

## EPI- AND ENDOBIONTS ON THE LATE SILURIAN (EARLY PRIDOLI) STROMATOPOROIDS FROM SAAREMAA ISLAND, ESTONIA

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**Abstract:** A diverse sclerobiont community is described from the Kaugatuma Formation (lower Pridoli) of Saaremaa, Estonia. The stromatoporoid substrates studied here vary from low-domical to high-domical shapes. The community is numerically dominated by microconchids, which may have been characteristic of the sclerobiont fauna in the Pridoli of Baltica. *Palaeoconchus* aff. *tenuis*, *Anticalyptraea calyptrata*, *Aulopora* sp., sheet-like bryozoans, branching bryozoans, erect bryozoan holdfasts, rugosans, favositids, discoidal crinoid holdfasts, star-like crinoid holdfasts and sheet-like stromatoporoids encrust the domical stromatoporoids. Endobionts are represented by embedded, symbiotic rugosans, *Aulopora* sp., and two rare borings *Trypanites*.

**Key words:** Encrustation, sclerobionts, stromatoporoids, symbiosis, bioerosion, Pridoli, Baltica.

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### INTRODUCTION

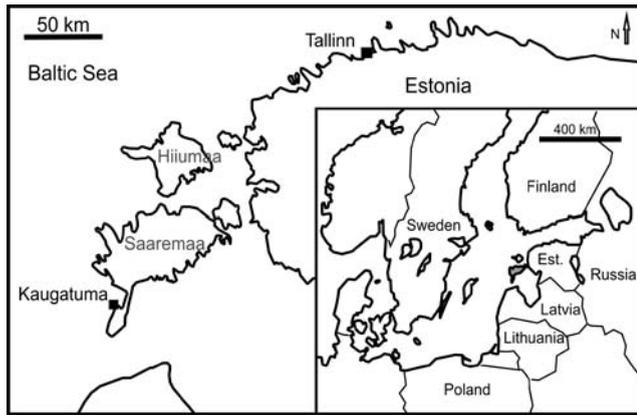
There is a considerable change in the composition of hard-substrate communities between the Silurian and Devonian. In general, Silurian encrusting faunas were dominated by bryozoans and echinoderms, similar to those of the Ordovician (Taylor and Wilson, 2003). In the Devonian, hard-substrate faunas were dominated by microconchids, hederelloids and tabulate corals, although bryozoans and echinoderms were still common (Sparks *et al.*, 1980; Bordeaux and Brett, 1990; Taylor and Wilson, 2003; Zapalski, 2005; Bose *et al.*, 2011; Rakociński, 2011; Zatoń and Krawczyński, 2011; Zatoń and Borszcz, in press). Encrusting faunas on Llandovery, Wenlock and Ludlow stromatoporoids have been studied in detail by several authors (e.g., Kershaw, 1980; Segars and Liddell, 1988; Lebold, 2000), but stromatoporoid encrusters from the Pridoli have not received such attention. Encrustation patterns and bioerosion are 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 and Wilson, 2010a, b). The only published record of Pridoli sclerobionts for Baltica is the description of a hardground fauna from the Ohesaare cliff, Saaremaa (Vinn and Wilson, 2010a). The encrusting faunas of the Pridoli are globally less studied than those of the rest of the Silurian, because of the smaller number of available localities.

The aims of this paper are: 1) to describe a hard-substrate association from the early Pridoli of the eastern Baltic for the first time; 2) to compare the early Pridoli hard-substrate association with the analogous associations in the Silurian of Baltica and beyond; and 3) to study both the upper surface and cryptic surface sclerobionts in order to find similarities and differences between these communities.

### GEOLOGICAL SETTING OF THE AREA

The Baltica palaeocontinent was located in equatorial latitudes during the late Silurian (Melchin *et al.*, 2004). The area of modern Estonia was covered by shallow epicontinental sea characterized by a wide range of tropical environments and diverse biotas (Hints *et al.*, 2008). On Saaremaa Island, the late Silurian succession is represented by carbonate rocks of shallow shelf origin. These rocks are rich in shelly faunas, usually of very good preservation. The most common fossil groups are brachiopods, corals, stromatoporoids, echinoderms, trilobites, ostracods, molluscs, fishes, eurypterids, bryozoans, conodonts, chitinozoans, scolecodonts, acritarchs, algae and stromatolites (see Kaljo, 1970; Hints *et al.*, 2008). The coastal cliffs are the best Pridoli exposures on Saaremaa.

