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Ichnogenus *Trypanites* in the Ordovician of Estonia (Baltica)

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ABSTRACT

Trypanites is a common boring in Ordovician hardgrounds of Estonia (Baltica). The depth of the sedimentary basin and sedimentation rates controlled the distribution of *Trypanites*. The trace-makers' community was diverse and changing over time. Three ichnospecies of *Trypanites* can be distinguished: *T. sozialis*, *T. weisei* and *Trypanites* isp. All three morphotypes can be recognized in the same hardground. It is impossible to distinguish between the different ichnospecies based only on the size of the boring aperture. The depth of early lithification of the seafloor determines the morphological variability seen in *T. sozialis*. The occurrence of elongated borings, such as *T. weisei* and *Trypanites* isp., is related to tropical environments, and their trace-makers strongly preferred substrates with a homogeneous and dense texture. The texture and available volume of hard substrate controls the ichnodiversity of *Trypanites* ichnospecies.

Introduction

Trypanites, a macroboring developed in fully lithified substrates, is common in the Palaeozoic of Baltica. This ichnogenus has been recognized in the Cambrian and has a wide distribution in Ordovician and Silurian carbonate hardgrounds and biogenic substrates (see Toom 2019 and references therein). Five *Trypanites* ichnospecies are regarded as valid. *T. weisei* Mägdefrau, 1932 (the type ichnospecies of *Trypanites*) from the Middle Triassic is more or less straight, oriented perpendicularly to the substrate surface, and has a length/diameter ratio of ca 20–50 (Knaust et al. 2023). *T. solitarius* (Hagenow, 1840) was described from Cretaceous biogenic substrates (Wisshak et al. 2017) and is the smallest (diameter much less than one millimetre) and a relatively long, simple, tubular boring, characterized by a winding course. *T. fosteryeomani* Cole and Palmer, 1999 was erected from Jurassic sediments and is the largest *Trypanites* ichnospecies. *T. mobilis* Neumann et al., 2008 occurs within subspherical bioclasts of Cretaceous to Palaeocene deposits. *T. sozialis* Eisenack, 1934 from the Ordovician and Silurian of Baltica is a short, straight or inclined boring with a small (0.5–15) length/diameter ratio (Knaust et al. 2023).

During the Early Palaeozoic, Estonia was covered by a shallow epeiric sea. Cool-water siliciclastic sediments were deposited in the Cambrian and Early Ordovician. The Middle and lowermost part of the Upper Ordovician succession was deposited in cool- and temperate-water environments and is characterized by a highly condensed succession of carbonates (e.g., Jaanusson 1973; Dronov and Rozhnov 2007). The upper part of the succession is characterized by warm-water carbonates. The sedimentary basin was influenced by changes in sea level, climate, and depositional conditions. The sediments of northern Estonia represent shallow-water settings and those of southern Estonia deeper-water settings (e.g., Nestor and Einasto 1997). Hardgrounds and omission surfaces are numerous and occur frequently. The main impregnation types are pyritic and phosphatic (Põlma 1982; Saadre 1992). Many of the hardgrounds are traceable for considerable distances and are used as markers for the separation of different stratigraphic units.

The aim of this work is to summarize and discuss the distribution patterns of *Trypanites* in the Ordovician of Estonia (Baltica).

Materials and methods

The study used palaeontological and lithological collections housed at Tallinn University of Technology (GIT) and the University of Tartu. To avoid problems related to the biogenic substrates, such as symbiotic structures or morphology of borings determined by the skeletal architecture of the host, only *Trypanites* borings from lithic substrates were investigated. A classical method of cutting and polishing rock faces was used to enhance the visibility of borings. Computed tomography (CT) was used to visualize borings hidden inside rocks. Measurements of the length/diameter ratio allowed us to determine borings on the ichnospecies level. Fiji image analysis software (https://imagej.net/Fiji) was used to measure specimens from calibrated digital photos. CT scanning was carried out at the Geological Survey of Finland using the GE phoenix v|tome|x s scanner.

The Supplementary material consists of measurements of boring apertures and length-frequency diagrams, it is available at SARV: Geoscience Data Repository (DOI 10.23679/516). Supplementary material 1: Väike-Pakri hardground, Dapingian, cold-water carbonates and Vasalemma hardground, Katian, tropical grain supported carbonates. Supplementary material 2: Sutlema hardground, Katian, pure tropical carbonates.

