

Encrustation and bioerosion on late Sheinwoodian (Wenlock, Silurian) stromatoporoids from Saaremaa, Estonia

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Abstract: A shallow shelf carbonate platform (pelletal limestone facies) stromatoporoid association from the late Sheinwoodian of Saaremaa (Baltica) contains a diverse assemblage of sclerobionts (both epi- and endobionts). The studied stromatoporoids vary from low domical to extended domical shapes. *Cornulites* sp. aff. *C. stromatoporoides*, *Conchicolites* sp., *Anticalyptrea calyptrata*, microconchids, tabulate (*Aulopora* sp., *Catenipora* sp. and favositids) and rugose corals, sheet-like trepostome bryozoans, and discoidal crinoid holdfasts encrust the stromatoporoids. The dominant sclerozoans were tabulate and rugose corals, which is significantly different from several analogous Silurian sclerobiont communities. There may have been taxonomic polarity between an upper surface and a cryptic sclerozoan community. Bioerosion occurs as macroborings in 45.5 % of studied (N=22) stromatoporoids. Endobionts were represented by *Trypanites* and *Palaeosabella* borings, as well as embedded symbiotic rugose corals and *Cornulites stromatoporoides*.

Key Words: Sclerobionts; symbiosis; bioerosion; Silurian; Saaremaa; Baltica.

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Résumé : *Encroûtement et bioérosion de stromatoporoïdes d'âge Sheinwoodien supérieur (Wenlock, Silurien) de Saaremaa (Estonie).*- Un peuplement de stromatoporoïdes de plate-forme carbonatée peu profonde (faciès calcaire péloïdal) d'âge Sheinwoodien supérieur (Wenlock inférieur) de Saaremaa (Estonie) recèle une association variée de sclérobiontes (épibiontes et endobiontes). Les stromatoporoïdes étudiés présentent différentes morphologies de dômes, basses à surélevées. Ces stromatoporoïdes sont encroûtés par *Cornulites* sp. aff. *C. stromatoporoides*, *Conchicolites* sp., *Anticalyptrea calyptrata*, des microconchidés, des tabulés (*Aulopora* sp., *Catenipora* sp. et des favositides), des tétracoralliaires, des bryozoaires trépostomes lamellaires et des crinoïdes dont subsistent les crampons discoïdes. Les sclérozoaires dominants sont des coraux (Tabulata et Rugosa), ce qui représente une différence significative par rapport aux nombreuses communautés analogues de sclérobiontes siluriens. Il y a pu avoir une polarité taxonomique entre une surface supérieure et une communauté cryptique de sclérozoaires. Sur les stromatoporoïdes étudiés (N=22), 45.5 % des cas de bioérosion correspondent à des perforations de grande taille. Les endobiontes sont représentés par des perforations de types *Trypanites* et *Palaeosabella*, ainsi que par des formes "enchâssées", tétracoralliaires (Rugosa) et *Cornulites stromatoporoides*.

Mots-Clefs : Sclérobiontes ; symbiose ; bioérosion ; Silurien ; Saaremaa ; Baltica ; Fenno-sarmatia.

1. Introduction

Marine invertebrate communities diversified rapidly during the Great Ordovician Biodiversification Event (GOBE; see, for review, SERVAIS *et al.*, 2009). There was also a dramatic increase in encrustation and bioerosion on hard substrates at this time (TAYLOR & WILSON, 2003). The diversification of bioeroders has been called the Ordovician Bioerosion Revolution (WILSON & PALMER, 2006). The Silurian was a time of further development of hard substrate communities after the GOBE. In general, Silurian hard substrate communities are similar to those of the Ordovician, being primarily dominated by

bryozoans and echinoderms (TAYLOR & WILSON, 2003). Encrusting faunas of the Silurian stromatoporoids have been studied in detail by several authors (KERSHAW, 1980; SEGARS & LIDDELL, 1988; LEBOLD, 2000). Encrustation patterns and bioerosion is relatively well known for western Baltica, especially for Gotland, Sweden (KERSHAW, 1980; NIELD, 1984; BEUCK *et al.*, 2008). However, little published data on sclerobionts are available from the Silurian of eastern Baltica (KALJO, 1970; VINN & WILSON, 2010a, 2010b).

