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Borings and bioclastrations in bryozoans from the Kunda Regional Stage (Darrwilian; Middle Ordovician) of northern Estonia and NW Russia

Olev Vinn, Andrej Ernst, Mark A. Wilson, and Ursula Toom

With 2 figures and 1 table

Abstract: Various borings are common in bryozoan colonies from the Kunda Regional Stage (early Darrwilian; Middle Ordovician) of northern Estonia and northwestern Russia. Three different boring types are found. In addition to post-mortem borings, bioclastrations that represent an early occurrence of such structures in the fossil record are also present in the bryozoan *Orbipora acanthophora*. The *syn vivo* nature of these structures is supported by changes in growth direction of zooecia around the shaft. The differences in morphology indicate that the bioclastration in *O. acanthophora* cannot be assigned to *Anoigmachnus* and likely represents a new ichnogenus. The new data do not change previously recorded bryozoan symbiont diversity trends in Baltica, and the diversity of bryozoan symbionts is still much lower in the Darrwilian than it is in the succeeding Sandbian.

Key words: Bryozoa, symbiosis, bioclastrations, bioerosion, Ordovician, Baltica.

1. Introduction

The Ordovician bryozoans of eastern Baltica are well known for containing borings (WYSE JACKSON & KEY 2007) and bioclastrations (VINN et al. 2014; VINN et al. 2016; VINN et al. 2017; VINN et al. 2018a; VINN et al. 2018b; VINN et al. 2019). Bioerosion was a common phenomenon in the Ordovician of the Baltic Basin (TOOM et al. 2019). Various endobionts have colonized Palaeozoic bryozoans (ERNST et al. 2014; SUÁREZ ANDRÉS 2014; SUÁREZ ANDRÉS et al. 2020; SUÁREZ ANDRÉS et al. 2021). The earliest bryozoan symbiotic endobionts have been recently described from the Tremadocian of China (MA et al. 2020). There is a possibility that the Middle and Late Ordovician diversification of ramose bryozoan forms may have stimulated the escalation of bioeroder and symbiont taxa in living colonies, and that in turn encouraged further trepostome evolution (ERICKSON 2020). In this paper we fol-

low the ‘de Bary’ definition and view symbiosis as any type of close and long-term biological interaction between two different organisms, be it mutualistic, commensalistic, or parasitic (MARTIN & SCHWAB 2013). Some of the early symbiotic endobionts of colonial animals may have been parasitic (ZAPALSKI 2007; ZAPALSKI 2009; ZAPALSKI 2011; ZAPALSKI & HUBERT 2011). This view has been questioned by TAYLOR (2015), who gave reasons why classifying endobionts as parasites is unwise in fossil material in which the exact costs and benefits of the interactions between host and symbiont cannot be determined.

The Ordovician bryozoans of northern Estonia and NW Russia are relatively well studied, and many systematic papers have been published (e.g., BASSLER 1911; MODZALEVSKAYA 1953; MÄNNIL 1959; PUSHKIN 1987; LAVRENTJEVA 1990; GORJUNOVA 1992; GORJUNOVA 1996; GORJUNOVA & LAVRENTJEVA 1993; KOROMYSLOVA 2004; KOROMYSLOVA 2007; KOROMYSLO-

VA 2011; KOROMYSLOVA & FEDOROV 2021). However, the bryozoan endobiont faunas of the Darriwilian have remained poorly known and deserve further study (ERNST 2022).

This paper: (1) describes the earliest bioclaustrations of endobiotic symbionts from Darriwilian bryozoans of Baltica; (2) discusses the palaeoecology of these bioclaustrations and their hosts; and (3) discusses bioerosion in the Darriwilian bryozoans of Estonia and NW Russia.

2. Geological background

In the Darriwilian, the palaeocontinent Baltica was located in a temperate climatic zone (TORSVIK et al. 2013). The area of modern northern Estonia and NW Russia was covered by a shallow epicontinental sea with little bathymetric variation in the Darriwilian. This basin had an extremely low sedimentation rate and a series of grey argillaceous and calcareous sediments accumulated along the ramp (NESTOR & EINASTO 1997). The content of clay increased and that of bioclasts decreased in the offshore direction (NESTOR & EINASTO 1997). In northern Estonia and NW Russia, the Kunda Regional Stage is represented by oolitic, glauconitic and sandy limestones, which formed in normal marine conditions in a shallow sea (MEIDLA 1997) (Fig. 1).