Results and discussion

The most common macroboring in Ordovician lithic substrates of Estonia is *Trypanites*, which is recorded from the Tremadocian to the Katian upper boundary. Hardgrounds typically develop in hydrodynamically active shallow environments with low sediment accumulation rates or periods of non-deposition (Christ at al. 2015) and provide a favourable environment for the borers. *Trypanites* occurs in northern Estonia, represented by the shallowest part of the sedimentary basin characterized by a highly condensed succession.

Carbonate hardgrounds from climatically different environments demonstrate a high variability in aperture size and boring depth within a given sample, locality, or stratigraphic unit. Measurements of the length/diameter ratio allowed us to determine borings on the ichnospecies level. Three different morphotypes of *Trypanites* are represented: shallow *T. sozialis*, long *T. weisei*, and course-changing undulating *Trypanite*s isp.

T. sozialis (Fig. 1A–G, I, O–T) is most abundant, with the earliest finds in the Tremadocian (Fig. 1Q) and the youngest occurrence in the Katian at its upper boundary (Fig. 1T). It occurs in cool-water siliciclastic sediments; in cool, temperate, and warm-water carbonates with coarse-grained and fine-grained textures. The borings demonstrate a high variation in length and diameter (Fig. 1B–D, F, O), but a length diameter ratio of less than 15 (see Knaust et al. 2023). The trace-maker of shallow *T.* s*ozialis* penetrates bioclasts (Fig. 1F), but may change its boring direction (Fig. 1R, S) to accommodate for variations of the hard substrate. The shape of the borings can be slightly conical, their termination pointed or proboscis-shaped, and some borings demonstrate a slightly enlarged lower portion (Knaust et al. 2023). Specimens from cool- and temperate-water environments (Fig. 1B–D) have a smaller length/diameter ratio than borings from warm-water settings (Fig. 1F, I, N, O). This higher variability is related to slower sedimentation rates (Fig. 1B, C), with these surfaces separating different lithologies or stratigraphic units (Fig. 1F, N, O).

All records of *T. weisei* (Fig. 1K–M) come from the Katian pure tropical carbonates with a very fine texture. The borings are recognizable in a hardground separating the Saunja and Kõrgessaare formations (fms) of the Nabala and Vormsi stages. In addition, the three hardgrounds from the Oandu and Vormsi stages contain *Trypanites* borings with a length/diameter ratio larger than 15 (Figs 1P, 2A, B).

The boundary beds of the Nabala and Vormsi stages (Saunja and Kõrgesaare fms) demonstrate tubular borings with a changing course, small diameter (far less than 1 mm) and a high length/diameter ratio (Fig. 1H, J). This morphotype differs from *T. weisei* in its changing course and small diameter. The borings resemble *T. solitaria*, but due to their presence in lithic instead of biogenic substrate, we currently do not assign it to that ichnospecies.

It should be emphasized that all three morphotypes of *Trypanites* are recognized in the same hardground (Fig. 1H–J, M). It is generally assumed that variation in boring diameter suggests several colonization stages of one and the same trace-making species (e.g., Kobluk and Nemcsok 1982; Nield 1984). The length-frequency diagrams of Estonian *T. sozialis* apertures measured in hardgrounds of the cold-water environment with extremely low sedimentation (Suppl. material 1, Väike-Pakri hardground) and in tropical grain-supported carbonates (Suppl. material 1, Vasalemma hardground) show a bimodal distribution and it allows us to assume that more than one species of borers was involved. The diagram of pure tropical carbonates with three *Trypanites* ichnospecies is not following a normal distribution curve (Suppl. material 2, Sutlema hardground). The Estonian hardground material demonstrates that it is impossible to distinguish between different ichnospecies based on the size of their apertures. Since the diagrams do not show a regular distribution, it is likely that a diverse group of bioeroders was responsible for substrate colonization.

