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# **Ordovician and Silurian Trace Fossils of Estonia**

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**Declaration:**

Hereby I declare that this doctoral thesis, my original investigation and achievement, submitted for the doctoral degree at Tallinn University of Technology has not been submitted for doctoral or equivalent academic degree.

Ursula Toom

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# **Ordoviitsiumi ja Siluri ajastu jäljekivistised Eestis**

URSULA TOOM





# Contents

|   |     |
|---|-----|
| List of Publications .....  | 7   |
| Author's Contribution to the Publications .....                             | 8   |
| 1 Introduction .....  | 9   |
| 2 Trace fossils .....   | 11  |
| 2.1 Basic concepts of ichnology.....  | 11  |
| 2.2 Classification of trace fossils.....                                    | 12  |
| 2.3 Ichnofacies model .....   | 13  |
| 2.4 Trace fossils in shallow-marine carbonates.....                         | 16  |
| 2.5 Bioerosion and hardgrounds .....  | 17  |
| 2.6 Ordovician and Silurian trace fossils and hardgrounds .....             | 18  |
| 3 Geological background.....  | 20  |
| 4 Materials and methods .....   | 22  |
| 5 Results and discussion.....   | 24  |
| 5.1 Systematic review of recorded trace fossils .....                       | 24  |
| 5.1.1 Bioturbation structures .....   | 24  |
| 5.1.2 Bioerosional trace fossils .....                                      | 38  |
| 5.1.3 Coprolites and structures with faecal pellets .....                   | 45  |
| 5.1.4 Bioclastration structures .....                                       | 51  |
| 5.2 Trace fossils and encrusters on hardgrounds.....                        | 51  |
| 5.3 The Bioerosion Revolution on Baltica.....                               | 55  |
| 5.4 Ichnodiversity in the Ordovician and Silurian deposits of Estonia ..... | 57  |
| 6 Conclusions and future directions .....                                   | 62  |
| References .....  | 64  |
| Acknowledgements.....   | 98  |
| Abstract.....   | 99  |
| Lühikokkuvõte.....  | 101 |
| Appendix .....  | 103 |
| Curriculum vitae .....  | 260 |
| Elulookirjeldus.....  | 263 |



## List of Publications

The thesis is based on the following publications:

- I **Toom, U.**, Vinn, O., Hints, O., 2019. Ordovician and Silurian ichnofossils from carbonate facies in Estonia: A collection-based review. *Palaeoworld* 28(1-2), 123–144. <https://doi.org/10.1016/j.palwor.2018.07.001>
- II **Toom, U.**, Vinn, O., Isakar, M., Madison, A., Hints, O., 2020. Small faecal pellets in Ordovician shelly fossils from Estonia, Baltoscandia. *Estonian Journal of Earth Sciences* 70(1). <https://doi.org/10.3176/earth.2020.01>
- III Vinn, O., **Toom, U.**, 2018. First description of rare *Teichichnus* burrows from the carbonate rocks of early Paleozoic of Estonia. *Carnets de Géologie* 18(13), 305–312. <https://doi.org/10.4267/2042/68550>
- IV Vinn, O., **Toom, U.**, 2016. Rare arthropod traces from the Ordovician and Silurian of Estonia (Baltica). *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen* 280(2) 135–141. <https://doi.org/10.1127/njgpa/2016/0570>
- V Vinn, O., **Toom, U.**, 2015. The trace fossil *Zoophycos* from the Silurian of Estonia. *Estonian Journal of Earth Sciences* 64(4), 284–288. <https://doi.org/10.3176/earth.2015.34>
- VI Vinn, O., Wilson, M.A., **Toom, U.**, 2015. Distribution of *Conichnus* and *Amphorichnus* in the Lower Paleozoic of Estonia (Baltica). *Carnets de Géologie* 15(19), 269–278. <https://doi.org/10.4267/2042/58180>
- VII Vinn, O., Wilson, M.A., **Toom, U.**, 2019. Earliest *Petroxestes* borings from Sandbian (earliest Late Ordovician) bryozoans of northern Estonia. *Palaios* 34(10), 453–457. <https://doi.org/10.2110/palo.2019.054>
- VIII Pohle, A., Klug, C., **Toom, U.**, Kröger, B., 2019. Conch structures, soft-tissue imprints and taphonomy of the Middle Ordovician cephalopod *Tragoceras falcatum* from Estonia. *Fossil Imprint* 75(1), 70–78. <https://doi.org/10.2478/if-2019-0006>
- IX Vinn, O., Wilson, M.A., Ausich, W.I., **Toom, U.**, 2015. *Tremichnus* in crinoid pluricolumnals from the Silurian of Western Estonia (Baltica). *Carnets de Géologie* 15(5), 239–243. <https://doi.org/10.4267/2042/57951>
- X Vinn, O., **Toom, U.**, 2016. A sparsely encrusted hardground with abundant *Trypanites* boring from the Llandovery of the Velise River, western Estonia (Baltica). *Estonian Journal of Earth Sciences* 65(1), 19–29. <https://doi.org/10.3176/earth.2016.01>
- XI Vinn, O., **Toom, U.**, 2016. Bioerosion of inorganic hard substrates in the Silurian of Estonia (Baltica). *GFF* 138(2), 306–310. <https://doi.org/10.1080/11035897.2015.1076513>
- XII Vinn, O., Wilson, M.A., **Toom, U.**, 2015. Bioerosion of inorganic hard substrates in the Ordovician of Estonia (Baltica). *PLOS ONE* 10(7), 1–17. <https://doi.org/10.1371/journal.pone.0134279>

## **Author's Contribution to the Publications**

Contribution to the papers in this thesis are:

- I The author studied the palaeontological material and collected new first-hand data, identified the fossils, assembled occurrence-level and literature databases, wrote the manuscript and acted as the first and corresponding author.
- II The author collected and prepared the palaeontological material, identified trace fossils, developed the scientific ideas, wrote the main part of the manuscript and acted as the first and corresponding author.
- III The author studied the palaeontological collections, made the determinations, developed the ideas, was responsible for the data management, and in part for writing the manuscript.
- IV The author studied the palaeontological collections, was responsible for the data in database, and in part for writing the manuscript.
- V The author studied the palaeontological collections, identified fossils, was responsible for database building, organized the fieldworks, and contributed to writing the manuscript.
- VI The author studied the palaeontological collections, made the determinations, assembled data, and wrote parts of the manuscript.
- VII The author studied the palaeontological collections, made the determinations, was responsible for data management, and in part for writing the manuscript.
- VIII The author organized and took part in fieldwork, collected material, studied the collections, identified fossils, and contributed to developing the ideas and writing the manuscript.
- IX The author studied the collections, collected data and partly wrote the manuscript.
- X The author studied the lithological collections, was responsible for data management, and wrote parts of the manuscript.
- XI The author studied the lithological collections, was responsible for the data in database, and contributed text to the manuscript.
- XII The author studied the lithological collections, was responsible for data and partly for writing the manuscript.



# 1 Introduction

Ichnology is the study, description, classification, and interpretation of various traces made by animals, plants, fungi, protists and microbes (Frey, 1973). Trace fossils, or ichnofossils (*ichnos* = “trace” in Greek), are often the only evidence of ancient life representing the behaviour of long-extinct organisms. Dinosaur trackways have fascinated people for centuries (Baucon et al., 2012) and well-preserved tracks of hominids have provided the first direct evidence of bipedalism (Meldrum et al., 2011). However, the vast majority of trace fossils encountered in sediments and sedimentary rocks represent communities of marine invertebrate animals and their habitats.

Bertling et al. (2006) defined trace fossils as ‘a morphologically recurrent structure resulting from the life activity of an individual organism, or homotypic organisms, modifying the substrate’. Palaeoichnology is commonly viewed as a branch of palaeontology, but it is closely connected to palaeoenvironments and sedimentology. Various palaeontological, biological, sedimentological and ecological methods are applied in ichnological studies (Bromley, 1996), and the analysis of trace fossils can contribute to palaeoecology, palaeoclimatology, biostratigraphy, sedimentology, sequence stratigraphy, palaeoceanography, reservoir characterization, palaeoanthropology, as well as archaeology (Mángano & Buatois, 2012).

Trace fossils have a long research history, which is divided into five distinct periods (Osgood, 1975; Pemberton et al., 2007; Baucon, 2010). The *Age of Naturalists*, spanning through the 15th to 17th centuries, includes Leonardo da Vinci, who used trace fossils for the first time to debate the marine origin of sedimentary rocks (Baucon, 2010). Brongniart (1823) interpreted trace fossils as petrified algae, called fucoids, which commenced the *Age of Fucoids* (1823–1881). Swedish naturalist Nathorst (1881) contested this interpretation and laid the foundation for the *Age of Controversy* (1881–1925). Development of the *Modern Approach* (1925–1953) started with the establishment of the Senckenberg Laboratory and neoichnological research. The subsequent *Modern Era of Ichnology* was initiated by Adolf Seilacher’s pioneering work in 1953. The taxonomic framework established by Walter Häntzschel (1962, 1975) also created the foundation for broader research and applications of ichnology (Pemberton & MacEachern, 2013).

A number of papers describe the oldest evidence for locomotion preserved in trace fossils (Seilacher et al., 1998; Rasmussen et al., 2002; Bengtson et al., 2007). The first traces were simple and relatively shallow (Jensen et al., 2005; Liu et al., 2010) and their separation from soft-bodied animals may be complicated. Several structures initially described among the earliest traces were subsequently re-interpreted as of abiological origin or as microbial structures (Mariotti et al., 2016; Retallack & Mao, 2019). For instance, the globally known *Palaeopascichnus linearis*, described from Ediacaran sediments of Baltica as a trace fossil (Fedonkin, 1976), appears to be a skeletal macroscopic organism (Kolesnikov et al., 2018).

According to Grosch & McLoughlin (2014), the oldest trace fossil – endolithic microboring in stromatolites reported by Zhang & Golubić (1987) from China – dates back to the Palaeoproterozoic Era, c. 1.7 Ga. The Precambrian time span clearly included environments as well as fossils that lack modern counterparts (Allison & Bottjer, 2011); for many soft-bodied animals of the Ediacaran Period, traces may be the only evidence of their presence and behaviour (Jensen et al., 2005). For instance, recent studies on

Ediacaran trace fossils have revealed an early occurrence of bilateralians (Chen et al., 2018) and sediment bulldozers (Buatois et al., 2018).

Trace fossils are also valuable indicators of past environments and a number of widely traced ichnofacies have been distinguished (Frey & Seilacher, 1980; Frey & Pemberton, 1987; Bromley & Asgaard, 1993; Gibert et al., 1998, 2007; MacEachern et al., 2007). When rocks are barren of conventional body fossils useful for biostratigraphy, traces may also become valuable tools for dating. They are nevertheless rarely taken as zonal index taxa, with a noteworthy exception of the base of the Cambrian System (Brasier et al., 1994; Buatois, 2018) – and thus the entire Phanerozoic Eon – which coincides with the first appearance of the trace fossil *Treptichnus pedum* (Seilacher, 1955).

Trace fossils are generally more common and better preserved in siliciclastic sediments compared to limestones, while the opposite is true for body fossils (Seilacher, 2007). This has been among the main reasons why trace fossils from Palaeozoic shallow-marine carbonates have received less research attention and are strongly underrepresented in ichnological literature (Knaust et al., 2012). This, in turn, results in a global knowledge bias that limits our understanding of the evolution and distribution of trace-making organisms both in time and space.

The Baltic Ordovician–Silurian sedimentary basin represents a well-preserved and well-known example of a Palaeozoic shallow-marine carbonate system with rich biotas and a long research history. In Estonia, palaeontological research commenced more than 180 years ago and all major fossil groups have since been thoroughly studied. However, trace fossils have received very little attention and taxonomic focus prior to the 21<sup>st</sup> century; resultingly, new data and knowledge have started to accumulate only recently (Paper I; and references therein).

The main working hypothesis of the current study is that trace fossils are much more common and taxonomically diverse in Estonia and the Baltic region than previously reported. This study proposes that thoroughly documented trace fossils may provide new insights into the ecology and diversification history of marine communities through the two major events in Earth history – the Great Ordovician Biodiversification Event and the end-Ordovician Mass Extinction. Several specific research questions can arise from these broad ideas. Examples include if and how the climate and facies changes resulting from the drift of Baltica towards the equator influenced the associations of trace-making organisms and the preservation potential of ichnofossils, or whether the so-called Ordovician bioerosion revolution can be documented in Baltoscandia. To answer these and other research questions, the following goals were set for the doctoral project:

(1) Compile a database of trace fossils in Estonia and neighbouring countries by systematically reviewing and identifying material in existing palaeontological collections, as well as reviewing previous literature and collecting new representative specimens from key stratigraphic intervals in Estonia.

(2) Analyse the temporal and spatial distribution of individual trace fossil taxa as well as ichnofossil abundance, diversity and disparity patterns, to allow a comparison between the diversity dynamics of body fossils, climate history, and regional facies changes through the Middle Ordovician to the late Silurian.

(3) Assess the potential biases of the data set, including collection and preservation bias, and set an agenda for successive research.

(4) Test novel study methods, such as 3D X-ray computed tomography imaging for a more thorough characterization of trace fossils in carbonate rocks, which has been rarely done before.

## 2 Trace fossils

### 2.1 Basic concepts of ichnology

The basic concepts and principles of trace fossil studies are the result of its long research history and the work of many researchers (see reviews and selected references in e.g. Seilacher, 1964; Frey, 1975; Bromley & Fürsich, 1980; Ekdale et al., 1984; Frey & Pemberton, 1984; Bromley, 1990, 1996; Buatois & Mángano, 2011). Trace fossils constitute a representative series of evidence of the behaviour of organisms (Seilacher, 1967), even though the biological affinity of the tracemakers often remains unknown (Knaust, 2017). One group of organisms may produce various traces that can be assigned to different ichnogenera, not to mention different ichnospecies. For instance, *Rusophycus* Hall, 1852, *Cruziana* d'Orbigny, 1842 and *Diplichnites* Dawson, 1873 are traces of trilobites (Crimes, 1970), and *Protovirgularia* McCoy, 1850, *Lockeia* James, 1879 and *Lophoctenium* Richter, 1850 could have been produced by bivalves (Ekdale & Bromley, 2001a). On the other hand, completely different organisms can produce morphologically indistinguishable traces that belong to one and the same ichnotaxon. For instance, vertical burrows of the ichnogenus *Skolithos* Haldeman, 1840 may have been produced by annelids, phoronids, priapulids, anthozoans, crustaceans, arachnids, insects and even plant roots (Schlirf & Uchman, 2005; Knaust, 2017).

Only in very rare cases the organisms producing traces have been preserved *in situ* and could thus be directly linked to a specific ichnotaxon. Gibb et al. (2010) described an asaphid trilobite placed directly over a *Rusophycus* trace, suggesting that the trilobite may have been trapped on top of a trace that it had just made. Soft-bodied organisms produced most of the traces (Pemberton et al., 1990) and can be preserved only under rare circumstances (Knaust & Desrochers, 2019), thus further reducing the chances to directly identify the biological origin of a trace fossil.

The same kind of burrowing activity might be preserved differently in various substrates, and the nature of the substrate can influence the morphology of trace fossils. Schlirf (2000) and Knaust (2017) showed that three different ichnogenera, *Ophiomorpha* Lundgren, 1891, *Thalassinoides* Ehrenberg, 1944, and *Spongeliomorpha* Saporta, 1887, were made in loose, soft, and firm substrate by the same organism.

Trace fossils usually have long or very long stratigraphic ranges. A large number of trace fossil genera appeared in the Palaeozoic (Buatois & Mángano, 2011), ranging from the Mesozoic and Cenozoic to present-day environments. Some traces nevertheless have limited stratigraphic ranges. The Cambrian *Cruziana* has a stratigraphically restricted distribution and has been used in biostratigraphy (Seilacher, 1970). However, trace fossil associations have narrow environmental ranges. Biogenic structures are strongly controlled by environmental factors; several traces can be common in shallow-marine environments or may only form in deep-marine settings (Buatois & Mángano, 2011).

Most of trace fossils are formed *in situ* and are an essential part of the sedimentary rock. This characteristic presents the strength of trace fossils in palaeoecological and palaeoenvironmental reconstructions (Buatois & Mángano, 2011). However, some traces can be transported with the host, like bioerosional and other traces related to shelly fossils or bioclasts. For instance, the Lower Ordovician *Siphonia cylindrica*, described initially as a sponge (Eichwald, 1840), appears to be a fragment of redeposited trace fossils (Männil et al., 1984; Fedorov, 2018).

## 2.2 Classification of trace fossils

Ichnotaxobase is a distinctive feature of a trace fossil, which can be used in ichnotaxonomic classification (Bromley, 1990, 1996). Rindsberg (2018) emphasizes that morphology is ultimately the only practical basis of ichnotaxonomy. Buatois & Mángano (2011) have discussed also other features, notably wall and lining, branching, fill, as well as presence or absence of spreite of the traces. Size, taphonomy or preservation, producer-related criteria, type of passive fill, substrate consistency, geological age, geographic location and facies are rejected as valid ichnotaxobases (Bertling et al., 2006). Only the principal type of substrate (lithic, soft sediment, etc.) is important for the identification of an ichnotaxon.

Often different trace fossils occur tightly together, making either compound or composite traces. Compound traces are produced by a single producer and occur due to the changing behaviour of the tracemaker (Ekdale & Bromley, 2001a). Composite structures are made by different producers and usually at different times, with the involvement of different ichnotaxa (Pickerill & Narbonne, 1995). Composite structures of different trace fossils that can also occur separately are not regarded as valid ichnotaxa (Bertling et al., 2006).

Systematic classification of trace fossils is complicated, and several alternative schemes are in use. For decades, Seilacher's (1953, 1964) ethological classification has been used as a standard. The traces are the primary evidence of animal behaviour, which is the basic concept of ethological classification. The first version of Seilacher's classification consisted of five basic categories: **resting traces** (cubichnia), **locomotion traces** (repichnia), **grazing traces** (pascichnia), **feeding traces** (fodinichnia), and **dwelling traces** (domichnia). The ethological classification is discussed in a large number of studies and has frequently been updated. Frey (1975) added **escape traces** (fugichnia) as a separate category and Ekdale et al. (1984) proposed agrichnia for **farming traces** and traps, and praedichnia for **predatory traces** that show interactions between the predator and its prey (Ekdale, 1985). Gibert et al. (2004) proposed fixichnia for the **attachment traces** on hard substrates. Vallon et al. (2016) made the latest major revision of ethological categories and proposed a new, updated scheme. Equilibrichna (Frey & Pemberton, 1985) including vertically repeated movements by the tracemakers, was reassigned to domichnia and fodinichnia (Vallon et al., 2016).

A custom simple toponomic classification of traces (Seilacher, 1964; Martinsson, 1965, 1970) with respect to their mode of preservation and relationship with the surrounding sedimentary layers also exists. According to Martinson (1965, 1970) **epichnia** is a structure preserved at the upper surface of the main body and **hypichnia** is preserved at the lower surface, both can be preserved as a ridge or a groove. **Endichnia** are fully inside of sediment and are made by infaunal organisms. Seilacher proposed the relevant terms epirelief, hyporelief and full relief.

Książkiewicz (1977) organized trace fossils in the basis of general morphology. Many subsequent authors (e.g. Hecker, 1980; Uchman, 1995, 2007; Schirf, 2000) have successfully used this system. Knaust (2012a) discussed the problems of trace-fossils systematics in detail and proposed a morphological classification scheme based on significant morphological features of burrows, trackways, imprints, trails and bioerosional traces. The idea of this proposed scheme was, in a longer term, utilization of structured database for classification.

Buatois & Mángano (2011, 2013) introduced the term ichnodisparity, which measures the variability of morphological body plans in biogenic structures, unlike ichnodiversity,

which refers to ichnotaxonomic richness. Ichnodiversity counts the number of ichnogenera and ichnodisparity the number of trace fossil architectural designs (Mángano & Buatois, 2014). Combination of ichnodisparity and ichnodiversity may provide valuable palaeobiological megatrends (e.g. Mángano & Buatois, 2014, 2016; Mángano et al., 2016). Buatois et al. (2017) discussed the term **category of architectural design** (CAD) and all trace fossil genera were grouped into 78 different CADs, 58 for bioturbation and 21 for bioerosion structures. This publication, with references to literature, is a very useful tool for the determination of the trace fossils. CADs are used to group and characterise Estonian carbonate facies ichnofossils in the main results part of this thesis.

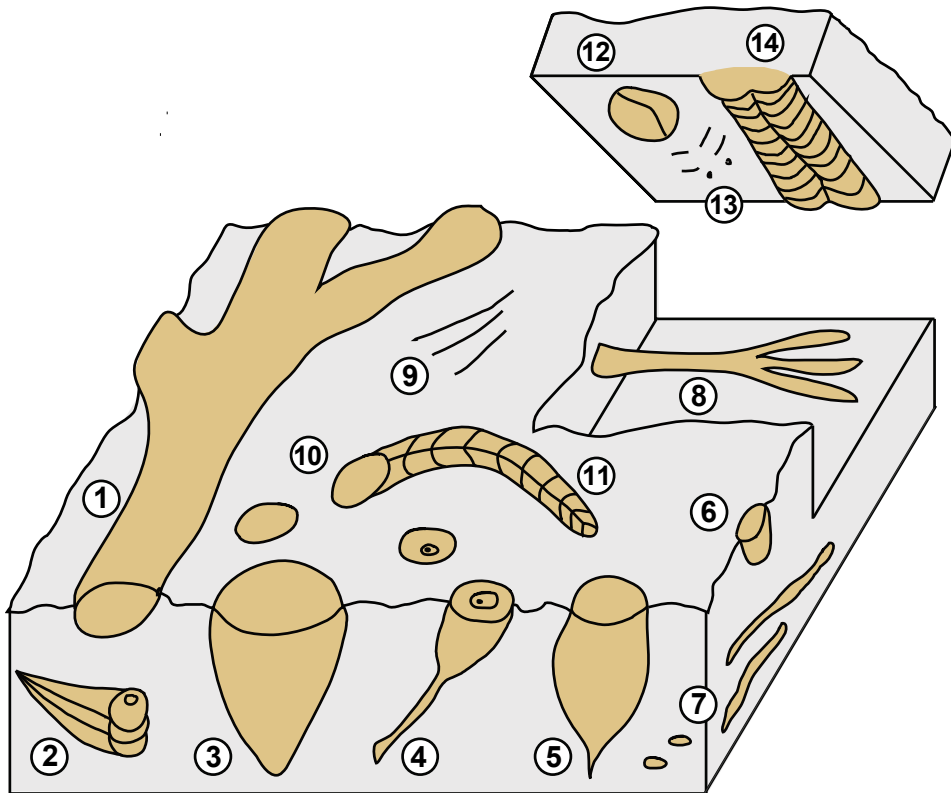
For now, the taxonomic classification of trace fossils is under the jurisdiction of the International Code of Zoological Nomenclature (ICZN, 1999). Trace fossils are included as an ichnotaxon (ichnogenus, ichnospecies) to separate them from categories of the Linnean taxonomy. Footprints, trackways, trails, burrows, borings, coprolites, gastroliths, regurgitaliths, nests, bite and gnaw structures are classified as traces under ICZN (Bertling et al., 2006; Rindsberg, 2012).

Trace fossils are mostly described on the ichnogenus and ichnospecies level. In recent decades, however, attention has been paid to establish a higher-level classification too. Several ichnotaxa are grouped into ichnofamilies and new ichnofamilies are introduced (e.g. Bromley et al., 2007; Knaust, 2015; Knaust & Neumann, 2016; Uchman et al., 2018; Wisshak et al., 2019). Concepts and reviews on ichnotaxonomic principles are further discussed and ichnotaxobases provided in many recent publications (e.g. Bertling et al., 2006; Bertling, 2007; Rindsberg, 2012, 2018; and references therein).

The trace fossils may also be divided into two informal groups based on their size: macro- and micro-traces (Knaust, 2012a), with the boundary between them commonly taken at 1 mm.

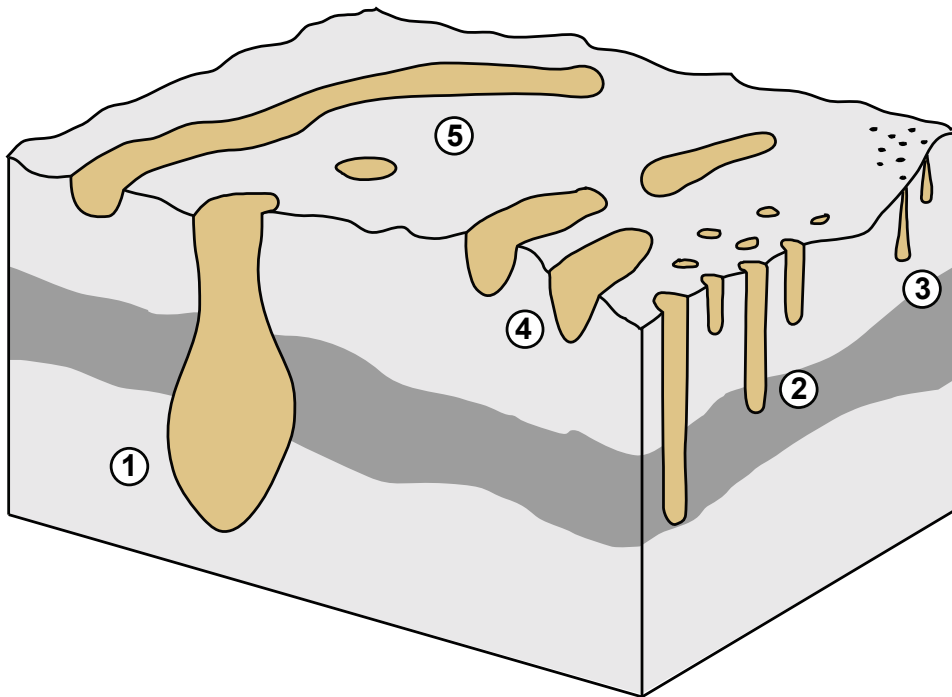
## 2.3 Ichnofacies model

Ichnofacies is an assemblage of trace fossils that provides indications about the environment that the trace-making organisms inhabited. The first comprehensive ichnofacies model was introduced by Seilacher (1954, 1964) and is based on invertebrate ichnotaxa. It is a tool to determine the ancient depositional setting. Originally, the model reflected water depth and distance from shoreline. Each ichnofacies is named after distinctive trace fossil(s) present in the assemblage. Seilacher's initial model has subsequently been improved (e.g. Frey & Seilacher, 1980; Frey & Pemberton, 1987; Bromley & Asgaard, 1993; Gibert et al., 1998, 2007; MacEachern et al., 2007), and in addition to the marine, softground and substrate-controlled ichnofacies, invertebrate and vertebrate continental ichnofacies have been established.



**Figure 1.** Trace fossils of the *Cruziana* ichnofacies. 1. *Thalassinoides*; 2. *Teichichnus*; 3. *Conichnus*; 4. *Rosselia*, 5. *Amphorichnus*; 6. *Bergaueria*; 7. *Planolites*; 8. *Chondrites*; 9. *Monomorphichnus*; 10. *Lockeia*; 11. *Protovirgularia*; 12. *Rusophycus*; 13 *Diplichnites*; 14. *Cruziana*.

Five softground marine ichnofacies are known: *Pylonichnus*, *Skolithos*, *Cruziana*, *Zoophycos* and *Nereites* ichnofacies, the first three of which occur in carbonate deposits. The *Pylonichnus* ichnofacies (Frey & Pemberton, 1987) represents a transitional zone between continental and marine depositional environments, containing traces of terrestrial and marine organisms. The *Skolithos* ichnofacies (Seilacher, 1963, 1967) is typical of beach foreshore and shoreface environments. It is characterised by the dominance of vertical, cylindrical, simple or U-shaped burrows, the presence of equilibrium burrows and escape traces, and an abundance of three-dimensional burrow systems with prevailing vertical components (Buatois & Mángano, 2011). The *Cruziana* ichnofacies (Seilacher, 1964, 1967) is characteristic of moderate- and low-energy offshore marine settings (shelves, epeiric seas, bays, lagoons, tidal flats), occurring between the fair-weather and storm wave base. It is characterised by the dominance of horizontal traces, a wide variety of ethological categories, and high ichnodiversity (Fig. 1), as well as an abundance of traces (Buatois & Mángano, 2011). According to Knaust et al. (2012), it is probably the most common ichnofacies in carbonates worldwide.



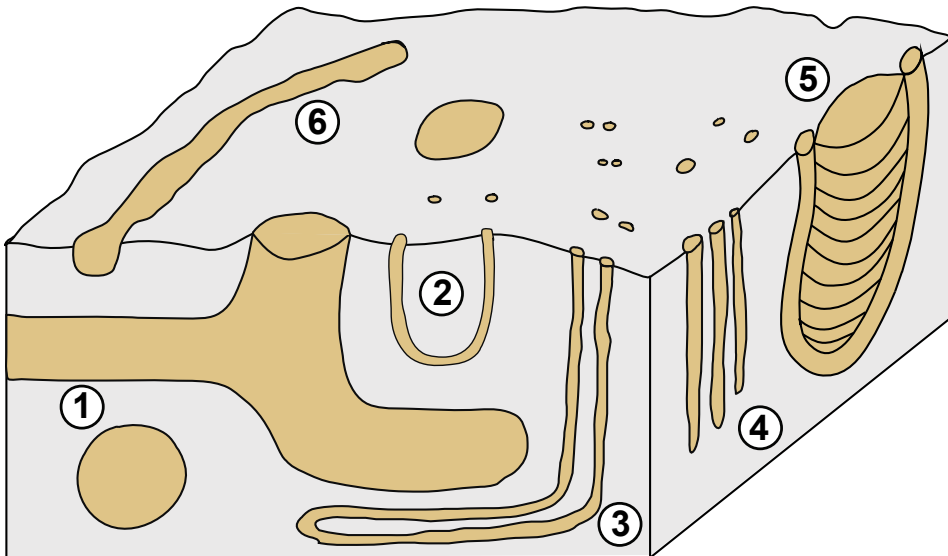
**Figure 2.** Trace fossils of the *Trypanites* ichnofacies. 1. *Gastrochaenolithes*; 2. *Trypanites*; 3. *Palaeosabella*; 4. *Petroxestes*; 5. *Sulcolithos*.

Four substrate-controlled ichnofacies are distinguished, and three of these have been described from carbonates: *Glossifungites*, *Trypanites* and *Gnatichnus* ichnofacies. The *Trypanites* ichnofacies (Frey & Seilacher, 1980) is characteristic of hardgrounds such as rocky coasts (beachrock, reefs, and coquinas). According to Bromley & Asgaard (1993), the *Trypanites* ichnofacies consists of two different ichnofacies: *Entobia* ichnofacies with deep tier borings, and *Gnatichnus* ichnofacies with shallow-tier raspings and etchings. MacEachern et al. (2007) noted that the trace fossil associations of *Entobia* and *Trypanites* ichnofacies are identical, and Buatois & Mángano (2011) regarded the *Entobia* association as an equivalent of the *Trypanites* ichnofacies. The latter ichnofacies is characterised by the dominance of deep tier borings, low to moderate ichnodiversity (Fig. 2), and a high abundance and density of traces. *Trypanites* ichnofacies is restricted to areas with rapid cementation, such as in subtidal and intertidal environments (Knaust et al., 2012). The *Gnatichnus* ichnofacies (Bromley & Asgaard, 1993) is related to shells and boulders. It is characterised by the dominance of shallow to very shallow-tier grazing structures and the presence of fixichnia, praedichnia, attachment scars, low ichnodiversity and a high abundance of traces (Buatois & Mángano, 2011). *Gnatichnus* ichnofacies occurs mostly on mobile shellgrounds and was common in the Mesozoic and Cenozoic (Gibert et al., 2007).

The *Glossifungites* ichnofacies (Seilacher, 1967) occurs on unlithified firmgrounds, where sediments are compacted and dewatered (carbonate ramps and platforms, lagoons, beaches, shoals). Occurrences of sharp-walled, passively filled burrows, the dominance of robust vertical structures (Fig. 3), a low ichnodiversity and high abundance of traces are characteristic of the *Glossifungites* ichnofacies (Buatois & Mángano, 2011). The *Glossifungites* ichnofacies may gradually change into *Trypanites* ichnofacies (Bromley, 1975a).

## 2.4 Trace fossils in shallow-marine carbonates

The number of ichnological studies from carbonate settings is small compared to those of siliciclastic environments, and Palaeozoic carbonate settings are especially underrepresented (Knaust et al., 2012). Ordovician shallow-marine carbonates have received somewhat more attention (e.g. Osgood, 1970; Pickerill & Forbes, 1979; Knaust et al., 2012; Zheng et al., 2018) than their Silurian counterparts (e.g. Archer, 1984; Narbonne, 1984). Bioerosional traces are important in shallow-marine carbonates and they have received attention with regard to the “Ordovician Bioerosion Revolution” (Wilson & Palmer, 2006).



**Figure 3.** Typical trace fossils of the *Glossifungites* ichnofacies. 1. *Balanoglossites*; 2. *Arenicolites*; 3. *Tisoo*; 4. *Skolithos*; 5. *Diplocraterion*.

Carbonate rocks have some peculiarities: early cementation and formation of hardgrounds and firmgrounds, the influence of organisms on early diagenesis, a lack of colour contrast, and heterogeneity in sediment composition and texture (Kennedy, 1975; Curran, 1994, 2007; Buatois & Mángano, 2011; Knaust et al., 2012). Many authors consider early cementation of carbonate substrates to be the most important factor for trace fossils, as lithification can take place before the burrow is abandoned. On the other hand, burrowing influences the early diagenesis, and diagenesis affects the preservation of traces (Narbonne, 1984; Buatois & Mángano, 2011). The compaction is less important in carbonate sediments and ensures better preservation of the traces (Knaust et al., 2012); however, a subsequent recrystallization of deposits can lead to poor preservation. Composition of the sediment is important, along with the distribution of benthic organisms as potential tracemakers. Most trace fossil forms occur in both carbonate and siliciclastic environments. Only few taxa are carbonate-specific with burrowing and boring techniques adapted to firmgrounds and hardgrounds; one such example is *Trypanites*, whose tracemakers used chemical dissolution (Knaust et al., 2012). In carbonates, microbial mats and biofilms, which cover the sediment surface and may increase the preservation of the trace fossils, are more typical.



An absence of colour contrast between the trace and matrix often hides the diagnostic features of trace fossils in carbonates (Curran, 1994, 2007). Discrete structures in carbonates have a higher textural and compositional contrast and thus better preservation potential (Archer, 1984). Several authors have noted that mixed carbonate-siliciclastic systems have a higher preserved ichnodiversity than carbonate settings (e.g. Rodríguez-Tovar et al., 2014; Mángano et al., 2016).

## 2.5 Bioerosion and hardgrounds

Neumann (1966) introduced the term “bioerosion” as the removal of consolidated minerals or lithic substrate by the direct action of organisms. Subsequently, the term has been discussed, reinterpreted and redefined (e.g. Ekdale et al., 1984; Tapanila, 2008a; Schönberg et al., 2017; Davidson et al., 2018). Bioerosion is mostly used for the breakdown of different hard substrates through the biological activities of animals, plants and microbes (Bromley, 1994) that produce both mechanical and chemical erosion. The earliest borings were made by endolithic cyanobacteria (Zhang & Golubić, 1987); the oldest predatory macroborings are known from the late Neoproterozoic (Bengtson & Zhao, 1992). The oldest representative of macroborings in carbonate substrate is the lower Cambrian *Trypanites* Mägdefrau, 1932 (James et al., 1977; Kobluk et al., 1978; Kobluk, 1981). Small *Trypanites* borings in early Cambrian phosphatic pebbles and cobbles are the earliest bioerosional traces known from Estonia (Vinn & Toom, 2016a).

Macroborings changed throughout the Phanerozoic (Taylor & Wilson, 2003). This diversification, with an increased intensity of carbonate substrate bioerosion, took place during the Middle and Late Ordovician (Kobluk et al., 1978; Bromley, 1994; Taylor & Wilson, 2003; Buatois et al., 2016a; Wisshak, 2017). Wilson & Palmer (2006) coined the term “Ordovician Bioerosion Revolution” for this change. Bioerosion needed an adaption by the bioeroding organisms (Ekdale & Bromley, 2001b; Mángano & Droser, 2004), which is often an integrated process involving both micro- and macrobiota (Taylor & Wilson, 2003; Golubić et al., 2019). One bioerosional ichnospecies may produce traces of different morphologies, depending on the resistance of the substrate (Schönberg & Tapanila, 2006).

A discontinuity surface indicates stratigraphic interference where an interruption of sedimentation is proven, and hardgrounds and simple omission surfaces are included (Bromley, 1975a; Clari et al., 1995). Hardgrounds are surfaces of synsedimentarily cemented carbonate layers that have been exposed on the seafloor; borings and encrusters aid in the recognition of fossil hardgrounds (Palmer, 1982; Wright & Chernes, 2016). Cavity-dwelling encrusters and *Trypanites* tracemakers from the lower Cambrian have been considered the oldest representatives of hardground faunas (James et al., 1977; Kobluk et al., 1978; Kobluk & James, 1979; Kobluk, 1981). In the Phanerozoic, hardgrounds are common in the Ordovician successions (Rozhnov, 2002; Taylor & Wilson, 2003; Palmer & Wilson, 2004; Christ et al., 2015; Paton et al., 2019), and are seemingly less abundant in the Silurian (Chernes, 1982; Vinn & Wilson, 2010a, Copper et al., 2012). Both periods represent calcite sea conditions (Palmer & Wilson, 2004), characterized by the rapid formation of hardgrounds and a contemporaneous dissolution of aragonitic shells (Chernes & Wright, 2000). Hard substrates and hardgrounds provide unique opportunities to study the encrusting and endolithic organisms in their life sites (Brett, 1988; Taylor, 2016). By the Middle Ordovician, the diversity of hardground faunas had

greatly increased, showing diverse encrusting and boring biotas (e.g. Kobluk et al., 1978; Wilson et al., 1992; Johnson & Baarli, 1999; Taylor & Wilson, 2003; Buatois et al., 2016a). Silurian hardground faunas have received somewhat less attention (e.g. Halleck, 1973; Cherns, 1980; Franzén, 1977; Sumrall et al., 2009; Vinn & Wilson, 2010a).

## 2.6 Ordovician and Silurian trace fossils and hardgrounds in the Baltic region

Until recently, trace fossils have received very little attention in Estonia, and have never been systematically collected and thoroughly studied from Ordovician and Silurian carbonate rocks. One reason for this has been the high abundance and availability of well-preserved shelly fossils. However, the abundance of different trace fossils is considered general knowledge (Põlma, 1982). Currently, only a very brief overview of Ordovician and Silurian traces has been provided in a single conference paper (Männil et al., 1984). These authors argued that ichnofossil diversity in the Ordovician and Silurian is generally lower than in the Cambrian and Devonian succession of the region.

The first papers on trace fossils in the region were published during the 19th century. Eichwald (1854) described and named numerous plants from the Baltic region, but some of them turned to be trace fossils. Kupffer (1874) was the first researcher who suggested that the deep pits in the Middle Ordovician discontinuity surface are of biogenic origin. The bioerosional traces, *Trypanites* borings and “amphora-like borings” were described from Dapingian and Darriwilian deposits of Estonia by Orviku (1940, 1960). Borings have been described from the Ordovician deposits of Russia, Sweden and Norway in a number of papers (e.g. Vishnyakov & Hecker, 1937; Hessland, 1949; Lindström, 1979; Opalinski & Harland, 1980; Nield, 1984; Pickerill & Harland, 1984; Ekdale & Bromley, 2001b; Ekdale et al., 2002). It is noteworthy that attention was also paid to the euendoliths (Podhalańska & Nölvak, 1995).

Männil (1966b) described only one globally known soft-sediment ichnogenus from the Upper Ordovician of Estonia – *Conichnus* and the less well-known *Amphorichnus*. At same time, rich assemblages of trace fossils with abundant trackways from the Ordovician and Silurian strata of the Oslo region were described (Seilacher & Meischner, 1965; Hanken & Størmer, 1975; Whitaker, 1979; Pollard & Walker, 1984; Stanistreet, 1989; Dam & Andreasen, 1990).

Investigations of Ordovician and Silurian trace fossils from the Baltic region were recently reinitiated in the onset of this century, and diverse associations have been described from Russia, Norway and Sweden (e.g. Dronov et al., 2002; Cherns et al., 2006; Davies et al., 2006; Ershova et al., 2006; Knaust et al., 2012; Knaust & Dronov, 2013; Hanken et al., 2016). Vinn (2004, 2005), Wyse Jackson & Key (2007), Vinn & Wilson (2010c), Vinn et al. (2014a) have described several bioerosional traces from Estonia: *Trypanites*, *Osprioneides* Beuck & Wisshak in Beuck et al., 2008, and *Sanctum* Erickson & Bouchard, 2003. In addition, some soft sediment ichnogenera have been discussed (Vinn & Wilson, 2013; Vinn, 2014). Trace fossils from carbonate erratic boulders of Baltic origin have been described in several papers (Stel, 1976; Chrzastek & Pluta 2017a; van Keulen & Rhebergen, 2017). Altogether, the literature database of Baltoscandian trace fossils includes more than 250 items.

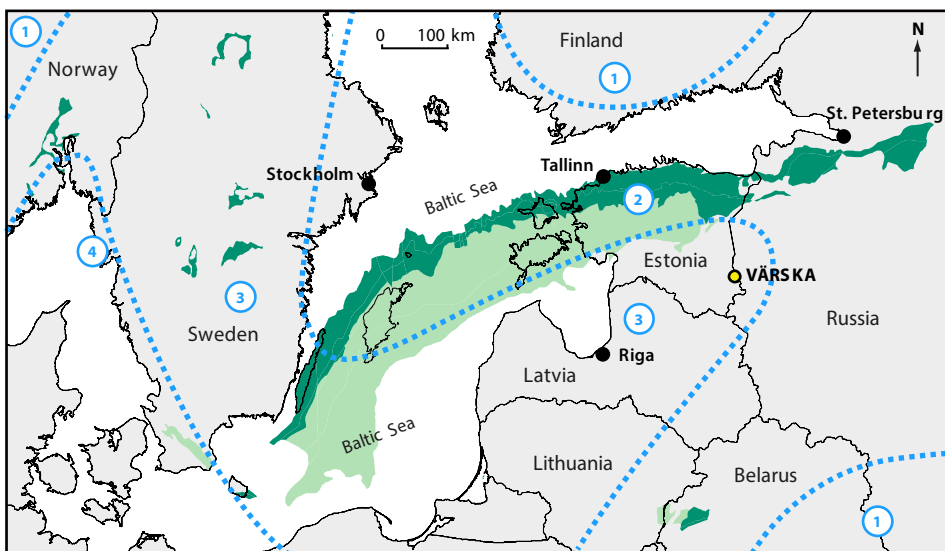
Hardgrounds and hardground faunas influenced the distribution of trace fossils and contributed to the bioerosion; thus, these aspects are specifically addressed in this study.

In Baltoscandia, hardgrounds and omission surfaces have been reported and studied for many years. Several papers are devoted to the Ordovician deposits of the St. Petersburg region (Kupffer, 1874; Lamansky, 1905; Vishnyakov & Hecker, 1937; Hecker, 1960, 1970; Rozhnov, 1994, 2002, 2017, 2018, 2019; Rozhnov & Palmer, 1996; Dronov et al., 1996; Fedorov, 2003; Knaust et al., 2012; Knaust & Dronov, 2013). Ordovician and Silurian hardgrounds and sedimentation breaks of Sweden have also been researched (Jaanusson, 1961; Lindström, 1963, 1979; Cherns, 1982; Nordlund, 1989; Ekdale & Bromley, 2001b; Ekdale et al., 2002). However, in Estonia they have received less attention, except in stratigraphy, where they are often used as markers for the separation of different stratigraphic units. Different morphologies of hardgrounds have been previously described (Orviku, 1940, 1960, 1961, 1962; Einasto, 1964), including types of impregnation (Saadre, 1992, 1993). Trace fossils and encrusting faunas have received attention in recent decades (Hints, L. & Miidel, 2008; Vinn & Wilson, 2010a, b; Vinn, 2015). Rozhnov's works on microbially induced sedimentary surfaces in the Ordovician deposits of the St. Petersburg region and Estonia have brought new developments and ideas into this field of research (Rozhnov, 2018). According to Põlma (1982), the number of different Ordovician discontinuity surfaces in northern Estonia exceeds 200, and at times they can occur very frequently (Nölvak, 1972). Many of the surfaces are traceable for considerable distances (Orviku, 1940; Männil, 1966a). The stratigraphic distribution of hardgrounds was influenced by changes in sea level, climate and depositional conditions. Low sedimentation in the Dapingian and Darriwilian (Jaanusson, 1973; Nestor & Einasto, 1997) created especially favourable conditions for hardground formation and habitation by organisms.

### 3 Geological background

During the Ordovician and Silurian periods, the study area was a part of a shallow sea that covered the western part of the Baltica craton. This epeiric sea extended from Norway to the Volga area in NW Russia, and from the Fennoscandian mainland in the north to the Sarmatian mainland in the south (Fig. 4; Nestor & Einasto, 1997). During the Ordovician and Silurian, the Baltica craton drifted from high southern latitudes to the equatorial area (Torsvik & Cocks, 2013; and references therein), resulting in gradual changes in climate and depositional conditions. In Estonia, carbonate sedimentation commenced in the end of the Floian and continued into the Early Ordovician in a vast flat-bottomed and relatively cool epicontinental basin (Dronov & Rozhnov, 2007); this sedimentation ended up in a restricted pericratonic sea in the late Pridoli, superseded by the tectonic uplift of the Caledonian mountain belt in the west (Nestor & Einasto, 1997).

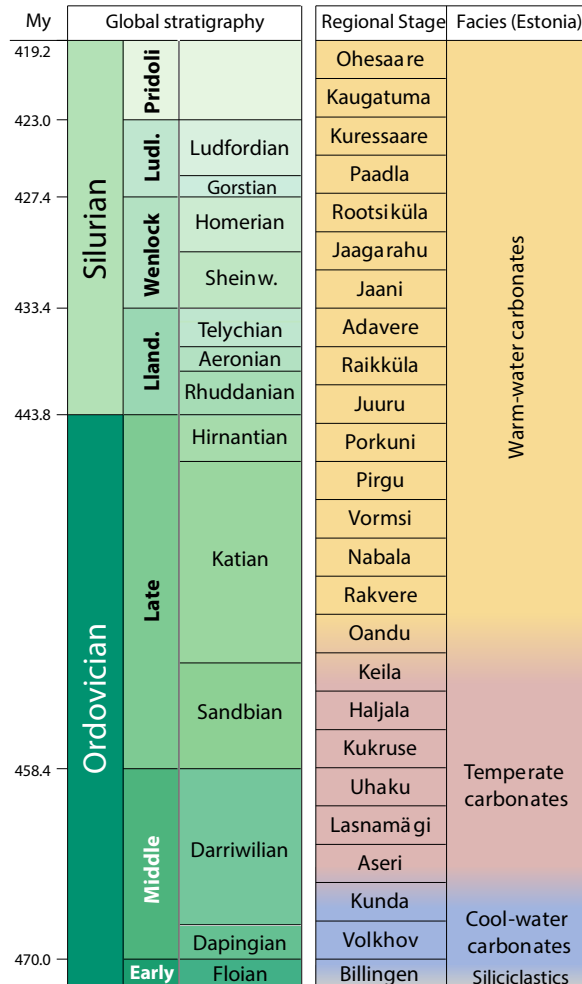
Generally, the area of Estonia, and the Ordovician–Silurian outcrop area in particular, represented the relatively shallow-water part of the Baltoscandian basin (Fig. 4), termed as the marginal facies belt or the Estonian shelf. Deeper-water settings were located in the south (the so-called Livonian basin) and west (Central Baltoscandian and Scanian facies belts). Details on the architecture and development of the Baltoscandian basin are provided by Männil (1966a), Kaljo et al. (1970) and Nestor & Einasto (1997; and references therein).



**Figure 4.** Locality map showing the outcrop area of Ordovician and Silurian rocks in the Baltic region and schematic configuration of the Baltoscandian basin (after Männil, 1966a and Nestor & Einasto, 1997). 1 – main land areas, 2 – shallow-water Estonian shelf, 3 – deeper-water Livonian basin and Central Baltoscandian facies belt, 4 – deep shelf of the Scanian facies belt (Paper I).

The Middle Ordovician and lowermost Upper Ordovician are characterised by a highly condensed succession of carbonates deposited in cool and/or temperate water environments (Fig. 5) with little bathymetric differentiation (Jaanusson, 1973). A major change in the sedimentation regime took place in the late Sandbian to the earliest Katian, when the first tropical reefs appeared in the region (Kröger et al., 2017) and the facies differentiation and sedimentation rates generally increased. The upper part of the

succession is characterised by warm-water carbonates and well-developed cyclicity at different scales (Nestor & Einasto, 1997). The maximum thickness of the Ordovician–Silurian succession is ca. 550 m in Estonia. The Ordovician–Silurian carbonate rocks in the region are characterised by virtually lacking thermal alteration, as indicated by conodont colour alteration index values c. 1 CAI unit (Männik, 2017) and other maturity proxies. The succession is rich in typical Palaeozoic shelly faunas (brachiopods, bryozoans, echinoderms, molluscs, corals, sponges, trilobites, etc.), as well as microfossils. Trace fossils are also abundant, and the degree of bioturbation is high (Harris et al., 2004).



**Figure 5.** Regional and international stratigraphy of the studied interval, showing transition from cool-water to warm-water carbonate deposits (Paper I).

The regional stratigraphic framework is historically based on Baltic regional stages (Fig. 5) and lithostratigraphy in Estonia. Time-correlations within the region and with the global standard are mostly based on high-resolution biostratigraphy, and notably conodont, chitinozoan and graptolite biozonations (Nölvak et al., 2006; Männik, 2014). Regional stages (as well as global series and stages are used throughout this study.

## 4 Materials and methods

The large palaeontological collections deposited in several institutions in Estonia form the basis for this study. The old collections, some dating back for more than 150 years, were complemented by new material collected by the author during fieldwork from 2010 onwards. The total number of Ordovician and Silurian macrofossils and rock samples in Estonian research collections is over 0.3 million; however, the number of ichnofossil specimens is significantly smaller – c. 3800 specimens have been identified from the Ordovician and Silurian carbonate succession and are referred to in this study.

The selection of study methods was based on the rock type and the size of trace fossils. Most specimens were initially inspected using a stereo zoom microscope (usually with magnifications  $\times 5$ – $25$ ); then, the material was cleaned and often photographed. For many types of traces, cutting and polishing was necessary before studying and imaging to reveal diagnostic features and enhance the contrast between the trace and the matrix. The uniqueness of the material was considered and destructive techniques were not applied to rare specimens. Cleaning with ultrasound equipment was tested but did not produce satisfactory results in solid Palaeozoic rocks; it was used in combination with mechanical preparation in cases where the matrix was relatively soft. Simple serial sectioning was used for larger specimens to reveal three-dimensional architecture.

Specimens were photographed with a Canon EOS 5DsR digital camera and a Leica Z16APO zoom microscope system. For measurements of specimens from calibrated digital photos, Fiji image analysis software (<https://imagej.net/Fiji>) was used. In some cases, scanning electron microscopy (SEM) was used for visualizing micro-coprolites. Energy-dispersive X-ray spectroscopy (EDS) was applied together with SEM to detect the chemical composition of selected trace fossil samples. Specimens demonstrating a large number of pellets on sectioned shells or steinkerns were used for measurements. To assess the relative abundance and distribution of pellet-filled shells, a random selection of shelly fossils was sectioned and examined, with 30 specimens of gastropods and 30 specimens of brachiopods from the Haljala quarry, and 30 specimens of gastropods from the Mõnuste quarry (respectively Sandbian and Katian stages).

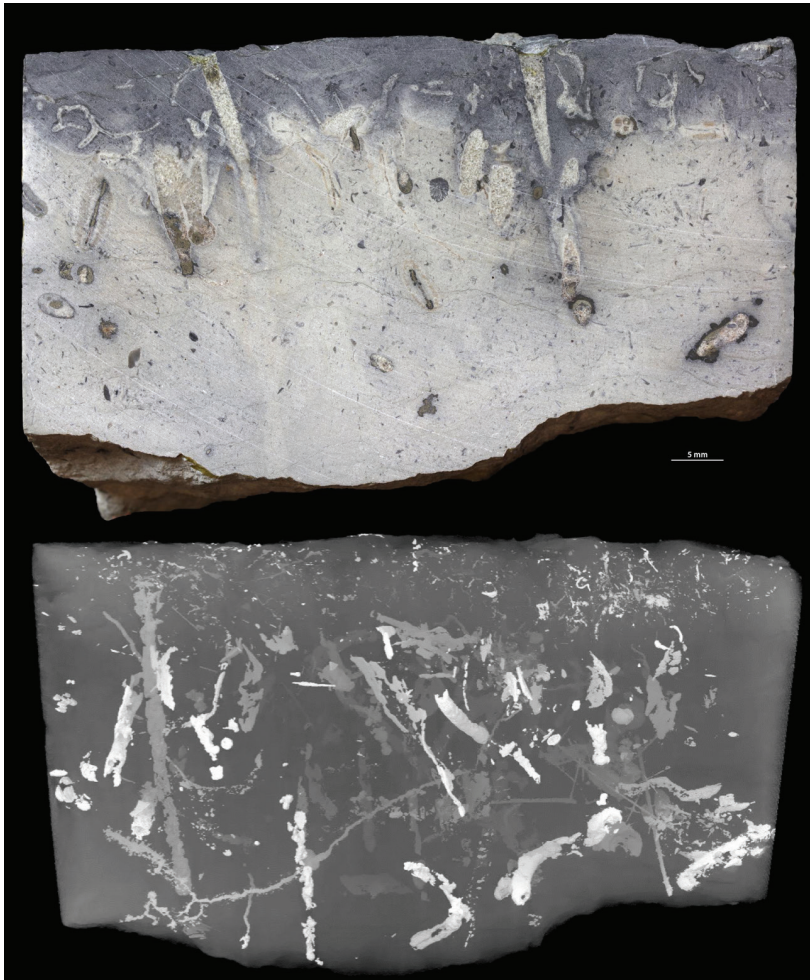
Conventional study methods turned to be insufficient for the determination of Lower Palaeozoic trace fossils, and especially bioerosional structures, in different shelly fossils. X-ray computed tomography (CT) and micro-CT have been successfully used in recent years for 3D visualisations of different trace fossils hidden in the hard substrates (e.g. Schönberg & Shields, 2008; Rodríguez-Tovar et al., 2018). This non-destructive method has been used to establish Palaeozoic sediment-filled macro- and microboring taxa (Beuck et al., 2008; Tapanila, 2008b; Wisshak et al., 2017).

X-ray CT was used for the first tests on different types of carbonate facies trace fossils from Estonia to reconstruct their 3D morphology and assess the potential of the method (Fig. 6; Toom et al., 2018). Within samples with pyritic impregnation and different structures on hardgrounds, the traces can be easily distinguished in considerable detail. Traces filled with denser carbonate are clearly distinct from the lighter kerogen-rich oil-shale matrix. Results from bioerosional traces within stromatoporoids and bryozoans that showed a rather faint difference in contrast between the trace infills and the matrix were problematic. These analyses were made at the Geological Survey of Finland with Phoenix v|tome|x s 240, running at 120–150 kV accelerating voltage with 1500–2700 projections, resulting in a 20–60 minute scan time and 20–100-micron voxel resolution. Further efforts are needed in this area.

For the maximum macroboring density (MMD), the method described in Tapanila et al. (2004) was used. MMD index values, ranging from 0 to 5, were determined from the number of macroborings centred in a 4 cm<sup>2</sup> grid. A maximum number of borings was counted in a 4 cm<sup>2</sup> area by using a grid drawn on a transparent film and calibrated photos. In addition, a millimetre grid drawn on a transparent film was used to measure the area covered by encrusters. The encrusting fauna was identified to the lowest possible taxonomic level.

The studied material is deposited at the Department of Geology, Tallinn University of Technology (GIT), Natural History Museum, University of Tartu (TUG) and the Estonian Museum of Natural History (TAMG). These three institutions make up the Estonian national geological collection. Data on individual trace fossil specimens (including images), localities and relevant literature are managed in the multi-institutional database of geoscientific collections, which is accessible online at <https://geocollections.info>.

For the identification of traces, the morphological classification scheme proposed by Knaust (2012a) and CADs introduced by Buatois et al. (2017) are used.



**Figure 6.** Surface photo and X-ray computed tomography 3D reconstruction of pyritized hardground with traces. Specimen GIT 362-587, Äiamaa drillcore, Oandu Stage, Katian.

## 5 Results and discussion

### 5.1 Systematic review of recorded trace fossils

In the following systematic review all trace fossil genera currently identified from Estonia are discussed. Trace fossils are grouped into three broad categories below: bioturbation structures, bioerosional trace fossils, coprolites and associated structures. These are further subdivided according to the CADs of Buatois et al. (2017). Additionally, bioclausturation structures, not trace fossils *sensu stricto*, are commented upon. All data are summarised in Table 1 at the genus level. The small number of named trace fossils and the large number of lithostratigraphic units in the carbonate succession of Estonia is why the occurrence of ichnofossils is provided in regional stages.

The review mostly follows the data published by Toom et al. (Paper I), but with some important updates based on most recent new finds and some re-interpretations of previous data. Wisshak et al. (2019) published a review of bioerosional traces with taxonomic inventory, and the updates are included or discussed below. Knaust (2019a) used the first results of X-ray CT on Estonian trace fossils from kukersite and established a new ichnogenus *Sulcolithos* (Knaust, 2019a), which appears to be common in the Ordovician deposits of the Baltic region. Recent fieldwork has also provided new material and data on the occurrence of some well-known taxa, including *Conichnus*, *Gastrochaenolithes*, *Rusophycus*, but also new ichnogenera for Estonia like *Archaeonassa*. The systematic work on collection of graptolites revealed the presence of pyritized thread-like trace *Trichichnus*, and research of micro-coprolites related to the body fossils (Paper II) brought up several new ichnogenera in the carbonate succession of Estonia. The work on bioerosional traces confirmed the occurrence of *Petroxestes* in Estonia (Paper VII). According to Toom et al. (Paper I) 45 trace fossil genera and five bioclausturation structures in total were identified. However, as of writing this thesis, Table 1 lists the occurrence of 52 ichnogenera, one ichnofamily, escape traces, unnamed peeling structures and bioerosional microstructures, in addition to the data on four bioclausturation genera.

#### 5.1.1 Bioturbation structures

**Simple horizontal trails** are represented by very simple trails. Surprisingly, the finds from this CAD are rare, represented by *Archaeonassa* Fenton & Fenton, 1937, and the problematic feeding trace *Circulichnis* Vialov, 1971 (Table 1). *Archaeonassa* furrows are tentatively identified on a rippled bedding plane of the Varbola Formation, Juuru Stage (Rhuddanian). Finding of poorly preserved *Circulichnis* comes from the same stratigraphic level. *Circulichnis* has been reported from shallow-water marine carbonates (Fillon & Pickerill, 1984). The tracemaker is discussed by Buatois et al. (1998) and Uchman & Rattazzi (2019). *Archaeonassa* is mostly interpreted as a grazing trail of gastropods (e.g. Fenton & Fenton, 1937; Buckman, 1994).

**Chevronate trails** are represented by *Protovirgularia*. All Estonian findings come from the Silurian and represent the ichnospecies *P. pennatus* (Fig. 7), which was initially described as a plant by Eichwald (1854), and later re-described by Uchman (1998). *Protovirgularia* commonly occurs together with *Lockeia*. The Estonian lower Silurian protovirgularians occur together with *L. cunctator* Schlirf & Uchman in Schlirf et al., 2001 and the upper Silurian specimens together with *L. siliquaria* James, 1879 (Paper I). *Protovirgularia* is a common element of the *Cruziana* ichnofacies, interpreted as a locomotion trace of bivalves (e.g. Mángano et al., 1998; Luo & Shi, 2017).







**Bilobate trails and paired grooves** are typically locomotion traces of deposit feeders. The best-known trace of this CAD is *Cruziana*. The trace defines the *Cruziana* ichnofacies. In Estonian carbonate succession *Cruziana* is very rare, and was recovered only from the upper Silurian (Vinn, 2014; Paper V). Some traces described initially as *Cruziana* (Paper V) actually represent *Protovirgularia*. The tracemaker and ethology of cruzianiforms are discussed in many papers (e.g. Crimes, 1970; Seilacher, 1985; Rodríguez-Tovar et al., 2014).

**Trackways and scratch imprints** are locomotion traces commonly made by arthropods. In Estonian material, this CAD is represented with few findings of tentatively identified *Diplichnites* and *Monomorphichnus* Crimes, 1970 (Paper I). These traces are common elements of the *Cruziana* ichnofacies. From the Baltic region, different trackways including *Diplichnites* have been previously reported from the upper Silurian of the Oslo region, Norway (Davies et al., 2006). Systematics and tracemakers are discussed in several papers (e.g. Crimes, 1970; Smith et al., 2003; Gibb et al., 2017; and references therein).



**Figure 7.** *Protovirgularia pennatus*, Rohuküla, Raikküla Formation, Raikküla Stage, Llandoverý, GIT 362-234-2.

**Bilaterally symmetrical short, scratched impressions and burrows** are mostly made by arthropods. The widely distributed resting trace *Rusophycus* (Fig. 8) belongs to this category and is a common element of the *Cruziana* ichnofacies. This trace is rare in the carbonate succession of Estonia (Paper V; Table 1). Further research may bring up new data, especially promising would be Silurian beds with occurrences of *Lockeia* and *Protovirgularia*. *Rusophycus* has been previously reported from the Oslo-Asker area (Stanistreet, 1989) and Middle Ordovician (Dapingian) of the St. Petersburg region (Dronov et al., 2002; Ershova et al., 2006). Trilobites are proposed as the tracemakers of Palaeozoic *Rusophycus* (e.g. Osgood, 1970; Brandt, 2007; Tarhan et al., 2012).



**Figure 8.** *Rusophycus*, Ohesaare cliff, Ohesaare Formation, Ohesaare Stage, Põidoli, GIT 362-681.

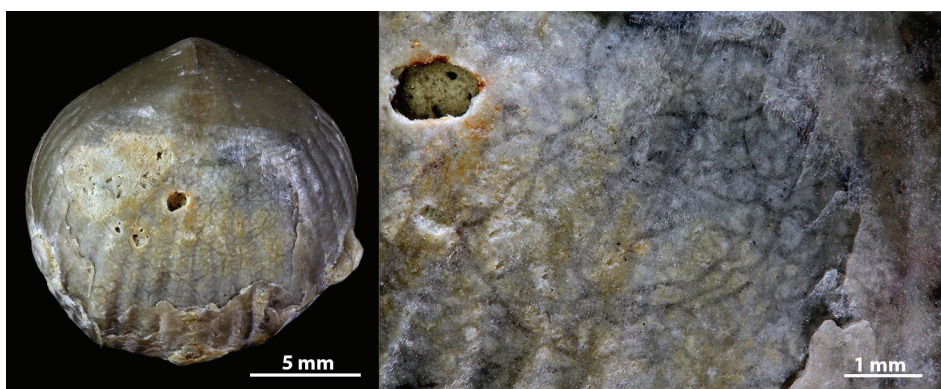
**Passively filled horizontal burrows** are represented in Estonia by the globally abundant ichnogenus *Palaeophycus* Hall, 1847 (Paper I; Table 1). This trace is a simple, lined, horizontal burrow, with an infill similar to the matrix (Pemberton & Frey, 1982). The lining is commonly characteristic in defining the ichnospecies (Buckman, 1995). Three different ichnospecies occur in the Estonian carbonate succession: the thin-walled *P. tubularis* Hall, 1847, the thick-walled *P. herberti* (Saporta, 1872), and *P. striatus* Hall, 1852 with characteristic parallel striae. In marine settings, *Palaeophycus* belongs mainly to the *Cruziana* ichnofacies. The trace is interpreted as a dwelling structure of vermiform animals (e.g. Pemberton & Frey, 1982; Jensen, 1997).

**Simple actively filled (massive) horizontal to oblique structures.** Horizontal structures with a homogeneous infill that is different from the host rock are included in this CAD. Two ichnogenera were identified from the Estonian carbonate succession: the globally abundant *Planolites* Nicholson, 1873 and the rare *Torrowangea* Webby, 1970 (Paper I; Table 1). *Planolites* is an actively filled feeding burrow and a common element of the *Cruziana* ichnofacies (Knaust, 2017). *Planolites* is common in Estonia and is probably represented by two species: tortuous *P. montanus* Richter, 1937, and straight to slightly curved *P. beverleyensis* Billings, 1862. *Torrowangea* is a trace that displays constrictions suggestive of peristalsis, interpreted as the feeding structure of a worm-like animal (Narbonne & Aitken, 1990). In Estonia, its identification is based on a poorly preserved specimen from Ohesaare Stage, Põidoli.

**Simple actively filled (meniscate) horizontal to oblique structures.** From this CAD, the feeding trace *Taenidium* Heer, 1877 is identified as an unlined, variably oriented, meniscate burrow. Ichnospecies are differentiated by the style of meniscate backfill (D'Alessandro & Bromley, 1987; Díez-Canseco et al., 2016). Meniscate traces are typical of the *Scoyenia* ichnofacies in sediments that are periodically exposed to air and submerged (Frey & Pemberton, 1987). However, the Estonian findings from the Kukruse Stage (Paper I) are not related to this kind of environment. The traces are reported from

both shallow- and deep-marine settings (D’Alessandro & Bromley, 1987; Uchman, 2007) and occur in the *Cruziana* ichnofacies (Bromley et al., 1999). *Taenidium* was previously reported from the upper Silurian of the Oslo region (Dam & Andreasen, 1990; Davies et al., 2006). Arthropods or worm-like organisms are thought to be the tracemakers (Bromley et al., 1999; Uchman, 2007; Rodríguez-Tovar et al., 2016).

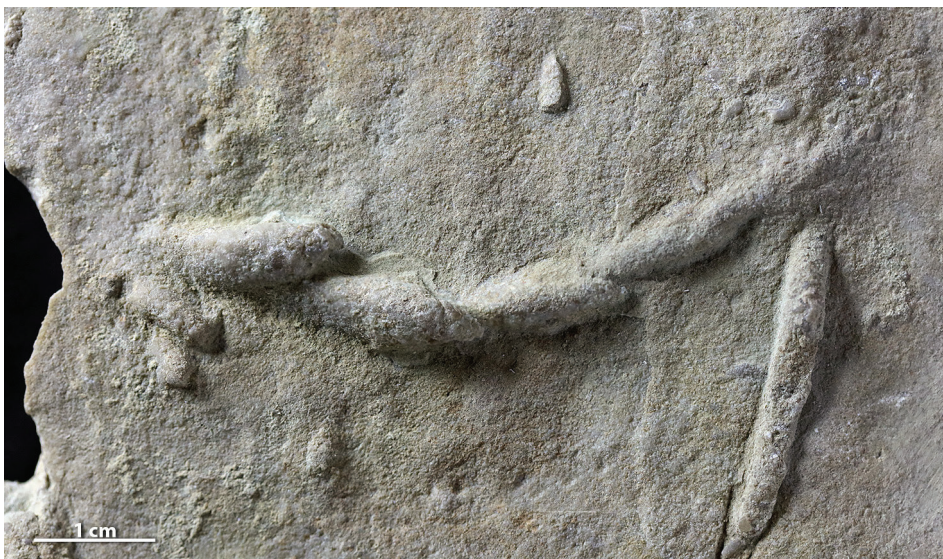
**Horizontal branching burrow systems.** Traces with a two-dimensional body plan are included in this CAD. Two ichnogenera *Archnostega* Bertling, 1992 and *Multina* Orłowski, 1968 (Paper I; Table 1) are identified from the Estonian carbonate succession. *Archnostega*, an irregular net-like burrow system on steinkerns, is widespread in the Ordovician deposits of Estonia and is related to different molluscs (Vinn et al., 2014a). An examination of Silurian trilobite and brachiopod collections revealed that *Archnostega* is relatively rare throughout the Silurian deposits of Estonia (Fig. 9). *Archnostega* has previously been reported from the Ordovician deposits of the St. Petersburg region (Dronov & Mikuláš, 2010) and erratic boulders of Baltic origin (Chrzastek & Pluta, 2017a). Similar traces were also described on the Ordovician trilobites of Sweden (Bohlin, 1960). The feeding trace *Multina* was erected from the upper Cambrian shallow-marine sediments of Holy Cross Mountains (Orłowski, 1968) and re-described by Orłowski & Żylińska (1996). Few specimens tentatively identified as *Multina* come from the upper Silurian sediments of Estonia.



**Figure 9.** 1. *Estonirhynchia estonica* Schmidt, 1954, GIT 700-204; 2. Closeup view of *Archnostega gastrochaenae* Bertling, 1992, GIT 700-204-2; Jaani Formation, Jaani Stage, Wenlock.

**Horizontal burrows with horizontal to vertical branches.** Two ichnogenera, *Phycodes* Richter, 1850 and *Treptichnus* Miller, 1889 represent burrow systems of this CAD (Figs 10–11). *Phycodes* is a common structure in the Estonian collection (Paper I; Table 1), demonstrating different morphologies. Most specimens belong to *P. rarus* Hanken et al., 2016 and found from the Nabala Stage (mid Katian). Rare *P. reniforme* Hofmann, 1979 is represented by a single find from the Oandu Stage (lower Katian) (Fig. 11). Further research is needed to clarify the taxonomic composition and occurrence of *Phycodes* in Estonia. This trace is a feeding structure and a constituent of the *Cruziana* ichnofacies (Osgood, 1970). The trace is common in the Baltic region – Dronov & Mikuláš (2010) reported it from the Ordovician of the St. Petersburg area, and Stanistreet (1989) and Hanken et al. (2016) made a similar report from Norway. *Treptichnus* is a widely distributed ichnogenus, with the best-known ichnospecies *T. pedum* (Sharma et al., 2018 and references therein). The trace is important for correlating the base of the Cambrian

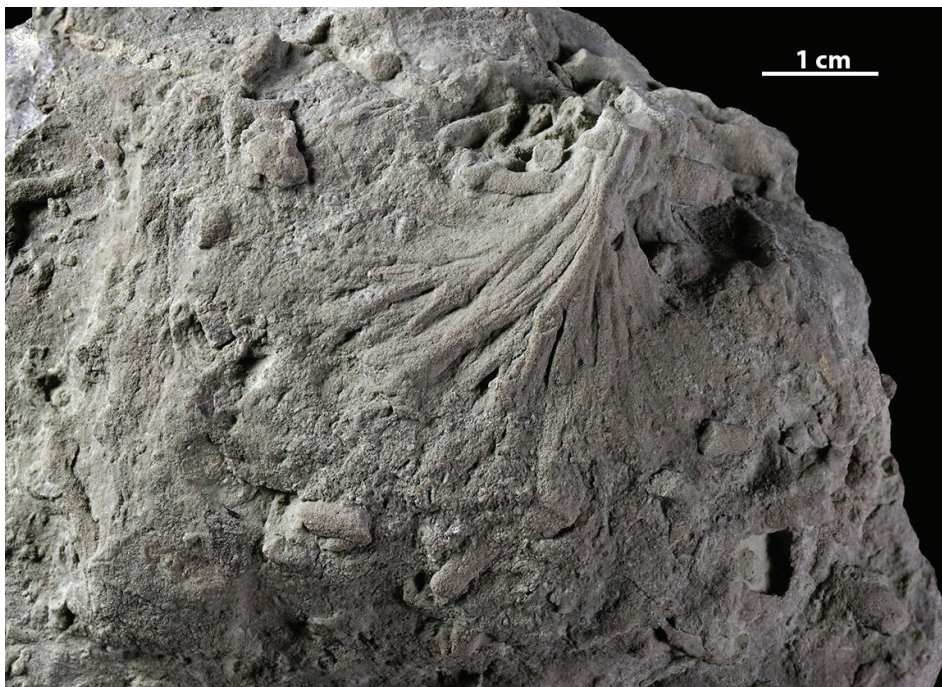
System (Buatois, 2018; discussion and references therein). It is commonly regarded as a feeding trace in shallow-marine environments. Stanistreet (1989) reported *T. pedum* from the Upper Ordovician of the Oslo-Asker region. The single Estonian specimen of *T. pedum* (Fig. 10) comes from the Raikküla Stage (lower Silurian) and may be the youngest representative of this ichnospecies (Paper I).