3. Material and methods

A collection of thin sections of bryozoans from the Kunda Regional Stage of northern Estonia and NW Russia was searched for bioclaustrations and signs of bioerosion (Table 1). This collection contains 134 thin sections of 39 bryozoan colonies that belong to 18 species (ERNST 2022). Following bryozoans contained ichnofossils: *Ceramopora* cf. *magnicellularis* MÄNNIL & PUSHKIN in PUSHKIN, 1990 with 1 specimen, *Dianulites collucatus* PUSHKIN in PUSHKIN & POPOV, 2001 with 2 specimens, *Esthoniopora communis* BASSLER, 1911 with 1 specimen, *Hemiphragma rotundatum* BASSLER, 1911 with 1 specimen, *Orbipora acanthophora* BASSLER, 1911 with 1 specimen, *Mesotrypa hystrowi* MODZALEVSKAYA, 1953 with 1 specimen, and *Pakripora cavernosa* ERNST, 2022 with 2 specimens. Thin sections with borings



Fig. 1. Locality map. Localities marked on the map with solid black squares.

and bioclaustrations were photographed using a Nikon Coolpix 7900 digital camera. Dimensions of borings and bioclaustrations were measured directly from thin sections using a caliper. The studied thin sections are deposited at the Department of Geology, Tallinn University of Technology.

4. Results

Various borings are common in small bryozoan colonies from the Kunda Regional Stage of northern Estonia and NW Russia (Table 1). In addition to these borings, there is a bioclaustration (Fig. 2A) in a colony of *Orbipora acanthophora* (GIT 155-2051) from the Loobu Formation, Harku Quarry trench, northern Estonia. The cylindrical bioclaustration occurs within the elevated region of the host colony and extends deep into the interior of colony. The bioclaustration has affected the growth direction of zooecia so that they are directed away from the bioclaustration at an approximate angle of 45°. The bioclaustration has a relatively constant diameter (2.0–2.5 mm) and is about four times as deep (8–12 mm) as wide. The floor of the bioclaustration is rounded. There are no obvious signs of bioerosion. There is another possible bioclaustration (Fig. 2B) in a *Dianulites collucatus* (GIT 155-1527) from Aseri, northern Estonia. This has a circular transverse section. The zooecia around the possible bioclaustration are smaller than they are further away from this structure.

Table 1. Bryozoans with borings and bioclaustrations from the Kunda Regional Stage.

Bryozoan species	Dimensions of bryozoan colony (mm)	Number of specimens with trace fossil	Trace fossil	Dimensions of trace fossil
<i>Pakripora cavernosa</i>	11×17	GIT 155-2047	<i>Trypanites?</i>	Diameter 1.1–2.0 mm; Length 4.5–8 mm
<i>Ceramopora</i> cf. <i>magnicellularis</i>	22×32	GIT 155-2041	Network of borings	Diameter 1–2 mm
<i>Diamulites collucatus</i>	30×50	GIT 155-1527	Transverse section of possible bioclaustration	Diameter 1.6–3.1 mm
<i>Diamulites collucatus</i>	6×17	GIT 852-6	Bowl-shaped boring	Diameter 4 mm Length 4 mm
<i>Esthoniopora communis</i>	16×22	GIT 155-2048	Unidentified borings	Diameter 0.8–1.5 mm
<i>Hemiphragma rotundatum</i>	14×18	GIT 155-287	Unidentified boring	Diameter 0.72–0.83 mm
<i>Mesotrypa bystrowi</i>	10×16	GIT 155-2055	<i>Trypanites</i> ; only transverse sections visible	Diameter 0.86–0.97 mm
<i>Orbipora acanthophora</i>	20×30	GIT 155-2051	Unidentified bioclaustration	Diameter 2–2.5 mm Length 8–12 mm
<i>Pakripora cavernosa</i>	15×20	GIT 537-2265	<i>Trypanites</i>	Diameter 0.58–0.95 mm, Length c. 3 mm

A small bowl-shaped boring (Fig. 2C) occurs in the growth surface of *Diamulites collucatus* from Putilovo, NW Russia. There is a 3D network of borings (Fig. 2D) or alternatively several intersecting solitary borings (diameter 1.05–2.00 mm) in *Ceramopora* cf. *magnicellularis* (GIT 155-2041) from the Pakri Formation, Väike-Pakri cliff, northern Estonia. Small cylindrical borings resembling *Trypanites* isp. occur in *Mesotrypa bystrowi* and *Pakripora cavernosa* (Fig. 2E). These borings are small for typical *Trypanites* (Table 1). Unidentified small borings also occur in *Hemiphragma rotundatum*. The borings in these bryozoan colonies do not show preference for any particular region of the colony; they can occur close to the growth surface or deep in the interior of the colony.

