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Earliest symbiotic rugosans in cystoporate bryozoan *Ceramopora intercellata* Bassler, 1911 from Late Ordovician of Estonia (Baltica)

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ABSTRACT

The earliest known endobiotic rugose corals are recorded in the Katian of Estonia. Multiple rugosans were partially embedded in colonies of the cystoporate bryozoan *Ceramopora intercellata* Bassler, 1911, leaving only their apertures free on the bryozoan growth surface. *Bodophyllum* sp. and *Lambelasma* sp. are rugosans that formed a symbiotic association with *C. intercellata* which may have been mutualistic. Rugosans presumably benefitted from growth within the stable substrate provided by the bryozoan, while bryozoans presumably benefitted by protection against some types of predators. Symbiosis between rugosans and the bryozoan *Ceramopora intercellata* was most likely facultative.

1. Introduction

Symbiotic interactions between different organisms are rather rarely preserved in the fossil record. The endobionts embedded (i.e. bioimmured) in the living tissues of host organisms also have great importance (see Taylor, 1990 for a review). The earliest microscopic invertebrate symbionts appeared in the Cambrian (Bassett et al., 2004). Macroscopic endobiotic invertebrate symbionts appeared later and became common in the Late Ordovician (see Tapanila, 2005 for a summary). Silurian and Devonian rugose corals were often bioimmured within the skeletons of stromatoporoids and slightly more rarely into other corals; they differ from bioclaustrations (Palmer and Wilson, 1988) by having their own skeletons. Several Paleozoic bioclaustrations may have been made by parasites, but it is better to consider them simply as symbionts (Zapalski, 2007, 2011; Zapalski and Hubert, 2011; Taylor, 2015). Endobiotic rugosans were hitherto unknown from the Ordovician. Moreover, there are no other reports of bryozoan-hosted endobiotic rugosans.

The faunas of bryozoans and rugose corals in the Ordovician of Estonia are relatively well studied (Bassler, 1911a, 1911b; Gorjunova, 1992, 1996; Gorjunova and Lavrentjeva, 1993; Kaljo, 1958, 1961; Lavrentjeva, 1990; Modzalevskaya, 1953; Männil, 1959; Neuman, 1969, 1986; Pushkin and Gataulina, 1992; Reiman, 1958), but symbiosis of rugosans and bryozoans needs a further study.

The aims of this paper are to: 1) describe the earliest known endobiotic rugosan symbionts, here reported from the Late Ordovician of Baltica; 2) describe the only known rugosan-bryozoan endosymbiosis; and 3) discuss the paleoecology of this rugosan-bryozoan association.

2. Geological background and locality

During the Ordovician Baltica moved from the temperate climatic zone into the subtropical realm (Torsvik et al., 1992; Nestor and Einasto, 1997; Cocks and Torsvik, 2005; Torsvik and Cocks, 2013). In the Sandbian, the area of modern Estonia was covered by a shallow epicontinental sea with little bathymetric variation and an extremely low sedimentation rate (Nestor and Einasto, 1997). Along the entire extent of the ramp a series of grey argillaceous and calcareous sediments accumulated. There was a trend of increasing clay and decreasing bioclasts in the offshore direction (Nestor and Einasto, 1997). In the Katian the climatic change resulted in an increase in carbonate production and sedimentation rate on the carbonate shelf (Nestor and Einasto, 1997).

The Dapingian to Hirnantian succession in Estonia is characterized by various normal marine carbonate rocks (Nestor and Einasto, 1997). In northern Estonia, mostly limestones are exposed, which accumulated in the shallow part of the basin. In addition to limestones, marls also occur in somewhat lesser amounts. The purest limestones are mostly

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in the Katian of northern Estonia. In northern Estonia, the Sandbian is characterized by a higher content of clay in carbonate rocks. In addition to limestones, kerogenous carbonates (oil shales) accumulated in the Sandbian of northern Estonia (Nestor and Einasto, 1997). The carbonate rocks of the Haljala Regional Stage are especially rich in clay. Carbonate buildups became common in the early Katian of the northern Estonia starting with the Keila Regional Stage (Nestor and Einasto, 1997).

The Kõrgessaare outcrop is an old abandoned quarry in Kõrgessaare village, Hiiumaa Island, NW Estonia. Thinly bedded (2–8 cm), bluish-grey to yellowish grey clayey nodular limestones with thin (<2 cm) marl intercalations were exposed. Kõrgessaare quarry was rich in various normal marine shelly fossils, including the rugosans *Streptelasma hiumica* (Reiman), *Kenophyllum siluricum* (Dybowski), *K. subcylindricum* Dybowski, *Rectigrewingkia anthelion* (Dybowski), *Grewingkia europaeum* (Roemer), *Bodophyllum* sp. and *Lambelasma* sp. The locality was also rich in bryozoans: *Anaphragma mirabile* Ulrich et Bassler, *Ceramopora intercellata* Bassler, *Corynotrypa barberi* Bassler, *Diplotrypa densitabulata* Modzalevskaya, *Orbignyella expansa baltica* Bassler, *Eichwaldictya flabellata* (Eichwald), *Constellaria constellata* (Dybowski) and *Cuffeyella arachnoidea* (Hall) (Rõõmusoks, 1962; D. Kaljo personal comm. 2016) (Fig. 1).