The aims of this paper are: 1) to describe a hard substrate association from the late Shein-

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woodian of East Baltic for the first time; 2) to discern whether this association is typical for the Silurian of Baltica and beyond; 3) to discover whether hard substrate cryptic niches were occupied; and 4) to determine whether the bioerosion was similar to that observed in the Silurian of North America and western Baltica (especially Gotland).

2. Geological background

During the Silurian the Baltica continent was located in equatorial latitudes drifting northwards (MELCHIN *et al.*, 2004). The pericontinental Baltica paleobasin in modern Estonia was characterized by a wide range of tropical environments and diverse biotas (HINTS *et al.*, 2008). In the outcrop area, including Saaremaa Island, the Silurian succession is represented by shallow shelf carbonate rocks rich in shelly faunas. The Silurian exposures on Saaremaa,

which are the best in Estonia, are mostly represented by coastal cliffs.

3. Locality and stratigraphy

The Abula cliff is situated on the eastern coast of Tagalaht Bay, 3 km north of the Mustjala-Veere road (58°27'12" N, 22°06'51" E) (Fig. 1). The cliff exposes the topmost Vilsandi Beds (lagoonal dolomitic marlstones) and the basal part of the Maasi Beds (HINTS *et al.*, 2008). The Maasi Beds form the middle part of the Jaagarahu Formation (Figs. 2 - 3). The studied stromatoporoids were collected from the pelletal limestone layers of the upper part of the section (the Maasi Beds). The stromatoporoid-rich layer is of normal marine origin. It is presumably deposited on a very shallow shelf in waves activity zone, what is indicated by occurrence of rare overturned stromatoporoids.



Figure 1: Location of Abula cliff (Maasi Beds, Jaagarahu Formation, late Sheinwoodian) on Saaremaa Island, Estonia. The map of Saaremaa is provided by Estonian Land Board.

4. Material and methods

Twenty-two stromatoporoids were collected from the pelletal limestone layers (Maasi Beds) of Abula cliff. Sample orientations were marked during collecting. The specimens were manually cleaned with water and a soft brush. *Trypanites-Palaeosabella* borings and endobiotic rugosans were counted in a 4 cm² grid. The surface areas of encrusting fossils were estimated using a millimeter grid. A centimeter grid was used to calculate the total surface area of the stromatoporoids. Upper surface and cryptic encrustations were measured separately.

Our classification of stromatoporoid shapes follows KERSHAW (1998). Three morphological categories of stromatoporoids were identified: 1) low domical, 2) high domical, and 3) exten-

ded domical. The preservation of our material is variable, and it is possible that some stromatoporoids may have lost some part of their original encrusters while broken free from the limestone matrix. Thus, encrustation densities on stromatoporoids reported here are minimums.

Endobiotic cornulitids from the same association were described by VINN and WILSON (2010c) and were not counted in this study as their abundance was determined by a different method (breaking the stromatoporoids into pieces by hammer).

Figured specimens are deposited at the Geological Museum, Museum of Natural History, University of Tartu (TUG).