The Kaugatuma cliff (2.5 m high) is on the western coast of the Sorve Peninsula, a few kilometers south from its northern neck and about 100 m from the coastline



**Fig. 1.** Location of Kaugatuma cliff (Äigu Beds, Kaugatuma Formation, early Pridoli) on Saaremaa Island, Estonia

(58°7'22"N, 22°11'36"E) (Fig. 1). The rocks belong to the middle part of the Äigu Beds of the Kaugatuma Formation (Fig. 2) (Hints *et al.*, 2008). Stromatoporoids were collected from the lowermost layer of greenish-grey, nodular, argillaceous wackestone, of open shelf origin (Hints *et al.*, 2008). Skeletal debris consists mostly of echinoderm and brachiopod fragments. Complete, large crinoid holdfasts and columnals occur in great numbers; *Enallocrinus* is especially common (Ausich *et al.*, 2012). There are also ostracods, trilobites, gastropods, bryozoans and fish fragments (Hints *et al.*, 2008).

## MATERIAL AND METHODS

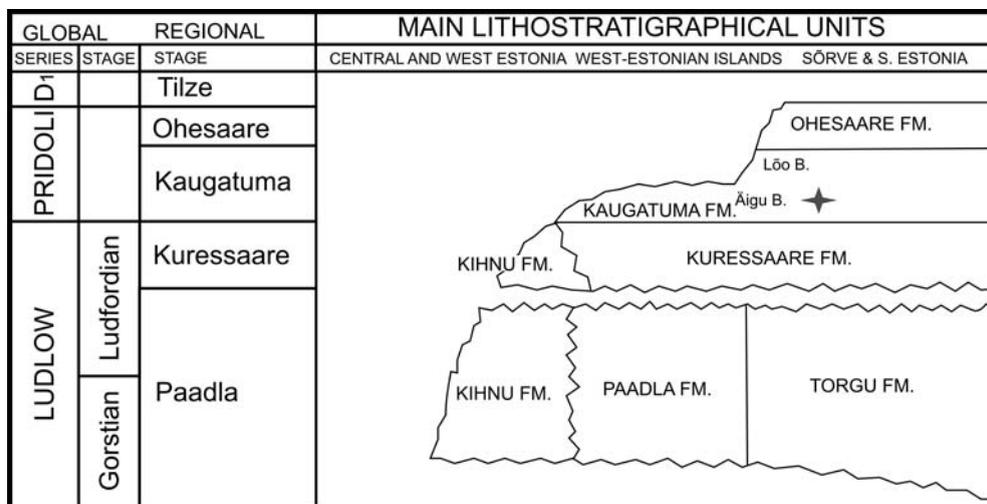
Eighteen stromatoporoids were collected from the Kaugatuma cliff (Saaremaa, Estonia) for a study of encrustation and bioerosion (Fig. 1). Five stromatoporoid species are known from the Äigu Beds: *Actinostromella vaiverensis*, *Densastroma astroites*, *Pachystylostroma* sp., *Parallelostroma typicum*, *P. minosi* (Kaljo, 1970). The stromatoporoids were removed from the shale matrix with a hammer and their orientation was indicated. Subsequently, the stro-

matoporoids were cleaned with brushes and water. The encrustation area was measured, using a centimetre grid on a transparent, plastic film. Only areas clean of matrix were counted. The area encrusted by fossils was measured, using a millimetre grid on a transparent, plastic film. For the branching colonial organisms, such as auloporids, the encrustation area was counted as the area within the perimeter of the encruster. The encrusting fossils and possible signs of bioerosion were studied using a binocular microscope. All figured specimens are deposited in the Museum of Natural History (Museum of Geology), University of Tartu (TUG), Estonia.