**Figure 10.** *Treptichnus pedum*, Rohuküla, Raikküla Formation, Raikküla Stage, Llandovery, GIT 362-232-1.

**Horizontal burrows with simple vertically oriented spreiten** are represented in Estonian collections by two ichnogenera: *Halopoa* Torell, 1870 and *Teichichnus* Seilacher, 1955 (Table 1). *Halopoa* is a feeding structure, known from both shallow and deep marine environments (Uchman, 1998; Mángano et al., 2002). This structure is rare in the carbonate succession of Estonia (Paper I). Two ichnospecies of *Teichichnus* (Paper III) were identified from the collections, widely known *T. rectus* Seilacher, 1955, and rare branching *T. patens* Schlirf, 2000 (Fig. 12). The Ordovician *Teichichnus* burrows from Estonia are large, and the single Silurian specimen related to a bentonite bed within the Adavere Stage is considerably smaller. This kind of small *Teichichnus* is known from stressful environments (Gibert & Ekdale, 2002; Buatois et al., 2005). *Teichichnus* is common in fully oxygenated shallow marine environments (Lima & Netto, 2012), but it also may be abundant in low energy environments with anoxic conditions (Savrda, 2007). *Teichichnus* is rare in carbonates and typical in siliciclastic systems (Knaust, 2017). Both Ordovician ichnospecies from Estonia show diminutive spreiten and are always associated with diverse shelly fauna. The pronounced stunting of the vertical spreiten may be related to the flimsy soft sediment layer, or may be due to less movement being needed to systematically process food in carbonates than in siliciclastic sediments. According to Vossler & Pemberton (1989), the *Teichichnus* behaviour type is not beneficial in areas of slow and steady sedimentation rate. Estonian finds are associated with deeper environments and periods of higher sedimentation rates (Paper III). From the Baltic region, *Teichichnus* was reported from the Darriwilian deposits of the St. Petersburg region (Dronov & Mikuláš, 2010) and from the Upper Ordovician deposits

of the Oslo-Asker region (Seilacher & Meischner, 1965; Stanistreet, 1989). The Palaeozoic *Teichichnus* is commonly interpreted as a feeding trace of polychaetes, arthropods or bivalves, or as a dwelling trace (Knaust, 2018; and references therein).



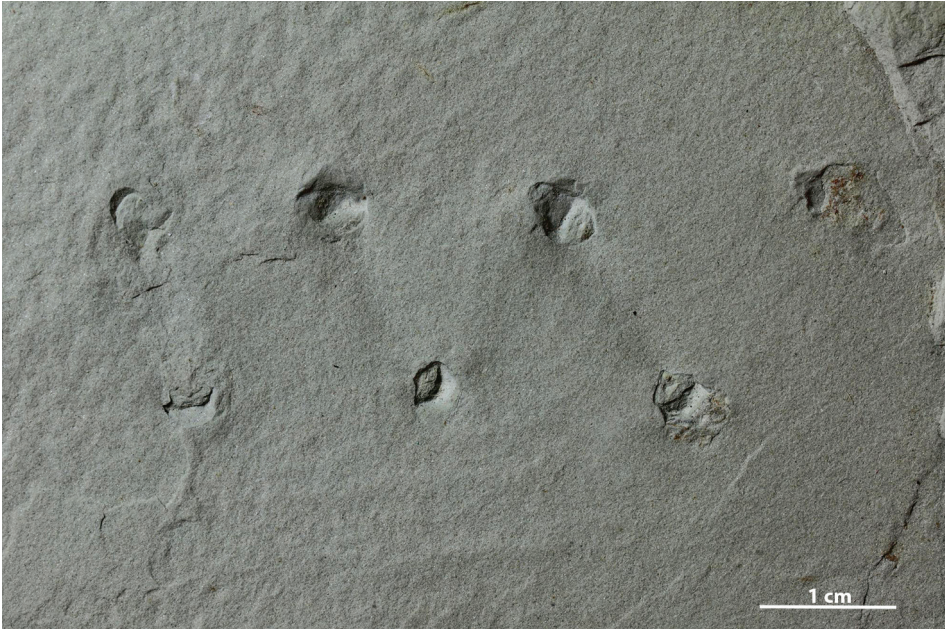
**Figure 11.** *Phycodes reniforme*, Saku quarry, Vasalemma Formation, Oandu Stage, Katian, GIT 362-13.

**Horizontal helicoidal burrows** are rare in the Estonian collections; only one corkscrew-shaped burrow (Fig. 13) from Ohesaare Stage (Přidoli) is identified as *Helicodromites* Berger, 1957 (Paper I; Table 1). The ichnogenus is rare and was previously described from the upper Silurian carbonates of the Canadian Arctic (Narbonne, 1984). The trace represents dwelling structures of vermiform organisms from shallow-marine settings (Poschmann, 2015).

**Burrows with horizontal spreiten** are rare in the Estonian carbonate succession. Only two poorly preserved specimens can be tentatively assigned to the ichnogenus *Rhizocorallium* Zenker, 1836 (Paper I; Table 1). The marine *Rhizocorallium* is discussed as a polychaete feeding trace (Knaust, 2013; Zhang et al., 2016). In the Palaeozoic, it is a common constituent of the *Cruziana* ichnofacies (Knaust, 2013).



**Figure 12.** *Teichichnus patens*, Narva opencast mine, Viivikonna Formation, Kukruse Stage, Sandbian, GIT 360-111-2.



**Figure 13.** *Helicodromites*, Ohesaare cliff, Ohesaare Formation, Ohesaare Stage, Pridoli, GIT 362-11.



**Burrows with helicoidal spreiten** include the well-known feeding structure *Zoophycos* Massalongo, 1855. During the Palaeozoic, the trace occurred in shallow environments and demonstrated thin planar spreiten (Gaillard & Racheboeuf, 2006). The morphological complexity of *Zoophycos* increased with the migration to deeper environments (Olivero, 2003). The Estonian specimens of *Zoophycos* are planar, cocktail shaped (Fig. 14), and frequent in the upper Silurian shallow water sediments (Paper V). Previously, *Zoophycos* traces have been reported from the Variku Formation (Katian) of Estonia (Ainsaar & Meidla, 2001) and from Norway (Seilacher & Meischner, 1965). The trace is discussed in several papers (e.g. Kotake, 2014; Zhang et al., 2015; and references therein). *Zoophycos* is commonly interpreted as a feeding structure of worm-like animals, but recently Zhang et al. (2015) expressed an opinion that it may represent feeding, gardening, resting and excreting strategies of the *Zoophycos* animal.

**Isolated and serial oval to almond-shaped burrows** are represented by the ichnogenus *Lockeia* (Table 1), which is frequent in the Silurian deposits of Estonia. Two ichnospecies have been identified: discrete *L. siliquaria*, and the clusters of *L. cunctator* (Paper I). *Lockeia* has been reported from different marine sediments (Mángano et al., 2002; and reference therein), being common in shallow-marine settings and a typical constituent of the *Cruziana* ichnofacies (Paranjape et al., 2013). Bivalves have been proposed as the tracemakers (e.g. Seilacher & Seilacher, 1994; Mángano et al., 1998).

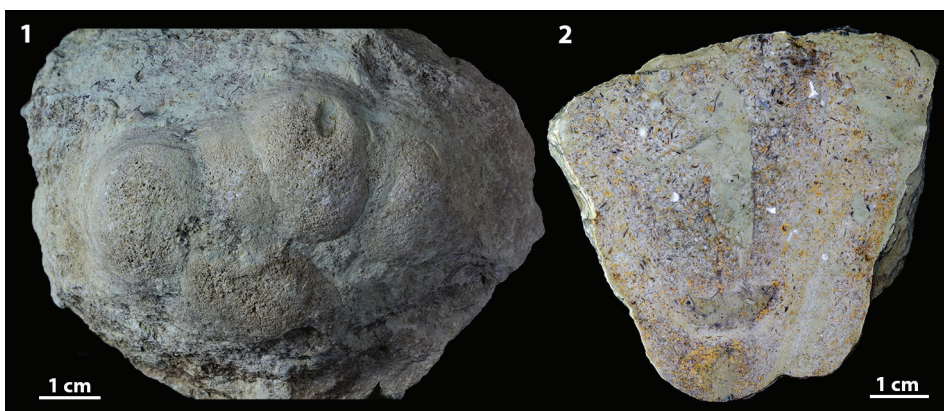


**Figure 14.** *Zoophycos*, Kaugatuma-Lõo coastal outcrops, Kaugatuma Formation, Kaugatuma Stage, Põldi, GIT 362-48.

**Vertical plug-shaped burrows** include three ichnogenera, *Amphorichnus* Männil, 1966b, *Conichnus* Männil, 1966b and *Bergaueria* Prantl, 1945 from Estonian carbonates. The *Conichnus* and *Amphorichnus* are by far the most numerous trace fossils in the Estonian collections (Papers I, VI; Table 1), ranging from the Kukruse to Keila stages

(from Sandbian to lower Katian). *Conichnus* occurs also in the Silurian (Adavere Stage). The traces are common constituents of the *Cruziana* ichnofacies in Estonia. The tracemakers seemingly preferred shallow water carbonate environments with a high clay input. *Conichnus* is unknown from the Cambrian of Estonia; it is possible that *Conichnus* tracemakers preferred temperate seas to their tropical equivalents. The Silurian specimens are somewhat wider than those from the Ordovician strata. The Ordovician *Conichnus* specimens show adjustment traces, with two to five stages in lateral directions and two stages in the vertical direction (Fig. 15). These kinds of lateral structures are more common than previously known (Paper VI). The *Amphorichnus* and Silurian *Conichnus* do not show any lateral adjustment structures. Frey and Howard (1981) placed the *Amphorichnus papillatus* Männil, 1966b to the ichnogenus *Conichnus*, but the general morphologies of the two traces are notably different; thus, it is reasonable to follow the original generic placement of *A. papillatus*.

In the Baltic region, *Conichnus* and *Amphorichnus* traces were known from the Lower and Middle Ordovician deposits of the St. Petersburg region (Dronov & Mikuláš, 2010), and only *Conichnus* has been reported from the Upper Ordovician deposits of the Oslo region (Hanken et al., 2016). *Bergaueria* is a shallow cylindrical trace common in siliciclastic deposits but also occurring in carbonates (Knaust, 2017). This trace was reported only from the Middle Ordovician deposits of the St. Petersburg region (Ershova et al., 2006; Dronov & Mikuláš, 2010; Knaust et al., 2012), being abundant in the sediments of the Volkhov Stage. *Bergaueria* of the St. Petersburg region varies in shape and the specimens are frequently relatively deep and sometimes have a narrow “neck”. Similar burrows occur in Estonia (in the Suhkrumäe outcrop, Tallinn, Toila Formation, Volkhov Stage) and were previously referred to as *Amphorichnus*? (Paper I). Dronov et al. (2019) suggested that this “neck” is a partly collapsed remnant of an escape structure. In Norway and Sweden, corresponding traces are missing and, according to the current data, are also rare in Estonian limestones. The *Bergaueria* and *Conichnus* are common in shallow-marine environments and were interpreted as dwelling or resting traces of sea anemones or similar organisms (Alpert, 1973; Shinn, 1968; Buck & Goldring, 2003; Curran, 2007; Paczešna, 2010).



**Figure 15.** *Conichnus conicus* adjustment traces. **1.** Five stages in lateral directions, GIT 720-463; **2.** Two stages in lateral and vertical directions; Aluvere quarry, Kahula Formation, Haljala Stage, Sandbian, GIT 156-1736.

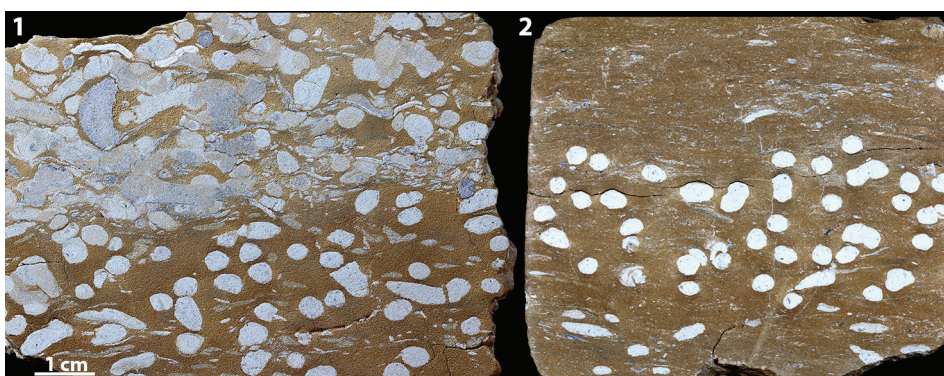
**Vertical unbranched burrows** are represented by two ichnogenera: *Oikobesalon* Thomas & Smith, 1998 and *Skolithos* (Paper I; Table 1). *Oikobesalon* is a dwelling trace, represented by *O. coricaceum* (Phillips in Phillips & Salter, 1848) in Estonia (Fig. 16), which is currently known only from the Uhaku Stage (Darriwilian) from the Osmussaar Island, NW Estonia (Vinn & Toom, 2014). *Skolithos* is a common trace fossil in the Palaeozoic, but from Estonia was described only a single bed with abundant burrows (Vinn & Wilson, 2013). *Skolithos* is an indicator of relatively high energy environments (Uchman et al., 2004). The Palaeozoic *Skolithos* is a dwelling structure, produced by various worms (Alpert, 1974; Knaust et al., 2018).



**Figure 16.** *Oikobesalon coricaceum*, Osmussaar Island, Kõrgekallas Formation, Uhaku Stage, Darriwilian. 1. GIT 697-16-1; 2. GIT 697-19-2.

**Vertical single U- and Y-shaped burrows** are represented by three feeding-dwelling ichnogenera: *Arenicolites* Salter, 1857, *Tisoa* Serres, 1840, and *Balanoglossites* Mägdefrau, 1932 (Table 1). *Arenicolites* is typical for high-energy shallow marine settings (Rindsberg & Kopaska-Merkel, 2005), belonging to the *Skolithos* and *Glossifungites* ichnofacies (Knaust et al., 2012). This genus is reported from the Upper Ordovician and upper Silurian deposits of Norway and Middle Ordovician deposits of the St. Petersburg region (Dam & Andreasen, 1990; Hanken et al., 2016; Mikuláš & Dronov, 2005). The trace is rare in Estonia, but it may occur in sediments of Kaugatuma Formation, Kaugatuma Stage (Přidoli). *Arenicolites* is a dwelling burrow that was probably created by polychaete

worms (e.g. Howard & Frey, 1984; Bradshaw, 2010). Haljala and Adavere stages contain horizontal cylindrical burrows, forming tight fork-like loops, identified previously as *Furculosus* Roniewicz & Pieńkowski, 1977 (Paper I). Similar burrows have been reported from the Ordovician carbonate deposits of eastern Canada (Fillon & Pickerill, 1984). X-ray CT analyses of carbonate burrows in a kerogen-rich oil-shale matrix bring up new data, showing that traces that were previously identified as *Planolites montanus* (Paper I) instead show U-shape loops and was thus assigned to the ichnogenus *Tisoo* Serres, 1840 by Knaust (2019a). The type ichnospecies, *T. siphonalis*, occurs in firmgrounds and is related to organic-rich and oxygen-poor substrates. In Estonia, *T. siphonalis* (Fig. 17) is known from the Viivikonna Formation, Kukruse Stage (Sandbian); with the burrows showing a vertical to inclined and horizontal orientation. Moreover, *Tisoo* co-occurred with tiny *Chondrites* traces. While the *Furculosus* is synonymized with *T. siphonalis* (Knaust, 2019b), the U-shaped softground traces from the Haljala and Adavere stages cannot be identified as *T. siphonalis*. Moreover, these specimens do not represent another species of *Tisoo*, *T. habichi* (Lissón, 1904), which occurs in the *Skolithos* ichnofacies (Knaust, 2019b). The ichnogenus *Balanoglossites* Mägdefrau, 1932 (redescribed by Knaust, 2008) consists of a tunnel and shaft system with several openings. Two valid species are known: the type species *B. triadicus* Mägdefrau, 1932 and the more irregular *B. ramosus* Knaust, 2008. The latter is known only from the Mesozoic (Knaust, 2008). *Balanoglossites* is common in the Palaeozoic of Baltoscandia (Männil et al., 1984; Knaust & Dronov, 2013). The trace has a complicated architecture and a complex nature: the tracemaker was able to simultaneously bioerode and burrow (Knaust & Dronov, 2013). The collection material and building stones used in Tallinn show an abundance of *B. triadicus* in the Middle Ordovician as well as in the Silurian (Tagavere Beds, Jaagarahu Stage, Wenlock) of Estonia (Table 1). The loosely consolidated high-energy beach deposits contain irregularly branching burrows of *B. ramosus* (Knaust, 2008). Similar traces may occur in the upper Silurian grainstones of the Äigu Beds, Kaugatuma Stage (Přidoli). *Balanoglossites* is common in shallow-marine carbonates, related to firmgrounds and hardgrounds, and is characteristic of the *Glossifungites* and *Trypanites* ichnofacies (Knaust et al., 2012). Eunicid polychaetes are regarded as possible tracemakers (Knaust, 2008).



**Figure 17.** *Tisoo siphonalis*, Viivikonna Formation, Kukruse Stage, kukersite seam C. 1. *Sine loco*, GIT 398-80; 2. Borehole No. 4325 from northeast Estonia, GIT 362-582.



**Figure 18.** *Chondrites intricatus*, Kùbassaare cliff, Rootsikùla Formation, Rootsikùla Stage, Gorstian, GIT 362-679.

**Burrows with shaft or bunch with downwards radiating probes** are represented by two ichnogenera *Chondrites* Sternberg, 1833 and *Trichichnus* Frey, 1970 (Table 1). *Chondrites* is a common trace fossil with a wide range of morphologies. Its systematics are discussed in multiple papers (e.g. Fu, 1991; Uchman, 1998, 2007; Uchman et al., 2012). Many data show that “*Chondrites* animals” lived in dysaerobic conditions (Bromley & Ekdale, 1984; Kotake, 1991; Gong & Droser, 2001), which are widespread in deep-marine environments, but may also occur in shelf and nearshore restricted basins (Knaust, 2017). Silurian shallow-water sediments of the Rootsikùla Stage (Homerian) in Estonia contain bedding plains with abundant monospecific assemblages of *Chondrites* (Fig. 18), possibly indicating poorly oxygenated bottom waters (Bromley & Ekdale, 1986). Otherwise, the *Chondrites* traces are not common in Estonia. The presence of two ichnospecies *C. intricatus* (Brongniart, 1823) and *C. cf. patulus* Fisher-Ooster, 1858 (Paper I) is possible. Previously, *Chondrites* have been described from the Ordovician of Norway (Seilacher & Meischner, 1965; Spjeldnæs, 1989; Stanistreet, 1989; Hanken et al., 2016). Dronov & Mikuláš (2010) reported *Chondrites* also from the Middle Ordovician of the St. Petersburg region. *Chondrites* is a facies-crossing feeding trace of unknown invertebrates (e.g. Osgood, 1970; Mángano et al., 2002). The pyritized thread-like *Trichichnus* burrows, probably made by meiofauna feeding on sulfide-oxidizing bacteria (Kędzierski et al., 2015) probably occurred in Estonia (Table 1). Previously, this taxon was reported from the Upper Ordovician deposits of Norway (Hanken et al., 2016).

**Vertical concentrically filled burrows** are represented by the dwelling structure *Rosselia* Dahmer, 1937. Few well-preserved specimens were identified from Estonia (Paper I; Table 1). The trace is a common constituent of the *Cruziana* ichnofacies, and possibly made by polychaetes (Uchman & Krenmayr, 1995; Buatois et al., 2016b; and references therein).

**Maze and boxwork burrows** display simultaneous branching. This category includes *Thalassinoides*, which is common in the Baltic region (Stanistreet, 1989; Dronov & Mikuláš, 2010; Hanken et al., 2016). The Estonian collections contain several samples of

large straight horizontal burrows, suggesting that *Thalassinoides* boxwork is common in the Ordovician and less abundant in Silurian sedimentary rocks (Paper I; Table 1). The ichnogenus is probably represented by several ichnospecies, including the rare *T. bacae* described by Ekdale & Bromley (2003) from the Middle Ordovician deposits of Sweden. The *Thalassinoides* is abundant in Ordovician marine limestones elsewhere (Sheehan & Schiefelbein, 1984), being typical of the *Cruziana* and *Glossifungites* ichnofacies. The Palaeozoic traces are produced by unidentified soft-bodied organisms or by trilobites (e.g. Myrow, 1995; Ekdale & Bromley, 2003; Carmona et al., 2004; Cherns et al., 2006).

### 5.1.2 Bioerosional trace fossils

**Cylindrical vertical to oblique borings.** *Trypanites* is one of the oldest macroborings and is common throughout the Phanerozoic (Bromley, 1994). It is also abundant in Estonia, occurring in different Ordovician and Silurian shelly fossils as well as in hardgrounds (Paper I). The *Trypanites* borings have a circular cross-section throughout their length and the axes of the borings may be straight, curved or irregular. Five valid ichnospecies are known and after Blissett & Pickerill (2007), two taxa are determined from the carbonate succession of Estonia. The type species *T. weisei* Mägdefrau, 1932 is mostly straight and vertical, occurring on hardgrounds, stromatoporoids and corals. *T. solitarius* (Hagenow, 1840) is curved, with its course running close beneath the substrate surface; its occurrence is mostly related to the large Upper Ordovician brachiopods. The occurrence of *T. fimbriatus* (Stephenson, 1952) in the Ordovician deposits of Estonia is unclear. Vinn (2005) described brachiopods with *T. aff. fimbriatus* from the Kukruse Stage (Sandbian) of Estonia. The traces were identified on casts made from the borings and cleaned by ultrasound equipment. This method does not guarantee a complete result even in cases where the borings are filled with kukersite. Borings of *T. fimbriatus* are similar to *Palaeosabella* Clarke, 1921, having a swollen distal portion. However, *Palaeosabella* borings are smaller and expand distally as a cone. Occasionally, the length and width ratio of the *Trypanites* borings was so small that their determination as *Trypanites* was questionable. These kinds of “shallow” borings are common in the Middle Ordovician of the St. Petersburg region, and were named as *Circolites* Mikuláš, 1992a (Dronov et al., 2002). Recently, Dronov & Mikuláš (2010) have named the traces as *Trypanites heckeri* (*nomen nudum*). *Trypanites* (= *Vermiforichnus* Cameron, 1969) is the most abundant bioerosional trace fossil in the carbonate succession of the Baltic region, and is related to hardgrounds, reefs and shelly fossils (e.g. Vishnyakov & Hecker, 1937; Opalinski & Harland, 1980; Nield, 1984; Vinn, 2004; Mikuláš & Dronov, 2005; Hanken et al., 2016). The high variability in the size of *Trypanites* borings would suggest several different tracemakers. Recent similar borings were made by polychaetes, sipunculans, and phoronids (Rice, 1969), and most authors have indeed discussed these worms as potential tracemakers. According to Bromley (1978) the fat and short *Trypanites* are produced by sipunculans and slender individuals by polychaetes.

**Borings with elliptical to sub-rectangular cross-sections.** *Osprioneides* belong to the ichnofamily Trypanitidae Mägdefrau, 1932 (Wisshak et al., 2019). It is the largest bioerosional trace fossil genus, with a single known species described from the Upper Visby Formation of Gotland (Sweden), where it occurs in stromatoporoids. These traces have been reported in Sheinwoodian stromatoporoids from Estonia (Vinn & Wilson, 2010c), occurring at the same stratigraphic level as on Gotland, and also in Sandbian bryozoans (Vinn et al., 2014b). The finds of *Osprioneides* in Estonia are related to

relatively deeper water muddy bottom environments. Soft-bodied organisms, most likely boring worms, were responsible for making the traces (Beuck et al., 2008).

**Circular holes and pit-shaped borings** are represented by three ichnogenera in Estonia: *Oichnus* Bromley, 1981, *Tremichnus* Brett, 1985, and *Circolites*. *Oichnus* is the simplest trace, a drill hole with a rounded outline, and was discovered in Ediacaran and Cambrian sediments (Bengtson & Zhao, 1992; Conway Morris & Bengtson, 1994). The earliest occurrence of *Oichnus* in the Ordovician is known from the Sandbian (Buatois et al., 2016a). Small hole-shaped bioerosional traces were discussed for many years until Wisshak et al. (2015) thoroughly revised the *Oichnus* and related genera. The ichnogenus was recently placed with the new ichnofamily Oichnidae (Wisshak et al., 2019). *Oichnus* is a common trace fossil globally but is surprisingly rare in Baltoscandia (Table 1). Previously, it was recorded from Estonia by Ausich et al. (2012) on an upper Silurian echinoderm (Kaugatuma Formation, Kaugatuma Stage), and more recently by Chrzęstek & Pluta (2017b) on Upper Ordovician trilobite (Viivikonna Formation, Kukruse Stage). *Oichnus* is the typical representative of predation traces. Gastropods are regarded as the tracemakers by many authors (e.g. Baumiller et al., 1999; Brett, 2003; Kong et al., 2015). A further examination of the Estonian large brachiopod collection may bring up new finds, but in cases where borings are filled with sediment it is difficult to distinguish the non-predatory domichnial *Trypanites* borings from predatory *Oichnus* traces.



**Figure 19.** *Tremichnus*, *Sepise*, Jaagarahu Formation, Jaagarahu Stage, Sheinwoodian, GIT 405-165.

*Tremichnus* occurs as an embedment structure in the ossicles of echinoderms. The ichnogenus was recently assigned to the ichnofamily Centrichnidae (Wisshak et al., 2019). *Tremichnus* represents the so-called ‘compound boring-bioclastrations’ structures (Tapanila & Ekdale, 2007). According to Wisshak et al. (2019) the trace is considered to be bioerosional, as the bioerosive action is predominant and largely independent from the host reaction. Outside Baltica, the occurrence of *Tremichnus* known from the Upper Ordovician (Sandbian) to Quaternary (Weichselian glaciation) deposits (Lewis, 1982; Pokorný & Štofik, 2017). *Tremichnus* is very rare in Estonia (Paper IX) – out of more than 1000 examined echinoderm columnals, only few contain the trace. The Rhuddanian (Juuru Stage) *Tremichnus* is not typical, and the outline of the boring is slightly irregular due to partial repair. The Sheinwoodian (Jaagarahu Stage) pluricolumnal bear several pits (Fig. 19) and is somewhat swollen. These kinds of traces have previously been described from the Sheinwoodian of Gotland (Franzén, 1974). In the eastern Baltics, *Tremichnus*

(= *Balticapunctum* Rozhnov, 1989) occurred in the Middle Ordovician deposits of the St. Petersburg region. These Dapingian (Volkhov Stage) specimens are the oldest representatives of the ichnogenus. The *Tremichnus* traces are possibly made by host-specific symbiotic parasites (Paper X; and discussion therein). Shallow circular excavations in the surface of lithic substrates belong to *Circolites*. Santos et al. (2015) described a set of bifurcating, sinuous grooves occasionally connected with *Circolites*. Recently, the traces were included to the new ichnofamily Circolitidae (Wisshak et al., 2019). Similar compound traces occurred also on the lower Silurian stromatoporoids (Juuru Stage). Regular echinoids were probably the tracemakers (Santos et al., 2015).

**Globular to spherical borings.** The ichnogenus *Cyclopuncta* Elias, 1958 is not listed within any CAD by Buatois et al. (2017). It was also not accepted by the Treatise (Häntzschel, 1962), but was recently included into the new ichnofamily Planobolidae by Wisshak et al. (2019). Since the similar ichnogenus *Planobulus* was placed into this CAD by Buatois et al. (2017), *Cyclopuncta* is discussed here under the same CAD. Different molluscs from Estonia (cephalopods, gastropods, bivalves) show relatively low encrustation densities (Vinn et al., 2018a), and the shells and steinkerns rarely bear bioerosional traces.

The Harku quarry in Tallinn, northern Estonia, is a well-known locality for Darriwilian cephalopods with phosphatized shells of excellent preservation (e.g. Mutvei, 2002; Kröger, 2012). A cephalopod *Tragoceras falcatum* (Schlotheim, 1820) from this locality shows shallow irregularly shaped pits in the adoral part of the body chamber (Paper VIII). These closely packed pits have diameters below 1 mm. It is unclear whether the pits are produced by boring organisms or if are they the result of diagenetic processes. The irregular outline and shallow depth support the latter explanation and may indicate that the dissolution of the shell had started. Similar structures were first described by Girty (1909), and Elias (1958) regarded them as attachments of epizoans and established the new ichnotaxon *Cyclopuncta*. These questionable traces were also reported by Hoare et al. (1980) and Niko (1996). The Estonian traces from the Kunda Stage are referred to as *cf. Cyclopuncta*.



**Figure 20.** *Petroxestes pera*, Aluvere quarry, Kahula Formation, Haljala Stage, Sandbian, GIT 720-5-1.



**Pouch-shaped borings** are pouch-shaped dwelling structures with a single elongated opening. Two ichnogenera were identified from this CAD: *Petroxestes* Wilson & Palmer, 1988 and *Rogerella* Saint-Seine, 1951. From the Katian of North America, shallow to deep elongate borings in lithic substrates are described as *Petroxestes*. The traces occur on cobbles, hardgrounds and biogenic substrates, and clumping behaviour of tracemakers is common (Pojeta & Palmer, 1976; Wilson & Palmer, 1988). In Estonia, traces of the species *P. pera* Wilson & Palmer, 1988 occur only on large trepostome bryozoans (Fig. 20), both on the upper- and undersides of colonies, and are often clumped and accompanied by *Trypanites* borings (Papers I, VII). The occurrence of *Petroxestes* was previously discovered from the upper Katian to Miocene (Wilson & Palmer, 1988; Tapanila & Copper, 1992; Pickerill et al., 2001). The Estonian specimens come from the Sandbian (Kukruse to Haljala stages) and probably from the lowermost Katian (Keila Stage). Only bivalves have been proposed as tracemakers for the Ordovician *Petroxestes* borings (Taylor & Wilson, 2003). *Rogerella* is a pouch-shaped boring from the ichnofamily Rogerellidae Codez & Saint-Seine, 1958 (Wisshak et al., 2019). The borings are uncommon in the lower Palaeozoic; all previous findings are from Laurentia. Baird et al. (1990) described traces from the Devonian and Wilson & Palmer (2006) mentioned undescribed material from the Katian. *Rogerella* is rare in Estonia, and the finds are restricted to heliolitid corals with fine skeletons from the upper Katian (Nabala and Vormsi stages). Barnacles are discussed as the tracemakers (e.g. Seilacher, 1969; Baird et al., 1990; Donovan et al., 2014).

**Clavate-shaped borings** are in Estonian collections represented by three different dwelling ichnogenera: *Gastrochaenolites* Leymerie, 1842, *Sanctum*, and *Palaeosabella*. *Gastrochaenolites* belong to the ichnofamily Gastrochaenolitidae (Wisshak et al., 2019) and contains 15 ichnospecies, most of which are known from post-Palaeozoic reef settings (Tapanila et al., 2004). The Palaeozoic occurrences are related only to hardgrounds (Wilson & Palmer, 1998; Benner et al., 2004). From Early Ordovician omission surfaces in Sweden, irregular vase-shaped ichnospecies *G. oelandicus* is described (Ekdale & Bromley, 2001b). These macroborings also occur in the Middle Ordovician hardgrounds of Norway and the St. Petersburg region (Ekdale et al., 2002; Knaust & Dronov, 2013), and have wider distribution and morphologies than previously suggested (Dronov et al., 2019). In Estonia, *Gastrochaenolites* is previously known from the lower boundary of the Volkhov Stage, and may occur on the lower boundary of the Vormsi Stage. *Gastrochaenolites* is a common constituent of the *Trypanites* ichnofacies (Buatois & Mángano, 2011), but it also occurs in the *Glossifungites* ichnofacies (Knaust et al., 2012). Bivalves are the tracemakers (Kelly & Bromley, 1984; Carmona et al., 2007). *Sanctum* is an irregular boring excavated into endozones of ramose and frondose bryozoans. Surprisingly, Wisshak et al. (2019) have placed *Sanctum* into the ichnofamily Rogerellidae Saint-Seine, 1958. It was initially described from the Upper Ordovician (Katian) of Laurentia, and it includes the single species *S. laurentiensis* Erickson & Bouchard, 2003. From Estonia, an abundant occurrence of *Sanctum* was previously reported, but only on ramose bryozoan colonies (Wyse Jackson & Key, 2007). An examination of the bryozoan collections from Estonia conveyed that endozones of hemispherical bryozoan colonies contain slightly clavate borings that are larger than the biggest *Trypanites* (*T. fosteryeomani* Cole & Palmer, 1999) and smaller than *Osprioneides*. These abundant traces should be identified as *Sanctum*. The occurrence of *Sanctum* in Estonian bryozoans is known from the Uhaku to Rakvere stages (Upper Darriwilian to Katian). Opalinski & Harland (1980) reported similar “large-scale” borings from the

Ordovician deposits of Norway. Erickson & Bouchard (2003) and Wyse Jackson & Key (2007) have proposed vermiform tracemakers. *Palaeosabella* is an unbranched, distally widened boring, with a long and complicated ichnotaxonomic history. The boring is very similar to *Trypanites* (Bromley, 2004; Wilson, 2007; Furlong & Roberts, 2014; Buatois et al., 2017) and therefore there is considerable confusion and probably misidentifications of these traces (Bromley, 2004; Wilson, 2007). In general, *Palaeosabella* is smaller and slightly cone shaped. From the Baltic region, the genus was reported twice, from the Sheinwoodian (Silurian) deposits of Sweden and Estonia (Beuck et al., 2008; Vinn & Wilson, 2010c). Notably, for the determination of Swedish specimens, an X-ray CT was used. *Palaeosabella* is rare in Estonia (Table 1), but further research will likely increase the number of occurrences. Bromley (2004) discussed the tracemaker of *Palaeosabella*.



**Figure 21.** *Pinaceocladichnus*, Ohesaare cliff, Ohesaare Formation, Ohesaare Stage, Põidoli, GIT 362-682.

**Fracture-shaped bioerosion traces** are represented by *Bicrescomanducator* Donovan et al. in Andrew et al., 2010. Aperture-attacking predation traces have been found worldwide (Alexander & Dietl, 2003). Repaired injuries on gastropods have been reported from the Ordovician and Silurian deposits of Sweden (Ebbestad & Peel, 1997; Ebbestad, 1998; Lindström & Peel, 2005). Stafford et al. (2015) described damages on gastropod shells as *Caedichnus*. Wisshak et al. (2019) synonymized *Caedichnus* with the ichnogenus *Bicrescomanducator* and subsequently included it in the new ichnofamily Belichnidae, which consists of fracture patterns in shells and other skeletal material. Isakar & Ebbestad (2000) described an Estonian specimen from the Sandbian (Viivikonna Formation, Kukruse Stage) in detail; it belongs to *Bicrescomanducator spiralis* (Stafford et al., 2015). Repaired injuries in the late Silurian (Kaugatuma Stage, Põidoli) encrusting

tentaculoid tubeworm (Vinn, 2012) also represent predatory traces of *Bicrescomanducator*.

**Camerate network borings** are produced by ctenostome bryozoans (Buatois et al., 2017). Ctenostome bryozoans have been known as tracemakers for a long time (e.g. d'Orbigny 1847; Pohowsky, 1978). Several of them are described based on the morphology of borings they have made and are treated as a body fossil or as a trace fossil (e.g. Ulrich, 1879; Pohowsky, 1978; Mayoral, 1988; Vogel et al., 1987; Barrier & D'Alessandro, 1985; Mayoral, 1991; Mayoral et al., 1994; Bertling, 1995; Wilson & Lazzuri, 2000; Taylor & Wilson, 2003; Beuck & Freiwald, 2005). A historical overview of this “great confusion” is given by Rosso (2008). Different shelly fossils in Estonian limestones (trilobites, brachiopods) bear ramifying tunnels with periodic expansions and openings to the surface (Fig. 21). Their occurrence is known from the Volkhov to Ohesaare stages (Dapingian to Přidoli). They are tentatively assigned to *Pinaceocladichnus*, the ichnogenus described by Mayoral (1988) as a trace fossil, and it was included in the list of valid bioerosional ichnotaxa (Wisshak et al., 2019). Dronov & Mikuláš (2010) reported this taxon from the Lower Ordovician (Volkhov Stage) of the St. Petersburg area, where numerous asaphid trilobites bear thin networks of “bryozoan borings”. These borings were named as *Ropalonaria* by Wilson & Palmer (2006).



**Figure 22.** *Dendrinidae*, Harku quarry trench, Kunda Stage, Darriwilian, GIT 362-738-1.

**Dendritic and rosette borings.** The microorganisms that penetrate carbonate substrates and live inside their self-made cavities are called euendoliths (Golubić et al., 2019); they include bacteria, cyanobacteria, chlorophytes, rhodophytes, and fungi. The microborings can be used as palaeobathymetric indicators (e.g. Golubić, 1972; Budd & Perkins, 1980; Vogel et al., 1995; Wisshak et al., 2005), as the tracemakers may be light dependent or light independent. Euendoliths are well-preserved in recent hard substrates; however, exceptional preservation is needed for the determination of the Palaeozoic material (Wisshak et al., 2008). Euendoliths have been described from

Ordovician and Silurian deposits in Poland (Campbell et al., 1979; Podhalańska, 1984). From the Middle Ordovician of Estonia, euendoliths of different morphologies have also been described from skeletal grains (Podhalańska & Nölvak, 1995). These traces were not taxonomically identified, however; based on the occurrence of these traces, the authors suggested photic conditions in the basin from the Kunda to Aseri time. Recently, Vogel & Brett (2009) described and named euendoliths from the Upper Ordovician marine shells of *Laurentia*. The ichnofamily *Dendrinidae* (Bromley et al., 2007) includes small bioerosional traces having a rosetted morphology; occurrence is known from Ordovician to recent deposits (Wisshak, 2017). The descriptions of microborings are mainly based on natural or resin casts. These traces cannot be accurately determined without special laboratory preparations. For now, the occurrence of microborings and different dendritic microstructures (Fig. 22) are identified from 13 regional stages of Estonian carbonate succession (Table. 1). Considering the excellent preservation of Estonian fossil shells and recent developments in euendolith research (e.g. Wisshak, 2012, 2017; Wisshak et al., 2017, 2018), it may be possible to find determinable euendoliths and provide palaeobathymetric data for several stratigraphical units; however, this is beyond the scope of the current study.

**Groove bioerosion traces.** Many different groups of fossils including gastropods and echinoids can abrade depressions into their substrate. Grazing animals feed on hard substrates by removing seaweed, algae and microbial coatings, all while eroding the substrate. Upper Ordovician large brachiopods *Porambonites wesenbergensis* bear several grazing traces. The traces consist of poorly preserved separated grooves that were previously identified as *Gnathichnus*? Bromley, 1975b (Paper I). Since then, better-preserved specimens have been found and these traces cannot be identified as *Gnathichnus*. Supposedly, these traces have not been described so far.

Santos et al. (2015) described the groove trace *Ericichnus*, consisting of bifurcating, sinuous grooves on the surface of lithic substrates. This kind of grooves with shallow pits occur on the lower Silurian stromatoporoids and were identified as peeling structures (Paper I). Only the grooves on the holotype of heliolitid coral *Coccosseris approximata* (Eichwald's collection in St. Petersburg University, No. 1/109, Kirna locality, central Estonia, Vormsi Stage) represent similar traces.

Two trace fossil genera that can simultaneously demonstrate the burrowing and boring activities of the tracemaker have been described. *Balanoglossites* Mägdefrau, 1932 and *Sulcolithos* Knaust, 2019a were found in the Triassic deposits of Germany and the Middle Ordovician deposits of the St. Petersburg region (Knaust, 2008, 2019a; Knaust & Dronov, 2013). The recently described ichnogenus *Sulcolithos* (Knaust, 2019a) is an elongate groove-like structure, burrow or boring, with a straight or slightly arched course on the bedding planes and organic substrates. According to Knaust (2019a), the traces are common in the Baltic region, known from the Middle Ordovician hardgrounds of the St. Petersburg region. Previously, these elongate grooves were described as *Sulcichnus* Martinell & Domènech, 2009 (Knaust et al., 2012; Knaust & Dronov, 2013). Notably, Knaust (2019b) attributed several groove traces described from Estonia to the new ichnogenus, including the unroofed *Osprioneides* borings in the Sheinwoodian stromatoporoids (Vinn & Wilson, 2010c) and relatively small canals on the surface of upper Ordovician stromatoporoids are identified as *Sulcichnus* (Paper I). Additionally, unnamed long bioerosional grooves on the surface of large trepostome bryozoans were illustrated in Paper I. This kind of trace occurs on large Middle Ordovician (Sandbian and lower Katian) bryozoans (Fig. 23). They can be straight or curved and may follow

the growth lines of bryozoans. Sheinwoodian (Mustjala Member, Jaani Stage) stromatoporoids are heavily bored. Preliminary observations suggest the simultaneous presence of *Osprioneides* and *Sulcolithos* Ordovician and Silurian sedimentary surfaces (bedding planes) bearing different shallow, more or less meandering grooves. Although the material is not systematically processed, the occurrence of *Sulcolithos* as a burrow is not shown in Table 1, and the trace is included only in the list of bioerosional traces.

**Escape traces** are structures produced by animals in response to rapid sedimentation to avoid burial. According to Buck & Goldring (2003), typical escape structures form cone-in-cone structures that are produced by vertical repeated movements. Vertical escape traces from the Ordovician and Silurian deposits of Estonia are mostly associated with rapidly deposited volcanic ash (bentonite) layers (Paper I).



**Figure 23.** *Sulcolithos variabilis*, Vasalemma quarry, Keila Stage?, Katian, GIT 362-672.

### 5.1.3 Coprolites and structures with faecal pellets

Coprolites and faecal pellets are a distinct category of trace fossils (Bertling et al., 2006) and represent feeding traces (fodinichnia). Fossil faeces, like all soft sediment fossils, have a generally low fossilization potential. Coprolites are nevertheless quite common in early Palaeozoic deposits, and are more widely known from non-carbonate sediments; resultingly, their discoveries are related to exceptional preservation conditions. Micro-coprolites in carbonate sediments are usually related to tropical shallow-marine environments (e.g. Folk & Robles, 1964; Shinn, 1968; Wanless et al., 1981) and are widely found in Mesozoic and Cenozoic deposits. Majority of these carbonate pellets have a characteristic inner structure and represent the ichnofamily Favreinidae Vialov, 1978.

| Regional Stage | Age          | Basin type     | Type of carbonate sediment | Type of pellets  | Trace fossil  | Gastropoda | Cephalopoda | Bivalvia  | Brachiopoda | Echinodermata | Trilobita | Total      | Length, mm     | Width, mm |
|----------------|--------------|----------------|----------------------------|--|---|------------|-------------|-----------|-------------|---------------|-----------|------------|----------------|-----------|
| Porkuni        | Hirnantian   | rimmed shelf   | tropical                   | N/A  | N/A   |            |             |           |             |               | 0         |            |                |           |
| Piigu          | Katian       | rimmed shelf   | tropical                   | oval; L/W ratio $\leq 2$ , 2-3   | <i>Coprolus</i> ,<br><i>Tubularina</i> ,<br>unidentified burrow                           | 2          | 2           |           |             |               | 4         |            | 0.23-0.34      | 0.09-0.23 |
| Vormsi         | Katian       | rimmed shelf   | tropical                   | oval; L/W ratio $\leq 2$ , 2-3   | <i>Coprolus</i>   | 4+11       | 1           |           |             |               | 16        |            | 0.46-0.95      | 0.19-0.45 |
| Nabala         | Katian       | rimmed shelf   | tropical                   | oval; L/W ratio $\leq 2$ , 2-3<br>oval, elongated oval,<br>rod-shaped; L/W ratio $\leq 2$ , 2-3, 5-6 | <i>Coprolus</i>   | 3          |             |           |             |               | 3         |            | 0.6-1.2        | 0.3-0.5   |
| Rakvere        | Katian       | rimmed shelf   | tropical                   |  | <i>Coprolus</i> ,<br><i>Tubularina</i>  | 38         |             | 9         | 3           |               | 50        |            | 0.2-1.8        | 0.1-0.75  |
| Oandu          | Katian       | rimmed shelf   | tropical                   | oval, elongated oval;<br>L/W ratio 2-3, 5  | <i>Coprolus</i> ,<br><i>Tubularina</i> ,<br>unidentified burrow                           | 1          |             | 2         | 12          |               | 15        |            | 0.3-0.7        | 0.1-0.3   |
| Keila          | Katian       | rimmed shelf   | tropical                   | oval; L/W ratio $\leq 2$   | <i>Coprolus</i> ,<br><i>Tubularina</i> ,<br><i>Alcyonidopsis</i> ,<br>unidentified burrow | 3          |             | 1         | 4           |               | 9         |            | 0.26-0.38      | 0.15-0.2  |
| Haljala        | Sandbian     | carbonate ramp | temperate                  | oval, rod-shaped; L/W ratio $\leq 2$ , 2-3, 4-5?   | <i>Coprolus</i> ,<br><i>Tubularina</i> ,<br><i>Alcyonidopsis</i>                          | 28+15      | 5           | 2         | 0+12        | 1             | 64        |            | $\leq 0.1-0.8$ | 0.08-0.4  |
| Kukuse         | Sandbian     | carbonate ramp | temperate                  | oval; L/W ratio $\leq 2$   | <i>Coprolus</i>   | 2          |             | 1         |             | 1             | 4         |            | 0.17-0.3       | 0.09-0.15 |
| Uhaiku         | Darriwillian | carbonate ramp | temperate                  | oval; L/W ratio $\leq 2$ , 2-3   | <i>Coprolus</i>   | 5          |             |           |             |               | 5         |            | 0.4-0.6        | 0.11-0.3  |
| Lasnamägi      | Darriwillian | carbonate ramp | temperate                  | oval; L/W ratio $\leq 2$   | <i>Coprolus</i>   | 3          |             |           |             |               | 3         |            | 0.13-0.14      | 0.25      |
| Aseri          | Darriwillian | carbonate ramp | temperate                  | oval; L/W ratio $\leq 2$   | <i>Coprolus</i>   | 1          |             |           |             |               | 1         |            | 0.24           | 0.12      |
| Kunda          | Darriwillian | carbonate ramp | temperate                  | oval; L/W ratio $\leq 2$ , 2-3   | <i>Coprolus</i>   | 4          |             |           |             |               | 4         |            | 0.3-0.5        | 0.15-0.2  |
| Volkhov        | Dapingian    | carbonate ramp | cool                       | oval; L/W ratio 2-3  | <i>Coprolus</i>   |            |             |           | 1           |               | 1         |            | 0.45           | 0.2       |
| <b>Total:</b>  |              |                |                            |  |   | <b>112</b> | <b>16</b>   | <b>15</b> | <b>32</b>   | <b>2</b>      | <b>2</b>  | <b>179</b> |                |           |

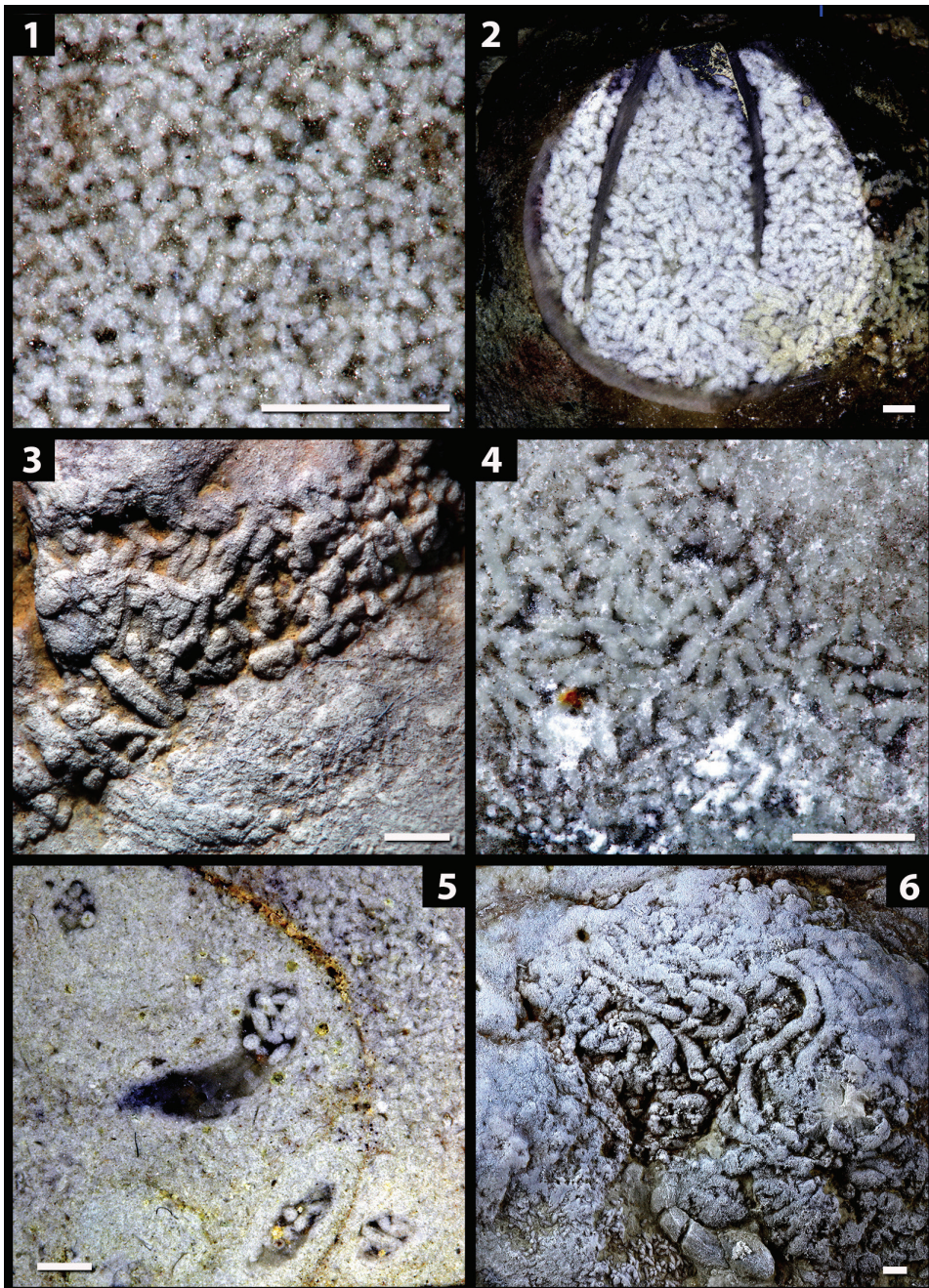
**Table 2.** Distribution and host shelly fossils of Ordovician coprolites from Estonia (from Paper II).

Small faecal pellets with an ornamented outer surface are described from several different ichnogenera (e.g. Heer, 1853; Elliott, 1963; Gramann, 1966; Gaździcki, 1974; Gaillard, 1978; Živković & Bogner, 2006). Isolated pellets without a characteristic internal structure and ornamentation were placed in the ichnofamily Coprolidae Knaust, 2008; very elongated coprolites represent the ichnofamily Lumbricariidae Schweigert, 2001. Pellets in carbonates are reported as the infill of different trace fossils (e.g. Fürsich, 1974; Knaust, 2008) as a part of composite traces (Gaillard et al., 1994) or as the infill of different mollusc shells (Mayer, 1955).

Different morphotypes of coprolites have been described from Cambrian deposits (e.g., Eriksson & Terfelt, 2007; Shen et al., 2014; Mángano et al., 2019). Pellets are common in the Ordovician deposits of Europe, usually related to the ichnogenus *Tomaculum* Groom, 1902 (for an overview of older references see Eiserhardt et al., 2001; Bruthansová & Kraft, 2003; Podhalańska, 2007; van Keulen & Rhebergen, 2017). Massalongo (1856) described similar rows of tightly packed pellets on bedding planes as *Alcyonidiopsis*. Several authors have considered that *Alcyonidiopsis* is a proper name for this kind of traces with pellets (e.g. Chamberlain, 1977; Uchman, 1995, Pickerill & Narbonne, 1995; Uchman et al., 2005, 2013; Buatois et al. 2017; Mángano et al., 2019). *Tomaculum* is indicative of a deep-water settings (e.g. Benton & Trewin, 1978; Podhalańska, 2007) and is rare in Palaeozoic carbonates (Chamberlain, 1977). Toom et al. (2017) reported *Coprulus* from the Ordovician shallow-marine carbonates of Estonia. From lower Palaeozoic sediments, the pellets are reported within shelly fossils, mainly from the Ordovician (Põlma, 1982; Gutiérrez Marco, 1984; Mikuláš, 1992b; Bruthansová & Kraft, 2003) and recently also from the Cambrian (Zhang et al., 2007; Mángano et al., 2019).

**Small faecal pellets** are common inside shelly fossils in the Ordovician carbonate succession of Estonia (Paper II) and are identified as infill inside over 180 shelly fossils. The majority of coprolites are represented by isolated loose pellets and belong to the ichnofamily Coprulidae; only one specimen was identified as representative of Lumbricariidae. Discoveries have occurred throughout the Ordovician outcrop area, from 40 different localities, and almost all represent normal shallow marine settings of the Estonian shelf (Fig. 4); only one discovery came from a deeper shelf environments (deeper-water Livonian basin, Fig. 4). Fossils with coprolites are found from cold-, temperate- and warm-water carbonates and come from wackestones, packstones and pure carbonate mudstones. Occurrence is known from the Volkhov to Pirgu stages (Dapingian to upper Katian) (Table 2). Two stratigraphic levels, tropical carbonates of the Rakvere Stage (Katian) and temperate water carbonates of the Haljala Stage (Sandbian), demonstrate a higher occurrence and better preservation of the faecal pellets. Several common Palaeozoic body fossils are represented as hosts for pellets, including gastropods, bivalves, cephalopods, brachiopods, echinoderms and trilobites (Table 2). Pellets have not been observed in the matrix. The prevalence of different molluscs, especially gastropods, as the hosts, is notable.

The size of faecal pellets is highly variable, ranging from 0.1 to 1.8 mm in length, and from 0.08 to 0.5 mm in diameter. However, within a single host specimen, the faecal pellets are principally stable in their dimensions. In shape, the pellets are elongated, always with a circular section, are mostly elliptical or rod-shaped length/diameter ratios of  $\leq 2$  and 2–3. A smaller number of shelly fossils show faecal pellets that are more elongated, elliptical or rod-shaped, with a length/diameter ratio of 4 to 6. All coprolites are devoid of internal structures, and no constructional wall or lining is observed. Chemical analysis with EDS showed that the carbonate mineralogy of faecal pellets is similar to the composition of matrix rock. The pellets from the Haljala Stage (Sandbian) were, however, somewhat silicified. Pellets inside the shells may be organised in two modes. The majority is represented by massive accumulations and c. 15 specimens contained faecal pellets within small burrows.



**Figure 24.** Micro-coprolites inside Ordovician shelly fossils. Scale bar is 1 mm. **1.** *Coprulus oblongus*, Värskä 6 borehole, 381.8 m, Adze Formation, Haljala Stage, Sandbian, GIT 156-1066-1; **2.** *Coprulus*, Oandu River outcrops, Rägavere Formation, Rakvere Stage, Katian, GIT 619-85-5; **3.** *Coprulus bacilliformis*, Rakvere, Rägavere Formation, Rakvere Stage, Katian, TUG 1779-477-1; **4.** *Coprulus*, Kullaaru ditch, Hirmuse Formation, Oandu Stage, Katian, GIT 694-93-3; **5.** *C. oblongus* as constituent of compound trace fossil *Tubularina*, Aluvere quarry, Kahula Formation, Haljala Stage, Sandbian; **6.** *Lumbricaria intestinum*, Rägavere quarry, Rägavere Formation, Rakvere Stage, Katian, TUG 73-148-2.



The number of pellets in individual accumulations varies widely, from less than a hundred to more than a thousand pieces. Faecal pellets in massive accumulations represent the ichnogenus *Coprulus* Mayer, 1952, which is known by two valid ichnospecies *C. oblongus* Mayer, 1952 (Fig. 24.1, 24.2) and *C. bacilliformis* Mayer, 1955 (Fig. 24.3). According to Knaust (2008), *C. oblongus* pellets are isolated pills with a smooth surface and are cylindrical to oval in shape, with a length/diameter ratio commonly between 1.5 and 2.0. The rod-shaped pellets of *C. bacilliformis* have a length/diameter ratio of around 6 (Mayer, 1955). Only half of Estonian shelly fossils demonstrated pellets with a length/diameter average value of less than 2, which can be identified as *C. oblongus*. Few gastropod steinkerns have faecal pellets with length/diameter values of 4-6, and only the rod-shaped pellets can be identified as *C. bacilliformis* (Fig. 24.3). Elliptical pellets with a length/diameter ratio of 2–3 may potentially be included with *C. oblongus*. However, it is questionable to include the faecal pellets' length/diameter values over 4 with *C. bacilliformis*. Since the material figured by Mayer (1952, 1955) is not available for re-investigation, the elongated oval faecal pellets with a length/diameter ratio over 2 (Fig. 24.4) can be identified only at the genus level (Paper II). The pellets were not related to the animals that inhabited the shells. Assigning the pellets to specific animals is complicated, as the pellets of most invertebrates lack specific morphological features (Flügel, 2004). However, there are many publications dealing with the excrements of different recent aquatic invertebrates, and a wide range of problems have been discussed (e.g. Moore, 1939; Kornicker, 1962; Arakava, 1970).

In general, the faeces of carnivorous animals are loose and irregular, whereas the faeces of deposit feeders are more resistant. Predators and scavengers have high assimilation efficiencies and produce a small number of faeces; mud-dwelling and suspension feeders produce large amounts of solid and resistant pellets (e.g. Pryor, 1975; Wotton & Malmqvist, 2001). Recent excrements similar to *Coprulus* are commonly produced by polychaetes (Bałuk & Radwański, 1979; Knaust, 2008; Kulkarni & Panchang, 2015). The Estonian pellets are composed of the same material as the host sediment and suggest that deposit feeders or suspension feeders were the main tracemakers. Considering the large number of pellets that the suspension feeders produce, the different cavities inside the shells were used as temporary hiding places rather than permanent domiciles. The fact that pellets have not been observed inside the largest shells, supports this idea. In addition, the size of apertures/holes in shells controlled the inhabiting community. The high variability in the size and shape of pellets is related to gastropod shells; their open apertures made them easily inhabitable (Paper II).

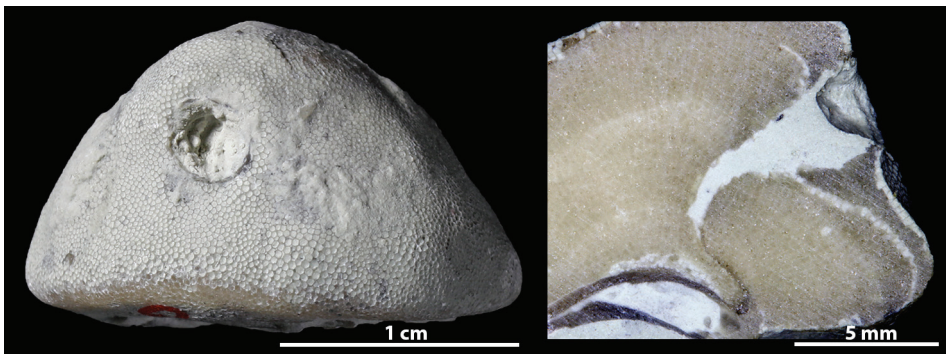
A single steinkern of a large gastropod revealed a very elongated (the length far exceeds the width), convolute, cylindrical coprolite without an internal structure, showing an overlapping pattern and exhibiting constrictions (Toom et al., 2019). This specimen comes from tropical carbonates of the Rakvere Stage (Katian) and is assigned to the rare ichnogenus *Lumbricaria* Münster in Goldfuss, 1831 (Fig. 24.4); it was recently emended by Kietzmann & Bressan (2019). The trace was found in Jurassic shallow subtropical carbonates (Schweigert, 2001). Different tracemakers have been discussed for *Lumbricaria*, most recently holothurians (Kietzmann & Bressan, 2019). Holothurians used different shelters for hiding and are known from the Upper Ordovician deposits of Estonia (Reich, 1999). The Estonian specimen from the Rakvere Stage is small (the diameter is about 0.7-0.8 mm, and the length of loops is more than 10 mm) and probably represents a juvenile tracemaker. Buatois et al. (2017) applied the scheme of architectural designs of traces only for structures filled with pellets, not coprolites.

**Simple, actively filled (pelletoidal) horizontal burrows** are represented in the Ordovician carbonate succession of Estonia by *Tubularina* Gaillard et al., 1994 and *Alcyonidiopsis* Massalongo, 1856 (Tables 1–2). These traces are classical examples of compound traces, consisting of two different ichnofossils – the burrows and pellets. *Tubularina* was previously described from the Jurassic lagoonal limestones; it is a relatively small burrow and circular in cross section (diameter up to 2 mm), filled with sparry calcite and loose pellets (Fig. 24.5). The trace is penetrating the sediment sinuously in very different directions. Burrows occurred inside molluscs' steinkerns from the Haljala to Oandu (Sandbian and lower Katian). Two specimens of trilobites from the Haljala and Keila stages (Sandbian and lower Katian) have curved ribbon-shape burrows filled with pellets and sparry calcite on the dorsal surface of steinkern. The location of burrows on steinkerns is similar to the position of *Arachnostega*, but the traces do not demonstrate the network characteristic of the latter; moreover, the pelletoidal infill of *Arachnostega* is unknown. The ribbon-shaped small burrows inside of trilobites are similar to *Alcyonidiopsis*. The pellets inside of *Tubularina* and *Alcyonidiopsis* represent the ichnogenus *Coprulus*. Polychaetes have been debated as the possible tracemakers (e.g. Chamberlain, 1977; Gaillard et al., 1994; Uchman et al., 2005; Mángano et al., 2019). Recently, palaeoscolecidans were also discussed as potential tracemakers for *Alcyonidiopsis* (= *Tomaculum* in Martin et al., 2016). Co-occurrence of the faecal pellets and *Arachnostega* was observed only in/on a few specimens. Estonian material confirms that *Arachnostega* producers were not related to the accumulations of pellets inside the shells.

Pellets are formed *in situ* inside the shells and were produced when the shell was lying on the sea floor. The shell was afterwards filled with sediments. However, it is possible that the pellets were formed when the shell was shallowly buried. The cementation is most complete just below the seafloor (Wilson & Palmer, 1992) and the rapid lithification was likely favoured by the small dimensions of the pellets. In addition, cementation resulting from aragonite dissolution may be confined to areas immediately adjacent to dissolving bioclasts (Wilson & Palmer, 1992). This may explain the large number of findings related to the different molluscs' steinkerns. The high number of discoveries and the wide range in shape and size of pellets came from the Upper Ordovician. This may be due to the better preservation conditions in warm waters. Increased numbers of findings in the Haljala Stage can be explained by the beginning of climate warming and supported by the silicification of sediments. Tarhan et al. (2016) and Liu et al. (2019) have discussed rapid silicification as an agent for preserving soft-bodied fossils. Slightly silicified rocks are common in Estonian shallow water carbonate rocks, especially in the Haljala Stage. The origin of silica is supposed to be biogenic (from sponges) or volcanic (Jürgenson, 1958; Siir et al., 2015). The microenvironment inside protective shells was probably an important factor in the preservation of pellets, especially in cool and temperate water environments (Paper II). The shells shielded pellets and burrows inside and allowed an early cementation to occur. Moreover, the shells regulated oxygen diffusion inside and may have behaved as traps for calcium ions. The preservation of pellets consists of interactions between several factors, including sea water and pore water chemistry, temperature, rapid lithification of small particles, a favourable microenvironment inside shells, and the composition of pellets and microbial communities (Paper II).

### 5.1.4 Bioclaustration structures

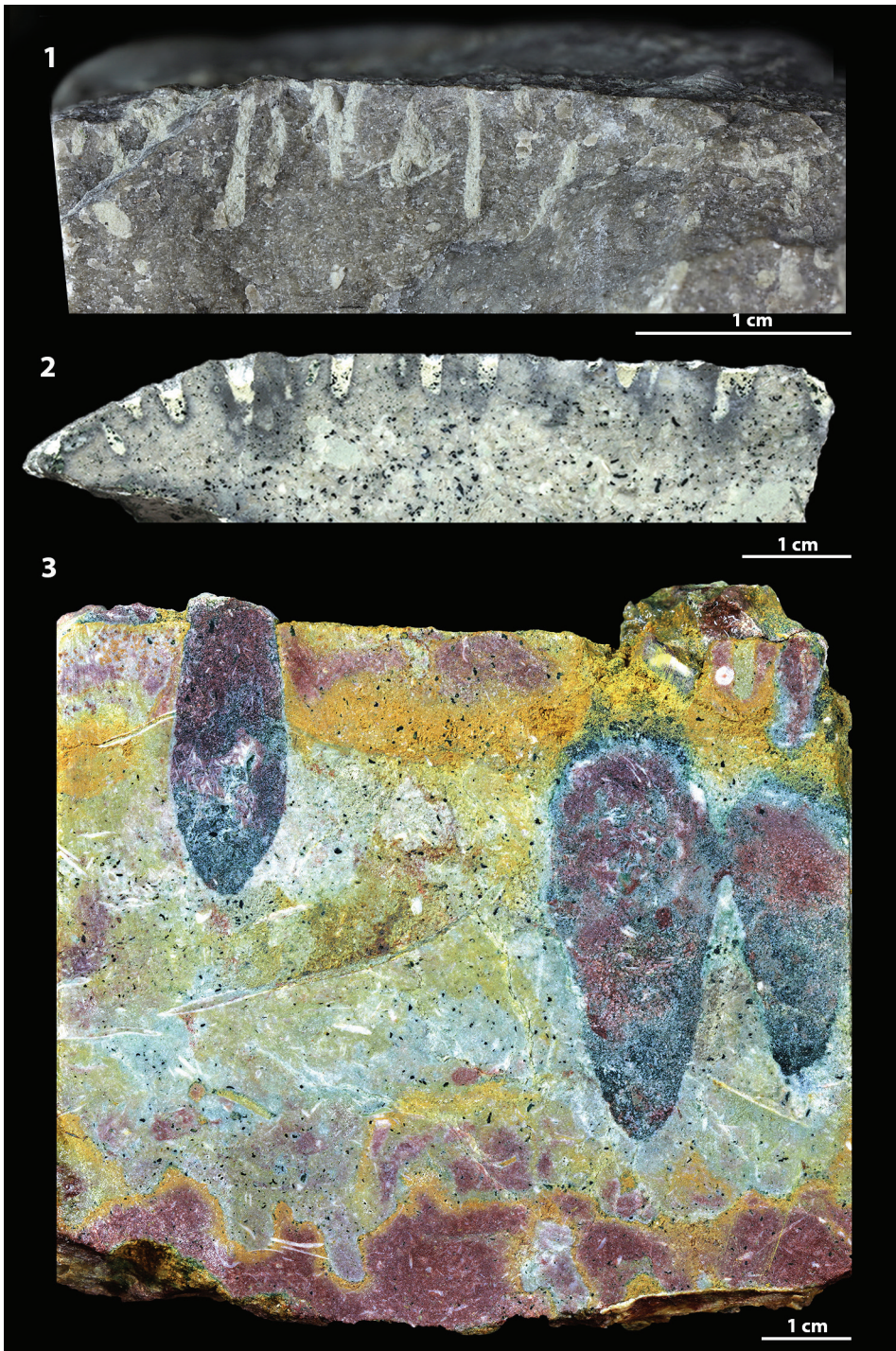
From the carbonate succession of Estonia several bioclaustration structures associated with tabulate corals and brachiopods have been described. *Chaetosalpinx* Sokolov, 1948 (Klaamann, 1959; Vinn & Mõtus, 2014), *Helicosalpinx* Oekentorp, 1969 (Vinn & Mõtus, 2014), and *Burrinjuckia* Chatterton, 1975 (Vinn et al., 2014c) are valid genera, but not listed as ichnotaxa (Wisshak et al., 2019). As some bioclaustration structures are very similar to trace fossils and some taxonomic questions cannot be fully solved at present, bioclaustration structures are included in this study. A symbiotic parasite *Anoigmaichnus* was described as a trace fossil on Darriwilian (Uhaku Stage) trepostome bryozoans from Estonia (Vinn et al., 2014d). *Anoigmaichnus* consists of shaft and terminally elevated aperture. In the Ordovician of Norway, a worm-tube boring in bryozoans is widespread (Spjeldnæs, 1989) and can also be referred to as *Anoigmaichnus*. Wisshak et al. (2019) regarded the *Anoigmaichnus odinsholmensis* Vinn et al., 2014d to be junior synonym of *Trypanites weisei*. Different structures with elevated apertures are common in Estonian bryozoans (Vinn et al., 2018b) and most of these structures are symbiotic with more complicated structures (Fig. 25) than the simple *A. odinsholmensis*. Synonymization of *A. odinsholmensis* with *T. weisei* remains questionable presently, and the small height of the bryozoan colony does not allow the trace to achieve the diagnostic length-to-width ratio of *Trypanites weisei*. Further research with non-destructive techniques is needed to clarify the occurrence of trace fossils and symbionts in bryozoans.



**Figure 25.** 1. *Mesotrypa expressa* Bassler, 1911 with ring structure, GIT 770-8; 2. *Anoigmaichnus bretti* (Vinn et al., 2018b), Kullaaru ditch, Hirmuse Formation, Oandu Stage, Katian, GIT 770-8.

## 5.2 Trace fossils and encrusters on hardgrounds

During the current study, eleven Ordovician and four Silurian hardgrounds were studied for bioerosional traces in detail (Papers X–XII; Vinn & Toom, 2015). The results must be considered preliminary, due to a sampling bias in the number of studied hardgrounds and the size of the samples being relatively small. All studied hardgrounds were impregnated with pyrite. The occurrence of ‘hiatus nodules’ (i.e., bioeroded limestone pebbles and cobbles in Paper XII) was recorded in the Volkhov and Kunda stages (Dapingian and early Darriwilian). The Päärdü hardground from the Adavere Stage, Llandovery, has been fractured into polygonal sections.

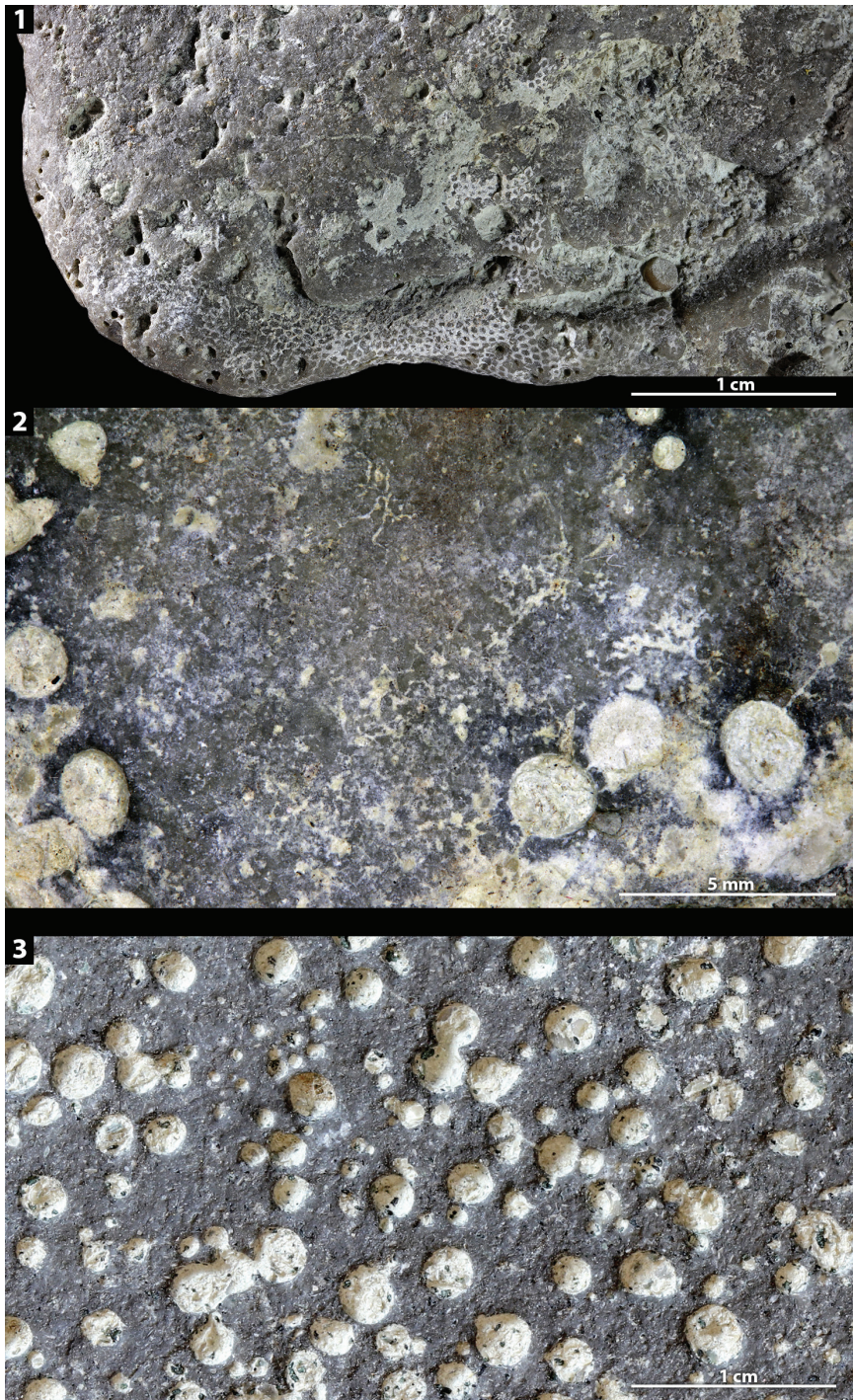


**Figure 26.** 1. *Palaeosabella* or *Trypanites*, Ohesaare cliff, Ohesaare Formation, Ohesaare Stage, Põidoli, GIT 362-562-1; 2. *Trypanites heckeri*, Väike-Pakri Island, Toila Formation, Volkhov Stage, Dapingian, GIT 381-595; 3. *Gastrochaenolites oelandicus*, Lelle D-102 drill core, Toila Formation, Volkhov Stage, Dapingian, GIT 362-537.

