RUGOSAN EPIBIONTS ON VERTICAL STEMS FROM THE LUDLOW AND PRIDOLI OF SAAREMAA, ESTONIA (BALTICA)

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ABSTRACT: The earliest known rugosans attached syn vivio to vertical stems occur in the late Silurian of Saaremaa, Estonia. These rugosans display vertical to subvertical attachment scars and are more common in the Ludfordian than in the Pridoli. The unknown hosts provided a higher tier for the feeding, making the association beneficial for the rugosans. Several rugosans were themselves syn vivio encrusted by bryozoans and unknown endobiotic tubicolous organisms, possibly cornulitids. Estonian rugosans appear to have been host size selective and preferred substrates of certain size. Silurian symbiotic rugosans are more often endobionts in stromatoporoids than epibionts on the vertical stems.

INTRODUCTION

Syn vivio interactions between different extinct organisms are seldom unequivocally identifiable in fossil material. The best studied examples of syn vivio interactions comprise various predatory borings (Huntley and Kowalewski 2007) and endobionts bioimmured (i.e., embedded) by the living tissues of host organisms (see Taylor 1990 for a review). Although the earliest microscopic invertebrate symbionts are known from the Cambrian (Bassett et al. 2004), macroscopic invertebrate symbionts are not common in the fossil record until the Late Ordovician, mostly as bioclaustrations (Palmer and Wilson 1988; Tapanila 2005). Rugosans have often been found bioimmured by living tissues of stromatoporoids or corals (Vinn and Wilson 2012; Vinn and Mõtus 2014; Vinn et al. 2015), but although the fauna of rugose corals from the Silurian of Estonia is relatively well studied (Kaljo 1958), there is no published record of syn vivio rugosan epibionts from the Silurian of Estonia and relatively little is known about symbioses involving Silurian rugosans in general (Kershaw 1987; Vinn and Wilson 2012; Vinn and Mõtus 2014; Vinn et al. 2015).

The aims of this paper are to describe the earliest known rugosan symbionts on vertical stems of unknown organisms from the Silurian of Baltica and to discuss the paleoecology of this rugosan-host association.

GEOLOGICAL BACKGROUND

During the Silurian, the area of present-day Estonia (Fig. 1) was part of the Baltica paleocontinent, which was located in equatorial latitudes (Melchin et al. 2004). The middle and western part of modern Estonia, including Saaremaa Island, was covered by the epicontinental Baltic paleobasin. This basin was characterized by diverse tropical faunas and extensive shelf environments (Hints 2008; Raukas and Teedumäe 1997). The sedimentary facies of the Silurian of Estonia are divided laterally into five facies belts along a reconstructed bathymetric profile (Nestor and Einasto 1977). The first three environments (i.e., tidal flat/lagoonal, shoal, and open shelf) comprised a carbonate platform, whereas the latter two (i.e., basin slope and basin depression) formed at greater water depths characterized by fine siliciclastic deposits. The tidal flat/lagoonal, shoal, open shelf, and basin slope sediments are represented in outcrops on Saaremaa Island, but rugosans occur only in rocks of shoal, open shelf, and basin slope origin. The Ludfordian fauna of studied localities includes rugosans, tabulates, stromatoporoids, trilobites, ostracodes, fish, conodonts, nautiloids and microconchids. The rugosans are most abundant among the Ludfordian fauna. The Pridoli fauna of studied localities includes rugosans, tabulates, stromatoporoids, brachiopods, crinoids, bryozoans, trilobites, ostracodes, conodonts, and microconchids.

MATERIAL AND METHODS

A collection of rugosans (N=59) from the late Silurian of Saaremaa (Figs. 1, 2) contains specimens with circular attachment scars. Fifty six (56) rugosans originate from four Ludfordian (Kuressaare Regional Stage) localities: Ipla (N=13), Kuressaare (N=10), Muratsi (N=30) and Kärsa (N=3). The remaining three rugosans come from the lower Pridoli (Kaugatuma Regional Stage) localities: Väike Rootsi (N=1) and Kaugatuma cliff (N=2). Both Ludfordian and Pridoli rugosans were from open shelf argillicose limestones and marls. The rugosans with attachment scars were photographed using a Nikon D7000 digital camera. The diameter and length of specimens as well as the diameter of attachment scars were measured from calibrated photographs. Thirteen rugosans were thin sectioned and identified to genus level. All epibionts cemented to the rugosans were counted and identified to the finest taxonomic level possible. The studied specimens are deposited at the Institute of Geology, Tallinn University of Technology (GIT).