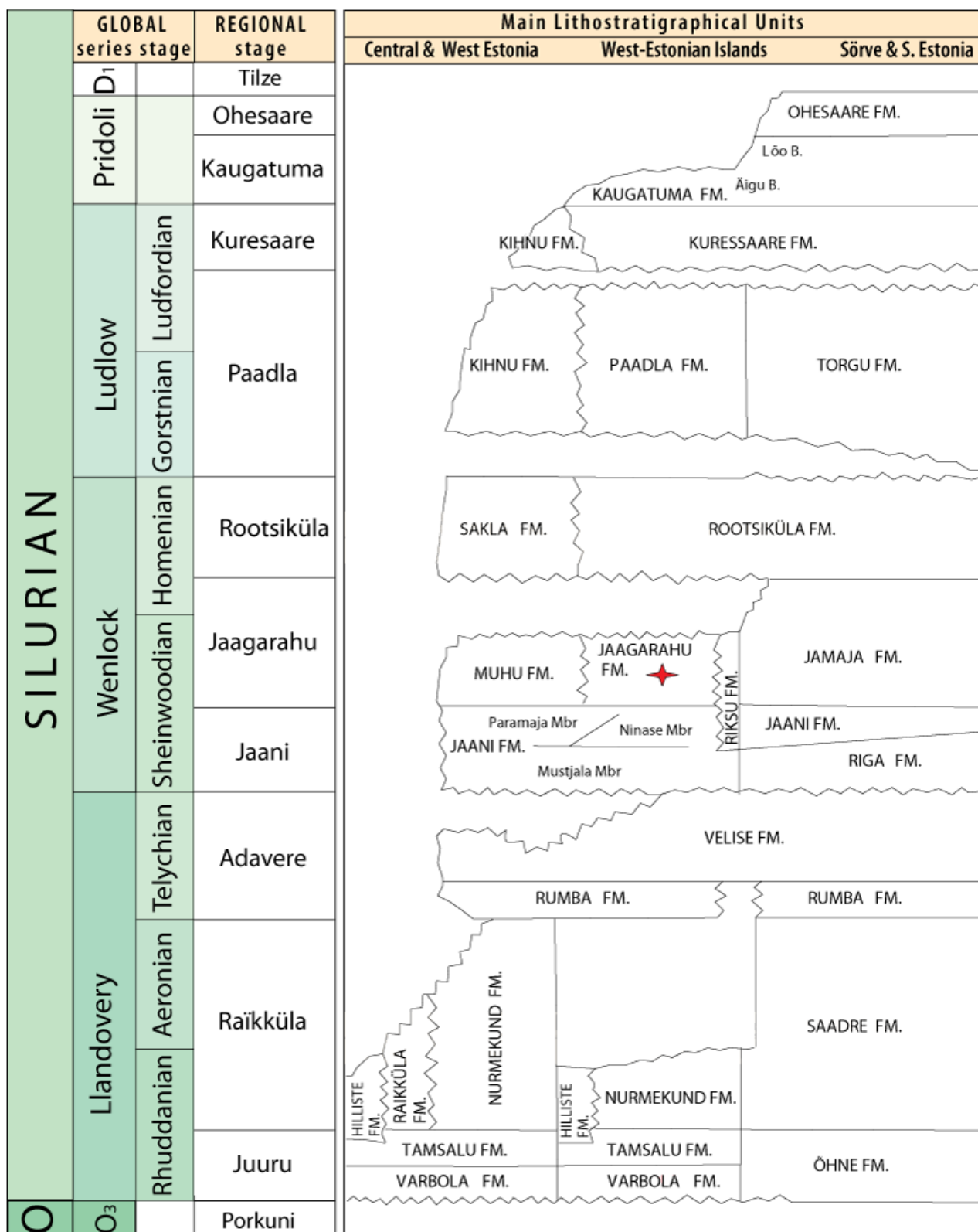


Figure 2: Stratigraphy of the Silurian of Estonia (after HINTS *et al.*, 2008). Location of Maasi Beds with stromatopora marked with red star.