Macroborer diversity in lower Palaeozoic hardgrounds is generally low (Tapanila et al., 2004). Preliminary research on Baltic material shows that Palaeozoic hardground boring faunas in Laurentia are more diverse (Paper XII). This can be explained by different environmental conditions caused primarily by climatic differences. In addition, it may be explained by collecting bias, as the North America hardground faunas have been more thoroughly studied. Four ichnogenera, *Trypanites*, *Gastrochaenolites*, *Petroxestes* and microbioerosional *Cicatricula* (= *Dictyoporus*) are known from the Ordovician deposits of North America (Palmer & Palmer, 1977; Wilson & Palmer, 1988, 1992; Benner et al., 2004) In Estonia, the Ordovician hardgrounds include *Trypanites* and *Gastrochaenolites* (Fig. 26.3) and the Silurian hardgrounds include *Trypanites*. *Trypanites* borings are prevalent (Papers X-XII), occurring in hardgrounds with pyritic impregnation. The samples frequently bear several different sizes of borings, thereby suggesting activities of several different tracemakers. The current level of research shows that there is no clear stratigraphic trend in the size and distribution of *Trypanites* borings and in the bioerosion intensity of hardgrounds through the Ordovician and Silurian succession of Estonia. There is a possibility that some of the borings identified as *Trypanites* may belong to *Palaeosabella* (Fig. 26.1). *Palaeosabella* is an elongated cylindrical boring with a swollen distal end but is smaller in diameter than *Trypanites* and can easily be confused (Wyse Jackson & Key, 2007). Notably, *Palaeosabella* is mostly known from different organic substrates of Laurentia and Baltica (Clarke, 1921; Wilson & Palmer, 2006; Beuck et al., 2008; Vinn & Wilson, 2010c; Mángano et al., 2016). The description of the shallow *Trypanites heckeri* (Fig. 26.2) introduces new data on the occurrence of macroborings in the Baltic region and in Estonian hardgrounds. The Estonian samples with *Gastrochaenolites* are recorded from the Volkhov Stage, Dapingian (Vinn & Wilson, 2010b, Papers I, X), on the lower boundary of the Middle Ordovician. This is an easily recognizable surface of non-deposition with large borings, traceable for hundreds of kilometres from Sweden to the St. Petersburg region (Jaanusson, 1961; Dronov & Holmer, 1999; Ekdale & Bromley, 2001b). Some Ordovician and Silurian hardgrounds from Estonia bear unidentified micro-bioerosional traces (Fig. 27.2) and possibly microbially induced microstructures (Papers I, IX). The diversity of Silurian hardgrounds has been reported as monospecific (Cherns, 1980; Vinn & Wilson 2010a; Papers X, XI) and the single boring that was recovered is *Trypanites*.

New material from the Ohesaare hardground (Ohesaare Stage, Põidoli) has brought up etching traces made by bryozoans. The latest findings from Estonia show that the occurrence of more diverse bioerosional trace fossil fauna on hardgrounds, including *Trypanites*, *Gastrochaenolites*, bryozoan's borings, Dendrinidae, and possible *Palaeosabella*, have been identified. Knaust (2019b) assumed an occurrence of *Sulcolithos* in Estonian firmgrounds/hardgrounds, but further research is needed to clarify the presence of this trace in Estonia. Moreover, the newest material shows the presence of *Gastrochaenolites* on the boundary of the Nabala and Vormsi stages.

MMD values (after Tapanila et al., 2004) for the studied Ordovician hardgrounds vary from 1 to 5 (Paper XII, Vinn & Toom, 2015). The most intensely bioeroded hardgrounds occur in the earliest Dapingian (Fig. 27.3) (Volkhov Stage) and the least eroded occur in the late Katian (Vormsi Stage). The MMD value for the Silurian hardgrounds is from 3 to 5, being lowest in the Telychian Põri hardground and highest in the Põidoli Ohesaare hardground (Papers X, XI). The latter value demonstrates the highest bioerosion density and likely reflects a longer colonisation window rather than an evolutionary trend (Vinn & Wilson, 2010a).



**Figure 27.** 1. Ohesaare hardground with borings and encrusting bryozoans, Ohesaare cliff, Ohesaare Formation, Ohesaare Stage, Põidoli, GIT 362-562; 2. Päärdu hardground with borings and microbioerosional traces, Rumba Formation, Adavere Stage, Llandoveri, GIT 362-104; 3. Väike-Pakri hardground with borings of several different sizes, Väike-Pakri Island, Toila Formation, Volkhov Stage, Dapingian, GIT 381-595.

The first hardground encrusters in Estonia appeared in the Dapingian, Middle Ordovician (Vinn & Toom, 2015), and are represented by bryozoans and echinoderms (eocrinoids or crinoids). In the Late Ordovician the hardground faunas changed, and edrioasteroids and cornulitids appeared in the Katian. The late appearance of edrioasteroids and cornulitids in Estonian hardground communities is noteworthy, they are already known from Darriwilian deposits in Estonia. In lower Silurian hardgrounds (Llandovery), bryozoans and echinoderms were accompanied by tabulate corals. The most diverse encrusting fauna was found at the Ohesaare hardground (Fig. 27.1; Vinn & Wilson, 2010a). The compositions of fauna encrusting hardgrounds are similar to the assemblage described by Taylor (2016).

The Ordovician and Silurian hardgrounds of Estonia are very sparsely encrusted. For the Middle and Upper Ordovician, around 1% of the hardground surface was encrusted. The North American analogues have much higher values (Brett & Liddell, 1978; Brett & Brookfield, 1984), and may cover c. 10% (Wilson et al., 1992). The low skeletal coverage has been explained by low nutrient availability and by a large community of soft-bodied organisms (Lescinsky et al., 2002). The high bioerosion density indicates that low productivity cannot be the cause of low encrustation. In case of amensalism, the abundance of boring organisms may prevent the formation of dense encrustation (Paper X). The substrates may have been covered by cyanobacterial biofilms, which prevented encrusters (Vinn & Wilson, 2010a; Rozhnov, 2018, 2019). The colonisation window is certainly important for the formation of the encrusting community. It seems that most of studied Estonian hardgrounds appear to have been formed under the low colonisation window conditions.

### 5.3 The Bioerosion Revolution on Baltica

The Middle Ordovician to latest Silurian carbonate succession of Estonia is rich in bioerosional trace fossils. According to the assembled data set, it hosts 15 macrobioerosional ichnogenera, 11 of which are recorded in the Ordovician and 10 in Silurian strata (Table 1). The siliciclastic Cambrian deposits of Estonia include a single bioerosional ichnogenus (Vinn & Toom, 2016). In addition to the macroscopic borings in various unidentified microstructures, dendriniids and traces assigned to cf. *Cyclopuncta* were found in Ordovician deposits. The Silurian strata also host unidentified microstructures and dendriniids. When Wilson & Palmer (2006) introduced the term “Ordovician Bioerosion Revolution,” they described seven macroboring ichnogenera from the Ordovician: *Trypanites*, *Palaeosabella*, *Gastrochaenolites*, *Petroxestes*, *Cicatricula* (= *Dictyoporus*), *Ropalonaria*, and *Sanctum*. A decade later, Mángano et al. (2016) listed 11 Ordovician ichnogenera, including *Trypanites* and *Oichnus*, ranging from the Cambrian, and 9 that first appeared in the Ordovician: *Palaeosabella*, *Peroxestes*, *Ropalonaria* (= *Pinaceocladichnus*), *Gastrochaenolites*, *Sanctum*, *Cicatricula* (= *Dictyoporus*), *Podichnus*, *Caedichnus* (= *Bicrescomanducator*) and *Tremichnus*.

The Ordovician Baltic region hosts 12 macroboring ichnogenera: *Trypanites* (= *Vermiforichnus* in Hanken et al., 2016), *Tremichnus* (= *Balticapunctum* in Rozhnov, 1989), *Gastrochaenolites*, *Pinaceocladichnus* (= *Ropalonaria* in Wilson & Palmer, 2006), *Sanctum*, *Oichnus*, *Osprioneides*, *Petroxestes*, *Sulcolithos*, *Bicrescomanducator*, *Rogerella*, and *Ericichnus*?. Moreover, several undescribed macroborings, bite marks and different microborings were found in Ordovician deposits of the region. Notably, the oldest representatives of several ichnogenera come from Baltoscandia: *Tremichnus*,

*Osprioneides*, *Pinaceocladichnus*, *Sulcolithos*, *Sanctum*, *Petroxestes*, and *Rogerella*. Additionally, the oldest Ordovician *Oichnus* has been reported from this region.

Three bioerosion ichnofacies are related to lithic and skeletal substrates: the *Trypanites*, *Entobia* and *Gnatichnus* ichnofacies (Gibert et al., 2007), and only *Trypanites* ichnofacies is typical of the Palaeozoic Era. The Estonian material from the Ordovician contains bioerosional traces that are also common in the *Gnatichnus* ichnofacies; for instance, *Rogerella* and undescribed peeling structures on large brachiopods (Paper I).

The majority of bioerosional ichnogenera are related to various shelly fossils: bryozoans, stromatoporoids, trilobites, brachiopods, echinoderms, rugose and tabulate corals, gastropods and other molluscs. However, the bioerosional traces are particularly common and diverse on bryozoans. In the Middle Ordovician, c. 80% of bryozoan colonies are bored (Wyse Jackson & Key, 2007). In this study, five ichnogenera were determined on Middle and Upper Ordovician bryozoans: *Trypanites*, *Sanctum*, *Osprioneides*, *Sulcolithos*, and *Petroxestes*. Moreover, the collection material is estimated to include at least four additional ichnogenera that are yet to be formally described. Macroborings were most common in the bryozoans occurring in muddy facies of the Kukruse and Haljala stages (Sandbian). Silurian stromatoporoids from the Jaani Stage (Sheinwoodian) bear macroborings with similar spread patterns. The borings are commonly clumping on the top of stromatoporoid colonies. Co-occurrence of several traces is frequent: *Osprioneides*, *Sulcolithos*, *Trypanites* of several sizes, possibly *Palaeosabella*, and microgrooves may be present together. Clumping behaviour of different borings is a common tendency. This kind of accumulation of tracemakers is common for macroboring taxa globally (Kobluk & Nemcsok, 1981; Wilson & Palmer, 1988). In addition, the overprinting of traces is common. It may be possible that some of the large borings are not domicinia, but predatory traces were instead made to catch the inhabitants of the smaller clumping borings. The morphology and size of the traces are controlled by the size and morphology of the host and large specimens, which tend to bear a large number of borings. This trend was described by Vinn (2005) in *Trypanites* borings in Ordovician brachiopods. Massive and large hosts can provide safer domiciles, more food and oxygen (Kershaw, 1984; Tapanila et al., 2004). In addition to bioerosional traces, the Middle Ordovician bryozoans were the most favourable hosts to different symbionts such as conulariids, cornulitids, rugose corals, and the problematic producer of the *Anoigmaichnus* structure (Vinn et al., 2016, 2017, 2018b, c, 2019).

In the Ordovician, some trepostome bryozoans produced very large colonies (Cuffey et al., 2000), and this period shows also a rapid diversification of bryozoans, with the peak in the Sandbian (Ernst, 2017). Stanley (2006) suggested that trepostome bryozoans become hypercalcified due to the “calcite sea” conditions that prevailed in the Ordovician and produced larger or thicker skeletons. Taylor & Kuklinski (2011) tested this hypothesis by comparing the values of branch diameter and exozonal skeletal wall thickness in trepostomes from the Ordovician (“calcite sea”) and Permian (“aragonite sea”). They concluded that trepostome bryozoans were not among the groups that responded to the low Mg/Ca seawater chemistry by producing hypercalcified skeletons. Instead, it is likely that bryozoans were strongly coupled with their food, which is mainly phytoplankton (Ernst, 2017), and their evolution in the Ordovician was directly related to the increasing phytoplankton availability reported by Servais et al. (2010).

Edwards et al. (2017) argued that the oxygen concentration was a key factor in early Palaeozoic biodiversity regulations, and oxygenation possibly drove the Great Ordovician Biodiversification Event. The estimated maximum atmospheric O<sub>2</sub> values were calculated



for the Middle Ordovician, Sandbian and early Katian (Edwards et al., 2017). From the upper Darriwilian to lower Katian, the sea level was generally high and stable (Haq & Schutter, 2008; Dronov et al., 2011), ensuring the relative stability of marine benthic communities. The increase of macrobioerosion in the Middle Ordovician is correlated with the increase of hardgrounds and heavy calcitic skeletons associated with “calcite sea” conditions (Palmer & Wilson, 2004; Mángano et al., 2016). In the Estonian Shelf, the upper Darriwilian to lower Sandbian interval corresponds to the period of massive kukersite kerogen accumulation. Kiipli et al. (2010) associated the rise of bioproduction with regional processes, notably seawater circulation and coastal upwelling. This time interval is characterised by a high diversity of both macro- and microfaunas in Baltoscandia (Kaljo et al., 2011; Hints, L. et al., 2018; Hints, O. et al., 2018), and the first appearance and rapid diversification of rugose corals (Kaljo, 1956) and echinoids (Männil, 1962). Reef development began during the latest Sandbian–early Katian interval in Baltoscandia (Kröger et al., 2017), and the main factor controlling the reef evolution was the drift of Baltica towards tropical latitudes. The diversification of bioerosional traces in the region started at the same period but is not related to the development of reefs. Large borers seemingly preferred a more stable environment than the high-energy reefal settings; this was also noted by Tapanila et al. (2004). The changes in the macrobioerosional trace fossil community reflect the facies and sea level changes. The predatory traces appear to have been characteristic of higher energy environments and were perhaps connected with higher competition for space and food.

The rapid diversification of bioerosional traces in the Ordovician of Baltoscandia was probably a coincidence of multiple global and regional factors. The major global factors were the sea water chemistry and oxygenation, stability of the sea level, and increasing phytoplankton availability. The main regional conditions supporting the bioerosion revolution were the warming climate and nutrient-rich well-oxygenated epeiric sea. The diversification of bioerosional trace fossils is strongly correlated with the development of different organisms possessing heavy calcite skeletons and low environmental stress.

#### **5.4 Ichnodiversity in the Ordovician and Silurian deposits of Estonia**

The number of well-preserved trace fossils collected from Estonia is not large, and several ichnogenera and species are as of now represented by few or even singular finds. Such taxa include, for instance, *Halopoa*, *Monomorphichnus*, *Diplichnites*, *Helicodromites*, *Treptichnus pedum* and *Phycodes reniforme*. The palaeontological collections from Estonia with several hundred thousand specimens contain only c. 3800 trace fossils, out of which c. 2500 are identified (Table 1). From the identified specimens, nearly half belong to the common and intensively collected ichnogenera *Conichnus* and *Amphorichnus*. Any identification of trace fossils is often complicated or impossible, as important diagnostic features may be hidden in solid Palaeozoic rocks or are not sufficiently well preserved. Altogether, 38 soft sediment ichnogenera and 15 bioerosional ichnogenera, one ichnofamily and unnamed peeling and macrobioerosional structures were identified. The distribution of traces in the Ordovician–Silurian carbonate succession is irregular. The data on the soft sediment trace fossils are especially patchy. However, weak trends in the distribution are nevertheless traceable.

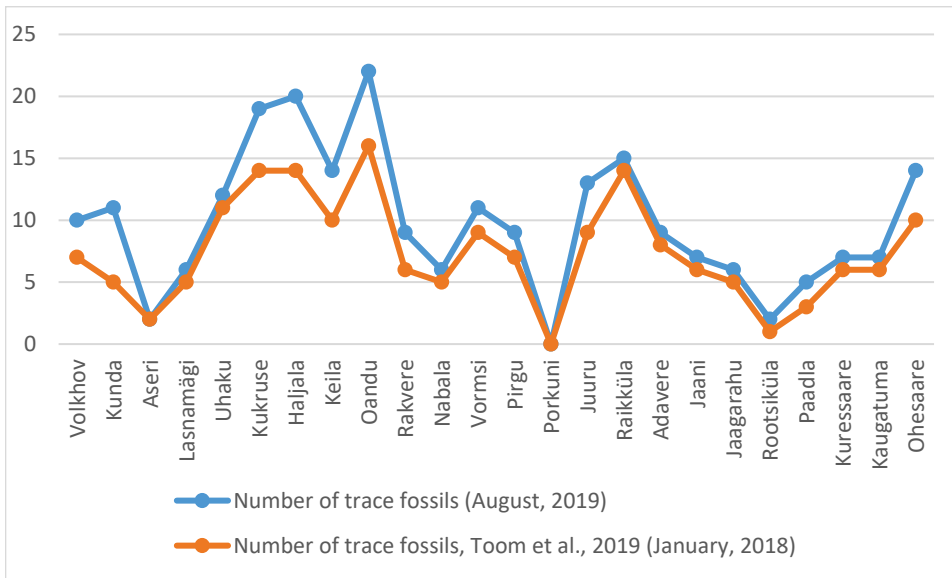
The general picture of the trace fossil distribution and associations reflects the geological succession of Estonia (Paper I): relatively stable conditions of sedimentation

in Middle Ordovician and a differentiation of the basin in the Upper Ordovician and Silurian. The Middle Ordovician succession of Estonia is characterised by slow sedimentation and a small number of trace fossil genera and CADs (Table 1). As noted by Stachacz et al. (2018), a slow sedimentation rate and the shallow burial of organic matter may negatively influence the diversity of trace fossils. The richness of trace fossils is associated with rock volume: the relatively smaller thickness of stratigraphic units reflects a smaller number of traces. For instance, the thickness of the Aseri Stage in northern Estonia varies from 0 to 4.6 m, being mostly less than 1 m (Hints, L., 1998). More diverse ichnofaunas from the Estonian carbonate succession are related to the intervals with greater sediment accumulation, like in the Kukruse and Haljala stages (Sandbian, Upper Ordovician).

The occurrence of trace fossils is also related to the type of sediments. Notably, the input of siliciclastic material to the sedimentary basin increased the number of the trace fossil genera as well as the number of CADs recovered (Papers I, IV). A similar trend where mixed carbonate-siliciclastic systems had a higher preserved ichnodiversity than purely carbonate settings has been reported by earlier authors (Rodríguez-Tovar et al., 2014; Mángano et al., 2016). Siliciclastic material influences the sediment composition and consistency, slowing down early cementation, and thus has an impact on the trace fossils' formation and preservation in carbonates. Continuous low sedimentation allows the mixing of the sediment and the destruction or overprinting of primary structures (Monaco, 1995). The input of siliciclastic material also contributes to the sedimentation rate and thus promotes preservation.

The identified trace fossils are rarely related to dolostones. Regional stages that contain more dolomite (Porkuni, Jaagarahu, Rootsiküla and Paadla) contain smaller numbers of traces (Table 1). On the other hand, in the Porkuni, Jaagarahu and Rootsiküla time the sedimentary environment was stressed, which seems to be reflected in the spread of traces. The Porkuni Stage faunas are affected by the Hirnantian glaciation. The Rootsiküla Stage contains sparsely distributed specific fossil biota (Einasto, 1970; Nestor, 1998). Additionally, the beds with lagoonal sediments of the Rootsiküla Stage were characterised by stressed settings, including the beds with abundant *Chondrites* traces that likely indicate dysaerobic conditions. A recrystallization of carbonates can alter trace fossils (Knaust et al., 2012). Dolomitization likely affected the preservation of traces, but the current level of research does not clearly demonstrate this supposition. A systematic characterisation of trace fossils of different lithological units is needed in the future; this may also bring up a new data on the influence of dolomitization.

Trace fossil richness in Estonian carbonates is broadly similar to body fossil diversity. For many fossil groups, a taxonomic richness peak is observed in the Sandbian and early Katian, both in Baltica and globally (e.g. Stigall et al., 2019; Franek & Liow, 2019). Warm-water faunas are commonly more diverse than temperate or cool-water faunas (Kröger, 2017), also exhibiting a wider spectrum of biofacies and behaviours. The less diverse faunas can explain a relatively small number of soft sediment traces in the Middle Ordovician. During the Late Ordovician, Baltica reached the subtropical climatic zone. The scolecodont-bearing polychaetes, which were probably among the most common tracemakers, reached their highest diversity in Baltoscandia during the Katian (Hints, O., 2000; Hints, O. et al., 2010) and thrived in the Silurian tropical seas (e.g. Tonarová et al., 2014). In Estonia, Sandbian and lower Katian strata (Kukruse to Oandu stages) also demonstrate a more diverse trace fossils association (Table 1).



**Figure 28.** Genus-level taxonomic richness of trace fossils through the Middle Ordovician to latest Silurian in Estonia, calculated per regional stages (see Fig. 5 for correlation with international stratigraphy); based on data in Table 1.

The ichnodisparity of Estonian Ordovician and Silurian traces (number of CADs in Table 1) correlates with trace fossils' richness (Fig. 28). The Estonian (and Baltoscandian) pattern of ichnodisparity is similar to the global trends, especially in the disparity of bioerosional traces. Globally, a rapid increase in bioerosional traces started in the Darriwilian and continued in the Sandbian (Mángano et al., 2016). Unique to the Estonian pattern is the relatively small number of shallow-marine bioturbation structures. However, the results may be biased due to insufficient data on the trace fossils' occurrence. The relatively abundant occurrence of post-Hirnantian traces is probably related to better preservation conditions.

For carbonate settings, many traces are associated with shelly fossils. In the Baltic region, this characteristic has been noted by several authors (e.g. Størmer, 1931a, 1931b; Regnéll, 1945; Bohlin, 1955; Spjeldnæs, 1989). The traces have formed inside defending shells and have therefore are abundant. For instance, the common feeding trace *Arachnostega* and the structures associated with microcoprolites have similar distribution patterns. The traces are usually associated with different groups of shallow-marine molluscs, and the dissolution of aragonitic shells have made ichnofossils easily visible. An examination of trilobites and brachiopods suggested that *Arachnostega* and micro-coprolites are frequent inside internal moulds. Nevertheless, the tracemaker of *Arachnostega* was not related to the small pellets inside the shells as was previously assumed by Bruthansová & Kraft (2003).

The Hirnantian glaciation strongly affected the distribution of trace fossils in Estonia. The complete absence of the identifiable traces in the Porkuni Stage (Hirnantian) in northern Estonia is noteworthy. The stage is represented by the Ärina Formation, comprising dolomites, stromatoporoid-tabulate reefs and oolitic or sandy limestones with a thickness up to 10 m (Hints, L. & Meidla, 1998). The absence of traces in the Porkuni Stage is probably a coincidence of several different causes. Dolomitization

affected the preservation of traces; colonies of corals and stromatoporoids bear pseudoborings. Additionally, the favositid and heliolitid corals of the Porkuni Stage have large corallites that were not a suitable substrate for borers. The same dynamic is true for halysitids.

Sampling bias also influenced the diversity curves of trace fossils. For instance, the number of outcrops of the Porkuni Stage (Hirnantian) is relatively small and the number of studied samples was insufficient. This may be one of the reasons why the *Trypanites* borings were not observed in the topmost Ordovician strata.

The Silurian bioerosional recovery faunas differ from the Ordovician bioerosional faunas. *Trypanites* borings, common throughout the Ordovician, are rare in the Juuru Stage (lower Rhuddanian). Shallow bioerosional traces such as *Oichnus*, *Tremichnus*, *Circolites*, and *Ericichnus* dominate, but current discoveries of them are few. Post-extinction shelly faunas (corals, echinoderms, bryozoan) show the so-called “lilliput phenomenon” (Kaljo, 1996; Ausich & Wilson, 2016). The small size of biogenic substrates may have also negatively affected the producers of bioerosional traces. The bioerosional traces confined to bryozoans like *Sanctum* were especially strongly affected. Silurian bryozoans also never reached the diversity and abundance they had in the Ordovician (Astrova & Kopaevich, 1970). However, corals and stromatoporoids diversified in Silurian (Kaljo, 1990; Nestor, 1990), providing a suitable substrate for different bioeroders.

*Arachnostega* was common in Ordovician (Vinn et al., 2014a), but was almost missing in the Silurian (Table 1). The Silurian *Arachnostega* traces are noticeably smaller in size, and their finds are related only to brachiopods (Fig. 9). The distribution curve of *Arachnostega* is related to the occurrence of different molluscs. The Silurian recovery fauna of bivalves and gastropods (Juuru Stage, lower Rhuddanian) contain only few genera (Isakar, 1998a, 1998b) and possibly affected the occurrence of *Arachnostega* tracemakers in the Silurian.

The number of vertical structures in the Estonian carbonate succession is small, with the exceptions of *Conichnus* and *Amphorichnus*. *Skolithos*, *Arenicolites*, *Oikobesalon*, *Tisoo*, common constituents of *Skolithos* and *Glossifungites* ichnofacies, and escape traces are related to rapidly deposited event beds. Notably, the Estonian succession includes some rare Laurentian ichnospecies like *P. reniforme*, with known occurrences only in the Ordovician (Hofmann, 1979), and *P. templus* was previously described only from the Devonian (Han & Pickerill, 1994).

Most soft sediment traces are constituents of the *Cruziana* ichnofacies, but representatives of the *Glossifungites* and *Skolithos* ichnofacies were also identified. However, the locomotion traces, characteristic of the *Cruziana* ichnofacies, as well as tool marks are very rare (Paper I; Vinn & Toom, 2016b). Hanken et al. (2016) noted the absence of trilobite traces in the Ordovician limestones of Estonia. The decrease in the abundance of trilobite traces in the Ordovician is a worldwide trend. Mángano et al. (2016) suggested two possible scenarios: (1) the biotic turnover and replacement of trilobite-dominated Cambrian fauna by the more diverse Palaeozoic fauna, where trilobites were “diluted”, and (2) preservation bias. The increase of bioturbation and the establishment of the mixed layer during the early Palaeozoic may have been harmful for the preservation of different sediment surface structures such as trilobite traces and tool marks (Tarhan et al., 2012; Tarhan, 2018). As noted by Mángano et al. (2016), both explanations may be complementary. The Estonian material and current level of research agrees with this view.

The general compositions of the trace fossil associations in the Ordovician and Silurian of Estonia are similar to those elsewhere in the Baltic region (Paper I). Estonian strata have a less diverse record of different arthropod trackways than, for instance, the Silurian of Norway. Estonian trace fossil associations are characterised by a high diversity of borings in biogenic substrates. The difference in surface structures is likely caused by sediment type and sedimentation rates. The diverse bioerosional trace fossils association of Estonia may also reflect sampling bias or may be related to differences in substrate faunas for the boring organisms. The distribution of trace fossils in shallow marine carbonates is closely connected to the distribution of shelly fossils, and most of the benthic organisms are potential tracemakers. The richness peaks of Ordovician macrofossils in the Baltic region and trace fossils in Estonia overlap. The factors controlling the occurrence of body fossils and trace fossils were therefore similar, like oxygen and food availability, climate, and sea-level changes. Heavy shells provide a suitable substrate for different boring organisms. Empty shells or shells filled with sediments are safe hiding places for different animal groups and supported the preservation of traces. The occurrence of trace fossils in the shallow-marine carbonates of Estonia was affected by the sedimentation rate and composition of sediments.

## 6 Conclusions and future directions

The Ordovician–Silurian shallow marine carbonate succession of Estonia contains a diverse association of trace fossils. During this study, 38 different soft sediment trace fossil genera, 15 bioerosion ichnogenera, the ichnofamily Dendrinidae, escape traces, and several new peeling structures and bioerosional microstructures were identified. This greatly increases the knowledge on trace fossils of the region – prior to this work, only 15 ichnogenera were mentioned from Estonia, and only 10 of these with some distributional data.

The composition of the trace fossil associations in the Ordovician and Silurian of Estonia is generally similar to that elsewhere in the Baltic region. However, during the study, several new ichnotaxa for the entire Baltica palaeocontinent were recovered, such as *Helicodromites*, *Petroxestes*, *Rogerella*, *Lumbricaria*, *Coprulus*, *Tubularina* and *Tisoa*, thereby providing new insights into the palaeobiogeographic distributions of the respective tracemakers. Additionally, some of the globally youngest and oldest finds were reported. For instance, the study revealed the youngest known specimen of *Treptichnus pedom*, and the oldest observations of *Osprioneides*, *Sanctum*, *Petroxestes*, *Rogerella*, *Lumbricaria*, and *Tubularina* worldwide. These and other data suggest that the Baltica palaeocontinent might have been a key region for the evolution of ichnofossil communities and especially bioerosional tracemakers.

The mixed carbonate-siliciclastic systems generally have a higher preserved ichnodiversity and better-preserved trace fossils than purely carbonate settings. It is characteristic of the shallow-marine carbonates of Estonia that many trace fossils are related to shelly fossils, using them as a substrate or domicile, or as preservational traps.

For the first time, an abundant occurrence and diversity of small coprolites preserved within shelly fossils was reported from Ordovician carbonate settings. These trace fossils represent ichnogenera *Coprulus* and *Lumbricaria* and range from the Dapingian to upper Katian. At some stratigraphic levels, nearly half of macrofossil shells contained coprolites. This indicates the abundance and diversity of cryptic coprolite-producing faunas that inhabited empty shells in different climates and environments in the Baltic palaeobasin. Specific chemical and physical conditions inside shells probably caused the rapid lithification of coprolites and ensured their preservation. The tracemaker of *Arachnostega* also apparently could not be related to the coprolites inside shells.

The diversity of bioerosional macroborers in Estonia is correlated with the development of different organisms possessing calcitic skeletons. The rapid diversification of bioerosional traces in the Ordovician of Baltoscandia was the coincidence of several regional and global factors, including a warming climate on Baltica, stability in the depositional environments and sea level, the availability of nutrients and the increasing phytoplankton abundance, as well as the calcitic sea geochemistry, including increasing oxygen levels. The Ordovician Bioerosion Revolution was a part of the Great Ordovician Biodiversification Event, and bioeroded hardgrounds are very common in the carbonate succession of Estonia. Macroboring density in hardgrounds were medium to high, but the hardgrounds were sparsely encrusted.

The distribution of trace fossil taxa and associations reflect the geological succession of Estonia. Differentiation of the basin in the Upper Ordovician and Silurian facilitated increasingly diverse trace fossil associations and the end-Ordovician mass extinction most strongly influenced the associations related to the shelly faunas.

From the methodological point of view, the conventional study methods were insufficient for the identification of fossils in consolidated carbonate rocks. Notably, the X-ray CT shows strong potential for observing features hidden in hard substrates. The first tests during this study provided accurate results if density contrast was present between the trace fossils and matrix. For instance, pyritic impregnation or organic-rich matrices revealed the 3D architecture of traces in great detail. However, in carbonate-in-carbonate cases, further methodological efforts are needed to artificially impregnate parts of a sample to create sufficient contrast.

Apart from the results highlighted above, several new research questions arose during the study that will require additional material to be collected and analysed using appropriate techniques. For instance, bioerosional traces and symbionts on bryozoans and stromatoporoids, bioerosional traces made by bryozoans, micro- and macrobioerosional traces on hardgrounds, currently undescribed peeling traces and bite marks on brachiopods, and the undescribed *Conichnus* material require further taxonomic efforts. A redescription of the type of material for the most abundant bioerosional ichnogenera *Trypanites* and the problematic *Palaeosabella* would notably benefit from modern methods.

The current study showed that a re-description of several old collections and type specimens is vital for creating a stable and justified ichnotaxonomic framework. For instance, the historical collections of Eichwald (1854), and Mayer (1952, 1955), and the type material of *Cyclopuncta* must be addressed. Mapping the occurrence of common bioerosional trace *Trypanites* may provide new data on the development of bioerosion and the *Trypanites* tracemaker. Further research of Estonian bioerosional trace fossils would bring up new ichnogenera and provide a more thorough understanding of the Ordovician Bioerosional Revolution and its roots.

A systematic ichnological characterisation of different lithological units in Estonia and neighbouring areas is also needed in the future. This would introduce new data on both temporal and spatial occurrences of trace fossils in shallow-marine carbonates and has the potential to more thoroughly characterise the environmental conditions, bathymetry and facies development within the early Palaeozoic Baltic basin.

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## **Abstract**

### **Ordovician and Silurian trace fossils of Estonia**

Trace fossils, or ichnofossils, are structures resulting from various activities of organisms modifying the substrate, and often constitute the only evidence of the occurrence, diversity and behaviour of extinct taxa that rarely preserve as body fossils. Trace fossils and their assemblages are useful tools in sedimentology and palaeoenvironmental studies reflecting substrate properties, nutrient availability, oxygenation, sedimentation rates and current energy.

Trace fossils are better preserved and studied in siliciclastic marine sediments. Shallow-water carbonate settings, especially those of the Palaeozoic age, are less well known worldwide. This has resulted a global knowledge bias that limits our understanding of the evolution and distribution of trace-making organisms both in time and space. The Ordovician–Silurian succession of Estonia represents an excellent archive of carbonate platform settings of the Baltic palaeobasin, which thoroughly characterizes shelly faunas and environments. However, trace fossils have remained very poorly understood in the region. This doctoral thesis is focused on filling this knowledge gap by documenting the taxonomic composition and distribution patterns of carbonate facies trace fossils in Estonia. This contribution would provide new insights into the ecology and diversification history of marine communities in the region as well as globally, and through the two major events in Earth history – the Great Ordovician Biodiversification Event and the end-Ordovician Mass Extinction.

Most of the data for this work come from the pre-existing palaeontological collections deposited in Estonia; however, complementary material was obtained from outcrops and drill cores at selected stratigraphic intervals. The resulting material, containing nearly 4000 specimens, was systematically studied, identified and arranged into categories of architectural designs. In addition to conventional study methods, X-ray computed tomography was applied to more thoroughly understand the 3D architecture of traces hidden in the solid rock matrix. The resulting occurrence-level ichnofossil database, complete with images and references, is available in the Estonian geocollections portal (<https://geocollections.info>), and forms the basis for analysing the distribution and diversity patterns of trace fossils in Estonia.

The results show that the Middle Ordovician to Silurian shallow marine carbonate sequence of Estonia contains a diverse association of trace fossils, composed of no less than 38 soft sediment ichnogenera, 15 bioerosion ichnogenera, and various other biogenic structures. This greatly increased the knowledge on trace fossils of the region, as only 15 ichnogenera in total were identified prior to this work.

The taxonomic composition of trace fossil associations appeared to be similar to those reported previously from neighbouring areas. The distribution of trace fossils broadly reflects the geological succession of Estonia, characterised by relatively stable conditions of sedimentation during the Middle Ordovician and a differentiated tropical basin in the Upper Ordovician and Silurian. The diversity of bioerosional macroborers is correlated with the development of different organisms possessing calcitic skeletons. The rapid diversification of bioerosional traces in the Ordovician deposits of Baltoscandia was a coincidence of several regional and global factors, including the warming climate on Baltica, stability in depositional environments and the sea level, an availability of nutrients and a growing phytoplankton abundance; calcitic sea geochemistry also was a contributing factor, including the increasing oxygen levels.

Several new ichnotaxa were discovered for the Baltica palaeocontinent during the study, such as *Helicodromites*, *Tisoa*, *Petroxestes*, *Rogerella*, *Lumbricaria*, *Coprulus*, and *Tubularina*; these discoveries provide new insights into the palaeobiogeographic distribution of the respective tracemakers. Additionally, some of the globally youngest and oldest discoveries were reported, including the youngest known specimen of *Treptichnus pedum*, and the oldest observations of *Osprioneides*, *Sanctum*, *Petroxestes*, *Rogerella*, *Lumbricaria*, and *Tubularina* worldwide. These and other data suggest that the Baltica palaeocontinent might have been a key region in the evolution of ichnofossil communities, and for bioerosional tracemakers in particular.

The study denotes the need for continuing ichnofossil research in the region to obtain a more complete picture of the distribution of trace fossils in individual lithostratigraphic units. Moreover, a redescription of poorly characterized type material of several widespread ichnotaxa is required in the future, using up-to-date techniques such as the X-ray CT.

## Lühikokkuvõte

### Ordoviitsiumi ja Siluri ajastu jäljekivistised Eestis

Jäljekivistised ehk ihnofossiilid on erinevate organismide elutegevuse tulemusel tekkinud settekivimite tekstuurid. Sageli on jäljekivistised ainsaks tõendiks väljasurnud organismidest ja nende eluviisist aidates seeläbi kirjeldada mineviku elurikkust ning selle arengut läbi geoloogilise aja. Ihnofossiile ja nende kooslusi kasutatakse laialdaselt sedimentoloogias ning paleokeskkonna uuringutes, tõendamaks vee liikumist, settimise kiirust, toitainete kättesaadavust, hapnikusisaldust jt parameetreid.

Jäljekivistised on paremini säilinud ja uuritud merelistes terrigeensetes setendites. Madalmerelise karbonaatse settekivimite jäljekivistised on märgatavalt vähem tähelepanu pälvinud, seda eriti Paleosoikumi osas. Seetõttu on senised arusaamad jäljekivistisi tekitanud organismide evolutsiooni ja leviku kohta nii ajas kui ruumis puudulikud ning globaalselt ühekülgised. Eesti Ordoviitsiumi–Siluri settekivimite läbilõige on esinduslik näide karbonaatse sedimentatsiooniga epikontinentaalsest merest. Baltoskandia paleobasseini elustik ja keskkonnamuutused on üldiselt hästi uuritud, kuid jäljekivistisi on Eestist kirjeldatud vähe ja nende levikumustreid ei ole varasemalt analüüsitud. Käesoleva doktoritöö eesmärgiks on seda lünka täita ning dokumenteerida karbonaatse madalmerelise jäljekivististe taksonoomilist koosseisu ja levikumustreid Eesti materjali alusel. See aitaks paremini mõista Baltoskandia ja kogu maailma madalmerelise fauna ökoloogiat ja selle arengut läbi murranguliste sündmuse Maa ajaloos (Ordoviitsiumi biomitmekestumise ja Ordoviitsiumilõpu massväljasuremine).

Doktoritöö alusmaterjal pärineb suuremas osas Eesti paleontoloogilistest kollektioonidest, kuid lisaks koguti täiendavaid andmeid valitud paljanditest ja puursüdamikest. Jäljekivististe kollektiooni, mis sisaldab kokku ligi 4000 eksemplari, uuriti süstemaatiliselt ning kivistised määrati ja süstematiseeriti nende morfoloogia järgi struktuuritüüpidesse. Lisaks tavapärastele uurimismeetoditele kasutati monoliitses kivimis olevate jälgede ruumilise ehituse selgitamiseks kompuutertomograafiat. Doktoritöö käigus koostati jäljekivististe andmebaas, mis sisaldab fotosid, levikuandmeid ja kirjandusviiteid ning on kättesaadav Eesti geokogude portaali kaudu (<https://geocollections.info>). Andmebaas oli aluseks jäljekivististe leviku, mitmekesisuse ja levikumustrite analüüsimisel.

Töö tulemused näitavad, et Eesti Kesk- ja Ülem-Ordoviitsiumi ning Siluri madalaveelised karbonaatkivimid sisaldavad mitmekesisest jäljekivististe kooslust, mis koosneb 38 bioturbatsioonilisest ja 15 bioerosioonilisest jäljekivististe perekonnast ning mitmetest identifitseerimata biogeensetest struktuuridest. Varasemaga võrreldes täienes Eesti jäljekivististe andmestik märgatavalt – eelnevalt oli teada vaid 15 perekonna esinemine ning nende hulgas 10 perekonna detailsem levik.

Eesti ala jäljekivististe kooslus sarnaneb üldjoontes naaberpiirkondade omale ja nende levik ning mitmekesisus jälgib Eesti geoloogilist ehitust: Kesk-Ordoviitsiumis valdasid stabiilsemad ning Ülem-Ordoviitsiumis ja Siluris mitmekesisusid settimistingimused. Töö tulemusena laiienes mitmete jäljekivististe perekondade paleogeograafiline levik. Näiteks kirjeldati Baltika paleokontinendilt esmakordselt perekondi *Helicodromites*, *Tisoa*, *Petroxestes*, *Rogerella*, *Lumbricaria*, *Coprulus* ja *Tubularina*. Samuti laiendati mitmete ihnotaksonite stratigraafilise leviku piire globaalselt, sh avastati noorim *Treptichnus pedum* ning vanimad *Osprioneides*, *Sanctum*, *Petroxestes*, *Rogerella*, *Lumbricaria* ja *Tubularina* leiud. Saadud tulemused viitavad, et Baltika paleokontinent oli

võtmetähtsusega regioon ihnofossiilide koosluste ning eriti bioerosiooniliste jäljekivististe mitmekesisuse arengus.

Bioerosioonsete jäljekivististe mitmekesisus Baltoskandia Ordoviitsiumis korreleerub organismide kaltsiitse skeleti arenguga ja on mitme regionaalselt ning globaalselt soodsa teguri kokkulangemise tulemus. Neist olulisimad on Baltika paleokontinendi soojenev kliima, settimiskeskkonna ja meretaseme stabiilsus, toitainete küllus ja fütoplanktoni kasvav arvukus ning „kaltsiitse mere“ geokeemia ja keskkonna suurenev hapnikusisaldus. Käesolev töö töö esile vajaduse jätkata ihnofossiilide uuringuid, et saada terviklikum pilt nende esinemisest litostratigraafilistes üksuste lõikes. Samuti on vajalik mitme laialt levinud ihnotaksoni tüüpmaterjali ümberkirjeldamine kasutades kaasaegseid meetodeid.

# Appendix

## Publication I

**Toom, U.**, Vinn, O., Hints, O., 2019. Ordovician and Silurian ichnofossils from carbonate facies in Estonia: A collection-based review. *Palaeoworld* 28(1-2), 123–144.  
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# Ordovician and Silurian ichnofossils from carbonate facies in Estonia: A collection-based review

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## Abstract

Trace fossils are common in the Ordovician and Silurian shallow marine carbonate succession of Estonia, with 45 ichnofossil genera and five bioclausturation structures identified, representing 31 categories of architectural designs and nine categories of ethological classification. Diverse soft sediment traces, bioerosional traces and bioclausturations occur both in the Ordovician and Silurian. Diversity of trace fossils is similarly high in the Late Ordovician and Silurian, but markedly lower in the Middle Ordovician. This could be explained by the fact that during the Late Ordovician, Baltica drifted to the subtropical climatic zone where ichnofauna is usually more diverse than in temperate climatic settings. In addition, the Great Ordovician Biodiversification reached its peak in the Late Ordovician for many groups of organisms, which further contributed to the increase in ichnodiversity. Distribution of trace fossils is also controlled by the type of sedimentation, so that the mixed carbonate-siliciclastic systems prevailing in the Late Ordovician and Silurian have higher ichnodiversity than the pure carbonate settings of Middle Ordovician age. Feeding and locomotion traces are relatively rare in the Ordovician and Silurian of Estonia with the exception of the feeding structure *Arachnostega*, which is formed inside of protective shells and therefore has abundant occurrences. Bioerosional trace fossils may be extremely common in places, with a large number of different genera in the Upper Ordovician, supporting the idea of the Ordovician Bioerosion Revolution.

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**Keywords:** Trace fossils; Shallow-marine carbonates; Ordovician; Silurian; Baltica; Baltoscandia

## 1. Introduction

Trace fossils (ichnofossils) record biological activity and are also useful for reconstructing past sedimentary environments. Study of burrows, trackways and borings has become a powerful tool that provides proxies to palaeoecology, sedimentology, sequence stratigraphy, biostratigraphy, evolutionary palaeoecology and palaeoclimatology (Buatois and Mángano, 2011). However, the knowledge of trace fossils from different time intervals and environments varies greatly. A relatively small number of ichnological studies are devoted to carbonate environments as compared to siliciclastic ones, and Palaeozoic shallow-marine carbonate settings are strongly underrepresented in ichnological literature (Knaust et al., 2012).

The Ordovician and Silurian strata of the Baltic region constitute an example of Palaeozoic shallow-marine carbonate basin for which few, if any, adequate modern analogues exist (Allison and Wells, 2006; Brady and Bowie, 2017). Such basins are generally characterised by low subsidence rates and an incomplete stratigraphic record, perhaps with only 1/10 of geological time being represented by deposits (Sloss, 1996). The conditions for preservation of biogenic traces in these settings are often limited (see discussion on carbonates ichnology in Ekdale and Bromley, 2003; Curran, 2007; Knaust et al., 2012; Mángano et al., 2016). In the classic Ordovician–Silurian outcrop area of Estonia the overall diversity of trace fossils has never been systematically collected, studied and summarised, even though many publications focusing on specific ichnotaxa exist (e.g., Vinn et al., 2014d, 2015b; Vinn and Toom, 2015b, 2016b, 2016c). However, in the course of palaeontological studies that started more than 150 years ago in Estonia, a large number of ichnofossils has been gathered and stored in the collections together with

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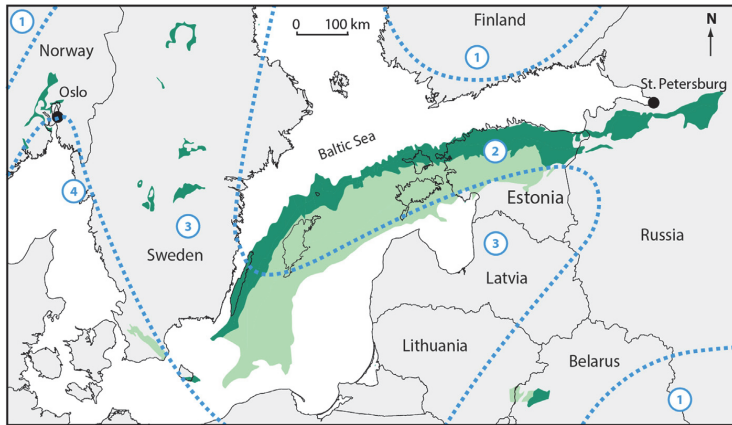


Fig. 1. Locality map showing the outcrop area of Ordovician and Silurian rocks in the Baltic region and schematic configuration of the Baltoscandian basin (after Männil, 1966 and Nestor and Einasto, 1997). 1 – main land areas, 2 – shallow-water Estonian shelf, 3 – deeper-water Livonian basin and Central Baltoscandian facies belt, 4 – deep shelf of the Scanian facies belt.

abundant shelly fossils. This material, mostly left unidentified thus far, could help understand the abundance and diversity of different trace fossils and bioclaustration structures throughout the Ordovician–Silurian carbonate succession and provide new insights into the development of biota as well as environments through the Great Ordovician Biodiversification and the Hirnantian mass extinction.

The main goal of this study is to provide an overview of carbonate facies ichnofossils deposited in Estonian palaeontological collections and summarise the trends in their taxonomic composition, abundance and diversity through the Ordovician–Silurian succession. Moreover, the study aims to compare the Estonian data with those of the neighbouring areas and discuss possible implications of the identified trends.

## 2. Geological background

During the Ordovician and Silurian periods, the study area was a part of a shallow sea, the Baltoscandian basin, which covered the western part of the Baltica craton and extended from Norway to the Volga area, and from the Fennoscandian mainland in the north to the Saratian mainland in the south (Fig. 1; Nestor and Einasto, 1997). The Baltica craton drifted from high southern latitudes to the equatorial area during the Ordovician and Silurian (Torsvik and Cocks, 2013), causing gradual change in climate and depositional conditions. In Estonia, carbonate sedimentation commenced in the end Floian (latest Early Ordovician) in a vast flat-bottomed, relatively cool epicontinental basin (Dronov and Rozhnov, 2007), and ended up in a restricted pericratonic sea in late Pridoli, superseded by the tectonic uplift of the Caledonian mountain belt in the west.

Generally, the area of Estonia and the Ordovician–Silurian outcrop area in particular (Fig. 1), was characterised by the relatively shallow-water part of the Baltoscandian basin, termed as the marginal facies belt or the Estonian shelf. Deeper-water settings were located in the south (the so-called Livonian basin) and

west (Central Baltoscandian and Scanian facies belts). Details on the architecture and development of the Baltoscandian basin are provided by e.g., Nestor and Einasto (1997, and references therein). In brief, the Middle Ordovician and lowermost Upper Ordovician are characterised by a highly condensed succession of cool water and temperate carbonates (Fig. 2). A major change in the sedimentation regime took place in late Sandbian to the earliest Katian, when the first reefs and tropical carbonate deposits appeared in the region and when the facies differentiation and sedimentation rates generally increased. The remaining part of the succession is characterised by warm-water carbonates and well-developed cyclicity at different scales (Nestor and Einasto, 1997).

The Ordovician–Silurian carbonate rocks in Estonia and elsewhere in the eastern Baltic region are flat-lying and characterised by virtually lacking thermal alteration as indicated by CAI (conodont colour alteration index) values ca. 1–1.5. The succession is rich in typical Palaeozoic shelly fauna (brachiopods, bryozoans, echinoderms, molluscs, corals, sponges, trilobites etc.), as well as microfossils and trace fossils. The maximum thickness of the Ordovician–Silurian succession is ca. 550 m in Estonia. The regional stratigraphic framework is historically based on regional stages (Fig. 2) and lithostratigraphy. Time-correlations within the region and with the global standard are mostly based on high-resolution biostratigraphy, notably conodont, chitinozoan and graptolite biozonations. In this paper, both regional stages (RS) as well as global series and stages are noted.

## 3. Material and methods

In Estonia, the first palaeontological studies were carried out more than 150 years ago. The long tradition of research is due to the large and representative bedrock exposures providing an excellent material for the study of Lower Palaeozoic rocks and well-preserved fossils. Fossil collections started to grow alongside with the first palaeontological studies and they

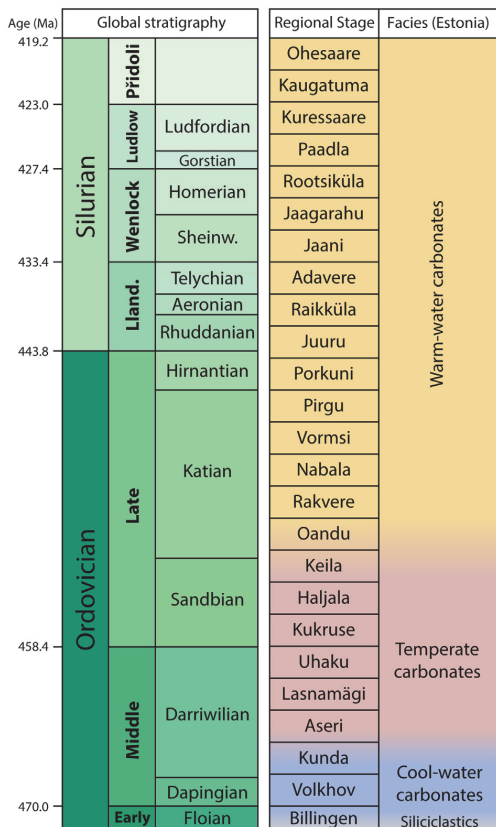


Fig. 2. Regional and international stratigraphy of the studied interval, showing transition from cool-water to warm-water carbonate deposits (compiled from various sources).

have actively been used by scientists since then. All Early Palaeozoic macrofossil groups are well represented in the collections, including trilobites, brachiopods, bryozoans, corals, molluscs, echinoderms. The total number of Ordovician and Silurian shelly macrofossils in Estonian collections is around 0.2 million, accompanied by more than 0.1 million rock samples from the same periods. The number of trace fossils deposited in the collections is considerably smaller — currently ca. 2700 specimens have been identified from the Ordovician–Silurian carbonate succession.

The selection of study methods was based on the rock type, the size of traces and takes into consideration the uniqueness of the material. After initial investigation using a stereo zoom microscope (magnifications usually  $\times 5$ – $25$ ), all material was photographed. Where necessary, the material was cut and polished to reveal diagnostic features and enhance the contrast between the trace and matrix. Cleaning with ultrasound equipment did not produce satisfactory results and was used only in combination with mechanical preparation in cases where the matrix was relatively soft. Serial sectioning was used for

large specimens in order to reveal three-dimensional structures. Destructive techniques were not used for studying rare specimens. X-ray computed tomography was tested, showing potential for future studies.

The studied material is deposited at the Department of Geology, Tallinn University of Technology (GIT), Natural History Museum, University of Tartu (TUG) and the Estonian Museum of Natural History (ELM). These three institutions make up the national geological collection. Data on individual trace fossil specimens (including images), localities and relevant literature are managed in the multi-institutional database of geocollections, which is accessible online at <http://geocollections.info>.

#### 4. Historical review of Baltoscandian trace fossils

Trace fossils in the Ordovician and Silurian carbonates of Estonia were not systematically collected and studied in the past. An abundance of different trace fossils is considered general knowledge, but there is only a single conference paper providing a very general overview of Ordovician and Silurian traces (Männil et al., 1984). The authors assumed that ichnofossil diversity in the Ordovician and Silurian is lower than in the Cambrian and Devonian of the region.

Kupffer (1874) suggested that the deeply pitted discontinuity surface from Middle Ordovician limestones of Estonia has biogenic origin. Middle Ordovician bioerosional traces have attracted the attention in Estonia, the *Trypanites* borings and “amphora-like borings” were described from Dapingian and Darrivilian deposits (Orviku, 1940, 1960). Männil (1966) described the globally widespread ichnogenus *Conichnus* and the less well known *Amphorichnus*.

Ordovician and Silurian trace fossils from the Oslo region, mostly trackways, were described in the last century (Seilacher and Meischner, 1964; Hanken and Størmer, 1975; Whitaker, 1979; Pollard and Walker, 1984; Stanistreet, 1989). Borings and microborings have been described from the Ordovician of Russia, Sweden, Norway and Estonia (Vishnyakov and Hecker, 1937; Hessland, 1949; Lindström, 1979; Opalinski and Harland, 1980; Nield, 1984; Pickerill and Harland, 1984; Podhalańska and Nölvak, 1995; Ekdale and Bromley, 2001a; Ekdale et al., 2002).

In the last decades, investigations of Ordovician and Silurian trace fossils of the Baltic region were reinitiated and diverse associations of trace fossils have been described in detail (Dam and Andreasen, 1990; Dronov et al., 2002; Cherns et al., 2006; Davies et al., 2006; Ershova et al., 2006; Knaust et al., 2012; Knaust and Dronov, 2013; Hanken et al., 2016). Recently, many soft sediment ichnotaxa such as *Skolithos*, *Conichnus*, *Amphorichnus*, *Arachnostega*, and *Zoophycos* have been reported from the Ordovician and Silurian of Estonia (Vinn and Wilson, 2013; Vinn et al., 2014d, 2015b; Vinn and Toom, 2015b). The most common bioerosional traces *Sanctum*, *Trypanites* and *Osprioneides*, have also received attention (Wyse Jackson and Key, 2007; Vinn and Wilson, 2010b; Vinn et al., 2014a; Vinn and Toom, 2016b, 2016c). Trace fossils from the erratic boulders of Baltic origin have been described by Stel (1976) and Chrzęstek and Pluta (2017b). Recently the number

of studies on carbonate hardgrounds and related bioerosional traces has increased (e.g., Vinn and Toom, 2015a, 2016b, 2016c; Vinn et al., 2015b, 2015c; Rozhnov, 2017).

## 5. Results

Systematics of trace fossils are complicated and several alternative classifications may be applied. For decades, the Seilacher's (1964) ethological classification has been used as the standard system. It has been discussed in a large number of studies (e.g., Frey and Seilacher, 1980; Ekdale, 1985; Bromley and Asgaard, 1993; de Gibert et al., 2004; MacEachern et al., 2012; Rindsberg, 2012; Vallon et al., 2016) and is still widely in use. Various criteria have been used to classify trace fossils such as preservation (Martinsson, 1965), overall morphology (Książkiewicz, 1977; Hecker, 1980; Uchman, 1995, 2007; Schlirf, 2000). Knaust (2012) proposed a morphological classification scheme based on significant morphological features of burrows, bioerosional traces, trackways, imprints and trails for the determination of the trace fossils. This system is applied in the present study.

Buatois and Mángano (2011, 2013, 2016) have discussed ichnodiversity, which refers to ichnotaxonomic richness, and ichnodisparity that is a measure of the variability of morphological plans in biogenic structures. Ichnodisparity may allow assessing major changes in trace fossil morphology that result from innovations in body plans and locomotory systems. Buatois et al. (2017) introduced the term “categories of architectural designs” (CADs), which could be used as a measure of ichnodisparity. They introduced 78 different CADs, 58 for bioturbation and 21 for bioerosion structures. We use these categories below to group and characterise Estonian carbonate facies ichnofossils. Representatives of each CAD are illustrated on Figs. 3–7 and all data are summarised on Tables 1 and 2.

### 5.1. Bioturbation structures

#### 5.1.1. Simple horizontal trails (Fig. 4E)

This CAD is represented by very simple horizontal trails. Buatois et al. (2017) included in this category the problematic feeding trace *Circulichnis* Vialov, 1971, which is a simple, smooth, circular to slightly ellipsoidal trace, common in deep marine environments (Buatois et al., 2001), but has also been reported from shallow-water marine carbonates (Fillon and Pickerill, 1984). In the Estonian collections, the shape of a single specimen resembles that of *Circulichnis*. The trace maker is discussed by Buatois et al. (1998).

#### 5.1.2. Chevronate trails (Fig. 3A, C)

This CAD includes horizontal trails with a chevronate morphology. In the Estonian collections this CAD is represented by *Protovirgularia* McCoy, 1850. It is a keel-like, horizontal bilobate locomotion trail, composed of chevronate ribs (Han and Pickerill, 1994b; Uchman, 1998). In the collection all studied finds come from the Silurian (Table 1) and belong to *P. pennatus*, which was first described as a plant by Eichwald (1854) and later redescribed by Uchman (1998). Fine morpho-

logical details including the shape and closely spaced chevrons (Fig. 3A, C) indicate de-watered substrate (Mángano et al., 1998; Carmona et al., 2010). Han and Pickerill (1994b), and Seilacher and Seilacher (1994) observed that *Protovirgularia* and *Lockeia* commonly occur together and represent different activities of the same trace maker. Estonian lower Silurian *protovirgularians* occur together with *L. cuncator* and the Upper Silurian ones with *L. siliquaria*. *Protovirgularia* is a common element of the *Cruziana* ichnofacies (Buatois and Mángano, 2011), representing typically shallow water environments. Trace makers are bivalves (Han and Pickerill, 1994b; Seilacher and Seilacher, 1994; Mángano et al., 1998; Luo and Shi, 2017; and references therein).

#### 5.1.3. Bilobate trails and paired grooves (Fig. 3F)

This CAD is made up of horizontal bilobate trails or parallel grooves, typically locomotion traces of deposit feeders, mostly from shallow tier structures. The best known representative of this category is *Cruziana* d'Orbigny, 1842, consisting of a straight or gently curved ploughed furrow, divided into two lobes. Ridges in the central part of the furrow usually have a herringbone shape, but details vary (Fortey and Seilacher, 1997; Gibb et al., 2009, 2017). *Cruziana* defines the *Cruziana* ichnofacies. In the Estonian succession *Cruziana* is very rare, described from the upper Silurian (Vinn, 2014; Vinn and Toom, 2016a). The trace maker and ethology of cruzianiforms are discussed in a large number of papers (e.g., Crimes, 1970; Seilacher, 1985; Hofmann et al., 2012; Rodríguez-Tovar et al., 2014).

#### 5.1.4. Trackways and scratch imprints (Fig. 3D, E)

Series of impressions left by individual locomotion appendages and scratch marks are included in this CAD, the trace makers being mostly arthropods (Buatois et al., 2017). In the Estonian collections two rare ichnogenera were identified: *Diplichnites* Dawson, 1873 and *Monomorphichnus* Crimes, 1970. The identification of *Diplichnites* was based strictly on trackway morphology having two parallel rows of similar tracks. The specimen (Fig. 3D) is very small, space between of rows is only 4 mm. Similar small trackways are reported from the Middle Ordovician Trenton Group of Canada (Fillon and Pickerill, 1984). From the Baltic region, trackways of e.g., *Diplichnites* have been reported previously from the upper Silurian sandstones of the Oslo Region, Norway (Davies et al., 2006). *Monomorphichnus* consists of clusters of elongate, straight striations (Crimes, 1970). The single Estonian specimen from the Upper Ordovician (Fig. 3E) shows more than two rows. *Diplichnites* and *Monomorphichnus* are common elements of the *Cruziana* ichnofacies. Systematics, ethology and trace makers are discussed in a large number of papers (e.g., Crimes, 1970; Crimes et al., 1977; Smith et al., 2003; Gibb et al., 2009, 2017; and references therein).

#### 5.1.5. Bilaterally symmetrical short, scratched impressions and burrows

Ichnotaxa included in this CAD are mostly resting traces made by arthropods. The most widespread representative of this category is *Rusophycus* Hall, 1852: a short (length to



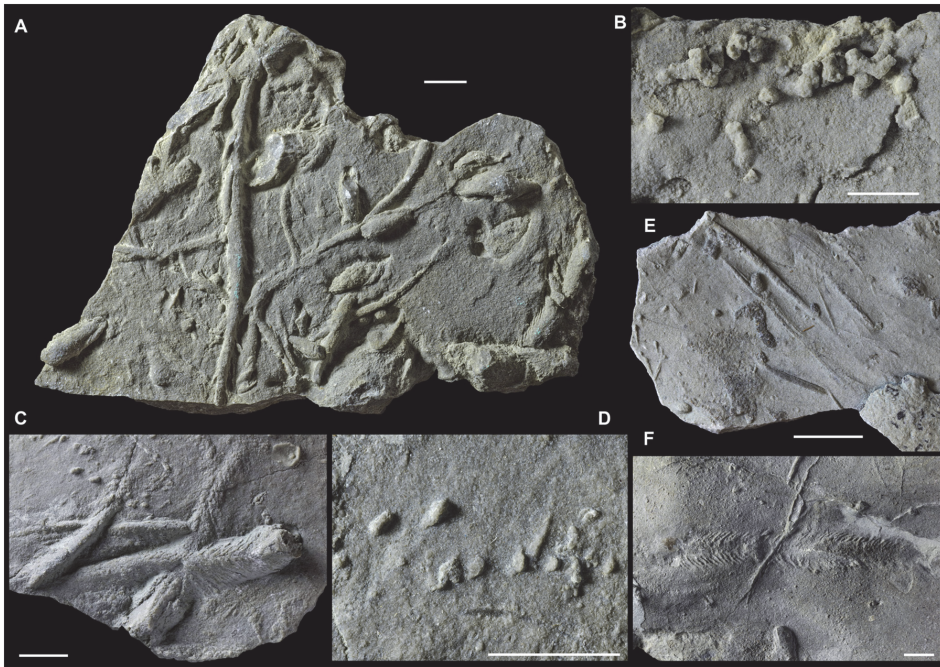


Fig. 3. Traces on bedding-planes, all preserved as positive hyporelief. (A) Composite traces *Protovirgularia pennatus-Lockeia siliquaria*, GIT 362-36, Kudjape ditch, Kuressaare RS, Ludlow. (B) *Lockeia cunctator*, GIT 379-222, Matsuküla, Raikküla RS, Llandoverly. (C) *Protovirgularia pennatus*, GIT 362-234-2, Rohuküla, Raikküla RS, Llandoverly. (D) *Diplichnites* isp., GIT 362-234-1, Rohuküla, Raikküla RS, Llandoverly. (E) *Monomorphichnus* isp., GIT 362-25, Saku quarry, Oandu RS, Katian. (F) *Cruziana plicata*, TUG 1670-1, Ohesaare cliff, Ohesaare RS, Pridoli. Scale bars: 1 cm.

Table 2

Summary of the different trace fossil groupings per global series. CAD – category of architectural design after Buatois et al. (2017).

| Ichnofossil category  | Middle Ordovician | Upper Ordovician | Llandoverly | Wenlock | Ludlow | Přidoli |
|-----------------------|-------------------|------------------|-------------|---------|--------|---------|
| Total ichnofossils    | 16                | 30               | 25          | 9       | 10     | 14      |
| Total CAD             | 12                | 24               | 19          | 8       | 8      | 11      |
| Bioturbation CAD      | 8                 | 14               | 15          | 2       | 6      | 9       |
| Bioerosion CAD        | 4                 | 10               | 4           | 6       | 2      | 2       |
| Fodinichnia           | 3                 | 9                | 10          | 1       | 3      | 4       |
| Fodinichnia/domichnia | 3                 | 2                | 1           | 2       | 0      | 2       |
| Domichnia             | 8                 | 9                | 5           | 3       | 1      | 4       |
| Cubichnia             | 0                 | 1                | 1           | 0       | 1      | 1       |
| Repichnia             | 0                 | 0                | 2           | 0       | 2      | 2       |
| Pasichnia             | 0                 | 2                | 1           | 0       | 0      | 0       |
| Praedichnia           | 0                 | 2                | 1           | 1       | 0      | 1       |
| Fixichnia             | 0                 | 1                | 0           | 0       | 0      | 0       |
| Impedichnia           | 2                 | 2                | 2           | 1       | 3      | 0       |
| Fugichnia             | 0                 | 1                | 1           | 0       | 0      | 0       |
| Microstructures       | 0                 | 1                | 1           | 1       | 0      | 0       |

width ratio less than 2:1) bilobate burrow (Keighley and Pickerill, 1996). In Estonian collections material only a single poorly preserved specimen is determined as *Rusophycus* (Vinn and Toom, 2016a). However, in neighbouring areas rare *Rusophycus* have been found in the Middle Ordovician (Dapingian) of the St. Petersburg region (Dronov et al., 2002; Ershova et al., 2006) and from the Oslo-Asker area (Stanistreet, 1989). *Rusophycus* occurs in softgrounds, mostly

in siliciclastic sediments, but has been found also in limestone successions. It is a common element of the *Cruziana* ichnofacies (Buatois and Mángano, 2011). Palaeozoic *Rusophycus* is mostly attributed to trilobites (Osgood, 1970; Seilacher, 1970; Gibb et al., 2010). Brandt (2008) and Tarhan et al. (2012) have provided comprehensive overviews of the *Rusophycus* trace makers.

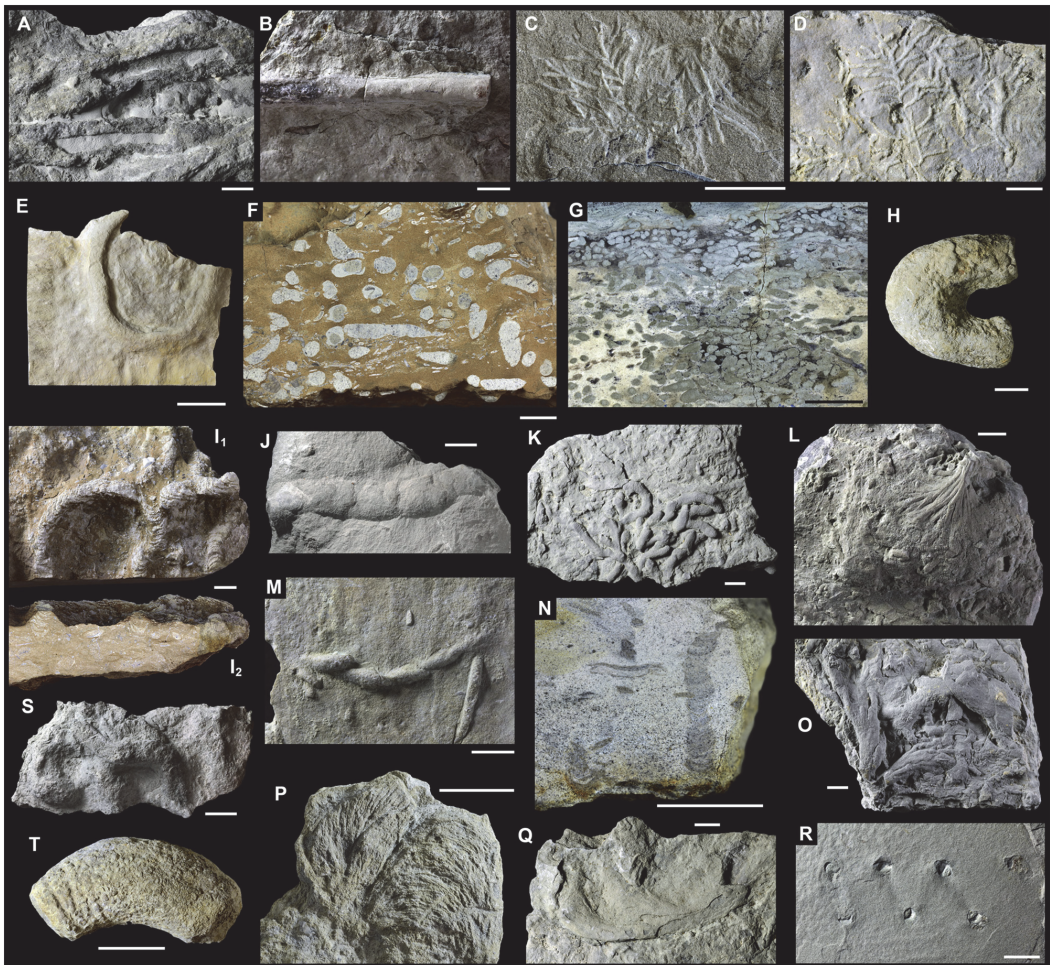


Fig. 4. Horizontal traces. (A) *Palaeophycus herberti*, epirelief, GIT 403-79, Ohesaare cliff, Ohesaare RS, Põidoli. (B) *Palaeophycus tubularis*, positive epirelief, GIT 362-544, Saxby shore, Vormsi RS, Katian. (C) *Chondrites intricatus*, negative epirelief, GIT 362-137, Ohesaare cliff, Ohesaare RS, Põidoli. (D) *Chondrites* cf. *patulus*, epichnal view?, GIT 379-224-1, Pullapää, Raikküla RS, Llandovery. (E) *Circularichnis*? isp., positive epirelief, GIT 362-257, Pirgu village, Juuru RS, Llandovery. (F) *Planolites montanus* in oil shale, vertical section, GIT 398-60, Tammiku mine, Kukruse RS, Sandbian. (G) *Planolites montanus* in bentonite, vertical section, GIT 340-302-1, Valgu trench outcrops, Adavere RS, Llandovery. (H) *Furculosus*? isp., full relief, GIT 362-154, Võiva outcrop, Adavere RS, Llandovery. (I1, I2) *Taenidium* isp. in oil shale, epichnal view (I1) and vertical section (I2), GIT 343-200, Põhja-Kiviõli opencast mine, Kukruse RS, Sandbian. (J) *Torrowangea*? isp., positive epirelief, GIT 362-122, Ohesaare cliff, Ohesaare RS, Põidoli. (K) *Phycodes* cf. *palmatus*, full relief epichnal view, GIT 362-136, Lubja quarry, Raikküla RS, Llandovery. (L) *Phycodes reniforme*, full relief epichnal view, GIT 362-13-1, Saku quarry, Oandu RS, Katian. (M) *Treptichnus pedom*, positive hyporelief, GIT 362-232-1, Rohuküla, Raikküla RS, Llandovery. (N) *Teichichnus rectus*, full relief in Osmundsberg bentonite, GIT 340-303-1, Valgu outcrops, Adavere RS, Llandovery. (O) *Halopoa imbricata*, positive epirelief, GIT 362-38, Saku quarry, Oandu RS, Katian. (P) *Zoophycos* isp., epirelief, GIT 362-45, Kaugatuma-Lõo coast, Kaugatuma RS, Põidoli. (Q) *Rhizocorallium* isp., epirelief, GIT 362-135, Anelma quarry, Jaagarahu RS, Wenlock. (R) *Helicodromites* isp., epirelief, GIT 362-11, Ohesaare cliff, Ohesaare RS, Põidoli. (S) Large burrow, positive epirelief, GIT 362-630, Paldiski, Volkhov RS, Dapingian. (T) Large burrow, full relief, GIT 398-519, Valgu outcrops, Adavere RS, Llandovery. Scale bars: 1 cm for (A–D), (F–O), (Q, R); 5 cm for (E), (P), (S), (T).

