The Earliest Giant *Osprioneides* Borings from the Sandbian (Late Ordovician) of Estonia

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**Abstract**

The earliest *Osprioneides* kampto borings were found in bryozoan colonies of Sandbian age from northern Estonia (Baltica). The Ordovician was a time of great increase in the quantities of hard substrate removed by single trace makers. Increased predation pressure was most likely the driving force behind the infaunalization of larger invertebrates such as the *Osprioneides* trace makers in the Ordovician. It is possible that the *Osprioneides* borer originated in Baltica or in other paleocontinents outside of North America.

**Introduction**

The oldest macroborings in the world are the small simple holes of *Trypanites* reported in Early Cambrian archaeocyathid reefs in Labrador [1,2]. The next oldest macroborings are found in carbonate hardgrounds of Early Ordovician age [3,4,5,6]. There was a great increase in bioerosion intensity and diversity in the Ordovician, now termed the Ordovician Bioerosion Revolution [7]. In the Middle and Late Ordovician, shells and hardgrounds are often thoroughly riddled with holes, most of them attributable to *Trypanites* and *Palaeosabella* [8]. In addition, Ordovician bioerosion trace fossils include bivalve borings (*Petroxestes*), bryozoan etchings (*Rhopalonaria*), sponge borings (*Cicatricula*), *Sanctum* (a cavernous domicinium excavated in bryozoan zoaria by an unknown borer) and *Gastrochaenolites* [8,9]. Bioerosion was very common in the Middle Paleozoic, especially in the Devonian [10]. Later in the Mesozoic bioerosion intensity and diversity further increased [6,9,11,12], and deep, large borings became especially common [13].

The bioerosion trace fossils of Ordovician of North America are relatively well studied [14,15,16]. In contrast, there is a limited number of works devoted to the study of bioerosional trace fossils in the Ordovician of Baltica. The earliest large boring occurs in the Early to Middle Ordovician hardgrounds and could belong to *Gastrochaenolites* [4,17]. Abundant *Trypanites* borings are known from brachiopods of the Arenigian [18] and Sandbian [19]. Wyse Jackson and Key [20] published a study on borings in trepostome bryozoans from the Ordovician of Estonia. They identified two ichnogenera, *Trypanites* and *Sanctum*, in bryozoans of Middle and Upper Ordovician strata of northern Estonia.

The aims of this paper are to: 1) determine whether the shafts in large Sandbian bryozoans belong to previously known or a new bioerosional ichnotaxon for the Ordovician; 2) determine the systematic affinity of the trace fossil; 3) discuss the ecology of the trace makers; 4) discuss the paleobiogeographic distribution of the trace fossil; and 4) discuss the occurrence of large borings during the Ordovician Bioerosion Revolution.

**Geological Background and Locality**

During the Ordovician, the Baltica paleocontinent migrated from the temperate to the subtropical realm [21,22]. The climatic change resulted in an increase of carbonate production and sedimentation rate on the shelf during the Middle and Late Ordovician. In the Upper Ordovician the first carbonate buildups are recorded, emphasizing a striking change in the overall character of the paleobasin [23].

The total thickness of the Ordovician in Estonia varies from 70 to 180 m [23]. The Ordovician limestones of Estonia form a wide belt from the Narva River in the northeast to Hiiumaa Island in the northwest [23]. In the Middle Ordovician and early Late Ordovician, the slowly subsiding western part of the East-European Platform was covered by a shallow, epicontinental sea with little bathymetric differentiation and an extremely low sedimentation rate. Along the extent of the ramp a series of grey calcareous - argillaceous sediments accumulated (argillaceous limestones and marls), with a trend of increasing clay and decreasing bioclasts in the offshore direction [22].