## RESULTS

Sixteen of the 18 stromatoporoids were preserved in the life position, while two were overturned. The stromatoporoid shapes are low- to high-domical (*sensu* Kershaw, 1981, 1984; Kershaw *et al.*, 2006). Both upper and cryptic surfaces were used by sclerobionts. The stromatoporoid sclerobionts on the upper surfaces are numerically (i.e., by number of specimens in the community) dominated by *Palaeoconchus* aff. *tenuis* (Microconchida) (51.4%, N = 43) (Fig. 3), bryozoans (20.3%, N = 17) (Fig. 4) and corals (14.4%, N = 12) (Fig. 5). The minor groups include root- and star-like crinoid holdfasts, *Anticalyptraea calyptrata* (Tentaculitida), and sheet-like stromatoporoids (Fig. 6, Table 1). The cryptic surfaces yielded only sheet-like (N = 2) and branching bryozoans (N = 1) (Table 1).

6.2% of stromatoporoids upper surfaces (total 892 cm<sup>2</sup>) and 9.5% of the cryptic surfaces (total 79 cm<sup>2</sup>) are covered by sclerobionts (Table 2). The largest area on the upper surfaces is covered by sheet-like stromatoporoids (54% of total skeletal cover), followed by bryozoans (24.5% of total skeletal cover) and corals (18.9% of total skeletal cover) (Fig. 7). Minor groups by skeletal cover include *Palaeoconchus* aff. *tenuis* (1.4%), crinoid holdfasts (0.6%) and *Anticalyptraea calyptrata* (0.3%) (Fig. 7, Table 2). Endobiotic rugosans (N = 2) occurred at the upper surface of a single stromato-



**Fig. 2.** Stratigraphy of Silurian of Estonia (after Hints *et al.*, 2008). Location of Äigu Beds, with stromatoporoids marked by a star



**Fig. 3.** *Palaeoconchus* aff. *tenuis* from Kaugatuma cliff, Saaremaa, Äigu Beds, Pridoli. TUG 1628-1. Scale bar is in millimeters



**Fig. 4.** Sheet-like bryozoan from Kaugatuma cliff, Saaremaa, Äigu Beds, Pridoli. TUG 1628-2. Scale bar is in millimeters

**Table 1**

Faunal composition of stromatoporoid-sclerobiont association

taxa	Upper surface		Cryptic surface	
	No. of specimens	No. of substrates (total N = 18)	No. of specimens	No. of substrates (total N = 3)
<i>Palaeoconchus</i> aff. <i>tenuis</i>	43 (51.2%)	8		
<i>Anticalyptraea calyptrata</i>	3 (3.6%)	2		
Sheet-like bryozoans	15 (17.9%)	9	2 (66.7%)	1
Erect bryozoans holdfasts	2 (2.4%)	2		
Branching bryozoans			1 (33.3%)	1
<i>Aulopora</i> sp.	4 (4.8%)	3		
Favositids	2 (2.4%)	2		
Rugosans (epibiont)	4 (4.8%)	3		
Rugosans (endobiont)	2 (2.4%)	1		
Root-like crinoid holdfasts	5 (5.9%)	3		
Star-like crinoid holdfasts	1 (1.2%)	1		
Stromatoporoids	1 (1.2%)	1		
borings <i>Trypanites</i>	2 (2.4%)	2		

poroid. They grew almost perpendicular to the surface of the stromatoporoid. Their apertures (4.9 to 8.0 mm in diameter) are slightly elevated above the stromatoporoid surface (Fig. 8). A single *Aulopora* sp. encrusted a sheet-like stromatoporoid; it grew endobiotically in the stromatoporoid, with its upward-turned aperture free on the stromatopo-



**Fig. 5.** *Aulopora* sp. from Kaugatuma cliff, Saaremaa, Äigu Beds, Pridoli. TUG 1628-3. Scale bar is in millimeters

roid's surface. Two microconchids have overgrown a sheet-like bryozoan. Only two stromatoporoid specimens showed a single boring, possibly belonging to *Trypanites*.