#### 5.1.6. Passively filled horizontal burrows (Fig. 4A, B)

This CAD includes simple horizontal burrows with passive infill. Worldwide abundant *Palaeophycus* Hall, 1847 is the most common representative of this category. This ichnogenus is a simple, lined, horizontal burrow (Pemberton and Fery, 1982; Fillon and Pickerill, 1990), with infill being similar to the host rock. The linings, produced by the consolidation of the burrow

wall by mucus (Christopher et al., 1994) are the most common characteristic used to define and identify individual ichnospecies (Buckman, 1995). From the Estonian collections three different species were determined. The thin-walled *P. tubularis* was the most common, the thick-walled *P. herberti* and *P. striatus* with characteristic parallel striae, are represented by few finds only. The collection material (Table 1) obviously underestimates the

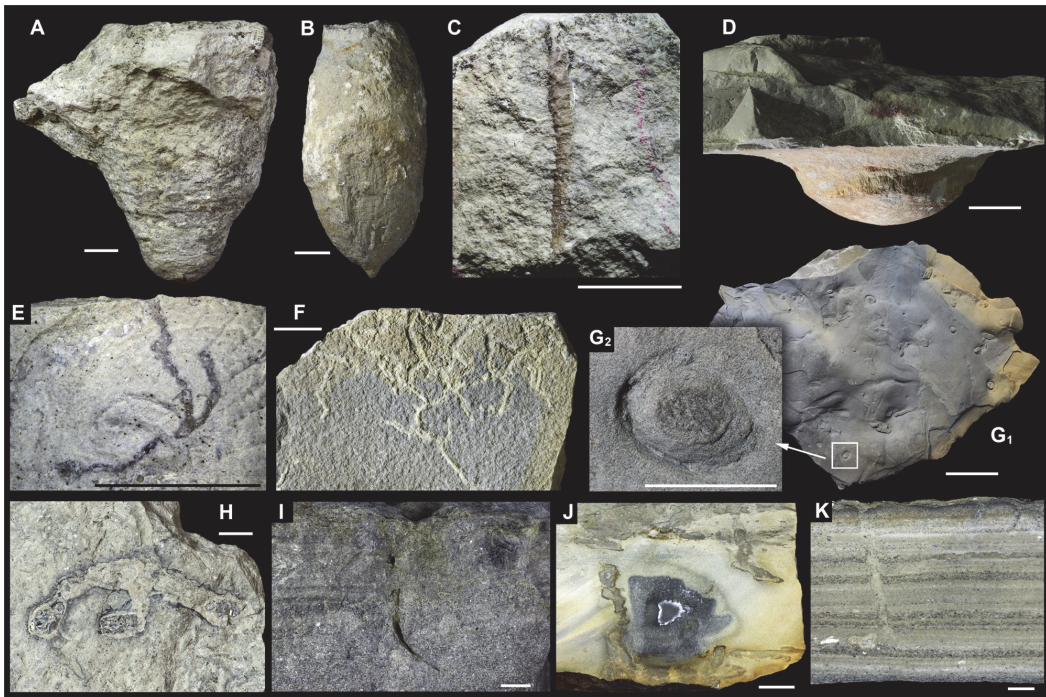


Fig. 5. Vertical and network traces. (A) *Conichnus conicus*, full relief in lateral view, GIT 107-4, holotype, Pääsküla, Keila RS, Katian. (B) *Amphorichnus papillatus*, full relief in lateral view, GIT 107-1, holotype, Anija, Haljala RS, Sandbian. (C) *Oikobesalon coriaceum*, full relief in lateral view, GIT 697-16-1, Osmussaar, Uhaku RS, Darrivilian. (D) *Bergaueria* isp., positive hyporelief in lateral view, GIT 362-273, Neitla quarry, Juuru RS, Llandovery. (E) *Arachnostega gastrochaenae* on brachiopod *Orthisocrania* sp., internal mold, GIT 362-657-1, Peetri hillock, Haljala RS, Sandbian. (F) *Multina?* isp., GIT 362-233, Rohuküla, Raikküla RS, Llandovery. (G1, G2) *Rosselia socialis*, top view from slab (G1) and close up (G2), GIT 362-20, Saku quarry, Oandu RS, Katian. (H) *Thalassinoides bacae*, top view, GIT 697-568, Osmussaar, Lasnamäe RS, Darrivilian. (I) *Arenicolites* isp., lateral view, GIT 362-560, Kaugatuma-Lõo coast, Kaugatuma RS, Pridoli. (J) Escape traces in bentonite, vertical section, GIT 340-295-2, Valgu trench outcrops, Adavere RS, Llandovery. (K) Escape traces, lateral view, GIT 362-583-1, Saku quarry, Oandu RS, Katian. Scale bars: 1 cm for (A–F), (G1), (H–K); 5 cm for (G2).

real occurrence of *Palaeophycus* in Estonian sediments. *Palaeophycus* occurs in siliciclastic and carbonate sediments, mainly in soft, but also in firm substrates (Knaust, 2017). In the marine realm *Palaeophycus* belongs mainly to the *Cruziana* ichnofacies, but also to various other ichnofacies. *Palaeophycus* is commonly interpreted as a dwelling structure of vermiform animals (e.g., Pemberton and Frey, 1982; Jensen, 1997; Knaust, 2017).

#### 5.1.7. Simple actively filled (massive) horizontal to oblique structures (Fig. 4F–H, J)

This CAD includes horizontal structures with homogeneous infill that is different from the host rock. From the studied material three ichnogenera were determined: the globally abundant *Planolites* Nicholson, 1873, the rare *Furculosus?* Roniewicz and Pieńkowski, 1977 and *Torrowangea?* Webby, 1970. *Planolites* is a feeding structure with a long stratigraphic range, produced by organisms that actively fill their burrows (Pemberton and Frey, 1982; Keighley and Pickerill, 1995). Taxonomy is based on the size, curvature and wall characteristic of the burrow. In the Estonian collections two most common ichnospecies are *P. montanus* (Fig. 4F, G) with a tortuous course, horizontal and incline

segments and more penetrative nature (Hofmann et al., 2012; Shahkarami et al., 2017), and horizontal, straight to slightly curved *P. beverleyensis*. *Planolites* is a characteristic component of softgrounds, occurring in both siliciclastic and carbonate sediments. It is most common in the *Cruziana* ichnofacies (Knaust, 2017), but has also been found in almost every depositional environment (Pemberton and Frey, 1982). Roniewicz and Pieńkowski (1977) described *Furculosus* (Fig. 4H) as cylindrical burrows-forming tight fork-line loops with parallel endings from flysch sediments of Poland. Fillon and Pickerill (1984) have reported these traces also from the Ordovician carbonate sediments of eastern Canada. The Estonian collections contain loop-like burrows resembling that of *Furculosus* occurrences within *Conichnus-Teichichnus* association (Table 1). Ethology of *Furculosus* is discussed in Pieńkowski and Westwalewicz-Mogilska (1986). *Torrowangea* is a structure that displays spaced constrictions suggestive of peristalsis and having an infill that contracts with the host rock matrix. This trace has been interpreted as a feeding burrow of a worm-like organism, common in sandstones but also occurring in limestones (Narbonne and Aitken, 1990). In the Estonian collections, the





Fig. 6. Bioerosional traces on hardgrounds and organic substrates. (A1, A2) *Trypanites wisei*, top view (A1) and vertical section (A2), GIT 381-595, Väike-Pakri Island, Volkhov RS, Dapingian. (B1, B2) Hardground with strong pyritic impregnation, *Trypanites* isp. and possibly microbially induced cracks, top view (B1) and vertical section (B2), GIT 362-587, Äiamaa borehole, Oandu RS, Katian. (C) *Sulcichnus* isp. on stromatoporoid, top view, GIT 362-551-1, Saxby shore, Vormsi RS, Katian. (D) *Osprioneides kampto* in stromatoporoid, top view, GIT 398-145, Panga cliff, Jaani RS, Wenlock. (E) *Trypanites solitarius* in weathered gonambonitid brachiopod, GIT 543-87-1, Vasalemma Partek Nordkalk quarry, Keila RS, Katian. (F) Peeling structure on stromatoporoid, top view, GIT 362-505-1, Reinu quarry, Juuru RS, Llandoverly. (G) *Trypanites wisei* in trepostome bryozoan, vertical section, TUG 1617-21-3, Kohla-Nõmme opencast, Kukruse RS, Sandbian. (H) *Trypanites wisei* and microborings on stromatoporoid, top view, GIT 362-554, Hosholm shore, Pirgu RS, Katian. (I, J) Macrobioerosional grooves on trepostome bryozoa, bottom view (I) and top view (J), GIT 720-5, Aluveru quarry, Haljala RS, Sandbian. (K) *Osprioneides kampto* (large borings) in trepostome bryozoa, top view, GIT 665-18, Hirmuse creek outcrop, Haljala RS, Sandbian. (L) *Sanctum* isp. in trepostome bryozoan, vertical section, GIT 720-788-2, Aluveru quarry, Haljala RS, Sandbian. (M) *Trypanites* isp. and various microborings on stromatoporoid, vertical section, GIT 362-266, Paluktila quarry, Vormsi RS, Katian. (N) *Balanoglossites* isp., horizontal section, GIT 398-668, Tagavere quarry, Jaagarahu RS, Wenlock. (O) *Oichnus* isp. on brachiopod *Plaesiomys saxbyana*, GIT 362-565-1, Saxby shore, Vormsi RS, Katian. (P) *Rogerella* isp. on heliolitid coral, TUG 3-535-2, Moe, Nabala RS, Katian. (Q) *Gastrochaenolites oelandicus*, vertical section, GIT 362-538, Uuga cliff, Volkhov RS, Dapingian. Scale bars: 5 mm for (E); 1 cm for (A–C), (F–H), (K–M), (O), (P); 5 cm for (D), (I), (J), (N), (Q).

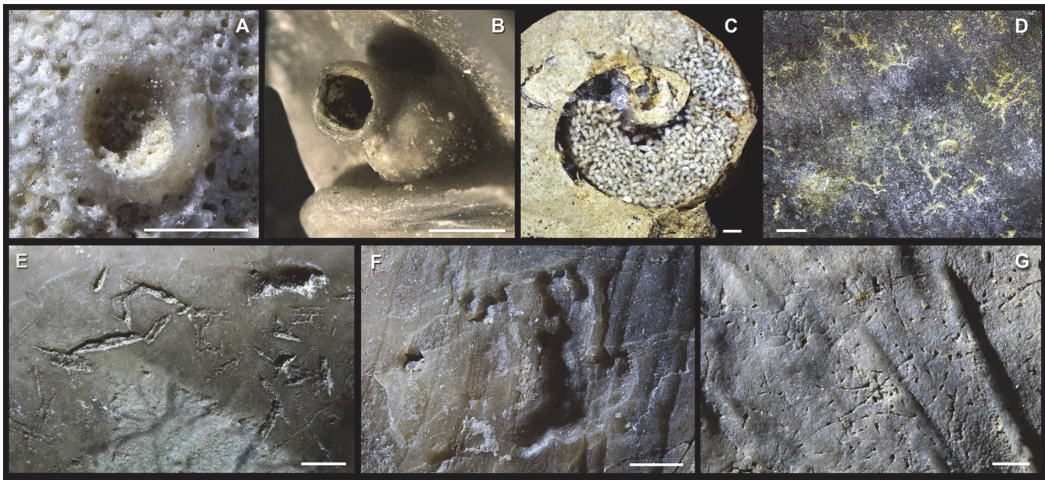


Fig. 7. Various microstructures: bioconstructions, coprolites and bioerosional structures. (A) *Anoigmaichnus* sp. on trepostome bryozoan, top view, GIT 720-754-1, Aluvere quarry, Haljala RS, Sandbian. (B) *Burrinjuckia clitambonitoflita*, inside of brachiopod *Clitambonites squamatus* shell, GIT 343-236-1, Estonia, Kukruse RS, Sandbian. (C) *Tomaculum?* isp. in gastropod mould, GIT 720-1, Aluvere quarry, Haljala RS, Sandbian. (D) Dendrinids on clitambonitid brachiopod shell, GIT 543-149-5, Pääsküla, Keila RS, Katian. (E) *Gnathichnus?* isp. on large brachiopod *Porambonites* sp., GIT 720-803-12, Aluvere quarry, Haljala RS, Sandbian. (F) Peeling structure on large brachiopod *Porambonites* sp., GIT 619-48-10, Oandu, Oandu RS, Katian. (G) *Pinaceocladichnus onubensis* on clitambonitid brachiopod shell, TUG 1750-3-3, Kohtla, Kukruse RS, Sandbian. Scale bars: 1 mm.

shape of a single specimen from the Silurian resembles that of *Torrowangea*.

#### 5.1.8. Simple actively filled (meniscate) horizontal to oblique structures (Fig. 4II, I2)

This CAD is represented by horizontal burrows, where the infill contrasts with the host rock and shows a meniscate structure. From this category the feeding structure *Taenidium* Heer, 1877 has been identified, which comprises of unlined, variably oriented, meniscate burrows (D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994; Díez-Canseco et al., 2016). Ichnospecies are differentiated by the style of meniscate backfill. Meniscate traces are typical of sediments periodically exposed to air and submerged (Frey and Pemberton, 1987). The Estonian material (Table 1) is not associated with structures indicative of subaerial exposure (raindrop imprints, desiccation cracks) and are thus not representative of the *Scoyenia* ichnofacies. *Taenidium* occurs also in shallow- and deep-marine deposits (D'Alessandro and Bromley, 1987; Uchman, 2007) and has been reported from the *Cruziana* ichnofacies (Bromley et al., 1999; Knaust, 2017). The ichnogenus is known from the upper Silurian of the Oslo Region (Dam and Andreasen, 1990; Davies et al., 2006). Possible trace makers of the marine *Taenidium* are arthropods or worm-like organisms (Bromley et al., 1999; Uchman, 2007; Rodríguez-Tovar et al., 2016; Knaust, 2017).

#### 5.1.9. Horizontal branching burrow systems (Fig. 5E, F)

This CAD include branching burrow systems that are confined to two-dimensional expression. In the Estonian collections two ichnogenera are known: *Arachnostega* Bertling, 1992 and *Multina?* Orłowski, 1968. *Arachnostega* is an irregular net-like

burrow system in the sediment fill of shells (Bertling, 1992). In Estonia, *A. gastrochaenae* is widespread in Ordovician (Table 1) and associated with different groups of shallow-marine molluscs (Vinn et al., 2014d). Examination of trilobite and brachiopod collections revealed that *A. gastrochaenae* is rather common on the surfaces of internal moulds, preserved as calcite-filled endoreliefs (Fig. 5E). It is interpreted mostly as feeding structure (e.g., Bertling, 1992; Fürsich et al., 1994; Chrzastek and Pluta, 2017b). *Multina* Orłowski, 1968 was erected from shallow-marine upper Cambrian sediments and redescribed by Orłowski and Żylińska (1996). It is a feeding structure consisting of irregularly meandering and winding horizontal burrows that display overlap and bifurcation forming irregular polygons (Buatois and Mángano, 2012). Lower Ordovician *Multina* occurs in deep-marine settings (Buatois et al., 2009). *Multina?* is rare in the Estonian collections (Table 1).

#### 5.1.10. Horizontal burrows with horizontal to vertical branches (Fig. 4K–M)

This CAD includes burrow systems that typically have a horizontal axis, but tend to branch out from it and thus result in a 3D system. In the Estonian collections, two well-known ichnogenera were found: *Phycodes* Richter, 1850 and *Treptichnus* Miller, 1889. The former is a horizontal branching burrow developed from a single proximal tunnel; individual ichnospecies are distinguished by the nature, style, disposition and degree of burrowing from the proximal structure (Han and Pickerill, 1994a). *Phycodes* is quite a common structure in the Estonian collection (Table 1), with five different ichnospecies identified: *P. curvipalmatum*, *P. cf. palmatum*, *P. rarus*, *P. reniforme* and *P. templus*. Elsewhere in the Baltic region *Phycodes* has been

reported from the Middle Ordovician of the St. Petersburg region (Dronov and Mikuláš, 2010) as well as Norway (Stanistreet, 1989; Hanken et al., 2016). *Phycodes* is a constituent of the *Cruziana* ichnofacies and interpreted as a feeding trace (Osgood, 1970). The taxonomic position of *Phycodes pedum* has been under discussion for many years. Geyer and Uchman (1995) favoured placement of *P. pedum* in *Trichophycus*, while Jensen (1997) placed *P. pedum* in *Teptichnus*. This ichnospecies has attracted great interest as it is important to the definition of the Precambrian/Cambrian boundary (Buatois, 2017). *T. pedum* is common in older Palaeozoic sediments, but certainly also extended into the Ordovician (Seilacher et al., 2005). *T. pedum* has been reported from the Upper Ordovician of the Oslo-Asker region (Stanistreet, 1989). The Estonian specimen originates from the lower Silurian Raikküla RS (Table 1; Fig. 4M) and may thus be the youngest representative of *T. pedum* worldwide. The trace maker, ethology and environments of *Teptichnus* have been discussed by several authors (Buatois, 2017; and references therein).

#### 5.1.11. Horizontal burrows with simple vertically oriented spreiten (Fig. 4N, O)

This CAD include horizontal burrows with spreiten oriented perpendicular to the bedding plane. From the Estonian collections two ichnogenes were identified: *Halopoa* Torell, 1870 and *Teichichnus* Seilacher, 1955. *Halopoa* is a horizontal trace covered with longitudinal ridges (Jensen, 1997; Uchman, 1998; Wetzel and Uchman, 2001). It is rarely found in Estonia (Table 1). Widely accepted as a feeding structure, it occurs in both shallow and deep marine environments (Jensen, 1997; Uchman, 1998; Mángano et al., 2002). *Teichichnus* is a horizontal wall-like feeding burrow with vertically retrusive spreiten (Martinsson, 1965), recently thoroughly revised with comprehensive overview by Knaust (2018). It is typical of siliciclastic settings and rare in carbonates (Pickerill and Forbes, 1979; Knaust, 2017). From the Estonian collections, *Teichichnus* was determined in two stratigraphic levels (Table 1). Ordovician burrows are large, and the single Silurian specimen related to a bentonite bed is small (Fig. 4N). This kind of small *Teichichnus* is described from restricted epicontinental sea sediments (de Gibert and Ekdale, 2002). Elsewhere in Baltoscandia, *Teichichnus* is reported from the Darrivilian of the St. Petersburg region (Dronov and Mikuláš, 2010) and from the Upper Ordovician of the Oslo-Asker region (Stanistreet, 1989). It is commonly interpreted as a feeding structure of worm-like animals (e.g., annelids) and arthropods (Seilacher, 1955; Tarhan et al., 2012; Knaust, 2017) or a dwelling trace (Knaust, 2018).

#### 5.1.12. Horizontal helicoidal burrows (Fig. 4R)

This CAD includes helicoidal burrows oriented parallel to the bedding. From Estonian collections (Table 1) only one corkscrew-shaped burrow was found that can be attributed to *Helicodromites* Berger, 1957. This ichnogenes is rare in lower Palaeozoic sediments, however Narbonne (1984) reported it from the upper Silurian carbonates of the Canadian Arctic. The

occurrence, ethology and trace maker are further discussed by Poschmann (2015).

#### 5.1.13. Burrows with horizontal spreiten (Fig. 4Q)

This CAD includes causative burrows that move horizontally to generate feeding spreiten. From the studied collections only two poorly preserved specimens can be assigned to this group (Table 1). They show U-shaped spreiten in which a marginal tube encloses an actively reworked area and represents the ichnogenes *Rhizocorallium* Zenker, 1836. Such traces are known from both siliciclastic and carbonate settings and occur in soft and firm substrates (Knaust, 2017). Palaeozoic *Rhizocorallium* is a common element of the *Cruziana* ichnofacies (Knaust, 2013). It is generally accepted that marine *Rhizocorallium* is a polychaete feeding trace (see Knaust, 2013, 2017; and Zhang et al., 2016 for discussion).

#### 5.1.14. Burrows with helicoidal spreiten (Fig. 4P)

Structures forming a J- or U-shaped causative burrow, which display helicoidal spreiten include the well-known feeding structure *Zoophycos* Massalongo, 1855. During the Cambrian–Devonian, *Zoophycos* predominantly occurred in the shallow-tier as thin planar spreiten (Gaillard and Racheboeuf, 2006). Estonian specimens of *Zoophycos* are planar, cock-tail shaped, occurring in Silurian shallow-water deposits (Vinn and Toom, 2015b) and are rather frequent in the upper Silurian (Table 1). This enigmatic trace fossil has been discussed in a large number of papers to determine its producer and environmental settings, for further details see Kotake (2014) and Zhang et al. (2015a, 2015b).

#### 5.1.15. Isolated and serial oval to almond-shaped burrows (Fig. 3A, B)

This CAD includes the almond-shaped burrow *Lockeia* James, 1879, common in marine environments (Uchman et al., 2004). *Lockeia* is frequent in the Silurian of Estonia (Table 1), represented by two different ichnospecies, the discrete *L. siliquaria* (Fig. 3A; see Mángano et al., 2002) and the clusters of *L. cunctator* (Fig. 3B; see Schlirf et al., 2001 and Paranjape et al., 2013). Bivalves are regarded as trace makers and the ethology is discussed by many authors (e.g., Seilacher and Seilacher, 1994; Mángano et al., 1998). *Lockeia* is a compound trace fossil with *Protovirgularia* (Ekdale and Bromley, 2001b).

#### 5.1.16. Vertical plug-shaped burrows (Fig. 5A, B, D)

This category includes conical and cylindrical burrows. Typical representatives of this category are *Amphorichnus* Männil, 1966, *Conichnus* Männil, 1966 and *Bergaueria* Prantl, 1945. It is by far the most numerous category in the Estonian collections, consisting of type material and more than a thousand specimens of *Amphorichnus* and *Conichnus* (Fig. 5A, B). *Bergaueria* is a vertical, shallow cylindrical trace common in siliciclastic deposits, but occurs also in carbonates (Alpert, 1973; Knaust, 2017) and has been interpreted as a dwelling or resting trace of sea anemones (Paczeńska, 2010). *Bergaueria* have been mostly reported from shallow-marine environments, but it also occurs in deep-marine deposits (Hofmann et al., 1994). *Bergaueria* is

reported from Middle Ordovician sediments of the St. Petersburg region (Ershova et al., 2006; Dronov and Mikuláš, 2010; Knaust et al., 2012), but not from Norway and is almost missing in Estonian collections (Table 1). In type area in Estonia *Conichnus* and *Amphorichnus* are constituents of the *Cruziana* ichnofacies. *Conichnus* is interpreted as a dwelling structure of sea anemones or similar organisms (Shinn, 1968; Pickerill, 1989; Buck and Goldring, 2003; Mikuláš and Dronov, 2005; Curran, 2007), or as an equilibrium structure associated with high sedimentation rates (e.g., Curran and Frey, 1977; Savrda, 2003).

#### 5.1.17. Vertical unbranched burrows (Fig. 5C)

Simple burrows oriented perpendicular to bedding are included in this CAD. From the Estonian collections two ichnogenera were determined: *Oikobesalon* Thomas and Smith, 1998, a vertical burrow with thin organic lining, and *Skolithos* Haldeman, 1840. *Oikobesalon* is described as a dwelling trace (Vinn and Toom, 2014) and it occurs in the Middle Ordovician (Table 1). *Skolithos* is a common trace fossil in the Palaeozoic, but from the Estonian succession it is only known from a single bed with abundant burrows (Vinn and Wilson, 2013). *Skolithos* is the nominal taxon for the *Skolithos* ichnofacies, occurring mostly in various shallow-marine settings and being an indicator of relatively high energy environments (Uchman et al., 2004). It is described as a dwelling structure, in the Palaeozoic, produced by various worms (Hallam and Swett, 1966; Alpert, 1974; Desjardins et al., 2010; Knaust, 2017).

#### 5.1.18. Vertical single U- and Y-shaped burrows (Figs. 5 I, 6 N)

This category contains vertical U- or Y-shaped burrows. Two feeding-dwelling ichnogenera were determined from the Estonian collections' material. *Arenicolites* Salter, 1857 is a simple vertical to subvertical U-shaped burrow with a passive fill (Bradshaw, 2010). From the Baltic region, *Arenicolites* has been described from the Middle Ordovician to upper Silurian (Dam and Andreasen, 1990; Mikuláš and Dronov, 2005; Davies et al., 2006; Hanken et al., 2016). Seemingly the collection specimens from Estonia do not reflect the full distribution of the taxon (Table 1). *Arenicolites* is characteristic of sandy (siliciclastic and carbonate) substrates typical of shallow marine settings, belonging to the *Skolithos* and *Glossifungites* ichnofacies (Crimes et al., 1977; Buatois and Mángano, 2011; Knaust et al., 2012). Trace makers for the Palaeozoic *Arenicolites* are polychaetes (Howard and Frey, 1984; Bradshaw, 2010). *Balanoglossites* Mägdefrau, 1932 (Fig. 6N) consists of branched galleries with several openings (Knaust, 2008) and simultaneously has a boring and burrowing character (Knaust and Dronov, 2013). These traces are common in the Palaeozoic rocks of Baltoscandia (Männil et al., 1984; Knaust and Dronov, 2013). Middle Ordovician (Dapingian) beds with abundant *Balanoglossites* ichnofabrics from the St. Petersburg region are also traceable in north-eastern Estonia (Knaust and Dronov, 2013). The collection material and building stones used in Tallinn show an abundant occurrence of *Balanoglossites* through the Middle Ordovician, especially in the Lasnamägi-Uhaku regional stages.

The Estonian *Balanoglossites* is mostly related to hardgrounds, but not only. In Table 1, *Balanoglossites* is included in both the bioerosional- and soft-sediment traces. Definitely, the abundant material needs more in-depth investigations. *Balanoglossites* occurs in shallow-marine carbonates, in firm- and hardgrounds and is characteristic of the *Glossifungites* and *Trypanites* ichnofacies (Knaust, 2008; Knaust et al., 2012). It is produced by eunicid polychaetes (Knaust, 2008; Knaust and Dronov, 2013).

#### 5.1.19. Burrows with shaft or bunch with downwards radiating probes (Fig. 4C, D)

This category includes regularly branching systems with a vertical burrow. From the Estonian collections the archetypal representative of the category *Chondrites* Sternberg, 1833 was determined. *Chondrites* has a wide range of morphologies, and its systematics is discussed in a large number of papers (e.g., Fu, 1991; Uchman, 1998, 2007; Uchman et al., 2012). It is a common trace fossil (Knaust, 2017), but not abundant in Estonia (Table 1) with only a few findings representing two different species: *C. intricatus* (Fig. 4C) and *C. cf. patulus* (Fig. 4D). Many papers demonstrate that “*Chondrites* animals” lived probably in dysaerobic conditions (Bromley and Ekdale, 1984; Kotake, 1991) which are common in deep-marine environments, but may also occur on the shelf and in nearshore restricted basins (Knaust, 2017). Most of the Estonian *Chondrites* specimens from the Silurian strata are large; only one specimen from Pridoli (Fig. 4C) is tiny as is characteristic of anoxic conditions (Gong and Droser, 2001). *Chondrites* is also reported from the St. Petersburg region (Dronov and Mikuláš, 2010) and is more common in Norway (Seilacher and Meischner, 1964; Spjeldnæs, 1989; Stanistreet, 1989; Hanken et al., 2016). *Chondrites* is a facies-crossing trace, mostly interpreted as a feeding structure. Its producer and ethology have received a lot of attention (e.g., Osgood, 1970; Mángano et al., 2002; Fernandez and Pazos, 2012; Knaust, 2017).

#### 5.1.20. Vertical concentrically filled burrows (Fig. 5G1, G2)

This CAD comprises of concentrically filled burrows oriented perpendicular to the bedding plane. The dwelling structure *Rosselia* Dahmer, 1937 represents this category. In the collections, a few well-preserved specimens were identified (Table 1). *Rosselia* is a common constituent of the *Cruziana* ichnofacies, mostly found in siliciclastic sediments, but occasionally occurring also in carbonates (Knaust, 2017). Polychaetes are the most likely producers of *Rosselia* (Uchman and Krenmayr, 1995; Buatois et al., 2016; Knaust, 2017; and references therein).

#### 5.1.21. Maze and boxwork burrows (Fig. 5H)

This CAD includes burrow systems displaying simultaneous branching. *Thalassinoides* Ehrenberg, 1944 is one of the most abundant ichnogenus of this category. It is a boxwork constituting a horizontal maze and vertical shafts, its branching is T- and Y-shaped, the burrow diameter is from a few millimeters to several centimeters (Frey and Howard, 1985; Knaust, 2017). Ichnospecies are distinguished on the basis of branching. *Thalassinoides* is common in the Baltic region (Stanistreet, 1989;

Dronov and Mikuláš, 2010; Hanken et al., 2016). Ekdale and Bromley (2003) described horizontal *T. bacae* as being with numerous short vertical shafts from Middle Ordovician (Dapingian) of Sweden. This kind of agrichnial traces is rare in the studied collections, but displayed in Estonian building stones. *Thalassinoides* occurs in a wide range of soft to firm substrates, being a common constituent of the *Cruziana* and *Glossifungites* ichnofacies in shallow marine carbonates (Knaust et al., 2012). It occurs abundantly in Ordovician marine limestones (Sheehan and Schiefelbein, 1984). Trace makers of the Palaeozoic *Thalassinoides* are trilobites or unidentified soft-bodied organisms (Ekdale, 1992; Myrow, 1995; Ekdale and Bromley, 2003; Cherns et al., 2006).

#### 5.1.22. Escape traces (Fig. 5J, K)

Escape traces (Fig. 5J, K) are structures produced in response to rapid sedimentation, when animals readjust their burrows to avoid burial. Typical escape structures are indicated by the vertical repetition of dwelling traces, commonly forming cone-in-cone structures (Buck and Goldring, 2003; Hofmann et al., 2012). Vertical escape burrows occur in several levels (Table 1) mostly associated with rapidly deposited bentonite layers.

#### 5.1.23. Structures with coprolites (Fig. 7C)

Bruthansová and Kraft (2003) described cylindrical pellets inside the shells of macrofossils, noticing that several of these specimens were associated with an *Arachnostega*-like ichnofossil. The Estonian collections contain Upper Ordovician gastropods (Fig. 7C) and brachiopods, which are partly filled with a tight concentration of small pellets (*Tomaculum*? in Table 1). Our material shows that the pellets may be the faeces of the enigmatic producers of *Arachnostega*, corroborating the observations from Bohemia. Bruthansová and Kraft (2003) considered that the shells were used as a domicile and were actively filled, not representing the real *Tomaculum* Groom, 1902 (after Eiserhardt et al., 2001). In this case, such pellets in shelly fossils may represent a new ichnogenus.

### 5.2. Bioerosion structures

#### 5.2.1. Cylindrical vertical to oblique borings (Fig. 6A1, A2, B1, B2, E, G, H)

This CAD consists of simple tubular borings with a circular cross section. One of the oldest macroborings *Trypanites* Mägdefrau, 1932 represents this category. The *Trypanites* borings have a circular cross-section throughout their length and the axes of the borings may be straight, curved or irregular. *Trypanites* is abundant in Estonia (Table 1) occurring both in Ordovician and Silurian hardgrounds as well as in bryozoans, brachiopods, stromatoporoids and corals. After Blissett and Pickerill (2007), two different ichnospecies of *Trypanites* were determined. *T. weisei* is more or less straight and vertical and *T. solitarius* is curved, with its course running close beneath the substrate surface. *Trypanites* occurs in hardgrounds with a pyritic impregnation, and samples bear several different sizes of borings (Fig. 6A1, A2, H), likely indicating the presence of different borers. The length and width ratio of the borings

was occasionally rather small, even so that its determination as *Trypanites* is questionable. *T. solitarius* is related to the large Upper Ordovician brachiopods (Fig. 6E). *Trypanites* (= *Vermiforichnus* Cameron, 1969) is common all over the region in the Ordovician and Silurian, related to hardgrounds, reefs and different shelly fossils (Vishnyakov and Hecker, 1937; Opalinski and Harland, 1980; Niels, 1984; Vinn, 2004; Mikuláš and Dronov, 2005; Hanken et al., 2016). *Trypanites* is the type taxon for the *Trypanites* ichnofacies, developed in fully lithified substrates, common throughout the Phanerozoic and produced by various trace makers (Bromley, 1994).

#### 5.2.2. Borings with elliptical to sub-rectangular cross sections (Fig. 6D, K)

This CAD includes *Osprioneides* Beuck and Wisshak in Beuck et al., 2008, the largest boring known from the Palaeozoic. This unbranched elongate boring with an oval cross section was first described from the Silurian of Sweden, where it occurs in stromatoporoids. These giant dwelling structures have been reported from (Table 1) stromatoporoids (Vinn and Wilson, 2010b) and bryozoans (Vinn et al., 2014a) in Estonia. The studied Estonian material shows the trend that *Osprioneides* is more common in the Upper Ordovician. The trace maker is a soft-bodied organism, likely a boring worm (for discussion see Beuck et al., 2008).

#### 5.2.3. Circular holes and pit-shaped borings (Fig. 6O)

This category includes simple circular holes and pits. In the Estonian collections this CAD is represented by *Oichnus* Bromley, 1981, a hole with a rounded outline, bored into calcareous substrates. *Oichnus* is rare, only with a few findings in brachiopods, echinoderms (Ausich et al., 2012) and trilobites (Chrzastek and Pluta, 2017a) (Table 1). For the systematics, ethology and trace maker see Wisshak et al. (2015), Breton et al. (2017), Donovan and Pickerill (2017).

#### 5.2.4. Pouch-shaped borings (Fig. 6I, J, P)

Borings in this CAD consist of pouch-shaped dwelling structures with a single elongated opening. In the Estonian collections, a few Upper Ordovician heliolitid corals bear *Rogerella* Saint-Seine, 1951 (Fig. 6P; Table 1). This kind of borings are uncommon in the lower Palaeozoic. Baird et al. (1990) described them from the Devonian and Wilson and Palmer (2006) noticed that there is undescribed material from the Katian of North America. Trace makers are barnacles (e.g., Seilacher, 1969; Baird et al., 1990; Donovan et al., 2014). *Petroxestes* Wilson and Palmer, 1988 consist of shallow elongate borings excavated into hardgrounds and bryozoans. The Estonian Upper Ordovician bryozoans bear similar borings (Fig. 6I, J).

#### 5.2.5. Clavate-shaped borings (Fig. 6L, Q)

This category includes club-shaped borings with narrow, circular openings. In Estonian collections it is represented by three different dwelling ichnogenera: *Gastrochaenolites* Leymerie, 1842, *Palaeosabella* Clarke, 1921, and *Sanctum* Erickson and Bouchard, 2003. Ekdale and Bromley (2001a) described omission surfaces with new ichnospecies *G. oelandicus*, having an

irregular vase-like shape and a roughly circular cross section from the Ordovician of Sweden. In Estonia, *G. oelandicus* occurs in the lower boundary of the Middle Ordovician (Vinn and Wilson, 2010a) (Table 1). This is an easily recognizable surface of non-deposition, traceable for hundreds of kilometers from Sweden to the St. Petersburg region (Jaanusson, 1961; Dronov and Holmer, 1999; Ekdale and Bromley, 2001a). These macroborings occur also in Norwegian Middle Ordovician hardgrounds (Ekdale et al., 2002). *Gastrochaenolites* is a common constituent of the *Trypanites* ichnofacies, also occurring in the *Glossifungites* ichnofacies (Knaust et al., 2012). Bivalves are commonly accepted as the trace maker (Kelly and Bromley, 1984; Wilson and Palmer, 1998; Carmona et al., 2007). Ekdale and Bromley (2001a) noticed that bivalves are unrepresented in Lower Ordovician in Sweden and no *in situ* inside of the *Gastrochaenolites* have been discovered. The Estonian material supports this opinion. *Sanctum* is an irregular boring excavated into endozones of ramose and frondose bryozoans. Wyse Jackson and Key (2007) examined bryozoans from the Ordovician of Estonia and emended the diagnosis for *Sanctum*, which occurs only on the ramose bryozoan colonies, and is abundant therein. Large Estonian bryozoan collections show that endozones of hemispherical bryozoan colonies contain borings that are of considerable size and larger than the biggest *Trypanites* (*T. fosteryemani*) and smaller than *Osprioneides*. In the authors' opinion, these abundant traces should be identified as *Sanctum* (Fig. 6L). Hemispherical bryozoans with “large-scale” borings are reported from the Ordovician of Norway (Opalinski and Harland, 1980), similar to the Estonian specimens. The trace maker is discussed by Erickson and Bouchard (2003) and Wyse Jackson and Key (2007). *Palaeosabella* Clarke, 1921 is an elongated cylindrical boring with a swollen distal end formed in carbonate substrates (Taylor and Wilson, 2003). It is similar to *Trypanites* (especially *T. fimbriatus*), having the swollen distal portion (Blissett and Pickerill, 2007), but being smaller in diameter. *Palaeosabella* was reported from the Silurian of Sweden and Estonia (Beuck et al., 2008; Vinn and Wilson, 2010b). It is rare in Estonia (Table 1), but further research will likely increase the number of occurrences. The trace maker of *Palaeosabella* is discussed by Bromley (2004).

#### 5.2.6. Fracture-shaped bioerosion traces

This category includes traces formed through biogenic fracturing of hard substrates. Stafford et al. (2015) described ichnogenus *Caedichnus* as an aperture-attacking predator on gastropod shells. It is a trace found worldwide (Alexander and Diel, 2003). Repaired *Caedichnus* injuries on gastropods have been reported from Ordovician and Silurian of Sweden (Ebbestad and Peel, 1997; Ebbestad, 1998; Lindström and Peel, 2005), as well as Estonia (Isakar and Ebbestad, 2000) (Table 1).

#### 5.2.7. Camerate network borings (Fig. 7G)

This category contains two-dimensional networks and all of these microborings are produced by ctenostome bryozoans (Buatois et al., 2017). Findings are rare in the Estonian collections, coming from the Dapingian and Sandbian (Table 1), and are represented by the ichnogenus *Pinaceocladichnus* Mayoral,

1988. Asaphid trilobites also bearing thin networks of “bryozoan borings” are known from the Dapingian of the St. Petersburg region (Dronov and Mikulaš, 2010). In Baltoscandia the Ordovician ctenostome bryozoans have only been reported from the Sandbian and lower Katian (Lavrentyeva, 1996).

#### 5.2.8. Dendritic and rosette borings (Fig. 7D)

This CAD includes microbioerosional traces that radiate mainly parallel to the substrate surface in dendritic or rosetted cavities representing the ichnofamily Dendrinidae (Bromley et al., 2007), recently thoroughly studied by Wisshak (2017). Large Upper Ordovician brachiopods as well as Silurian rugose corals bear these kinds of structures (Table 1). Besides, some stromatoporoids bear internal micro-bioerosional structures (Fig. 6H, M; Table 1) and preliminary observations found the presence of simple unbranching structures with cavities having a more complicated architecture.

#### 5.2.9. Elongate or branched attachment bioerosion traces (Fig. 6C)

Martinell and Domènech (2009) described a new ichnogenus *Sulcichnus*, which consists of canals running along the surface of the rugose corals made by commensal eunicid polychaetes. This kind of canals are recovered only in a single Upper Ordovician stromatoporeid (Table 1).

#### 5.2.10. Groove bioerosion traces (Fig. 7E)

This CAD includes rasping traces, left when grazers remove the substrate. Ichnogenus *Gnathichnus*, Bromley, 1975 is a grazing structure consisting of grooves and pits. This kind of traces are found on the surface of Upper Ordovician brachiopods (Table 1) and may belong to the ichnogenus *Gnathichnus*. The oldest similar trace-making behaviour is described and discussed from the Lower Triassic (Chen et al., 2012). The traces are produced by echinoids (e.g., Bromley, 1975; de Gibert et al., 2007). Echinoids occur in the Upper Ordovician of Baltics (Männil, 1962; Bockelie and Briskeby, 1980) and are represented by two genera *Bothriocidaris* and *Neobothriocidaris* in the Estonian succession. In addition, we included different peeling structures on Upper Ordovician brachiopods (Fig. 7F) and Silurian stromatoporoids (Fig. 6F; Table 1) to this category.

### 5.3. Bioclastration structures

Bioclastration structures (Fig. 7A, B) are produced by the activity of the endosymbiont that inhibits skeletal accretion of the host, and by the host which alters skeletal growth to accommodate the infesting organism (Tapanila, 2005; Buatois and Mángano, 2011). Diversity of bioclastrational species is that highest in colonial animals. *Helicosalpinx* Oekentorp, 1969 and *Chaetosalpinx* Sokolov, 1948 are reported from Silurian stromatoporoids and tabulate corals in Estonia (Klaamann, 1959; Vinn et al., 2013; Vinn and Mõtus, 2014; Vinn, 2016) and Silurian tabulate corals from Gotland (Stel, 1976). *Anoigmaichnus*, first described from Estonia (Vinn et al., 2014b), occurs rather frequently in Upper Ordovician trepostome bryozoans colonies.

In the Ordovician of Norway, a worm-tube boring, probably symbiotic in bryozoans (Spjeldnæs, 1989), and possibly attributable to *Anoigmaichnus*, is widespread. A rare brachiopod parasite *Burrinjuckia cliambonitofilia* (Fig. 7B) in a rhychonelliform brachiopod is described from the Late Ordovician (Vinn et al., 2014c). The controversial ichnogenus *Tremnichnus* Brett, 1985, lately debated by Wisshak et al. (2015) and Donovan and Pickerill (2017) occurs as an embedment structure in the ossicles of echinoderms. The large Estonian collection of echinoderms contains only a few specimens (Table 1) that were attributed to *Tremnichnus* (Vinn et al., 2015a). *Tremnichnus* (= *Balticapunctum* Rozhnov, 1989) occurs also in the Middle Ordovician of the St. Petersburg region.

## 6. Discussion

In general, the number of the well-preserved ichnofossils is relatively small and their distribution is irregular in the Ordovician–Silurian carbonate succession of Estonia. The identification of traces was often complicated and sometimes impossible, as the important diagnostic characteristics tend to be poorly preserved. Most of the classic study methods turned to be inappropriate or insufficient for the determination of Lower Palaeozoic trace fossils, especially bioerosional structures, in consolidated carbonate rocks. New techniques, such as X-ray computed tomography (CT) hold great potential for studying three-dimensional architectures hidden in hard substrates as discussed in Beuck et al. (2008) and Wisshak et al. (2017). The first tests with CT scanning of Estonian trace fossils produced good results when the ichnofossils and the matrix had different composition (such as carbonate burrows within kerogen-rich oil-shale). Further efforts are needed in this area in order to select appropriate settings, resolutions etc. For instance, type material for the most abundant bioerosional ichnogenes, such as *Trypanites* and the problematic *Palaeosabella*, are in the need of redescription using modern methods. There are currently five valid ichnospecies of *Trypanites*, but all need better characterisation and diagnostics (Wilson and Palmer, 2006).

Another aspect of the present study is that the material was collected during a long time interval and from a multitude of localities, therefore offering more chances to find rare and well-preserved specimens, whereas common but less spectacular specimens are clearly underrepresented in the collection. Several of the genera and species discussed above are represented by single findings only, such as *Halopoa*, *Monomorphichnus*, *Diplichmites*, *Helicodormites*, *Trepticus pedum* and *Phycodes reniforme*. This results a relatively high overall diversity of ichnofossils in the Ordovician and Silurian carbonate succession of Estonia, but stratigraphically and geographically scattered distribution of individual genera and species.

Altogether we were able to identify 50 different biogenic structures, including 33 soft-sediment, 13 bioerosional ichnotaxa and 5 bioclaustration genera, representing 31 CADs and 9 categories of ethological classification (Tables 1 and 2). General picture of the trace fossil distribution and association reflects the geological succession of Estonia: the more stable conditions of sedimentation in Middle Ordovician and differentiation of the

basin in Upper Ordovician and Silurian. The Middle Ordovician trace fossils association is characterised by relatively smaller number of CADs (Table 2). In addition, most of the genera are represented by a large number of finds. The identified trace fossils are common elements of the *Trypanites*, *Glossifungites* and *Cruziana* ichnofacies. The Upper Ordovician and Silurian trace fossil associations are more diverse and characterised by a larger number of CADs (Table 2). The identified trace fossils are constituents of three different ichnofacies in the Upper Ordovician (*Cruziana*, *Trypanites* and *Gnaticchnus*), and five ichnofacies in the Silurian (*Cruziana*, *Trypanites*, *Gnaticchnus*, *Skolithos* and *Glossifungites*). A relatively small number of CADs in the Middle Ordovician could be explained by the less diverse faunas of trace makers during that interval as compared to the Late Ordovician and Silurian. Also, a slow sedimentation rate and shallow burial of organic matter in the Middle Ordovician negatively influenced the diversity of trace fossils (Stachacz et al., 2018). During the Late Ordovician, Baltica reached subtropical climatic zone and warm-water faunas are commonly more diverse than temperate or cool-water ones, exhibiting also wider spectrum of biofacies and behaviours. Moreover, for many groups of organisms the Great Ordovician Biodiversification Event (GOBE) reached peak richness during the Late Ordovician. For instance, the scolecodont-bearing polychaetes, which were likely among the most common trace makers, reached their highest diversity in Baltoscandia during Katian (Hints, 2000; Hints et al., 2010) and thrived in the Silurian tropical seas (e.g., Tonarová et al., 2014 and references therein).

Input of siliciclastic material to the sedimentary basin also increased the number of the trace fossil genera as well as the number of CADs in Estonia (Table 1). Mixed carbonate-siliciclastic systems have higher preserved ichnodiversity than carbonate settings (Rodríguez-Tovar et al., 2014; Mángano et al., 2016), and the summarised Estonian material supports this observation. Input of siliciclastic material contributes to the increase of the sedimentation rate and influences sediment composition and substrate consistency, and thus has a significant impact on the trace fossil associations. More diverse trace fossil faunas are related to the intervals with greater sediment accumulation in the Upper Ordovician and lower Silurian (Tables 1 and 2). Continuous and slow sedimentation allows to mix the sediment and destroy all primary structures (Monaco, 1995). Overprinting and time-averaging, resulting from the long interval of colonization, is a plausible explanation for the rarity of trace fossils common elsewhere in the Palaeozoic, like the locomotion traces. Hanken et al. (2016) assumed that structures attributed to trilobites are rare in the region and the Estonian material confirms this observation. The decrease in the abundance of trilobite traces in the Ordovician is a worldwide trend discussed recently by Mángano et al. (2016). Locomotion traces (repichnia) of the region are mostly related to the siliciclastic sedimentation in Norway (Dam and Andreassen, 1990; Davies et al., 2006). Well-preserved material of locomotion traces like *Protovirgulara* in the Silurian (Fig. 3A, C; Tables 1 and 2), accompanied by trilobite traces, prove that the taphonomic overprint is an important factor and affects the general scheme of trace fossil associations.

Feeding structures (fodinichnia) are represented by a large number of genera (Table 2). Surprisingly, the most common feeding trace *Arachnostega* (Table 1) formed inside of defending shells and has therefore rather abundant occurrence. *Arachnostega* in the Baltic region has been associated with different groups of shallow-marine molluscs (Dronov and Mikuláš, 2010; Vinn et al., 2014d), and rarely other groups (Chrzastek and Pluta, 2017a, 2017b). Dissolution of aragonitic shells have made the traces easily visible. Examination of trilobite and brachiopod collections brought out that *Arachnostega* is frequent at the surfaces of internal moulds, preserved as calcite-filled endoreliefs (Fig. 5E). Quite common are fodichichnia *Planolites* and *Phycodes* (Table 1), but the collection material does likely not reflect the real distribution of these ichnotaxa. *Planolites montanus* (Fig. 4F, G) is abundant in the beds with kukersite kerogen (Kukruse Regional Stage, Sandbian) and in the rapidly deposited bentonite bed (Adavere Regional Stage, Llandovery).

*Phycodes* was represented by five different species, of which *P. rarus* was the most common. Noteworthy is the presence of rare Laurentian ichnospecies *P. reniforme*, with known occurrences only in the Ordovician (Hofmann, 1979), and *P. templus* previously described only from the Devonian (Han and Pickerill, 1994a). The general peculiarity of the Estonian trace fossil collection is the presence of many rare genera and species. According to Keighley and Pickerill (1994) *Taenidium* and similar ichnogenera are very rare in the Ordovician and Silurian. In the Estonian collections finds come from the Upper Ordovician (Table 1). The present collection contains a large number of pieces of straight horizontal burrows. These finds suggest that *Thalassinoides* boxwork is common in the Ordovician, and less abundant in the Silurian of Estonia (Table 1). The collection contains also large arcuate burrows, which do not belong to *Thalassinoides* (Fig. 4S, T). These traces need to be studied in outcrops for proper identification.

The small number of vertical structures in collections, with the exception of *Conichnus* and *Amphorichnus* is notable. Vertical structures, e.g., *Skolithos*, *Arenicolites* and *Oikobesalon* (Table 1) are mostly related to certain event beds. In Estonian succession abundant *Conichnus* and *Amphorichnus* occur in the Ordovician (Kukruse and Haljala regional stages, Sandbian) and Silurian (Adavere Regional Stage), together with elements of the *Cruziana* ichnofacies, such as *Teichichnus*, *Planolites* and *Thalassinoides* (Table 1). They are representing deeper environments than shoreface (Nestor and Einasto, 1997). In the Ordovician of Estonia, *Teichichnus* is characterised by very stunted vertical spreiten, which may be related to the flimsy soft sediment layer. Alternatively, less movements are needed for the systematic processing of food in carbonates than in siliciclastic sediments.

Bioerosional trace fossils may be locally very common. Noteworthy is the occurrence of a large number of different genera in the Upper Ordovician (Tables 1 and 2). This supports the idea of the Ordovician Bioerosion Revolution of Wilson and Palmer (2006), based on dramatic diversification of macroboring ichnotaxa during the Middle and Late Ordovician, and also on the increased intensity of carbonate substrate bioerosion. The studied collection material shows also that the diversity

of traces in inorganic substrates is lower than in organic ones. Three genera of macroborings occur in the hardgrounds (*Trypanites*, *Balanoglossites* and *Gastrochaenolites*) and 11 in various biogenic substrates (*Trypanites*, *Osprioneides*, *Sanctum*, *Sulcichnus*, *Rogerella*, *Oichnus*, *Pinaceocladichnus*, *Gnathichnus?*, *Palaeosabella*, *Tremnichnus*, *Caedichnus*), which additionally bear a number of yet undescribed structures. Three bioerosion ichnofacies occur in the mineral hardgrounds (lithic and skeletal): *Trypanites*, *Entobia* and *Gnathichnus* (de Gibert et al., 2007). The former is typical of the Palaeozoic. Estonian Ordovician–Silurian collection contains different bioerosional traces common for the *Gnathichnus* ichnofacies, like *Rogerella* and *Gnathichnus?*, and the yet undescribed peeling structures.

The increase of macroborers in the Late Ordovician may be correlated with the increase in carbonate hardgrounds and heavy calcitic skeletons associated with Calcite Sea geochemistry (Palmer and Wilson, 2004), in accession with the ocean-atmosphere oxygenation that possibly drove the Great Ordovician Biodiversification (Edwards et al., 2017). Tapanila et al. (2004) described positive correlation between bioerosion and skeletal density for Palaeozoic substrates and the Baltic material supports this idea. The Estonian macroborings were most common in muddy facies, clumping in large skeletons of Upper Ordovician bryozoans (early Sandbian Kukruse and Haljala regional stages) and a similar situation occurs in the Silurian (Jaani Regional Stage, Wenlock) with stromatoporoids (Fig. 6D, I–L; Table 1). Borers prefer massive hosts, which allow to provide safer domicile (Tapanila et al., 2004) and/or availability of food and oxygen (Kershaw, 1984). It must be added, however, that bioerosion diversification in the Baltic region is not related to reef development, which began across the region during the late Sandbian–early Katian interval (Kröger et al., 2017).

Composition of the trace fossils associations in the Ordovician and Silurian of Estonia is, in general, similar to that elsewhere in the Baltic region, including the absence of traces made by trilobites and the presence of *Phycodes pedum*. Estonian trace fossil associations are characterised by the high diversity of borings in biogenic substrates.

## 7. Conclusions

Collection-based study revealed a diverse association of trace fossils in the Ordovician and Silurian shallow marine carbonate succession of Estonia. Altogether 45 trace fossil and 5 bio-claustation genera were identified, many for the first time in Estonia, representing 31 categories of architectural designs, and 9 categories of ethological classification.

The diversity of ichnofossils is lowest in the Middle Ordovician, and higher in the Upper Ordovician and Silurian. No clear distinction could be made between the Upper Ordovician and Silurian trace fossil assemblages, pointing to generally similar facies and faunas during these periods. The ichnotaxonomic composition revealed from the Estonian collections is closely similar to what has been reported from the St. Petersburg region, Sweden and Norway. The Upper Ordovician bioerosional trace fossils in biogenic substrates are very diverse and contain traces common for the *Gnathichnus* ichnofacies.



In conclusion, our study has revealed a much higher ichnodiversity in the Ordovician–Silurian carbonate succession of Estonia than was previously known. These data and observations should nevertheless be regarded as preliminary, and higher diversity and wider distribution of many ichnotaxa would be expected if additional targeted collecting will be carried out in the future. New material and methods are moreover necessary in order to more fully describe and identify the trace fossils in consolidated carbonate rocks.

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## **Publication II**

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# Small faecal pellets in Ordovician shelly fossils from Estonia, Baltoscandia

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**Abstract.** Coprolites (fossil faeces) constitute a group of soft sediment trace fossils that provide useful palaeoecological and sedimentological information, but have generally low preservational potential. In this paper we report abundant occurrence and high diversity of small faecal pellets preserved inside different shelly fossils from Middle and Upper Ordovician carbonates of the Baltoscandian palaeobasin. The material contains ca 180 body fossils with faecal pellets from 40 localities, corresponding to a range of shallow-marine environments from cool-water carbonate ramp to tropical open shelf settings. Stratigraphically the finds range from the Volkhov to Pirgu regional stages (Dapingian to uppermost Katian). The pellets are elliptical or rod-shaped, 0.1–1.8 mm long and 0.08–0.75 mm diameter, with length/diameter ratio ranging from less than 2 to ca 6. They occur in shells of gastropods, bivalves, cephalopods, brachiopods, echinoderms and trilobites and represent two ichnospecies, *Coprulus oblongus* and *Coprulus bacilliformis*, and some intermediate forms belonging to the same ichnogenus. Additionally, two compound traces were identified: *Tubularina* (pellets inside small burrows with circular cross-section) and *Alcyonidiopsis* (pellets inside ribbon-shaped burrows). The pellets were produced when the empty shells were located on seafloor, or possibly during shallow burial in the oxic zone. The preservation of faecal pellets is due to an interaction of several factors, notably protection by the shells and a rapid mineralization. The origin of trace makers remains speculative, but polychaete worms having compatible size and body plan and living representatives who produce similar faecal pellets, are among the most likely groups. Possibly organisms with different feeding strategies were involved in producing the faecal pellets. Systematic examination of shelly fossils from selected localities showed that up to about half of the pellets may contain pellets, which indicates great abundance and diversity of pellet-producing organisms in the Ordovician Baltoscandian basin. Our material also shows that the trace maker of *Arachnostega* was not related to the faecal pellets inside the shells.

**Keywords:** micro-coprolites, faecal pellets, *Coprulus*, *Tubularina*, *Alcyonidiopsis*, shallow-marine carbonates, Ordovician, Estonia

## Introduction

Trace fossils are important environmental indicators and provide valuable knowledge on animal behaviour in the geological past (Seilacher 2007). Trace-fossil assemblages of the Ordovician of the Baltica craton are comparatively well studied (e.g. Dronov et al. 2002; Mikuláš & Dronov 2005; Knaust & Dronov 2013; Hanken et al. 2016), but the number of studies devoted to material from Estonia is limited (Männil 1966b; Vinn et al. 2014, 2015; Vinn & Toom 2016; Toom et al. 2019a,b).

Coprolites (fossil faeces) represent a distinct category of trace fossils common since the early Palaeozoic – different morphotypes are known already from the Cambrian (e.g. Vizcaïno et al. 2004; Eriksson & Terfelt 2007; Shen et al. 2014; Kimming & Strotz 2017; Mángano et al. 2019). The term pellet denotes grains of faecal origin according to Flügel (2004); however, some authors have used it

without reference to their oridin. The term is frequently used for the small invertebrate excrements of mm scale, with simple elliptical or rod-shaped form. Like all soft-bodied organisms, coprolites have generally a low preservation potential. From Palaeozoic siliciclastic sediments, their findings are mostly related to deeper-water settings with high sedimentation rates and specific preservation conditions. The occurrence of pellets in carbonate sediments is commonly related to tropical shallow-marine environments (Folk & Robles 1964; Shinn 1968; Wanless et al. 1981) and is widely reported from Mesozoic and Cenozoic strata. Rapid lithification has played an important role in their preservation in carbonates (Knaust et al. 2012). The majority of faecal pellet ichnotaxa in carbonates have characteristic inner structure and belong to the ichnofamily Favreinidae. Small faecal pellets with ornamented outer surface are assigned to a number of different ichnogenera (e.g. Heer 1853; Elliott 1963; Gramann 1966; Gaździcki 1974; Gaillard 1978; Agarwal 1988; Živković & Bogner 2006), whereas isolated faecal pellets without internal structure and ornamentation are representing the ichnofamily Coprulidae (Knaust 2008).

Faecal pellets are common in the Ordovician rocks of Europe (Häntzschel 1962; Benton & Hiscock 1996), first mentioned from Bohemia by Barrande (1872) and commonly related to the ichnogenus *Tomaculum* Groom, 1902 (e.g. Eiserhardt et al. 2001 and references therein; Pickerill & Forbes 1979; Mikuláš & Slavičková 2001; Bruthansová & Kraft 2003; Neto de Carvalho & Farinha 2006; Podhalańska 2007; Martin et al. 2016; Neto de Carvalho et al. 2016; van Keulen & Rhebergen 2017). Groom (1902) left open the question of the origin of the small pellets, but later authors have suggested a faecal origin for these particles (e.g. Frič 1908; Gutiérrez-Marco 1984; Mikuláš 1991; Eiserhardt et al. 2001; Bruthansová & Kraft 2003, Neto de Carvalho & Farinha 2006).

Faecal pellets may be associated with other trace fossils (e.g. Fürsich 1974; Seilacher 2007; Knaust 2008), constitute composite traces (Gaillard 1994), or fill shells of mollusks and other invertebrates (e.g. Mayer 1955, 1958; Zhang et al. 2007; Mángano et al. 2019). From the Ordovician, faecal pellets in burrows have been described as *Syncoprulus* (= *Tomaculum*) (Richter & Richter 1939; Pickerill et al. 1987), *Alcyonidiopsis* (Chamberlain 1977; Pickerill 1980; Pickerill & Narbonne 1995; Orr 1996; Uchman et al. 2005), in branching burrows as *Quebecichnus* (Hofmann 1972), and in burrows with segmented fill as *Compaginatichnus* (Pickerill 1989). Gutiérrez Marco (1984) described a cylindrical elongated cluster filled with small pellets inside of a gastropod as *Cilindrotomaculum*.

The reports of pellets inside Ordovician shelly fossils are few and most come from siliciclastic basins (Gutiérrez Marco 1984; Mikuláš 1992; Bruthansová & Kraft 2003). From carbonate settings, the occurrence of pellets in shells has only been mentioned by Pölma (1982), more recently by Toom et al. (2017, 2019a,b) and van Keulen & Rhebergen (2017). All referring to the material from the Baltic region.

The aim of this study is to report the abundance of small faecal pellets inside various shelly fossils in the Ordovician shallow-marine carbonates of the Baltoscandian basin, describe their morphology, and discuss the taxonomic, sedimentological and palaeobiological aspects.

## Geological background

During the Ordovician, the study area was part of a shallow sea, which covered the western part of the Baltica craton. This epicontinental sea, the Baltoscandian basin, extended from Norway to the Volga area in western Russia, and from the Fennoscandian mainland in the north to the Sarmatian mainland in the south (Fig. 1; Nestor and Einasto 1997). The Ordovician outcrop area in northern Estonia, where most of the material of the present study derives from, was characterized by relatively shallow-water settings of the basin, whereas deeper shelf environments – the so-called Livonian basin – were located in the south (Fig. 1). Baltica drifted from high southern latitudes to the tropical area (Torsvik & Cocks 2013, and references therein), causing a gradual change in climate and

depositional conditions. In Estonia, carbonate sedimentation commenced in the end of Floian (latest Early Ordovician) in a relatively cool, flat-bottomed epicontinental basin (Dronov & Rozhnov 1997). In the Middle and early Late Ordovician, the basin was characterized by extremely low sedimentation rates and with little bathymetric differentiation (Jaanusson 1973). In the Late Ordovician, the climatic change resulted in an increase in carbonate production and sediment accumulation rates on the platform. The basin started to differentiate particularly in the early Katian (Nestor & Einasto 1997). At that time the first tropical carbonate buildups appeared in the region (Kröger et al. 2017, and references therein).

The total thickness of the Ordovician succession in Estonia reaches ca 180 m (Nõlvak 1997). The Ordovician carbonate rocks in Estonia are rich in shelly fossils such as brachiopods, bryozoans, cephalopods, gastropods, echinoderms, trilobites, corals etc. Trace fossils are also common and diverse (Toom et al. 2019a), and the degree of bioturbation is generally high (Harris et al. 2004). A notable feature of Palaeozoic rocks of Estonia and the entire eastern Baltic region is a very low burial temperature indicated by conodont color alteration index (CAI) values ca 1 (Männik 2017). The stratigraphic framework and time-correlations in the region are based on Baltic regional stages and high-resolution biostratigraphy, notably trilobite, conodont, chitinozoan and graptolite zones (Nõlvak et al. 2006). We refer to both regional as well as global stages and series in the present study (Fig. 2).

## Material and methods

The large palaeontological collections of Ordovician fossils from Estonia, housed at the Department of Geology, Tallinn University of Technology (GIT) and the Natural History Museum, University of Tartu (TUG), were searched for shelly fossils containing small coprolites. In addition, the extensive lithological collection of eastern Baltic Ordovician rocks by Lembit Põlma (housed at GIT) was examined in order to reveal similar pellets dispersed in carbonate matrix.

The main method to identify the pellets was non-destructive observation of steinkerns, broken shelly fossils, and rock samples already cut during previous studies. Better-preserved specimens were studied on steinkern surfaces only; the less valuable material was sectioned and polished for the determination and measurements of pellets. Only the specimens containing, large number of individual pellets on sectioned shells or steinkerns were used for measurements.

Additionally, a selection of shelly fossils from two localities were sectioned and examined in order to assess the relative abundance and distribution of pellet-filled shells. In this way, 30 gastropods and 30 brachiopods from the Aluverre quarry (Haljala Stage, Sandbian), and 30 gastropods from the Mõnuste quarry (Vormsi Stage, Katian) were studied.

Specimens were photographed with a Canon EOS 5DS R digital camera and a Leica Z16 APO zoom microscope system at GIT. Measurements were taken from calibrated digital photos using Fiji image analysis software (<https://imagej.net/Fiji>). Selected specimens were additionally studied under a scanning electron microscope and analyzed for chemical composition with EDS (TESCAN VEGA II XMU SEM with an X-Ray Energy Dispersive INCA ENERGY 450 microanalysis system at the A.A. Borissiak Paleontological Institute, Moscow). Data of individual specimens and related pellets (including images and localities) are deposited in the database of Estonian geocollections, which is accessible online at <https://geocollections.info>.

## Results and discussion

### Characterization of faecal pellets and host shells

In total the small pellets are identified inside ca 180 shelly fossils coming from 40 localities across the Ordovician outcrop area in Estonia and representing normal shallow-marine settings of the Estonian shelf (Table 1). So far only one specimen has been recovered from the deeper-shelf Livonian basin (Fig. 1). Stratigraphically the pellets in shells are known from the Volkhov (Dapingian) to Pirgu regional stages (Upper Katian); however, the majority comes from temperate and tropical carbonates (Table 1), with only a single record from cool-water limestone of the Volkhov Stage. The host rocks of shelly fossils with pellets are varied, ranging from wackestones and packstones to pure carbonate mudstones. Notably, so far, the loose pellets have not been found from the host rocks.

Host shells containing faecal pellets belong to common Palaeozoic fossil groups: gastropods, bivalves, cephalopods, brachiopods, echinoderms and trilobites (Table 1). In general, the host dimensions range from ca. 10 to 45 mm; for cephalopods the diameter of body chamber is less than 25 mm. The size of pellets is very variable, ranging from 0.1 to 1.8 mm in length, and 0.08 to 0.5 mm in diameter. Within a single host shell, however, pellets are principally similar in their dimensions. The pellets are elongated, mostly elliptical or rod-shaped and always with circular cross-section. Their length/diameter ratio is mostly less than 2 (Figs. 3A, D; 4F-H; 5J, K) or 2–3 (Figs. 3I; 4A, B, D, I; 5C). Only few specimens show more elongated pellets, with length/diameter ratio between 4 and 6 (Figs. 3F; 5B). All pellets are devoid of internal structure, and no constructional wall or lining has been observed. EDS chemical analysis suggested similar carbonate composition for pellets and rock matrix, only a single specimen from the Haljala Stage (Sandbian) showed traces of silicification.

Pellets inside shells are organized in two different modes: the majority is represented by massive accumulations (Figs. 3A-I; 4A-I; 5A-F), and in fewer cases (15 specimens), pellets are associated with small burrows (Fig. 5F-K). The massive accumulations consist of randomly oriented pellets, which are not mixed with the sediment. The boundary between the sediment and pellets may be distinct (Fig. 3A) or transitional (Fig. 3G). The degree of preservation of pellets is variable, especially for the sets of massive accumulations. Decomposition process may affect an entire set (Fig. 3C), or only the periphery of an accumulation (Fig. 3G-I). Probably the sediment inside the shells consists of decomposed pellets, especially if it does not contain bioclastic material. Some specimens contain two different sizes of pellets, located in separate sets (Figs. 3E, 4I). The number of pellets in accumulations varies widely: for large pellets, less than hundred pieces make up an accumulation, but for the smallest pellets a set may contain more than a thousand pellets (Fig. 3A).

Small burrows (diameter about 1–3 mm, traceable length less than 10 mm), sinuous, branching may contain micritic, randomly oriented isolated elliptical pellets with length/diameter ratio around 2 (Fig. 5F-J). Such pellets are well preserved, randomly oriented and loose. The outline of burrows is sharp, their cross-section is circular and mostly constant in diameter, without ornamentation or lining. In most cases the burrows with pellets are found within gastropods, but few are known inside brachiopods and bivalves. These burrows are oriented in different directions, but their total length and general configuration is difficult to establish as the pellets are mostly visible in cross section (Fig. 5G, H). A massive accumulation of pellets and burrows with pellets may occur together inside the same shell (Fig. 5I, J). However, the pellets inside the burrows are not coming from the massive accumulations, as they are different in size and preservation, and are thus likely made by the producers of the burrows. Additionally, a few trilobite specimens demonstrate specific ribbon-shaped, pellet-filled burrows with varying diameter (Fig. 5K).

The majority of pellet-filled fossils belong to mollusks, especially gastropods (Figs. 3E, F-I; 4A-D; 5D, E, I, J), with a total of 112 specimens. All common Ordovician gastropod genera are represented, but most finds are related to oblong and conical forms such as *Subulites*, *Murchisonia*, *Hormotoma*, *Lophospira*, *Holopea*, *Liospira*, and *Deaehospira*. Fewer specimens belong to the depressed

gastropod shells (the diameter is much larger than the height) like *Pachystrophia*, *Lesueurilla*, *Cymbularia*, *Bucanella*, *Megalomphala*, and *Salpingostoma*. The gastropods vary in size, the smallest measured specimen being 10.1 mm high and 16.4 mm wide, and the largest 102.1 mm high and 53.8 mm wide. Massive clusters of pellets are typically located in the apical parts of gastropod shells (Fig. 3H, I). For smaller shells, the entire whorl may be filled with pellets. In larger specimens, like *Hormotoma insignis* from the Rakvere Stage, the pellets may be accumulated in one side of the shell and the occurrence of pellets may be observed also in body whorl (Fig. 4C). Clusters, clusters together with burrows (Fig. 5I, J) and only burrows filled with pellets are observed in gastropod shells, the latter case being rather exceptional. Stratigraphically the pellet-filled gastropods are recorded from the Uhaku (late Darriwillian) to Pirgu stages (late Katian), with higher number of finds from two levels: the Haljala (Sandbian) and Rakvere stages (Katian). The pellets inside gastropods show the highest variability in size and shape, including the largest pellets recovered during this study (Fig. 4A). Elliptical and rod-shaped pellets with a length of 0.23–1.8 mm, diameter 0.09–0.75 mm and various length/diameter ratio ( $\leq 2$ , 2–3 and 4–5) are known. Notably, there is no correlation between the size of the shells and the size of the pellets they contain. Probably the large open aperture of the gastropods made them easy to inhabit and may have controlled the occurrence and variability of pellets. However, the higher variability of pellets in gastropod shells may also result from the largest number of specimens studied. On the surface of some gastropod steinkerns the trace fossil *Arachnostega* is observed (Fig. 4C, D).

Sixteen specimens of cephalopods contain pellets. Infills have been found in the body chamber, phragmocone between septae (Fig. 4E), as well as siphuncle (Fig. 4C). Frequently only one chamber between septae is filled (Fig. 4E) and bioturbation is common. Finds of pellets in cephalopods are mostly related to coiled and medium-size specimens with a diameter of aperture less than 25 mm. Stratigraphically the occurrences range from the Kunda to Lasnamägi stages (Darriwillian), the Haljala Stage (Sandbian), and from the Vormsi to Nabala stages (Upper Katian). Most of the pellets are poorly preserved and relatively small in size (length 0.23–0.5 mm, diameter 0.09–0.2 mm), with length/diameter ratio below 2 or 2–3. Most finds are coming from temperate-water carbonates, which may be the cause for a relatively small size of the pellets in cephalopod shells. In addition, small holes in damaged phragmocones allowed inhabiting by small animals with slender body plan only. The small number of cephalopod specimens with pellets may be biased due to insufficient study, although, a recent thorough examination of a large number of lower Katian cephalopods by Kröger & Aubrechtová (2018) did not reveal any finds with pellets.

Fifteen specimens of bivalves representing the genera *Modiolopsis*, *Aristerella* and *Cypricardinia* contain pellets (Fig. 5A-C, F-H). Shells with length of 28–61 mm, height 16–44 mm and width 23–44 mm are partially filled with irregular clusters. Only the largest *Cypricardinia* contain several small burrows filled with pellets (Fig. 5F). Bivalves filled with pellets are recorded from the Kukruse to Rakvere stages (Sandbian to Katian). The pellets observed are elliptical (length 0.26–0.76 mm; diameter 0.18–0.43 mm), elongated elliptical (length 0.61 mm; diameter 0.16 mm) or rod-shaped (length 1.19 mm; diameter 0.22 mm), with the length/diameter ratio of  $\leq 2$ , 2–3, or 4–6. A relatively small number of finds shows surprisingly high variability of the shape of pellets. Few bivalve steinkerns show the presence of *Arachnostega*.

Thirty-two specimens of brachiopods containing pellets have been recorded (examples on Figs. 3C, D; 4G-I). Shell sections may be filled only with pellets (Fig. 3C), or more commonly, the irregular accumulations of pellets occur in some parts of the shell sections examined, like the spondylium (Fig. 4G). The smallest brachiopod with pellets is *Platystrophia* with a height of 9.4 mm and a width of 21.6 mm, the largest being *Porambonites wesenbergensis* with a height of 45.4 mm and width of 33.9 mm. Bioturbation and multiple accumulations with different size of pellets are related to the larger specimens (Fig. 4I). A single occurrence is recorded from the Volkhov Stage, other finds come from the Haljala to Rakvere stages (Sandbian to Katian). Only elliptical pellets are observed with length 0.2–1.1 mm, diameter 0.1–0.5 mm and length/diameter ratio  $\leq 2$  or 2–3. Commonly the large

pellets occur inside large brachiopods, which it may be related to the size of the pedicle opening. Few specimens of brachiopods also show the presence of *Archnostega*.

Two echinoderm specimens belonging to *Echinosphaerites* and *Sphaeronites* contain irregular accumulations of small, elliptical pellets with length 0.1–0.4 mm, diameter 0.08–0.24, and length/diameter ratio below 2. The *Sphaeronites* shell is so far the only specimen characterizing the deeper shelf environments. It is noteworthy that the pellets it contains are the smallest recorded during the present study (Fig. 3A). The two specimens come from the Kukruse and Haljala stages (Sandbian).

Two trilobites have ribbon-shape burrows located on the dorsal surface of sediment infill of the cephalon of *Oculichasmops* and the pygidium of an asaphid trilobite (Fig. 5K). Stratigraphically the finds come from the Haljala and Keila stages (Sandbian and lower Katian). The pellets inside trilobites are elliptical in shape, with length 0.13–0.19 mm, diameter 0.32–0.36 mm, and length/diameter ratio below 2 or 2–3.

To some extent the data on pellet occurrences presented in Table 1 is biased by the different detection and study methods and the number of previous studies on different fossil groups. Pellets can rarely be observed on natural break surfaces – the lack of color difference between the pellets and matrix makes them virtually indistinguishable. However, sectioning and polishing surfaces reveals the pellets inside. The number of finds also depends on the degree of preservation of the shelly fossils. For instance, brachiopods have commonly well-preserved shells and pellet finds are related only to damaged specimens or material which was sectioned for other purposes. The prevalence of mollusks, and especially gastropods, can be explained by the conditions of ‘calcite sea’, where aragonitic shells dissolved rapidly (Palmer et al. 1988; Palmer & Wilson 2004) and therefore the internal molds with pellets became visible. Pellets were particularly well observable on the steinkerns of gastropods and bivalves derived from pure tropical lime-mudstones of the Rakvere and Nabala stages (Katian). These specimens were redeposited on the sediment surface before complete lithification of steinkerns had taken place but after the dissolution of the shells. Steinkerns are deformed, with crush marks (Fig. 5D), may contain small cracks (Fig. 5E), are overgrown by trepostome bryozoans (Fig. 5D, E) and covered by pyrite threads (Fig. 5A). It can be easily identified on which side a gastropod or bivalve was lying on the sea floor after redeposition, as a selective erosion by dissolution has made the pellets more distinct (Fig. 5D, E). The dominance of gastropods among pellet substrates can also be explained by a more favourable microenvironment inside the empty gastropod shells for the pellet producers. Appropriate shape and size of the shells may have supported a better preservation. In addition, the open apertures of gastropod shells made them easily habitable, which is supported by the high variability in the size and shape of pellets.