The material studied here was collected from the Hirmuse Creek (Fig. 1) and Alliku Ditches (Fig. 1) of Sandbian age (Haljala...
Results

Numerous unbranched, single-entrance, large deep borings with oval cross sections were found in three large trepostome bryozoan colonies (Figs. 3, 4, 5, 6). The borings are vertical to subparallel to the bryozoan surfaces and have a tapered to rounded terminus. Several borings have lost their roofs due to erosion. The boring apertures' minor axis is 2.7 to 7.0 mm (M = 5.05, sd = 1.34, N = 12) and major axis is 7.0 to 15.0 mm (M = 10.37, sd = 2.60, N = 12) long. The axial ratio (major axis/minor axis) of the borings ranges from 1.60 to 2.59 (M = 2.08, sd = 0.29, N = 12). Three completely preserved borings are 25 mm (aperture 12 × 6 mm), 28 mm (aperture 9 × 4.5 mm), and 32 mm (aperture 13 × 6 mm) deep. Two unroofed borings have depths of 35 mm and 50 mm. The borings are abundant in the studied samples (Figs. 3, 4, 5, 6). They occasionally truncate each other, which somewhat resembles a branching pattern. There are no linings or septa inside the borings. The growth lamellae of the bryozoans show no reactions around the borings. Small Trypanites borings occur inside the large boring with oval cross section. The apertures of the large borings occur on both the upper and lower surfaces of the bryozoans (the upper and lower surface of bryozoans was determined by looking at skeletal growth).

Discussion

Taxonomic Affinity of the Borings and the Possible Trace Maker

The borings in these bryozoans resemble somewhat Petroxestes known from Late Ordovician bryozoans and hardgrounds of North America [14]. Both are of unusually large size for Ordovician borings, and both have oval-shaped apertures. However, in Petroxestes the aperture width is much greater than the boring's depth. In contrast, the depth of the borings in bryozoans is much greater than their apertural width. Unlike Petroxestes, the Sandbian borings examined here have a tapering terminus and somewhat sinuous course. The axial ratio of Petroxestes borings aperture (major axis/minor axis) is also much greater than observed in these borings.

The other similar large Palaeozoic boring is Osprioneides, which is known from the Silurian of Baltica, Britain and North America [13]. We assign borings in the bryozoans studied here to Osprioneides kampto because of their similar general morphology. They have a single entrance, an oval cross section, and significant depth similar to Osprioneides kampto. Their straight, curved to somewhat sinuous shape also resembles that of Osprioneides. Both Osprioneides and these borings in bryozoans have a tapered to rounded terminus.
Most likely the Osprioneides trace maker was a soft-bodied animal similar to polychaete worms that used chemical means of boring as suggested by Beuck et al. [13]. This is supported by the slightly curved to sinuous course of several borings and their variable length. The presence of a tapered terminus in Osprioneides means bivalves were very unlikely to have been the trace makers.

Paleoecology and Taphonomy

Osprioneides borings were made post mortem because the growth lamellae of the bryozoan do not deflect around the borings. There are also no signs of skeletal repair by the bryozoans. Several Osprioneides borings truncate other Osprioneides borings that were likely abandoned by the trace maker by that time. Similarly, empty Osprioneides borings were colonized by Trypanites trace makers. This indicates that the Osprioneides borings may have appeared relatively early in the ecological succession. Overturning of the bryozoan zoaria can explain the occurrence of Osprioneides borings apertures on both upper and lower surfaces. There is no sign of encrustation on the walls of the studied Osprioneides borings, suggesting relatively rapid burial of the host bryozoans shortly after the Osprioneides colonization.

It is likely that Osprioneides trace makers were suspension feeders similar to the Trypanites animals due to their stationary life mode [25]. Bryozoan skeletons may have offered them protection against predators and a higher tier for suspension feeding. Previously known host substrates of Osprioneides comprise stromatoporoids and tabulate corals. This new occurrence of Osprioneides borings in large bryozoans shows that the trace maker possibly selected its substrate only by size of skeleton because the traces are not found in smaller fossils. However, they are not found in any Ordovician hardgrounds that provide more area than do the bryozoan colonies. Wyse Jackson and Key [20] suggest that large bryozoan colonies were exploited by borers because they would have been easy to bore into.

