Symbiotic endobiont biofacies in the Silurian of Baltica

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ABSTRACT

The distribution of symbiotic endobionts in Silurian stromatoporoids of Estonia is correlated with the diverse sedimentary facies formed in this portion of the Baltica palaeocontinent. These depositional environments are characterized by different symbiotic endobiont associations. There are two onshore shallow water and one offshore deeper water symbiotic endobiont associations. Water depth was not the only controlling factor for their distribution: seawater nutrient levels, hydrodynamics (especially substrate stability), sedimentation rates and distribution of stromatoporoid hosts may have also played important roles.

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1. Introduction

The earliest macroscopic endobiotic invertebrate symbionts are known from the Late Ordovician of North America and Baltica (Elias, 1986; Tapanila, 2005; Dixon, 2010; Vinn and Mõtus, 2012). These endobionts are among the best examples of symbiotic interactions in the fossil record (Taylor, 1990; Taylor and Wilson, 2002). Symbiotic endobionts are usually completely embedded in the tissues of a host organism, except for an opening on the host surface for feeding. Skeletal endobionts have their own mineral wall separating them from the tissues of the host. Endobionts without mineralized skeletons can leave a living cavity within the hard tissues of the host skeleton. The cavities left by embedment are termed bioclaustrations (Palmer and Wilson, 1988; Tapanila, 2005). Originally Sokolov (1948) interpreted bioclaustrations as the traces of commensal endobionts. The later studies have suggested a parasitic nature (i.e., the organisms have a harmful effect on the host) for most of these traces (Stel, 1976; Zapalski, 2007, 2009, 2011; Zapalski and Benoît, 2011).

Worms (Vinn et al., in press), rugosans (Nestor, 1966; Vinn et al., in press), syringoporids (Nestor, 1966) and cornulitids (Vinn and Wilson, 2010) occur as the endobiotic stromatoporoid symbiotic bioclaustrations in the Silurian of Estonia. All these endobiont groups first appeared in the Ordovician (Scrutton, 1997; Tapanila, 2005; Vinn, 2010). Palaeozoic worm bioclaustrations range into the Late Devonian (Zapalski et al., 2008), cornulitids into the Late Carboniferous (Vinn, 2010), and rugosans and syringoporids into the Permian (Scrutton, 1997). Stromatoporoids themselves have a stratigraphic range from the Ordovician through the Devonian (Stock, 2001).

Recent symbiotic polychaetes often produce habitation tunnels very similar to the worm bioclaustrations of the Palaeozoic (Tapanila, 2005). Thus, it is likely that at least some of the Palaeozoic worm bioclaustrations may have also been made by polychaete annelids. However, without data on soft body anatomy, the zoological affinities of these ancient worms will remain unresolved. Both syringoporids and rugosans are corals, though they are not direct ancestors of modern corals (Scrutton, 1997). Cornulitid tubeworms have recently been classified as encrusting tentaculitoids (Vinn, 2010). Cornulitids were common encrusters on various biogenic substrates, especially in the middle Paleozoic (Zatoń and Borszcz, 2013). They are presumably ancestors of free-living tentaculitoids (Vinn and Mutvei, 2009; Vinn, 2010). The biological affinities of cornulitids have long been debated. Recently Vinn and Zatoń (2012) showed that they most likely belong to the Lophotrochozoa, and could represent stem-group phoronids (Taylor et al., 2010).

There are sclerobiofacies of encrusting and endolithic communities on shells in the geological past and in modern seas (Brett et al., 2011, 2012). The taxonomic composition of sclerobiont suites has a predictable variation in marine environments (e.g., based upon depth), but these sclerobiofacies are primarily useful within local areas and limited time frames (Brett et al., 2011, 2012). There is no published synthesis of the facies distribution of symbiotic endobionts in the Silurian. However, it is possible that symbiotic endobionts may form various biofacies in the Silurian analogous to the bioeroding organisms and epibionts.

The aims of this paper are: 1) to describe the symbiotic endobiont associations of stromatoporoids in the Silurian of Saaremaa (Baltica),...
and 2) to discuss whether the distribution of these symbiotic endobionts of stromatoporoids depended on sedimentary rocks.