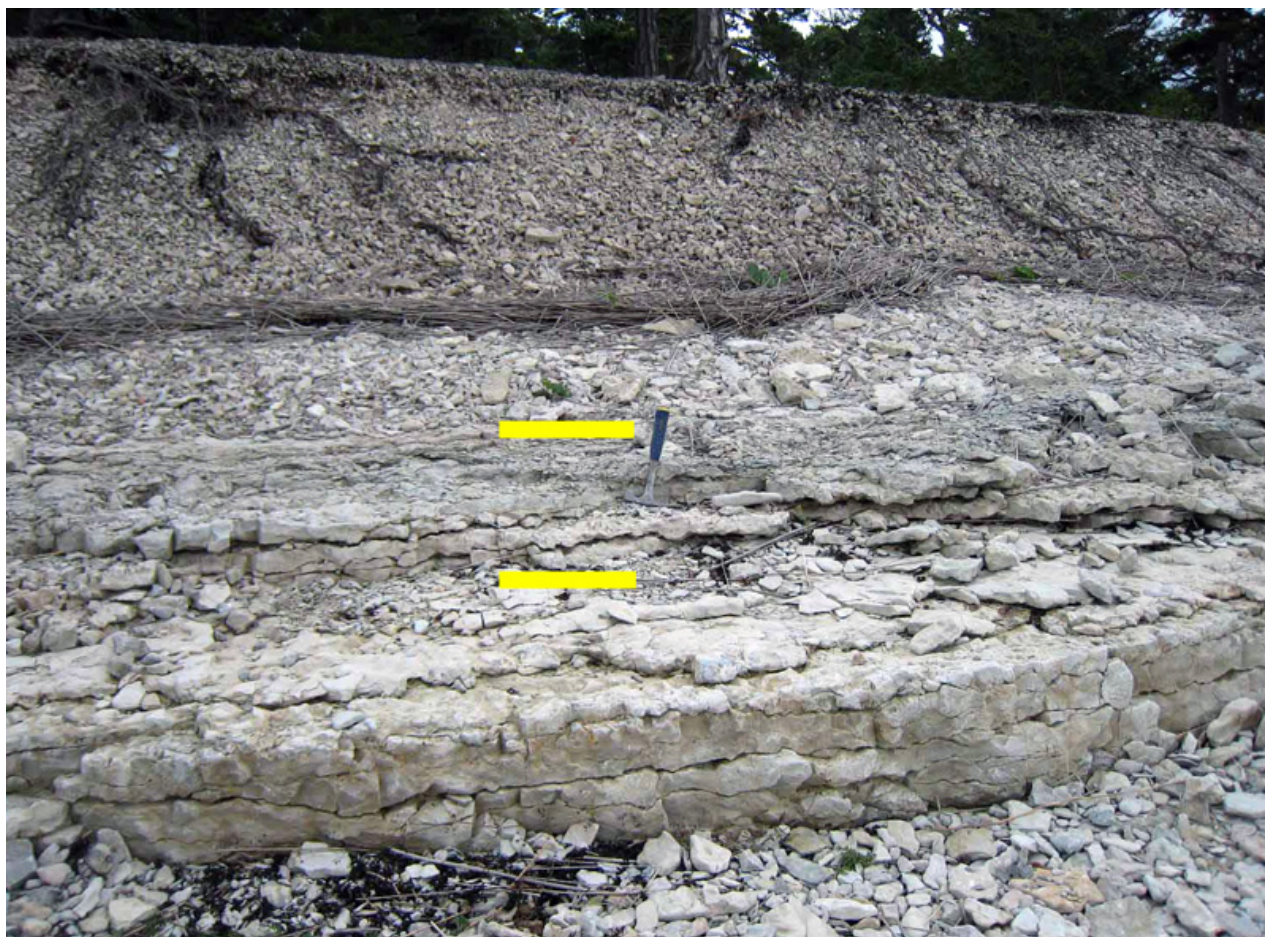


Figure 3: Abula cliff, Maasi Beds, Jaagarahu Formation. Stromatoporoid-rich horizon is indicated by yellow lines.

Taxon	Upper surface Number of specimens	Cryptic surface Number of specimens	Total number of specimens	Number of stromatoporoids with particular encruster
<i>Cornulites</i> aff. <i>stromatoporoides</i>	8 (13.3%)	-	8 (10.7%)	2
<i>Anticalyptraea calyptrata</i>	-	2 (13.3%)	2 (2.7%)	1
<i>Conchicolites</i> sp.	-	1 (6.7%)	1 (1.3%)	1
Microconchids	15 (25%)	-	15 (20%)	1
Sheet-like trepostome bryozoans	3 (5%)	4 (26.7%)	7 (9.3%)	5
Rugosans	17 (28.3%)	-	17 (22.7%)	6
Auloporids	5 (8.3%)	7 (46.6%)	12 (16%)	5
Favositids	6 (10%)	1 (6.7%)	7 (9.3%)	5
<i>Catenipora</i> sp.	2 (3.3%)	-	2 (2.7%)	2
Crinoid holdfast (discoidal)	4 (6.7%)	-	4 (5.3%)	3
Total	60	15	75	

Table 1: Faunal composition of the stromatoporoid sclerobiont association.

