Revista Brasileira de Paleontologia, 28(1):e20250542, 2025
A Journal of the Brazilian Society of Paleontology

doi: 10.4072/rbp.2025.1.0542

Article

PALEOENVIRONMENT OF *TAENIDIUM BARRETTI* FROM THE MIDDLE DEVONIAN OLD RED SANDSTONES OF ESTONIA

OLEV VINN
Department of Geology, University of Tartu, Ravila 14A, 50411, Tartu, Estonia.
olev.vinn@ut.ee (Corresponding author)

RADEK MIKULÁŠ
Institute of Geology, Czech Academy of Sciences, Rozvojová 269, 16500, Prague 6 - Lysolaje, Prague, Czech Republic.
mikulas@gli.cas.cz

MARE ISAKAR
Natural History Museum, University of Tartu, Vanemuise tn 46, 51003, Tartu, Estonia.
mare.isakar@ut.ee

MAGDY EL HEDENY
Geology Department, Faculty of Science, Alexandria University, 5WR5+65 Moharam Bek, Egypt.
magdy.elhedeny@alexu.edu.eg

MANSOUR ALMANSOUR & SALEH ALFARRAJ
Zoology Department, College of Science, King Saud University, P.O. Box 2455, Riyadh 11451, Saudi Arabia.
almansour@ksu.edu.sa, alfarraj@ksu.edu.sa

ABSTRACT – Trace fossils are good indicators of paleoenvironment and help us to re-evaluate the contradicting paleoenvironmental setting of the Middle Devonian Old Red Sandstones in Estonia. In this paper, the first ichnofossils are systematically described from the Eifelian of southern Estonia and the eastern Baltic in general. *Taenidium barretti* (Bradshaw) is abundant in laminated siltstone at two horizons. Eifelian sandstones also contain rare *Planolites* isp. These traces were most likely produced by deposit- or detritus-feeding worms or small arthropods. The main difference between the two tracemakers was in the lack of sediment push-back in the case of *Planolites* isp. The lack of sediment push-back in *Planolites* isp. resulted from the different locomotor behavior of the animal and not from the sediment's material properties, which were similar in the case of both traces. There could have been two species of deposit-feeding invertebrates in the Eifelian of Tamme, though a single organism producing different traces could not be ruled out. The discovered traces are either characteristic of nonmarine environments (*T. barretti*) or are facies-crossing traces that occur in nearly all depositional environments (*Planolites* isp.). The trace fossils at Tamme suggest that the paleoenvironment was a fluvially dominated, subaqueous delta plain environment, as suggested by previous sedimentological studies, but contrary to studies based on fossil fish.

Keywords: trace fossils, delta plain, nonmarine environment, terrigenous sedimentation, Eifelian, Baltics.

INTRODUCTION

The trace fossils of the Eastern European Platform from the Cambrian to Silurian periods are well documented (Toom *et al*., 2019). In contrast, ichnofossils from the Middle Devonian Old Red Sandstone facies of the East European Platform are not well understood in an aspect of the paleoenvironment (Mikuláš *et al*., 2013). However, there is extensive knowledge about the fish faunas of the region, which were previously interpreted as marine (Mark-Kurik, 1991, 1995). The Old Red Sandstone facies were deposited during the Middle and Late Devonian in the Laurussia supercontinent (Mikuláš *et al*., 2013). It is widespread across the Eastern European Platform, representing its easternmost region (*e.g*., Friend *et al*., 2000). Other significant occurrences of this facies are found in Spitzbergen, Greenland, Norway, Great Britain, the USA, and Canada, where it is primarily represented by terrigenous siliciclastic deposits from late- to post-orogenic foreland and intramontane molasse basins with occasional marine influence (*e.g*., Friend *et al*., 2000). The Middle Devonian Old Red sandstones of Estonia have previously been suggested to be deposited in non-marine conditions due to the rarity or complete lack of trace fossils (Vinn, 2023). Nearby, in northwest Russia, sedimentary structures suggest that the Old Red deposits of the Andoma Formation (early Frasnian) accumulated under the influence of wave and tidal activity (Tovmasyan & Stinkulis, 2008). Remains of vertebrates, invertebrates such as bivalves, gastropods, and lingulids, as well as plants, have been discovered in several beds of the Andoma Formation. The latter formation has also yielded trace fossils including *Cochlichnus*, *Cruziana*, *Diplocraterion*, *Glockerichnus*, *Lockeia*, *Palaeophycos*, *Planolites*, *Rusophycus*, *Skolithos*, *Teichichnus*, and *Undichna* (Mikuláš *et al*., 2013).

The aim of the paper is: (i) to analyze trace fossils in the Eifelian Old Red Sandstones of Estonia, (ii) to discuss the behavior of tracemakers, (iii) to interpret the paleoenvironment, and (iv) to discuss the paleobiogeography of the identified trace fossils.

