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Earliest known rugosan-stromatoporoid symbiosis from the Llandovery of Estonia (Baltica)

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ABSTRACT

A stromatoporoid, *Petridiostroma simplex*, from the Llandovery of Estonia was infested by numerous rugosan endobiotic symbionts of the species *Petrozium losseni* (Dybowski, 1874). These rugosans presumably benefitted from the stable growth substrate provided by the stromatoporoid. The effects of the endobiotic rugosans on the stromatoporoid are not known, but it is possible that they reduced its feeding efficiency. The relatively thick skeletons of the rugosans could indicate a short evolutionary history for this symbiotic association. The elevation of the symbionts' apertures above the host stromatoporoid may have been to achieve a feeding advantage if the host stromatoporoid and rugosans competed for nutrients. This record and others suggest that complex ecological interactions such as symbiosis were common among the macroscopic invertebrates of the Ordovician–Silurian mass extinction recovery fauna.

1. Introduction

Endobiotic rugosans often had symbiotic relationships with stromatoporoids, and such interactions are especially common in the Silurian of Baltica (Kershaw, 1987; Vinn and Wilson, 2012; Vinn and Mõtus, 2014a). In addition to rugosans, the tabulate coral *Syringopora* is also a common endobiotic symbiont in Silurian stromatoporoids of Baltica (Kershaw, 1987; Vinn et al., 2014). The Silurian of Baltica has a relatively rich record of symbiotic interactions between various other macroscopic invertebrates (Kershaw, 1987; Vinn and Wilson, 2010, 2012; Vinn and Mõtus, 2014a,b). Vinn and Wilson (2010) recently described a symbiotic cornulitid and stromatoporoid association from the late Sheinwoodian of Estonia in which they recorded large numbers of stromatoporoids (77% of the preserved population) as infested by cornulitid endobionts.

Syn vivo interactions between different organisms are rather rare in the fossil record. The best studied examples comprise various predatory borings. Similarly important are the endobionts embedded (*i.e.* bioimmured) by the living tissues of host organisms (see Taylor, 1990 for a review). Microscopic invertebrate symbionts are known from the Cambrian (Bassett et al., 2004). Macroscopic endobiotic invertebrate symbionts appeared later in the Late Ordovician (see Tapanila, 2005 for a summary). Palaeozoic rugosans were sometimes bioimmured by living tissues of stromatoporoids or corals; they differ from bioclaustrations (Palmer and Wilson, 1988) by having their own skeleton. Endobiotic lingulid brachiopod symbionts in stromatoporoids appeared earlier (*i.e.* Llandovery) than rugosan symbionts (*i.e.* Wenlock until this work) and are the earliest known skeletal endobiotic symbionts of stromatoporoids (Tapanila, 2005). Lingulids often occupied empty borings in the stromatoporoids, and in some cases these borings have been overgrown indicating *syn vivo* interaction (Stewart et al., 2010).

The fauna of stromatoporoids and rugose corals of the Silurian of Estonia is relatively well studied (Nestor, 1964, 1966; Kaljo, 1958). The symbiotic interactions between different animal groups must obviously be after their first evolutionary appearance. In order to better understand the evolution of symbiosis it is important know the times these interactions appeared.

The aim of this paper is: 1) to describe the earliest known rugosan symbionts in stromatoporoids of the Silurian of Baltica; and 2) to discuss the palaeoecology of this rugosan-stromatoporoid association.

2. Geological background and localities

During the Silurian the Baltica continent was located in equatorial latitudes and drifting northwards (Melchin et al., 2004). The area of modern Estonia was mostly covered by the shallow epicontinental

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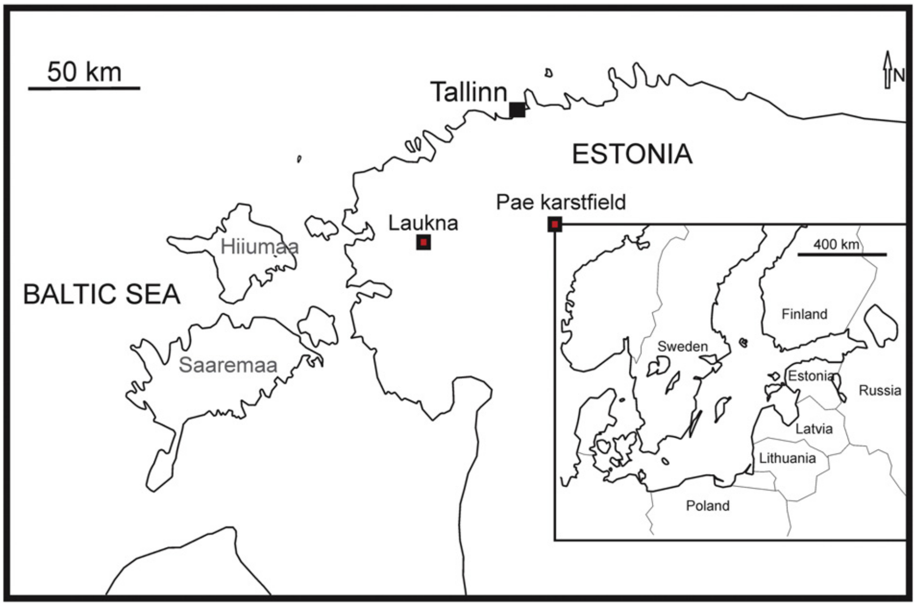

Fig. 1. The location of Laukna quarry and Pae karstfield in Estonia.