The Ordovician was a period of extensive early cementation occurring near the sediment-seawater interface on shallow-marine seafloors (Palmer and Wilson 2004). Early cementation depends on several prerequisites. In the Baltic basin, cyanobacterial films covering sediments played the leading role in the rapid development of hardgrounds in cold- and warm-water sediments (Rozhnov 2018). Borers are the first inhabitants of the hard substrate. *T. sozialis* demonstrates deviations from the direction (Fig. 1R, S), the conical shape and expanded terminations of borings (for details, see Knaust et al. 2023). The trace-makers of *Trypanites* are highly selective in their choice of substrate and are strongly controlled by the hardness and extent of the substrate (e.g., Kobluk and Nemcsok 1982; Nield 1984; Kočová Veselská et al. 2021). More likely, deviations from the normal boring shape are trace-makers' reactions to a decrease in the hardness of the substrate and the volume, and depth of early lithified seafloor determined the high variability of *T. sozialis*.

The finds of elongated borings from the Ordovician of Estonia (*T. weisei* and *Trypanites* isp.) are related to tropical environments and their trace-makers strongly preferred substrates with a homogeneous and dense texture.

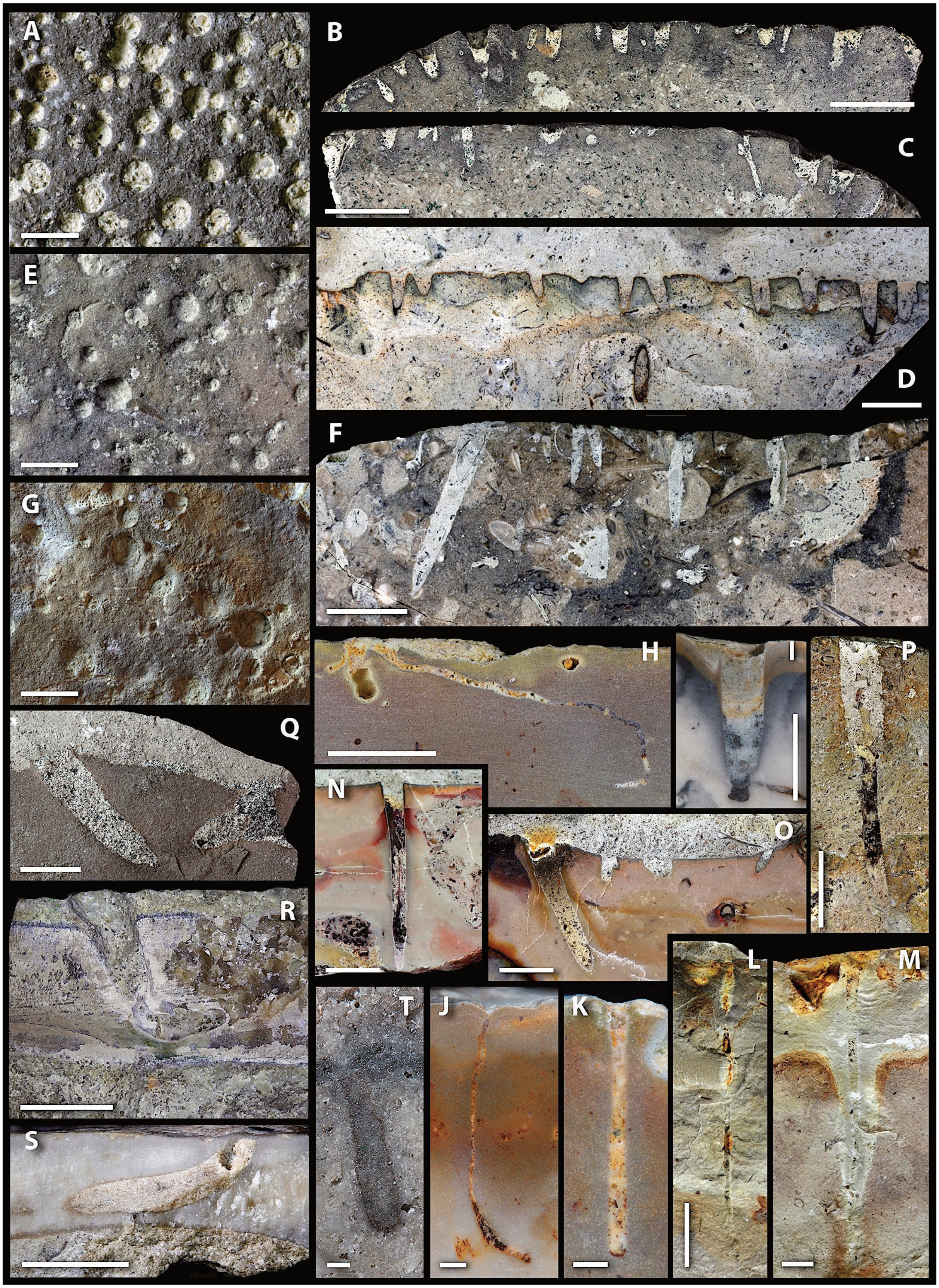

Fig. 1. *Trypanites* from the Ordovician of Estonia. **A–G, I, N–T** – *T. sozialis* Eisenack, 1934; **A–C** – cool-water carbonates of the Toila Formation (Fm), Dapingian, GIT 381-595, Väike Pakri; **D** – cool-water carbonates of the Väo Fm, Darriwilian, GIT 858-1, Keila River; **E, F** – coarse-grained tropical carbonates of the Pääsküla Member, Katian, GIT 362-95, Vasalemma; **T** – upper boundary of the Adila Fm, Katian, GIT 362-889-2, Reinu quarry; **I, N, O** – pure tropical fine-grained carbonates of the Saunja