2. Geological background

The Silurian System is represented by various sedimentary rocks in Estonia, but carbonates dominate in shallow water settings (Fig. 1). The exposed strata range from the Rhuddanian to the Pridoli (Fig. 2). In the outcrop area, including Saaremaa and Hiiumaa islands, the Silurian succession is represented by shallow water carbonate rocks rich in shelly faunas (Hints et al., 2008).

During the Silurian, Baltica was located in equatorial latitudes and thereafter drifted northwards (Melchin et al., 2004). The area of modern Estonia was variously part of the epicontinental Baltic paleobasin. This basin was characterized by a wide range of tropical environments and diverse biotas, especially shelly faunas (Hints et al., 2008). Nestor and Einasto (1977) recognized five depositional environments in the Baltic Silurian Basin. The three most onshore environments formed a carbonate platform containing tidal flat/lagoon, shoal, and open shelf facies zones. Two offshore environments (i.e. basin slope, and a basin depression facies zones) formed a deeper basin with fine-grained siliciclastic deposits (Raukas and Teedumäe, 1997).

3. Material and methods

Stromatoporoids from Hilliste Quarry (N = 40), Panga cliff (N = 43), Undva cliff (N = 20), Suuriku cliff (N = 6), Abula cliff (N = 60), Katri cliff (N = 18) and Kaugatuma cliff (N = 18) were searched for endobionts by external observation with magnifying lenses and by breaking them with a hammer (Fig. 1). Several stromatoporoid specimens with endobionts were cut longitudinally and transversely in the laboratory with a rock saw. Longitudinal and transverse sections were then polished and photographed with a Leica IC80 HD digital camera. Several thin-sections were made from both transverse and longitudinal sections. All thin-sections were scanned using an Epson 3200 optical scanner. The number of stromatoporoids infested by particular endobionts was recorded, as were the number of endobiont specimens per stromatoporoid host. Areal coverage of stromatoporoids by the endobionts was calculated only for rugosans from Abula cliff.

3.1. The lithologic characteristic of the studied beds

Hilliste quarry, Hiiumaa Island (Rhuddanian, Hilliste Formation): Moderately thick horizontal layers of bluish grey packstones with thin marl interlayes. Massive coral and stromatoporid skeletons are common in the section, but they are not interconnected.

Panga cliff, Saaremaa Island (lower Sheinwoodian, Mustjala Member): Bluish grey dolomitic marlstone with argillaceous dolostone interbeds and nodules.

Undva cliff, Saaremaa Island (lower Sheinwoodian, Mustjala Member): Blue-green marlstones containing nodules of biomicritic limestone. The unit contains abundant brachiopods, crinoids, bryozoans, corals and stromatoporoids.

Suuriku cliff, Saaremaa Island (lower Sheinwoodian, Mustjala Member): Blue-green marlstones containing nodules of biomicritic limestone. The unit contains abundant corals (especially halystitids) and stromatoporoids.

Abula cliff, Saaremaa Island (upper Sheinwoodian, Maasi Beds): Light-grey wavy-bedded pelletal limestones with several discontinuity surfaces. Stromatoporoids and brachiopods are common.

Katri cliff, Saaremaa Island (Ludfordian, Uduvere Beds): Section contains a biostrome rich in argillaceous material and with lenses and/or irregular lensoidal interbeds of light-beige pelletal limestone. Stromatoporoids, corals and cephalopods are common.

Kaugatuma cliff, Saaremaa Island (lower Pridoli): Section contains greenish-grey argillaceous limestones and marls. The marl and argillaceous limestone layer is extremely rich in fossils and contains abundant in situ buried large crinoid holdfasts (Enallocrinus sp.). It also contains in situ buried tabulate corals and stromatoporoids.