## DISCUSSION

The Kaugatuma stromatoporoids inhabited a soft bottom, on a shallow shelf. They presumably lived in the zone between the fair-weather and storm wavebases, as indicated by the common occurrence of overturned stromatoporoids and considerable, shelly lag debris.

Table 2

## Skeletal cover of upper and cryptic surfaces of stromatoporoids

Taxa	Upper surface (892 cm <sup>2</sup> )			Cryptic surface (79 cm <sup>2</sup> )		
	Encr. area (cm <sup>2</sup> )	% of encrusted area	% of substrate area	Encr. area (cm <sup>2</sup> )	% of encrusted area	% of substrate area
<i>Palaeoconchus</i> aff. <i>tenuis</i>	0.80	1.4	0.09			
<i>Anticalyptraea calyptrata</i>	0.17	0.3	0.02			
Sheet-like bryozoan	12.10	21.8	1.36	7.0	93.3	8.86
Erect bryozoan holdfast	1.50	2.7	0.17			
Branching bryozoan				0.5	6.7	0.63
<i>Aulopora</i> sp.	6.17	11.1	0.69			
Favositids	0.70	1.3	0.08			
Rugosans (epibiont)	2.85	5.1	0.32			
Rugosans (endobiont)	0.75	1.4	0.08			
Root-like crinoid holdfasts	0.30	0.5	0.03			
Star-like crinoid holdfasts	0.08	0.1	0.01			
Stromatoporoids	30.00	54.1	3.36			
Total	55.42 (6.2% of upper surface)			7.50 (9.5% of cryptic surface)		

The diversity of the higher taxonomic groups of Kaugatuma sclerobiont fauna is comparable with several, other examples of Silurian hard-substrate associations (Brett and Liddell, 1978; Segars and Liddell, 1988; Lebold, 2000). The faunal composition of the Kaugatuma stromatoporoids is characteristic of the Silurian. The high number of bryozoans (20.3% upper-surface community) in the community is especially typical for the Silurian. However, the numerical dominance of microconchids (51% of the upper-surface community) is striking (Fig. 6). In this aspect, the Kaugatuma sclerobiont association is similar to the Ohessaare hardground fauna from the late Pridoli of Saaremaa. However, in Ohessaare the microconchids (87.8 % of sclerobiont specimens in the upper-surface community) are even more common than in Kaugatuma. Thus, the high numerical abundance of microconchids may have been characteristic of Pridoli hard-substrate communities on Baltica.

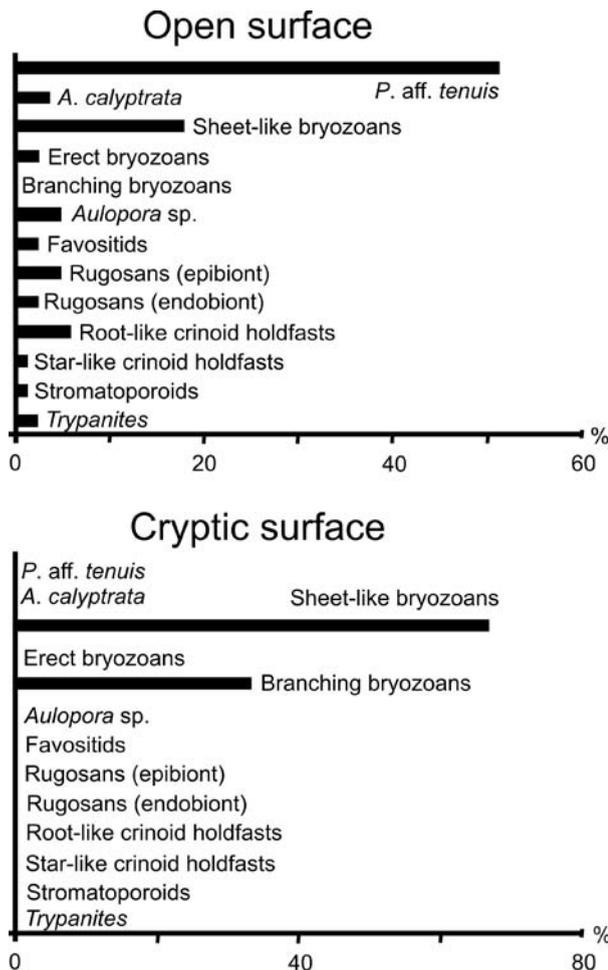
Echinoderms are usually a very important component of Silurian hardground communities (Halleck, 1973; Franzén, 1977; Keeling and Kershaw, 1994). The Kaugatuma stromatoporoid sclerobiont community differs from several other earlier Silurian communities by a low number of echinoderms (Fig. 6). The scarcity of echinoderms among sclerobionts here is peculiar because the bioclasts in the surrounding rock matrix mostly belong to crinoids. However, these rock-forming crinoid taxa were soft-bottom dwellers (Ausich *et al.*, 2012). This is supported by the large number of soft-bottom crinoid holdfasts found in the life position, in the same layer with the stromatoporoids studied.