RESULTS

Fifty nine (59) rugosans of the total examined (391) have a single lateral scar with vertical to subvertical orientation (Figs. 3A–3F, 4A, 4B, 5A–5D); in one case, two merged rugosans have a common scar. Scars are sometimes complete cylindrical shafts through the lateral part of the corrallum, but more commonly they are semicylindrical furrows (Neumann 1968). Cylindrical shafts and semicylindrical furrows are not morphologically variable, have a smooth surface, and do not vary much in size (Fig. 6); they are more common in smaller than larger specimens (Figs. 7, 8). Scars occur in four genera: Entelophyllum Wedekind 1927, Hedstroemophyllum Wedekind 1927, Kyphophyllum Wedekind 1927, and Pilophyllum Wedekind 1927, but are most numerous in Entelophyllum (seven of 13 identified) (Figs. 3D, 4B). Cylindrical shafts and semicylindrical furrows are more common in the Ludfordian (56 of total 202 rugosans) than
Fig. 1.—Locality map. Key: 1, Kaugatuma cliff; 2, Kuressaare; 3, Muratsi; 4, Ilpla; 5, Vääke-Rootsi; and 6, Kärta.

Fig. 2.—Stratigraphic distribution of rugosans with cylindrical attachment scars in the Silurian of Estonia.
in the Pridoli (three of total 189 rugosans). The diversity of rugosans in both the Kuresaare (Ludfordian) and Kaugatuma (Pridoli) are the same and the same genera display scars in both units. Eleven of the rugosans with attachment scars have epibiont encrusters. Eight specimens are encrusted by microconchids (Fig. 3E, 3F) which are the most numerous encrusters of the rugosans (N=518), with up to five microconchids per single coral. Three rugosans are encrusted with bryozoans and Anticalyptraea sp., with a maximum of two Anticalyptraea sp. on a single specimen. Microconchids and Anticalyptraea sp. are observed occurring together on a single rugosan, as are microconchids and bryozoans. A single sheet-like bryozoan follows the contour of a rugosan attachment scar (Fig. 3E). In one specimen an encrusting trepostome bryozoan was overgrown by a microconchid. A single rugosan has

![Fig. 3.](image-url)
possible cornulitids embedded in the wall near the attachment scar (Fig. 3C); a single microconchid and a bryozoan are cemented inside the attachment scar of this specimen.

**DISCUSSION**

*Nature of the Substrate*

The semicircular to circular morphology of most attachment scars is consistent with the morphology of crinoid stems, which were abundant in the late Silurian of Saaremaa (Ausich et al. 2012, 2015). Symbiotic rugosans attached to crinoid stems are known from the Devonian (Berkowski and Klug 2011; Bohatý et al. 2012). However, crinoid stems and rugosans are calcitic, and taphonomically, both should have behaved very similarly. The lack of crinoid remains indicates that most likely crinoid stems were not substrates for the rugosans. Epibionts on crinoid stems commonly caused malformations of columnals and epibionts are often partially embedded within the crinoid skeleton (Franzén 1974). This did not happen with the studied rugosans. In addition, some attachment scars have an oval cross section, which is not characteristic of a crinoid host. Thus, alternative explanations are required.

The absence of an organism to which the coral was attached indicates that it was either a skeleton comprised of aragonite or organic stems that did not fossilize. Organic stems occur in algae which were common in shallow seas (i.e., photic zone) during the Silurian, although no fossilized stems of algae are known from the Ludfordian and Pridoli of Saaremaa. Sando (1977) and Ausich and Smith (1982) reported rugosans with the juvenile portion of the coral being planispirally coiled and hollow. They inferred attachment to planktonic algae, thus a pseudoplanktonic lifestyle. Ausich and Smith (1982) also reported a different rugosan in which the juvenile portion of the skeleton was coiled around a fenestrate bryozoan branch.

*Dimensions of Scars*

The dimensions of attachment scars have little variability (Fig. 6) indicating that rugosans were attached to substrates of certain sizes. The attachment presumably occurred in the early growth stage of the rugosan, based on the presence of attachment scars in the beginning of corallum. In the initial phase of attachment, rugosans were attached to one side of the host stem and later grew around it. Alternatively, only substrates with limited sizes were available for rugosans. However, this is less likely as most biological vertical stems have growth stages with different diameters. It is possible that, stems with a smaller diameter (i.e., possible juveniles) also occurred in the community, but rugosans may have been size selective and preferred hosts of certain size. It is likely that possible thinner stems were not strong enough to carry the adult rugosans. Thus, larva of rugosans may have been able to detect the size of a potential host if thinner stems were present in the community.

