentological and palaeontological information is available from the Ludza-15 core, where the Lontova Formation spans both the Lontova and Rovno Regional Stages (BIRKIS et al. 1972). The Atasiene-9 core (Fig. 1) can be readily compared with the Ludza core, except that here the Lontova Formation belongs entirely to the Lontova Regional Stage (BRANGULIS 1985). The Lontova Formation in eastern Latvia, as well as over most of its distribution in the Baltic region, is largely represented by little compacted greenish-grey or variegated argillaceous rocks with minor beds of sand- and siltstone (MENS et al.1990). It lies transgressively on sedimentary rocks of the Rovno Regional Stage, on Vendian rocks, or on crystalline basement. Bedding is poorly developed and more often absent. Deposition was in relatively shallow waters (MENS 1987). ARTJUSHOV et al. (1997) suggest water depths of about 40-50 m in the Leningrad region.

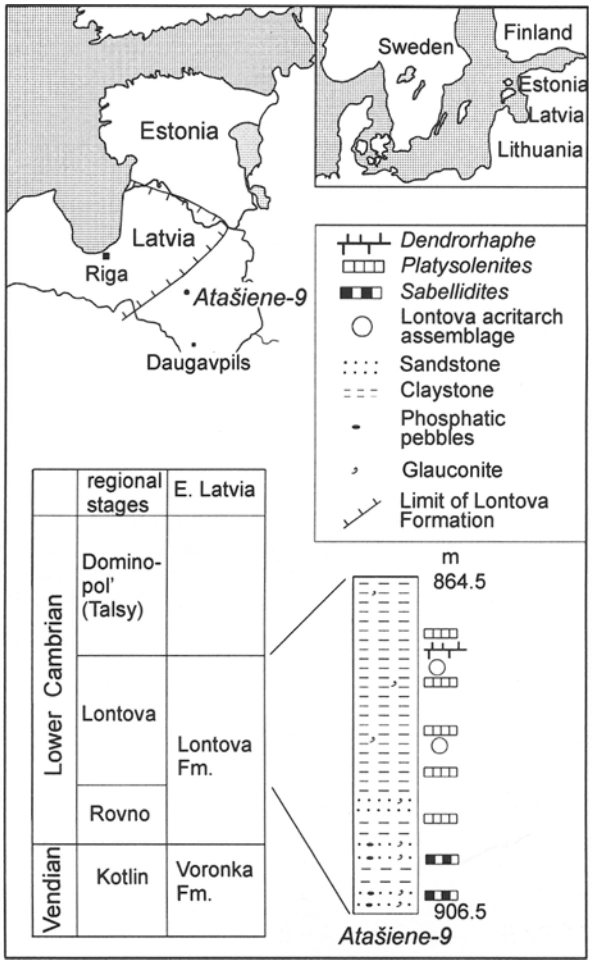

Fig. 1. Geographical location and stratigraphic context of Lower Cambrian *Dendrorhaphe* isp. Lithological log based on BRANGULIS (1985) and observations by K. MENS.

A characteristic feature of the argillaceous portions of the Lontova Formation is the presence of trace fossils preserved as thin pyrite (or pyrite derivative) films (e.g. PALIJ et al. 1983; TAMMEAID 1990). These are often relatively abundant but because of the general absence of bedding only small portions of the trace fossils are visible, making the recognition of morphologies difficult. The most common forms can be broadly classified as *Planolites*, with *Helminthopsis* and *Cochlichnus* also occurring (PALIJ et al. 1983). More conventional preservation of trace fossils occurs in sandier portions of the Lontova Formation, including the Cambrian-type trace fossil *Treptichnus pedum* (PALIJ et al. 1983: pl. 63, fig. 5) near the base of the Lontova Formation in Estonia.

Systematic ichnology

Ichnogenus *Dendrorhaphe* SEILACHER 1977

Emended diagnosis: Endogenic horizontal trace fossil with straight or slightly winding axial string, extending from which are irregularly arranged arcuate or straight simple branches.

Dendrorhaphe isp.