5. Results

Encrusting tentaculitoid tubeworms (*Cornulites* sp. aff. *C. stromatoporoides*, *Conchicolites* sp., microconchids), tabulate corals (*Aulopora* sp., *Catenipora* sp., favositids), rugose corals, sheet-like trepostome bryozoans, and discoidal crinoid holdfasts were found encrusting the stromatoporoids. *C.* aff. *stromatoporoides*, microconchids, *Catenipora* sp., rugosans, and crinoid holdfasts were attached only to the upper surface of stromatoporoids, while *Anticalyptrea calyptata* and *Conchicolites* sp. were found only on cryptic surfaces (those other than upward-facing) (Table 1; Fig. 4). Corals are numerically the most important encrusters (50.7 %, N=38) (Fig. 5), followed by tentaculitoid tubeworms (34.7 %, N=26) and bryozoans (9.3 %, N=7) (Fig. 6). Numerically least important are crinoids (5.3 %, N=4) (Fig. 7). There is a difference in taxonomic composition between the upper surface community and the cryptic community.

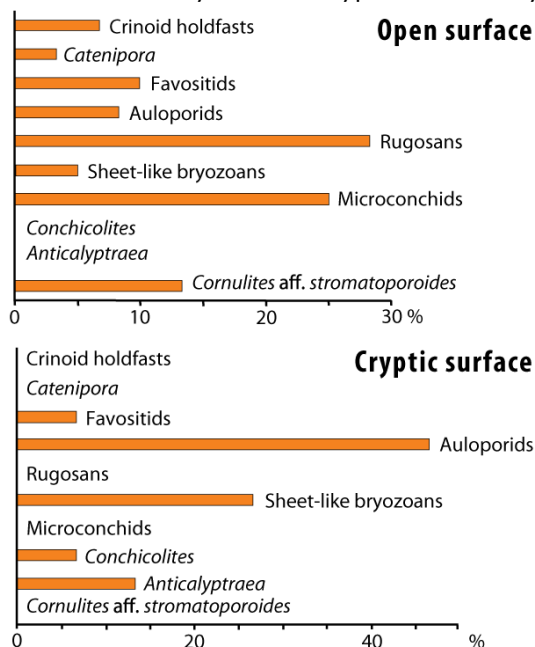


Figure 4: Diagrams showing abundance of sclerobionts on Abula cliff stromatoporoids.

The stromatoporoids in this study are sparsely covered by skeletal sclerobionts. Both upper (2.5 % encrusted) and cryptic surfaces (3.5 % encrusted) are similar in this respect (Table 2; Fig. 8). Colonial encrusters have the largest area of skeletal cover. In the upper surface community, tabulate corals dominate by area of skeletal cover (72.2 %), followed by bryozoans (10.1 %). The least important in the upper surface community by area of skeletal cover are crinoids (3.0 %). In the cryptic community, bryozoans have the largest area of skeletal cover (85.8 %) followed by tabulate corals (13 %) (Table 2). Skeletal overgrowth was not observed between the encrusters in either the open or cryptic communities.

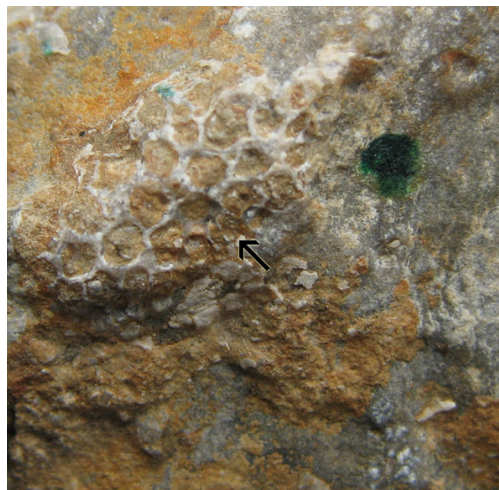


Figure 5: A favositid coral colony cemented to the cryptic surface of a stromatoporoid. Abula cliff, Saaremaa (Estonia), Maasi Beds, Jaagarahu Formation, late Sheinwoodian. TUG 1627-1.



Figure 6: Bryozoans on the cryptic surface of a high domical stromatoporoid. Abula cliff, Saaremaa (Estonia), Maasi Beds, Jaagarahu Formation, late Sheinwoodian. TUG 1627-2.



Figure 7: Discoidal crinoid holdfast on the upper surface of an extended domical stromatoporoid. Abula cliff, Saaremaa (Estonia), Maasi Beds, Jaagarahu Formation, late Sheinwoodian. Diameter of the disc 9 mm. TUG 1627-3.