Baltic Basin (Fig. 1). The Baltic Basin was characterized by a wide range of tropical environments that included coral-stromatoporoid reefs and lagoons. The biota of this basin was diverse (Hints et al., 2008).

Nestor and Einasto (1977) described the paleoenvironments of the basin as composed of following facies belts: tidal flat/lagoonal, shoal, open shelf, transitional (*i.e.* basin slope), and a basin depression. The first three facies belts formed a shallow carbonate shelf (*i.e.* carbonate platform). The latter two facies belts formed a deeper pericratonic basin where fine-grained clastic deposits were deposited (Raukas and Teedumäe, 1997).

Laukna (58.929152, 24.186950) is an old quarry in an ancient coastal terrace, about 5 km to north from Koluvere Castle in western Estonia (Fig. 1). A flaggy micritic and coral-stromatoporoid limestone is exposed from the middle part of the Raikküla Formation (middle Llandovery) (Mõtus and Hints, 2007). Other fauna includes the tabulates *Multisolenia tortuosaeformis*, *Parastriatopora celebrata*, *Sinopora operta*, and the rugosans *Dokophyllum* sp.

Pae karstfield (58.99619, 24.916086) is located in western Estonia (Fig. 1). Limestones of the Raikküla Regional Stage containing stromatoporoids are exposed there (H. Nestor, personal comm.). In addition to stromatoporoids, solitary rugosans also occur at Pae karstfield.

3. Material and methods

Thirty stromatoporoids were collected from the Raikküla Regional Stage at the Laukna outcrop and five stromatoporoids from Raikküla Regional Stage of Pae karstfield (Fig. 2, Table 1). The studied stromatoporoids were sectioned using a stone saw, and then three thin-sections were made. The thin-sections were scanned with an Epson 4490 scanner.

All of the studied specimens are deposited in the collections of the Institute of Geology, Tallinn University of Technology (GIT).

4. Results

Among the total stromatoporoid population collected at the Laukna outcrop, symbiosis with rugosans was rare; only a single stromatoporoid (*Petridiostroma simplex*) specimen of the 30 studied was infested by the symbiotic rugosan *Petrozium losseni* (Dybowski, 1874) (Fig. 3). Among the five stromatoporoids from Pae karstfield, one (*Clathrodictyon turritum* = *P. simplex*) was infested with *P. losseni* (Dybowski, 1874) (Fig. 4). Both of the infested stromatoporoids had numerous endobiotic rugosans (>20) (Fig. 3A).

The growth surface of the infested *P. simplex* is evenly covered with apertures of symbiotic rugosans at various growth stages (Fig. 3A). The apertures of the rugosans are elevated above the growth surface of the host stromatoporoid. There is no regular distribution of the symbiont apertures relative to the stromatoporoid morphology; symbionts are numerous at the edges of stromatoporoid as well as in the central regions.

The rugosan symbionts are located perpendicularly to subperpendicularly relative to the growth surface of the stromatoporoid. There is a notable change in orientation of the host stromatoporoid growth lamellae around each rugosan symbiont. The growth lamellae of the

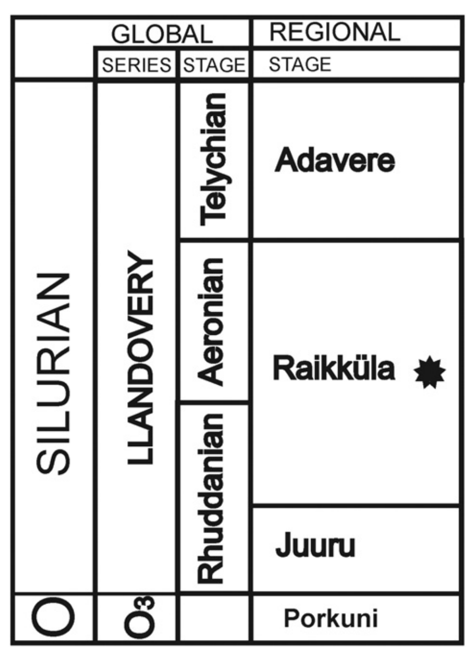

Fig. 2. The stratigraphy of the Llandovery of Estonia. Location of earliest rugosan symbionts in stromatoporoids marked with asterisk.