GEOLOGICAL BACKGROUND AND LOCALITY

Siliciclastic rocks dominate the Devonian sequence of Estonia, with exceptions in the lower Middle Devonian (Narva Regional Stage) and Upper Devonian (from the Pļaviņas RS to the Daugava RS), where carbonate and carbonate-terrigenous rocks are more prevalent (Mark-Kurik & Põldvere, 2012; Tänavsuu-Milkeviciene *et al*., 2009) (Figure 1). In southern Estonia, Middle Devonian sandstone layers from the Pärnu, Narva, Aruküla, Burtnieki, Gauja, and Amata formations are exposed in an ENE–WSW trend (Kleesment, 1997). The older (Eifelian) part of the Middle Devonian is represented by tide-dominated estuarine deposits of the Pärnu Formation, where sediments fine seawards, the tidal bars have sharply defined bases, and prodelta muds are absent (Tovmasyan, 2004). The Givetian Aruküla Formation is characterized by gradational tidal-bar and tidal-flat successions, which fine seawards into prodelta muds (Tänavsuu-Milkeviciene & Plink-Björklund, 2009). Channel deposits and paleosols are rare within the Aruküla Formation (Tänavsuu-Milkeviciene & Plink-Björklund, 2009).

The Tamme outcrop extends approximately 200 m and reaches a height of up to 5 m; it is located on the eastern shore of Lake Võrtsjärv near the village of Tamme. Exposed at this site are the sandstones of the Kureküla Member of the Aruküla Formation. These rocks consist of well-sorted, brownish red, very fine- to fine-grained sandstone, with bed thicknesses ranging from 0.5 to 0.9 m. The main part of the outcrop features very fine- to fine-grained, cross-stratified sandstone (Figure 2). In the upper portion of the section, laminated siliciclastic mudstone, siltstone, and dolomitic marl are also present (Tänavsuu-Milkeviciene & Plink-Björklund, 2009). Sedimentological analysis suggests that the depositional setting was a fluvially dominated subaqueous delta plain (Plink-Björklund & Björklund, 1999).

MATERIAL AND METHODS

The trace fossils were collected during an excavation for fossil fishes at Tamme (Figure 2) in 1993 and were recently rediscovered in the collection of the Natural History Museum, University of Tartu (TUG 741-103, TUG 741-104, TUG 741-105, TUG 741-106, TUG 741-107 and TUG 741-109). Samples containing trace fossils were partially embedded in gypsum during the fieldwork in order to avoid their disintegration. The specimen was digitally photographed in an uncoated state with a CANON EOS R6 camera. The stratigraphic position of traces was identified using the detailed description of the excavation from 1993 and corroborated during the later visit to Tamme in 2023.

Figure 1. Location of Tamme outcrop, south Estonia.

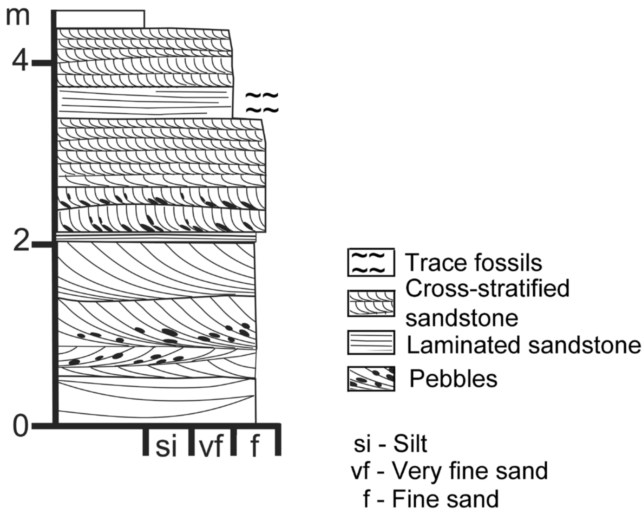

Figure 2. Geological section of Tamme outcrop (after Zirk, 2007). Location of trace fossils indicated.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Taenidium* Heer, 1877

Diagnosis (emended by Bromley *et al.*, 1999**).** Unlined, unbranched, cylindrical trace fossils with a meniscate backfill. These trace fossils are typically straight, curved, or sinuous, and the menisci (curved segments) are evenly spaced and uniformly thick.

Taenidium barretti (Bradshaw, 1981)
(Figure 3A–C)

Material. Four slabs with multiple burrows from the Tamme outcrop, south Estonia, Eifelian, Middle Devonian (TUG 741-103, TUG 741-105, TUG 741-106, TUG 741-107).

Remarks. Burrows are very small (3.5-5.0 mm in diameter) for the ichnospecies and are preserved in full relief. They are unbranched, straight to meandering. Intersections may occur. Tubes lack any lining. The fill is meniscate. Menisci are hemispherical and much shorter than the diameter of the burrow, relatively tightly packed, sometimes forming discrete meniscate segments. The menisci are quite heterogeneous, of different thicknesses and even their diameter is not completely constant. Moreover, at the beginning of one of the traces, there is a more pronounced oval body that can be interpreted as a cubichnion. Some parts of the fill represent a chevron-like rather than a purely meniscate form. The surface of the burrow is often somewhat uneven, sometimes with individual meniscate segments slightly offset from one another. The rock matrix is light yellowish-brown to beige siltstone, whereas the burrow infill is bluish-grey clayey siltstone. The burrows are subparallel to stratification. Menisci are interpreted to represent sediment push-back traces produced by arthropod appendages (Gouramanis & McLoughlin, 2016).