The present collection is probably too small and taxonomically biased to fully assess the distribution of pellet-containing shells, including differences between fossil groups. However, the 90 randomly examined gastropod and brachiopod shells from two localities provides useful insights into these questions. Shelly fossils with pelletoidal infill were especially common in the Haljala and Rakvere stages (middle Sandbian and middle Katian; Table 1). 30 random gastropods and 30 brachiopods from the fossil collection of the Aluveru quarry (Haljala Stage, Sandbian), without external indications of pellet occurrence, were sectioned and examined. The previous data from the same locality had shown high abundance of pellets inside gastropods and their absence inside brachiopods. From the selected 60 shells, 15 gastropods and 12 brachiopods contained pellets, suggesting that nearly half of the shells preserved pellets in both fossil groups. For comparison, 30 gastropods from the Mõnuste quarry (Vormsi Stage, upper Katian) were sectioned. This stratigraphical interval had only few previous finds of shelly fossils with pellets. However, the study of 30 gastropod steinkerns revealed pellets in 11 cases, that is, in every third shell. This approach clearly shows that the pelletoidal infill is a very common phenomenon related to different shelly

fossil groups and stratigraphical intervals within the Middle and Upper Ordovician carbonate succession of Estonia.

### Ichnogenus *Coprulus* – pellets in massive accumulations and inside burrows

Richter & Richter (1939) proposed the term *Coprulus* as an informal name. The formal ichnogenus *Coprulus* was erected by Mayer (1952) for isolated small pellets. Two ichnospecies, *C. oblongus* and *C. sphaeroideus*, were described and later *C. bacilliformis* was added (Mayer 1955). Knaust (2008) revised the diagnoses for the ichnogenus *Coprulus* and ichnospecies *C. oblongus*; he brought out an important diagnostic feature for small pellets – the length/diameter ratio. *C. sphaeroideus* and the ichnogenus *Tibiokia* Hatai et al., 1970 were regarded as junior synonyms of *C. oblongus*; thus, the ichnogenus *Coprulus* includes two ichnospecies, *C. oblongus* and *C. bacilliformis* (Knaust 2008). The pellets of *C. oblongus* are isolated pills with smooth surface, cylindrical to oval in shape, and length/diameter ratio commonly between 1.5 and 2.0 (Knaust 2008). The pellets of *C. bacilliformis* have length/ diameter ratio around 6 and are rod-shaped (Mayer 1955).

It should be noted that diagnoses of *C. oblongus* by Mayer (1952) and by Knaust (2008) are based on material where pellets are partly or completely washed in different burrows. By Mayer's (1952) diagnosis *C. oblongus* has "long-oval" shape, but Knaust (2008) refers to "cylindrical to oval" shape. In case when pellets may be washed in, instead of being formed *in situ*, they may represent composite traces (structures made by combined activity of two or more species) and, according to Bertling et al. (2006), have no ichnotaxonomic standing. Arakawa (1970) introduced a detailed morphological classification of bivalve faeces. The faeces were divided into several types according to the structure and form. Three basic types were erected: oval, rod-shaped, and ribbon-like pellets; including a large number of subtypes (pellet-types by Arakawa). According to Knaust (2008), *C. oblongus* includes pellets from oval to cylindrical shape, thus from two different basic types of Arakawa (1970). It has to be noted that for badly preserved very small pellets with small length/diameter ratio values, distinguishing between elliptical and rod-shaped forms may be complicated (see Fig. 3B).

Estonian faecal pellets in accumulations are mostly elliptical in shape, with length/diameter ratio below 2 or 2–3 (Table 1), and few specimens demonstrate value between 4 and 6 with two different outlines: elliptical (Fig. 4F) and rod-shaped (Fig. 5B). From the Estonian material, only half of shelly fossils demonstrated faecal pellets with length/diameter average value around 2 and these can be confidently identified as *Coprulus oblongus*. A small number of rod-shaped faecal pellets have length/diameter ratio about 4–6, and these can be named as *C. bacilliformis*. However, a large number of pellets are elliptical with length/diameter ratio over 2 – these cannot be named at present without erecting a new species or emending the diagnoses of existing species (Figs. 3E, F, H; 4A, B, D; 5C). Péneau (1941) described this type of pellets as *Tomaculum*. The Estonian material suggests that it is reasonable to include the elliptical pellets with length/ ratio 2–3 in the ichnospecies *C. oblongus*. However, it is questionable if there is good basis to assign the oblong elliptical pellets with length/diameter values over 4 to *C. bacilliformis*. As far as the original material of *C. oblongus* and *C. bacilliformis* described and figured by Mayer (1952, 1955) is not available for re-examination, we identify the elongated elliptical pellets with length/diameter ratio over 2 only at the genus level.

### Compound trace *Tubularina* – pellets in small burrows

Compound traces consist of combined individual traces with different morphologies that would be named differently if they were preserved in isolation (Miller 2003). Compound traces can only be named if all structures have been produced simultaneously (Bertling et al. 2006). For simple burrows

filled with pellets, the two compound trace-fossil genera *Alcyonidiopsis* Massalongo, 1856 and *Tomaculum* Groom, 1902 are most commonly identified and discussed from Palaeozoic strata. From Jurassic lagoonal limestones, *Tubularina* Gaillard et al. 1994, a small (diameter up to 2 mm) firmground burrow, filled with sparry calcite and loose pellets has been described. The walls of *Tubularina* are smooth, without ornamentation, branching is observed. *Tubularina* is penetrating the sediment sinuously in very different directions. Burrows inside of shelly fossils from the Haljala to Oandu stages (Sandbian and lower Katian) are very similar to the Jurassic material. Skeletal debris displaced concentrically around the burrows, and also the sharp contours and circular cross-section of the burrow indicate that the traces were made into a coherent substrate.

### Ichnogenus *Alcyonidiopsis* – ribbon-shaped burrows with pellets inside trilobites

Two specimens of trilobites from the Haljala and Keila stages contain curved ribbon-shape burrows inside, filled with sparry calcite and pellets (Fig. 5K). No constructional wall or lining is observed, the boundary of the structure is marked by calcite. The burrows are located on the dorsal surface of the sediment infill, one on the cephalon and a second on the pygidium. The burrows are 1.7–2.9 mm and 1.1 mm wide, the width is somewhat variable. The pellets are elliptical in shape and representing the ichnogenus *Coprulus*. These burrows are different from *Tubularina*, which has a circular cross-section (Gaillard et al. 1994), and from *Phymatoderma*, which is a subhorizontally branching burrow system filled with pellets (Izumi 2012). The location of burrows on steinkerns is similar to *Arachnostega*, but the traces are not demonstrating network characteristic of the latter; besides, the pelletoidal infill is unknown in *Arachnostega*. Bruthansová & Kraft (2003) described pellets arranged in rows inside Ordovician trilobites as *Tomaculum*. However, several authors have considered that *Alcyonidiopsis* is the proper name for tubular burrows filled with faecal pellets (Chamberlain 1977; Uchman 1995, 1999; Pickerill 1980; Pickerill & Narbonne 1995; Orr 1996, Uchman et al. 2005, 2013; Buatois et al. 2017; Mángano et al. 2019). *Tomaculum* consist of tightly packed pellets on bedding planes and is indicative of deep-water settings (e.g. Benton & Trewin 1978; Zagora 1997; Podhalańska 2007). The trace is rare in Palaeozoic carbonates (Chamberlain 1977), but is also known from non-marine settings (Metz 2015). Mángano et al. (2019) described small burrows with pellets inside Cambrian bivalved arthropods as *Alcyonidiopsis*. The Estonian ribbon-shaped small burrows inside trilobites are most similar to *Alcyonidiopsis*. Additionally, a few shelly fossils with pellets inside demonstrate poorly preserved burrows with unclear shape and cross section (Table 1); these cannot be named at present.

### Notes on the preservation of pellets

For all sectioned specimens, the taphonomic evidence suggests that the large accumulations of pellets were formed *in situ*, inside the shells. This is also proved by the specimens containing only pellets inside (Fig. 3C). The massive accumulations of pellets are not evenly mixed with sediment, which also indicates that the pellets were not washed into the shells together with sediment. Random placement of skeletal grains around the sets of pellets suggests that the sediment was not affected by the formation of pellets and proves that the pellets were not made in shells filled with sediment. In case of shells with large apertures, like in gastropods, it is more likely that the pellets were produced when the empty shell was lying on the sea floor and was afterwards filled with sediment. However, it is also possible that the dead body closed the aperture of the gastropods and pellets were formed when the shell was shallowly buried. More likely, the shells with small openings, like brachiopods or echinoderms, could also be colonized by meiofauna and small macrofauna after shallow burial and the pellets were produced by infauna. According to Wilson & Palmer (1992), the cementation is fastest just below the water - sediment interface. Rapid lithification is important for the forming and preservation of trace fossils in carbonates (Knaust et al. 2012). Eriksson et al. (2011) expressed the same opinion for the preservation of coprolites. The rapid lithification was likely



favoured by the small dimension of pellets examined in our study. Cementation by calcite resulting from aragonite dissolution may be confined to the areas immediately adjacent to dissolving bioclasts (Wilson & Palmer 1992). This may be the explanation for the large number of finds related to the different mollusk shells.

In the Ordovician sediments of Estonia, the occurrence of pellets is recoded from cool-water to tropical carbonates (Table 1). Two stratigraphical levels, tropical carbonates of the Rakvere Stage (Katian) and temperate water carbonates of the Haljala Stage (Sandbian) demonstrate higher occurrence and better preservation of pellets. According to Flügel (2004), carbonate pellets can be preserved in warm water environments with low energy and reduced sedimentation rates. The fossilization of the originally soft particles requires bacterial decomposition of organic mucus and intra-granular cementation by Mg-calcite. The higher number of findings and large scale in shape and size of pellets is related to the Upper Ordovician. This may be due to the better preservation conditions in warm waters.

Increased number in the Haljala Stage could be explained by the beginning of climate warming and supported by silicification of sediments. Extremely well-preserved pellets inside shelly fossils from Bohemia also showed high degree of silicification (Bruthansová & Kraft 2003). Tarhan et al. (2016) and Liu et al. (2019) have discussed rapid silicification for the preservation of soft-bodied fossils. Slightly silicified rocks have a wide distribution in Estonian shallow-water carbonate rocks, especially in the Haljala Stage. The source of silica is supposed to be organic, especially from siliceous sponges, and/or volcanic (Jürgenson 1958; Siir et al. 2015).

Environmental conditions, such as low oxygen levels in the sediment and/or fast burial, related to increasing of sedimentation rates, may have supported the preservation of pellets. Anoxic conditions slowed down or stopped the decomposition of pellets. Processes occurring at the oxic/anoxic boundaries are controlled by a temperature, supply of organic matter, light, water currents, and bioturbation (Kristensen 2000). The bioturbation inside large number of steinkerns and on their surfaces indicates the existence of oxic environmental conditions inside the shells after the burial and before lithification. In addition, the activities of infaunal benthos stimulate microbial activity (Aller & Aller 1982) and may in turn accelerate the decomposition of pellets. The physical mixing of sediments lowered the carbonate cementation (Wright & Cherns 2016) and may have supported the degradation process of pellets. The best preserved pellets were recorded inside shells where bioturbation was not recorded. The tropical pure carbonates of the Rakvere Stage are, in general, characterized by relatively low bioturbation rate and small number of soft-sediment traces (Toom et al. 2019a).

High-energy environments with enhanced oxygen exposure are generally characterized by a very low burial efficiency of organic matter (Arndt et al. 2013). Microenvironment inside the shells was probably less affected, the oxygen diffusion into the sediment was decreased and the degradation of pellets was slowed down. The shells also shielded pellets and pellet-filled burrows with pellets from compaction and allowed an early cementation to occur as suggested by Mángano et al. (2019). This may explain the absence of pellets in the host rocks. However, water circulation in the uppermost sediment column favours the lithification (Coimbra et al. 2009), and the shells may acted as traps for calcium ions and favor early cementation of small pellets. Supposedly, the microenvironment inside the protective shell was an important factor for the preservation of pellets in cool and temperate water environments of the Ordovician of Estonia.

Microbial communities are important in the decomposition process of organic matter (Solan & Wigham 2005; Morata & Seuthe 2014). Microbes on pellets could originate from the water or sediment, or the gut of pellet producers and ingested with the food. The accumulations of fresh pellets, which contained less microorganisms, had a better preservation potential (Hargrave 1976). The decomposition process, which started from the outer edge of the set, did not reach the end of

the set inside an elongated and narrow whorl (Fig. 3H). This may be the reason for a large number of finds of pellets in the apical parts of gastropod steinkerns. The organic matter may have played a major role in inhibiting precipitation of sedimentary carbonates (Morse et al. 2007).

In conclusion, it is difficult to identify one main reason for the observed preservation of pellets. Most likely it is due to the interaction of several factors including sea water and pore water chemistry, temperature, rapid lithification of small particles, favourable microenvironment inside of shells, and the composition of pellets and microbial communities.

### The tracemakers

Flügel (2004) summarized a modern view on trace makers of small pellets: the assignment of pellets to specific pellet-producing animals is difficult because the pellets of most invertebrates lack specific morphological features. However, there are many publications dealing with excrements of different recent aquatic invertebrate groups (e.g. Moore 1931a, 1931b, 1939; Moore & Kruse 1956; Manning & Kumpf 1959; Kornicker 1962; Arakawa 1970, 1971; Krauter & Haeven 1970; Pryor 1975; Martens 1978; Ladle & Griffiths 1980; Wotton & Malmqvist 2001; Kulkarni & Panchang 2015). In addition to detailed descriptions and classifications of pellets, a wide range of problems have been discussed. Moore (1939) concluded that in general carnivorous animals tend to produce faeces of loose consistency, and faeces of deposit feeders are the most resistant of all. Arakawa (1970) noted that variations in pellets are related to feeding habits and mode of life, and that the pellets of carnivores are very soft and irregular in shape. Excrements of a loose consistency cannot be preserved as fossils (Kornicker 1962). Nature and form of faecal pellets are related to the structure and function of the digestive organs (Stamhuis et al. 1998). Unsculptured faecal rods are formed, as mid-gut is very simple and circular (Arakawa 1970). The exact shape of pellets may vary; for instance, the excrements of stressed or starved animal may be thinner and irregular in shape (Arakawa 1971).

Similar pellets inside different shells are described and discussed by Bruthansová & Kraft (2003). These authors demonstrated that the pellets were not related to the animals that originally inhabited the shells. Our observations on the Ordovician material from Estonia confirm this conclusion – the pellets located on the ventral muscle scar of a brachiopod shell and in cephalopod phragmocone could not be produced by a brachiopod and cephalopod, respectively.

It is possible that some pellets were made by scavengers feeding on soft parts after the death of the animal with the shell (Bruthansová & Kraft 2003), or feed on microbial halo formed around the decaying soft body. Deposit feeders appear to be limited largely to worms longer than 1 cm; in general, juveniles and small worms are restricted to ingest highly digestible organic matter and rich food items (Jumars et al. 2015) and may be the tracemakers, especially in case of complete brachiopod shells, where a slender body shape was needed to enter the shell. Priapulids and arthropods, trilobites included, with mobile epifaunal lifestyle, are discussed as crayon feeders (Hu 2005). In addition, nematodes could feed on bacteria, fungi, algae and protozoans (Sun et al. 2014). Predators and scavengers have high assimilation efficiencies and produce small numbers of faecal pellets (Wotton & Malmqvist 2001). The accumulations with a relatively small number of pellets (much less than 100 pellets per cm<sup>2</sup> according to Wotton & Malmqvist 2001) can be made by scavengers. However, in some cases the pellets were located in parts of the shell which did not contain a soft body, like between septae in the phragmocone. Other animals than scavengers should have been producing these clusters. Estonian pellets composed of the same material as the host sediment suggest that deposit feeders or suspension feeders were trace makers rather than predators and scavengers.

In shallow-marine environments, a cryptic environment inside shells provides shelter and food to different encrusters (Vinn et al. 2018). Our unpublished material of steinkerns brought up new data showing that encrusting community is widespread and consist of different bryozoans, cornulitids and

inarticulate brachiopods. It confirms that in shallow-marine conditions the empty shells provided suitable living environments. However, co-occurrence of pellets and different encrusters has not been observed. Considering the large number of pellets that the suspension feeders produce (Pryor 1975; Wotton & Malmqvist 2001, and references therein), the different cavities inside the shells were used as temporary hiding places rather than permanent domicile. Mobile trilobites used empty cephalopod shells for hiding (Davis et al. 2001). Bruthansová & Kraft (2003) suggested that producers selected the shells according to their body dimensions. Our material supports this idea – pellets have not been observed inside the largest shells. In addition, the apertures/holes in shells that controlled the inhabiting community of shells were important.

García-Ramos et al. (2014) discussed a situation where pellets were stored to use them as a bacteria-enriched resource. Gardeners have low turbative activity, inhabiting relatively simple and almost permanent burrows with storage rooms (Stamhuis et al. 1998), and pellets may be stored inside of shells by gardeners. Invertebrates may live in a mixture of faecal pellets and fine particles (Levinton 2017).

Mayer (1952, 1958) originally interpreted *Coprulus* as faecal pellets of annelids. Recent excrements similar to *Coprulus* are commonly produced by polychaetes (Bałuk & Radwański 1979; Gaillard et al. 1994; Knaust 2008; Kulkarni & Panchang 2015). Kraeuter & Haven (1970) investigated pellets of six modern shallow-marine phyla represented by 70 species and described thoroughly several characteristics. Elliptical or rod-like shape was common, but faecal pellets of polychaetes were characterized by rod-like or ellipsoidal shape, with circular cross-section, lacking sculpture and having mostly solid consistency. Various mud-dwelling and suspension feeding polychaetes form solid and resistant pellets of very constant shape (Moore 1931b; Pryor 1974). *Alcyonidiopsis* and *Tubularina*, burrows actively filled with pellets, were interpreted as a feeding structure of polychaetes (Chamberlain 1977; Gaillard et al. 1994; Uchman et al. 2005; Mangano et al. 2019). Recently, palaeoscolecids were discussed as potential trace makers (see Martin et al. 2016 and references therein). Based on evidence of scolecodonts, polychaetes were abundant and diverse in the Ordovician of Baltoscandia, especially starting from the Darriwilian (Hints 2000; Hints & Eriksson 2007; Eriksson et al. 2013), and might have been responsible for various trace fossils, including the herein reported pellets. However, in ichnology the identity of the trace makers mostly remains speculative and we may have the case of unknown feeding strategies, and the animals that made the pellets may have no close living representatives.

Bruthansová & Kraft (2003) described several *Coprulus* (as *Tomaculum*) specimens inside of shells associated with *Arachnostega*-like traces and suggested that the pellets could be the faeces of the cryptic producers of *Arachnostega*. The latter is a feeding trace inside the body fossils found at the contact of sediment filling and the inner surface of body fossils. *Arachnostega* is common also in the Ordovician of Estonia (Vinn et al. 2014). Our observations show co-occurrence of the faecal pellets and *Arachnostega* only in few specimens, indicating that the trace maker of *Arachnostega* was probably not the producer of pellets inside the shells. Moreover, *Arachnostega* and *Tubularina* were made within coherent sediment, whereas the faecal pellets were put into empty shells. Thus, the two traces could not be created simultaneously.

Bruthansová & Kraft (2003) concluded that the producers of pellets inside shells come from different growth stages of a limited number of non-deposit-feeding taxa. The Estonian material inside shells is similar to the Bohemian pellets; they were made by trace makers with similar feeding strategies. Most likely filter feeders and scavengers looking for shelter were the producers of the herein described pellets. However, the large variation in size, shape and the number of pellets in accumulations and burrows suggest a wide spectrum of potential trace makers.

## Conclusions

- Small faecal pellets are common inside shelly fossils (gastropods, bivalves, cephalopods, brachiopods, echinoderms and trilobites) in the Ordovician carbonate succession of Estonia, and may fill up half of the fossil shells.
- The faecal pellets are representing the ichnogenus *Coprulus* Mayer, 1952 and ichnospecies *C. oblongus* Mayer, 1952 *sensu* Knaust 2008, *C. bacilliformis* Mayer, 1955 and transitional unidentified forms.
- Compound traces consist of small burrows with circular cross-section and filled with faecal pellets inside of various shelly fossils are representing the ichnogenus *Tubularina* Gaillard et al., 1994. Ribbon-shape burrows with faecal pellets inside trilobites are representing the ichnogenus *Alcyonidiopsis* Massalongo, 1856.
- Stratigraphically, the faecal pellets occur from the Volkhov to the Pirgu regional stages (Dapingian to upper Katian), showing that they can be preserved in cool, temperate and warm-water shallow-marine conditions; although the highest number of finds and largest morphological diversity is encountered in the Upper Ordovician sediments.
- The size and the shape of host shells controls the occurrence of pellets in two ways: shells with large apertures were easier to inhabit by animals with different size and body plan; and in narrow and elongated shells, the process of decomposition was slowed down.
- Preservation of pellets has been due to interaction of several factors: chemical and physical processes that affect rapid lithification, factors that disturb mechanical and biological decomposition and the composition of pellets. In some cases, silicification may have supported the preservation of pellets in carbonates.
- Fauna inhabiting various empty shells was diverse through the Middle and Late Ordovician in Estonia, consisting of mobile trace makers with different feeding strategies.
- The trace maker of *Arachnostega* was most probably not the producer of the faecal pellets inside shells.

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## Mikrokoproliidid Eesti Ordoviitsiumi makrofossiilides

Fossiilsed ekskrementid ehk koproliidid on halvasti säiluvad jäljekivistised, mis kannavad olulist paleoökoloogilist ja sedimentoloogilist teavet. Artiklis on kirjeldatud Eesti Kesk- ja Ülem-Ordoviitsiumist (Baltoskandia paleobassein) makrofossiilide kodade sisemuses säilunud mikrokoproliti ning nende levikut ja mitmekesisust. Uuritud materjal sisaldab üle 180 koproliti sisaldava makrofossiili, mis on kogutud enam kui 40 leiukohast ja esindavad mitmesuguseid madalaveelisi keskkondi alates jahedaveelisest karbonaatsest platvormist troopilise avašelfini. Stratigraafiliselt pärinevad mikrokoprolitiidide leiud Volhovi lademest kuni Pirgu lademeni (Dapingi kuni Katy globaallade). Mikrokoproliidid on ovaalsed või pulkjad, 0.1–1.8 mm pikkused ja 0.08-0.75 mm läbimõõduga; pikkuse/läbimõõdu suhe ulatub 6-ni. Mikrokoproliidid esinevad tigude, karpide, peajalgsete, käsijalgsete, okasnahksete ja trilobiitide kodades ning kuuluvad valdavalt liikidesse *Coprolus oblongus* ja *Coprolus bacilliformis*. Lisaks tuvastati kaks kompleks-jäljekivistist: *Tubularina* (koproliidid ümmarguse ristlõikega käikudes) ja *Alcyonidiopsis* (koproliidid lintjates käikudes). Mikrokoproliidid tekitati siis, kui organismide tühjad kodad asusid merepõhjas või olid veidi settesse mattunud. Koproliidid säilusid tõenäoliselt tänu kodade mehaanilisele kaitsele ja kiirele mineraliseerumisele. Mikrokoprolitiidide tekitajate bioloogiline päritolu jääb spekulatiivseks, kuid tõenäolisemate rühmade hulka kuuluvad polüheedid, kellel on sobiv suurus ja kehakuju ning kelle tänapäevased esindajad tekitavad sarnaseid fekaale. Võimalik, et mikrokoprolitiidide tekitamisel osalesid erineva toitumisstrateegiaga organismid. Valitud leiukohtade makrofossiilide süstemaatiline uuring näitas, et kuni pooltes kodades esineb mikrokoprolite. See näitab koproliti tootvate organismide suurt arvukust ja mitmekesisust Baltoskandia Ordoviitsiumi basseinis. Meie materjal näitas ka, et *Arachnostega* jäljekivististe tekitaja ei olnud tõenäoliselt mikrokoprolitiididega seotud.

## Figure and table captions

**Fig. 1.** Locality map showing the outcrop area of Ordovician rocks in the Baltic region (green) and schematic configuration of the Baltoscandian basin (after Männil 1966a and Nestor & Einasto 1997).

1 – main land areas, 2 – shallow-water Estonian shelf, 3 – deeper-water Livonian basin and Central Baltoscandian facies belt, 4 – deep shelf of the Scanian facies belt (modified after Toom et al. 2019a).

**Fig. 2.** Regional and international stratigraphy of the studied interval, showing transition from cool-water to warm-water carbonate deposits (modified after Toom et al. 2019a).

**Fig. 3.** Faecal pellets inside Ordovician shelly fossils from Estonia. Scale bars: 1 cm for A, C, H; 1 mm for B, E, D, F, G, I. **A**, Echinoderm *Sphaeronites*, massive accumulation of pellets, vertical section, GIT 156-1066, Värskä 6 drillcore, 381.8 m, Haljala Stage, Sandbian. **B**, Detail from GIT 156-1066, *C. oblongus*. **C**, Brachiopod *Porambonites*, two sets of pellets inside, boundary between sets is distinct, one of the sets is almost completely decomposed, GIT 399-1961, Aluvere quarry, Haljala Stage, Sandbian. **D**, Detail from GIT 399-1961, *C. oblongus*. **E**, Gastropod *Hormotoma insignis*, surface of steinkern, two different sizes of *Coprulus* (L/W ratio 2,7), TUG 80-484, Piilse, Rakvere Stage, Katian. **F**, Bivalve *Aristerella*, detail from surface, *Coprulus* (L/W ratio 4), GIT 694-93, Kullaaru ditch, Oandu Stage, Katian. **G**, Gastropod *Subulites wesenbergensis*, horizontal section through the apical part of steinkern, boundary between the accumulation of pellets and sediment is transitional, decomposition of pellets has almost finished. GIT 404-639, Mõnuste quarry Harjumaa, Vormsi Stage, Katian. **H**, Gastropod *Lesueurilla*, horizontal section through the apical part, *Coprulus* (L/W ratio 2.3), GIT 720-1, Aluvere quarry, Haljala Stage, Sandbian. **I**, Detail from GIT 720-1, on the left side of the image are decomposed pellets.

**Fig. 4.** Faecal pellets inside Ordovician shelly fossils from Estonia. Scale bars: 1 mm for A-B, D, F-I; 1 cm for C, E. **A**, Gastropod *Liospira wesenbergense*, weathered steinkern, largest *Coprulus* (L/W ratio 2.5), TUG 1780-380, Rägavere quarry, Rakvere Stage, Katian. **B**, Gastropod *Hormotoma insignis*, polished surface of steinkern, *Coprulus* (L/W ratio 2.4), TUG 76-63, Rägavere quarry, Rakvere Stage, Katian. **C**, Gastropod *Hormotoma insignis*, steinkern surface with pellets and trace fossil *Arachnostega*. TUG 2-393, Rakvere, Rakvere Stage, Katian. **D**, Detail from TUG 2-393, *Coprulus* (L/W ratio 3), *Arachnostega* and openings of small burrows filled with sparry calcite. **E**, Section through the cephalopod phragmocone, only one chamber is filled with pellets, GIT 362-740, Viki borehole, 360.9 m, Kunda Stage, Darriwilian. **F**, Section of cephalopod *Estonioceras*, detail from siphuncle filled with *C. oblongus*, GIT 146-7, Valkla outcrop, Kunda Stage, Darriwilian. **G**, Section of brachiopod *Clinambon anomalus*, detail from spondylium filled with *C. oblongus*. GIT 543-1367, Saku 1098 borehole, 10.3 m, Keila Stage, Katian. **H**, Brachiopod *Porambonites*, polished surface, *C. oblongus* (L/W ratio 2), GIT 619-85, Oandu River outcrops, Rakvere Stage, Katian. **I**, Brachiopod *Porambonites wesenbergensis*, detail from sectioned surface, bioturbated pellets different in shape and size. TUG 1766-141, Oandu, Oandu Stage, Katian.

**Fig. 5.** Faecal pellets inside Ordovician shelly fossils from Estonia. Scale bars: 1 cm for A, D, F, I; 1 mm for B, C, E, J, G, H, K. **A**, Bivalve *Modiolopsis*, wethered steinkern covered by pyrite threads, TUG 1779-477, Rakvere, Rakvere Stage, Katian. **B**, detail from TUG 1779-477, rod shape pellets *C. bacilliformis*. **C**, Bivalve *Modiolopsis*, detail from strongly wethered steinkern surface, *Coprulus* (L/W ratio 3), TUG 1779-439, Estonia, Rakvere Stage, Katian. **D**, Gastropod *Hormotoma insignis*, redeposited steinkern with crush mark, cracks, overgrown by trepostome bryozoans, TUG 76-62, Rägavere quarry, Rakvere Stage, Katian. **E**, Detail from TUG 76-62, steinkern surface with pellets and small bryozoan colony. **F**, Bivalve *Cypricardina*, vertical section, bioturbated sediments and composite trace fossil *Tubularina*, GIT 156-1079, Oandu, Keila Stage, Katian. **G, H**, Detail from GIT 156-1079, *Tubularina* filled with *C. oblongus*, cross-sections at different angles. **I**, Gastropod

*Subulites amphora*, vertical section, bioturbated accumulations of pellets and trace fossil *Tubularina* filled with *C. oblongus*, GIT 399-999, Aluvere quarry, Haljala Stage, Sandbian. J, Detail from GIT 399-999. K, Pygidium of asaphid trilobite, *Alcyonidiopsis* filled with *C. oblongus*, GIT 362-726, Vasalemma quarry, Keila Stage, Katian.

**Table 1.** Stratigraphic distribution of shelly fossils with pellets inside in the Ordovician carbonate succession of Estonia. Basin margin and type of sediments after Dronov & Rozhnov (1997). The numbers after plus sign denote finds from 30 randomly selected sliced shells. Note that pellets have not been recorded in the topmost Ordovician Porkuni Stage so far.

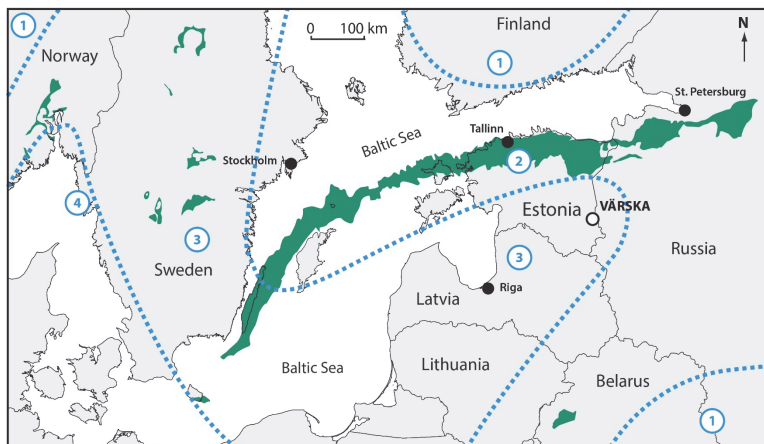


Fig. 1.

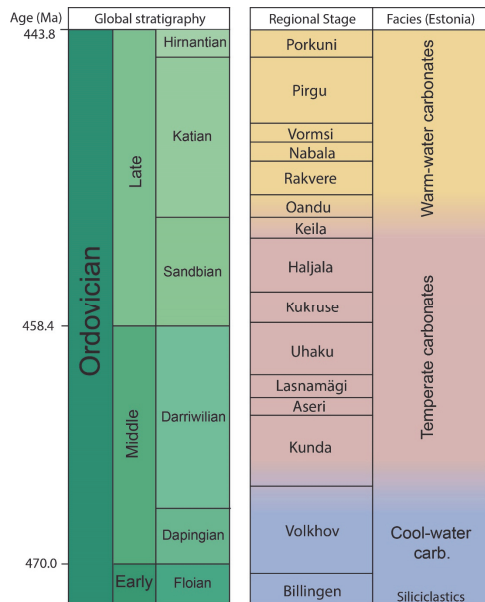


Fig. 2.

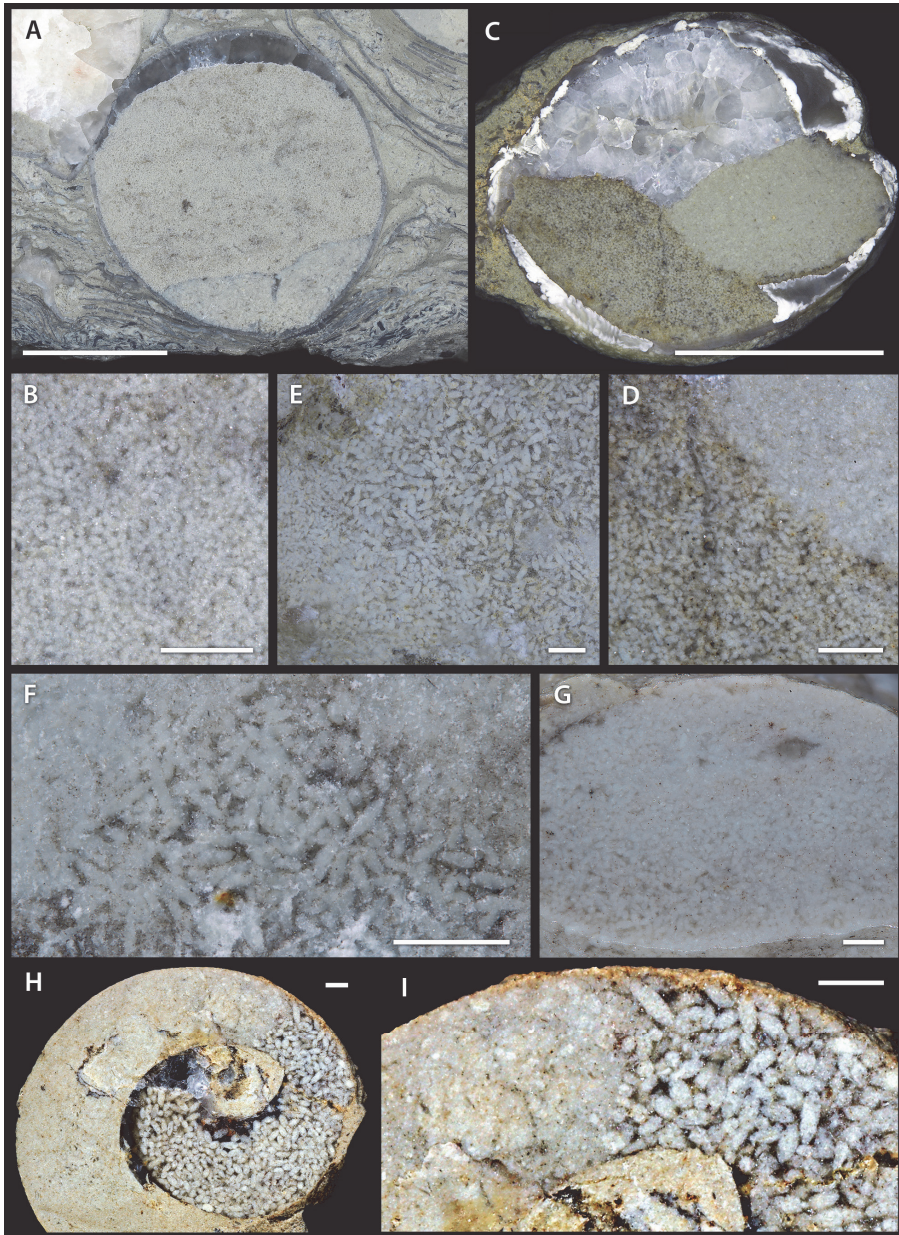


Fig. 3.

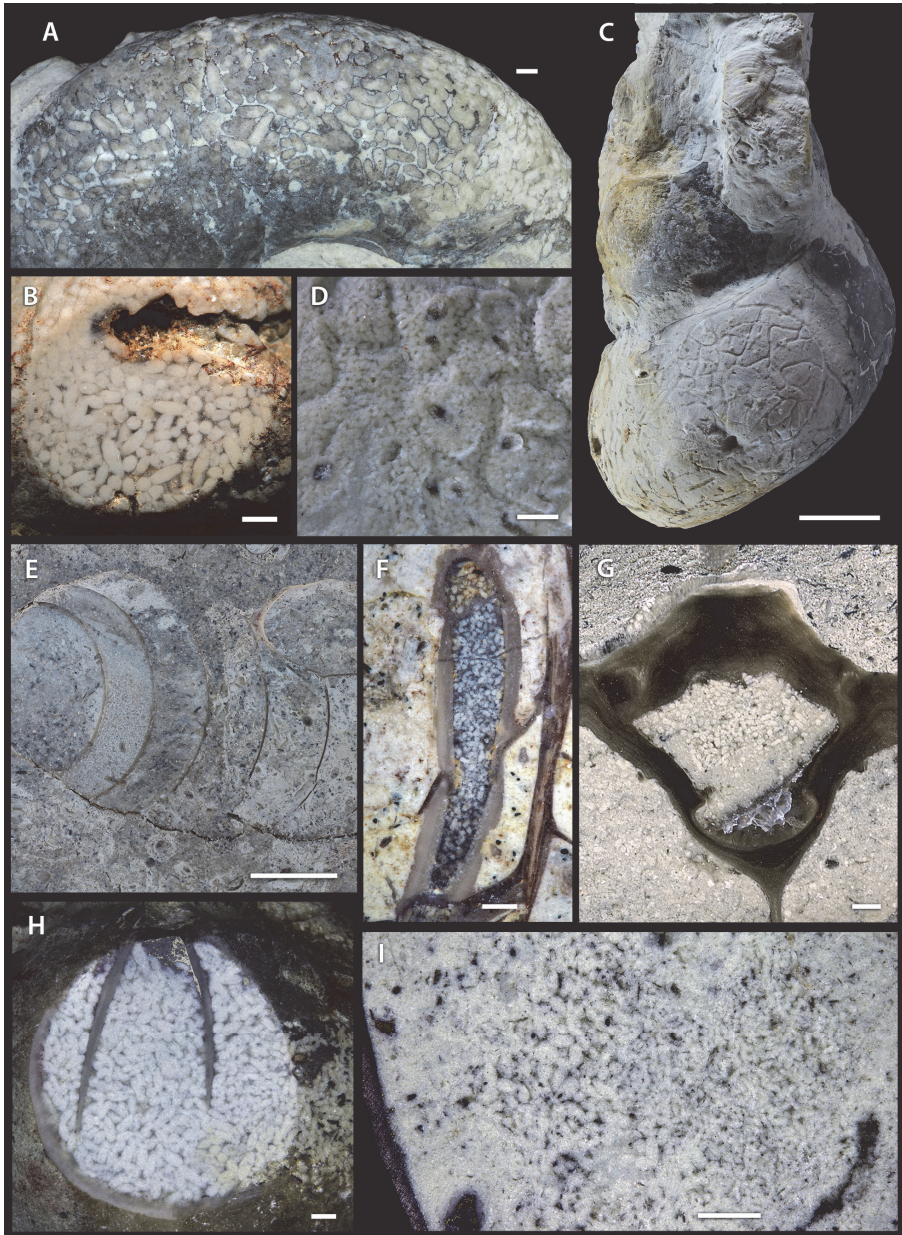


Fig. 4.





Fig. 5.

| Regional Stage | Age          | Basin type     | Type of carbonate sediment | Type of pellets  | Trace fossil   | Gastropoda | Cephalopoda | Bivalvia | Brachiopoda | Echinodermata | Trilobita | Total | Length, mm | Width, mm |
|----------------|--------------|----------------|----------------------------|--|--|------------|-------------|----------|-------------|---------------|-----------|-------|------------|-----------|
| Porkuni        | Hirnantian   | rimmed shelf   | tropical                   | N/A  | N/A  |            |             |          |             |               |           | 0     |            |           |
| Pirgu          | Katian       | rimmed shelf   | tropical                   | elliptical; L/D ratio s2, 2-3  | <i>Coprulius, Tubularina</i> , unidentified burrow                         | 2          | 2           |          |             |               |           | 4     | 0.23-0.34  | 0.09-0.23 |
| Vormsi         | Katian       | rimmed shelf   | tropical                   | elliptical; L/D ratio s2, 2-3  | <i>Coprulius</i>   | 4+11       | 1           |          |             |               |           | 16    | 0.46-0.95  | 0.19-0.45 |
| Nabala         | Katian       | rimmed shelf   | tropical                   | elliptical; L/D ratio s2, 2-3  | <i>Coprulius</i>   | 3          |             |          |             |               |           | 3     | 0.6-1.2    | 0.3-0.5   |
| Rakvere        | Katian       | rimmed shelf   | tropical                   | elliptical, elongated elliptical, rod-shaped; L/D ratio s2, 2-3, 5-6 | <i>Coprulius, Tubularina</i>   | 38         |             | 9        | 3           |               |           | 50    | 0.2-1.8    | 0.1-0.75  |
| Oandu          | Katian       | rimmed shelf   | tropical                   | elliptical, elongated elliptical; L/D ratio 2-3, 5                   | <i>Coprulius, Tubularina</i> , unidentified burrow                         | 1          |             | 2        | 12          |               |           | 15    | 0.3-0.7    | 0.1-0.3   |
| Keila          | Katian       | rimmed shelf   | tropical                   | elliptical; L/D ratio s2   | <i>Coprulius, Tubularina</i> , <i>Alcyonidiopsis</i> , unidentified burrow | 3          |             | 1        | 4           |               | 1         | 9     | 0.26-0.38  | 0.15-0.2  |
| Hajjala        | Sandbian     | carbonate ramp | temperate                  | elliptical, rod-shaped; L/D ratio s2, 2-3, 4-5?                      | <i>Coprulius, Tubularina</i>   | 28+15      | 5           | 2        | 0+12        | 1             | 1         | 64    | ≤0.1-0.8   | 0.08-0.4  |
| Kukruuse       | Sandbian     | carbonate ramp | temperate                  | elliptical; L/D ratio s2   | <i>Coprulius</i>   | 2          |             | 1        |             | 1             |           | 4     | 0.17-0.3   | 0.09-0.15 |
| Uhaku          | Darriwillian | carbonate ramp | temperate                  | elliptical; L/D ratio s2, 2-3  | <i>Coprulius</i>   | 5          |             |          |             |               |           | 5     | 0.4-0.6    | 0.11-0.3  |
| Lasnamägi      | Darriwillian | carbonate ramp | temperate                  | elliptical; L/D ratio s2   | <i>Coprulius</i>   | 3          |             |          |             |               |           | 3     | 0.13-0.14  | 0.25      |
| Aseri          | Darriwillian | carbonate ramp | temperate                  | elliptical; L/D ratio s2   | <i>Coprulius</i>   | 1          |             |          |             |               |           | 1     | 0.24       | 0.12      |
| Kunda          | Darriwillian | carbonate ramp | temperate                  | elliptical; L/D ratio s2, 2-3  | <i>Coprulius</i>   |            | 4           |          |             |               |           | 4     | 0.3-0.5    | 0.15-0.2  |
| Volkhov        | Dapingian    | carbonate ramp | cool                       | elliptical; L/D ratio 2-3  | <i>Coprulius</i>   |            |             |          | 1           |               |           | 1     | 0.45       | 0.2       |
| Total:         |              |                |                            |  |  | 112        | 16          | 15       | 32          | 2             | 2         | 179   |            |           |

Table 1

### **Publication III**

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## First description of rare *Teichichnus* burrows from carbonate rocks of the Lower Paleozoic of Estonia

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**Abstract:** *Teichichnus* burrows occur in the Sandbian, Katian and Telychian of Estonia associated with carbonate rocks. It is possible that *Teichichnus* is more common in the Sandbian than in the Lower to Middle Ordovician and in the Silurian. Two ichnospecies, *T. rectus* and *T. patens*, have been identified from the Lower Paleozoic of Estonia. This is the first record of *T. patens* in the Ordovician of Baltica. *Teichichnus* in the Sandbian, Katian and Telychian of Estonia is restricted to the shallowest tier levels. The rarity of *Teichichnus* in the carbonate sequences of the Ordovician and Silurian of Estonia reflects little bathymetric variability and an extremely low sedimentation rate in the shallow epicontinental basin.

**Key-words:**

- trace fossils;
- *Teichichnus*;
- carbonate rocks;
- Upper Ordovician;
- Telychian;
- Baltica

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**Résumé :** *Première description de rares terriers de Teichichnus à partir de roches carbonatées du Paléozoïque inférieur de l'Estonie.*- Les terriers de *Teichichnus* sont présents dans le Sandbien, le Katien et le Telychien d'Estonie, associés à des roches carbonatées. Il est possible que *Teichichnus* soit plus commun dans le Sandbien que dans l'Ordovicien inférieur et moyen ainsi que dans le Silurien. Deux ichno-espèces, *T. rectus* et *T. patens*, ont été identifiées dans le Paléozoïque inférieur d'Estonie. Il s'agit du premier enregistrement de *T. patens* dans l'Ordovicien de Baltica. *Teichichnus* dans le Sandbien, le Katien et le Telychien d'Estonie est limité aux niveaux les moins profonds. Sa rareté dans les séquences carbonatées de l'Ordovicien et du Silurien en Estonie reflète une faible variabilité bathymétrique combinée à une vitesse de sédimentation extrêmement faible dans le bassin épicontinental peu profond.

**Mots-clefs :**

- trace fossiles ;
- *Teichichnus* ;
- roches carbonatées ;
- Ordovicien supérieur ;
- Télychien ;
- Baltica

### 1. Introduction

Trace fossils are common and diverse throughout the Phanerozoic. They are valuable environmental indicators and help us understand the behaviour of extinct organisms (SEILACHER, 2007). The trace fossils of the Ordovician and Silurian have been relatively well studied (SEILACHER, 2007). The Ordovician and Silurian of Estonia (Baltica) has an excellent record of sedimentary rocks and associated fossils, including trace

fossils (RAUKAS & TEEDUMÄE, 1997). MÄNNIL *et al.* (1984) report that trace fossils are abundant and distributed all over the palaeobasin, but their diversity is lower than in the Cambrian and Devonian of the region. Recent studies show that Ordovician and Silurian trace fossil association are more diverse than previously expected (TOOM *et al.*, 2017). However, trace fossils of the carbonate rocks from the Ordovician and Silurian of Estonia (MÄNNIL, 1966) have historically received less attention than various groups of shelly fossils. In

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contrast, Lower Paleozoic trace fossils have systematically been described from Scandinavia and northwestern Russia (STANISTREET, 1989; DRONOV *et al.*, 2002; ERSHOVA *et al.*, 2006; KNAUST & DRONOV, 2013; HANKEN *et al.*, 2016). Recently, several traces have been described from the Ordovician and Silurian limestones of western and northern Estonia (VINN & WILSON, 2013; VINN & TOOM, 2015, 2015; VINN *et al.*, 2014, 2015c). Bio-erosional trace fossils (ORVIKU, 1960, 1961; DRONOV *et al.*, 2000; WYSE JACKSON & KEY, 2007; VINN *et al.*, 2015b) and various bioclastrations (VINN *et al.*, 2015a) have the best record among trace fossils in the Ordovician and Silurian of Estonia. Soft bottom trace fossils of the Ordovician and Silurian of Estonia deserve to be studied in more detail in order to use their full potential as paleo-environmental indicators. The diversity of soft bottom trace fossils are also indirect indicators of biological diversity in the past seas.

*Teichichnus* is a fodinichnial burrow that has a good record in Phanerozoic rocks (BUCKMAN, 1996). *Teichichnus* burrows are spreite structures which are characterized by a spreite lamina that formed through the displacement of a limb (SCHLIRF & BROMLEY, 2007). The lamina is composed of successively placed floors of the rising burrow limb, which are designated lamellae (SCHLIRF & BROMLEY, 2007). Eighteen ichnospecies have been described due to high variation of burrow morphology (KNAUST, 2018). However, only four ichnospecies are currently regarded as valid: *Teichichnus rectus*, *T. zigzag*, *T. patens* and *T. duplex* (STANTON & DODD, 1984; FREY & BROMLEY, 1985; SCHLIRF, 2000; SCHLIRF & BROMLEY, 2007; MÁNGANO & BUATOIS, 2011; KNAUST, 2018). Combined modes of feeding are involved in formation of *Teichichnus*, including deposit and suspension-feeding, suggesting that *Teichichnus* is a dwelling trace rather than a feeding trace (KNAUST, 2018). *Teichichnus* is considered the best example of the architectural category "Horizontal burrows with simple vertically oriented spreiten" by BUATOIS *et al.* (2017). In addition to the classical interpretation of polychaetes as producers, many features fit with an interpretation of dwelling echinurans and holothurians (KNAUST, 2018, in press). Arthropods, vermiform organisms and especially annelids have been suggested as possible trace-makers of *Teichichnus* (VOSSLER & PEMBERTON, 1989; DAM, 1990). In Baltica, *Teichichnus* occurs in the Cambrian of Sweden (MARTINSSON, 1965; JENSEN, 1997), Middle Ordovician of the St. Petersburg region of Russia (DRONOV & MIKULÁŠ, 2010) and Upper Ordovician of the Oslo-Asker region in Norway (STANISTREET, 1989).

This paper addresses the following question: how common and diverse are *Teichichnus* burrows in the Ordovician and Silurian of Estonia?

## 2. Material and methods

A large collection of more than 2500 specimens of trace fossils from the Department of Geology, Tallinn University of Technology, and the University of Tartu Natural History Museum geological collections were searched for *Teichichnus* burrows. All *Teichichnus* specimens were photographed with scale bar using a Canon EOS 5Dsr digital camera.

There are hundreds of well-studied Ordovician outcrops in the northern Estonia covering all the international stages. Similarly, all Silurian stages are present, well exposed and studied in middle and western Estonia. Only relatively shallow water rocks are cropping out in the Ordovician and Silurian exposures of Estonia. In carbonate rocks it is common that color contrast is absent, which impacts preservation of biogenic structures (CURRAN, 1994). Delicate traces or parts of them are rarely well preserved (KNAUST *et al.*, 2013) in carbonates. *Teichichnus* usually occurs in lower shoreface to offshore deposits (PEMBERTON *et al.*, 2012) and is typical for low- to moderate-energy conditions (KNAUST, 2017). Given the above, it may be assumed that *Teichichnus* is an under-sampled trace fossil in Estonia, especially in drill cores representing deeper environments.

## 3. Geological background

During the Ordovician, the palaeocontinent Baltica drifted from the temperate climatic zone into the subtropical realm (NESTOR & EINASTO, 1997; TORSVIK *et al.*, 2013). In the Middle Ordovician and lower Upper Ordovician (Sandbian), the area of modern Estonia (Fig. 1) was covered by a shallow, epicontinental sea. It was characterized by little bathymetric variability and an extremely low sedimentation rate (NESTOR & EINASTO, 1997). Along the entire extent of the ramp a series of grey argillaceous and calcareous sediments accumulated with a trend of decreasing clay and increasing bioclasts in the onshore direction (NESTOR & EINASTO, 1997). During the Katian, the climatic change resulted in an increase in carbonate production and sedimentation rate. The Katian was the time of appearance of the first carbonate buildups in the basin.

During the Silurian, Baltica was located in equatorial latitudes and moving northwards (COCKS & TORSVIK, 2005; TORSVIK *et al.*, 2013). A shallow epicontinental basin covered middle and western Estonia (Fig. 1) with a wide range of tropical environments and diverse biotas (NESTOR & EINASTO, 1997). Five main facies belts have been described from the Baltic basin: tidal flat/lagoon, shoal, open shelf, basin slope and a basin depression (NESTOR & EINASTO, 1977). The first three facies belts formed are confined to a carbonate platform (RAUKAS & TEEDUMÄE, 1997).

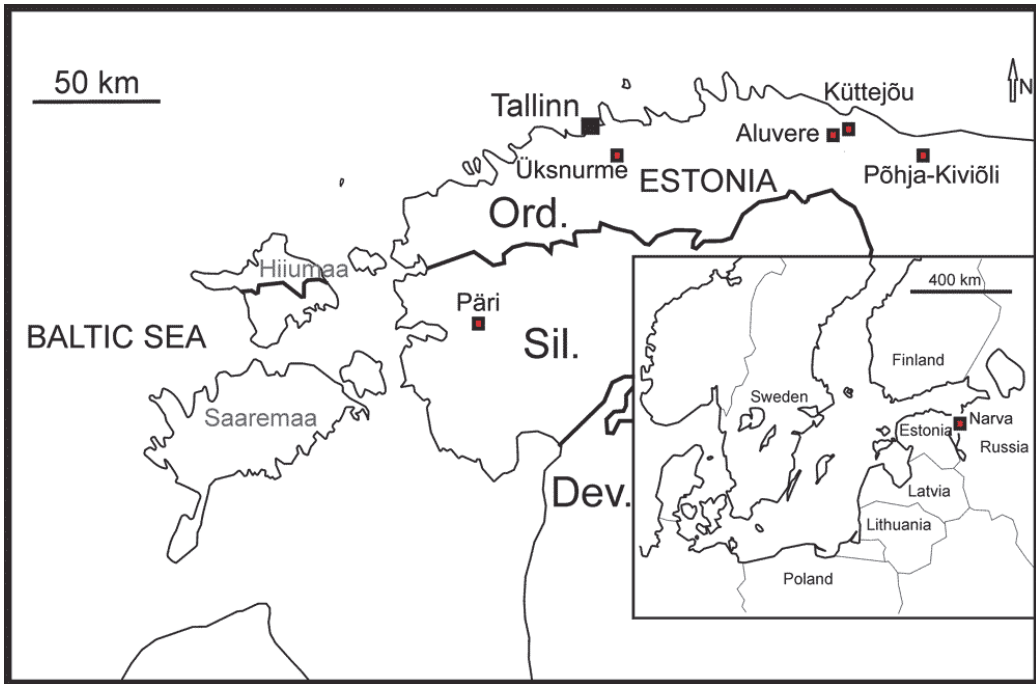


Figure 1: Locality map. Modified after VINN *et al.* (2017).

#### 4. Systematic ichnology

##### **Ichnogenus *Teichichnus* SEILACHER, 1955**

Type ichnospecies. *Teichichnus rectus* SEILACHER, 1955 - p. 378, Pl. 24, fig. 1; by monotypy.

##### ***Teichichnus rectus* SEILACHER, 1955**

(Fig. 2)

Material: Ten burrows preserved in full relief, eight from Sandbian, one from Katian and one from Telychian.

Localities: Narva open pit, Põhja-Kiviõli open pit and Ubja open pit (Sandbian, Kukruse Regional Stage); Aluvere quarry (Sandbian, Haljala Regional Stage); Üksnurme (Katian, Oandu Regional Stage); Päre quarry (Telychian, Adavere Regional Stage) (Fig. 1).

Stratigraphic distribution: lower Sandbian (Kukruse Regional Stage) to lower Telychian (Adavere Regional Stage).

Observations: Horizontal, sometimes slightly inclined, straight to slightly winding, unbranched burrows. The trace fossil consists of convex-down lamellae, forming a wall-like spreite structure. All laminae are arranged retrusively. Terminal burrow tube preserved in some specimens; without strongly upward bending terminal tubes. In lateral view, parallel, more-or-less horizontal lamina

form a spreite structure, topped by a tube in some specimens. In transverse section, slight lateral displacements of the lamina can occur. Height of the trace is 1.5 to 6.0 cm. Length of the trace is 7.2 to 14.2 cm. Width of a single trace can be slightly variable. Maximal width of the trace is 0.25 to 3.5 cm. Thickness of individual laminae varies from 0.8 to 12 mm. Silurian burrows are markedly smaller than Upper Ordovician ones.

Note: KNAUST (2018) has provided a detailed synonymy of *Teichichnus rectus*.

##### ***Teichichnus patens* SCHLIRF, 2000**

(Fig. 3)

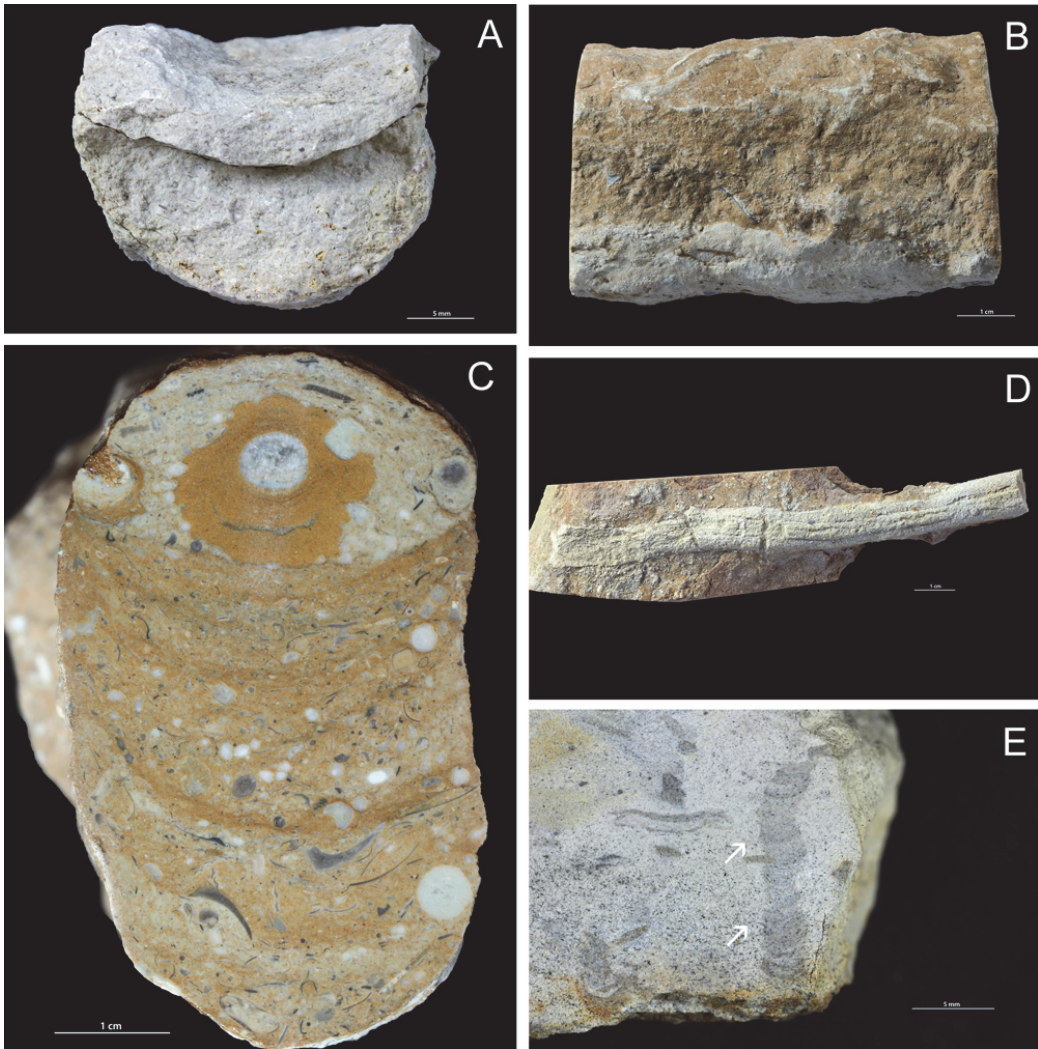
1992 *Teichichnus* ichnosp. (ichnosp. nov.) MIKULÁŠ, p. 328, Fig. 2; Pl. 7 fig. 2C.

2000 *Teichichnus patens* SCHLIRF, p. 173, Pl. 6, fig. 5.

Material: Single burrow preserved in full relief.

Locality: Narva open pit (Sandbian, Kukruse Regional Stage) (Fig. 1).

Observations: Horizontal, predominantly straight, branching burrows. Burrows consist of gutter-shaped retrusive laminae. Terminal burrow tube not preserved. Branching via bifurcation at acute angles, branching with up to three branches from a central burrow. Total height of burrow 1.0 cm, burrow width 0.4 to 0.9 cm, total length of burrow 12 cm.



**Figure 2:** A, Cross section of *T. rectus* from the Haljala Regional Stage (Sandbian), northern Estonia (GIT 720-796). B, Lateral view of *T. rectus* from the Kukruse Regional Stage (Sandbian), northeastern Estonia (GIT 398-203). C, Cross section of *T. rectus* from the Kukruse Regional Stage (Sandbian), northeastern Estonia (GIT 398-203). D, Horizontal view of *T. rectus* from the Kukruse Regional Stage (Sandbian), northeastern Estonia (GIT 343-201). E, Cross section of *T. rectus* from the Adavere Regional Stage (Telychian), western Estonia (GIT 340-303). Arrows point to *Teichichnus* burrow.

## 5. Discussion

All *Teichichnus* burrows occur in the carbonate part of the section (Middle Ordovician to Silurian). The rarity of *Teichichnus* is not surprising in the Ordovician and Silurian of Estonia. It is a common ichnofossil in the Phanerozoic sediments and it occurs mainly in low-energy depositional systems. *Teichichnus* is usually recorded in fully oxygenated substrates (LIMA & NETTO, 2012), but

it also occurs in substrates with stressful conditions and in this case specimens are generally smaller and with diminutive spreiten (BUATOIS *et al.*, 2005). Ordovician *Teichichnus* material from Estonian collections shows diminutive spreiten but it is always associated with relatively diverse ichnofauna (*Conichnus*, *Amphorichnus*, *Planolites*, *Thalassinoides*, *Taenidium*, *Phycodes*) and abundant shelly fauna. VOSSLER and PEMBERTON (1989)





**Figure 3:** Horizontal view of *T. patens* from the Kukruse Regional Stage (Sandbian), northeastern Estonia (GIT 360-111).

noted that *Teichichnus* behavior type is not beneficial in areas of slow and steady sedimentation rate; Estonian material originated from such areas of shallow epeiric sea and is in agreement with this idea. Findings of *Teichichnus* burrows are related with deeper environments than shoreface and also with periods of higher sedimentation rate in the Ordovician and Silurian. *Teichichnus* burrows have mostly been reported from siliciclastic rocks (SEILACHER, 1955; BUCKMAN, 1996; SEILACHER, 2007; SCHLIRF & BROMLEY, 2007; KNAUST, 2018). Fewer findings are reported from carbonates, mostly from Mesozoic chalk (e.g., FREY, 1970; FREY & BROMLEY, 1985). There are important differences between the formations of trace fossils in carbonate versus siliciclastic sediments (CURRAN, 1994; KNAUST *et al.*, 2012). In carbonate rocks it is common that colour contrast is absent, which impacts the preservation of trace fossils (CURRAN, 1994). This may explain the more frequent occurrence of *Teichichnus* in kukersite bearing beds in lower Sandbian of Estonia where clear color contrast occurs between the trace filling and rock matrix.

The majority of studied *Teichichnus* specimens from Estonia have been collected from lower Upper Ordovician (Sandbian) rocks. It is likely that the more common *Teichichnus* in the lower Upper Ordovician is reflecting favorable sedimentation

conditions rather than the increase in number of trace makers.

In the Cambrian, *Teichichnus* along with other Cambrian feeding burrows, is only known from shallow tier levels (BUCKMAN, 1996). Already by the Upper Cambrian-Lower Ordovician *Teichichnus* occurred at depths of up to 150 mm within deep-sea flysch sediments (PICKERILL & WILLIAMS, 1989). An Upper Cretaceous *Teichichnus* reached a depth of emplacement in excess of 1 meter (FREY & BROMLEY, 1985). *Teichichnus* in the Ordovician of Estonia seems to be confined to the shallowest tier levels. Some *Teichichnus* traces may be quite a long and not very deep as was described by LEGG (1985) from the Middle Cambrian sediments. Similar shallow traces occur in Estonian kukersite. A very stunted vertical spreiten may be related to the flimsy soft sediment layer. Alternatively, the carbonate muds contain a high content of organic matter in comparison to sands. Estonian kukersite originated from organic material (FOSTER *et al.*, 1990) and offered an environment especially rich in deposited organics. In this kind of organic rich sediment the *Teichichnus* producer could move around less frequently for successful feeding than in organic poor sediments. Thus, amount of food in the sediment could influence the tier of *Teichichnus* traces. In the Silurian of Estonia *Teichichnus* occurs in the



Osmundsbergen bentonite, where it is considerably smaller and shows relatively deeper spreiten than the Ordovician traces. It was formed in conditions where sediment accumulated rapidly; this kind of trace is interpreted as an equilibrium feeding structure (CORNER & FJALSTAD, 1993).

Different ichnospecies of *Teichichnus* have different palaeogeographic distributions. The only ichnospecies with global distribution in the Lower Paleozoic is *T. rectus* (KNAUST, 2018). Another Lower Paleozoic ichnospecies, *T. patens*, has more restricted distribution being hitherto known only from the Upper Ordovician of Bohemia (MIKULÁŠ, 1992). New findings from the Upper Ordovician of Estonia demonstrate that this ichnospecies had a wider geographic distribution than previously known.

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## Rare arthropod traces from the Ordovician and Silurian of Estonia (Baltica)

Olev Vinn and Ursula Toom

With 3 figures and 1 table

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**Abstract:** Arthropod trace fossils are rare and of very limited diversity in Ordovician and Silurian strata of Estonia. Only two ichnogenera have been documented: *Rusophyucus* is known from a single occurrence in the Late Ordovician (Katian) and *Cruziana* from several specimens in the Late Silurian (Ludlow to Pridoli). In contrast, body fossils of large arthropods are relatively common in these rocks, suggesting that the poor trace fossil record is related to their lower preservation potential in the dominantly carbonate mud and sand lithologies on wide epeiric carbonate platform.

**Key words:** Trace fossils, arthropods, Katian, Ludfordian, Pridoli, epeiric carbonate platform.

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### 1. Introduction

Trace fossils are common throughout the Phanerozoic being useful environmental indicators and tools for understanding the behaviour of extinct organisms (SEILACHER 2007). Early Paleozoic trace fossils have been relatively well studied (SEILACHER 2007). The Early Paleozoic of Estonia (Baltica) has an excellent record of sedimentary rocks and associated fossils (RAUKAS & TEEDUMÄE 1997). Early Paleozoic trace fossils have systematically been described from Scandinavia and NW Russia (DRONOV et al. 2002; KNAUST 2004; DAVIES et al. 2006; ERSHOVA et al. 2006; KNAUST et al. 2012; KNAUST & DRONOV 2013; MIKULÁŠ et al. 2013). There are several papers dealing with the Ordovician (VINN & TOOM 2014; VINN et al. 2014) and Silurian trace fossils (VINN & WILSON 2013; VINN 2014) of Estonia. The Ordovician and Silurian carbonate rocks of Estonia are rich in arthropod body fossils, but their traces have remained poorly studied (VINN 2014). The ichnology of siliciclastic systems is better studied compared to that

carbonate sedimentary systems such as studied here. Early-diagenetic processes in carbonate systems can lead to rapid lithification with trace-fossil accentuation, but can also result in little to no sediment color contrast between burrows and rock matrix and bears a high potential for diagenetic alternation of trace fossils and hosting rocks (KNAUST et al. 2012).

This paper addresses questions about the abundance, diversity, and stratigraphic distribution of arthropod trace fossils in Ordovician and Silurian carbonate rocks of Estonia.

### 2. Geological background and localities

During the Ordovician and Silurian Estonia was part of shallow cratonic sea. In the Dapingian, Darriwilian and Sandbian, the area of modern Estonia (Fig. 1) was covered by a shallow epicontinental sea with little bathymetric variability and an extremely low sedimentation rate (JAANUSSON 1972; HINTS et al. 1994; NIELSEN

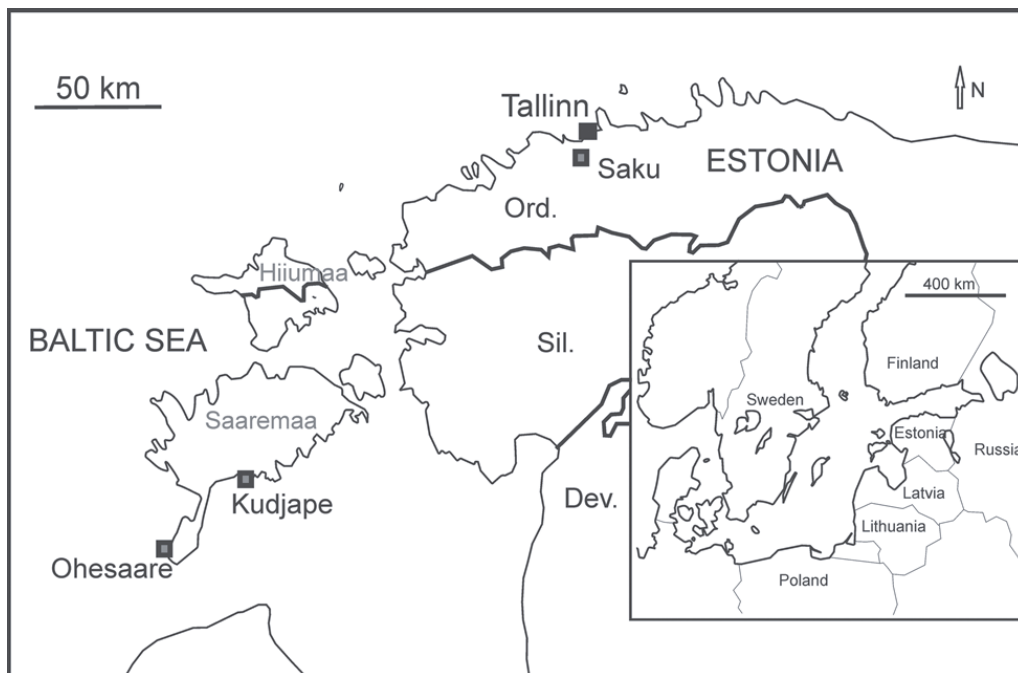


Fig. 1. Locality map. Ord. = Ordovician; Sil. = Silurian; Dev. = Devonian.

2004) and input of terrigenous sediments was limited. The deposits are settled nearly horizontally, with numerous breaks caused by repeated fluctuation of the sea depth. The Ordovician strata of the region is some 100–200 m (LINDSKOG et al. 2012) and average net accumulation rates were of the order of 1–9 mm/1,000 years (NIELSEN 2004). During the Ordovician, the palaeocontinent Baltica moved from the temperate climatic zone into the subtropical realm (NESTOR & EINASTO 1977; TORSVIK et al. 1992). Climatic change in the Late Ordovician resulted in an increase in carbonate production and sedimentation rate on the shelf; the first carbonate buildups appeared in the Baltic Basin. In the latest Ordovician during the Caledonian Orogeny the Baltica continent collided with Avalonia. During the Silurian, Baltica was located in equatorial latitudes and it continued its drift northwards (COCKS & TORSVIK 2005). Central and western Estonia (Fig. 1) were covered by an epicontinental sea that was characterized by wide range

of tropical environments and diverse biotas (KALJO & HINTS 1996). Five main facies belts occur in the Estonian part of Baltic basin: tidal flat/lagoonal, shoal, open shelf, slope and depression, the first three comprising a carbonate platform (NESTOR & EINASTO 1977).

Studied arthropod traces originate from Saku Quarry, Kudjape ditch and Ohesaare cliff (Table 1).

### 3. Material and methods

A large collection (more than 2000 specimens) of trace fossils at the Institute of Geology, Tallinn University of Technology (TUT) was searched for arthropod traces. Selected specimens were photographed using a Nikon 7000 digital camera. The electronically databased part of Estonian trilobite collections contains 3849 specimens from the Silurian and 4815 specimens from the Ordovician.

Northern Estonia has hundreds of well-studied Ordovician outcrops covering all international stages. Similarly, rocks representing all Silurian stages are well exposed and



**Table 1.** Locality information.

| Locality       | Coordinates<br>World<br>Geodetic<br>System 84 | Description   | References                         |
|----------------|---|---|------------------------------------|
| Saku quarry    | 59.299934;<br>24.646433                       | A 3.5 m thick section of argillaceous wackestone and coarse-grained packstones-grainstones of Saku Member. In addition to the rich shelly fauna, <i>Planolites</i> , <i>Phycodes</i> , <i>Palaeophycus</i> , <i>Rosselia</i> , <i>Chondrites</i> , tool marks and <i>Rusophycus</i> occur.  | KRÖGER et al. 2014                 |
| Kudjape ditch  | 58.266500;<br>22.517360                       | A section of nodular argillaceous biomicritic limestones of Kudjape beds which contain coquinoid interlayers. Abundant shelly fossils, <i>Zoophycos</i> , and <i>Cruziana</i> traces occur.   | VINN & TOOM 2015                   |
| Ohesaare Cliff | 58.000405;<br>22.019223                       | An approximately 3.5 m thick section of intercalating thin-bedded marlstones and limestones of normal marine shelf origin. Thicknesses of individual beds (they are lenticular and slightly wavy) vary throughout the outcrop. Shelly fossils, <i>Skolithos</i> , <i>Trypanites</i> , <i>Palaeophycus</i> and <i>Cruziana</i> traces occur. | NESTOR 1990;<br>VINN & WILSON 2013 |

studied through central and western Estonia. Surface exposures of both Ordovician and Silurian age comprise relatively shallow water deposits. In southern Estonia, deeper water Ordovician and Silurian rocks are well sampled by hundreds of drill cores and have been thoroughly studied by numerous palaeontologists from the Institute of Geology (RAUKAS & TEEDUMÄE 1997). Some ichnotaxa that are easily identified in outcrops may be impossible to recognize in cores, locomotion traces fall into this category (BUATOIS & MÁNGANO 2011). There is only one published record of ichnofossils on genus level from drillcore (AINSAAR & MEIDLÄ 2002) from Estonia. It is possible that in Estonian cores arthropod trackways are described only as burrows. Thus, the collections under investigation herein are presumably not biased towards any particular stratigraphic interval or depositional environment.