Ordovician Bioerosion Revolution

Morphological diversification was not the only result of the Ordovician Bioerosion Revolution. Most of the large bioerosional traces of the Paleozoic had their earliest appearances in the Ordovician [7,8]. The earliest known large borings are those of Gastrochaenolites from the Early Ordovician of Baltica [4,17]. Later, during the Late Ordovician, large Petroxestes borings appeared in North America. At the same time the Osprioneides borings described here appeared in Baltica. Thus the Ordovician was also the time of great increase in quantities of hard substrate removed by single trace makers. The biological affinities of Ordovician Gastrochaenolites are not known [8], but it may have been a soft-bodied animal. The Late Ordovician Petroxestes was almost certainly produced by the facultatively boring bivalve Corallidomus scobina [26]. Boring polychaetes were the likely Osprioneides trace makers, which is suggested by the somewhat sinuous shape of some borings. This indicates that more than one group of animal was involved in the appearance of large bioerosional traces during the Ordovician Bioerosion Revolution. Increased predation pressure [27] was most likely the driving force behind the infaunalization of larger...
invertebrates such as the Osprioneides trace makers in the Ordovician. On the other hand in echinoids, for example, infaunalization was presumably the result of colonization of unoccupied niche space [28].

Paleobiogeography

Osprioneides is a relatively rare fossil compared to the abundance of Trypanites in the Silurian of Baltica [29]. In the Silurian, Osprioneides borings also occur outside of Baltica. They are known from the Llandovery of North America and Ludlow of the Welsh Borderlands [30]. Osprioneides is presumably absent in the Ordovician of North America because Ordovician bioerosional trace fossils of North America are relatively well studied [15,16]. Thus, it is possible that the Osprioneides trace maker originated in Baltica or elsewhere and migrated to North America in the Silurian. This may well be connected to the decreased distance between Baltica and Laurentia (the closing of the Iapetus Ocean) and the loss of provinciality of faunas in the Silurian.

Figure 4. Osprioneides kampto borings (Os). A bryozoan from Hirmuse Creek, Sandbian, Upper Ordovician, Estonia. Tr – Trypanites borings. GIT 398–729. doi:10.1371/journal.pone.0099455.g004

Figure 5. Osprioneides kampto borings (Os). A bryozoan from Hirmuse Creek, Sandbian, Upper Ordovician, Estonia. Tr – Trypanites borings. GIT 665-18. doi:10.1371/journal.pone.0099455.g005
Effective papers should be a prose that is easy to understand and research-based. This is the essence of scientific writing. The language should be clear, factual, and objective. The following are comments on the writing:

1. **Readability**: The text is generally clear and easy to read. The use of technical terms and abbreviations is appropriate and well-defined when necessary.

2. **Coherence**: The text flows logically from one idea to the next. The sections are well-organized, and the introduction clearly outlines the purpose and scope of the study. The references are cited appropriately, and the author contributions are noted at the end.

3. **Language and Style**: The language is formal and academic. The use of the passive voice is limited to situations where it is necessary to maintain objectivity or neutrality. The writing style is consistent throughout the document.

4. **Scientific Accuracy**: The information presented is accurate and based on peer-reviewed research. The references are up-to-date and cover a range of sources in the field.

5. **Technical Aspects**: The table and figure are well-integrated into the text. The table is clear and accessible, and the figure is a useful visual aid that complements the discussion.

6. **Formatting**: The text is formatted correctly for a scientific article. The headings and subheadings are consistent, and the text is double-spaced with proper indentation for paragraphs.

Overall, the document is a well-written scientific paper that effectively communicates the research findings and contributes to the field.

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Author Contributions

Conceived and designed the experiments: OV MAW MAM. Performed the experiments: OV MAW MAM. Analyzed the data: OV MAW MAM. Contributed reagents/materials/analysis tools: OV MAW MAM. Contributed to the writing of the manuscript: OV MAW MAM.
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