The burrows of *Taenidium barretti* are often found in nonmarine environments (Keighley & Pickerill, 1994), while the ichnogenus *Taenidium* overall is also a relatively common trace fossil in marine and even deep-sea environments (D'Alessandro & Bromley, 1987; Frey & Howard, 1990; Bosetti *et al*., 2021). *T. barretti* is a common constituent of *Scoyenia* ichnofacies, chiefly in moist to wet substrates of fluvial settings, forming composite ichnofabrics including *Skolithos*, *Arenicolites*, *Camborygma*, and *Beaconites* (Savrda *et al*., 2000; Buatois & Mángano, 2004; Melchor *et al*., 2006, 2012; Buatois *et al*., 2007, 2020; Guimarães Netto, 2007; Krapovickas *et al*., 2009; Mancuso *et al*., 2020; Sciscio *et al*., 2021; Nascimento *et al*., 2023). *T. barretti* has a stratigraphic range from the Ordovician to the Recent (Keighley & Pickerill, 1994).

Planolites isp.
(Figure 4)

Material. Single burrow from Tamme outcrop, south Estonia, Eifelian, Middle Devonian (TUG 741-104).

Remarks. Unlined, very gently meandering, smooth surface, circular or elliptical in cross-section, with homogeneous, structureless infill. Burrow diameter varies between 3.0 to 4.0 mm. The burrow infill differs in color (yellowish grey versus brownish grey) and lithology from the host rock (pure siltstone versus clayey siltstone). The burrow is branching via bifurcation at an angle of about 30°. *Planolites* is understood as feeding burrows (fodinichnia) created by deposit-feeders (Pemberton & Frey, 1982), with an age range spanning the Ediacaran or Cambrian to the Holocene (Häntzschel, 1975; Barroso *et al*., 2014; Mángano & Buatois, 2014). It is present in nearly all depositional environments (Pemberton & Frey, 1982).

DISCUSSION

Behavior

Taenidium barretti has usually been classified as a locomotion trace (repichnion) and/or a feeding structure (fodinichnion). The meniscate fill represents active backfill resulting from mechanical manipulation or ingestion by the animal (*e.g*., Buatois & Mángano, 2011). This burrow could be produced during ingestion and excretion of an animal that transports sediment through its body, as it has been associated with deposit- or detritus-feeding habits, most likely of worm-like invertebrates (Bown & Kraus, 1983; D'Alessandro & Bromley, 1987; Sarkar & Chaudhuri, 1992; Retallack, 2001; Schlirf *et al*., 2001). Oligochaetes, millipedes, crustaceans, cicada nymphs, and beetle larvae have been suggested as potential *T. barretti* tracemakers (D'Alessandro & Bromley, 1987; Keighley & Pickerill, 1994; Savrda *et al*., 2000; Buatois *et al*., 2007; Guimarães Netto, 2007; Verde *et al*., 2007; Bedatou *et al*., 2009; Counts & Hasiotis, 2009; Hembree, 2009, 2019; Smith & Hasiotis, 2008; Good & Ekdale, 2014; Rodríguez-Tovar *et al*., 2016; Nascimento *et al*., 2023). Only millipedes, myriapods, and crustaceans could have occurred in the Middle Devonian. The other groups appeared later in geological time. The large burrows are usually assigned