5. Discussion

5.1. Symbiotic endobionts in Kundan bryozoans

The shaft within the *Orbipora acanthophora* specimen does not cut through the bryozoan colony, and there are no obvious signs of bioerosion associated with it. This suggests that it is a bioclaustration rather than a boring. This is similar to the classic case of “pseudoborings” and bioclaustrations in the Upper Ordovician bryozo-

ans from North America (PALMER & WILSON 1988). The *syn vivo* nature of the structure is also supported by the changes in growth direction of zooecia around the shaft. The aperture of the bioclaustration was open on the growth surface of the host bryozoan and the endobiont almost certainly used the aperture on the host's surface for suspension feeding. The architecture of the studied bioclaustration and its similarity to other bioclaustrations in Palaeozoic colonial animals suggests that it was likely inhabited by a suspension feeding invertebrate. Presumably, the bioclaustration was formed around a worm-like invertebrate, but arthropods also may live in cylindrical tunnels. The endobiont likely benefitted from being partially embedded within the bryozoan colony because such a life mode provided it with additional protection against predators. The bryozoan also provided the endobiont with a relatively stable substrate for growth, and may also have gathered suspended food particles from the feeding currents of the zooids. Even if the endobiont was a kleptoparasite we cannot know if it caused any further harm to the bryozoan. The influence of the endobiont on the host bryozoan remains problematic as no skeletal malformations of the bryozoan are associated with the bioclaustration.

Somewhat similar bioclaustrations that open on the surface of Darrivilian bryozoans belong to *Anoigmaichnus* (VINN *et al.* 2014) but their apertures are

known. This is not surprising as diverse bryozoan bioclaustrations have recently been reported from the Tremadocian trepostomes of China (MA et al. 2020). Nevertheless, our new data do not change previously documented bryozoan symbiont diversity trends in Baltica (VINN et al. 2021). The diversity of bryozoan symbionts is still much lower in the Darriwilian than it is in the Sandbian of Baltica.

5.2. Bioerosion of Kundan bryozoans

Colonies of several bryozoans in the Darriwilian of Estonia and NW Russia were targeted by boring organisms. However, there are no signs of changes in bryozoan growth, which indicates that the borings were likely made post-mortem. WYSE JACKSON & KEY (2007) analyzed borings in the Ordovician bryozoans of Estonia and found that 50% of Kundan bryozoans are bored. Our material is in the form of thin sections and does not allow us to estimate the proportion of bored bryozoans in the community, but borings are not very common in our samples (nine colonies of 39). We did not observe any site selectivity in our borings and it is possible that the borers in the Kunda Stage did not prefer any particular regions in the bryozoan colonies. The diversity of our borings is rather high for the early Darriwilian, comprising *Trypanites* and possibly two undescribed borings. WYSE JACKSON & KEY (2007) reported only *Trypanites* from the Kundan bryozoans of Estonia. Later in the Ordovician of Estonia a second type of boring appears identified as *Sanctum* (WYSE JACKSON & KEY 2007; TOOM et al. 2019). The apertures of our borings are not narrower than their main body and thus differ from *Sanctum* (WYSE JACKSON & KEY 2007). The bowl-shaped boring in *Dianulites colucatus* differs from all known Baltic borings. It was likely created by a radially-symmetrical sessile animal for a domicile. The bowl-shaped architecture of the domicile would not have offered much protection against the predators, so it must have had a different adaptive value for the boring organism. *Trypanites* and network-like borings in *Ceramopora* cf. *magnicellularis* were likely created by worm-like animals that did seek refuge from predators. *Trypanites* borings may be small in this collection because of the small size of bryozoan colonies, which could not accommodate larger borings.

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