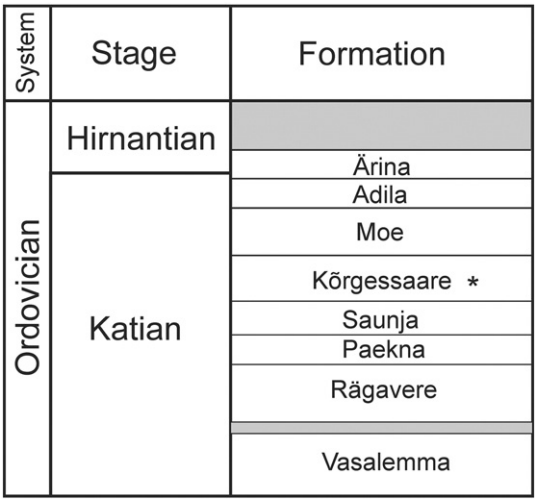

Fig. 2. The stratigraphy of the Katian of Estonia. Location of rugosan symbionts in bryozoans marked with an asterisk.

3. Material and methods

The collections of the Institute of Geology, Tallinn University of Technology (GIT) contain 113 bryozoans and 320 rugosans from the Kõrgessaare Formation (Katian) (Fig. 2) of the Kõrgessaare outcrop, Hiiumaa Island, NW Estonia. The bryozoans in the collection were searched for the presence of symbionts. Two specimens of *Ceramopora intercellata* Bassler, 1911 contained rugosans. The bryozoans with rugosans were photographed using a Nikon D7000 digital camera. The dimensions of both rugosan and bryozoan were obtained from calibrated photographs.

4. Results

Two of 113 bryozoans from the Kõrgessaare outcrop contain partially embedded rugosans (Fig. 3). Rugosans occur only in the cystoporate bryozoan *Ceramopora intercellata* Bassler, 1911. There are multiple rugosans embedded in both bryozoan colonies. The rugosans are oriented perpendicular to the surface of bryozoan colonies. Bryozoan zooids around the partially embedded rugosans are the same size as those in other regions of the colonies. One *C. intercellata* colony (GIT 666-22) contains the rugosan *Bodophyllum* sp., but some juvenile specimens probably belong to the other species. The other bryozoan colony (GIT 666-23) contains the rugosan *Lambelasma* sp., but some juvenile specimens may also belong to other species. Bryozoan colony GIT 666-22 is 5.8 cm in diameter and 1.5 cm thick, forming slightly hemispherical disk with a somewhat irregular shape. Bryozoan colony GIT 666-23 has a diameter of 5.6 cm and a slightly hemispherical shape.

There are thirteen rugosans in *C. intercellata* colony GIT 666-22. The growth stages of the rugosans vary. Individuals of *Bodophyllum* sp. rugosans in this colony have their apertures elevated above the

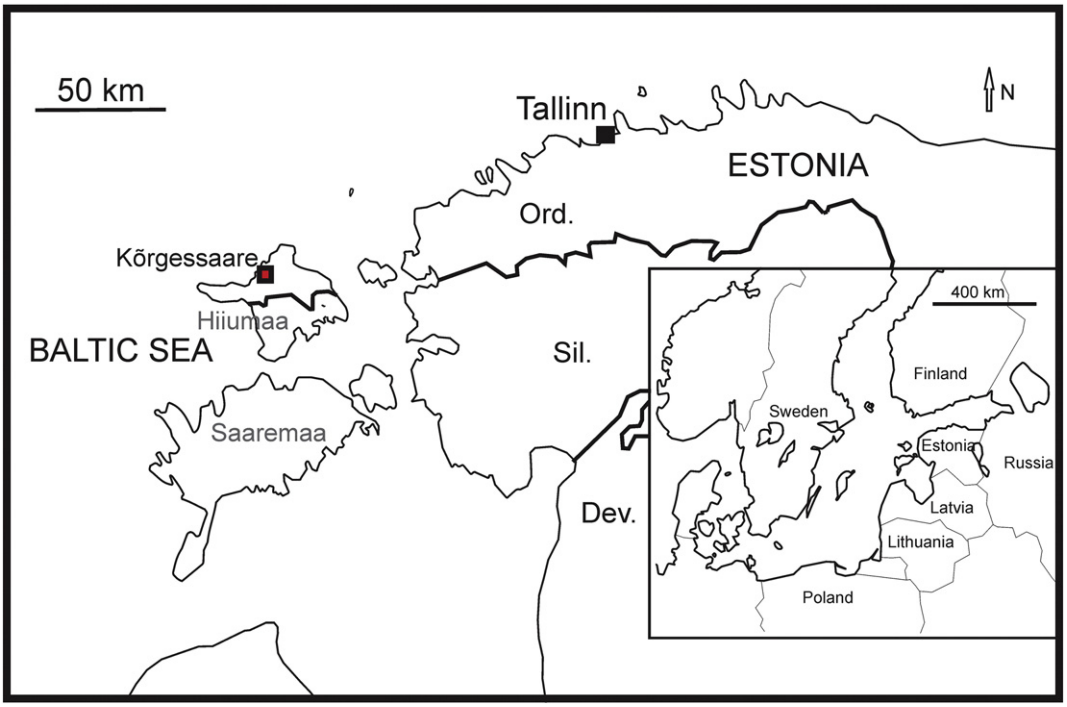

Fig. 1. The location of Kõrgessaare quarry on Hiiumaa Island in NW Estonia.