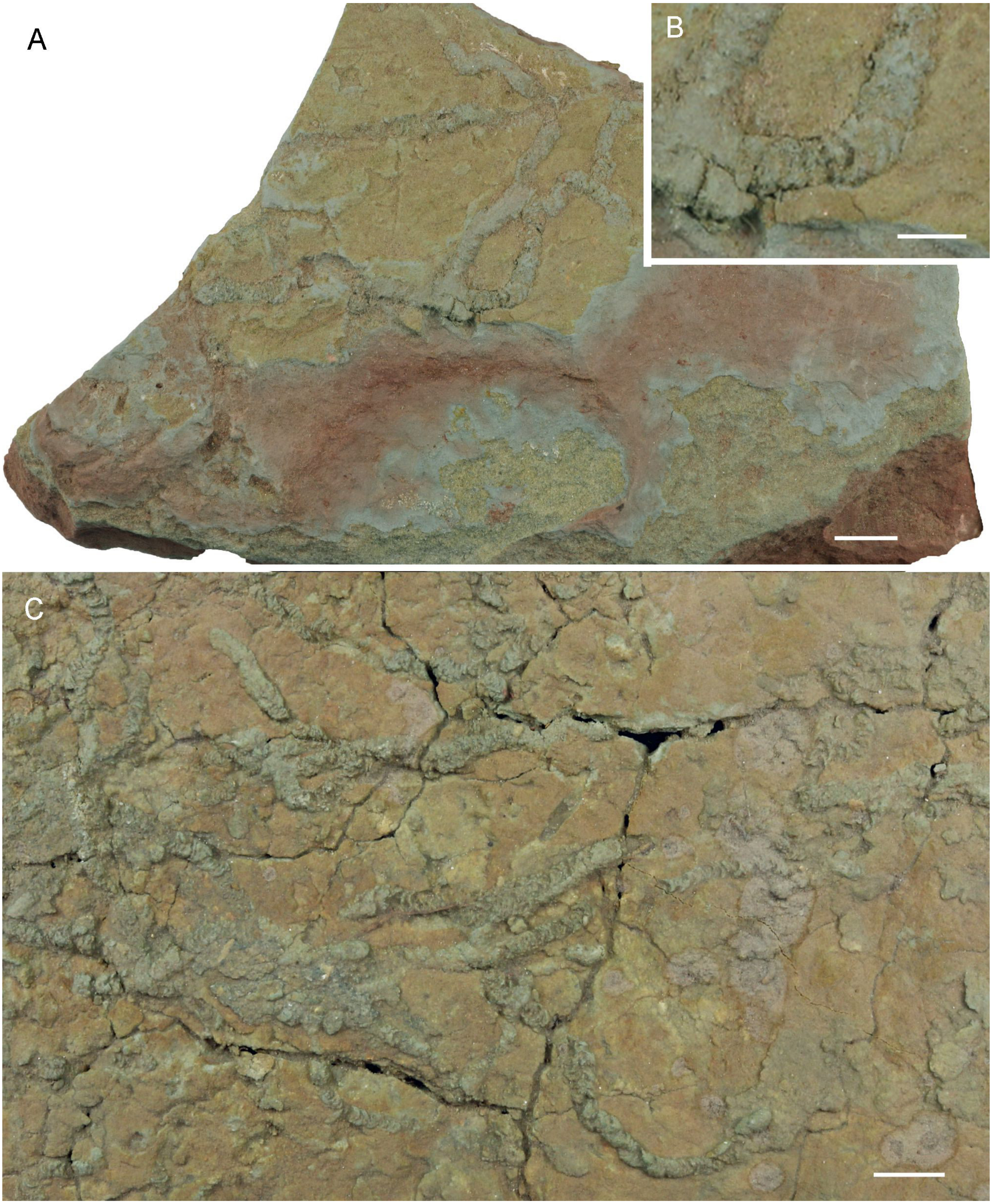

Figure 3. *Taenidium barretti* (Bradshaw, 1981) from Eifelian of Tamme, southern Estonia. **A**, general view of meniscate burrows on the bedding plane (TUG 741-103). **B**, detail view of menisci (TUG 741-103). **C**, general view of meniscate burrows on the bedding plane (TUG 741-105). Scale bars: A, C = 10 mm; B = 5 mm.

to large arthropods. The relatively narrow burrows in the Eifelian of Estonia were produced by animals of a correspondingly small diameter. It makes it more plausible that these traces were produced by deposit- or detritus-feeding arthropods.

Figure 4. *Planolites* isp. from Eifelian of Tamme, southern Estonia (TUG 741-104). Scale bar = 5 mm.

The architecture of *Planolites* isp. suggests that the tracemaker was also a deposit-feeding worm, though exhibiting a different behavior than organisms responsible for the creation of *Taenidium*. The main difference was in the lack of sediment push-back in the case of *Planolites* isp. tracemaker. The lack of sediment push-back most likely resulted from the animal's different locomotor behavior from the sediment's material properties, which were similar in the case of both traces. Thus, there could have been two species of deposit-feeding organisms in the Eifelian of Tamme, though a single organism with two distinct behaviors could not be ruled out.

Paleoenvironment

The lack of *Skolithos* and other shallow-marine trace fossils in the Middle Devonian sections studied by Vinn (2023) has led to the conclusion that the sedimentary environment of Old Red sandstones was likely nonmarine in Estonia. The same would be true for the Russian Pskov area (Ivanov, 2005), where outcrops of the Old Red Sandstone are devoid of any trace fossils and contain fishbone coquinas. The depositional environment of these sandstones at Tamme has been interpreted alternatively as shallow-marine (Kleesment, 1997), a fluvially dominated subaqueous delta-plain (Plink-Björklund & Björklund, 1999), or, in parts of the cross-stratified sandstone, a tidally influenced delta front, with the thin-bedded upper section representing a delta plain environment (Tänavsuu-Milkeviciene & Plink-Björklund, 2009). Vinn (2023) argued that in the case of a normal marine sedimentary environment, one would expect to find a rich ichnofauna characteristic of the shallow tropical sea. He concluded that the lack of such trace fossils suggests that the depositional environment was likely not fully marine, pointing to deposition in a brackish to freshwater environment (Vinn, 2023). This is contradictory to the opinion of Mark-Kurik (1991, 1995), suggesting that Old Red Sandstone fish in the Middle Devonian of Estonia must have been marine as there are numerous species of fish, both large and small, with a wide range of body form, and none having the deep, laterally compressed body typical of riverine inhabitants. Mark-Kurik (1991) suggested that the most probable environment of these fish was a comparatively shallow sea with ample space for migration, rich in oxygen and food. However, the newly discovered traces are either characteristic of nonmarine environments (*i.e.*, *T. barretti*) or are facies-crossing traces that occur in nearly all depositional environments (*i.e.*, *Planolites* isp.). The only facies-specific traces among the extremely sparse trace-fossil record of the Middle Devonian in Estonia point to nonmarine environments. Thus, a fluvially dominated subaqueous delta plain (Plink-Björklund & Björklund, 1999) or delta-plain environment (Tänavsuu-Milkeviciene & Plink-Björklund, 2009) are more in accord with the ichnological record at Tamme than a shallow-marine shelf (Kleesment, 1997). It is possible that some fish fed on these burrowing invertebrates. The discovery of traces of invertebrate fauna fills the gap in the food web of the Estonian Old Red sandstone facies.

