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Symbiotic endobionts in Paleozoic stromatoporoids

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ABSTRACT

Stromatoporoids hosted a diverse fauna of symbiotic endobionts during the Silurian and Devonian. Assemblages of symbiotic endobionts from the Ordovician, Silurian and Devonian differ significantly. The only symbiotic association in the Ordovician is cornulitid-stromatoporoid. The diversity of Silurian and Devonian symbiotic associations is similar, but the taxonomic compositions of the Silurian (i.e. rugosans, syringoporids, cornulitids, lingulids, *Chaetosalpinx* and *Helicosalpinx*) and Devonian (i.e. syringoporids, *Torquaysalpinx*, *Chaetosalpinx*, *Streptindytes*, and rugosans) associations are different. Symbiotic corals dominated both Silurian and Devonian associations, rugosans dominated the Silurian associations, and syringoporids dominated the Devonian associations.

1. Introduction

Stromatoporoids are extinct sponges with calcareous skeletons. In the paleontological literature the term "stromatoporoid" has been assigned to various taxa ranging in age from the Cambrian through the Paleogene (Stock, 2001). From a phylogenetic point of view, only those organisms that have been demonstrated to have a phyletic connection with *Stromatopora* should be considered as true stromatoporoids (Stock, 2001). True stromatoporoids occur from the Lower Ordovician through the Upper Devonian (Stock, 2001).

Symbiotic interactions play an important role in the ecology of organisms in the modern biosphere. The evolutionary history of symbiotic interactions helps us better understand modern ecosystems. Symbiotic interactions were important in the Palaeozoic fauna (Tapanila, 2005). Symbiotic relationships can be recognized in fossil material when one organism has caused changes in the growth of another's skeleton. Commonly, symbionts are embedded within the skeleton of a host organism, such as a stromatoporoid, leaving only small apertures exposed for feeding. Embedment structures left by organisms without biomineralized skeletons are called bioclaustrations (Palmer and Wilson, 1988).

The aims of this study are as follows: (1) to summarize the stromatoporoid-hosted symbiotic associations found in the Ordovician to Devonian; (2) to discuss trends in the distribution of symbiosis between stromatoporoids and their endobiotic symbionts.

2. Stromatoporoid symbionts

The most common stromatoporoid symbionts in the Silurian and Devonian were syringoporoids and rugose corals. Slightly less important were "worms" such as *Chaetosalpinx*, *Helicosalpinx* and tentaculitoid tubeworms such as cornulitids, *Streptyndites* and *Torquaysalpinx*. Lingulids had a lesser role in the history of stromatoporoid symbiosis.

2.1. Rugosans

Most rugose corals, both solitary and colonial, encrust various substrates or grow freely on sea floor. They have a stratigraphic range from Middle Ordovician to Permian. Symbiotic rugosan endobionts are embedded within a host stromatoporoid, leaving only the coral's apertures exposed on the growth surface of the stromatoporoid (Fig. 1). The number of symbionts in the coenostea of stromatoporoids can vary from a single specimen to hundreds of individuals depending on the taxa (Vinn and Wilson, in press). Endobiotic rugosan symbionts presumably benefitted from the stable growth substrate provided by stromatoporoids. The effects of the symbionts on the stromatoporoid host are not known, but it is possible that they reduced its feeding efficiency (Vinn et al., 2015). On the other hand, calcareous rigid skeletons of rugosans may have reinforced the skeletons of stromatoporoids. Symbiotic rugosans occur in at least in 17 species and 11 genera of stromatoporoids (Nestor, 1966; Soto and Méndez Bedia, 1985; Kershaw, 1987; May, 2005; Vinn and Mõtus, 2014b; Vinn et al., 2015). There are at least 18 species and 14 genera of rugosans in Paleozoic stromatoporoids (Nestor, 1966; Soto and Méndez Bedia, 1985; Kershaw, 1987; May, 2005; Vinn and Mõtus, 2014a, 2014b; Vinn et al.,

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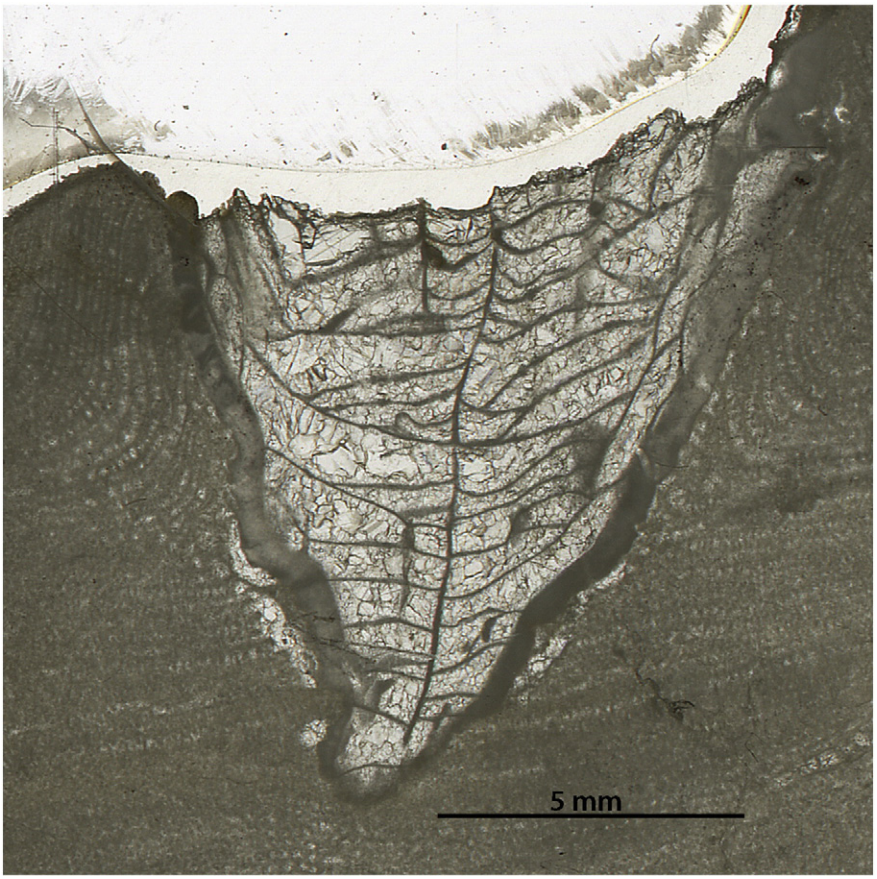