Fig. 2

Material: One specimen (IG Va 1844) from the early Cambrian Lontova Formation, Lontova Regional Stage, eastern Latvia, Atasiene-9 core, depth 874.0 m. Specimen collected by Dr. ERIKA POSTI.

Description: Horizontal trace fossil consisting of a more or less straight stem from which at least six irregularly spaced branches arise on either side (Fig. 2). The stem and branches lie in essentially one plane, though there is a small variation in the level of the branches. Preserved as an endogenic thin reddish film in a silty, micaceous, claystone. The branches are straight to gently curved and arranged almost perpendicular to the main stem. The branches show an unidirectional and relatively abrupt curvature immediately before they join the main stem (Fig. 2). Width of central stem 0.3 mm, branches 0.25-0.3 mm wide. Preserved length of central stem 35 mm. The branches terminate abruptly, evidently representing preservational rather than original ends; greatest preserved length is just over 3 mm.

The trace has a higher content of iron than the surrounding sediment but there is not a significant difference in sulphur (SEM analyses). This film probably is a diagenetic remnant of pyrite. X-ray radiography does not produce an image of the trace, probably because of the thinness of the film.

Interpretation: The unusual preservation for this object makes it first necessary to consider alternative interpretations. Specifically, is it a vendotaenid metaphyte? These ribbon-shaped objects are widely reported from late Vendian beds of the East-European platform, though in the Lontova Regional Stage only the fragmentary *Dvinia* occurs (GNILOVSKAYA 1988). The absence of a carbonaceous envelope does not exclude this possibility, because of its potential loss during diagenesis. The specimen described here, however, does not exhibit any expected features for a vendotaenid, such as twisting or angular terminations. Additionally, the regular development of the structure suggests a greater rigidity than that of typical vendotaenids. In this respect a possible exception is *Daltaenia mackenziensis*, from the early Neoproterozoic Little Dal Group of north-west Canada. This is preserved as black carbonaceous or pyritized compressions, which appear to have had a considerable rigidity and possibly had lateral branches (HOFMANN 1985). Nevertheless, considering the length of the branches in the described specimen this interpretation appears unlikely. Circumstantial evidence for the trace fossil origin comes from similarly preserved unequivocal trace fossils. This includes pyritized traces with a vertical or inclined orientation on the same core fragment, including the vertical spiral *Gyrolithes* isp. (Fig. 2). The trace fossil nature of these can be further seen in samples with co-occurrence of specimens with different style of preservation. For example, in the Voosi Formation in Estonia (a western, generally sandier equivalent of the Lontova Formation; KALA et al. 1981) the vertical spiral *Gyrolithes* is preserved as a passive fill of coarse sediment but also as flat iron-impregnated films (Fig. 3). On balance, all evidence strongly favour the interpretation of this object as a trace fossil.

Fig. 2. Branching trace fossil, *Dendrorhaphe* isp., from the Lower Cambrian Lontova Formation, Latvia (IG Va1844). Specimen preserved as horizontal flattened film of iron-impregnated fine sediment in muddy siltstone. Up-down direction not known. In the upper part of the picture is a partially preserved vertical spiral trace fossil, *Gyrolithes* isp. Also seen are fragments of other non-diagnostic trace fossils. – Scale bar = 3 mm.

The branches arise as a direct continuation of the central stem, with successive branches having a consistent direction in their initial curvature. The stem, therefore, represents the overall direction of movement with lateral tunnels made at acute angles to either side, either by the

Fig. 3. Two different preservational styles of the vertical spiral trace fossil *Gyrolithes* isp. (IG Va 1845), Lower specimen filled with medium sand, in part leaving distinctive impressions. Specimen near top preserved as pyrite impregnated material. Kõnnu-300 core, 391.5 m, Taebla Member, Voosi Formation, Estonia. – Scale bar = 2.5 mm.