Paleogeography

Taenidium barretti has been reported from the upper Silurian of Baltica (Dam & Andreasen, 1990), and their tracemakers could have migrated to the eastern Baltic by the Middle Devonian. Large *T. barretti*, probably produced by arthropods, are relatively common in the Siluro–Devonian strata of eastern Gondwana (Webby, 1968; Bradshaw, 1981; Trewin & McNamara, 1994; Draganits *et al*., 2001; Gouramanis *et al*., 2003). However, the large *T. barretti* of Gondwana were likely produced by different tracemakers that did not migrate to the Baltic part of Euramerica. *T. barretti* has not been previously reported from the Devonian of the Baltic region, though these traces are known from the Devonian of Great Britain (Allen & Williams, 1981). Rather than the faunal exchange between remote regions, the convergent evolution of similar burrowing behavior could explain the wide distribution of nonmarine *T. baretti* in the Devonian and other periods. *Planolites* had a global distribution in the Devonian and does not suggest any paleobiogeographic connections to other regions.

CONCLUSIONS

This study provides the first systematic description of ichnofossils from the Eifelian of southern Estonia, offering insights into the paleoenvironment of the region. The traces of *Taenidium barretti* and *Planolites* isp., observed in the laminated siltstones and sandstones of the Eifelian strata, suggest the presence of deposit- or detritus-feeding organisms, such as annelid worms or small arthropods. The distinct locomotor behaviors of the tracemakers, particularly the absence of sediment push-back in *Planolites* isp., highlight the variations in trace fossil formation due to different feeding strategies rather than material properties of the sediment. These ichnofossils, characteristic of nonmarine and facies-crossing environments, are indicative of a fluvially dominated, subaqueous delta plain paleoenvironment, aligning with previous sedimentological interpretations of the region. This conclusion contrasts with earlier environmental reconstructions based on fossil fish, suggesting a shallow marine environment.

DATA AVAILABILITY STATEMENT

Data will be available upon request.

ACKNOWLEDGEMENTS

Reviewers greatly improved this paper.

FUNDING

The Estonian Research Council project PRG2591 and a Sepkoski Grant from the Paleontological Society provided financial support to OV. This project was supported by the Ongoing Research Funding program (ORF-2025-900), King Saud University, Riyadh, Saudi Arabia. Through the contribution of RM, the publication is in concordance with the Research Plan of the Institute of Geology of the Czech Academy of Sciences (No. RVO 67985831).

AUTHOR CONTRIBUTIONS

Olev Vinn: writing – original draft, editing, visualization, investigation, formal analysis, software, resources, data curation, writing – review, final approval for publication, accountability for the work performed. Radek Mikuláš: editing, methodology, investigation, formal analysis, writing – review, final approval for publication, accountability for the work performed. Mare Isakar: writing – review, final approval for publication, accountability for the work performed. Magdy El Hedeny: writing – review, final approval for publication, accountability for the work performed. Mansour Almansour: writing – review, final approval for publication, accountability for the work performed. Saleh Alfarraj: writing – review, final approval for publication, accountability for the work performed.

DECLARATION OF AI USE

We have used AI-assisted technologies to improve the English of this article.

ETHICS

This work did not require ethical approval, collecting licenses, or previous authorizations.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

REFERENCES

Allen, R.J.L. & Williams, B.P.J. 1981. Beaconites antarcticus: a giant channel-associated trace fossil from the Lower Old Red Sandstone of South Wales and the Welsh Borders. *Geological Journal*, **16**:255–269. *doi:10.1002/gj.3350160405*.

Barroso, F.R.G.; Viana, M.S.S.; Lima Filho, M.F. & Agostinio, S.M.O. 2014. First Ediacaran Fauna Occurrence in Northeastern Brazil (Jaibaras Basin? Ediacaran-Cambrian): Preliminary Results and Regional Correlation, *Anais da Academia Brasileira de Ciências*, **86**:1029–1042. *doi:10.1590/0001-3765201420130162*.