The presence of only bryozoans on the cryptic surfaces could either be explained by taxonomic polarity between the upper-surface and cryptic-surface communities, or by a sampling bias, since the upper-surface area studied was 11 times larger than that of the cryptic surface (Table 2). The dominance of bryozoans on cryptic surfaces is also characteristic for a late Sheinwoodian (Wenlock) sclerobiont association from Saaremaa (Vinn and Wilson, 2012). In addition,

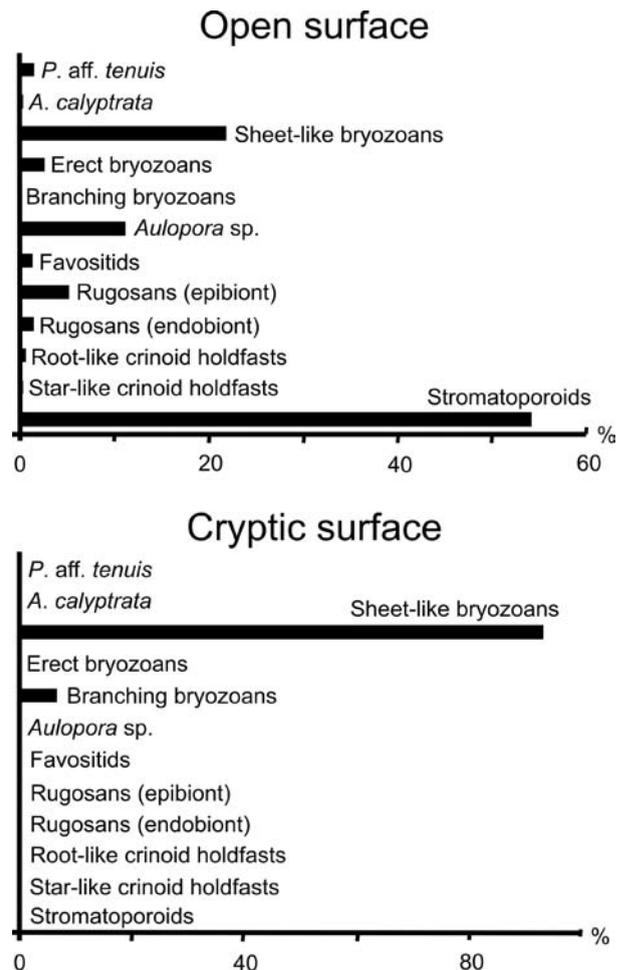
cryptic surfaces of a late Pridoli hardground from Saaremaa are similarly dominated by bryozoans (Vinn and Wilson, 2010a). However, the open surface sclerobiont associations from Wenlock (Vinn and Wilson, 2012) and late Pridoli (Vinn and Wilson, 2010a) of Saaremaa were dominated by corals and bryozoans respectively. Thus, in spite of differences between the upper surface communities of these Baltic Silurian sclerobiont associations, it is possible that dominance by bryozoans may represent a general characteristic of cryptic sclerobiont communities of the Silurian of Baltica.