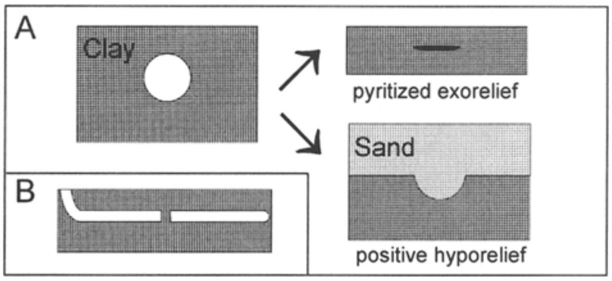

Fig. 4. – **A:** Two preservational histories of an open burrow in fine-grained sediment. Exhumation and casting, for example by turbidity current, leads to preservation in positive hyporelief on sole of coarse bed. Without contrasting sediment, the trace can only fossilize by the formation of diagenetic minerals, as seen in *Dendrorhaphe* isp. described herein. **B:** Two possible morphologies of branches in *Dendrorhaphe* isp. from the Lower Cambrian of Latvia.

whole animal or an extensible portion, such as a proboscis. The initial sharp curvature makes the former alternative the more likely. The slightly greater width of the central stem may be the result of repeated passages of the animal. The state of preserved branches is probably incomplete, but it appears that they were not arranged in opposite pairs. Neither is there any evidence that they alternated in a regular fashion. Fragmentary preservation prevents recognition of whether the branches ended blindly or turned up to intersect the sea-floor (Fig. 4b). This, of course, frustrates further speculation on the ethology. Nevertheless, the preservation as a flat film of iron-enriched sediment indicates that it was originally an open burrow. This does not automatically rule out a deposit-feeding origin. However, the wide spacing of the branches suggest that alternative interpretations must be considered. If the branches connected to the sea-floor (Fig. 4b) the trace would fit Seilacher's (1977) graphoglyptid model, perhaps representing microbial gardening. Alternatively, if the branches ended blindly it would fit a model of chemosymbiosis (Seilacher 1990; Fu 1991).

Taxonomic remarks: In its general morphology this specimen shows similarity with *Dendrotichnium haentzscheli* Farrés 1967 (Fig. 5d). The type material from the Late Cretaceous (Maastrichtian) of Spain is about an order of magnitude larger, and preserved as positive hyporelief on the sole of a turbidite bed (Farrés 1967). In terms of general morphology and preservation this trace is also similar to *Chondrites patulus* Fischer-Ooster 1858, or portions of this (Fig. 5e, f). *Chondrites patulus* is an atypical species of *Chondrites* in that there only rarely is secondary branching (Fig. 5e). The Cambrian specimen shows no sign of secondary branching though this could be due to incomplete preservation.

In recent papers the mode of preservation has been included in the diagnosis of *Dendrotichnium* (Seilacher 1977; Wetzel & Uchman 1997). Seilacher (1977: 308) explicitly stated that similar forms should not be classified as *Dendrotichnium llarenai* if not preserved as sole casts. We feel that difference in mode of preservation (Fig. 4a), should not be used as a taxonomic criterion when the morphology can be reasonably demonstrated to have been equivalent. In an analogous situation, Seilacher (1977: pl. 1, fig. a) illustrates, and identifies as *Paleodictyon*, a rare occurrence of a network graphoglyptid preserved as an iron-stained flattened contour in mud.

Dendrotichnium is a rare form of uncertain origin, but it appears likely that it was an open mud burrow (Seilacher 1977). *Chondrites patulus* is a rare form reported from Cretaceous-Tertiary flysch deposits of central Europe (Fu 1991), and from similar depositional settings to that in which *Dendrotichnium* is found. Most *Dendrotichnium* are larger than *Chondrites patulus* but this, at least in part, could be caused by the different styles of preservation, since exhumation is likely to result in some widening of the trace. Furthermore, Tunis & Uchman (1996) reported a specimen of *Dendrotichnium llarenai* with branches as small as 0.6-0.7 mm wide. Consequently, hypichnial preservation of a portion of a *Chondrites patulus* presumably would result in a trace identical to *Dendrotichnium* (cf. Fig. 5b-f). We suggest that this possibility needs further consideration. Since it