#### 4. Systematic ichnology

*Rusophycus* HALL, 1852  
*Rusophycus* isp.  
Fig. 2A-B

**Material:** One complete trace, Saku quarry.

**Stratigraphy:** Oandu regional stage (lower Katian).

**Description:** Bilobate trace with oval outline preserved in positive hyporelief; 12 cm long and 5.5 cm in maximum width. Maximum height 2.5 cm, located slightly closer to presumed anterior end. Well-developed median groove, 7 mm wide. Scratches and other surface features absent.

**Remarks:** *Rusophycus* is considered an arthropod resting trace. Trilobites may have been the *Rusophycus* trace makers (SEILACHER 2007; DONOVAN 2010).

*Cruziana* D'ORBIGNY, 1842  
*Cruziana* isp.  
Fig. 2C-F

2014 *Cruziana* isp. – VINN, p. 2, fig. 4.

**Material:** Eleven traces, Ohesaare cliff and Kudjape ditch.

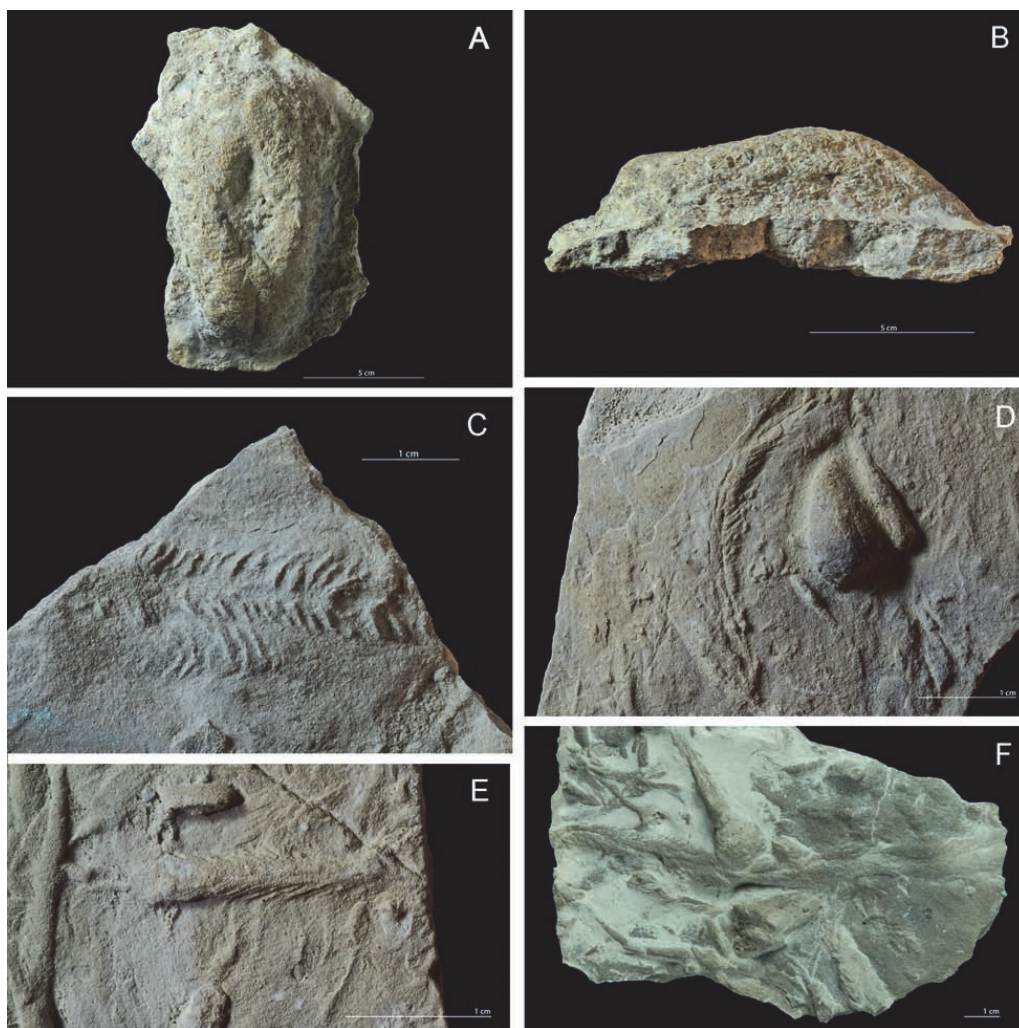
**Stratigraphy:** Kuressaare (Ludfordian) and Ohesaare (Pri-doli) regional stages.

**Description:** The bilobate scratch marks are up to 23 cm long and have a V-shaped pattern. The minimum width of the trace is 3.0 mm and the maximum width is 11 mm. Traces are characterized by well-developed relatively deep linear scratch marks on both sides of the wide median ridge or groove which is about 1/4 to 1/3 as wide as the whole trace. The angle between scratch marks and the median groove or ridge is 40 to 47 degrees. Six to seven scratch marks per 10 mm occur laterally on both sides of the trace. The scratch marks are 0.4 to 0.8 mm deep. Some traces have variable width. A single trace with variable width can be divided into sectors with increasing diameter. Traces are preserved as hyporelief on the bed's upper surface.

**Remarks:** *Cruziana* is considered to be the arthropod digging trace. Trilobites could be among the *Cruziana* trace makers (SEILACHER 2007; DONOVAN 2010).

#### 5. Discussion

Arthropod trace fossils are rare and their diversity is low in the Ordovician and Silurian of Estonia. *Rusophycus* isp. (Fig. 2A-B) occurs in the early Katian (Oandu regional stage) of northern Estonia. *Cruziana*



**Fig. 2.** **A, B** – *Rusophycus* isp. from Saku Member (Katian), Saku quarry, northern Estonia (GIT 362-14). **C-E** – *Cruziana* isp. from Kuressaare Formation (Ludfordian), Kudjape, Saaremaa Island; C, GIT 362-32, D, GIT 362-35, E, GIT 362-33. **F** – *Cruziana* isp. from Ohesaare Formation (Pridoli), Ohesaare cliff, Saaremaa Island (GIT 156-996).

isp. (Fig. 2C-F) occurs both in the Ludfordian (Kuressaare regional stage) and late Pridoli (Ohesaare regional stage). *Cruziana* isp. is the most common ichnofossil in the studied collection; it is more numerous in the Ludfordian. All arthropod trace fossils occur in the carbonate part of the section (Middle Ordovician to Silurian).

*Cruziana* isp. is usually associated with carbonates rich in fine terrigenous silt.

The rarity of arthropod trace fossils is surprising as trilobites are very common in the Ordovician and Silurian of Estonia (MÄNNIL 1997; RÕÖMUSOKS 1997) (Fig. 3). In addition to trilobites, other large arthropods are

| System     | Series     | Stage       | Regional stage |                     |                   |      |  |
|------------|------------|-------------|----------------|---------------------|-------------------|------|--|
| SILURIAN   | Priddali   |             | Ohesaare *     | 4/6                 | ← <i>Cruziana</i> |      |  |
|            |            |             | Kaugatuma      | 4/0                 |                   |      |  |
|            |            |             | Kuressaare ●   | 2/5                 | ← <i>Cruziana</i> |      |  |
|            | Ludlow     | Gorstian    | Ludford.       | Paadla              | 10/0              |      |  |
|            |            |             |                | Rootsiküla          | 4/0               | ←    |  |
|            | Wenlock    | Homer.      |                | Jaagarahu           | 9/0               |      |  |
|            |            |             |                | Jaani               | 11/0              |      |  |
|            |            | Sheinw.     |                | Adavere             | 11/0              |      |  |
|            | Llandovery | Telych.     | Aer.           | Raikküla            | 7/0               |      |  |
|            |            |             |                | Juuru               | 12/0              | ←    |  |
|            |            | Rhudd.      | Him.           | Porkuni             | 12/0              |      |  |
|            |            |             | Kalian         |                     | Pirgu             | 15/0 |  |
|            |            |             |                |                     | Vormsi            | 16/0 |  |
|            |            | Nabala      |                | 17/0                |                   |      |  |
|            | Rakvere    | 15/0        |                |                     |                   |      |  |
|            |            | Oandu *     | 23/1           | ← <i>Rusophycus</i> |                   |      |  |
| ORDOVICIAN | Upper      | Sandbian    | Keila          | 25/0                |                   |      |  |
|            |            |             | Hajjala        | 28/0                | ←                 |      |  |
|            |            |             | Kukruse        | 27/0                | ←                 |      |  |
|            |            |             | Uhaku          | 24/0                |                   |      |  |
|            |            |             | Lasnamägi      | 20/0                |                   |      |  |
|            | Middle     | Darnivilian | Aseri          | 11/0                |                   |      |  |
|            |            |             | Kunda          | 20/0                | ←                 |      |  |
|            |            |             | Volkhov        | 16/0                |                   |      |  |

**Fig. 3.** Distribution of arthropod traces in the carbonate rocks of the Ordovician and Silurian of Estonia. Arrows point to influx of terrigenous material. First number shows large arthropod genera per regional stage, second number shows arthropod traces per regional stage (i.e. trilobites, eurypterids and xiphosurans).

known from the Silurian of Estonia, including eurypterids (i.e. *Eurypterus*, *Pterygotus* etc.) and xiphosurans (i.e. *Bunodes*) (KALJO 1970). It is possible that arthropod traces which are commonly associated with silici-

clastic sediments (SEILACHER 2007) did not preserve well in the carbonate muds and sands of the Ordovician and Silurian of Estonia, as there are important differences between the formation of trace fossils in carbonates versus siliciclastics (CURRAN 1994). Burrowing in stiff mud poses a fabrication problem: the animal has to work hard and must be equipped with strong claws or setae (trilobite limbs would not do) (SEILACHER 2007). Stiff mud due to low sedimentation rate may have been the main reason why the arthropod traces are so rare in the Ordovician and Silurian of Estonia. In addition diagenetic processes may have played important role in destruction of arthropod traces as diagenesis is capable to total alteration of the deposits (KNAUST et al. 2012). The majority of studied arthropod traces from Estonia have been collected from late Silurian rocks. The Late Silurian has not been better sampled than the rest of Silurian and Ordovician of Estonia, which is indicated by the stratigraphic distribution of specimens in the studied collection. Thus, it is possible that arthropod traces are more common in the Late Silurian and Ordovician. It is possible that the numerous *Cruziana* traces in the Late Silurian are rather reflecting favourable sedimentation condition than the increase in number of trace making arthropods. Trilobites do not seem to be more common in the Late Silurian than in the Early Silurian and Ordovician. Paleontological collections of Estonia yield 273 trilobite specimens in average per regional stage for the Late Silurian, 369 trilobite specimens in average per regional stage for Early Silurian and 267 trilobite specimens in average per regional stage for the Ordovician. The taphonomic filter played the stronger role in rarity of trilobite traces in Baltica, as preservation of trilobite trace fossils is highest in heterolithic siltstone-sandstone deposits. The calcareous, commonly condensed sediments of Baltica were not suitable for preservation of trilobite burrows (RODRIGUEZ-TOVAR et al. 2014). In addition to Baltica, trilobite traces are known from carbonate rocks of North-America (PICKERILL et al. 1984) and South America (PERALTA et al. 1995). Late Silurian (Ludlow) rocks are characterized by increased amount of terrigenous material, but similar intervals occur also earlier in the Silurian section (JÜRGENSON 1988). In general, arthropod traces are not rare in the Early Palaeozoic of Baltica (DAVIES et al. 2006). DAVIES et al. (2006) described diverse traces from the Silurian of Oslo region: *Cruziana*, *Rusophycus*, *Diplichnites*, *Oniscoidichnus*, *Merostomichnus*, *Paleohelcura*, *Palmichnum*, *Siskema*, and *Steinsfjordichnus*. In the Baltic Basin closer to Estonia, *Rusophycus* has rarely

been found in a transgressive system tract (Zheltiaki) of the Volkhov Sequence at the Putilovo Quarry (DRONOV et al. 2002; ERSHOVA et al. 2006).

## 6. Conclusions

Abundance of arthropod body fossils in the section cannot be directly correlated with the abundance of arthropod trace fossils on epeiric carbonate platform.

Arthropod traces did not preserve well in carbonate muds and sands of the Ordovician and Silurian of Estonia on epeiric carbonate platform.

While still rare, a slight increase in the frequency of *Cruziana* traces in the Late Silurian part of the section can be attributed to a higher influx of terrigenous clastics and greater preservation potential, rather than an increase in the abundance of trace makers.

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## The trace fossil *Zoophycos* from the Silurian of Estonia

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**Abstract.** Trace fossils of the ichnogenus *Zoophycos* have been described for the first time from the Silurian of Baltica. They occur in Llandovery pure limestones of middle Estonia and in Ludfordian argillaceous limestones and early Pridoli crinoid grainstones of western Estonia (Saaremaa). The occurrence of *Zoophycos* in the Silurian of Estonia was not restricted to a particular facies, though all finds come from shallow-water sediments. *Zoophycos* had a wide geographic distribution in the Silurian.

**Key words:** trace fossils, burrows, *Zoophycos*, carbonate rocks, Ordovician, Silurian.

### INTRODUCTION

Trace fossils are an important tool for palaeoenvironmental reconstructions (Seilacher 2007). They are relatively poorly known in the Silurian of Baltica, especially the Estonian and eastern Baltic ones (Raukas & Teedumäe 1997). Recently, several hard substrate ichnofossils, such as *Trypanites* and *Osprioneides* (Vinn & Wilson 2010) and bioclaustrations were described from the Silurian of Estonia (Vinn et al. 2014). However, soft substrate trace fossils, such as *Skolithos* and *Cruziana*, have only seldom been described from the Silurian of Estonia (Kaljo 1970; Vinn & Wilson 2013; Vinn 2014).

The earliest *Zoophycos* Massalongo, 1855 occurs in the Lower Cambrian strata of the lower member of the Wood Canyon Formation in southeastern California (Sappenfield et al. 2012). *Zoophycos* is a helical spreite that marks successive, former positions of the burrow (Häntzschel 1975; Olivero 2007; Sappenfield et al. 2012). The lamellae are often composed of secondary lamellae. *Zoophycos* may be present either as simple lobes or ornate spiral structures, which are enclosed by a marginal burrow (Bromley 1991; Seilacher 2007; Sappenfield et al. 2012). The marginal burrow may not always exist or be preserved (Sappenfield et al. 2012). *Zoophycos* constitutes a feeding trace of a worm-like organism (Seilacher 2007). It has often been associated with certain water depth and facies conditions (Osgood & Szmuc 1972). It gives the name to the *Zoophycos* ichnofacies. In the Palaeozoic it is usually found in shallow-water environments, but from the Mesozoic it shifted almost entirely to deep-sea sediments (Seilacher 2007).

The aims of this paper are (1) to describe *Zoophycos* traces for the first time from the Silurian of Baltica, (2) to discuss the stratigraphic and environmental distribution of the traces and (3) to discuss the palaeogeographic distribution of the traces.

### GEOLOGICAL BACKGROUND AND LOCALITY

During the Silurian, the Baltica palaeocontinent was located in equatorial latitudes and continued its journey northwards (Melchin et al. 2004). The western part of modern Estonia was covered by the shallow epicontinental Baltic Basin (Fig. 1). The tropical Baltic Basin was characterized by diverse biota and environments. Organic buildups were common, especially coral-stromatoporoid reefs (Raukas & Teedumäe 1997).

Nestor & Einasto (1977) described the palaeoenvironments of the Baltic Basin in detail. They distinguished the following facies belts: tidal flat/lagoonal, shoal, open shelf, transitional (i.e. basin slope) and basin depression. The first three facies belts formed a carbonate platform. A deep pericratonic basin with fine-grained clastic deposition formed the last two facies belts (Raukas & Teedumäe 1997).

Kalana abandoned quarry (58.713586, 26.045208 by World Geodetic System 84) (Fig. 1) is located 200 m east of Põltsamaa–Kalana road at the southern border of Kalana village. A ca 4 m thick section of pure slightly dolomitized limestones with thin lenses rich in fossil debris of the Raikküla Regional Stage (Aeronian–Telychian) are exposed (L. Põlma, unpublished field notes 1981).



Fig. 1. Schematic map showing the location of Kaugatuma, Kudjape ditch and Kalana quarry.

Kudjape ditch (58.266500, 22.517360 by World Geodetic System 84) (Fig. 1) lies near the road from Kudjape cemetery to Kuressaare–Orissaare road. The Kudjape beds of the Kuressaare Formation (Ludfordian) are represented by nodular argillaceous biomicritic limestones containing coquinoid interlayers. *Atrypoida* and colonial rugose corals *Entelophyllum* are numerous (Mõtus & Hints 2007).

Kaugatuma Beach (58.113890, 22.184080 by World Geodetic System 84) (Fig. 1) is located between Kaugatuma and Lõo cliffs. Dark bluish-grey slightly argillaceous to pure skeletal packstones and grey sorted crinoid grainstones of the Kaugatuma Formation (early Pridoli) are exposed on a 200 m long seashore (H. Nestor, unpublished field notes 1985).

## MATERIAL AND METHODS

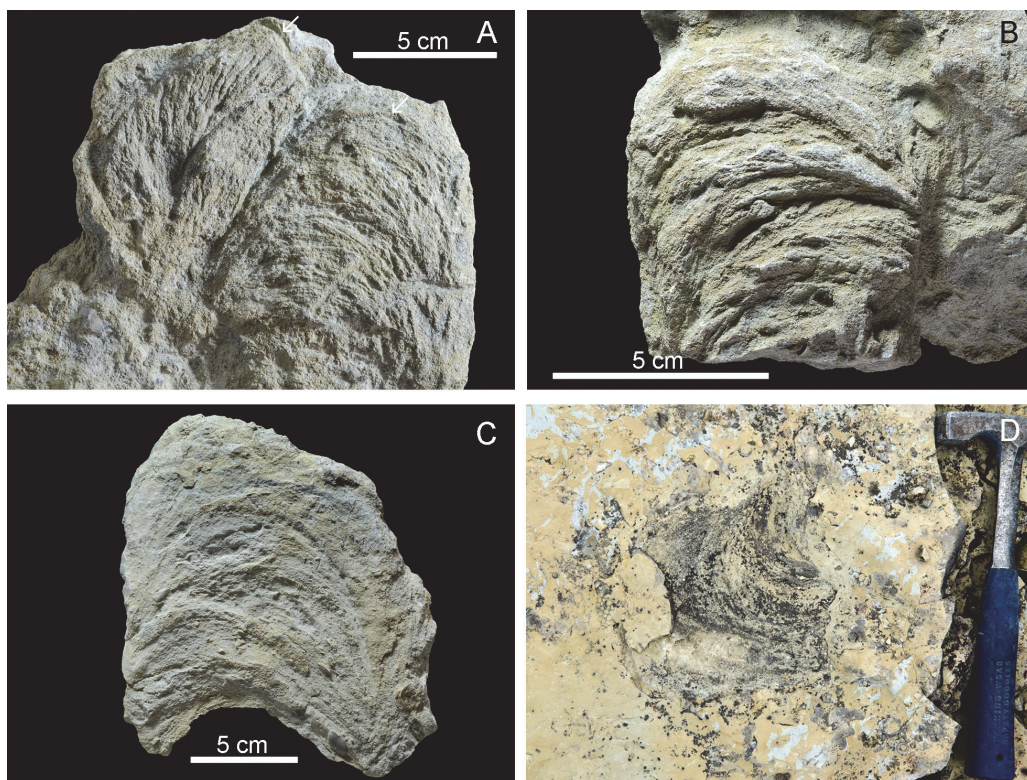
The authors observed *Zoophycos* in the field during several field trips and collected three specimens. The studied collection ( $N = 10$ ) is deposited at the Institute

of Geology at Tallinn University of Technology (GIT 362-43 to GIT 362-52). It contains specimens from several collectors obtained during the past fifty years but nobody had interpreted the finds before us. The trace fossil samples with *Zoophycos* burrows were photographed with scale bar using Nikon D7000.

## RESULTS

*Zoophycos* traces are common in the Kaugatuma Formation (Fig. 2A, B) and slightly less common in the Kuressaare Formation (O. V. field observations) (Fig. 2C). They also occur in the Raikküla Regional Stage (U. T. field observations) (Fig. 2D). Complete traces have not been found in either formation. The Kaugatuma Formation traces were made in crinoid grainstone with marl interlayers, those of the Kuressaare Formation in clayey limestone containing fine fossil debris.

In the studied traces, the marginal tube, though not well preserved in all traces, corresponds to the external border of a lamina. The laminae are formed by numerous



**Fig. 2.** A, B, *Zoophycos* isp. from the Kaugatuma Formation (lower Pridoli) from Saaremaa, Kaugatuma (TUG 362-45 and 362-50). Arrows point to the marginal tube. C, *Zoophycos* isp. from the Kuressaare Formation (Ludfordian) from Saaremaa, Kudjape (TUG 362-44). D, *Zoophycos* isp. from the Raikküla Regional Stage (Llandovery) of middle Estonia, Kalana quarry. Hammer for scale is 28 cm.

thin arched lamellae. There are up to seven lamellae per 1 cm. The lamellae are deformed, filled tunnels, which mark the previous position of the same single tunnel penetrating through the sediment. The marginal tube marks the most advanced position of this tunnel. Only this part of the burrow system remained open during the life of the trace-maker. The marginal tunnel of some Saaremaa specimens is discontinuous and does not contour the whole spreite (Fig. 2A). It seems to regularly jet-out to initiate a new lobe. The lobes are 6 to 8 cm in diameter.

## DISCUSSION

### Ichnotaxonomy

The transitions between *Rhizocorallium* and *Zoophycos* are known (Knaust 2013). The Estonian material differs

from *Rhizocorallium* in having a proportionately much thinner marginal tube and a burrow outline in the form of a widely rounded curve. The spreite organization of one Kaugatuma specimen (Fig. 2A) resembles most the alate (wing-like) form of *Zoophycos* (Seilacher 2007). These Devonian specimens have secondary lamellae, however, we found no evidence of secondary lamellae in the Estonian material. *Zoophycos* has been interpreted as a burrow system. In these burrows the trace-maker avoids the marginal tunnel from becoming too long by making new entrances (Seilacher 2007). The spreite shape and structure of most of the studied specimens cannot be identified due to incomplete preservation of the trace. However, the preserved parts of most traces do not resemble the classical spiral form of *Zoophycos* (Seilacher 1967a, 1967b; Bromley & Ekdale 1984). The Estonian forms resemble mostly planar *Zoophycos* spreites known from the Devonian storm deposits

(Miller 1991). Their marginal curvature is similarly broadly arcuate to lobate and their marginal tunnels are weakly developed or lacking.

### Stratigraphy and palaeoenvironment

In Estonia, *Zoophycos* seems to be common only in the late Silurian in the Kuressaare (Ludfordian) and Kaugatuma (early Pridoli) formations. During the late Silurian, the Baltic Basin had retreated to the southwest part of Estonia and was filled with sediments (Raukas & Teedumäe 1997). Water was relatively shallow (Raukas & Teedumäe 1997). Clayey limestones of the Kuressaare Formation were formed in the open shelf zone in deeper water and grainstones of the Kaugatuma Formation in shallower shoal conditions (Raukas & Teedumäe 1997). It seems that *Zoophycos* preferred shallow water, salinity normal marine sediments with high skeletal debris content (i.e. Kaugatuma Formation) in the Silurian of Estonia. However, *Zoophycos* also occurred in slightly deeper-water sediments of the Kuressaare Formation, thus, it was not restricted to certain facies. Several facies types similar to the Silurian of Estonia were also present in the Late Ordovician of Estonia when the climatic conditions were similar to the Silurian. In the Ordovician of Estonia, silty beds of the Variku Formation are known to contain abundant *Chondrites* and *Zoophycos* ichnofauna (Ainsaar & Meidla 2001).

### Palaeogeography

*Zoophycos* occurred in several palaeocontinents already in the Cambrian (Doucek & Mikuláš 2014). The Ordovician records of *Zoophycos* seem to be relatively common (Mikuláš 1993; Ainsaar & Meidla 2001; Kakuwa & Webb 2007; Pak et al. 2010). Few records of *Zoophycos* are also known from the Silurian rocks. *Zoophycos* has been reported from the Rhuddanian of Saudi Arabia (Melvin 2015). It probably also occurs in the Silurian of Bolivia and in Australia (Gondwana) (Toro et al. 1990; Shi et al. 2009). Their traces are also known from the Silurian rocks of Canada (Laurentia) (Pickerill et al. 1977). The Estonian occurrences add the Baltica palaeocontinent to the Silurian record of *Zoophycos*.

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## ***Zoophycos*'e jälgede esmaleid Eesti Silurist**

Olev Vinn ja Ursula Toom

*Zoophycos*'e jäljed on esmakordselt kirjeldatud Baltika kontinendi Silurist. *Zoophycos* esineb Raikküla lademe puhastes lubjakivides, Kuressaare lademe savikates lubjakivides ja Kaugatuma lademe krinoidlubjakivis. Jälgede levik ei ole piiratud kindla faatsiesega, kuid need esinevad madalaveelistes setendites.



#### **Publication VI**

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## Distribution of *Conichnus* and *Amphorichnus* in the Lower Paleozoic of Estonia ( Baltica)

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**Abstract:** *Conichnus conicus* and *Amphorichnus papillatus* occur in clay-rich carbonate rocks in the Ordovician of Estonia. *Conichnus conicus* also occurs in clay-rich carbonates of the early Silurian of Estonia. Lateral adjustment traces are more common in *C. conicus* than previously recorded. The lack of adjustment traces in *Amphorichnus*, together with its morphology, does not support synonymy of *Conichnus* and *Amphorichnus*. The *Conichnus conicus* and *Amphorichnus papillatus* tracemakers preferred shallow water carbonate environments with high clay content. They were rare or did not occur in deeper water muddy environments or where shallow water carbonates accumulated. A high content of volcanic ash in the depositional environment is characteristic of both the Ordovician and Silurian maxima of *Conichnus conicus* occurrence. *C. conicus* may have been more common in the temperate seas of Baltica than in the tropics.

**Key Words:** Ichnofossils; burrows; endichnia; Ordovician; Silurian; Baltica.

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**Résumé : Répartition de *Conichnus* et d'*Amphorichnus* dans le Paléozoïque inférieur d'Estonie (bouclier balte).**- *Conichnus conicus* et *Amphorichnus papillatus* sont présents dans des roches carbonatées riches en argiles de l'Ordovicien d'Estonie. *Conichnus conicus* est également présent dans des roches carbonatées riches en argiles du Silurien inférieur d'Estonie. Les signes d'ajustements latéraux sont plus fréquents chez *C. conicus* que ce que nous connaissions auparavant. L'absence de signes d'ajustements chez *Amphorichnus*, conjointement à sa morphologie, ne vient donc pas corroborer la synonymie de *Conichnus* et d'*Amphorichnus*. Les organismes à l'origine des traces de type *Conichnus conicus* et *Amphorichnus papillatus* préféraient des environnements peu profonds, carbonatés mais présentant une teneur élevée en argile. Ils sont, par contre, rares ou absents dans des environnements peu profonds mais où les carbonates s'accumulent ou dans des environnements plus profonds et boueux. Une forte teneur en cendres volcaniques dans l'environnement de dépôt représente un trait caractéristique des pics d'abondance ordoviens et siluriens de *Conichnus conicus*. *C. conicus* semble avoir été plus fréquent dans les mers tempérées du bouclier balte que dans celles sous les tropiques.

**Mots-clefs :** Ichnofossiles ; terriers ; endichnia ; Ordovicien ; Silurien ; bouclier balte.

### 1. Introduction

Ichnofossils are important environmental indicators, and they provide us with valuable information on animal behavior in the geological past (SEILACHER, 2007). Ichnofossil assemblages of the Ordovician and Silurian in many areas are relatively well known (SEILACHER, 2007), but the number of studies devoted to the Ordovician and Silurian ichnofaunas of Estonia and the eastern Baltic is limited (MÄNNIL, 1966; DRONOV *et al.*, 2002; MIKULÁŠ & DRONOV, 2005; ERSHOVA *et al.*, 2006; KNAUST *et al.*, 2012; KNAUST & DRONOV, 2013; VINN *et al.*, 2014b). The Ordovician ichnofossils of Estonia that have been described are mostly hard substrate borings (VINN, 2005; VINN & WILSON, 2010; VINN *et al.*, 2014a).

*Conichnus* MÄNNIL, 1966 and *Amphorichnus* MÄNNIL, 1966 are common ichnogenera of plug-shaped burrows (MÄNNIL, 1966; FREY & HOWARD, 1981; PEMBERTON *et al.*, 1988). They are found in various sedimentary rocks of marine origin from the Cambrian onwards (MÄNNIL, 1966; FREY & HOWARD, 1981; JONES & PEMBERTON, 1989; PICKERILL *et al.*, 1992; KNAUST, 2007; PACZEŚNA, 2010; METZ, 2011). *Conichnus* has been interpreted as the resting trace or dwelling structure of anemone-like animals (FREY & HOWARD, 1981). Ordovician *Conichnus* traces were described in detail by MÄNNIL (1966), but their Silurian occurrences have remained problematic (MÄNNIL, 1966).

This paper addresses the following questions:

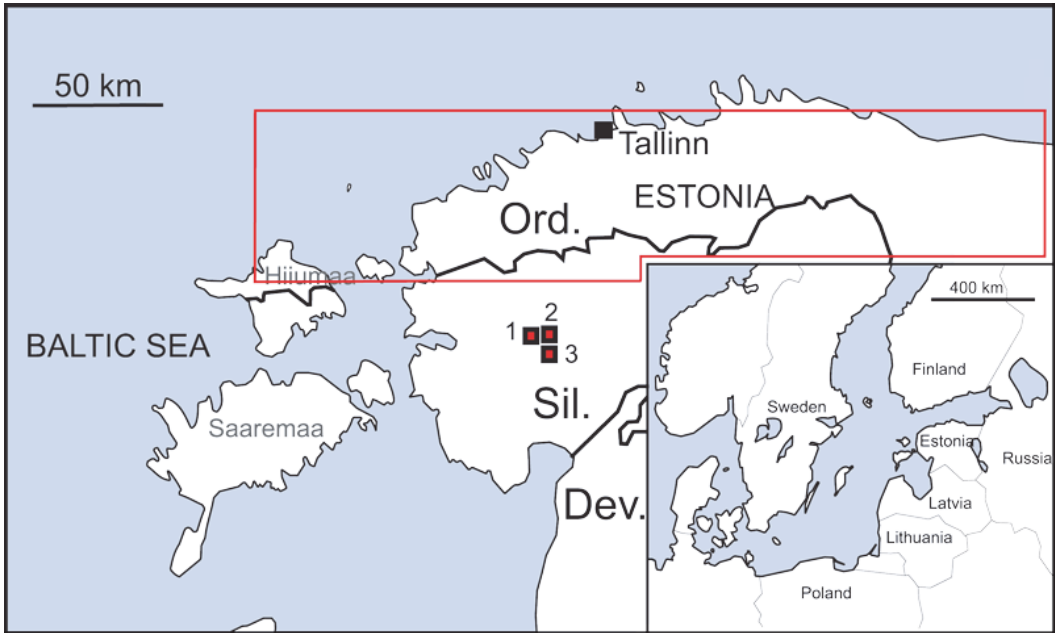
1) To which ichnospecies does the *Conichnus* in

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**Figure 1:** Schematic line drawing showing the Estonia and localities (red-area covered with samples from Ordovician). 1 - Valgu River, 2 - Valgu ditch, 3 - Velise-Kõrgekalda.

the Silurian of Estonia belong? 2) How are *Conichnus* and *Amphorichnus* traces distributed in the Lower Paleozoic of Estonia? 3) How does the abundance of *Conichnus* change in the Ordovician and Silurian of Estonia? Are such abundance changes correlated with climatic change (temperate *versus* tropical climate) and changes in sedimentation? 4) How do the dimensions and morphology of *Conichnus* differ in the Ordovician and Silurian of Estonia?

## 2. Paleoenvironments

### Paleogeography and sedimentation in Baltic basin

During the Ordovician, the paleocontinent Baltica moved from the temperate climatic zone into the subtropical realm (TORSVIK *et al.*, 1992; NESTOR & EINASTO, 1997; TORSVIK *et al.*, 2013). In the Middle Ordovician and Sandbian, the area of modern Estonia (Fig. 1) was covered by a shallow, epicontinental sea with little bathymetric variability and an extremely low sedimentation rate (MÖTUS & HINTS, 2007). Along the entire extent of the ramp a series of grey calcareous and argillaceous sediments accumulated with a trend of increasing clay and decreasing bioclasts in the offshore direction (NESTOR & EINASTO, 1997). In the Late Ordovician the climatic change resulted in an increase in carbonate production and sedimentation rate on the carbonate shelf and the occurrence of the first carbonate buildups in the basin.

During the Silurian, Baltica was located in equatorial latitudes and drifting northwards (COCKS & TORSVIK, 2005; TORSVIK *et al.*, 2013). An epicontinental basin covered middle and western Estonia (Fig. 1) with wide range of tropical environments and diverse biotas (HINTS *et al.*, 2008). Five main facies belts have been recognized in the Estonian part of Baltic basin: tidal flat/lagoonal, shoal, open shelf, basin slope and a basin depression (NESTOR & EINASTO, 1977). The first three facies belts formed a carbonate platform (RAUKAS & TEEDUMÄE, 1997).

### Sedimentation in study area

The Tremadoc to Floian section of the Ordovician of Estonia is characterized by a terrigenous sedimentation in relatively shallow normal marine basin. Various sandstones dominate the succession (Pakerort, Hunneberg and Billingen regional stages), along with kerogenous argillites (Varangu Regional stage) and phosphatic brachiopod coquinas (Pakerort Regional Stage) (RAUKAS & TEEDUMÄE, 1997).

The Dapingian to Hirnantian succession is characterized by various normal marine carbonate rocks, mostly limestones, in northern Estonia, which accumulated in the shallow part of the basin. In addition to limestones, marls occur in lesser amounts. The purest limestones are in the Dapingian-Darriwilian and most of the Katian of northern Estonia. The Sandbian is characterized by a higher content of clay in carbonate rocks. In addition to limestones, oil shales (*i.e.*,

kerogenous carbonates) accumulated in the Sandbian (Kukruse Regional Stage) of northern Estonia. The carbonate sediments of the Haljala Regional Stage are especially rich in clay. Carbonate buildups are common in the northern Estonia starting in the early Katian (Oandu Regional Stage). The Dapingian to Hirnantian succession of southern Estonia is characterized by terrigenous sediments, mostly marls and argillites, which accumulated in the deeper part of the basin (RAUKAS & TEEDUMÄE, 1997).

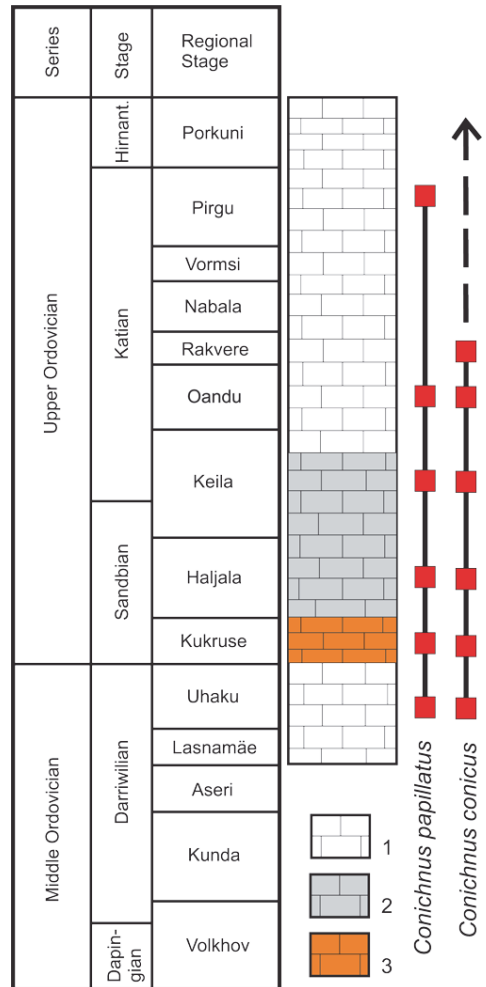
The Silurian succession in middle and western Estonia is characterized by various normal marine carbonate rocks, mostly limestones and secondary dolomites, which accumulated on a carbonate platform. Bioherms are common throughout the Silurian in the middle and western Estonia (KALJO, 1970; RAUKAS & TEEDUMÄE, 1997). Marginal marine lagoon dolomites also occur in the Silurian of western Estonia; they may have formed in elevated salinities (KALJO, 1970; RAUKAS & TEEDUMÄE, 1997). In some parts of the section argillaceous limestones and marls are common (*i.e.*, Adavere Regional Stage and Jaani Regional Stage) (KALJO, 1970). The Silurian succession in southern Estonia is characterized by an alternation of marls and argillaceous rocks that accumulated in the deeper part of the basin (KALJO, 1970; RAUKAS & TEEDUMÄE, 1997).

### 3. Material and methods

A collection of 461 *Conichnus conicus* from the Ordovician and Silurian of Estonia was studied, along with a collection of 611 *Amphorichnus papillatus* traces from the Ordovician of Estonia. These collections are deposited at the Institute of Geology, Tallinn University of Technology. The best preserved *Conichnus conicus* (n=69) and *Amphorichnus papillatus* (n=63) specimens were measured with calipers to an accuracy of 0.1 mm. Selected traces were photographed using a Nikon D7000 camera. Some traces were cut longitudinally and transversely in order to study their internal structure.

### 4. Geological background

Northern Estonia has abundant well-studied Ordovician outcrops. Similarly, the Silurian is well exposed and studied in middle and western Estonia. The deeper water Ordovician and Silurian sections of southern Estonia are well covered by hundreds of drill cores and thoroughly studied by numerous palaeontologists from the Institute of Geology (TUT) during the past fifty years (RAUKAS & TEEDUMÄE, 1997). Thus the samples in the collections of the Institute of Geology, Tallinn University of Technology, are not biased towards certain stratigraphic intervals or depositional environments.



**Figure 2:** Stratigraphic distribution of *Conichnus conicus* and *Amphorichnus papillatus* in the Ordovician of Estonia. 1 - limestones, 2 - clay rich limestones, 3 - oil shale (kukersite) with limestone.

The thickness of the Uhaku Stage (Fig. 2) in northern Estonia varies from 5-10 m in the west to about 20-25 m in the east. In northern Estonia the lower part of the Uhaku Stage is composed of hard bioclastic limestones belonging to the Vão Formation. The formation has a rather consistent thickness (4-5 m). The upper part of the Uhaku Stage is made up of relatively thin-bedded argillaceous limestones of the Kõrgekallas Formation that contain *Conichnus conicus*. The formation is subdivided into the Koljala, Pärtlioru and Erra members (HINTS, 1997). In the upper part of the section there are also thin layers of oil shale. The argillaceous limestones of the Uhaku Stage were deposited in a relatively shallow epicontinental sea with normal salinity (RAUKAS & TEEDUMÄE, 1997).

The thickness of the Kukruse Regional Stage (Fig. 2) in northern Estonia ranges from about 3 m in the west to more than 20 m in the east (HINTS, 1997). The stage consists of three formations. The argillaceous bioclastic limestones with intercalations of oil shale (kukersite) and marls of the Viivikonna Formation occur northeast of the line Osmussaar Island - south coast of Lake Peipsi. Oil shale contains 15-46 % kerogen, 26-5 % carbonates and 18-42 % terrigenous material (HINTS, 1997). Based on the abundance of kukersite seams, the Viivikonna Formation is subdivided into the Kiviõli, Peetri and Maidla members. Viivikonna Formation yields numerous *C. conicus*. The boundaries of the Viivikonna Formation are diachronous due to the facies shift of the kukersite beds. The upper part of the Viivikonna Formation (Peetri Member) is absent in northeastern Estonia (HINTS, 1997). The Viivikonna Formation was deposited in a shallow epicontinental sea with normal salinity.

The Haljala Regional Stage (Fig. 2) is divided into the Idavere and Jõhvi substages. The lower part of the Idavere Substage (Tatruse Formation) comprises the regularly bedded hard bioclastic limestones. The upper part of the Idavere substage (Vasavere Formation) yields abundant *Conichnus conicus* and *Amphorichnus papillatus*. The Vasavere Formation contains argillaceous limestones with intercalations of marls and some thin K-bentonites (HINTS, 1997). The Idavere substage has the most reduced sequence in northern Estonia, and in some places in the vicinity of Tallinn it is entirely absent (HINTS, 1997). The Vasavere Formation contains usually two, but in the west up to 18 K-bentonite beds, which belong to the Grefsen complex of bentonites (Vasavere Formation) (KIIPLI *et al.*, 2014). Argillaceous limestones and marls of Vasavere Formation were deposited in a relatively shallow epicontinental sea with normal salinity (RAUKAS & TEEDUMÄE, 1997).

In most of northern Estonia, the Keila Regional Stage (Fig. 2) comprises the argillaceous bioclastic limestones of the Kahula Formation (HINTS & MEIDLA, 1997). Argillaceous limestones of the Kahula Formation contain intercalations and occasionally thicker (up to 4 m) intervals of relatively pure limestones. The argillaceous layers yield *Conichnus conicus* and *Amphorichnus papillatus*. The total thickness of the Kahula Formation is about 30 m, and in northwestern Estonia its main part corresponds to the Keila Stage (HINTS & MEIDLA, 1997). The thickness of the Keila Stage part of the formation (usually 10-15 m) decreases in the southeast direction. In the same direction, the formation becomes lithologically more homogeneous and argillaceous. In a restricted area in northwestern Estonia, the upper part of the Kahula Formation is replaced by the Vasalemma Formation where the greatest thickness of the

Keila Stage (more than 30 m) has been recorded (HINTS & MEIDLA, 1997). The argillaceous limestones of the Kahula Formation were deposited in a relatively shallow epicontinental sea with normal salinity (RAUKAS & TEEDUMÄE, 1997).

In northern Estonia, the Oandu Regional Stage (Fig. 2) comprises rocks of two different lithofacies forming the Vasalemma and Hirnuse formations. The Vasalemma Formation is distributed in northwestern Estonia. It consists of fine- to coarse-grained bioclastic limestones with irregular bodies of carbonate buildups (HINTS & MEIDLA, 1997). The argillaceous limestones and marls of the Hirnuse Formation are exposed on the banks of the Oandu River in northeastern Estonia (HINTS & MEIDLA, 1997). The Hirnuse Formation thins out within a rather short distance in the southern direction. Hirnuse Formation contains *Conichnus conicus* and *Amphorichnus papillatus*. The argillaceous limestones and marls of the Hirnuse Formation were deposited in onshore shallow epicontinental sea with normal salinity (RAUKAS & TEEDUMÄE, 1997).

In northern Estonia, the Rakvere Regional Stage (Fig. 2) is characterized by pure micritic (fine-grained) limestones that intercalate with more or less argillaceous varieties. The clayey parts of the cycles are characterized by the appearance of abundant new taxa (HINTS & MEIDLA, 1997). The Rakvere Stage consists of the Piilse and Tudu members of the Rägavere Formation. The stage is at its thickest (28 m) in western Estonia and its thickness decreases notably in the southeastern direction (HINTS & MEIDLA, 1997). The lower Piilse Member with a thickness of up to 27 m consists of pure limestones with a low content of terrigenous material (3 - 9 %) and skeletal sand (< 5 %). The member is characterised by abundant pyritized burrows (HINTS & MEIDLA, 1997). The upper Tudu Member is up to 10 m thick and contains more skeletal sand (about 15 %) and thin, up to 3 cm thick kukersite layers. Tudu Member yields rare *Conichnus conicus*. It was deposited in a relatively shallow epicontinental sea with normal salinity (RAUKAS & TEEDUMÄE, 1997).

In northern Estonia, the Pirgu Regional Stage (Fig. 2) contains two successive rock units of grey-colored limestones: the - lower - Moe and the - upper - Adila formations (HINTS & MEIDLA, 1997). The Moe Formation is up to 40 m in thickness, it consists of micritic and bioclastic nodular or bedded limestones with argillaceous intercalations (HINTS & MEIDLA, 1997). The calcareous alga *Palaeoporella* is abundant in the lower part of the formation. In some places carbonate mounds are developed, quite similar to the Boda mounds in the Siljan district of Sweden (HINTS & MEIDLA, 1997). The Adila Formation contains predominantly bioclastic limestones with a thickness of 10-15 m. Cyclically alternating pure and argillaceous limestones and numerous discontinuity surfaces characterize the

upper part of the formation. The Adila Formation yields *A. papillatus*. The sediments of the Adila Formation were deposited in a relatively shallow epicontinental sea with normal salinity (RAUKAS & TEEDUMÄE, 1997).

The Adavere Regional Stage (Fig. 2) is distributed in the southernmost part of Hiiumaa Island, on Saaremaa and Muhu islands and in the southwestern part of mainland (NESTOR, 1997). The Stage is represented by thin-bedded to nodular wackestones and packstones with marl- to mudstones above (Velise Formation). The clay content increases westwards. The Velise Formation contains rather rich shelly fauna of *Clorinda* communities (NESTOR, 1997). Velise Formation yields *C. conicus*. The argillaceous limestones and marls of Velise Formation were deposited in a relatively shallow epicontinental sea with normal salinity (RAUKAS & TEEDUMÄE, 1997). Metabentonite layers are very common (HINTS *et al.*, 2006; KIIPLI *et al.*, 2008, 2014).

**Table 1:** Distribution of *Conichnus* and *Amphorichnus* in the Ordovician and Silurian of Estonia.

| Regional Stage                      | Number of localities | <i>Conichnus conicus</i> | <i>Conichnus papillatus</i> |
|-------------------------------------|----------------------|--------------------------|-----------------------------|
| Adavere (upper Llandovery)          | 2                    | 15                       | -                           |
| Pirgu (upper Katian)                | 1                    | -                        | 1                           |
| Rakvere (middle Katian)             | 1                    | 1                        | -                           |
| Oandu (lower Katian)                | 1                    | 2                        | 1                           |
| Keila (upper Sandbian-lower Katian) | 21                   | 55                       | 31                          |
| Haljala (middle Sandbian)           | 18                   | 356                      | 571                         |
| Kukruse (lower Sandbian)            | 9                    | 29                       | 6                           |
| Uhaku (upper Darriwilian)           | 3                    | 3                        | 1                           |

## 5. Distribution of plug-shaped burrows in the Lower Paleozoic of Estonia

There are two species of plug-shaped burrows, *Conichnus conicus* and *Amphorichnus papillatus*, in the Ordovician and one species, *Conichnus conicus*, in the Silurian of Estonia. *Conichnus* occurs in shallow water epicontinental carbonate rocks in the Ordovician of northern Estonia. Similarly, it is found in argillaceous limestones of shallow water epicontinental on-shore settings in the Silurian. *Conichnus* is abundant only in the most clay-rich shallow-water carbonates in the Ordovician and Silurian of Estonia. *Conichnus* is most abundant in the

interval of numerous metabentonite layers in the Ordovician. Similarly, active volcanic ash deposition also characterizes the Silurian environments in which *Conichnus* formed. *Conichnus* seems to be more common in the temperate climate part of the Ordovician (Sandbian) than in the tropics of the Silurian (Telychian) as there are 385 Sandbian records *versus* 15 in the Telychian (Table 1).

## 6. Systematic ichnology

### Ichnogenus *Conichnus* MÄNNIL, 1966

Type ichnospecies: *Conichnus conicus* MÄNNIL, 1966.

#### *Conichnus conicus* MÄNNIL, 1966

Fig. 3C-E, Fig. 4B-C

1966 *Conichnus conicus* MÄNNIL, p. 201, Figs. 1B, 1C, Pl. 1, figs. 4-6, Pl. 2, figs. 1, 4.

1975 *Conichnus conicus*, HÄNTZSCHEL, p. W52, Fig. 31.3.

1981 *Conichnus conicus*, FREY & HOWARD, p. 800-801, Figs. 1A, 2A-2E.

1982 *Conichnus conicus*, FREY & HOWARD, Fig. 20.

1983 *Conichnus conicus*, PEMBERTON & FREY, p. 61, Pl. 1, figs. 1-2.

1984 *Conichnus conicus*, HOWARD & FREY, p. 203, Fig. 7.

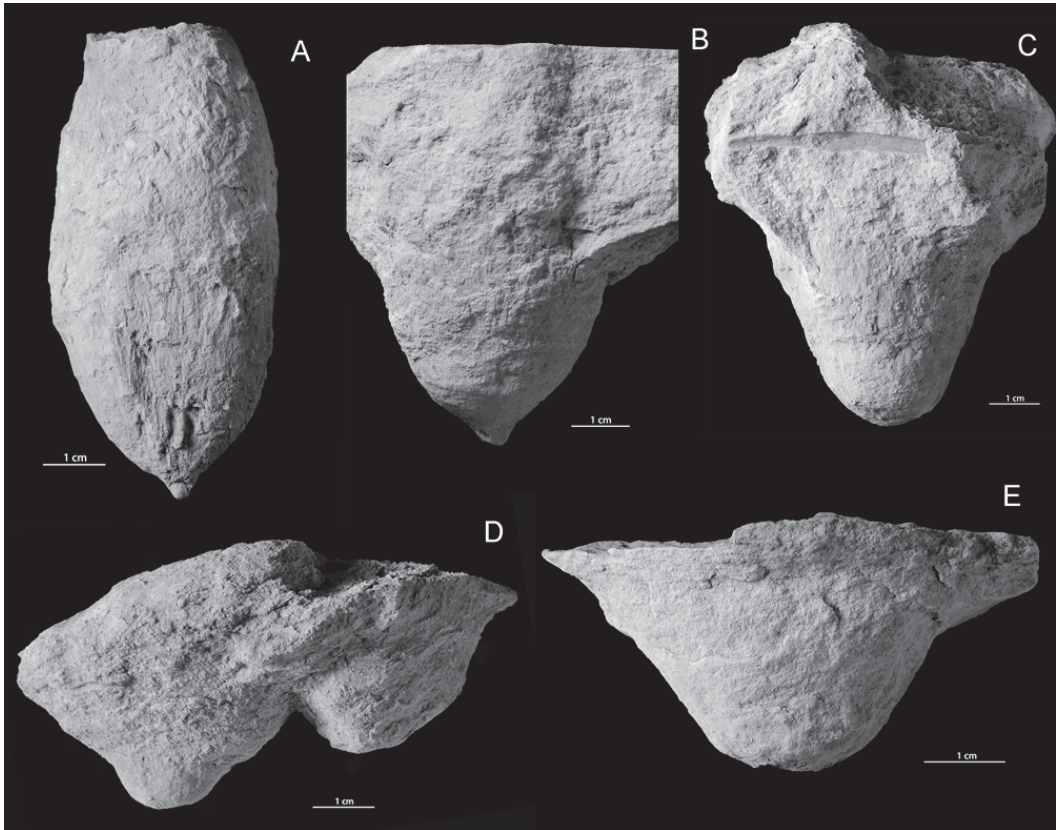
? 2006 *Conichnus* isp. ERSHOVA *et al.*, p. 420, Fig. 5A-B.

Holotype: GIT 107-4 from Pääsküla, northern Estonia, Keila Regional Stage.

Material: 15 Silurian specimens, 10 well preserved; 488 Ordovician specimens.

Occurrence: Silurian (Telychian): Valgu River, Valgu ditch, Velise-Kõrgekald and Võiva, western Estonia; Ordovician (Darriwilian to Katian): all of northern Estonia.

Description: Short conical, limestone filled burrows with unornamented shafts, circular to elliptical in a transverse section. Limestone filling is often rich in fossil debris. No linings occur. The morphology of the Ordovician and Silurian specimens is slightly different. Silurian specimens are somewhat wider relative to their height than the Ordovician specimens. The Ordovician specimens are in average slightly higher than wide. Their diameter/height ratio is 0.59 to 1.59 (n=59, mean 0.98). Ordovician forms are 1.52 cm to 8.91 cm high (n=59, mean 5.31 cm, sd=1.77) and 1.82 cm to 9.53 cm wide (n=59, mean 5.22 cm, sd=1.68). Silurian forms are remarkably wider than high. Their diameter/height ratio is 0.80 to 2.20 (n=10, mean 1.70). They are 1.02 to 5.81 cm high (n=10, mean 2.54 cm, sd=1.47) and 1.72 to 6.51 cm wide (n=10, mean 3.91 cm, sd=1.63). Some Ordovician forms often show adjustment traces, usually two or three but in some cases up to five stages in lateral directions and up to two stages in vertical directions. The Silurian specimens do not show any lateral adjustment structures. Both Ordovician and Silurian burrows are often filled



**Figure 3:** **A.** *Amphorichnus papillatus* MÄNNIL, 1966 (Holotype GIT 107-1) from Anija, northern Estonia, Jõhvi Formation (Sandbian). **B.** *A. papillatus* (GIT 107-2) from Kämbemäe, northern Estonia, Jõhvi Formation (Sandbian). **C.** *Conichnus conicus* MÄNNIL, 1966 (GIT 107-5) from Rae, northern Estonia, Jõhvi Formation (Sandbian). **D.** *C. conicus* (GIT 107-6) from Aluverve quarry, northern Estonia, Vasavere Formation (Sandbian). **E.** *C. conicus* (GIT 362-483) from Valgu, Velise Formation (Llandovery).

with coarse fossil debris. Basal part smooth and rounded, without apical protuberance. The burrows are preserved in full relief as endichnia.

Remarks: The oval transverse section of some Telychian burrows links them to forms described from the Upper Cretaceous of Utah, USA (FREY & HOWARD, 1981; HOWARD & FREY, 1984). The described Silurian forms differ from typical *Conichnus* (PEMBERTON *et al.*, 1988) by being in average significantly wider than high. According to MÄNNIL (1966), the maximum length of *C. conicus* from the Ordovician of Estonia is 12 cm, which is slightly more than that measured in new material (8.91 cm). New material shows that lateral adjustment traces are more common in the Ordovician *C. conicus* than previously known.

### **Ichnogenus *Amphorichnus* MÄNNIL, 1966**

Type ichnospecies: *Amphorichnus papillatus* MÄNNIL, 1966.

### ***Amphorichnus papillatus* MÄNNIL, 1966**

Fig. 3 A-B, Fig. 4A

1966 *Amphorichnus papillatus* MÄNNIL, p. 202, Figs. 1A, 1D; Pl. 1, figs. 1-3; Pl. 2, figs. 2-3, 5.

1975 *Amphorichnus papillatus* HÄNTZSCHEL, p. W36, Fig. 24.3.

1979 *Amphorichnus* sp., HURST (partim), Figs. 12B, C.

? 2006 *Amphorichnus* isp., ERSHOVA *et al.*, p. 419, Figs. 3B-L, 4A-I.

Holotype: GIT 107-1 from Anija, northern Estonia, Haljala Regional Stage (Sandbian).

Material: 637 Ordovician specimens.

Occurrence: Uhaku to Pirgu Regional Stages (Darriwilian to upper Katian), northern Estonia.

Description: Short to elongate nearly cylindrical to amphora-shaped, limestone filled burrows with unornamented shafts and slightly constricted apertures, circular to slightly elliptical in a transverse section. Maximal diameter is between 1/3 to 2/3 of the burrow height. Burrows are 1.10 to 7.71 cm height (n=63, mean 4.73 cm,

sd=1.60). Aperture of the burrows is 0.60 to 3.31 cm wide (n=63, mean 1.91 cm, sd=0.53). Maximal diameter of the burrows is 0.91 to 3.62 cm (n=63, mean 2.50 cm, sd=0.65). Limestone filling is often rich in fossil debris. In most of specimens burrow filling is homogeneous, but in some specimens it contains indistinct laminae. These laminae indicate successive stages in filling of the burrow with sediments. No linings occur. Burrows are often filled with coarse fossil debris. Basal part smooth rounded to conical, with an apical protuberance. The development of apical protuberance is variable. The burrows are preserved in full relief as endichnia.

Remarks: FREY & HOWARD (1981) transferred *Amphorichnus papillatus* to the ichnogenus *Conichnus* MÄNNIL, 1966 based on similar plug-shaped morphology of *C. conicus*. However, the morphology of *Amphorichnus papillatus* considerably differs from *Conichnus* by its amphora-like shape and the papillate termination and is better accommodated under its original name, *Amphorichnus*. *Amphorichnus* also differs from *Conichnus* by presence of lateral adjustment traces. In addition, its shape resembles *Gastrochaenolites oelandicus*. However, *G. oelandicus* is a hard substrate boring, not a soft-sediment burrow, implying completely different behavior.

## 7. Discussion

### Comparison of Ordovician and Silurian forms of *Conichnus conicus* in Estonia

MÄNNIL (1966) found that *C. conicus* traces in the oil shale of the Kukruse Regional Stage are larger than the other Ordovician *C. conicus* traces. This is confirmed by our study. It seems that *C. conicus* traces were larger in the Ordovician than in the Silurian of Estonia. The smaller size of the Silurian traces probably correlates with the smaller size of the trace makers, as *Conichnus* has been interpreted as the living burrow of a cnidarian (FREY & HOWARD, 1981; JONES & PEMBERTON, 1989). The Silurian specimens are somewhat wider relative to their height than the Ordovician specimens, probably because of taxonomic differences between the Ordovician and Silurian *C. conicus* trace makers. Alternatively, Ordovician *C. conicus* specimens differ because of vertical adjustment in response to higher sedimentation rates. The lack of lateral adjustment traces in the Silurian forms of *C. conicus* may be a result of differences in the mud substrate dynamics. The muddy bottom of the Telychian (Adavere Regional Stage) may have been more stable than the bottoms in the Sandbian of Estonia. Alternatively, it could be an artefact of sampling bias (*i.e.*, there are many more specimens known from the Ordovician than from the Silurian) and future *C. conicus* finds from the Silurian Estonia could reveal also the lateral adjustment traces.

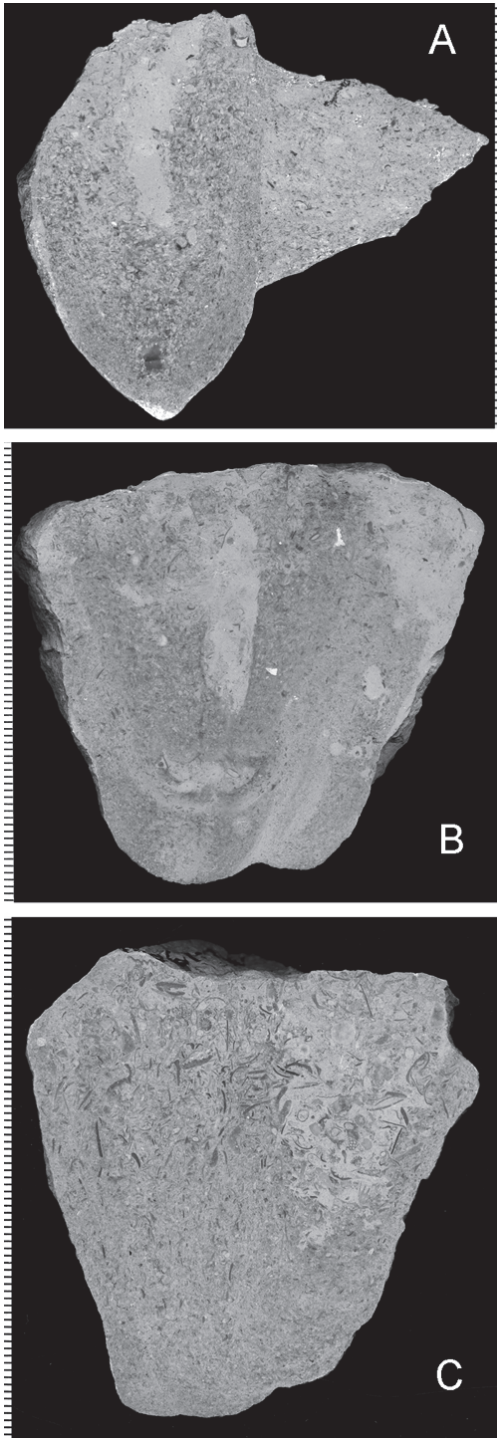
### Sedimentation environment

It appears that the sedimentary environment controlled the distribution of *Conichnus* in the Ordovician and Silurian of Estonia. Most likely the *Conichnus* traces were made by shallow-water animals in the Ordovician and Silurian of Estonia. One should also consider that preservation bias may have influenced the distribution of *Conichnus* traces. However, it seems reasonable to assume that the preservation potential in deeper and calm water marls and argillites was not lower than in shallow-water clayey limestones. Thus, the *Conichnus* trace makers were likely present only in the shallow water parts of the Ordovician and Silurian basin in Estonia. The lack or rarity of *Conichnus* in shallow water pure limestones possibly reflects the trace maker's preferences for the substrate, but alternatively it may represent a preservation bias. Either the *Conichnus* trace maker's substrate preference or preservation bias is responsible for the lack of *Conichnus* in the Lower Ordovician sandstones and argillites. However, *Conichnus* is not known from the Cambrian of Estonia and it is possible that *Conichnus* trace makers may have arrived in the Estonian part of the Baltic Basin during the Middle Ordovician.

The maximum abundance of *Conichnus* traces coincides with the highest amount of volcanic ash in the sedimentation environment both in the Sandbian and Telychian (HINTS *et al.*, 2006; KIPLI *et al.*, 2008, 2014). This may be a coincidence, but it is possible that numerous volcanic ash sedimentation episodes created ecologically favorable conditions for the *Conichnus* trace makers, such as better sediment cohesion with elevated clay content. Reduced bioturbation intensities may have also been favorable for *Conichnus* trace makers.

### Climate change

During the Katian, Baltica moved into the tropics (Cocks & Torsvik 2005; TORSVIK *et al.*, 2013). *Conichnus conicus* occurred both in temperate climate (Darriwilian) and tropics (Llandovery). The clayey limestones containing *C. conicus* in the Sandbian are very similar to those found in the Telychian of Estonia (KALJO, 1970; JÜRGENSON, 1988; RAUKAS & TEEDUMÄE, 1997). Thus, it is unlikely that the differences in the substrate or preservation caused the differences in the abundance of *C. conicus* between the Sandbian and Telychian. Instead, it is possible that *C. conicus* trace makers may have preferred muddy bottoms of the temperate seas more than their tropical equivalents. Tropical seas have different and more abundant benthos, which may have caused the decrease of *C. conicus* abundance. It is also possible that the increased water temperature could affect *C. conicus* abundance.



### Comparison to other occurrences of *Conichnus* and *Amphorichnus*

*Conichnus* isp. and *Amphorichnus* isp. are known from the Lower Ordovician of St Petersburg region, Russia (Baltica) (ERSHOVA *et al.*, 2006). PACZEŚNA (2010) described *Conichnus conicus* and *C. papillatus* from Lower Cambrian sandstones of southern Poland, which formed a part of Brunovistulian terrane. *Conichnus* has also been described from the Upper Cretaceous of North America (FREY & HOWARD, 1981; HOWARD & FREY, 1984). JONES and PEMBERTON (1989) described *C. conicus* traces from shallow carbonate sediments of the Pleistocene of Grand Cayman. It is interesting that *C. conicus* occurs only in certain parts of the Ordovician and Silurian of Estonia (Baltica), while globally it occurs in various sedimentary rocks from Cambrian onwards. This could be explained by the different ecological requirements of *Conichnus* trace makers. These traces were presumably made by various animals with different environmental preferences.

### 8. Conclusions

1. *Conichnus conicus* and *Amphorichnus papillatus* are common in the Ordovician of Estonia. They are more common in the clay-rich carbonate rocks of the Sandbian than in the pure carbonates of the Katian. Only *Conichnus conicus* occurs in argillaceous carbonates of the Lower Silurian (Llandovery). The peaks in the abundance of *Conichnus* traces coincide with the highest amount of volcanic ash in the sedimentation environment in the Sandbian and Telychian. Thus, tracemakers of both *C. conicus* and *Amphorichnus papillatus* preferred clay-rich carbonate sediments over the pure carbonate muds.

2. *Conichnus conicus* is more abundant in the temperate Sandbian and than in the tropical Telychian. It is possible that *C. conicus* trace makers may have preferred muddy bottoms of the temperate seas more than their tropical equivalents.

3. The morphology of the studied traces does not support synonymy of *Conichnus* and *Amphorichnus*. *Amphorichnus* differs significantly from *Conichnus* by its amphorous shape, papillate terminations, and the presence of lateral adjustment traces

◀ **Figure 4:** **A.** Longitudinal section of *Amphorichnus papillatus* MÄNNIL, 1966 (GIT 107-17) from Aluvere, northern Estonia, Vasavere Formation (Sandbian). **B.** Longitudinal section of *Conichnus conicus* MÄNNIL, 1966 (GIT 156-1736) showing lateral adjustment traces from Aluvere quarry, northern Estonia, Vasavere Formation (Sandbian). **C.** *C. conicus* (GIT 156-1910) showing lateral adjustment traces from Küttejõu, northern Estonia, Kiviõli Formation (Sandbian). Scale bar in mm.



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#### **Publication VII**

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## EARLIEST PETROXESTES BORINGS FROM SANDBIAN (EARLIEST LATE ORDOVICIAN) BRYOZOANS OF NORTHERN ESTONIA

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**ABSTRACT:** The earliest *Petroxestes* borings were excavated in large trepostome bryozoans in the Sandbian (earliest Late Ordovician) of Estonia. The Estonian specimens are morphologically similar to the type material from the later Katian of North America. *Petroxestes pera* is rare in the Sandbian of Estonia and occurs only in biogenic hard substrates. *Petroxestes* borings occur in muddy environments that were preferred by macroborers in the Hirnantian and early Silurian of North America. It is possible that muddy environments supported higher bioerosion intensities and higher diversity of bioerosional traces in the shallow epicontinental seas of the Late Ordovician. The discovery of *Petroxestes* in the Sandbian of Estonia supports the idea that there was an earliest Late Ordovician peak in the diversification of borings in Baltica. It is possible that there was a migration of bioerosional trace makers from Baltica to Laurentia in the Late Ordovician.

### INTRODUCTION

Among the oldest signs of macrobioerosion in the world are the small simple holes of *Trypanites* described from the early Cambrian archaeocyathid reefs in Labrador (James et al. 1977; Kobluk et al. 1978). These early macroborings are common in carbonate hardgrounds (Vinn et al. 2015), but they occur also in phosphatic pebbles and cobbles in the early Cambrian of Estonia (Vinn and Toom 2016). Bioerosion intensity and diversity increased markedly during the Ordovician, an event termed the Ordovician Bioerosion Revolution (Wilson and Palmer 2006). Bioeroded shells and hardgrounds are common in the Middle and Upper Ordovician of Baltica, and they are mostly *Trypanites* and *Palaeosabella* (Vinn et al. 2015). Less abundant, but still important, Ordovician bioerosion trace fossils in Baltica include *Bicescomanducator* (= *Caedichmus*, see Wisshak et al. 2019 for synonymy), *Gastrochaenolites*, *Gnathichmus*?, *Osprioides*, *Oichmus*, *Pinaceoladichmus*, *Rogerella*, *Ropalonaria*, *Sanctum*, and *Sulcolithus* (*Sulcichmus*, see Knaust, 2019 for synonymy) (Toom et al. 2019). In the Ordovician of Baltica, the diversity of bioerosional trace fossils was much higher in biogenic substrates than in hardgrounds and calcareous pebbles (Vinn et al. 2015; Toom et al. 2019). There is much information available about the bioerosional trace fossils of the Ordovician of North America, but only a limited number of works are devoted to their study from coeval successions of Baltica (Toom et al. 2019). The earliest signs of bioerosion in Estonia appear in the early Cambrian as small *Trypanites* borings in phosphatic pebbles and cobbles (Vinn and Toom 2016). The first larger borings belonging to *Gastrochaenolites*, occur in Lower to Middle Ordovician hardgrounds (Ekdale and Bromley 2001). *Trypanites* borings are common in brachiopods from the Arenig (Vinn 2004) and Sandbian (Vinn 2005) of Estonia. According to Wyse Jackson and Key (2007), two ichnogenera, *Trypanites* and *Sanctum*, occur in bryozoans in the Middle and Upper Ordovician of northern Estonia. Toom et al. (2017, 2019) mentioned possible *Petroxestes* borings in bryozoans from the Haljala Regional Stage (middle Sandbian) in northern Estonia,

but this information deserves a more detailed discussion as these are the earliest of their kind in the world.

*Petroxestes pera* borings have previously been reported from hardgrounds and bryozoan colonies from the Ordovician of Ohio and Kentucky (Wilson and Palmer 1988, 2006) and the lower Silurian of eastern Canada (Tapanila and Copper 2002). *Petroxestes* also occurs in the Upper Cretaceous of Belgium (Jagt et al. 2009) and the middle Miocene of Carriacou (Pickerill et al. 2001). General opinion is that a facultative rock-boring modiomorphid bivalve, *Corallidomus scobina*, produced the North American Ordovician *P. pera*, based on the presence of a bivalve specimen preserved *in situ* within the boring (Whitfield 1895; Pojeta and Palmer 1976; Wilson and Palmer 1988, 2006). The ichnospecies *Petroxestes altera* was described from the late Maastrichtian of northeast Belgium; it was likely produced by sipunculan worms (Jagt et al. 2009). Francischini et al. (2016) described a boring they named *Asthenopodichnium fallax* from the Upper Cretaceous of Brazil. Wisshak et al. (2019) consider *A. fallax* to be a junior synonym of *P. altera*. The terrestrial *Petroxestes* reported by Xu et al. (2018) from China is more likely a soft-sediment burrow similar to *Palaeophycus*.

The aims of this paper are to: (1) determine whether the large borings in Sandbian bryozoans belong to *Petroxestes*; and to discuss (2) the paleoecology of the *Petroxestes* trace makers; (3) the paleobiogeographic distribution of the trace fossil; and (4) the diversification of large borings during the Ordovician Bioerosion Revolution in Baltica.

### GEOLOGICAL BACKGROUND

In Estonia, Middle and Upper Ordovician limestones are well-exposed and form a broad belt from the Narva River in the northeast to Hiiu Island in the west (Nestor and Einasto 1997) (Fig. 1). The Ordovician System in Estonia varies from 70 to 180 m thick, being thickest in the southern part of the country (Nestor and Einasto 1997). In the Sandbian, the western part of the East-European Platform, which includes Estonia, was covered by a shallow, epicontinental sea. This shallow sea was

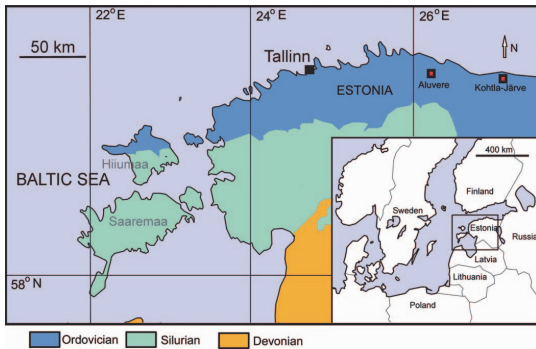


FIG. 1.—Locality map. Kohtla-Järve locality (lower Sandbian) and Aluvere quarry (middle Sandbian) marked with squares. Modified after Vinn et al. (2019).

characterized by little bathymetric differentiation and a low sedimentation rate (Nestor and Einasto 1997). In the study area of northern Estonia, a series of gray calcareous–argillaceous sediments accumulated along the entire extent of the basin ramp. The sedimentation trend is decreasing bioclasts and increasing clay in the offshore direction (Nestor and Einasto 1997). During the Ordovician, the paleocontinent of Baltica drifted from the temperate climatic zone to the subtropics (Cocks and Torsvik 2005; Torsvik et al. 2013). Due to Baltica’s drift towards the tropics, a climatic change took place in the Late Ordovician that caused an increase in carbonate production and sedimentation rate on the northern Estonian carbonate platform. Later in the Katian the first tropical carbonate buildups appeared, marking a notable change in the overall character of the paleobasin (Nestor and Einasto 1997). Both of the specimens studied here derive from shallow water, normal marine carbonates (Nestor and Einasto 1997).