*Dimensions of Rugosans*

It is possible that the lack of smallest rugosans (diameter < 6 mm) in the collection represents collecting bias. Early rugosan growth stages do not have morphology characteristic of an attachment scar (i.e., small flat area instead of a cylindrical shaft or semi-cylindrical furrow). The abundance of small rugosans with scars indicates that most of the specimens did not achieve large size. It is impossible to detect on the fossil material whether most of the specimens stopped growing further after achieving the optimal size for the life on the stems or if they died before achieving large size. Life on relatively thin stems sets limits on the maximal size of the rugosans, as very large endobionts would have gravitationally and presumably also hydrodynamically destabilized the host organism. Larger unattached rugosan specimens are known from the studied localities.

*Ecology of the Rugosans with the Scars*

Rugosans as a whole grew aperture upward (Hill 1981), therefore, the fact that the observed attachment scars are oriented perpendicular to subperpendicular to the aperture of the corals indicates that they were growing on vertical stems. (If the studied rugosans were attached to stems lying on the seafloor, the attachment scars would have formed parallel or subparallel to the aperture of rugosans.) The vertical stems likely belonged to living organisms.
FIG. 5.—A) *Entelophyllum* sp. with semicylindrical attachment scar in transverse section, from the Kuressaare Formation (Ludfordian), Muratsi, Saaremaa (GIT 713-30). B) *Entelophyllum* sp. with semicylindrical attachment scar in transverse section, from the Kuressaare Formation (Ludfordian), Muratsi, Saaremaa (GIT 713-29). C) Longitudinal section through rugosan with cylindrical shaft from the Kuressaare Formation (Ludfordian), Kuressaare, Saaremaa (GIT 713-20). D) *Pilophyllum* sp. longitudinal section through cylindrical shaft, from the Kuressaare Formation (Ludfordian), Muratsi, Saaremaa (GIT 713-40). Abbreviation: sc = attachment scar.

FIG. 6.—Distribution of attachment scar diameter.

FIG. 7.—Distribution of rugosan diameter.
Thus, the rugosans presumably had a *syn vivo* association with an organism with thin vertical stems. Whether the relationship was mutualistic, commensal or parasitic, the hosts benefited rugosans by providing a higher tier for feeding. The influence of the rugosans on their hosts is difficult to estimate, but a large number of rugosan epibionts on a single host probably would have destabilized the stems.

**Encrusters**

In one of the rugosan specimens, a single sheet-like bryozoan follows the contour of the rugosan attachment scar. Such growth indicates *syn vivo* encrustation. There are also tubicolous organisms embedded in the skeleton of one rugosan specimen. These *syn vivo* encrusting organisms belong to suspension feeders, which similar to their rugosan hosts, presumably also benefited from a higher tier for feeding provided by stems of the unknown organism. The other cases of encrustation probably represent both *syn vivo* and post-mortem encrustation. The microconchids and bryozooans inside the attachment scars represent encrustation after the separation of rugosans from their hosts and certainly did not belong to the described *syn vivo* association.

**Other Cases of Symbiosis Involving Silurian Rugosans**

Silurian rugosans formed symbiotic associations most commonly with stromatoporoids (Kershaw 1987; Vinn and Wilson 2012; Vinn and Mõtus 2014; Vinn et al. 2015). In these associations, rugosan endobionts were partially embedded within the host stromatoporoid skeleton. Endobiotic rugosans benefited from a stable substrate and protection against predators provided by the stromatoporoid skeleton. Rugosans have also been reported to form symbiotic associations with tabulate corals and crinoids. *Streptelasma* sp. occurs as an endobiont in the tabulate coral *Paleofavosites prolificus* in the Llandovery of Ohio (Sorauf and Kissling 2012). Endobiotic rugosans in tabulates similarly benefitted from a stable substrate and protection against predators. Living crinoid stems were encrusted by rugose corals in the Devonian of Morocco and Germany (Berkowski and Klug 2011; Bohaty et al. 2012). Crinoid hosts provided rugosans with a higher tier for feeding and made this symbiotic association beneficial for the rugosans. It seems that Silurian endobionts are more common than epibionts among the symbiotic rugosans. It is likely that rugosans more commonly needed additional protection via partial embedding within a host’s skeleton than a higher tier for feeding provided by living on stems.

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**REFERENCES**


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