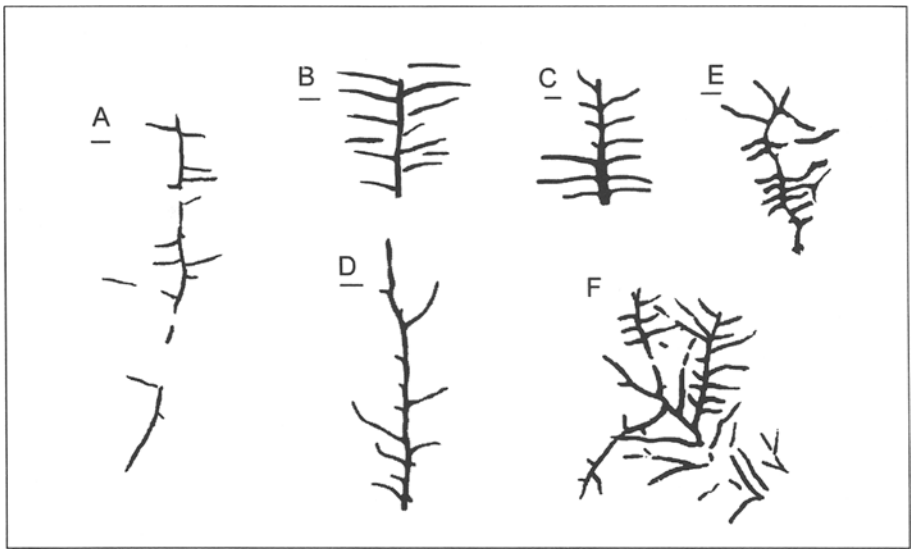

Fig. 5. Schematic tracings of branching trace fossils. – **A:** Lower Cambrian specimen described in this paper. Scale bar = 2 mm. **B:** *Ubinia wassoevitschi* from the Cretaceous of southern Russia (from Grosshejm 1961: pl. 1, fig. 1). Scale bar = 20 mm. **C:** *Dendrotichnium llarenai* from the Cretaceous of Spain (from Farrés 1967: pl. 1, fig. 4). Scale bar = 20 mm. **D:** *Dendrotichnium haentzscheli* from the Cretaceous of Spain (from Farrés 1967: pl. 1, fig. 2). Scale bar = 20 mm. **E:** *Chondrites patulus* from the Cretaceous of Switzerland (from Fu 1991: pl. 2, fig. b). Scale bar = 2 mm. **F:** *Chondrites patulus* from the Cretaceous of Switzerland (from Fischer-Ooster 1858: pl. 8, fig. 7). – Notice similarity of individual branches of the specimens in A-D. About 1/3 natural size.

is possible that there are trace fossils with only one order of branching, the maintenance of separate ichnotaxa seems sensible. In some *Dendrotichnium* the branches do clearly go up at an angle from the stem (Han & Pickerill 1994). This, however, is not a universal trait. The Cambrian specimen described here is comparable to specimens of *Dendrotichnium*, although it is possible that it, and possibly other reports of *Dendrotichnium*, is a partially preserved *Chondrites patulus*.

Wetzel & Uchman (1997) treated *Dendrotichnium* as a subjective junior synonym of *Ubinia* Grosshejm 1961. There is indeed great similarity between *Ubinia wassoevitschi* and *Dendrotichnium llarenai* (Fig. 5b, c) but it may be more questionable if all species currently included in *Dendrotichnium* belong to one ichnogenus. Six species are attributable to *Ubinia* (or *Dendrotichnium*). Besides of its smaller size, the Cambrian specimen differs from *Dendrotichnium seilacheri* Kozur, Krainer & Mostler 1996 and *Dendrotichnium llarenai* Farrés 1967, both of which have regularly arranged lateral branches (Fig. 5c). *Dendrotichnium alternans* Seilacher 1977 has a zig-zag shaped central stem and regularly alternating branches (this is a feature also seen in some *Chondrites patulus*, see Fu 1991: fig. 1b): *Ubinia wassoevitschi* Grosshejm 1961, has more closely spaced and regular branches (Fig. 5b) and may be a subjective senior synonym of *Dendrotichnium llarenai* (Wetzel & Uchman 1997). The description and photographs of *Dendrotichnium pachycladus* Yang 1992, do not permit comparison. As mentioned above, the Cambrian specimen is most similar to *D. haentzscheli*. Because of its simple straight stem and the irregularly arranged branches Seilacher (1977) erected the new monospecific genus *Dendrorhaphe* for this species. Seilacher (1977: 318) suggested that the three specimens of the holotype slab of *Dendrotichnium haentzscheli* are part of a radial system, further pointing to possible links with *Chondrites patulus*. Seilacher's decision to separate *Dendrotichnium haentzscheli*, has not been positively received (Kozur et al. 1996; Wetzel & Uchman 1997). In view of the simple morphology and uncertain relation to more regular forms it seems sensible to maintain this separation at present, and we assign the Cambrian find to *Dendrorhaphe* isp. It probably represents a new species of *Dendrorhaphe*, but formal designation must await more material.