Fig. 1. Longitudinal section of rugosan *Petrozium losseni* (Dybowski) in stromatoporoid *Petridiostroma simplex* Raikküla Regional Stage, Llandovery of Laukna quarry, western Estonia. GIT 666-5.

2015). Solitary rugose corals often form symbiotic associations with the stromatoporoids (Nestor, 1966; Kershaw, 1987; Vinn and Mõtus, 2014b; Vinn et al., 2015). Colonial rugose coral and stromatoporoid intergrowth also occur in the Silurian (Kershaw, 1987; May, 2005). However, these examples are relatively rare in the Llandovery, and have been observed almost exclusively in the reefal units of Anticosti Island. One example includes a phaceloid rugosan, *Paleophyllum*, with corallite diameters of ca. 3–5 mm, intergrown with *Ecclimadictyon* in the East Point Member (Aeronian) (Nestor et al., 2010). The earliest example of stromatoporoid-rugosan intergrowth is a streptelasmid coral fixed by *Ecclimadictyon anticostiense* from the Hirnantian Laframboise Member of Anticosti Island (Nestor et al., 2010). However, the latter association may have been accidental, rather than symbiotic (Nestor et al., 2010). Symbiotic associations between solitary rugosans and stromatoporoids are known from the Rhuddanian of Estonia (Vinn personal obs.) and Anticosti Island (Nestor et al., 2010). Symbiotic associations between stromatoporoids and rugosans seem to be especially common in the Ludlow of Gotland, Sweden (Kershaw, 1987), and Saaremaa, Estonia (Nestor, 1966; Kershaw and Mõtus, 2016). It is possible that the late Silurian represents the acme of rugosan-stromatoporoid symbiosis. There are records of endobiotic rugosans from the Devonian (Soto and Méndez Bedia, 1985; May, 2005), but these are less common as compared to the Silurian. Rugosan-stromatoporoid symbiosis has a stratigraphic range from Rhuddanian (Nestor et al., 2010) to Givetian (May, 2005).

2.2. Syringoporids

Syringoporids are tabulate corals that have a range from Late Ordovician to the Early Permian. They can grow separately or as symbiotic endobionts within stromatoporoids. Endobiotic *Syringopora* is always completely embedded within a host stromatoporoid, leaving only its apertures free on the growth surface of the stromatoporoid (Vinn and Wilson, in press) (Fig. 2). It is possible that calcareous rigid skeletons of syringoporids may have reinforced skeletons of stromatoporoids. Syringoporids occur in twenty-seven stromatoporoid genera, but five of them only have more than five species with syringoporids (Mistiaen, 1984). There are five *Syringopora* species in the Devonian stromatoporoids of Bohemia (May, 2005). The *Caunopora*-type of syringoporid-stromatoporoid symbiosis, so common in the Devonian (Carter, 1878; Carter, 1879; Roemer, 1880; Mistiaen, 1984; May, 1999), does not occur in the early Silurian of Anticosti Island, Canada, even though auloporids or syringoporids were common in the East Point Member and Pavillon Member (Nestor et al., 2010). Similarly, syringoporids are missing in the Late Ordovician and early Silurian stromatoporoids of Estonia and Sweden (Nestor, 1964; Mori, 1968). The Late Silurian examples are known from Gotland (Sweden) (Mori, 1970; Kershaw, 1987) and Saaremaa (Estonia) (Nestor, 1966), though much less common than in the Devonian (Mistiaen, 1984; Da Silva et al., 2011). It is likely that syringoporid-stromatoporoid symbiosis evolved in the middle Silurian and achieved its maximum in the Devonian. Syringoporid-stromatoporoid symbiosis has a stratigraphic range from Ludlow (Nestor, 1966; Mori, 1970; Kershaw, 1987) to Frasnian (Da Silva et al., 2011).

2.3. Cornulitids

Cornulitids were suspension feeding tentaculitoid tubeworms that encrusted various organic and inorganic substrates in the Middle Ordovician to Carboniferous. They share affinities with lophophorates (Vinn