Taxa	Upper surface area studied 2588 cm ²		Cryptic surface area studied 373 cm ²	
	Area covered cm ²	% of skeletal cover	Area covered cm ²	% of skeletal cover
<i>Cornulites aff. stromatoporoides</i>	4.2	6.5		
<i>Anticalyptraea calyptrata</i>			0.1	0.8
<i>Conchicolites</i> sp.			0.05	0.4
Microconchids	0.3	0.5		
Sheet-like trepostome bryozoans	6.5	10.1	11.2	85.8
Rugosans	4.9	7.6		
Auloporids	30.2	47	0.5	3.8
Favositids	8.1	12.6	1.2	9.2
<i>Catenipora</i> sp.	8.1	12.6		
Crinoid holdfast (discoïdal)	1.9	3.0		
Total area encrusted	64.2 cm ² (2.5 %)		13.05 cm ² (3.5%)	

Table 2: Skeletal cover of upper and cryptic surfaces of the stromatoporoids.

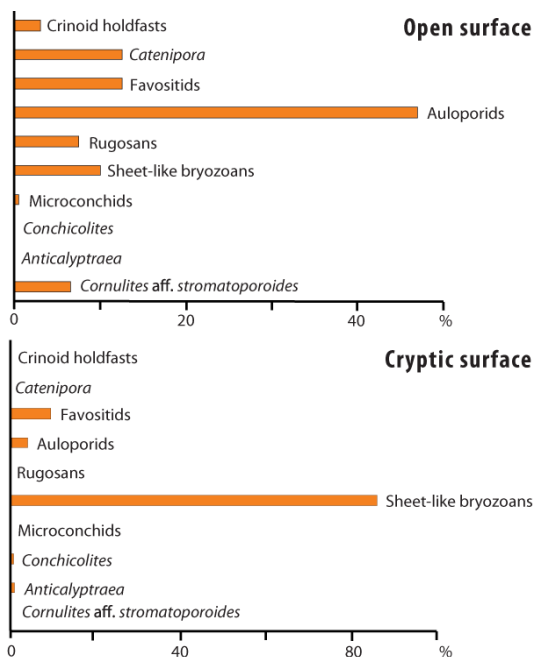


Figure 8: Percent of skeletal cover of upper and cryptic surfaces of the stromatoporoids by sclerobiont taxa.

Endobiotic rugosan symbionts were found in two stromatoporoids (9.1 %, N=22) (Figs. 9 - 10). Both stromatoporoids with endobiotic rugosans have a low domical shape. There are 10 to 20 endobiotic rugosans per 4 cm², counting more than 100 rugosans per stromatoporoid. The apertures of the rugosans are 0.5 to 3.0 mm wide and are usually situated at the level of the surrounding stromatoporoid surface. A few

rugosans show slightly elevated apertures (< 0.5 mm). The endobiotic rugosans are spread all over the stromatoporoid upper surface without any preference for certain regions.

Ten stromatoporoids of 22 studied (45.5 %) were bioeroded, mostly by *Trypanites* (Fig. 11). Among ten exposed borings, one resembled *Palaeosabella*. Maximum boring density was eight borings per 4 cm², but average density was one to five for the same area. *Palaeosabella* differs from cylindrical *Trypanites* by its flared distal end. *Palaeosabella-Trypanites* range from 0.30 to 4.00 mm in diameter and extend to a maximum depth of 1.0 cm below the substrate surface. Distribution of the borings is patchy on the stromatoporoid upper surfaces. In high domical and extended domical stromatoporoids, borings are often more numerous in the most elevated part of the substrate.

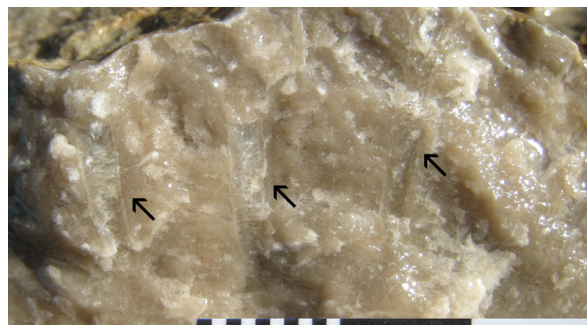


Figure 9: Symbiotic rugosan corals in a stromatoporoid in longitudinal section. Abula cliff, Saaremaa (Estonia), Maasi Beds, Jaagarahu Formation, late Sheinwoodian. TUG 1627-4.