4. Results

Symbiotic endobionts range from the Rhuddanian to the Pridoli in the Silurian of Estonia (Baltica). They occur in Silurian stromatoporoids of Estonia throughout several facies zones. Packstones of the Hilliste Formation (exposed in the Hilliste quarry, Rhuddanian, of Hiiumaa) (Fig. 1) yielded a single stromatoporoid specimen with 15 Chaetosalpinx? sp. bioclaustrations (Vinn et al., in press) (Fig. 2, Table 1). Marlstones of the Mustjala Member (Undva cliff, Panga cliff, Suuriku cliff; all early Sheinwoodian) yielded 19 stromatoporoids (of 69 examined) with cornulitid endobionts Cornulites stromatoporoides (one to twenty per
host) (Vinn and Wilson, 2010) (Figs. 2–3, Table 1). Pelletal limestones of the Jaagarahu Formation (Abula cliff, late Sheinwoodian) yielded 48 stromatoporoids (of 60 total) with endobionts. The endobionts included the abundant *C. stromatoporoides* (one to three per host) in 75% (*N* = 60) of stromatoporoids and rare rugosans (several hundred per host, ten to 20 endobiotic rugosans were counted per 4 cm²) in 5% of stromatoporoids (*N* = 60) (Vinn and Wilson, 2010, 2012a) (Figs. 2, 4, Table 1). The biostromal limestones of the Paadla Formation (Katri cliff, Ludfordian) yielded stromatoporoids with rugosan (in three of 18 stromatoporoids, tens of specimens per host) and syringoporid endobionts (in four of 18 stromatoporoids, hundreds of corallites per host) (Figs. 2, 5, Table 1), and abundant worm-like bioclaustrations without mineral tubes (in 14 stromatoporoids of 18 with tens of bioclaustrations per host) (i.e., Chaetosalpinx sp. and Helicosalpinx sp.) (Nestor, 1966; O. Vinn personal obs.) (Figs. 2, 6, Table 1). Packstones of the Kaugatuma Formation (Kaugatuma cliff, early Pridoli) yielded one stromatoporoid (of 18 examined) with a single endobiotic rugosan (Vinn and Wilson, 2012b) (Table 1).

5. Discussion

5.1. Depositional environments

The packstones of the Hilliste Formation (Rhuddanian) are interpreted as having been deposited in an onshore shallow sea environment due to the occurrence of normal marine fauna and deposition of calcareous skeletal debris in large accumulations. Marls of the Mustjala Member presumably formed offshore in a relatively deeper sea environment with relatively calm waters (no overturned stromatoporoids were found). Pelletal limestones of the Jaagarahu Formation likely represent an onshore shallow sea environment. The packstones of the Kaugatuma Formation appear to have formed in an onshore shallow sea environment. The packstones and wackestones of the Kaugatuma Formation formed in an onshore environment of a relatively shallow sea with high-energy waters (overturned...
stromatoporoids are common) (see Kaljo, 1970, for review of sedimentary environments in the Silurian of Estonia).

5.2. Symbiotic endobiont associations

1) Association A is characterized by the co-occurrence of abundant cornulitid (in 75% of stromatoporoids) and rare rugosan endobionts (in 5% of stromatoporoids). This association is established on the stromatoporoid endobiont fauna in the Jaagaru Formation at Abula cliff (Figs. 1, 2, Table 1). Chaetosalpinx? bioclaustrations in a Hilliste Formation stromatoporoid from the Hilliste Quarry on Hiiumaa Island may also belong to this association (Figs. 1–2). Association A occurred in an onshore shallow sea with a carbonate facies.

2) Association B is indicated by the co-occurrence of abundant endobiotic rugosans, syringoporids and abundant bioclaustrations of worm-like organisms (i.e., Chaetosalpinx? and Helicosalpinx sp.). This association is established on the stromatoporoid endobiont fauna in the Paadla Formation exposed at Katri cliff (Figs. 1–2, Table 1). Association B inhabited an onshore shallow sea in biostromes and possibly also reefs. A similar association of biostrome stromatoporoids and endobiotic cornulitids was therefore not entirely controlled by water depth. In contrast, endobiotic cornulitids occur in both shallow and relatively deep water. The occurrence of symbioses between stromatoporoids and endobiotic cornulitids was therefore not entirely controlled by water depth. The diversity of symbiotic endobiont groups was greatest in shallow water (associations A (number of groups two) and B (number of groups three)) and lowest in relatively deep water (association C; number of groups one).

3) Association C is characterized by the occurrence of abundant endobiotic cornulitids (in 16.7–30.2% of stromatoporoids) (Table 1). This association is established on the stromatoporoid endobiont fauna in the Mustjala Member at Panga, Suuriku and Undva cliffs (Fig. 1). Association C inhabited a relatively deep-water offshore environment with a siliciclastic muddy bottom.