The Kohtla-Järve locality (Fig. 1) of the Kukruse Regional Stage (lower Sandbian; Fig. 2) exposes intercalations of limestone with oil shale (kukersite) of various thickness. The Aluvere quarry (Fig. 1) of the Haljala Regional Stage (middle Sandbian; Fig. 2) exposes marly limestones and marls.

MATERIAL AND METHODS

The collection of the Department of Geology, Tallinn University of Technology, contains large numbers of Middle and Late Ordovician hemispherical bryozoans (70 specimens with a colony diameter about 80 mm from Aluvere quarry and 30 similarly large specimens from different localities of Kukruse Regional Stage). The bryozoan collection was searched for *Petroxestes* borings. Some Middle Ordovician hardground samples and samples from the Kukruse Regional Stage (earliest Sandbian), Keila Regional Stage (latest Sandbian–earliest Katian), Oandu Regional Stage (early Katian) and Vormsi Regional Stage (late Katian) were searched for *Petroxestes* borings. Studied specimens were cleaned from sedimentary matrix with a needle under the binocular microscope and photographed with a Canon EOS 5DS R digital camera. Measurements of the borings were taken from calibrated digital photos of specimens. All studied specimens are deposited at the Department of Geology, Tallinn University of Technology.

RESULTS

*Petroxestes* borings are rare in the Upper Ordovician of Estonia, occurring only in large trepostome bryozoan skeletons. The hardground samples studied here did not reveal any *Petroxestes* borings. Shallow to

| Series           | Stage    | Regional Stage        | Graptolite Zone           |
|------------------|----------|-----------------------|---------------------------|
| Upper Ordovician | Hirnant. | Porkuni               | <i>N. persculptus</i>     |
|                  |          |                       | <i>N. extraordinarius</i> |
|                  | Katian   | Pirgu                 | <i>D. anceps</i>          |
|                  |          |                       | <i>D. complanatus</i>     |
|                  |          | Vormsi                | <i>P. linearis</i>        |
|                  |          | Nabala                |                           |
|                  |          | Rakvere               | <i>D. clingani</i>        |
|                  |          | Oandu                 |                           |
|                  |          | Keila                 |                           |
|                  |          | Haljala               |                           |
| Sandbian         | Kukruse  | <i>D. multidentis</i> |                           |
|                  |          | <i>N. gracilis</i>    |                           |

FIG. 2.—Stratigraphy of *Petroxestes* in northern Estonia. Occurrences marked with hexagons. Stratigraphic column modified after Meidla et al. (2008).

relatively deep elongate borings with blunt ends occur in two large trepostome bryozoans from the Kukruse Regional Stage (earliest Sandbian) (Fig. 3A) and Haljala Regional Stage (middle Sandbian) (Fig. 3B–3D). The walls of these borings are commonly parallel, but can be also slightly convex or concave in horizontal view. The borings have rounded terminations in transverse and longitudinal section. Most specimens are relatively large, but size varies considerably; small borings occur more seldom. The depth of borings varies from a shallow groove on the surface of the bryozoan to a deep hole. Borings are up to 0.80 mm deep. The Kukruse specimens are 12.1 to 21.0 mm long and 2.3 to 4.2 mm wide (Table 1). The Haljala specimens are 9.2 to 25.1 mm long and 2.0 to 4.0 mm wide (Table 1). The morphology of these borings is most similar to the ichnospecies *Petroxestes pera* Wilson and Palmer, 1988, described from the Katian of North America. No remains of trace makers were found within the Estonian borings. Borings from the Haljala Regional Stage were clean of sedimentary matrix, presumably due to weathering. Borings from the Kukruse Regional Stage were originally filled with oil shale (kukersite). Both bryozoan specimens were intensely bioeroded by *Petroxestes*. *Trypanites* borings occur together with *Petroxestes* in both specimens. In the Haljala specimen the contribution of *Trypanites* to bioerosion was important, but in Kukruse specimen it was minor compared

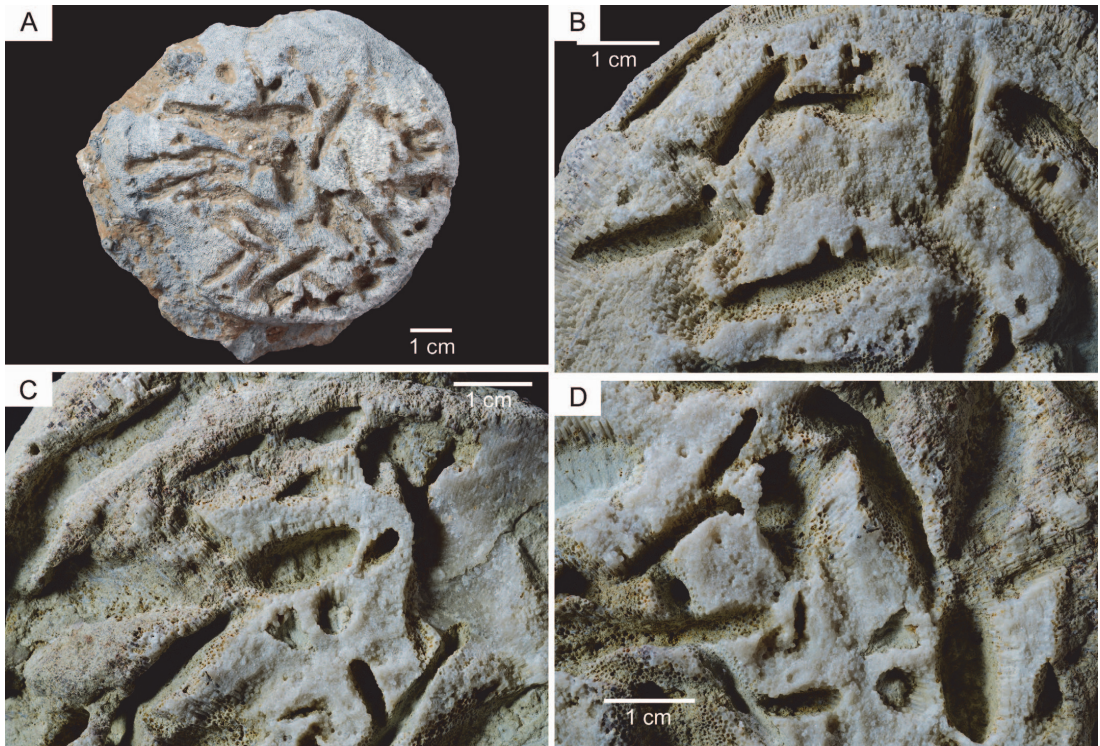


FIG. 3.—*Petroxestes pera* (elongate borings) from trepostome bryozoans, Late Ordovician, northern Estonia. A) Kohtla-Järve, Viivikonna Formation, Kukruse Regional Stage, earliest Sandbian (GIT 343-182-1). B–D) Aluvere quarry, Kahula Formation, Haljala Regional Stage, middle Sandbian (GIT 720-5-1).

to *Petroxestes*. Both upper and lower side of the Haljala specimen show signs of bioerosion.

#### DISCUSSION

##### *Morphology of Petroxestes*

The morphology of Estonian *Petroxestes pera* borings does not differ in any significant way from the North American specimens (Wilson and Palmer 1988). The dimensions of the Estonian *Petroxestes pera* specimens are very similar to their American equivalents, though the maximal length of Estonian specimens (25.1 mm) slightly exceeds the American ones (20.3 mm). The Estonian material markedly differs from *P. altera* (late Maastrichtian, Belgium) in displaying no chipped margins and no sculpture of undulating grooves or small scratches on the bottom of the trace (Jagt et al. 2009).

##### *Paleoecology*

Trepostome bryozoans living on soft, muddy seafloors constituted benthic islands that provided a habitat for hard substrate colonizers. Trepostome colonies were relatively common in the mud-dominated environments of the Sandbian in Estonia. Due to its relatively large size, the tracemaker of *Petroxestes pera* needed large substrates. Most common brachiopods, echinoderms and small bryozoans were not massive enough to accommodate *Petroxestes*. The rarity of *Petroxestes* among borings in

biogenic substrates was therefore at least partially caused by the relatively small number of sufficiently large hard substrates available in soft bottom regions of the Baltic Basin during the Sandbian.

*Trypanites* borings are common in environments with strong winnowing such as hardgrounds and rocky coastlines (Palmer 1982; Tapanila et al. 2004). Rocky shores often have lower predation levels compared to other regions in the sea (Johnson and Baarli 1999), which could be beneficial for some boring organisms. Some hardgrounds with phosphatic crusts had enhanced nutrient supply (Wilson and Palmer 1992), making them preferred environments by many suspension feeders. In the Late Ordovician of North America, *Petroxestes* is commonly associated with hardgrounds (Wilson and Palmer 1988). However, Late Ordovician hardgrounds from Baltica are typically rich in *Trypanites*, but devoid of *Petroxestes* (Vinn et al. 2015). It is possible that environmental conditions associated with hardgrounds were different in the Baltic Basin compared to those in North America (Laurentia). Muddy bottom regions of the Baltic Basin definitely supported different fauna and flora than hardgrounds. There also may have been differences in productivity. Productivity and faunal and floral compositions strongly influence the survival of any organism in a particular environment. The Ordovician *Petroxestes* probably constituted a domicile of a suspension feeding animal, most likely a bivalve (Wilson and Palmer 1988). One possible explanation is that there were better feeding conditions for suspension feeders in muddy regions of the sea. Mud bottom regions of the Baltic Ordovician Basin also may have been more productive. On the other hand, hardgrounds were

TABLE 1.—Measurements of best preserved *Petroxestes* borings. Abbreviation: *sd* = standard deviation.

| Specimen                 | Length (mm)                             | Width (mm)                           | Total number of borings per substrate | Approximate number of bryozoans |
|--------------------------|---|--------------------------------------|---------------------------------------|---------------------------------|
| Kukruse bryozoan (total) | 12.1–21.0<br>mean 14.4<br>sd 3.1<br>N=6 | 2.3–4.2<br>mean 3.2<br>sd 0.6<br>N=6 | 24                                    | 30                              |
| Specimen 1               | 21.0                                    | 3.1                                  |                                       |                                 |
| Specimen 2               | 15.2                                    | 2.3                                  |                                       |                                 |
| Specimen 3               | 12.1                                    | 3.0                                  |                                       |                                 |
| Specimen 4               | 12.3                                    | 4.2                                  |                                       |                                 |
| Specimen 5               | 13.0                                    | 3.3                                  |                                       |                                 |
| Specimen 6               | 12.9                                    | 3.1                                  |                                       |                                 |
| Haljala bryozoan (total) | 9.2–25.1<br>mean 15.9<br>sd 5.4<br>N=8  | 2.0–4.0<br>mean 2.8<br>sd 0.7<br>N=8 | 23                                    | 70                              |
| Specimen 1               | 25.1                                    | 4.0                                  |                                       |                                 |
| Specimen 2               | 11.0                                    | 2.2                                  |                                       |                                 |
| Specimen 3               | 9.2                                     | 3.1                                  |                                       |                                 |
| Specimen 4               | 15.3                                    | 2.1                                  |                                       |                                 |
| Specimen 5               | 24.1                                    | 3.4                                  |                                       |                                 |
| Specimen 6               | 13.0                                    | 2.3                                  |                                       |                                 |
| Specimen 7               | 16.4                                    | 3.1                                  |                                       |                                 |
| Specimen 8               | 13.2                                    | 2.0                                  |                                       |                                 |

often associated with cyanobacterial biofilms in the Ordovician of Baltica (Rozhnov 2019). These could have been toxic to some organisms and prevented colonization by *Petroxestes*. Tapanila et al. (2004) found that bored biogenic hard substrates are most common in muddy off-reef facies, less common in sandy off-reef facies and least common in reefs. Thus, the studied *Petroxestes* borings occurred in an environment that was preferred by macroborers in the Hirnantian and early Silurian of North America. It is possible that this gradient in bioerosion intensities could have coexisted with a gradient in diversity of bioerosional traces in shallow epicontinental seas in the Late Ordovician. In any case, organic substrates from muddy off-reef facies (Toom et al. 2019) show much higher diversity of bioerosional traces than hardgrounds in the Ordovician of Baltica (Vinn et al. 2015).

#### Ordovician Diversification of Macroboring in Baltica

There was an increase in the number of bioerosional ichnogenera at the beginning of the Sandbian (Kukruse regional Stage) in Baltica (Toom et al. 2019). The same applies for the number of categories of architectural design (Buatois et al. 2017) of bioerosional trace fossils in the Baltic Basin (Toom et al. 2019). Several groups of organisms capable of boring reached peak richness during the Late Ordovician due to the Great Ordovician Biodiversification Event (GOBE) (Toom et al. 2019). Stigall et al. (2019) found that the GOBE is primarily Darrivilian and was facilitated by simultaneous biotic/abiotic events. Wilson and Palmer (2006) termed the interval of drastic diversification of macroboring ichnotaxa during the Middle and Late Ordovician the Ordovician Bioerosion Revolution. During this rapid diversification of traces, the intensity of carbonate substrate bioerosion also increased markedly (Wilson and Palmer 2006). The data of Toom et al. (2019) showed that the Ordovician Bioerosion Revolution reached its peak in the Late Ordovician in Baltica, and it seems that the major diversification of bioerosional traces took place at the very

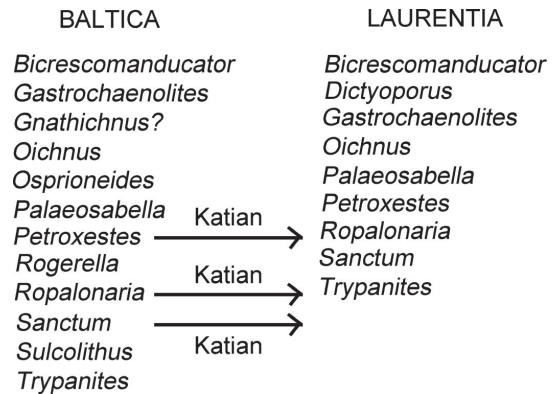


FIG. 4.—Bioerosional trace fossils diversity in the Ordovician of Baltica and Laurentia and possible migrations of trace makers in the Katian. Data for Baltica are based on Toom et al. 2019 and Wilson and Palmer 2006. Data for Laurentia are based on Wilson and Palmer 2006.

beginning of the Sandbian. The *Petroxestes* reported here support the earliest Late Ordovician peak in the diversification of borings in Baltica. However, it is possible that the global peak of the Ordovician Bioerosion Revolution could have predated the beginning of the Sandbian as the Late Ordovician is associated with the warming of the climate in Baltica due to its drift towards the tropics. The tropical fauna was more diverse than the temperate fauna of the Middle Ordovician of Baltica. The tropical fauna also likely contained more boring taxa than the temperate fauna of Baltica.

#### Paleobiogeographic Notes

The faunas of Laurentia and Baltica were distinct in the Middle Ordovician and early Late Ordovician. Similarly, there are some differences between Baltica and Laurentia in the ichnotaxonomic composition and diversity of bioerosional trace fossils. Vinn et al. (2015) found that North American hardground borings were more diverse than those in Baltica. They explained this by different environmental conditions, such as substrate texture, oxygen levels, nutrient content, depositional energy and sedimentation rate due to climatic differences during most of the Ordovician (Vinn et al. 2015). Laurentia was located in the tropics during the Ordovician while Baltica was located in a temperate climate zone from the earliest Ordovician to the Sandbian (Vinn et al. 2015). It would be reasonable to speculate that tropical Laurentia in the Middle Ordovician to late Sandbian (Lam et al. 2018) with its diverse fauna was the center of origination for many bioerosional trace fossils, and that many Late Ordovician borings in Baltic are of Laurentian origin. However, Ordovician bioerosional trace fossils are more diverse in Baltica than in Laurentia (Toom et al. 2019; Wilson and Palmer 2006). During the Dapingian through late Sandbian ages, dispersal of invertebrate species occurred among major paleocontinents, and was facilitated by major ocean currents and gyre systems (Lam et al. 2018). Our new data on *Petroxestes* suggests that this boring appeared earlier in Baltica (earliest Sandbian) than in Laurentia (earliest Katian). Thus, *Petroxestes* likely originated in Baltica. Similarly, *Sanctum* appears earlier in the Baltica (latest Darrivilian) than in Laurentia (Katian) (Erickson and Bouchard 2003; Toom et al. 2019). Same is true for the *Ropalonaria* that appeared earlier in the Baltica (Dapingian–earliest Darrivilian) than in Laurentia (Katian) (Wilson and Palmer 2006). This indicates that there possibly was a migration of bioerosional trace makers from Baltica to Laurentia in the Late Ordovician (Fig. 4).



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#### **Publication VIII**

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## CONCH STRUCTURES, SOFT-TISSUE IMPRINTS AND TAPHONOMY OF THE MIDDLE ORDOVICIAN CEPHALOPOD *TRAGOCERAS FALCATUM* FROM ESTONIA

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**Abstract:** *Tragoceras falcatum* (SCHLOTHEIM, 1820) is a common, loosely coiled estonioceratid (Tarphyserida, Cephalopoda) occurring in the Kunda Regional Stage (early Darriwilian, Middle Ordovician) of Estonia. Although the species is quite well-known, we document some features for the first time. For example, one specimen from the Harku quarry (Estonia) with a phosphatized replacement shell exhibits growth halts (megastriae) on the body chamber. As they are not preserved in smaller specimens, we suggest that these megastriae formed at the approach of maturity, possibly also reflecting sexual dimorphism and cycles of reproduction (iteroparity?). Additionally, the specimen shows minute soft-tissue imprints (drag bands and pseudosutures). These imprints are comparable to patterns in other cephalopods such as ammonoids, bactritids and other nautiloids, but have not yet been reported from Palaeozoic nautiloids. However, they might have been misinterpreted as oncomyarian muscle attachment scars previously. Lastly, we discuss the taphonomy of the specimen, which was encrusted by multiple bryozoan colonies post-mortem. Furthermore, it shows questionable traces of bioerosion.

**Key words:** Tarphyserida, Estonioceratidae, Darriwilian, megastriae, bryozoa, Baltoscandia

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### Introduction

Representatives of the order Tarphyserida were the earliest cephalopods with a coiled conch, a feature that evolved independently multiple times e.g. in modern day *Nautilus* and *Spirula*, but also in many other fossil groups such as ammonoids and lituitids (Dzik 1984, Kröger 2005). Some of the earliest tarphyserids, belonging to the family Estonioceratidae, were not yet fully coiled. They either had gyroconic shells where the whorls do not touch each other, or were only coiled in the early ontogenetic stages, with later stages of the conch diverging (Furnish and Glenister 1964). Estonioceratids are common in the Kunda Stage of Estonia, from which a number of genera and species have been described (King 2014).

Here, we present a remarkable specimen of *Tragoceras falcatum* (SCHLOTHEIM, 1820) that was encrusted by a bryozoan colony with another colony on top. Furthermore, we discuss two conspicuous constrictions near the base of the body chamber. Lastly, we describe the clearly visible soft-tissue imprints and discuss their origins.

### Material and methods

The specimen was collected from the Harku quarry, near Tallinn, Estonia (lat.: 59.398371 N, long.: 24.563784 E). The locality is well-known for yielding excellent cephalopod remains of the Kunda Regional Stage (early Darriwilian, Middle Ordovician), such as endocerids, actinocerids and tarphyserids, which are commonly phosphatized (e.g. Mutvei 1997a, b, 2002, Kröger 2012). Furthermore, the different localities in Harku Hillcock yield abundant benthic organisms and trace fossils. The studied cephalopod specimen is housed in the Institute of Geology at Tallinn University of Technology (Estonia) under the number GIT 819-1 (Text-fig. 1a, d). Further comparative material also originates from the Harku quarry and the nearby locality of Maardu (lat.: 59.4505556 N, long.: 25.0338889 E).

The convex side of the *Tragoceras* conch curvature has long been recognized as the ventral side (e.g. Dewitz 1880, Teichert 1964), which is followed here. Accordingly, the term dorsal refers to the concave side of the curvature,



**Text-fig. 1.** Megastriae and post mortem epicoles on *Tragoceras falcatum* (SCHLOTHEIM, 1820). Arrows and M1–M3 indicate megastriae, bryozoan colonies are indicated by B1 and B2. a: GIT 819-1, left lateral view; b: body chamber of GIT 819-1, dorsal view; c: body chamber of GIT 819-1, left lateral view; d: GIT 819-1, right lateral view; e: PIMUZ 37299, right lateral view; f: detail of the body chamber of GIT 819-1, right lateral view, encrusted by bryozoans; g: bryozoan colony with *Trypanites* borings growing on an older bryozoan crust GIT 819-1. Specimens oriented with aperture downwards. Scale bars 10 mm.

while length, height and width refer to the longitudinal, dorsoventral and lateral axes, respectively.

#### Institutional abbreviations

GIT – Department of Geology, Tallinn University of Technology, Estonia

TUG – University of Tartu Natural History Museum, Estonia

PIMUZ – Paläontologisches Institut und Museum, University of Zürich, Switzerland

#### Systematic remarks

Dzik (1984) synonymized a number of loosely coiled estonioceratids, namely *Aserioceras* STUMBUR, 1962, *Bentoceras* STUMBUR, 1962, *Pyncoceras* HYATT, 1894 and with reservation *Falcilituites* REMELÉ, 1886, with *Tragoceras* REMELÉ, 1890. However, we follow King (2014), who accepted these genera as separate taxa in his review of the Estonioceratidae. Thus, the genus *Tragoceras* has a distinctly curved, slender, slowly expanding conch with a compressed

cross section and sutures with broad lateral saddles. Although the genus is fairly common, the apex and juvenile stages of the conch are unknown. Nevertheless, it appears likely that they were tightly coiled (Dzik 1984, King 2014). Also, note that the genus was previously referred to *Planctoceras* SCHRÖDER, 1891 on many occasions (e.g. Ulrich et al. 1942, Flower and Kummel 1950, Balashov 1953, Mutvei 1957, 2002, Sweet 1958, Stumbur 1962); however, after Furnish and Glenister (1964) and King (2014), *Tragoceras* has priority and is the valid name for the genus.

According to King (2014), *Tragoceras* contains only the type species, *Tragoceras falcatum* (SCHLOTHEIM, 1820) and the species “*T. arciforme*” (BALASHOV, 1953) is most likely synonymous. However, two additional species have been described which were omitted by King (2014). “*Planctoceras*” *quenstedti* HYATT, 1894 (Hyatt 1894: 446) was only very briefly mentioned and is probably also synonymous with *T. falcatum*. *T. yichangense* XU et LAI, 1987 (Xu and Lai 1987: 289, pl. 24, fig. 9) has been described from the Early Ordovician of China, but from the description and figure it is not clear whether the species really belongs to *Tragoceras*. If true, *T. yichangense* would represent the only known *Tragoceras* outside Baltoscandia.

## Megastriae

Adult modifications of the body chamber occur in many lineages of Palaeozoic cephalopods and are often caused by a change in growth patterns. In most cases, these involve changes in apical angle, curvature or a contraction or constriction of the aperture (e.g. Stridsberg 1981, Dzik 1984, cf. Bucher et al. 1996, 2003, Urdu et al. 2010). Some more unusual modifications are longitudinal imprints in *Orthoceras* and *Ctenoceras* (e.g. Troedsson 1931, Kröger 2004, Kröger and Isakar 2006), a strongly laterally contracted aperture with a separation of head and hyponome in the Silurian discosorid *Phragmoceras* (e.g. Manda 2008) or lateral outgrowths and visor-like apertures in the Devonian rutoceratids *Ptenoceras* and *Hercoceras* (Turek 2007, 2008).

The preserved part of the body chamber of the herein studied specimen GIT 819-1 is 75 mm long, 23 mm high and 21 mm wide at the base and shows a different modification. The shell is sharply constricted almost immediately adorally to the base of the body chamber, parallel to the growth lines of the shell (Text-fig. 1b, c). Similar constrictions in a specimen of *Tragoceras* were described by Dewitz (1880: 176, pl. 4, fig. 3); however, according to him, the constrictions are only present on the internal mould and were caused by shell thickening. In GIT 819-1, the constrictions are definitely present on the external surface of the shell. On the dorsum, the first constriction can be seen 10 mm from the base of the body chamber. In contrast to Dewitz's (1880) specimen, the constriction is only faintly visible on the internal mould, which is exposed at the left ventrolateral side of the conch. The right ventrolateral side is covered by a bryozoan on the body chamber and thus not visible. Nevertheless, as the constriction is parallel to the growth lines, which slope in an adaperatural direction on the dorsum (prorsiradiate), the constriction probably begins very close to the ventral base of the body chamber.

A second constriction (Text-fig. 1b, c) occurs at a distance of 21 mm adorally from the first and is even more pronounced. After both constrictions, the shell expands rapidly in width by about 1 mm, but contracts shortly thereafter, producing a convex outline. Thus, the largest dorsoventral diameter of 25 mm occurs after the second constriction.

Another 21 mm adaperaturally from the second constriction at the most anteriorly preserved part of the specimen, there is a third constriction, this time only a shallow constriction (Text-fig. 1b, c), measuring slightly over 23 mm in height.

The constrictions described above resemble growth halts (megastriae) found in certain ammonoids (e.g. Bucher et al. 1996, 2003, Klug et al. 2007). Furthermore, the shell adoral of the constriction is apparently attached to the inside of the shell adapical of the constriction, i.e., the older shell material overlies the more recently formed shell. Thus, we interpret the constrictions as megastriae, representing phases during which the animal stopped growing and later resumed growth. In contrast to ammonoids, however, they appear to be restricted to the adult body chamber in *Tragoceras*. In ammonoids, megastriae are often formed throughout the majority of post-embryonic ontogeny. Thus, they may mark the boundaries between growth phases and therefore are also present on the phragmocone. It is possible

that ontogenetically younger constrictions are not visible in our *Tragoceras* specimen because the left side lacks shell remains and the right side is covered by a bryozoan. However, the constrictions mentioned by Dewitz (1880) are also restricted to the body chamber and another specimen illustrated by Schröder (1891: pl. 6, fig. 1a; re-figured by King 2014: fig. 3c) shows two similar constrictions in the adult part of the specimen (although it is not clear from the illustration, where the base of the body chamber is located).

Although *Tragoceras falcatum* is relatively common and several dozens of specimens are deposited at the collections in Tallinn and Tartu, the constrictions are only visible in a limited number of the specimens. This is partly because many of the specimens are broken and only a small part of the conch is preserved. These fragments do not all represent the same ontogenetic stage and the body chamber is not always preserved. Furthermore, the remains are often corroded, making it difficult to discern whether constrictions are present. However, the constrictions are visible in at least one additional specimen, TUG 860-1642 and perhaps also in TUG 1393-57-1, TUG 856-5-2 and GIT 426-125.

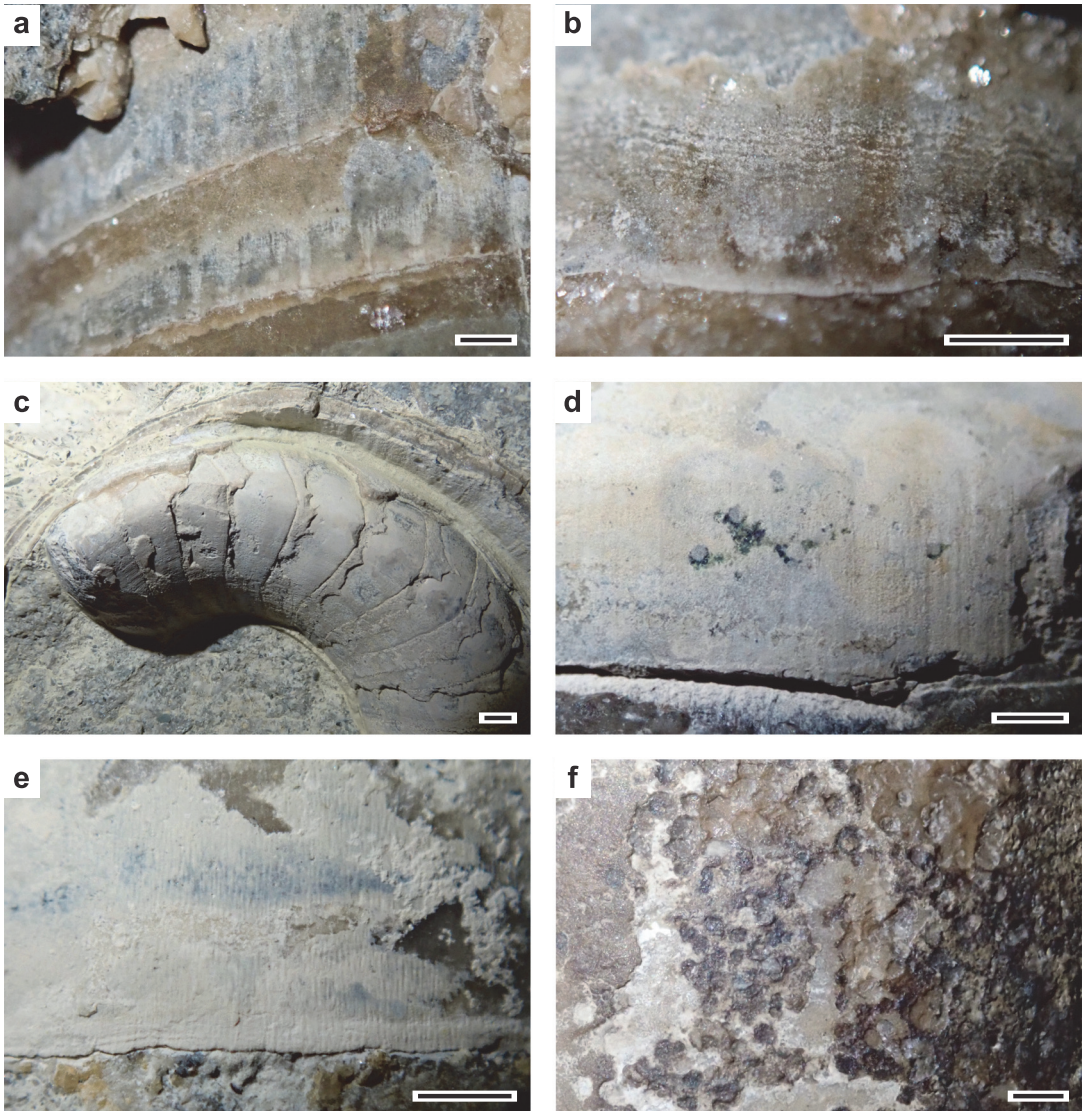
Another well-preserved specimen from Harku (PIMUZ 37299; Text-fig. 1e) shows no sign of any pronounced constrictions, only somewhat irregularly developed growth lines and lirae. These probably represent minor growth cycles or halts, but they did not produce the convex outline as in GIT 819-1. PIMUZ 37299 has a dorsoventral whorl cross section of 20 mm at the base of the body chamber, which only increases to 21 mm over the remaining 90 mm of the body chamber. This corroborates the assumption that the constrictions/megastriae are restricted to the adult body chamber.

As GIT 819-1 is somewhat larger than PIMUZ 37299, this leaves four explanations for the constrictions: 1) the specimens belong to different species; 2) the constrictions represent a pathological condition or reflect other syn vivo-disturbances (injuries, other adverse conditions); 3) PIMUZ 37299 represents an ontogenetically younger stage; 4) the specimens are antidimorphs of one species and thus reflect sexual dimorphism.

We favour explanations 3) or 4), since the constrictions are too regular and occur too commonly to be pathological. It is possible that they belong to different species, but more detailed investigations are needed to confirm this hypothesis. The fact that the difference is confined to the adult stage suggests that ontogeny and sexual dimorphism represent plausible explanations. It is also conceivable – though difficult to test – that the animal ceased growth during phases of reproduction (iteroparity). The number of megastriae would then indicate the number of times that the animal reproduced. By comparison, the iteroparous recent *Nautilus* terminates growth completely at the approach of maturity (Collins and Ward 2010).

## Soft-tissue imprints

Soft-tissue imprints from fossil nautiloids are rarely documented and are mostly restricted to muscle attachment scars (e.g. Mutvei 1957, Sweet 1959, King and Evans 2019).



**Text-fig. 2.** Soft-tissue imprints and traces of bioerosion on Middle Ordovician cephalopods from Estonia. a: GIT 819-1, *Tragoceras falcatum* (SCHLOTHEIM, 1820), drag bands; b: GIT 819-1, *T. falcatum*, pseudosutures; c: GIT 819-2, *Estonioceras* sp., drag bands; d: GIT 819-3, cf. *Anthoceras vaginatum* (SCHLOTHEIM, 1820), drag bands; e: GIT 819-4, cf. *Orthoceras regulare* SCHLOTHEIM, 1820, drag bands; f: Pits on the body chamber of GIT 819-1, *T. falcatum*. Specimens oriented with aperture downwards. Scale bars 1 mm.

These were already described in *Tragoceras falcatum* as “Verwachungsband” (= adhesion band) by Dewitz (1880) and later by Mutvei (1957) as annular elevation. In *T. falcatum*, the muscle attachment scars are ventromyarian (sensu Sweet 1959). In GIT 819-1, the muscle attachment scars are mostly covered by shell and are thus only partially visible.

Some other imprints are more remarkable. The surface of the internal mould of the phragmocone (where the shell broke off) carries minute, but clearly visible longitudinal markings, so-called “drag bands” (Text-fig. 2a). Similar imprints have been documented by several authors in

ammonoids, bactritids and Mesozoic and extant nautilids (Zaborski 1986, Hewitt et al. 1991, Richter 2002, Richter and Fischer 2002, Kröger et al. 2005, Klug et al. 2008, Polizzotto and Landman 2010, Polizzotto et al. 2015). In contrast, they have not yet been described to our knowledge in Palaeozoic nautiloids apart from a few Devonian orthocerids (Kröger et al. 2005). The drag bands are usually interpreted as imprints of muscle fibers of the mantle. The homology of the structures in different groups is not clear and differences exist. In the case of *Tragoceras*, the drag bands are not confined to the mural band but rather continue from one septum to the next.



Further structures are visible in the same specimen, GIT 819-1, namely small undulating transverse lines on the dorsal side of the phragmocone (Text-fig. 2b). As the ventral side of the phragmocone is not exposed, it is not clear, whether these structures are restricted to the dorsum. It is clear that they become weaker towards the flanks and in the other fragment, which exposes the left flank of the phragmocone, they are not visible, although drag bands are clearly discernible in the same position. Nevertheless, the fact that they disappear slightly adorally suggests that these delicate structures might not always be preserved. We interpret these structures as pseudosutures, which are occasionally associated with drag bands but run parallel to the sutures instead of in the direction of growth (Polizzotto et al. 2015). Note that the pseudosutures are distinct from the wrinkle layer (“Runzelschicht”) well known in ammonoids and certain nautiloids (e.g. Teichert 1964, Mapes 1979, Kulicki et al. 2001, Korn et al. 2014).

It is interesting to note that the same continuous drag bands occur not only in the closely related *Estonioceras* (GIT 819-2; Text-fig. 2c), but also in endocerids (cf. *Anthoceras vaginatum* (SCHLOTHEIM, 1820); GIT 819-3; Text-fig. 2d), both of which also originate from the Harku quarry. We furthermore found drag bands in a stratigraphically slightly younger (Lasnamägi Regional Stage, late Darriwilian, Middle Ordovician) orthocerid (cf. *Orthoceras regulare* SCHLOTHEIM, 1820; GIT 819-4; Text-fig. 2e) from the Maardu quarry. In the latter case, the drag bands also occur on the entire free part of the septum. Pseudosutures are not visible in either of the aforementioned specimens. However, the presence or absence of soft-tissue imprints is more likely related to taphonomic processes (e.g. grain size, etc.) rather than phylogeny.

Within the last decade, isolated cases of longitudinal tracks or ridges on the surface of internal moulds of Palaeozoic nautiloid phragmocones have been interpreted as evidence for oncomyarian muscle attachment scars (Evans and King 2012, Mutvei 2013, King and Evans 2019). These structures occur in late Cambrian plectronocerids (King and Evans 2019: 68), Early Ordovician bisonocerids (Evans and King 2012: 25), late Silurian ascocerids (Mutvei 2013: 176) and a number of other specimens of various taxa (see King and Evans 2019: supplementary material). In contrast, the material documented here shows that longitudinal tracks on the phragmocone do not necessarily imply the presence of oncomyarian muscle attachment scars, because they are known to be dorsomyarian in *Orthoceras* and *Anthoceras* and ventromyarian in *Estonioceras* and *Tragoceras* (Mutvei 1957, 2002). In addition, most specimens that have been interpreted previously as oncomyarian based on phragmocone tracks lack actual muscle attachment scars (including the annular elevation) on the body chamber. Thus, the only evidence supporting an oncomyarian condition in these species is the presence of similar longitudinal structures on the body chamber of oncocerids, discosorids and certain ellesmerocerids (e.g. Mutvei 1957, 2002, 2013, Sweet 1959, Kröger 2007, Manda and Turek 2009). In summary, it appears likely that drag bands have been misinterpreted as oncomyarian muscle attachment scars on some occasions and caution is advised when using this character for phylogenetic inferences.

## Taphonomy

The shell of GIT 819-1 is thickly encrusted by bryozoans (Text-fig. 1f). Two larger colonies are present which cover the shell over a length of 39 mm and 42 mm respectively, the latter being located more adapically. These occur only on the left side of the conch, thus suggesting that the specimen was deposited with the right side facing the sediment and the bryozoans colonized the shell later. Post-mortem epicoles on cephalopod conchs are well documented throughout the Ordovician (e.g. Davis et al. 1999, Wyse Jackson and Key 2014). In Estonia, encrusting bryozoans on different Ordovician molluscs occur mostly on internal moulds of gastropods and bivalves (own data). This observation can be explained by Calcite Sea conditions, where aragonitic shells dissolved rapidly (Palmer et al. 1988, Palmer and Wilson 2004). Cephalopods with encrusting bryozoans are less common in Estonia, but locally abundant in reef environments such as the Late Ordovician Vasalemma Formation (Kröger and Aubrechtová 2018). Recently, Vinn et al. (2018) described encrusting bryozoans on cryptic surfaces (e.g. cephalopods from the Kunda Regional Stage) and noticed that cephalopods from the Ordovician of Estonia usually show relatively low encrustation densities. Cases of bryoimmuration as recently described by Wilson et al. (2019) are unknown in the Ordovician of Estonia.

Apparently, the large bryozoan colony which is located more adapically (Text-fig. 1d: B1) was later encrusted by another small bryozoan colony (Text-fig. 1g). The small bryozoan colony is hemispherical with a diameter of 6 mm and shows around 20 small circular pits. They are mostly less than 0.5 mm in diameter and likely represent *Trypanites* (e.g. Wyse Jackson and Key 2007), the most abundant bioerosional trace fossil in the Ordovician of Estonia, which often spread on bryozoans (Toom et al. 2019). Clumping behavior is common for macroborers, especially for the trace makers of *Trypanites* (Kobluk and Nemcsok 1981). There are different hypotheses regarding the identity of its producer, however, according to Wyse Jackson and Key (2007), a sessile annelid polychaete worm is the most likely candidate. Further questionable instances of *Trypanites* are visible on the cephalopod shell itself and look very similar to the ones on the bryozoan in Text-fig. 1g.

Distinct from these possible cases of *Trypanites* are some other traces on specimen GIT 819-1. The most adoral part of the body chamber is densely covered by shallow, somewhat irregularly shaped pits, which have a slightly larger diameter than those on the bryozoan (Text-fig. 2f). In many cases, these pits are closer to each other than their own diameter. It is not clear whether the latter pits were produced by boring organisms or diagenetic processes. The latter explanation is supported by the irregular outline and shallow depth of the pits, potentially indicating that the shell was starting to dissolve. However, it is also possible that bacteria or fungi played a role. Thus, at present we leave the questions regarding formation of these structures open.

Similar structures were first described by Girty (1909: 53–54, pl. 6, fig. 6) on a Carboniferous bacritid and by Elias (1958: 50–51, pl. 3, figs 14, 16) on a Carboniferous ammonoid. Based on these findings, the latter author established the new ichnotaxon *Cyclopuncta girtyi* ELIAS,

1958. Further questionable cases of *Cyclopuncta* were reported on Devonian pseudorthocerids (Niko 1996: 355, fig. 6.2–3). While Girty (1909) considered the punctual traces as an integral part of the shell, Elias (1958) regarded them as having been produced by the attachment of epizoans. In contrast, Hoare et al. (1980) favoured an inorganic origin. The ichnogenus was not accepted by the Treatise (Hantzschel 1962) because the authors considered it as unrecognisable. More recently, Wisshak et al. (2019) classified *Cyclopuncta* within the ichnofamily Planobolidae.

There are differences between our material and the above-described cases of *Cyclopuncta*. Firstly, some of Girty's (1909) original material consists of elevations, rather than depressions. Secondly, *Cyclopuncta* appears to be generally more widely spaced. Nevertheless, the overall appearance is similar. Thus, we refer to the traces as cf. *Cyclopuncta*.

The above suggests that the specimen GIT 819-1 was deposited in a well-oxygenized but low energy environment and was lying on the muddy sea floor for some time after death, allowing bryozoans to use the shell as a substrate. This is in agreement with the slow sedimentation rates proposed by Jaanusson (1972) for the Ordovician of Estonia. Furthermore, the well preserved taphonomic bottom side of the shell suggests that there was limited post-mortem transport, as otherwise the shell would exhibit more characteristic breakage patterns (cf. Wani 2004, Yacobucci 2018).

## Conclusions

We describe a specimen of *Tragoceras falcatum* (SCHLOTHEIM, 1820) from the Kunda Regional Stage (early Darriwilian, Middle Ordovician) which is unusual in several aspects:

1. The body chamber carries at least two conspicuous constrictions which we interpret as adult growth halts (megastriae), potentially linked to mature growth and possibly reflecting sexual dimorphism since only some specimens show this pattern.

2. The internal mould of the phragmocone exhibits soft-tissue imprints such as drag bands and pseudosutures, which have not been documented before in Palaeozoic nautiloids, although possibly they have been misinterpreted as tracks of oncomyarian muscle scars. We also compare them to other Ordovician cephalopods.

3. The specimen is heavily overgrown by bryozoans, but only on the left side of the conch, which suggests that these are post-mortem encrustations. Further traces of bio(?) erosion (*Trypanites* and cf. *Cyclopuncta*) are also present on the specimen.

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## ***Tremichnus* in crinoid pluricolumnals from the Silurian of western Estonia (Baltica)**

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**Abstract:** Rare pits attributed to *Tremichnus* have been found in crinoids from the Silurian of Estonia. The Rhuddanian *Tremichnus* is the earliest symbiont in crinoid columnals of Baltica. These pits presumably were domiciles of unknown organisms. *Tremichnus* had a negative effect on the host crinoid as demonstrated by swollen columnals. *Tremichnus* in the Silurian of Estonia is less common than similar traces in the Silurian of nearby Gotland. The most important aspect of this study is the rarity of this interaction in these samples in contrast to most other samples of comparable age elsewhere. These structures have a very patchy distribution.

**Key Words:** Trace fossils; *Tremichnus*; symbiosis; crinoids; Silurian; Estonia.

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**Résumé :** *Tremichnus dans des segments de tiges de crinoïdes du Silurien d'Estonie occidentale (bouclier balte).*- Quelques petites cavités attribuées à *Tremichnus* ont été trouvées dans des crinoïdes provenant du Silurien d'Estonie. Ce *Tremichnus* rhuddanien est le symbiote le plus ancien observé dans des segments de tiges de crinoïdes du bouclier balte. Ces cavités correspondent vraisemblablement à des habitats d'organismes inconnus. *Tremichnus* a eu un impact négatif sur le crinoïde hôte comme en attestent les renflements des tiges. *Tremichnus* est moins fréquent dans le Silurien d'Estonie que des traces semblables dans le Silurien du Gotland voisin. L'aspect le plus significatif de cette étude est la rareté de cette interaction dans ces échantillons à la différence de la plupart des échantillons du même âge provenant d'autres localités. Ces structures ont une répartition très irrégulière.

**Mots-clefs :** Traces fossiles ; *Tremichnus* ; symbiose ; crinoïdes ; Silurien ; Estonie.

### **1. Introduction**

The Phanerozoic record of symbiosis often relies on trace fossils (TAPANILA, 2005). These trace fossils commonly include borings associated with shell repair in various invertebrates. The earliest symbiotic borings are known from Ordovician brachiopods, bryozoans and echinoderms (PALMER & WILSON, 1988; VINN, 2004; THOMKA *et al.*, 2014). Paleozoic symbiotic borings are especially common in echinoderms (BRETT, 1985; THOMKA *et al.*, 2014) and in the shells of brachiopods and mollusks (VINN, 2004). The Ordovician was a time of major diversification of invertebrates, and many new symbiotic interactions appeared by the Late Ordovician involving mostly larger colonial animal hosts, but also echinoderms (TAPANILA, 2005). During the Silurian the diversity of symbiotic interactions increased further (TAPANILA, 2005). The most

common endobiotic symbiont in crinoids is *Tremichnus* (BRETT 1978, 1985). *Tremichnus* is an embedment structure formed by an organism that inhibited growth of the crinoid host stereom (BRETT, 1978, 1985; ZONNEVELD & GINGRAS 2014; WISSHAK *et al.*, 2015).

Trace fossils in the Silurian of Baltica are poorly known, and most are not related to symbiosis. Traces caused by symbionts have previously been described from Silurian corals and stromatoporoids of Estonia (VINN *et al.*, 2014; VINN & MÖTUS, 2014a, 2014b). Silurian crinoids of Estonia are relatively well studied (AUSICH *et al.*, 2012, 2015), but their ichnofossils have mostly remained undescribed.

The aims of this paper are: 1) to describe *Tremichnus* from crinoids of the Silurian of Estonia; 2) to assess the frequency of *Tremichnus* in crinoids; 3) to discuss the ethology of *Tremichnus* in the crinoids.

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**Figure 1:** Locality map of crinoids with symbiotic borings.

## 2. Geological background and localities

During the Silurian the Baltica palaeocontinent was located in equatorial latitudes, slowly moving northward (MELCHIN *et al.*, 2004; COCKS & TORSVIK, 2005). The western part of modern Estonia was covered by the shallow epicontinental Baltic Basin (Fig. 1). The tropical Baltic Basin was characterized by diverse biota and environments. Organic buildups were common, especially coral-stromatoporoid reefs (RAUKAS & TEEDUMÄE, 1997).

NESTOR & EINASTO (1977) described the paleoenvironments of the Baltic Basin in detail. They reported the following facies belts: tidal flat/lagoonal, shoal, open shelf, transitional (*i.e.*, basin slope), and a basin depression. The first three facies belts formed a carbonate platform. A deep pericratonic basin with fine-grained siliciclastic deposition formed the latter two facies belts (RAUKAS & TEEDUMÄE, 1997).

Hilliste quarry (GPS: 58.873889; 22.971944) (Fig. 1) is located 1km east from Pühalepa Church. The fossiliferous limestones of the Hilliste Formation (Rhuddanian) have abundant favositids, stromatoporoids, and encrusting algae; they belong to the shoal facies belt. Sepise alvar (GPS: 58.455128; 22.007986) (Fig. 1) is a low escarpment limestone exposure located in Sepise Village.

Fossiliferous limestones of the Jaagarahu Formation (Sheinwoodian) exposed here are rich in tabulate corals and stromatoporoids.

## 3. Material and methods

An echinoderm collection from the Silurian of Estonia containing more than 1000 crinoid specimens, mostly columnals, was searched for signs of *syn vivo* borings. The studied collection, acquired by numerous collectors during the past 50 years, is housed in the Institute of Geology, Tallinn University of Technology. In addition, crinoid specimens collected during fieldwork in the Hilliste quarry were examined for borings. Hilliste quarry specimens are housed in the Natural History Museum (Museum of Geology), University of Tartu.

## 4. Results

*Tremichnus* is very rare in the Silurian crinoids of Estonia. It occurs only in a single specimen from the Hilliste Formation and in a single specimen from the Jaagarahu Formation.

One crinoid pluricolumnal with a single *Tremichnus* was found in the Rhuddanian (Hilliste Formation) of Hiiumaa Island (Fig. 2). The boring is oval with a somewhat irregular outline, and is moderately deep in the column wall. It has a rounded edge and shows partial repair. The columnal is strongly swollen around the pit. The pit is 4.7 mm long and 2.0 mm wide.



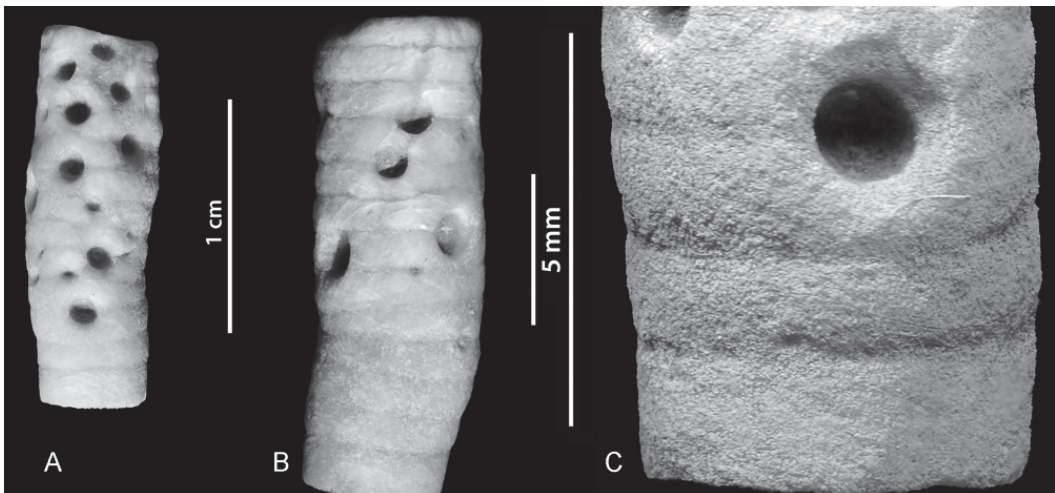
◀ **Figure 2:** A crinoid pluricolumnal with single *Tremichnus* from the Rhuddanian (Hilliste Formation) of Hiiumaa Island (Hilliste quarry) (TUG 1692-1).

One crinoid pluricolumnal (Fig. 3A-C) with multiple ( $n=14$ ) *Tremichnus* was found in the Jaagarahu Formation (Sheinwoodian) of Saaremaa Island. The borings are smaller and larger conical pits that penetrate the column wall around the circumference of the stem. These pits have circular outlines, rounded edges and straight-sided walls. The crinoid pluricolumnal appears to be slightly swollen at the pits. The diameter of the outer edge is 0.2 to 1.9 mm ( $n=14$ , mean 0.9 mm,  $sd=0.47$ ).

## 5. Discussion

### *Tremichnus* in a Rhuddanian pluricolumnal

The *syn vivo* nature of the pit is indicated by the strongly swollen column. In addition, the edges of the pit show partial repair. This is the earliest record of a symbiont in the columnals of crinoids from Baltica. The shape of the pit defies simple characterization. It differs from typical *Tremichnus* by its slightly irregular outline, but this may be due to partial repair. Overall, the structure is subelliptical. The top is broadly rounded, but the lowest portion tapers to a point until the final portion which is expanded into small bulb. The Rhuddanian specimen is a typical embedment structure formed by an organism that inhibited growth of the crinoid host stereom. There is evidence of the exterior columnal surface in the floor of the pit. This suggests that an epizoan settled on the exterior of the column but did not bore in but occupied space as the crinoid secreted extra stereom around it (BRETT, personal comm.). The most likely motive for settling on a crinoid columnal was to create a domicile. The exact nature of this crinoid-symbiont association is uncer-



**Figure 3: A-C.** A crinoid pluricolumnal with multiple *Tremichnus* from the Sheinwoodian (Jaagarahu Formation) of Saaremaa Island (Sepise) (GIT 405-165).

tain, but occupying a portion of the columnal wall may have had a negative effect on the host. The swollen pluricolumnal also indicates a negative effect of the symbiont on its host. It is possible that the symbiont may have consumed nutrients from the host crinoid tissues. Alternatively, it may have simply benefited from a higher tier for feeding if it was a suspension feeder. This trace resembles somewhat the barrel-shaped inflations of crinoid stems with one entrance hole described by FRANZÉN (1974). They also have edges around the pit often bent slightly inward, indicating that crinoid tried to close the opening. FRANZÉN (1974) suggested that metabolic waste products from the parasite might be responsible for the malformation of the surrounding columnals. She also argued that in some cases the contact with alien tissue might have been the stimulus for a histological response by the crinoid.

#### ***Tremichnus* in a Sheinwoodian pluricolumnal**

The pits in the Sheinwoodian pluricolumnal are slightly different from typical *Tremichnus* because they are more conical than bowl-shaped. The Sheinwoodian pluricolumnal is somewhat swollen at the pits. If this is not an artefact of preservation, it may indicate reaction of the crinoid. In this case the pits are similar to the parasitic pits known from crinoids since the Ordovician (BRETT, 1985; THOMKA *et al.*, 2014). The *syn vivo* origin of the pits is also supported by their distribution around the column. It is difficult to estimate the exact nature of this crinoid-symbiont relationship. Numerous deep pits in the column may have had negative effects on the host. The symbionts may have benefitted from a higher tier if they were suspension feeders. Alternatively, or in addition, they may have consumed nutrients from the crinoid. The symbionts also likely benefitted from a domicile and additional protection by the crinoid skeleton against the predators. Similar symbiotic pits (Type 1), possibly created by parasites, have been described from crinoid columns of the Sheinwoodian of Gotland (FRANZÉN, 1974). These pits (type 1 in the Gotland crinoids) are also located all around the stem and contain both smaller and larger pits. The crinoid collection studied here was comprised of numerous specimens from the Sheinwoodian of Saaremaa, but no other symbiotic pits were discovered. This kind of symbiotic pit may have not been common everywhere in the Silurian of Baltica. The producers of *Tremichnus* were potentially host-specific, as demonstrated by their decidedly non-random distribution among crinoid taxa in the Silurian of New York (BRETT, 1978). The absence of pits in most stems may simply reflect the fact that these were not the required hosts, which were rare in this setting.

#### **Symbiosis on Paleozoic crinoids**

Symbiosis was common in Paleozoic crinoids. There is a rich record of various invertebrates living symbiotically with crinoids, mostly various symbiotic boring organisms that lived within the crinoid columns. Symbionts in crinoid columnals are often common (FRANZÉN, 1974; WARN, 1974; WELCH, 1976; BRETT, 1978, 1985; MEYER & AUSICH, 1983; BAUMILLER, 1990; GUENSBURG, 1992; WILSON *et al.*, 2014). In addition to symbiotic boring organisms, there were also cornulitid worms, microconchids, tabulate corals, bryozoans and rhynchonellid brachiopods (FRANZÉN, 1974; PETER & BORK, 1998) that grew attached to the stems of living crinoids. Crinoids could also attach to an erect column of other crinoids (GUENSBURG, 1992). The Silurian of Estonia is well studied and rich in shelly fossils (RAUKAS & TEEDUMÄE, 1997). However, crinoid symbionts have not been reported previously. This probably represents a study bias as the earlier literature is mostly devoted to the stratigraphic distribution of fossils and less to paleoecology.

Crinoid symbionts have been previously described from Baltica only by FRANZÉN (1974), and it is clear that they did not form an important part of symbiotic interactions in this region at this time. Most records of symbiosis involve colonial organisms with massive skeletons, such as stromatoporoids and tabulate corals (KERSHAW, 1987; VINN & MÖTUS, 2014a, 2014b). Skeletal volume probably played an important role in symbiont host selection, although why this was is unclear. Crinoids, with their relatively low-volume skeletons, were less attractive hosts than the large colonial animals.

## **6. Conclusions**

*Tremichnus* is an embedment structure formed by an organism that inhibited growth of the crinoid host stereom. This is particularly likely in the case of the Rhuddanian specimen in which there is evidence for exterior surfaces of columnals in the floor of the pit. This suggests that an epizoan settled on the exterior of the column, did not bore into it but occupied space while the crinoid secreted extra stereom around it.

*Tremichnus* is rare in the crinoid columns from the Silurian of Estonia. This is not a study bias and can presumably be explained by the small number of suitable host species among the crinoid fauna. The rarity of crinoid-*Tremichnus* interactions here contrasts with other examples of comparable age elsewhere.

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# A sparsely encrusted hardground with abundant *Trypanites* borings from the Llandovery of the Velise River, western Estonia (Baltica)

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**Abstract.** The Päärdu hardground from the Telychian (Rumba Formation) of western Estonia is sparsely encrusted (0.4% of the studied surface) by possible tabulate corals, sheet-like bryozoans and discoidal echinoderm holdfasts. Both the upper and cryptic sides of the hardground are intensely bioeroded by *Trypanites* borings. The taxonomic composition of the Päärdu hardground association is rather different from the characteristic Silurian association in being dominated by tabulate corals, while bryozoans and echinoderms played a minor role in the association. The Päärdu hardground is more sparsely encrusted than common for the Late Ordovician and Silurian hardgrounds, but this may be a characteristic feature of the hardgrounds of Baltica. The Päärdu hardground is important among the Silurian hardgrounds because it has unusually low encrustation combined with high bioerosion.

**Key words:** bioerosion, *Trypanites*, hardgrounds, tabulates, bryozoans, echinoderms.

## INTRODUCTION

Carbonate hardgrounds are surfaces of carbonate layers that have been syndimentarily cemented and exposed on the seafloor. Such hardgrounds are more common in calcite seas than in aragonite ones because of favourable conditions for early cementation of carbonate sediments in the seafloor (Wilson & Palmer 1992). Hardgrounds form excellent attachment surfaces for encrusting and bioeroding organisms (Palmer 1982). The Silurian Period was characterized by calcite seas (Stanley 2006), and hardgrounds were common, though probably less abundant than in the Ordovician (Taylor & Wilson 2003).

Silurian hardground faunas, especially the early Silurian ones, are similar to those of the Ordovician (Taylor & Wilson 2003; Vinn & Toom 2015). Silurian hardgrounds are dominated by bryozoans and echinoderms, particularly crinoids (Taylor & Wilson 2003), but late Silurian (Pridoli) hardground faunas include also numerous microconchids (Vinn & Wilson 2010) (Table 1). Devonian encrusting communities differ from the Silurian ones in being dominated by microconchids, hederelloids and tabulate corals instead of bryozoans and echinoderms, although the latter two groups are still common (Kesling et al. 1980; Brett & Cottrell 1982; Alvarez & Taylor 1987; Taylor & Wilson 2003). During some time intervals microconchids may be absent or have a low abundance (Zatoń et al. 2015). However, Devonian encrusting communities are better known on shells than other hard substrates (Taylor & Wilson 2003).

Only seven detailed studies are known on Silurian hardground communities. Halleck (1973) described hardground encrusting crinoids, corals and brachiopods from the Wenlock of Indiana. Thomka & Brett (2014, 2015) found various echinoderm encrusters also from the Wenlock of Indiana. Franzén (1977) described hardground encrusting echinoderm holdfasts from the Silurian of Gotland. Cherns (1980) found a bioeroded hardground from the Ludlow of the Welsh Borderland. Sumrall et al. (2009) described edrioasteroids cemented to the hardground from the middle Silurian of Pennsylvania (Table 1).

Two hardground faunas have previously been described from Baltica (Einasto 1964), including crinoids from Gotland, Sweden (Franzén 1977) and a microconchid-dominated association from the Pridoli of Saaremaa, Estonia (Vinn & Wilson 2010). Hardground faunas of the Llandovery of Baltica have remained undescribed. These early Silurian communities are especially interesting regarding to the question of how and when typical Ordovician sclerobiont communities recovered after Ordovician–Silurian mass extinction.

This paper aims to (1) describe for the first time a hardground association of Llandovery age from Baltica, (2) test whether the Päärdu hardground association is typical for the Silurian, (3) test whether the density of bioerosion is negatively correlated with the encrustation density and (4) compare the hardground fauna from the Llandovery of western Estonia to other Silurian and Late Ordovician analogues.

**Table 1.** Silurian hard substrate faunas from Estonia and beyond

| Location                          | Lithology (substrate)   | Encrusting fauna<br>(in order of importance)   | Bioerosion                      | Age                | Reference                      |
|-----------------------------------|---|--|---------------------------------|--------------------|--------------------------------|
| Estonia (Baltica)                 | Dolomitized limestone<br>(hardground)                             | Tabulates, bryozoans,<br>echinoderms   | <i>Trypanites</i><br>(abundant) | Llandovery         | Present study                  |
| Estonia                           | Intrabiosparite<br>(hardground)                                   | Microconchids,<br><i>Anticalyptraea</i> ,<br>trepostome bryozoans,<br>crinoids, graptolites,<br>cornulitids, tabulates | <i>Trypanites</i><br>(abundant) | Pridoli            | Vinn & Wilson (2010)           |
| Estonia (Baltica)                 | Pelletal limestone<br>(stromatoporoids)                           | Rugosans,<br>microconchids,<br>auloporids, cornulitids,<br>trepostome bryozoans,<br>favositids, crinoids               | <i>Trypanites</i><br>(abundant) | Wenlock            | Vinn & Wilson (2012a)          |
| Estonia (Baltica)                 | Argillaceous limestones<br>(stromatoporoids)                      | Microconchids,<br>bryozoans, tabulates,<br>rugosans, crinoids  | <i>Trypanites</i><br>(rare)     | Pridoli            | Vinn & Wilson (2012b)          |
| Welsh<br>Borderland<br>(Avalonia) | Conglomeratic limestone<br>(hardground)                           | Absent   | <i>Trypanites</i><br>(abundant) | Ludlow             | Cherns (1980)                  |
| Indiana<br>(Laurentia)            | Limestone (hardground)  | Crinoids, blastozoan<br>echinoderms  | Absent                          | Wenlock            | Thomka & Brett (2014,<br>2015) |
| Indiana<br>(Laurentia)            | Limestone (hardground)  | Crinoids, auloporid<br>corals, craniid<br>brachiopods  | Absent                          | Wenlock            | Halleck (1973)                 |
| Pennsylvania<br>(Laurentia)       | Ostracode grainstones to<br>brachiopod packstones<br>(hardground) | Edrioasteroids   | Absent                          | Wenlock–<br>Ludlow | Sumrall et al. (2009)          |

## GEOLOGICAL BACKGROUND AND LOCALITY

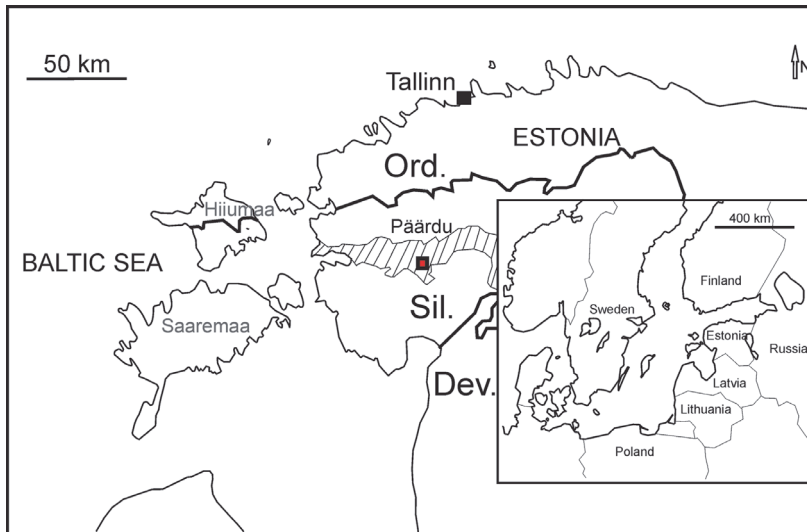
In the Silurian the Baltica continent was located in equatorial latitudes drifting northwards (Melchin et al. 2004). An epicontinental Baltic palaeobasin was located on the area of modern Estonia (Fig. 1). This basin was characterized by a wide range of tropical environments and diverse biotas (Hints 2008).

Nestor & Einasto (1977) established a general facies model for the basin including the following facies belts: tidal flat/lagoonal, shoal, open shelf, transitional (basin slope), and a basin depression. The first three facies belts formed a carbonate platform (i.e. carbonate shelf), the latter two a deeper pericratonic basin with fine-grained clastic deposits (Raukas & Teedumäe 1997).

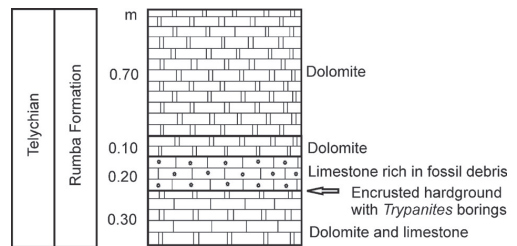
The Päärdu outcrop is located on the right bank of the Velise River 200 m west of the Tallinn–Pärnu highway bridge in western Estonia. Marls and nodular dolomitic limestones of the Rumba Formation are exposed at Päärdu (Fig. 2).

## MATERIALS AND METHODS

Twelve samples have been collected by scientists of the Institute of Geology at Tallinn University of Technology from the hardground of the Velise River outcrop during the past several decades. The samples were cleaned with water and brushes and then their upper and lower sides were photographed with scale bar using Nikon 7000. The studied total hardground surface area was 580.11 cm<sup>2</sup>. Unfortunately the orientation is not marked on the pieces of the hardground in the collection of the Institute of Geology (GIT), so the upper and lower surface features are not distinguished in this study. A maximum number of *Trypanites* borings was counted in 4 cm<sup>2</sup> using a grid drawn on a transparent film and calibrated photos. The 4 cm<sup>2</sup> area was chosen to follow the methodology of Tapanila et al. (2004) for the study of Ordovician and Silurian hard substrates. On calibrated photos a grid was also used to measure the area of the studied hardground surface and a grid drawn on a transparent film was used to measure the area covered by encrusters. The



**Fig. 1.** Location of the Päärdu outcrop at the Velise River, western Estonia. Exposure of the Adavere Regional Stage (incl. Rumba Formation) is marked with slanting lines.



**Fig. 2.** Section of limestones and dolomites of the Rumba Formation (early Telychian) in the Päärdu outcrop; modified after field notes of Rein Einasto.

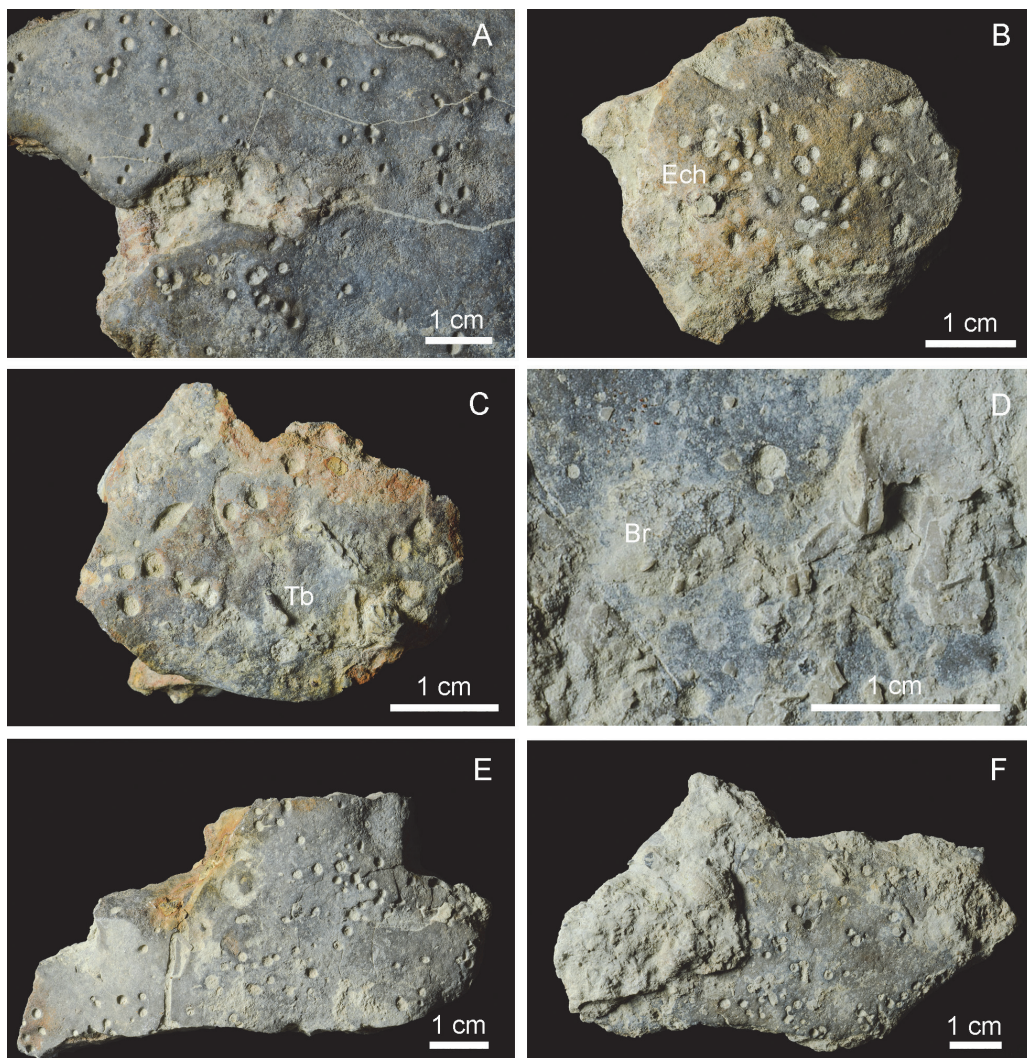
encrusting fauna was identified to the lowest possible taxonomic level. Several papers on hard substrate faunas were used as guides to aid the identification (Halleck 1973; Franzén 1977; Brett & Liddell 1978; Tapanila et al. 2004).

## RESULTS

The hardground surface is relatively flat, but in some places it can be bumpy with pronounced relief. Its surface is mostly relatively smooth, but it also has regions which have rougher microrelief. Both upper and lower hardground surfaces are strongly mineralized by pyrite and have a dark colour, in contrast to the light grey colour of the matrix. The hardground is strongly

abraded and partially broken into cobbles. There are also few somewhat linear fractures that reach through the hardground. Signs of possible microbio-erosion are observed on both surfaces of the hardground. Numerous *Trypanites* borings occur in the upper as well as the lower surface of the hardground (Fig. 3A). The intensities of the borings seem to be similar on both surfaces. The *Trypanites* borings have a somewhat patchy distribution, with a maximum of 27 borings found per 4 cm<sup>2</sup>. The diameter of the borings is 0.5 to 2.4 mm ( $N = 17$ , mean 1.2 mm,  $sd = 0.5$ ). Their apertures are mostly circular, in some cases slightly oval or subcircular. The apertures of some borings are merged.

The hardground surface is very sparsely encrusted by possible tabulates (Fig. 3C), sheet-like trepostome



**Fig. 3.** Päärdu hardground surfaces with encrusters and abundant *Trypanites* borings from the Rumba Formation, early Telychian of the Velise River, western Estonia. **A**, *Trypanites* borings (GIT 362-100); **B**, discoid echinoderm holdfast (GIT 362-101); **C**, possible tabulate corals (auloporids?) (GIT 362-105); **D**, bryozoa (possibly trepostome) (GIT 362-104); **E**, hardground surface with *Trypanites* borings (GIT 362-102); **F**, hardground surface with *Trypanites* borings (GIT 362-104).

bryozoans (Fig. 3D) and echinoderm holdfasts (only 0.4% of the studied 580.11 cm<sup>2</sup>; Fig. 3B). Presumed tabulates are the dominant group by number ( $N = 3$ ) and also by the area of encrustation. Tabulates include two possible auloporids with the encrustation area of 0.3 cm<sup>2</sup> and remains of an eroded tabulate with the encrustation area of 1.5 cm<sup>2</sup>. Both sheet-like bryozoa

with the encrustation area of 0.25 cm<sup>2</sup> and a discoidal echinoderm holdfast with the encrustation area of 0.2 cm<sup>2</sup> are represented by one specimen. The preservation of encrusters is variable; some are well preserved (i.e. not eroded) as a single large discoidal echinoderm holdfast, while remains of a plausible tabulate are strongly eroded. We did not notice any consistent differences between

encrustation intensities and the encrusting fauna across the hardground relief, but *Trypanites* borings seem to be more common in elevated regions.

## DISCUSSION

### Mineralization, fractures and palaeoenvironment

In Laurentia, many hardgrounds are strongly impregnated by minerals, but it is commonly phosphate that has developed (Sullivan et al. 2014). This contrasts with the pyrite mineralization of the Päärdu hardground. It is possible that pyrite mineralization may reflect the differences between palaeocontinents. Alternatively, the absence of phosphate can rule out the hypothesis that excess nutrients triggered anomalously high bioerosion frequencies.

The Päärdu hardground has been fractured into a series of polygonal sections (Fig. 3). Carlton Brett and James Thomka (pers. comm. 2015) have found very similar ‘platter hardgrounds’ in the Llandovery-age Brassfield Formation of the midcontinent USA, as well as within tentatively correlative units in the Medina Group in the Appalachian Foreland Basin. It is possible that hardgrounds of this type are widely traceable marker beds reflecting some underlying stratigraphic or palaeoceanographic process.

The encrusting echinoderm holdfast has a discoidal morphology. It likely indicates a very stable, clean, hard substrate rather than something that was slightly shifting, poorly winnowed or poorly sorted (Thomka & Brett 2015).