Bedatou, E.; Melchor, R.N. & Genise, J.F. 2009. Complex palaeosol ichnofabrics from Late Jurassice Early Cretaceous volcaniclastic successions of central Patagonia, Argentina. *Sedimentary Geology*, **218**:74–102. *doi:10.1016/j.sedgeo.2009.04.005.*

Bosetti, E.P.; Guimarães Netto, R.; Tognoli, F.M.W.; Sedorko, D. & Matsumura, W.M.K. 2021. Continental input on shelfal deposits unveiled by integration of ichnology, sedimentology, and taphonomy: a case study in Givetian beds of the Paraná Basin, Brazil. *Journal of South American Earth Sciences*, **110**:103342. *doi:10.1016/j.jsames.2021.103342.*

Bown, T.M. & Kraus, M.J. 1983. Ichnofossils of the alluvial Willwood Formation (lower Eocene), Bighorn Basin, northwest Wyoming, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **43**:95–128. *doi:10.1016/0031-0182(83)90050-0.*

Bradshaw, M.A. 1981. Paleoenvironmental interpretations and systematics of Devonian trace fossils from the Taylor Group (lower Beacon Supergroup), Antarctica. *New Zealand Journal of Geology and Geophysics*, **24**:615–652. *doi:10.1080/00288306.1981.10421537.*

Bromley, R.G.; Ekdale, A.A. & Richter, B. 1999. New Taenidium (trace fossil) in the Upper Cretaceous chalk of northwestern Europe. *Bulletin of the Geological Society of Denmark*, **46**:47–51. *doi:10.37570/bgsd-1999-46-05.*

Buatois, L.A. & Mangano, M.G. 2004. Animal-substrate interactions in freshwater environments: applications of ichnology in facies and sequence stratigraphic analysis of fluvial-lacustrine successions. *In*: D. McIlroy (ed.) *The application of ichnology to palaeoenvironmental and stratigraphic analysis*, London, Geological Society, p. 311–333 (Special Publications 228). *doi:10.1144/GSL.SP.2004.228.01.14*.

Buatois, L.A. & Mángano, M.G. 2011. *Ichnology: organism-substrate interactions in space and time*, Cambridge, Cambridge University Press. *doi:10.1017/CBO9780511975622*.

Buatois, L.A.; Mángano, M.G.; Minter, N.J.; Zhou, K.; Wisshak, M.; Wilson, M.A. & Olea, R.A. 2020. Quantifying ecospace utilization and ecosystem engineering during the early Phanerozoic—The role of bioturbation and bioerosion. *Science Advances*, **6**:eabb0618. *doi:10.1126/sciadv.abb0618*

Buatois, L.A.; Netto, R.G. & Mángano, M.G. 2007. Ichnology of Permian Marginal- to shallow-marine coal-bearing successions Rio Bonito and Palermo formations, Paraná Basin, Brazil. *In*: J.A. MacEachern; K.L. Bann; M.K. Gingras & S.G. Pembebrton (eds.) *Applied Ichnology Applied Ichnology*, SEPM, p. 1–11.

Counts, J.W. & Hasiotis, S.T. 2009. Neoichnological experiments with masked chafer beetles (Coleoptera: Scarabaeidae): implications for backfilled continental trace fossils. *Palaios*, **24**:74–91. *doi:10.2110/palo.2008.p08-026r.*

D'Alessandro, A.R. & Bromley, G. 1987. Meniscate trace fossils and the *Muensteria Taenidium* problem. *Palaeontology*, **30**:743–763.

Dam, G. & Andreasen, F. 1990. High-energy ephemeral stream deltas; an example from the Upper Silurian Holmestrand Formation of the Oslo Region, Norway. *Sedimentary Geology*, **66**:197–225. *doi:10.1016/0037-0738(90)90060-7.*

Draganits, E.; Braddy, S.J. & Briggs, D.E.G. 2001. A Gondwanan coastal arthropod ichnofauna from the Muth Formation (Lower Devonian, Northern India): paleoenvironment and tracemaker behavior. *Palaios*, **16**:126–147. *doi:10.1669/0883-1351(2001)016<0126:AGCAIF>2.0.CO;2.*

Frey, R.W. & Howard, J.D. 1990. Trace fossils and depositional sequences in a clastic shelf setting, Upper Cretaceous of Utah. *Journal of Paleontology*, **64**:803–820. *doi:10.1017/S0022336000019004*.

Friend, P.F., Williams, B.P.J., Ford, M., & Williams, E.A. 2000. Kinematics and dynamics of Old Red Sandstone basins. In: P.F. Friend & B.P.J. Williams (eds.) *New perspectives on the Old Red Sandstone*, Geological Society of London, p. 29–60 (Special Publication 180). *doi:10.1144/GSL.SP.2000.180.01.04*.

Good, T.R., & Ekdale, A.A. 2014, Paleoecology and taphonomy of trace fossils in the eolian Upper Triassic/Lower Jurassic Nugget Sandstone, northeastern Utah. *Palaios*, **29**:401–413. *doi:10.2110/palo.2014.013.*

Gouramanis, C. & McLoughlin, S. 2016. Siluro-Devonian trace fossils from the Mereenie Sandstone, Kings Canyon, Watarrka National Park, Amadeus Basin, Northern Territory, Australia. *Alcheringa*, **40**:118–128. *doi:10.1080/03115518.2016.1099957*.