6. Discussion

Both bioerosional trace fossils, *Trypanites* and *Palaeosabella*, had a global distribution in the Silurian (TAYLOR & WILSON, 2003). Among the Abula cliff stromatoporoids, *Trypanites* borings are most prominent, which is similar to the situation in the Silurian of Gotland (western Baltica) (NIELD, 1984) and Anticosti (North America) (TAPANILA *et al.*, 2004). TAPANILA *et al.* (2004) found for the Silurian of Anticosti Island that samples from the reef are bored least frequently (28 %). Among the sandy off-reef samples, they found 41 % bored substrates, and 50 % of muddy facies samples were bored. The boring frequency among Abula cliff stromatoporoids (45.5 %) is similar to both off-reef samples described by TAPANILA *et al.* (2004). However, the Abula cliff pelletal limestones can best be compared to the sandy off-reef facies by TAPANILA *et al.* (2004). Similarity in the boring frequency of large skeletal substrates between North America and Baltica in the early Silurian is not surprising considering their similar paleoclimates and paleogeographic proximity. The low bioerosion density for the Silurian (TAPANILA *et al.*, 2004) presumably indicates a relatively short exposure time of the Abula stromatoporoids to borers, or a relatively small number of borers in the community, or extensive occupation of the stromatoporoid surfaces by soft-bodied encrusters. Occurrence of more numerous borings in the most elevated parts of the substrate in high domical and extended domical stromatoporoids has several known analogues. The organisms that produced *Trypanites* borings preferentially drilled the high points on hard substrates in the Ordovician and Silurian, probably for better filter-feeding opportunities (BRETT & LIDDELL, 1978; BRETT & BROOKFIELD, 1984; NIELD, 1984; WILSON & PALMER, 1992).

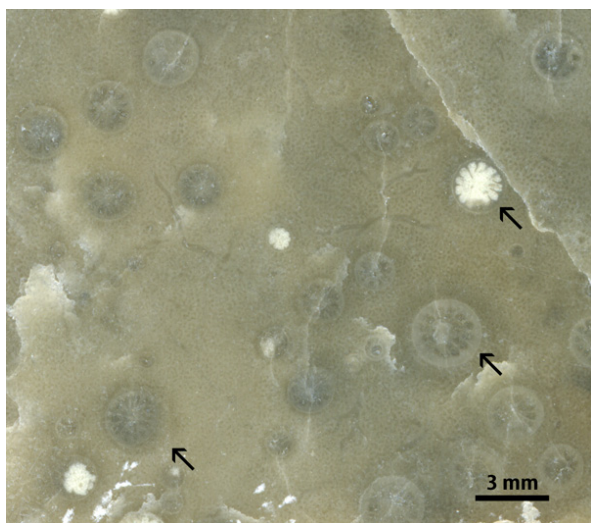


Figure 10: Symbiotic rugosan corals in a stromatoporoid in cross section. Abula cliff, Saaremaa (Estonia), Maasi Beds, Jaagarahu Formation, late Sheinwoodian.

The taxonomic composition of encrusters recorded on the Abula stromatoporoids is characteristic of the Silurian (Table 1; Fig. 4). However, there are some peculiarities among the Abula stromatoporoid encrusters considering the numerical abundance and relative area covered by skeletons. In general, typical Silurian encrusting faunas were similarly to those of the Ordovician dominated by bryozoans and echinoderms (TAYLOR & WILSON, 2003). In contrast, the Abula stromatoporoids show a very high number of corals (50.7%, N=38) and tentaculitoid tubeworms (34.7 %, N=26) in the association. Corals also have the largest area of skeletal cover in the upper surface community. Though numerically important, tentaculitoid tubeworms covered only small areas on the stromatoporoids as compared to tabulate corals and bryozoans. Echinoderms are both numerically and by area of skeletal cover the least important encrusters on the Abula stromatoporoids (Tables 1 - 2; Figs. 4 & 8). Microconchids are common encrusters in the Silurian. The presence of microconchids in large numbers only on a single stromatoporoid specimen could either be explained by an original patchy distribution (gregariousness) or by weak preservation potential compared to other encrusters with more massive skeletons. The dominance of corals over the bryozoans make the Abula stromatoporoid epibiont fauna different from the reef stromatoporoid fauna of the Ludlow of Gotland (SEGARS & LIDDELL, 1988) where bryozoans dominate the upper surface community.