The sheet-like stromatoporoids are most important in this Kaugatuma fauna in terms of area of encrustation on the upper-surface community (54.1% of the encrustation area), which differs from that of Ohessaare hardground fauna, whereas the sheet-like bryozoans form 63.3% skeletal cover on the upper surface and 92.3% on the cryptic surface (Fig. 7, Table 2). However, bryozoans are also important by area of encrustation on the Kaugatuma stromatoporoids (24.5% of skeletal cover). In contrast to the Ohessaare hardground fauna, microconchids are unimportant by the area of encrustation on Kaugatuma stromatoporoids. Another difference between the Kaugatuma stromatoporoid sclerobiont fauna and the Ohessaare hardground fauna is the presence of encrusting corals in the former. Kaugatuma stromatoporoids exhibit moderate, total-encrusting coverage as compared to the other Ordovician to Devonian analogues from North America and Baltica (Brett and Liddell, 1978; Segars and Liddell, 1988; Lebold, 2000).

Overgrowth was not common in the Kaugatuma sclerobiont community, indicating low competition for space between the sclerobionts. In most cases, it is likely that the stromatoporoids were encrusted *post mortem* because sclerobionts have not disturbed their growth. However, rare embedded symbiotic rugosan endobionts (Fig. 8) represent a *syn vivo* association occurring only in a single stromatoporoid (total N = 18). Similar *syn vivo* stromatoporoid-rugose



**Fig. 6.** Faunal composition of stromatoporoid-sclerobiont association from Kaugatuma cliff, Saaremaa, Äigu Beds, Pridoli



**Fig. 7.** Encrustation area of upper and cryptic surfaces of stromatoporoids by sclerobiont taxa from Kaugatuma cliff, Saaremaa, Äigu Beds, Pridoli

associations are known from the Sheinwoodian of Saaremaa (Vinn and Wilson, 2012), the Silurian of Gotland (Mori, 1969, 1970; Kershaw, 1981, 1987) and the Devonian of Spain (Soto and Méndez-Bedia, 1985). The exact nature of these symbiotic associations is difficult to interpret from fossil material, leaving anything between parasitism and mutualism possible. An *Aulopora* sp. tube, embedded within a stromatoporoid, with a free aperture on the stromatoporoid surface, represents a symbiotic association of some kind.

The virtual lack of bioerosion on the Kaugatuma stromatoporoids is a striking characteristic of this hard-substrate association. The extremely low rate of bioerosion in Kaugatuma contrasts with the situation on the Ohesaare hardground (late Pridoli). Bioerosion is dependent on the time of exposure and also on the sedimentary environment. Palaeozoic bioerosion was generally higher in muddy bottom environments and lower in reef and sand facies (Tapanila *et al.*, 2004). The Kaugatuma stromatoporoids grew on a muddy bottom with a high amount of carbonate debris (mostly crinoidal). Thus, one would expect to find moderate to high bioerosion on the Kaugatuma stromatoporoids on the basis of the sedimentary environment. If there were very short exposure times, one also would expect a low encrustation rate. However, the moderate encrustation rate of the Kaugatuma stromatoporoids indicates that the exposure



**Fig. 8.** Endobiotic rugosan in stromatoporoid from Kaugatuma cliff, Saaremaa, Äigu Beds, Pridoli. TUG 1628-4. Scale bar is in millimeters

time of stromatoporoids was not short. Lescinsky *et al.* (2002) found that in modern oceans bioerosion is higher at the more productive sites. They also found that the higher encrustation rates are associated with more productive sites.

Thus, if the moderate encrustation rate for the Kaugatuma stromatoporoids is explained by moderate productivity, then the bioerosion rate would also be similarly moderate. The moderate encrustation rate, combined with the very low bioerosion rate of the Kaugatuma stromatoporoids, would be better explained by a low abundance of boring organisms in the Kaugatuma environment, combined with a relatively long exposure time of the substrate, indicating rather low productivity. However, the Lescinsky *et al.* (2002) productivity hypothesis was based on limited material from the modern ocean, so the Kaugatuma stromatoporoid bioerosion and encrustation patterns alternatively might be explained by factors, other than productivity, such as exposure time and sediment cover.

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