Discussion

This trace fossil has a strongly controlled regular morphology of a type othwerwise principally known from Mesozoic and Cenozoic deep-water flysch deposits. Apparently, however, it has not previously been reported from the Cambrian. Kim et al. (1992) report *Dendrotichnium haentzscheli* from the Ordovician Yeongheung Formation of Korea. These specimens have an unusual preservation in that they occur as convex epirelief in a dolomitic packstone. The assignment to *Dendrotichnium* can not be substantiated from the photograph (Kim et al. 1992: pl. 1, fig. 8) so this report needs further confirmation. The next youngest occurrence is Han & Pickerill's (1994) report of *Dendrotichnium haentzscheli*, from the

Lower Devonian Wapske Formation of eastern Canada. This, however, was not placed in a specific depositional environment. TWITCHETT & WIGNALL (1996) report *Dendrotichnium* isp. from Triassic storm beds of Italy. This identification may be open to question since one of the branches is said to itself branch. The status of supposed *Dendrotichnium* from Triassic shallow-water carbonates in China (BI et al.1996; YANG 1992) is unclear. All post-Triassic occurrences known to us come from deep-water deposits (CRIMES et al. 1981; FARRÉS 1967; GROSSHEJM 1961; LESHCHUKH 1988; MACSOTAY 1967; SEILACHER 1977; TUNIS & UCHMAN 1996; WETZEL & UCHMAN 1997). The number of reports is low but does indicate that *Dendrorhaphe* (or *Ubinia* sensu lato) is another example of an ichnotaxon with an early Palaeozoic shallow water origin, followed by either displacement or expansion (if the Mesozoic shallow-water reports above can be verified) in deeper waters (cf. CRIMES et al. 1992; CRIMES & FEDONKIN 1994).

Traces in the Nereites ichnofacies, such as meanders and spirals, are generally considered K-selected ichnotaxa developed in stable and predictable environments. Deposition in the Lontova basin was dominated by fine-grained material and arguably would have provided an environment reminiscent of deep-sea settings. Together with the apparently low degree of bioturbation, this may have been a setting conductive to ecologic specialists. As yet, the specimen described here from the Lontova Formation is a unique find of a possible graphoglyptid, making unresolved their overall abundance and diversity in the Lontova basin. Regardless, the Lontova Formation displays preservation of open mud burrows that are preserved by virtue of mineral impregnation and exceptionally low levels of compaction. These conditions may have been particularly conducive for the preservation of such slender and supposedly shallow-tier trace fossil and hints at the possibility that this type of trace fossil was more widely distributed in the Cambrian.

Acknowledgment

This paper is part of an ongoing study of Lower Cambrian trace fossils in Estonia (ESF, grant No 3237). We thank SIMON CONWAY MORRIS and PETER CRIMES for comments on an earlier manuscript, FRANZ T. FÜRSICH for review and IAN MARSHALL for SEM analyses. JENSEN's visit to Estonia in 1995 was financed through the exchange program of the Royal Swedish Academy of Sciences and the Estonian Academy of Sciences. JENSEN acknowledges financial support in Cambridge from the Leverhulme Trust, and currently from NERC. Cambridge Department of Earth Sciences Publication 5269.

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Eingang des Manuskriptes am 24. März 1998;
Annahme durch die Schriftleitung am 31. Juli 1998.