There is a likely taxonomic polarity between the upper surface and cryptic communities in the Abula stromatoporoids. Most notable is a lack of rugose corals on the cryptic surfaces



Figure 11: *Trypanites* borings in the upper surface of a high domical stromatoporoid. Abula cliff, Saaremaa (Estonia), Maasi Beds, Jaagarahu Formation, late Sheinwoodian. TUG 1627-5.

(Table 1; Fig. 4). Similarly, a taxonomic polarity of epibionts has been reported from the reef stromatoporoids from the Ludlow of Gotland (SEGARS & LIDDELL, 1988). *Anticalyptraea* has previously been reported from cryptic surfaces under the late Silurian hardground from Ohesaare, Saaremaa (VINN & WILSON, 2010a). Cryptic surfaces in the Silurian were similar to the Ordovician, being mostly populated by the bryozoans, and cornulitids may also have been locally important (KERSHAW, 1980; TAYLOR & WILSON, 2003). Considering the small cryptic area studied, it is impossible to draw firm conclusions for the Abula stromatoporoids, but bryozoans were also found to be dominant encrusters by area of skeletal cover (85.8%) (Table 2; Fig. 8). In contrast to the Ohesaare hardground (Pridoli) and reef stromatoporoid from Gotland (SEGARS & LIDDELL, 1988), no clear difference in skeletal cover was observed in the Abula stromatoporoids between cryptic and upper surface communities.

LESCINSKY *et al.* (2002) found that modern bioerosion is higher at more productive sites in the ocean. They also found that more productive sites have higher encrustation rates. The Abula stromatoporoids have a relatively low encrustation density (SEGARS & LIDDELL, 1988; LEBOLD, 2000) combined with low bioerosion density for the Silurian (TAPANILA *et al.*, 2004). Thus, if these relations were valid in the late Silurian, the relatively low skeletal coverage of the stromatoporoids as compared to the other Ordovician to Devonian analogues (BRETT & LIDDELL, 1978) may be explained by low productivity (low nutrient levels) in the sea water (LESCINSKY *et al.*, 2002) or by a large number of soft-bodied organisms in the community that were not preserved.

VINN & WILSON (2010c) described a cornulitid (*Cornulites stromatoporoides*) and stromatoporoid association from the Abula cliff assemblages. They found symbiotic cornulitid endobionts in 77 % of studied stromatoporoids. In maximum there were three cornulitid specimens counted per stromatoporoid host. The symbiotic rugosan endobionts here are more rare compared to the cornulitids, occurring only in 9 % (N=22) of studied stromatoporoids. However, their total number in the population is not insignificant as there may be about a hundred rugosans per infested stromatoporoid host. Similar stromatoporoid-rugose associations are known from the Silurian of Gotland (MORI, 1969, 1970; KERSHAW, 1981, 1987) and the Devonian of Spain (SOTO & MENDEZ-BEDIA, 1985). These associations are interpreted as commensal relationships by these authors. Similarly to endobiotic rugosan symbionts from the Silurian of Gotland (KERSHAW, 1987), the Abula endobiotic rugosans have small apertural diameters (0.5-3.0 mm). Further studies should show whether this rugosan-coral symbiotic relationship occurred only between certain taxa. The

presence of both symbiotic cornulitid and rugosan endobionts indicates that symbiotic interactions were important among the Abula stromatoporoids. However, it is difficult to identify with fossil material whether this *syn vivo* association of stromatoporoids and rugosans was parasitic or mutualistic (ZAPALSKI, 2011).

7. Conclusions

1) The Sheinwoodian Abula sclerobiont assemblage differs from the analogous western Baltic (SEGARS & LIDDELL, 1988) and North American equivalents (LEBOLD, 2000) by dominance of corals in the assemblage.

2) Bioerosion on the Abula stromatoporoids was similar to the Early Silurian of North America (TAPANILA, 2004) and Gotland (NIELD, 1984), but the density of *Trypanites-Palaeosabella* boring was low in Abula as compared to the maximum in North America.

3) The Abula cliff stromatoporoids are rich in endobiotic symbionts, including both cornulitids and rugosans.

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