Gouramanis, C.; Webb, J.A. & Warren, A.A. 2003. Fluviodeltaic sedimentology and ichnology of part of the Silurian Grampians Group, western Victoria. *Australian Journal of Earth Sciences*, **50**:811–825. *doi:10.1111/j.1440-0952.2003.01028.x.*

Guimarães Netto, R. 2007. Skolithos-dominated pipe rockin nonmarine environments: An example from the Triassic Caturrita Formation, Southern Brazil. In: R.G. Bromley; L.A. Buatois; M.G. Mángano; J.F. Genise & Melchor, R.N. (eds.) *Sedimente organism interactions: a multifaceted ichnology*, Society for Sedimentary Geology, p. 109–121 (SEPM Special Publication 88). *doi:10.2110/pec.07.88.0107*.

Häntzschel, W. 1975. Trace fossils and problematica In: C. Teichert (ed.) *Treatise on invertebrate paleontology, part W, supplement 1*, Geological Society of America, University Press of Kansas.

Hembree, D.I. 2009. Neoichnology of burrowing millipedes: Linking modern burrow morphology, organism behavior, and sediment properties to interpret continental ichnofossils. *Palaios*, **24**:425–439. *doi:10.2110/palo.2008.p08-098*r

Hembree, D.I. 2019. Burrows and ichnofabric produced by centipedes: modern and ancient examples. *Palaios*, **34**:468–489. *doi:10.2110/palo.2019.059.*

Ivanov, A. 2005. Early Permian Chondrichthyans of the Middle and South Urals. Revista Brasileira de *Paleontologia*, **8**:127–138. *doi:10.4072/rbp.2005.2.05*

Keighley, D.G. & Pickerill, R.K. 1994. The ichnogenus *Beaconites* and its distinction from *Ancorichnus* and *Taenidium*. *Palaeontology*, **37**:305–337.

Kleesment, A. 1997. Devonian sedimentation basin In: A. Raukas & A. Teedumäe (eds.) *Geology and mineral resources of Estonia*, Estonian Academy Publishers.

Krapovickas, V.; Ciccioli, P.L.; Mangano, M.G.; Marsicano, C.A. & Limarino, C.O. 2009. Paleobiology and paleoecology *of an* aridesemiarid Miocene South American ichnofauna in anastomosed fluvial deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **284**:129–152. *doi:10.1016/j.palaeo.2009.09.015*.

Mancuso, A.C.; Krapovickas, V.; Benavente, C.A. & Marsicano, C.A. 2020. An integrative physical, mineralogical, and ichnological approach to characterize underfilled lake-basins. *Sedimentology*, **67**:3088–3118. *doi:10.1111/sed.12736*.

Mángano, M.G. & Buatois, L.A. 2014. Decoupling of body-plan diversification and ecological structuring during the Ediacaran-Cambrian transition: evolutionary and geobiological feedbacks. *Proceedings. Biological Sciences*, **281**:20140038. *doi:10.1098/rspb.2014.0038.*

Mark-Kurik, E. 1991. On the environment of Devonian fishes. *Proceedings of the Estonian Academy of Sciences Geology*, **40**:122–125. doi:10.3176/geol.1991.3.06.

Mark-Kurik, E. 1995. Trophic relations of Devonian fishes. *Geobios*, **28**:121–123. doi:10.1016/S0016-6995(95)80098-0.

Mark-Kurik, E. & Põldvere, A. 2012. Devonian stratigraphy in Estonia: current state and problems. *Estonian Journal of Earth Sciences*, **61**:33–47. *doi:10.3176/earth.2012.1.03*.

Melchor, R.N.; Genise, J.F.; Buatois, L.A. & Umazano, A.M. 2012. Fluvial environments In: D. Knaust & R. Bromley (eds.) *Trace fossils as indicators of sedimentary environments, developments in sedimentology, Elsevier*, *doi:10.1016/B978-0-444-53813-0.00012-5*.

Melchor, R.N.; Bedatou, E.; de Valais, S. & Genise, J.F. 2006. Lithofacies distribution of invertebrate and vertebrate trace-fossil assemblages in an Early Mesozoic ephemeral fluvio-lacustrine system from Argentina: Implications for the Scoyenia ichnofacies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **239**:253–285. *doi:10.1016/j.palaeo.2006.01.011.*

Mikuláš, R.; Meškis, S.; Ivanov, A.; Lukševičs, E.; Zupinš, I. & Stinkulis, G. 2013. A rich ichnofossil assemblage from the Frasnian (Upper Devonian) deposits at Andoma Hill, Onega Lake, Russia. *Bulletin of Geosciences*, **88**:389–400. *doi:10.3140/bull.geosci.1358*

Nascimento, D.L.; Guimarães Netto, R.; Batezelli, A.; Ladeira, F.S.B. & Sedorko, D. 2023. *Taenidium barretti* ichnofabric and rainfall seasonality: Insights into dryland suites of Scoyenia ichnofacies. *Journal of Palaeogeography*, **12**:28–49. doi:10.1016/j.jop.2022.10.001.

Pemberton, S.G. & Frey, R.W. 1982. Trace fossil nomenclature and the Planolites–Palaeophycus dilemma. *Journal of Paleontology*, **56**:843–871.

Plink-Björklund, P. & Björklund, L. 1999. Sedimentary response in the Baltic Basin to postcollisional events in the Scandinavian Caledonides. *GFF*, **121**:79–80.