5.3. Depth distribution of symbiotic endobionts

The exact water depths of deposition have not been estimated for the studied sections of the Baltica palaeobasin in the Silurian of Saaremaa, but they were all less than 200 m deep (Kaljo, 1978). Most likely none were deeper than 90 m (Kaljo, 1978). Endobiotic rugosans and syringoporids occur only in relatively shallow waters; however, their fossils are not restricted to onshore environments. The same may be true for tubeless worm-like bioclaustrations (i.e., Chaetosalpinx?, Helicosalpinx?) in stromatoporoids that have only been found in shallow water sediments. Thus, it is possible that rugosans and syringoporids formed symbiotic associations with stromatoporoids only in shallow waters. In contrast, endobiotic cornulitids occur in both shallow and relatively deep water. The occurrence of symbioses between stromatoporoids and endobiotic cornulitids was therefore not entirely controlled by water depth. The diversity of symbiotic endobiont groups was greatest in shallow water (associations A (number of groups two) and B (number of groups three)) and lowest in relatively deep water (association C; number of groups one).

5.4. Controlling factors on symbiotic endobiont facies distribution

Symbiotic endobiont associations (A and B) of both shallow sea facies are different, indicating that the water depth alone did not control the distribution of symbiotic endobionts. Seawater nutrient levels and hydrodynamics (such as substrate stability) and sedimentation may have also played an important role.

Modern coral reefs thrive in nutrient poor waters (Muscatine and Porter, 1977). If this was also true for Silurian reefs and biostromes (Kershaw, 1993), differences in nutrient levels may explain the taxonomic differences between shallow sea and biostrome symbiotic endobiont associations. Cornulitids that are absent in the biostrome association may have preferred the more nutrient rich waters of other
onshore shallow seafloors and shoals. Alternatively, the taxonomic differences may be explained by different stromatoporoid hosts in these two settings if the endobionts were host-specific.

Why are endobiotic rugosans more abundant in biostromes (association B) and syringoporids lacking in the shallow water association (A)? Modern reef environments are very diverse ecosystems. If this was also true for the Silurian reefs and biostromes in Baltica, it may well explain the highest diversity of endobionts at group and possibly species level in the biostrome association (B). The higher abundance of endobiotic rugosans in the biostrome association (B) as compared to shallow water association (A) could be explained by the specific favorable environmental conditions of the biostrome environment. These favorable conditions may include a lack of space competition by cornulitid endobionts (in maximum up to 20 individuals per host) and a large number of available stromatoporoids in a small area (up to 15 stromatoporoids per 1 m²). The endobionts may have also preferred the possible lower sedimentation rates in the biostromes (Kershaw, 1993) as compared to other areas of shallow sea.

In addition to environmental conditions, the taxonomy of the host stromatoporoids may have influenced the taxonomic composition of their endobiont fauna. Different stromatoporoid taxa have a different facies distribution in the Silurian of Baltica (Nestor, 1999). It is unlikely, but possible, that stromatoporoids may have also been selectively tolerant with regard to their endobionts. Even if the facies distribution of stromatoporoid species had some effect on the taxonomic composition of their endobiont associations, it was not strong as there are endobiont taxa that occur both in deeper water and shallow water stromatoporoids, such as *C. stromatoporoides*.

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Fig. 3. *Cornulites stromatoporoides* from the Jaani Formation (Sheinwoodian) of Panga cliff, Saaremaa. Scale bar 10 mm. TUG-1328-1.

Fig. 4. *Palaeophyllum* sp. in *Ecclimadictyon astroloaxum* from the Jaagarahu Formation of Abula cliff, Saaremaa. Scale bar 5 mm. TUG1627-4.

Fig. 5. Syringoporids in a stromatoporoid from the Paadla Formation (Ludfordian) of Katri cliff, Saaremaa. Scale bar 10 mm. TUG 1653-1.

Fig. 6. *Helicosalpinx* sp. in a stromatoporoid from the Paadla Formation (Ludfordian) of Katri cliff, Saaremaa. Scale bar 2 mm. GIT-656-82.
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