Fm, Katian; **I** – GIT 881-2-3, Sutlema; **N, O** – GIT 858-2, Aulepa; **Q** – siliciclastic sediments of the Türisalu Fm, Tremadocian, GIT 858-8, Tallinn; **R** – bioclast from the Pakri Fm, Darriwilian, GIT 426-707-1, Muraste; **S** – fragment of coral from the Kõrgessaare Fm, Katian, GIT 520-256-1, Saxby; **K–M** – *T. weisei* Mägdefrau, 1932 in pure tropical fine-grained carbonates, Saunja Fm, Katian; **K** – GIT 881-9-4; **L** – GIT 881-1-2; **M** – GIT 881-1-1, all from Sutlema; **P** – *T. sozialis* overprinted by *T. weisei*, Kõrgesaare Fm, Katian, GIT 362-865, Sutlema; **H, J** – course-changing *Trypanites* isp. in pure tropical fine-grained carbonates of the Saunja Fm, Katian; **H** – GIT 881-9-3; **J** – GIT 881-17-5, both from Sutlema. Scale bars for **B–F, L, M** = 1 cm; **E, G–I, N, O** = 5 mm; **J, K, T** = 1 mm.

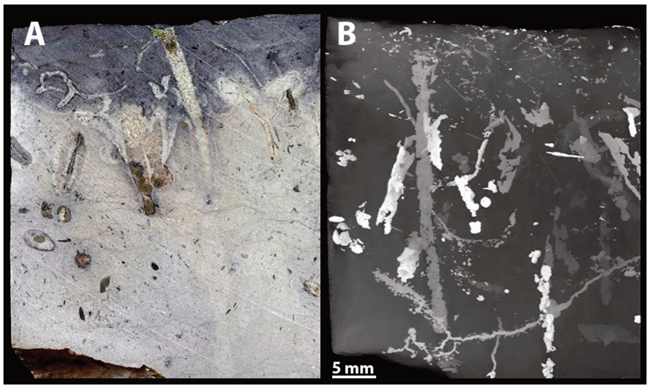

Fig. 2. Pyritized hardground with *Trypanites weisei* Mägdefrau, 1932, GIT 362-587, Äiamaa drillcore, Katian. **A** – image of vertical section; **B** – X-ray computed tomography 3D reconstruction.

Seawater chemistry and temperature control lithification, and appropriate water temperatures ensure a sufficient supply of carbonate minerals for cementation (Flügel 2010: subtropical and tropical shallow waters, supersaturated with calcium carbonate, contribute significantly to rapid cementation) and it enhanced the formation of surfaces with suitable thickness for the elongated *Trypanite*s borings.

Conclusions

The primary controls on the occurrence of *Trypanites* in the Ordovician of Estonia (Baltica) are the depth of the sedimentary basin and the sedimentation rate. The trace-makers' community was diverse and has changed over time. The texture and volume of the hard substrate controlled the ichnodiversity of *Trypanites*.

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