Retallack, G.J. 2001. *Scoyenia* burrows from Ordovician palaeosols of the Juniata Formation in Pennsylvania. *Palaeontology*, **44**:209–235. *doi:10.1111/1475-4983.00177.*

Rodríguez-Tovar, F.J.; Alcala, L. & Cobos, A. 2016. *Taenidium* at the lower Barremian El Hoyo dinosaur track site (Teruel, Spain): assessing palaeoenvironmental conditions for the invertebrate community. *Cretaceous Research*, **65**:48–58. *doi:10.1016/j.cretres.2016.04.013.*

Sarkar, S. & Chaudhuri, A.K. 1992. Trace fossils in Middle to late triassic fluvial redbeds, Pranhita-Godavari Valley, South India. *Ichnos*, **2**:7–19. *doi:10.1080/10420949209380071*.

Savrda, C.E.; Blanton-Hooks, A.D.; Collier, J.W.; Drake, R.A.; Graves, R.L.; Hall, A.G. & Wood, H.A. 2000. Taenidium and associated ichnofossils in fluvial deposits, Cretaceous Tuscaloosa Formation, eastern Alabama, southeastern USA. *Ichnos*, **7**: 227–242. *doi:10.1080/10420940009380162.*

Schlirf, M.; Uchman, A. & Kümmel, M. 2001. Upper Triassic (Keuper) non-marine trace fossils from the Hassberge area (Franconia, south-eastern Germany). *Palaontologische Zeitschrift*, **75**:71–96. *doi:10.1007/BF03022599.*

Sciscio, L.; Broderick, T.J.; Barrett, P.M.; Munyikwa, D.; Zondo, M. & Choiniere, J.N. 2021. Invertebrate and plant trace fossils from the terrestrial Late Triassic of Zimbabwe. *Palaios*, **36**:129–140. *doi:10.2110/palo.2020.071.*

Smith, J.J. & Hasiotis, S.T. 2008. Traces and burrowing behaviors of the cicada nymph *Cicadetta calliope:* Neoichnology and paleoecological significance of extant soil dwelling insects. *Palaios*, **23**:503–513. *doi:10.2110/palo.2007.p07-063r.*

Tänavsuu-Milkeviciene, K. & Plink-Björklund, P. 2009. Recognizing tide-dominated versus tide-influenced deltas: Middle Devonian strata of the Baltic Basin. *Journal of Sedimentary Research*, **79**:887–905. *doi:10.2110/jsr.2009.096.*

Tänavsuu-Milkeviciene, K.; Plink-Björklund, P.; Kirsimäe, K. & Ainsaar, L. 2009. Coeval versus reciprocal mixed carbonate–siliciclastic deposition, Middle Devonian Baltic Basin, Eastern Europe: Implications from the regional tectonic development. *Sedimentology*, **56**:1250–1274. *doi:10.1111/j.1365-3091.2008.01032.x*.

Toom, U.; Vinn, O. & Hints, O. 2019. Ordovician and Silurian ichnofossils from carbonate facies in Estonia: a collection-based review. *Palaeoworld*, *28*:123–144. *doi:10.1016/j.palwor.2018.07.001*.

Tovmasyan, K. 2004. Tidal features in siliciclastic deposits of Pärnu Formation, Middle Devonian, Estonia. *In*: INTERNATIONAL GEOLOGICAL CONGRESS, 32, 2004. *Résumés*, p. 902–903.

Tovmasyan, K. & Stinkulis, G. 2008. Implications of fluvial, tidal and wave processes to the deposition of siliciclastic sequence of Devonian, Andoma Hill, 71. In: O. Hints, L. Ainsaar; P. Männik & T. Meidla (eds.) *THE SEVENTH BALTIC STRATIGRAPHICAL CONFERENCE*, 2008. *Abstracts*, Tallinn, Geological Society of Estonia.

Trewin, N.H. & McNamara, K.J. 1994. Arthropods invade the land: trace fossils and palaeoenvironments of the Tumblagooda Sandstone (?late Silurian) of Kalbarri, Western Australia. *Transactions of the Royal Society of Edinburgh. Earth Sciences*, **85**:177–210. *doi:10.1017/S026359330000359X.*

Verde, M.; Ubilla, M.; Jimenez, J.J. & Genise, J.F. 2007. A new earthworm trace fossil from paleosols: Aestivation chambers from the late Pleistocene Sopas Formation of Uruguay. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **243**:339–347. *doi:10.1016/j.palaeo.2006.08.005.*

Vinn, O. 2023. Old Red Sandstones in the Middle Devonian of Estonia: where are the trace fossils? *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, **310**:83–89. *doi:10.1127/njgpa/2023/1170.*

Webby, B.D. 1968. Devonian trace fossils from the Beacon Group of Antarctica. *New Zealand Journal of Geology and Geophysics*, **11**:1001–1008. *doi:10.1080/00288306.1968.10420766*.

Zirk, E. 2007. *Kesk-Devoni Aruküla lademe deltasetted*. MSc Thesis, University of Tartu, Tartu, 47 p.

Received: 01 March 2025. Accepted: 22 March 2025.

Associated editor: Rodrigo Horodyski
Editor-in-chief: Matias do Nascimento Ritter