### Päärdu hardground association

It is interesting that boring intensities of the upper and lower hardground surfaces seem to be similar. According to Niell (1984), *Trypanites* organisms prefer open surfaces and elevations, because they probably were suspension feeders. As the Päärdu hardground includes large cryptic areas densely covered by *Trypanites* borings, it possibly had voluminous cryptic spaces with a good influx of suspended nutrients, necessary for *Trypanites* organisms. James Thomka (pers. comm. 2015) has found that the undersides or edges of raised substrata (i.e. tabulate coral colonies) are often densely encrusted in the Palaeozoic Laurentian hardgrounds. These areas might represent areas where horizontally flowing currents ‘swirl up’ over the encrusted obstructing substratum, making them sites of elevated current velocity or more consistent flow; hence, they might be preferred settlement sites (J. Thomka pers. comm. 2015). Our material was not large enough to study the possible

polarity (i.e. upper surface *versus* cryptic fauna) of the hardground association. The Päärdu hardground association is strongly dominated by endobenthic organisms (i.e. *Trypanites*), presumably both by the number of specimens and biomass, while the skeletal epibenthos forms the minor part of the association. However, it is possible that the extremely low skeletal cover of the hardground was due to its being pre-occupied by soft-bodied encrusters that did not fossilize. Soft-bodied encrusters such as sponges are common in modern seas. Alternatively, microbial mats might have covered some portion of the hardground and prevented encrustation (J. Thomka pers. obs. 2015). A similar hypothesis for a Devonian edrioasteroid-encrusted hardground was elaborated by Cornell et al. (2003). In the latter case the association may have been less tilted towards the dominance of endobenthos. Among the epibenthic organisms not elevated surface dwellers dominated (sheet-like bryozoans and possible tabulates), while elevated stemmed forms (i.e. echinoderms) formed a minor part.

### Taxonomic composition

Typical Ordovician–Silurian hardground associations are in general similar and dominated by bryozoans and echinoderms (Taylor & Wilson 2003). One would expect the early Silurian associations to be very similar to the Ordovician ones. Thus, the taxonomic composition of the Päärdu hardground association is rather different from the characteristic Silurian association in being dominated by tabulate corals, while bryozoans and echinoderms play a minor role. Regarding the position of tabulates in the association, the Päärdu hardground fauna is surprisingly modern, slightly Devonian-like, where tabulates form an important part of the associations. An association of stromatoporoid encrusters from the late Sheinwoodian of Saaremaa, Estonia, is somewhat similar to the Päärdu association (Vinn & Wilson 2012a). Sheinwoodian stromatoporoids of Saaremaa had also an unusually high number of encrusting corals (i.e. rugosans and tabulates). Bryozoans occur also in all other hard substrate associations described from the Silurian of Estonia (Vinn & Wilson 2010, 2012a, 2012b). Similarly, crinoids are usually found in hardground associations (Vinn & Wilson 2010) of Baltica (Franzén 1977; Vinn & Wilson 2010). Several Silurian hardgrounds from North America (Sumrall et al. 2009; Thomka & Brett 2014, 2015) differ from the Päärdu hardground by the lack of boring organisms in the association. In addition, the group diversity (i.e. number of higher taxa) of the Päärdu hardground is higher than in many North American examples (Sumrall et al. 2009;

Thomka & Brett 2014, 2015). Only the hardground fauna described by Halleck (1973) shows a group diversity similar to the Päärdu hardground. However, its taxonomic composition is different (Table 1). The lack of cornulitids in the association is taxonomically interesting. Cornulitids are common on the Late Ordovician hardgrounds of Baltica (Vinn & Toom 2015). Another interesting aspect is related to the lack of microconchids (Zatoń & Vinn 2011; Zatoń et al. 2015). These tiny tentaculitoid tubeworms appeared in the Late Ordovician of Baltica (Vinn 2006) and form an important part of the Pridoli hardground faunas in Estonia (Vinn & Wilson 2010). Thus, it is possible that microconchids were primarily organic substrate dwellers in the Late Ordovician and early Silurian of Baltica, and adapted to life on hardgrounds later in the Silurian.

### Encrustation intensity

The Päärdu hardground is relatively sparsely encrusted for the Late Ordovician and Silurian hardgrounds (Halleck 1973; Sumrall et al. 2009; Vinn & Wilson 2010; Thomka & Brett 2015). In general the Ordovician and Silurian hardgrounds of Baltica seem to be more sparsely encrusted (Vinn & Wilson 2010; Vinn & Toom 2015) than the North American analogues (Brett & Liddell 1978; Brett & Brookfield 1984; Wilson et al. 1992). However, due to numerous boring organisms that inhabited the Päärdu hardground, its general population density was not low for the Silurian.

### Bioerosion

Bioerosion of the Päärdu hardground was rather intense for the Early Palaeozoic with maximum boring intensities of >20 *Trypanites* per 4 cm<sup>2</sup>. Tapanila et al. (2004) considers >20 *Trypanites* per 4 cm<sup>2</sup> to be very high bioerosion intensity for the stromatoporoids of the Late Ordovician–earliest Silurian of Anticosti Island, North America. Relatively high bioerosion intensities seem to be characteristic of the Ordovician (Vinn et al. 2015) and probably also Silurian hardgrounds of Baltica (Vinn & Wilson 2010). Such high bioerosion intensities could either indicate high nutrient contents in seawater (Lescinsky et al. 2002) or long exposure times of the hardgrounds (Wilson & Palmer 2006). The encrusters of the Päärdu hardground are taphonomically variable. This shows that multiple generations are preserved within a single, time-averaged assemblage (Thomka & Brett 2014), indicating fairly convincingly that the hardground was characterized by a long exposure time. The long exposure time might help to explain the origin

of high bioerosion rates of the Päärdu hardground. The hardground described by Thomka & Brett (2014, 2015) from the Wenlock of Indiana is totally devoid of *Trypanites* borings. It is densely encrusted by diverse biota, but bioerosion structures occur entirely within large bioclasts and not in the hardground surface itself.

### Bioerosion versus encrustation

Bioerosion and encrustation are two fundamentally opposite processes in the oceans that shape the hard substrates. Bioerosion leads to loss of the weight and density of the substrate, while encrustation leads to the accretion of additional mineral and organic layers on top of the hard substrate. It is important to know how these two opposite processes were working together in the Silurian on the same substrate. The Päärdu hardground fauna indicates that high bioerosion densities could correlate with low encrustation densities. This may not be a general rule because bioerosion and encrustation can have a patchy distribution as in the case of the Ohessaare hardground from the Pridoli of Saaremaa (Vinn & Wilson 2010). However, when the hardground surface was first colonized by numerous boring organisms, it could have prevented the formation of dense encrustation. This might be a form of trophic group amensalism, wherein the abundance of bioeroders precluded the settlement of larvae of encrusters and/or prevented the growth of the existing encrusting colonies (J. Thomka pers. comm. 2015).

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## **Hõredalt asustatud *Trypanites*'e käikudega tsementeerunud Llandovery-aegne kihipind Lääne-Eestist Velise jõe äärest**

Olev Vinn ja Ursula Toom

Sedimentatsiooniga samaaegselt tsementeerunud kihipinna külge olid hõredalt kinnitunud okasnahksed, korallid ja sammalloomad. Tsementeerunud kihipind sisaldas arvukalt sinna sisse uuristatud *Trypanites*'e käike. Enkrusteerivate loomade hõre asustus ja arvukad *Trypanites*'e käigud tunduvad olevat iseloomulikud Baltika kontinendi Ordo-viitsiumi ning Siluri tsementeerunud merepõhjale.



#### **Publication XI**

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## Bioerosion of inorganic hard substrates in the Silurian of Estonia (Baltica)

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**Abstract:** Carbonate hardgrounds are unevenly distributed in the Silurian of Estonia, with only three bioeroded hardgrounds in the Telychian and one in the late Pridoli. There seem to be no trends in the bioerosion intensities and ichnotaxonomical diversity in the Silurian of Estonia. Only *Trypanites* occurs in the hardgrounds of the Silurian of Estonia and ichnological diversity of bioeroded organic hard substrates, containing *Trypanites*, *Palaeosabella* and *Osprioneides* is higher than inorganic substrates. The small number of bioeroded inorganic substrates could indicate that these substrates were probably less important than the organic hard substrates for the development of seafloor ecological niches in the Silurian of Estonia. The average bioerosion intensities of the hardgrounds are relatively high, but not unusual for the Silurian.

**Keywords:** borings, *Trypanites*, hardgrounds, early Palaeozoic, Baltic basin

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### Introduction

Only seven detailed studies of Silurian hardground communities have previously been published. Hardground encrusting crinoids, corals and brachiopods from the Wenlock of Indiana were described by Halleck in 1973. Thomka and Brett (2014, 2015) discovered hardgrounds encrusted with various echinoderm also from the Wenlock of Indiana. Hardground encrusting echinoderm holdfasts from the Silurian of Gotland have been mentioned by Franzén (1977). A bioeroded hardground from the Ludlow of the Welsh Borderland was described by Cherns (1980). Sumrall et al. (2009) found edrioasteroids cemented to a hardground from the middle Silurian of Pennsylvania. Hardground faunas and bioerosion of inorganic hard substrates of Baltica are in general relatively poorly studied (Einasto 1964; Franzén 1977; Vinn & Wilson 2010a). Especially poorly studied is the bioerosion of inorganic hard substrates in the Silurian of Estonia (Einasto 1964). The study of inorganic hard substrates is important because it helps us better understand their role in the evolution and distribution of encrusting faunas in the Silurian. The only record of bioerosion intensity is that of Vinn and Wilson (2010a) for a late Silurian (Pridoli) hardground from Saaremaa.

Sedimentary discontinuity surfaces in the Silurian of Estonia are often marked by pyrite mineralization (Einasto 1964; Raukas & Teedumäe 1997). There are several types of sedimentary discontinuity surfaces in the Silurian of Estonia (Einasto 1964), but not all of them are hardgrounds. Several of these surfaces could constitute various geochemical barriers (i.e. surfaces of diagenetic mineralization) and may be related to sea level regressions with short periods of dry land or no sedimentation in shallow water. True hardgrounds are surfaces of syndimentarily cemented carbonate layers that have been exposed on the seafloor. These

surfaces usually show evidence of bioerosion and/or encrustation (Palmer 1982), which in turn can be used to identify the hardgrounds, as in this study.

Hardgrounds were common during times of calcite seas in which geochemistry (low Mg/Ca ratios) favoured early calcite cementation of carbonate sediments on the seafloor (Wilson & Palmer 1992). Balthasar and Cusack (2015) found that calcite sea intervals were characterized by the co-precipitation of aragonite and calcite in environments above 20 °C. The continuous prominence of aragonite precipitation in Phanerozoic warm-water environments could explain the Phanerozoic increase of aragonite over calcite skeletal composition in calcifying organisms (Balthasar & Cusack 2015). The Silurian was characterized by calcite sea and hardgrounds were abundant, but slightly less abundant than in the Ordovician (Brett & Liddell 1978; Brett & Brookfield 1984; Taylor & Wilson 2003). Silurian hardgrounds and their bioerosional trace fossils are better known for North America than Baltica (Einasto 1964).

This paper attempts in the Silurian of Estonia to: (1) identify bioeroded inorganic hard substrates, (2) identify the bioeroding ichnotaxa, (3) find trends in the record of bioerosion, (4) find controls of the bioerosion of inorganic hard substrates, (5) find controls on the distribution of hardgrounds, and (6) compare Silurian bioerosion in Baltica with North America.

### Geological background

Silurian rocks are exposed in a wide outcrop belt in middle and western Estonia, mostly in quarries and small cliffs along river

banks. However, the best Silurian outcrops are located on Saaremaa Island, mostly in small coastal cliffs (Raukas & Teedumäe 1997).

Nestor and Einasto (1977) established a general facies model for the Silurian basin in Estonia and described the following facies belts: tidal flat/lagoonal, shoal, open shelf, transitional (basin slope), and a basin depression. The carbonate platform (i.e. carbonate shelf) includes the first three facies belts. The last two facies belts characterize a deeper pericratonic basin with fine-grained siliciclastic deposits (Raukas & Teedumäe 1997).

During the Silurian Baltica, including the area of modern Estonia, was located in equatorial latitudes and drifting northwards (Melchin et al. 2004). The area of modern Estonia was covered by the relatively shallow epicontinental Baltic paleobasin. This basin was characterized by diverse biotas and a wide range of tropical environments, including coral-stromatoporoid reefs and lagoons (Hints 2008).

## Material and methods

Silurian hardgrounds from Estonia (Fig. 1) were cleaned and photographed with a scale bar using a Nikon 7000 digital camera from both upper and cryptic sides; maximum number of *Trypanites* borings on the hardground pieces was counted in 4 cm<sup>2</sup> using a grid drawn on a transparent film and calibrated photographs. A grid was also used to measure the area of the studied hardground surface on calibrated photos.

### Studied hardgrounds

#### *Metsküla, Raiküla Regional Stage (early Telychian)*

The Metsküla outcrop is located 10 km SW of Raikküla (middle Estonia) (Fig. 1). Limestones and nodular limestones of the Adavere Regional Stage (Fig. 2) are exposed in a small quarry. The hardground pieces have a total area 1240 cm<sup>2</sup> (full descriptions will follow later in the paper).

#### *Päri, Rumba Formation (early Telychian)*

Päri quarry is located 5 km southwest of Kullamaa village, on a flat limestone hillock (Fig. 1). Argillaceous nodular limestones

of the Rumba Formation of the Adavere Regional Stage (Fig. 2), containing numerous brachiopods, mainly *Pentamerus oblongus*, are exposed there. Bored bioclasts (*Pentamerus* shells) from the hardground surface and pieces of sedimentary hardground with total area 750 cm<sup>2</sup> were collected (full descriptions will follow later in the paper).

### Previously studied hardgrounds

#### *Päärdu, Rumba Formation (early Telychian)*

The hardground surface is relatively flat, but there are also bumpy regions with strong relief. Its surface is generally smooth, but in some places microrelief can be rougher. Both upper and cryptic hardground surfaces have a dark color due to mineralization by pyrite. This contrasts with the light grey color of the matrix. The hardground is partially broken into cobbles indicating either discontinuous cementation (i.e. like a concretion) or bioturbational breakage. Abundant *Trypanites* borings are found in both the upper and cryptic surfaces of the hardground. Boring intensities on the upper and cryptic surfaces of the hardground are similar. The distribution of these borings is somewhat patchy on both surfaces. We counted a maximum of 27 *Trypanites* per 4 cm<sup>2</sup> of the hardground upper surface. *Trypanites* diameters vary from 0.5 to 2.4 mm ( $N = 17$ , mean 1.2 mm,  $sd = 0.5$  mm). The apertures of *Trypanites* are mostly circular, but may also be slightly oval or subcircular (Vinn & Toom in press) (Figs. 1 and 2).

#### *Ohesaare hardground, Ohesaare Formation (late Pridoli)*

The hardground surface is darker than the rock matrix due to pyrite mineralization; it is abraded and has numerous cryptic spaces formed under the hardground ledges. (Vinn & Wilson 2010a). *Trypanites* range from 0.50 to 2.50 mm in diameter and extend to a maximum depth of 0.5 cm. There is a maximum of 28 *Trypanites* borings per 4 cm<sup>2</sup> of the hardground upper surface, but their distribution is patchy. There is a maximum of only one *Trypanites* per 4 cm<sup>2</sup> on the cryptic surfaces of the hardground. The hardground is sparsely encrusted by sclerobionts (6.4% of lower surface and 1.5% of the upper surface area) (Vinn & Wilson 2010a) (Figs. 1 and 2).

All studied samples are deposited in the collections of the Institute of Geology, Tallinn University of Technology (GIT).

## Results

### Hardgrounds

#### *Metsküla*

The hardground surface is strongly mineralized by pyrite and has a dark brown color, possibly indicating slight oxidation. The surface is relatively smooth and has a moderate relief. Only the upper surface was studied. It contains a few eroded brachiopod bioclasts indicating some abrasion of the hardground. The hardground is moderately bored by *Trypanites*. The borings have a patchy distribution. A maximum of 18 *Trypanites* can be found per 4 cm<sup>2</sup>. They have a diameter of 0.5–2.1 mm ( $N = 17$ , mean 1.2 mm,  $sd = 0.53$  mm). The shape of the apertures of *Trypanites* is mostly circular, but some borings are slightly oval. Some apertures of *Trypanites* have been merged with each other, usually no more than two

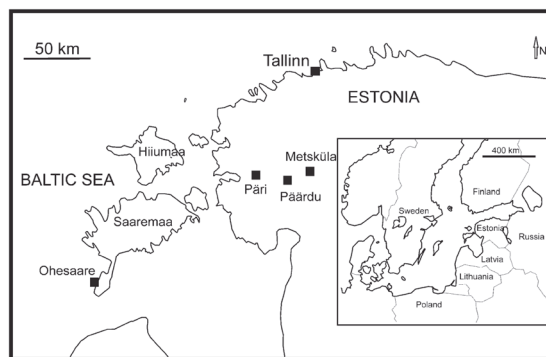


Fig. 1. Location of western Estonia. Location of outcrops with the studied hardgrounds is shown.

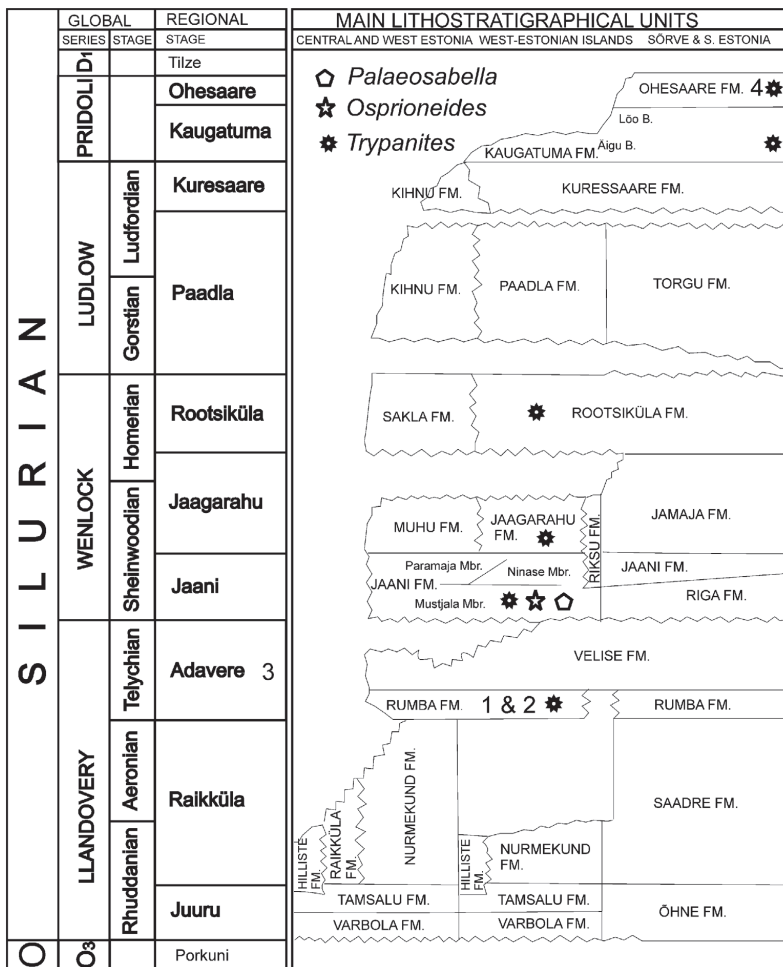


Fig. 2. Stratigraphic distribution of hardgrounds and borings in the Silurian of Estonia.

borings overlap. The hardground is sparsely encrusted by discoidal echinoderm holdfasts (Fig. 3A, B).

*Päri*

The hardground surface is relatively rough with large *Pentamerus* bioclasts. The surface is moderately eroded and strongly mineralized by pyrite and due to oxidation of pyrite the weathered surface has a reddish brown color. There are no encrusters on the hardground. Only the upper surface was exposed for study. There are signs of possible microbioerosion on this surface. The hardground is mostly sparsely bored by *Trypanites*. It contains a maximum of 12 *Trypanites* per 4 cm<sup>2</sup>. *Trypanites* borings have a diameter 0.8 to 1.4 mm (N = 12, mean 1.0 mm, sd = 0.17 mm). The apertures of *Trypanites* are mostly circular, but some are slightly oval. The distribution of *Trypanites* borings on the hardground is relatively patchy (Fig. 4A, B).

*Characteristics of bioerosion of inorganic hard substrates in the Silurian of Estonia*

*Boring sizes*

Diameters of *Trypanites* borings in hard inorganic substrates of the Silurian of Estonia are relatively similar with a mean from 1.0 to 1.2 mm in the studied samples and a range from 0.5 to 2.5 mm.

*Boring intensity*

The maximum bioerosion density of the studied samples does vary somewhat, being lowest in the Telychian Päri hardground (12 *Trypanites* per 4 cm<sup>2</sup>) and highest in the Pridoli Ohesaare hardground (28 *Trypanites* per 4 cm<sup>2</sup>). There is no difference in maximum bioerosion densities between studied early Silurian and late Silurian samples (Telychian maximum 27 *Trypanites* per 4 cm<sup>2</sup> compared to Pridoli maximum 28 *Trypanites* per 4 cm<sup>2</sup>).



Fig. 3. Trypanites borings in Metsküla hardground from the Adavere Regional Stage (Telychian), early Silurian of western Estonia. A. GIT 362-112. B. GIT 362-113.

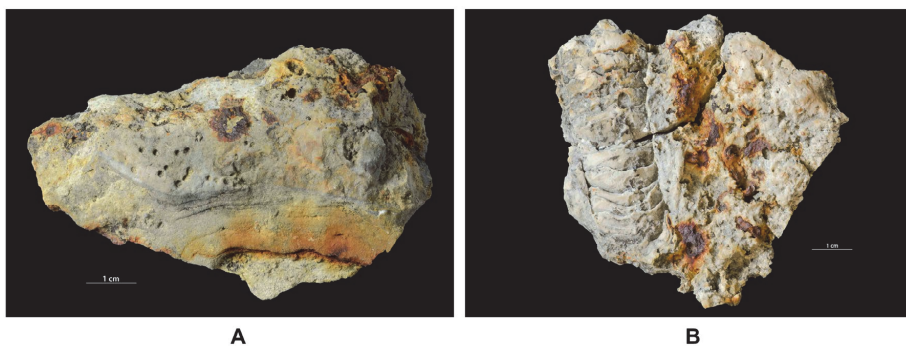


Fig. 4. Trypanites borings in Pääri hardground from the Rumba Formation (early Telychian) of western Estonia. A. GIT 362-88. B. There is a steinkern of an orthocone cephalopod in the hardground surface. GIT 362-92.

*Ichnotaxonomy*

The ichnological diversity of the studied hardground samples from the Silurian of Estonia is low, with only one ichnogenus – *Trypanites* – present. However, only a few longitudinal sections of the borings were studied, so some of the borings identified as *Trypanites* may actually belong to *Palaeosabella*. *Palaeosabella* is a tubular boring that, in contrast to *Trypanites* has a distal enlargement.

**Discussion**

*Distribution of hardgrounds*

Hardgrounds were common during calcite sea periods such as in the Silurian (Taylor & Wilson 2003). The distribution of hardgrounds in the Silurian of Estonia is uneven (Fig. 2). There are three hardgrounds in the Telychian and one record in the Pridoli. While this record may be somewhat sample biased, in general the whole Silurian section of Estonia has been relatively evenly studied (Raukas & Teedumäe 1997). Thus, it is possible that the middle Silurian of Estonia was a less favourable time for hardground formation in the Paleobaltic Basin, than earlier and later

times. Alternatively, hardgrounds formed just as frequently at this time but were less often preserved if sediment erosion rates were greater in the middle Silurian.

*Cryptic versus open surfaces bioerosion in organic and inorganic substrates*

In the case of the Ohessaare hardground (Pridoli) the cryptic side of the hardground was much less bioeroded than the upper surface. In contrast, the Päärdü hardground contains numerous *Trypanites* borings on both sides. Organic hard substrates usually show higher bioerosional densities for upper and especially elevated surfaces (Nield 1984). Wilson (1998) found that cryptic spaces became progressively restricted by the accumulation of sediment within, which caused a biotic change from a fauna nearly identical to that on the exposed hardground surfaces above to a typical shallow marine cavity-dwelling community. The obscure communities inhabiting the dark recesses of Mediterranean caves have low biomass and they cover the substrate sparsely (Harmelin 1986). Thus, the differences between exposed and cavity-dwelling communities could influence the bioerosion rate in the case of the Ohessaare hardground.

### Bioerosion trends in inorganic and organic hard substrates

Borings in organic substrates have been reported from the early Sheinwoodian to early Pridoli of Saaremaa, Estonia (Vinn & Wilson 2010a, 2010b; Vinn & Wilson 2012a, 2012b). The highest boring frequencies seem to be associated with stromatoporoids and corals in relatively deep water, muddy sediments of the Jaani Formation (early Sheinwoodian), but high boring frequencies are common also in stromatoporoids of the relatively shallow water Jaagarahu Formation. The highest ichnotaxonomic diversity occurs in stromatoporoids and corals of the Jaani Formation where *Trypanites*, *Palaeosabella* and giant *Osprioneides* occur together. Thus, there may have been a peak in diversity and intensity of bioerosion in the Sheinwoodian of Estonia (Vinn & Wilson 2010a, 2010b; Vinn & Wilson 2012a, 2012b). However, it is also possible that this could represent a sampling bias as the number of bioerosion studies is relatively small and concentrated to certain stratigraphic intervals. In contrast to organic substrates, boring in inorganic substrates of the Silurian of Estonia do not show any temporal trend regarding diversity and bioerosion intensity. The small number of bioeroded inorganic substrates in the Silurian of Estonia indicates that these substrates were probably less important than the organic hard substrates for the development of seafloor ecological niches in the Silurian of Estonia.

### Comparison with other early Paleozoic examples

The diameters of *Trypanites* in inorganic hard substrates of the Silurian of Estonia are typical for such borings at that time (see Tapanila et al. 2004). They do not differ from analogous North American examples (Tapanila et al. 2004; Thomka & Brett 2014) and British examples (Cherns 1980).

More than 20 *Trypanites* per 4 cm<sup>2</sup> is considered high bioerosion intensity for the Late Ordovician and early Silurian stromatoporoids of Anticosti Island, North America (Tapanila et al. 2004). Similarly to the Silurian of Estonia some North American hardground samples show high bioerosion intensities (Thomka & Brett 2014).

The diversity of borings in inorganic hard substrates seems to be monospecific everywhere in the Silurian (Cherns 1980; Vinn & Wilson 2010a) and the sole boring ichnotaxon is *Trypanites*.

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## **Publication XII**

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RESEARCH ARTICLE

# Bioerosion of Inorganic Hard Substrates in the Ordovician of Estonia (Baltica)

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## Abstract

The earliest bioeroded inorganic hard substrates in the Ordovician of Estonia appear in the Dapingian. Hardgrounds are also known from the Sandbian and Katian. Most of the bioerosion of inorganic hard substrates occurs as the boring *Trypanites* Mägdefrau, 1932 along with some possible *Gastrochaenolites* borings. North American hardground borings are more diverse than those in Baltica. In contrast to a worldwide trend of increasing boring intensity, the Estonian record seems to show no increase in boring intensities during the Middle and Late Ordovician. Hardgrounds seem to be more common during the temperate climate interval of the Ordovician calcite sea in Estonia (seven hardgrounds during 15 my) than in the part with a tropical climate (four hardgrounds during 12 my). Bioerosion is mostly associated with carbonate hardgrounds, but cobbles and pebbles broken from the hardgrounds are also often penetrated by *Trypanites* borings. The general diversity of boring ichnotaxa in Baltica increased from one ichnospecies in the Cambrian to seven by the end of Ordovician, showing the effect of the GOBE on bioeroding ichnotaxa. The diversity of inorganic hard substrate borers increased by only two times. This difference can be explained by the wider environmental distribution of organic as compared to inorganic substrates in the Ordovician seas of Baltica, and their more continuous temporal availability, which may have caused increased specialization of several borers. The inorganic substrates may have been bioeroded only by the generalists among boring organisms.



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## Introduction

Sedimentary discontinuity surfaces in the Ordovician of Estonia are often marked by mineralization, either with iron minerals or phosphates [1]. All sedimentary discontinuity surfaces are not hardgrounds; many may represent geochemical barriers or were erosional surfaces due to exposure caused by regression. In this study we have counted only hardgrounds that show bioerosion and/or encrustation, which are indications of a true synsedimentarily cemented sea-floor surface. Carbonate hardgrounds are common in calcite sea conditions that favored early cementation of carbonate sediments in the seafloor [2]. Hardgrounds form suitable surfaces for bioeroding and encrusting organisms [3]. There was a calcite sea in the Ordovician and

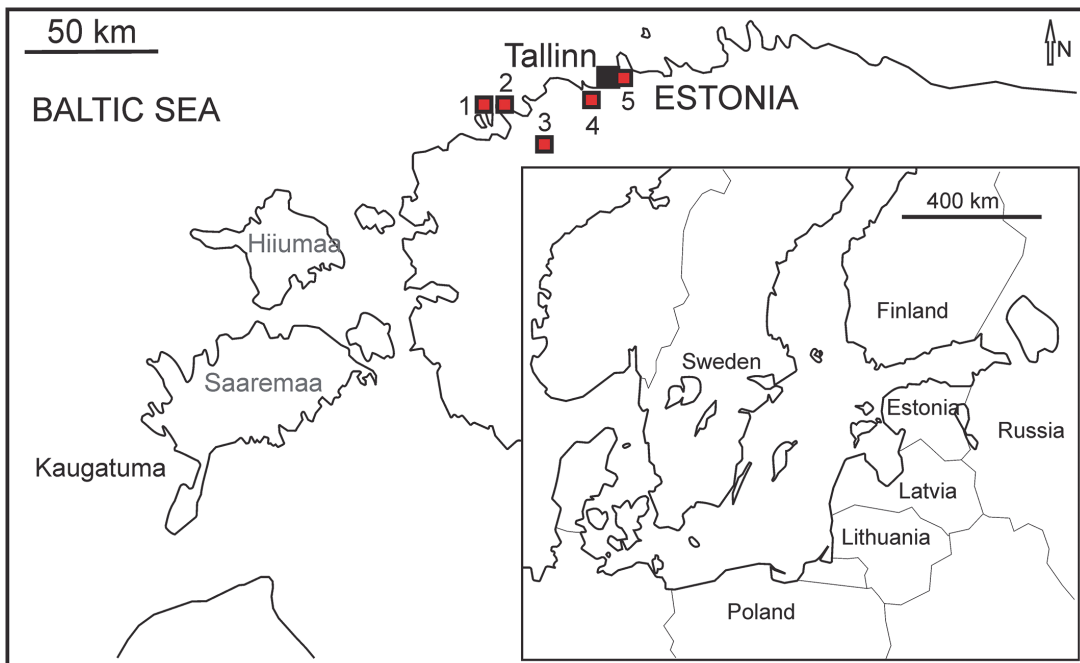
hardgrounds were globally abundant during this period [4, 5, 6]. The Ordovician hardgrounds and their bioerosional trace fossils are best known in North America [2]. The western Baltic, especially Sweden, also has a relatively good record of bioerosional trace fossils associated with hardgrounds in the Lower Ordovician [7, 8]. Relatively little is known about the borings in the Estonian and eastern Baltic Ordovician hardgrounds, especially in the Upper Ordovician [9, 10, 11, 12, 13, 14, 15, 16]. Studies of bioerosion of the Ordovician of Estonia have mostly been based on organic substrates such as brachiopods [17, 18] and bryozoans [19, 20].

This paper: 1) records bioeroded inorganic hard substrates in the Ordovician of Estonia, 2) identifies their bioeroding ichnotaxa of inorganic hard substrates, 3) examines trends in the record of this bioerosion, 4) suggests the controls on the bioerosion process of these inorganic hard substrates, 5) finds patterns for the distribution of hardgrounds, and 6) compares the bioerosion in the Ordovician of Baltica with that of North America.

### Previously Studied Hardgrounds

The Saka hardground forms the base of Volkhov Regional Stage (earliest Dapingian) in NE Estonia (Fig 1); it contains possible *Gastrochaenolites* borings in dolomitized limestone [16]. The density of its bioerosion has not been studied.

The Pakri hardground is a surface in the middle of a sandy limestone within the Pakri Formation (Kunda Regional Stage, early Darriwilian) at Pakri Cliff, near Paldiski Town (Figs 1 and 2). This hardground is sparsely encrusted by bryozoans and echinoderms. No bioerosion has been reported [21].



**Fig 1. Locality map.** Localities in Estonia. 1 Väike-Pakri, 2 Cape Pakri, 3 Vasalemma, 4 Alliku, 5 Suhkrumägi.

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The Väike-Pakri hardground forms the upper surface of a sandy limestone in the Pakri Formation (Kunda Regional Stage, early Darriwilian) on Väike-Pakri Island (Figs 1 and 2). This hardground is sparsely encrusted by large echinoderm holdfasts. Bioerosion has not been recorded [22].

## Geological Background and Localities

During the Ordovician the paleocontinent of Baltica moved from the temperate climatic zone to the subtropical realm [23]. In the Middle and Late Ordovician the climatic change caused an increase in carbonate production and sedimentation rate on the carbonate platform. The appearance of the first carbonate build-ups during the Late Ordovician led to a striking change in the overall character of the Baltic paleobasin in Estonia [24].

The exposure of Ordovician limestones in Estonia forms a wide belt from the Narva River in the northeast to Hiiumaa Island in the west [24]. The total thickness of the Ordovician system in Estonia is moderate, varying from 70 to 180 m [24]. Little bathymetric differentiation characterized the Middle to early Late Ordovician shallow epicontinental sea that covered the western part of the East-European Platform. This basin had an extremely low sedimentation rate [24]. Argillaceous limestones and marls accumulated along the entire extent of the ramp. There was a sedimentological trend of decreasing bioclasts and increasing clay in the offshore direction [23].

Suhkrumägi outcrop (Fig 1): Hardground in the lower part of the Toila Formation (Volkhov Regional Stage, Dapingian); greenish grey dolomitized glauconitic limestones of onshore normal marine origin [1].

Väike-Pakri Island cliff: Hardground (Figs 1 and 2) in the middle of the Toila Formation (Volkhov Regional Stage, Dapingian); greenish grey dolomitized glauconite rich limestones of onshore normal marine origin. Hardground (Figs 1 and 2) in the lower part of the Pakri Formation (Kunda Regional Stage, early Darriwilian); brownish grey calcareous sandstones and sandy limestones of onshore normal marine origin [1].

Alliku quarry: Hardground in the middle of the Kukruse Regional Stage (early Sandbian); intercalation of limestone and oil shale (kukersite) layers of various thicknesses; normal marine origin [1].

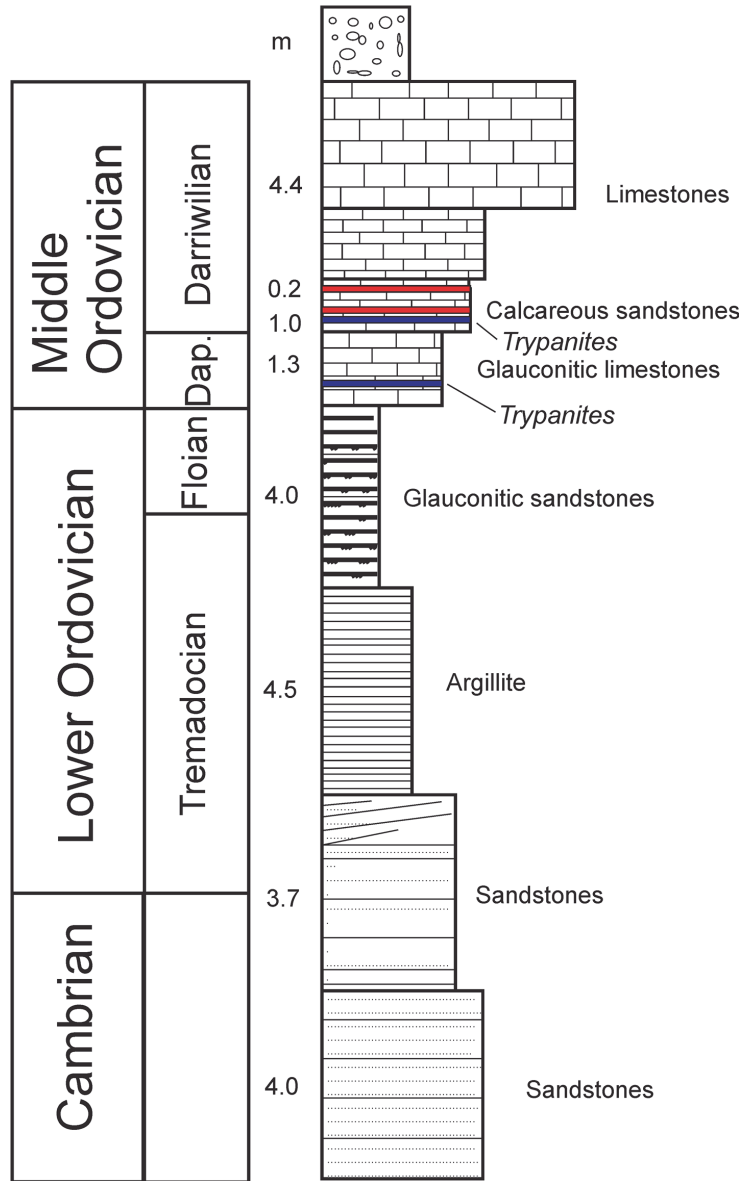
Vasalemma quarry: Hardground (1) forms the boundary between the Kahula and Vasalemma Formations (Keila Regional Stage, early Katian) (Figs 1 and 3); marly limestones and bioclastic limestones of shallow normal marine origin [1]. Hardground (2) forms the upper boundary of the Vasalemma Formation (Keila Regional Stage, early Katian) (Figs 1 and 3); top of reef bodies, composed of bryozoan framestone-bindstone, echinoderm bindstone, receptaculitid-bryozoan-microbial framestone, and tabulate bafflestone of onshore shallow normal marine origin [1].

Kautla 7034 borehole: Hardground forms the boundary between the Hirmuse Formation and the Tõremägi Member in the Oandu Regional Stage (early Katian); marly limestones and bioclastic limestones of shallow normal marine origin [1].

Vormsi Island (Saxby costal outcrop): Hardground in the upper part of the Vormsi Regional Stage (late Katian); marly limestones with thin layers of marls of shallow normal marine origin [1].

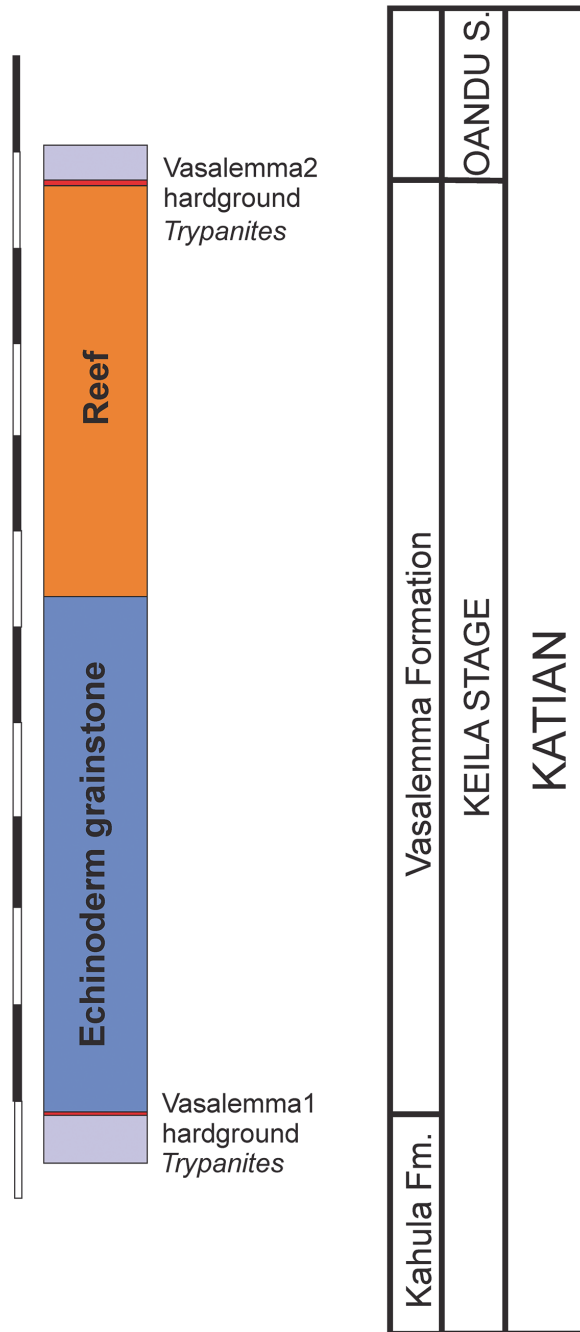
## Material and Methods

All studied samples were collected on public land where permits are not required, complying with all Estonian regulations. (Collecting hardground samples on public land is not regulated in Estonia.)



**Fig 2. Stratigraphy of Pakri cliff.** Modified after Hints et al. (2008). Red-hardgrounds. Blue-cobbles and pebbles.

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**Fig 3. Stratigraphy of Vasalemma quarry.** Modified after Kröger et al. (2014).

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## Hardgrounds of this study

Two large hardground samples were collected from the Alliku quarry (Kukruse Regional Stage, early Sandbian) (Figs 1 and 4).

Eight large hardground samples were collected from the Vasalemma quarry. This hardground forms the boundary between the Kahula and Vasalemma Formations (Keila Regional Stage, early Katian) (Figs 1 and 4).

Four large hardground samples were collected from the upper surface of reefs in the Vasalemma quarry. This hardground forms the upper boundary of the Vasalemma Formation (Keila Regional Stage, early Katian) (Figs 1 and 4).

Possible hardground or cobble samples from the Kautla 7034 borehole with a total area about 25 cm<sup>2</sup>. This is at the boundary between the Hirmuse Formation and Tõrremägi Member in the Oandu Regional Stage (early Katian) (Fig 4).

Two large hardground samples were collected by Ursula Toom during field work in 2012 on Vormsi Island (Saxby costal outcrop) in the Vormsi Regional Stage (late Katian) (Figs 1 and 4).

## Pebbles and cobbles

Cobbles from the Toila Formation (Volkhov Regional Stage, Dapingian) of Väike-Pakri Island; with diameters 6 to 8 cm. All surfaces are bioeroded.

Pebbles from Suhkrumägi, Toila Formation (Volkhov Regional Stage, Dapingian), with diameters 4 to 6 cm. All surfaces are bioeroded.

Cobbles from the Pakri Formation (Kunda Regional Stage, early Darriwilian) on Väike-Pakri Island; with diameters 7 to 10 cm. All surfaces are bioeroded.

The samples were cleaned and photographed with a scale bar. Borings were measured on calibrated photos. Some samples were longitudinally cut using a rock saw. The sections were thereafter photographed with a scale bar. Borings were counted in 4cm<sup>2</sup> using a grid drawn on a transparent film, and on calibrated photos. A cm grid was used to measure the area of the studied surface on calibrated photos.

All studied samples are deposited at the Institute of Geology, Tallinn University of Technology, Ehitajate tee 5, Tallinn, Estonia, with specimen numbers (GIT) 381–595, 381–22, 381–1149, 362–114, 362–115, 156–998, 362–98, 362–99, 156–356, 362–95, 362–96, 222–498, 222–449, 222–500, 222–501, 222–502, 222–503, 222–504.

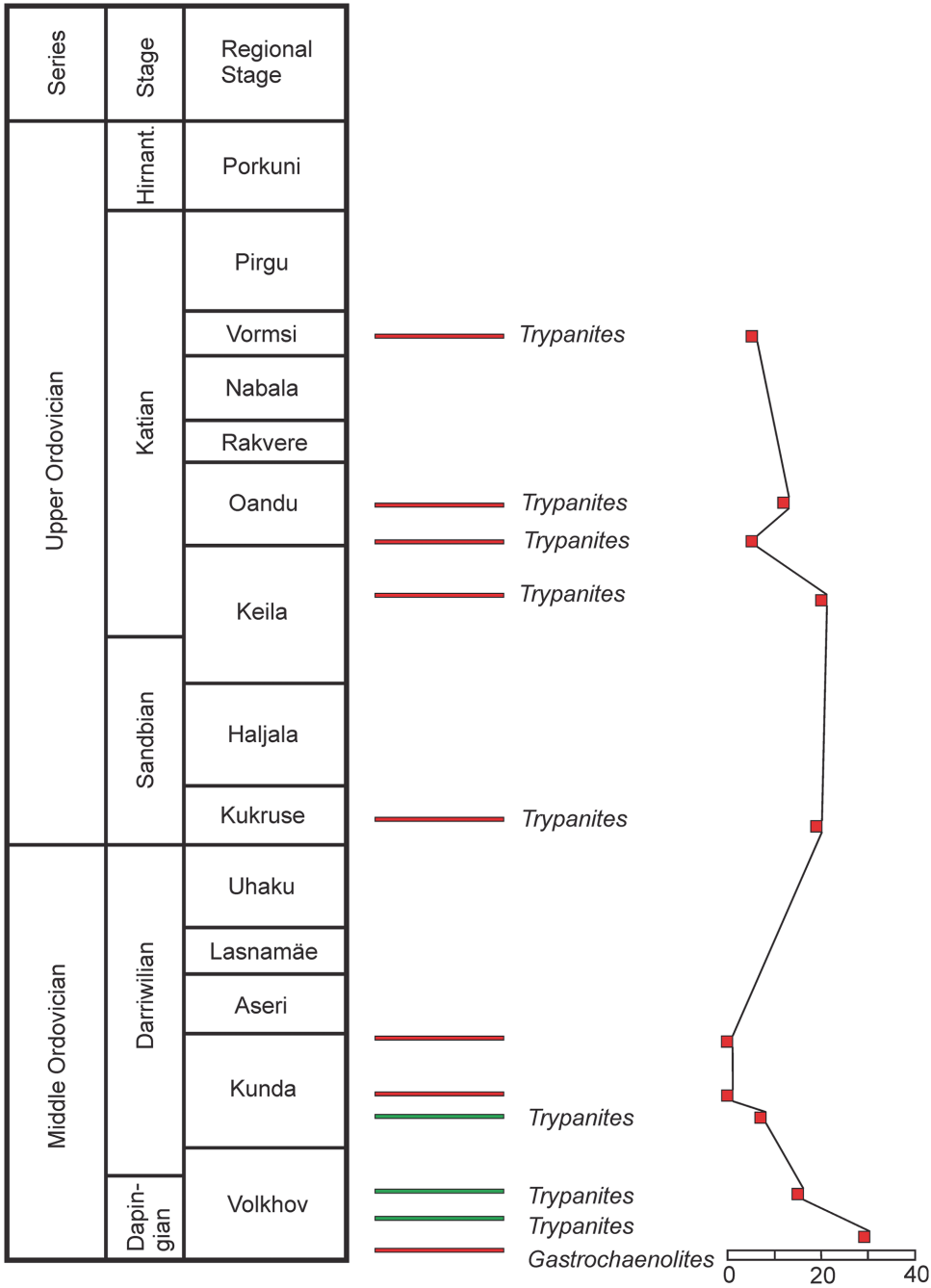
## Results

### Hardgrounds

**Alliku hardground.** The Alliku hardground (early Sandbian) has a relatively even surface with a rough microrelief. The surface of this hardground has a darker grey color than the limestone matrix due to mineralization by iron minerals (presumably pyrite). There are no visible cryptic surfaces. There are no encrusters on the studied hardground slabs. Borings are assigned to *Trypanites* because they are simple cylindrical shafts with single entrances. *Trypanites* borings are very frequent. There are 19 *Trypanites* borings per 4cm<sup>2</sup>. Maximum macroboring density index [25] ranges 3 to 4. *Trypanites* borings have a diameter 0.9 to 2.0 mm (N = 12, mean 1.3 mm, sd = 0.37). The apertures of *Trypanites* are mostly circular, but some can be slightly oval. The distribution of *Trypanites* borings on the hardground surface is patchy (Figs 5, 6 and 7). *Trypanites* borings are not filled with sediment.

**Vasalemma hardground (lower) 1.** The Vasalemma hardground 1 (earliest Katian) is ripple-marked and has a relatively even surface. The surface of the hardground has slightly darker brownish-grey color than the limestone matrix due to mineralization by iron minerals





**Fig 4. Stratigraphic scheme.** The Middle and Upper Ordovician in Estonia with inorganic hard substrates and *Trypanites* shown. Modified after Hints et al. (2008). Scale showing *Trypanites* per 4 cm<sup>2</sup>. One unit on scale = 10 *Trypanites* borings. Red-hardgrounds. Green-pebbles/cobbles.

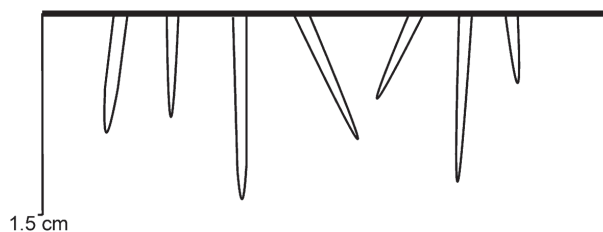
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(presumably pyrite). The surface is eroded and cuts various bioclasts. There are no visible cryptic surfaces. A single eroded cornulitid was found cemented to the hardground. Hints and Müdel [15] reported encrustation by the edrioasteroid echinoderm *Cyathocystis*. *Trypanites* borings are very frequent. The hardground contains 20 *Trypanites* borings per 4cm<sup>2</sup>. Maximum macroboring density index [25] ranges from 3 to 5. The *Trypanites* borings have diameters of 0.5 to 3.3 mm (N = 16, mean 1.5 mm, sd = 0.9). The apertures of *Trypanites* are mostly circular, but some can be slightly oval or subcircular. The distribution of *Trypanites* borings on the hardground is somewhat patchy, but there are no large areas without the borings (Figs 5, 8 and 9). *Trypanites* borings are filled with argillaceous limestone.

**Vasalemma hardground (above reefs) 2.** The Vasalemma hardground 2 (earliest Katian) surface has a darker grey color due to strong pyritization. The rest of rock matrix is light grey. The hardground occurs on the upper surface of a reef limestone layer. The surface is eroded and cuts several bioclasts. Hardground ledges are rounded. Cryptic spaces are formed under the hardground ledges, which are 2 to 9 mm thick. The hardground is sparsely encrusted by cornulitids and bryozoans. *Trypanites* borings are not frequent. *Trypanites* borings range from 0.2 to 2.1 mm in diameter (Fig 5). There are five *Trypanites* per 4 cm<sup>2</sup> of the hardground upper surface, but some large areas (up to 10 cm<sup>2</sup>) have no borings. The maximum macroboring density index [25] ranges from 0 to 2. The *Trypanites* borings are filled with argillaceous limestone.

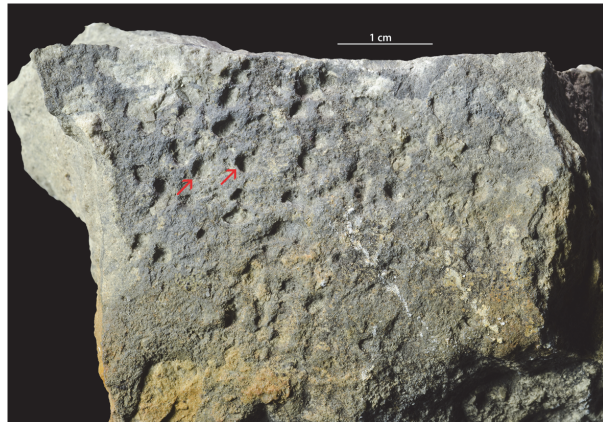
**Possible hardground or cobble from Kautla borehole 7034.** The Kautla hardground of early Katian age, the boundary between Hirmuse Formation and Tõrremägi Member in Oandu Regional Stage, is a surface in a limestone with a dark color due to strong pyritization. The rest of rock matrix is light grey in color. *Trypanites* borings are relatively frequent. The hardground surface is relatively smooth and evenly bored by *Trypanites* (Fig 5). There are no encrustations on the studied hardground slab. The hardground contains a maximum 13 *Trypanites* borings per 4cm<sup>2</sup>. The maximum macroboring density index [25] ranges from 2 to 3. *Trypanites* borings have a diameter 0.6 to 4.4 mm (N = 16, mean 2.1 mm, sd = 1.17). The apertures of *Trypanites* are mostly circular, but some can be slightly oval or subcircular. The apertures of some borings are merged. The *Trypanites* borings are filled with argillaceous limestone.

**Saxby hardground.** The Saxby hardground (middle Katian) has an uneven surface and is darker grey than the limestone matrix due to mineralization by iron minerals (presumably pyrite). The surface is eroded and cuts large bioclasts, such as a spiral nautiloid shell. There are no visible cryptic surfaces. There are no encrustations on the studied hardground slabs. *Trypanites* borings are not frequent. It has four *Trypanites* borings per 4 cm<sup>2</sup>. The maximum macroboring density index [25] ranges from 0 to 1. The *Trypanites* borings have diameters 2 to 3.5 mm



**Fig 5. Longitudinal sections of *Trypanites*.** A generalization from studied samples.

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**Fig 6. Hardground with *Trypanites*.** The Alliku hardground, limestone (early Sandbian) from northern Estonia. GIT 362–115.

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( $N = 7$ ; mean 2.6 mm,  $sd = 0.62$ ). The apertures of *Trypanites* are circular. *Trypanites* borings are sparsely located on the hardground surface (Figs 5 and 10). The *Trypanites* borings are not filled with sediment.

### Cobbles and pebbles

**Cobbles from the Toila Formation of Väike-Pakri Island.** The studied Dapingian cobble is a platy limestone with slightly lens-shaped profile. Its surface is strongly mineralized (presumably with pyrite) and has a dark color. *Trypanites* borings are very frequent. The surface of the cobble is relatively smooth and evenly bored by *Trypanites* (Fig 5). There is a small holdfast of a possible echinoderm cemented to the cobble. The cobble contains 29 *Trypanites* borings



**Fig 7. Hardground with *Trypanites*.** The Alliku hardground, limestone (early Sandbian) from northern Estonia. GIT 362–114.

doi:10.1371/journal.pone.0134279.g007

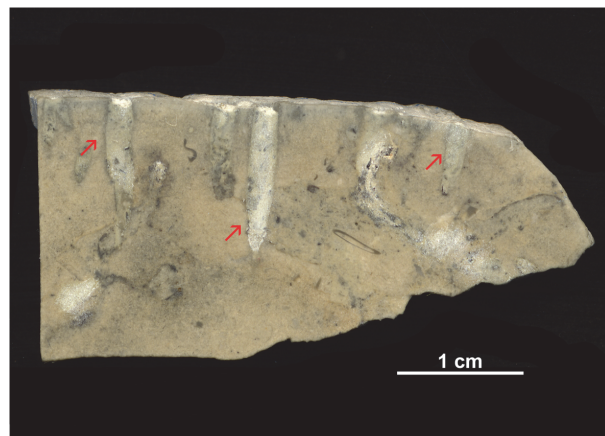


**Fig 8. Hardground with *Trypanites*.** The Vasalemma hardground 1, micritic-peloidal limestone (earliest Katian) from NW Estonia. GIT 362–95.

doi:10.1371/journal.pone.0134279.g008

per  $4\text{cm}^2$ . Maximum macroboring density index [25] ranges from 4 to 5. The *Trypanites* borings have diameters 0.6 to 2.8 mm ( $N = 16$ , mean 1.7 mm,  $sd = 0.75$ ). The apertures of *Trypanites* are mostly circular, but some are slightly oval or subcircular and some are merged. The *Trypanites* borings are filled with argillaceous limestone.

**Pebbles from the Toila Formation of Suhkrumägi.** The studied Dapingian limestone pebble has an irregular shape and slightly lens-shaped profile. Its surface is strongly mineralized (presumably with pyrite) and has a dark color. *Trypanites* borings are frequent (Fig 5). The surface of the pebble is slightly bumpy and bored by *Trypanites* from both sides. The distribution of *Trypanites* borings on the pebble is patchy. There are three possible small eroded bryozoans cemented to the pebble. The pebble contains 15 *Trypanites* borings per  $4\text{cm}^2$ . The



**Fig 9. Hardground with *Trypanites*.** Longitudinal section through Vasalemma hardground 1, micritic-peloidal limestone (earliest Katian) from NW Estonia. GIT 222–499.

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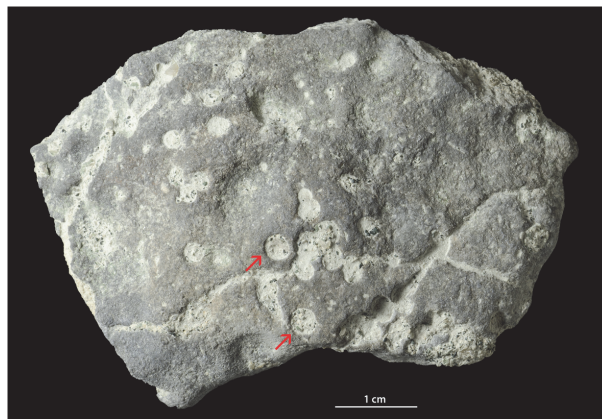


**Fig 10. Hardground with *Trypanites*.** Saxby hardground (limestone) from the late Katian of Vormsi Island, western Estonia. GIT 362–98.

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maximum macroboring density index [25] ranges from 3 to 4. The *Trypanites* borings have diameters 0.7 to 2.9 mm ( $N = 19$ , mean 2.3 mm,  $sd = 0.62$ ). The apertures of *Trypanites* are mostly circular, but some are slightly oval or subcircular, and some are merged (Fig 11). The *Trypanites* borings are filled with argillaceous limestone.

**Cobbles from Pakri Formation of Väike-Pakri Island.** The early Darriwilian limestone cobbles have flat to slightly rounded shape. Their surfaces are mineralized (presumably with pyrite), have a much darker color than their interiors, are slightly bumpy, and are sparsely bored by *Trypanites* on both sides. The surface of one cobble has a relatively rough microrelief. There is a small bryozoan holdfast cemented to one cobble. The cobbles contain maximum seven *Trypanites* borings per  $4\text{cm}^2$  (Fig 5). Maximum macroboring density index [25] ranges



**Fig 11. Pebble with *Trypanites*.** Toila Formation (Dapingian) from Suhrumägi, dolomitized glauconitic limestone, northern Estonia. GIT 156–356.

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from 1 to 2. *Trypanites* borings have diameters 1.1 to 4.4 mm ( $N = 12$ , mean 2.4 mm,  $sd = 0.87$ ). The apertures of *Trypanites* are mostly circular, but some can be slightly oval or sub-circular and a few are merged. The *Trypanites* borings are filled with calcareous sandstone.

### Distribution of bioeroded inorganic hard substrates

Bioeroded limestone pebbles and cobbles occur only in the Middle Ordovician of Estonia, from the early Dapingian (Volkhov Regional Stage) to the early Darriwilian (Kunda Regional Stage) (Fig 4). They are most numerous in the Dapingian (Volkhov Regional Stage). Bioeroded hardgrounds appear in the earliest Dapingian (lower part of the Volkhov Regional Stage) and continue upwards into the middle Katian (Vormsi Regional Stage) (Fig 4). There is a single bioeroded hardground in the Dapingian, two bioeroded hardgrounds in the Darriwilian, a single bioeroded hardground in the Sandbian, and four bioeroded hardgrounds in the Katian.

There are three records of bioeroded hard substrates each in the Dapingian, Darriwilian and early Katian. One more is found in the middle Katian while the Sandbian has just one record.

### Bioerosion of inorganic hard substrates in the Ordovician of Estonia

**Dimensions.** The largest borings occur in the earliest Dapingian (Volkhov Regional Stage) and are possibly *Gastrochaenolites* [16]. On average the largest *Trypanites* borings (mean 2.6 mm) occur in the late Katian (Vormsi Regional Stage) and the smallest (mean 1.3 mm) in the early Sandbian (Kukruse Regional Stage). There is no clear stratigraphic trend in the size distribution of *Trypanites* borings in the Ordovician of Estonia. The size of *Trypanites* borings is not correlated with hard substrate characteristics, such as extent of surface erosion, mineralization or relief. The borings in cobbles, pebbles and hardgrounds have similar sizes.

**Intensity.** The most intensely bioeroded hard substrates occur in the Dapingian (Volkhov Regional Stage) and the least bioeroded in the late Katian (Vormsi Regional Stage). The Dapingian boring intensities are 7–15 *Trypanites* per 4 cm<sup>2</sup>, the Darriwilian boring intensity is 7 *Trypanites* per 4 cm<sup>2</sup>, the Sandbian boring intensity is 19 *Trypanites* per 4cm<sup>2</sup> and Katian boring intensities are four to 20 *Trypanites* per 4cm<sup>2</sup>. There is no stratigraphic trend in the bioerosion intensity in the Ordovician of Estonia. Both high and low intensities occur in short stratigraphic intervals. Bioerosion intensity does not correlate with the hard substrate characteristics included in this study (see above).

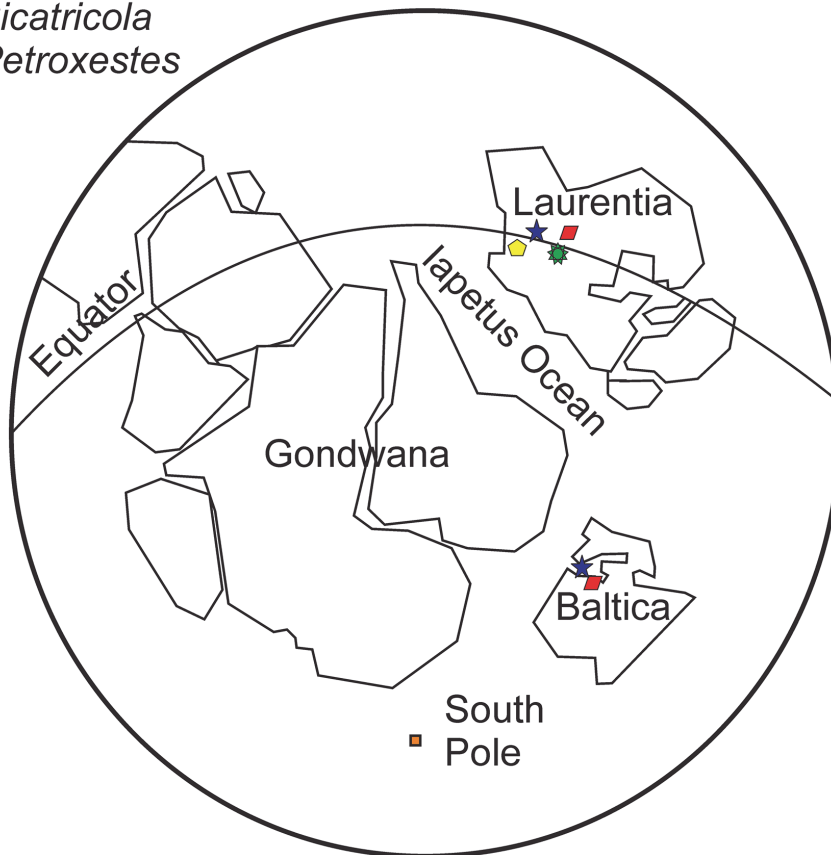
**Ichnotaxonomy.** Most of the bioerosion of Ordovician inorganic hard substrates consists of the boring *Trypanites*. *Gastrochaenolites* is reported only from the earliest Dapingian. It is possible that some of the *Trypanites* reported here may actually belong to *Palaeosabella*, as only a few longitudinal sections of the borings were available.

## Discussion

### Comparison with the other Early Paleozoic inorganic hard substrates

*Trypanites* and possible *Gastrochaenolites* are the only bioerosional trace fossils of inorganic hard substrates common between Estonia (Baltica) and North America (Laurentia) (Fig 12). In addition to these ichnotaxa, North American hardground faunas include *Petroxestes* and *Cicatricula* [26]. *Petroxestes* is a surficial elongate boring produced by bivalves and is known from hardgrounds from the Ordovician of North America [26, 27] (Fig 12). Similarly, *Cicatricula* is found on Middle Ordovician hardground surfaces in Iowa [28] (Fig 12). It is a shallow ramifying boring. It is likely that North American hardground borings were more diverse than those in Baltica. This could be explained by different environmental conditions, such as substrate texture, oxygen levels, nutrient content, depositional energy and sedimentation rate, caused by

- *Trypanites*
- ★ *Gastrochaenolites*
- ◆ *Cicatricola*
- ✱ *Petroxestes*



**Fig 12. Paleobiogeography of borings.** Inorganic hard substrates in the Ordovician. The paleogeographic map of Middle Ordovician is modified after Levin (2006). Data are based on Palmer and Palmer (1977), Wilson and Palmer (1988), Ekdale and Bromley (2001) and present work.

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climatic differences during most of the Ordovician. Most of North America was located in the tropics during the Ordovician while Baltica was located in a temperate climate zone from the earliest Ordovician to the Sandbian. An alternative explanation would be collecting bias, as the North American hardground faunas have been more thoroughly studied than the Estonian ones.

*Trypanites* borings are most intense in the Late Ordovician of North America [27]. However, the Estonian inorganic hard substrates do not show a consistent trend in boring intensities (i.e., number of borings per unit of hard substrate area) during the Middle and Late Ordovician, but this could be explained by the insufficient sample size and different exposure times of Middle Ordovician and Late Ordovician substrates. The sedimentation rates were

lower in the Middle Ordovician of Estonia than in the Late Ordovician [1]. Thus, it is likely that the Middle Ordovician hard substrates were in general exposed longer to bioeroding organisms than the Late Ordovician substrates.

The dimensions of Estonian *Trypanites* borings in the inorganic hard substrates do not differ from analogous records from the Ordovician of North America and other regions of Baltica [25].

### Stratigraphic distribution of hardgrounds

Hardgrounds are often broken into cobbles and larger pebbles due to hydrodynamic activity. The above described bioeroded cobbles and pebbles from the Ordovician of Estonia are interpreted here as the reworked remains of contemporaneous hardgrounds because of their plate-like shape. The earliest bioeroded hardground occurs almost immediately after the beginning of carbonate sedimentation in the Paleobaltic Basin (Fig 4). However, the lack of hardgrounds in the latest Ordovician (latest Katian and Hirnantian) of Estonia needs an explanation. This could be due to less favorable conditions for hardground formation or by higher sedimentation rates in the latest Ordovician of Estonia. Alternatively, it could reflect a collecting bias, but this is unlikely as the whole Ordovician of Estonia has been equally well sampled.

The temporal distribution of hardgrounds reveals a possible trend (Fig 4). There are seven hardgrounds in the Dapingian to early Sandbian (15 my) and only four hardgrounds in the late Sandbian to Hirnantian (12 my) (Fig 4). This may indicate that there were unfavorable conditions for hardground formation during most of the Katian and Hirnantian. The uneven stratigraphic distribution of bioeroded inorganic hard substrates is explained by the varying availability of these substrates in the Ordovician of Estonia.

### Bioerosion trends in organic hard substrates

Among Ordovician organic hard substrates in Estonia, bioerosion has been studied only in bryozoans [19, 20] and brachiopods [17, 18] (Table 1). Bioerosion has a relatively good stratigraphic record only for bryozoans in the Ordovician of Estonia, but no trends can be detected. Data published by Wyse Jackson and Key [19] show that both in the Middle Ordovician (N = 25) and the Late Ordovician (N = 115) 80% of bryozoans were bored by *Trypanites*. However, their data for the early Middle Ordovician are insufficient for statistical analysis, and the Late Ordovician record lacks the middle Katian to Hirnantian part of the section, so it is impossible to draw any firm conclusions. The latest Sandbian to earliest Katian (Keila Regional Stage) is characterized by relatively intense bioerosion (90% of bryozoan specimens) [19]; similarly, the Vasalemma 1 hardground has relatively high bioerosion intensity (20 *Trypanites* borings per 4 cm<sup>2</sup>). It is possible that this may indicate slightly more favorable environmental

**Table 1. Comparison of *Trypanites* borings in organic and inorganic substrates.** The Ordovician of Estonia.

| Character                    | Organic hard substrates                                  |  | Inorganic hard substrates                                |  |
|------------------------------|--|--|--|--|
|                              | Bryozoans  | Brachiopods  | Cobbles/pebbles  | Hardgrounds  |
| Diameter (mm)                | Mean 2.1–2.6   | 0.2–1.6, mean 0.2–1.0                                    | 0.6–4.4, mean 1.7–2.4                                    | 0.2–4.4, mean 1.3–2.6                                    |
| Length (mm)                  | Mean 4.9–7.1   | 2–8  | 7–12   | 6–15   |
| Morphology                   | Simple cylindrical                                       | Simple cylindrical                                       | Simple cylindrical                                       | Simple cylindrical                                       |
| Typical bioerosion intensity | Medium to high   | Low  | High   | Medium   |
| Bioerosion environment       | Shallow marine, carbonate platform (Onshore to offshore) | Shallow marine, carbonate platform (Onshore to offshore) | Shallow marine, carbonate platform (Onshore to offshore) | Shallow marine, carbonate platform (Onshore to offshore) |

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conditions for bioerosion in the latest Sandbian to earliest Katian (Keila) time. Bryozoan data suggest that bioerosion intensities were similar in the Middle and Late Ordovician of Estonia.

### Climatic change, bioerosion and hardground formation

A possible explanation for the uneven stratigraphic distribution of hardgrounds in the Ordovician of Estonia may be in sedimentation rate differences. The Dapingian and early Darriwilian are characterized by low net sedimentation in the Paleobaltic basin [1]. The Early Katian Vasalemma Formation may have similarly been affected by low sedimentation rates. The sedimentation pattern during the latest Keila, Sandbian/Katian boundary (Vasalemma Formation) interval has been described as unique as it represents a time of pronounced non-deposition over most parts of northern Estonia [29].

The Ordovician was a time of calcite seas, which produced favorable conditions for hardground formation [30]. According to a recent review by Balthasar and Cusack [31], calcite sea intervals were characterized by the co-precipitation of aragonite and calcite in environments above 20°C. They concluded that continuous prominence of aragonite precipitation in Phanerozoic warm-water environments could explain the Phanerozoic increase of aragonite over calcite skeletal composition in calcifying organisms. Thus, the geochemical regimes in tropical and temperate calcite seas were different. During the Ordovician, Baltica moved from a temperate climate (Tremadocian to Sandbian) to the tropics (late Katian and Hirnantian). Hardgrounds seem to be more common in the temperate climate part of the Ordovician calcite sea in Estonia (seven hardgrounds during 15 my) than in the tropical portion of the record (four hardgrounds during 12 my). If there is a trend, it is possible that the temperate climate geochemical regime of calcite seas could have been more favorable for hardground formation than the tropical equivalent. Future studies should show whether there is a climate-related trend in the distribution of hardgrounds in Baltica.

There seems to be no correlation between hardground formation and minor climatic perturbation, such as the GICE (Guttenberg  $\delta^{13}\text{C}$  excursion), for example, in the Ordovician of Estonia. There is no event associated clearly with numerous hardgrounds.

### GOBE and the Ordovician Bioerosion Revolution

The Great Ordovician Biodiversification Event (GOBE) is reflected in the record of bioerosional trace fossils and is termed the Ordovician Bioerosion Revolution. During the Ordovician Bioerosion Revolution, the diversity of boring ichnotaxa dramatically increased. There are two macroborings in the Cambrian, which contrasts with nine ichnotaxa known from the Ordovician [26, 20].

The evolution of bioerosion in Baltica follows a similar pattern, but there are some differences in diversity and taxonomic composition between North America and Baltica [20, 26]. The following borings occur in the Ordovician of Baltica: *Trypanites*, *Palaeosabella*, *Gastrochaenolites?*, *Osprioneides*, *Ropalonaria*, and *Sanctum* [17, 19, 20, 26]. *Trypanites* and *Gastrochaenolites* are the only known inorganic hard substrate borings in the Ordovician of Baltica. Interestingly, when the general diversity of boring ichnotaxa in Baltica increased from one to seven during the Ordovician, the diversity of inorganic hard substrate borings increased only two times. This difference in diversity increase may be explained by the wider environmental distribution of organic substrates as compared to inorganic ones in the Ordovician seas of Baltica, and their continuous temporal availability. These factors may have encouraged specialization of several borers. The inorganic substrates were probably bored only by the generalists.

## Conclusions

- Bioeroded hardgrounds, limestone pebbles and cobbles are common in the Ordovician of Estonia.
- Bioerosional trace fossils in inorganic hard substrates are less diverse than those on organic skeletons in the Ordovician of Baltica.
- The major bioerosional ichnotaxon of inorganic hard substrates is *Trypanites* in the Ordovician of Baltica.
- Hardground borings in North America are more diverse than those in Estonia (Baltica).

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Conceived and designed the experiments: OV MAW UT. Performed the experiments: OV MAW UT. Analyzed the data: OV MAW UT. Contributed reagents/materials/analysis tools: OV MAW UT. Wrote the paper: OV MAW UT.

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