FIRST RECORD OF *CHAETOSALPINX* BIOCLAUSTRATIONS IN THE RUGOSE CORALS FROM THE LATE ORDOVICIAN OF BALTICA

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ABSTRACT – Bioclaustrations are extremely rare in the rugose corals from the Ordovician of Estonia. A specimen of *Kenophyllum subcylindricum* from the Vormsi Regional Stage (Katian) contains multiple shafts of *Chaetosalpinx siberiensis*?. The latter bioclaustration also occurs in the Pirgu Regional Stage (Katian). The growth lines of the host coral show a reaction to the infesting organism, suggesting that the shafts in the calyx are bioclaustrations and not post-mortem borings (*Trypanites*). The worm-like *Chaetosalpinx* tracemaker initially caused damage to the coral's soft tissues and used the coral's resources to build its domicile, resulting in a negative impact. The symbiotic worms benefited from having a domicile and protection against predators from the host's nematocysts. *Chaetosalpinx siberiensis*?-*Kenophyllum subcylindricum* association was likely parasitic.

Keywords: symbiosis, rugosans, worms, parasites, Katian, Estonia.

RESUMO – Bioclaustrações são extremamente raros nos corais rugosos do Ordoviciano da Estônia. Um espécime de *Kenophyllum subcylindricum* do estágio regional Vormsi (Katiano) contém eixos múltiplos de *Chaetosalpinx siberiensis*?. Essa última bioclaustração também ocorre no estágio regional de Pirgu (Katiano). As linhas de crescimento do coral hospedeiro mostram uma reação ao organismo infestante, sugerindo que os eixos no cálice são bioclaustrações e não perfurações *post-mortem* (*Trypanites*). *Chaetosalpinx,* produtor do traço semelhante a um verme, inicialmente causou danos aos tecidos moles do coral e usou os recursos do coral para construir seu domicílio, resultando em um impacto negativo. Os vermes simbióticos se beneficiaram do fato de terem um domicílio e proteção contra predadores dos nematocistos do hospedeiro. A associação *Chaetosalpinx siberiensis*?-*Kenophyllum subcylindricum* foi provavelmente parasitária.

Palavras-chave: simbiose, rugosas, vermes, parasitas, Katiano, Estônia.

INTRODUCTION

Macroscopic endobiotic invertebrate symbionts have been documented more often since the Late Ordovician, as reviewed by Tapanila (2005). Fossils of these endobionts, including bioclaustrations and skeletal organisms, represent some of the most compelling examples of symbiotic interactions in the fossil record. Initially, these interactions were thought to be commensal (Oekentorp, 1969), but later suggestions proposed a parasitic nature, particularly for the bioclaustrations (Stel, 1976; Zapalski, 2007, 2011). Contrary to this view, Taylor (2015) disputed the classification of endobionts as parasites in fossil specimens. Taylor argued that in the absence of clear evidence regarding the precise costs and benefits of interactions between the host and symbiont,

it is not appropriate to label them definitively as parasites. Bioclaustrations, as defined by Palmer & Wilson (1988), are cavities formed by the growth-interfering behavior of a symbiont residing within the host's skeleton (Słowíński *et al*., 2020). Late Ordovician bioclaustrations, likely left by parasites, have been discovered in bryozoans as well (Palmer & Wilson, 1988). *Chaetosalpinx* is a bioclaustration that has a stratigraphic range extending from the Late Ordovician to Late Devonian (late Famennian) (Elias, 1986; Tapanila, 2005; Zapalski *et al*., 2008). The exact biological affinity of the organisms responsible for *Chaetosalpinx* bioclaustrations remains unknown, but they are presumed to have had a worm-like body plan.

The fauna of rugosans in the Ordovician of Estonia is relatively well studied (Kaljo, 1958, 1961; Neuman, 1986),

but the symbiosis of rugosans with other organisms needs further study. Previously discovered findings of symbiosis between rugosans and other invertebrates in the Ordovician of Estonia primarily concern rugosan-bryozoan associations (Vinn *et al*., 2016).

The aim of this paper is to (i) report the *Chaetosalpinx* bioclaustrations in the rugosans from the Ordovician of Baltica for the first time; (ii) discuss the paleoecology of the *Chaetosalpinx*-rugosan association; and (iii) compare the distribution of bioclaustrations in tabulates and rugosans.

GEOLOGICAL BACKGROUND AND LOCALITIES

During the Ordovician, the paleocontinent of Baltica drifted from the temperate climatic zone to the subtropical realm (Nestor & Einasto, 1997; Cocks & Torsvik, 2005; Torsvik & Cocks, 2013). The succession from the Dapingian to the Hirnantian in Estonia is characterized by various normal marine carbonate rocks (Nestor & Einasto, 1997). In northern Estonia, limestone formations predominate, indicating deposition in shallow parts of the basin. Marls are also present to a lesser extent. The purest warm-water limestones are primarily found in the Katian of northern Estonia. Carbonate buildups became increasingly common here during the Katian (Nestor & Einasto, 1997).

The Nõmmküla quarry of western Estonia (Lat 59.075744; Long 23.612872) is currently a gravel pit and limestone quarry capped by a layer of 0.5–1 m of Quaternary sand gravel,

and, beneath it, is the bedrock. The rugosans originate from limestones of the Vormsi Stage (Figure 1).

Hosholm (Lat 58.963019; Long 23.162005) is located on Vormsi Island. In the case of low water levels, limestones of Pirgu Stage are exposed on the beach along a stretch of approximately 0.5 kilometers (Figure 1).

MATERIAL AND METHODS

The collection of the Tallinn University of Technology, Department of Geology (**GIT**) contains hundreds of thin sections of rugose corals from the Ordovician and Silurian of Estonia. Over two hundred specimens of unidentified Ordovician and Silurian rugosans were searched for bioclaustrations in thin sections using detailed digital photographs. In addition, thin sections of *Phaulactis* (N = 80), *Streptlasma* (N = 37), *Entelophyllum* (N = 34), *Grewingkia* (N = 32), *Paliphyllum* (N = 27), *Tryplasma* (N = 17), *Cystiphyllum* (16), *Rhegmaphyllum* (N = 15), *Pycnactis* (N = 13), *Strereoxylodes* (N = 11) and *Kenophyllum* (N = 10) were searched for bioclaustrations and endobionts. Only two specimens of *Kenophyllum subcylindricum* (N = 5) from the Katian of Estonia contained bioclaustrations.

RESULTS

A single transverse thin section of *Kenophyllum subcylindricum* (GIT 80-8) from the Vormsi Regional Stage (Katian) contains 11 shafts of *Chaetosalpinx siberiensis*?
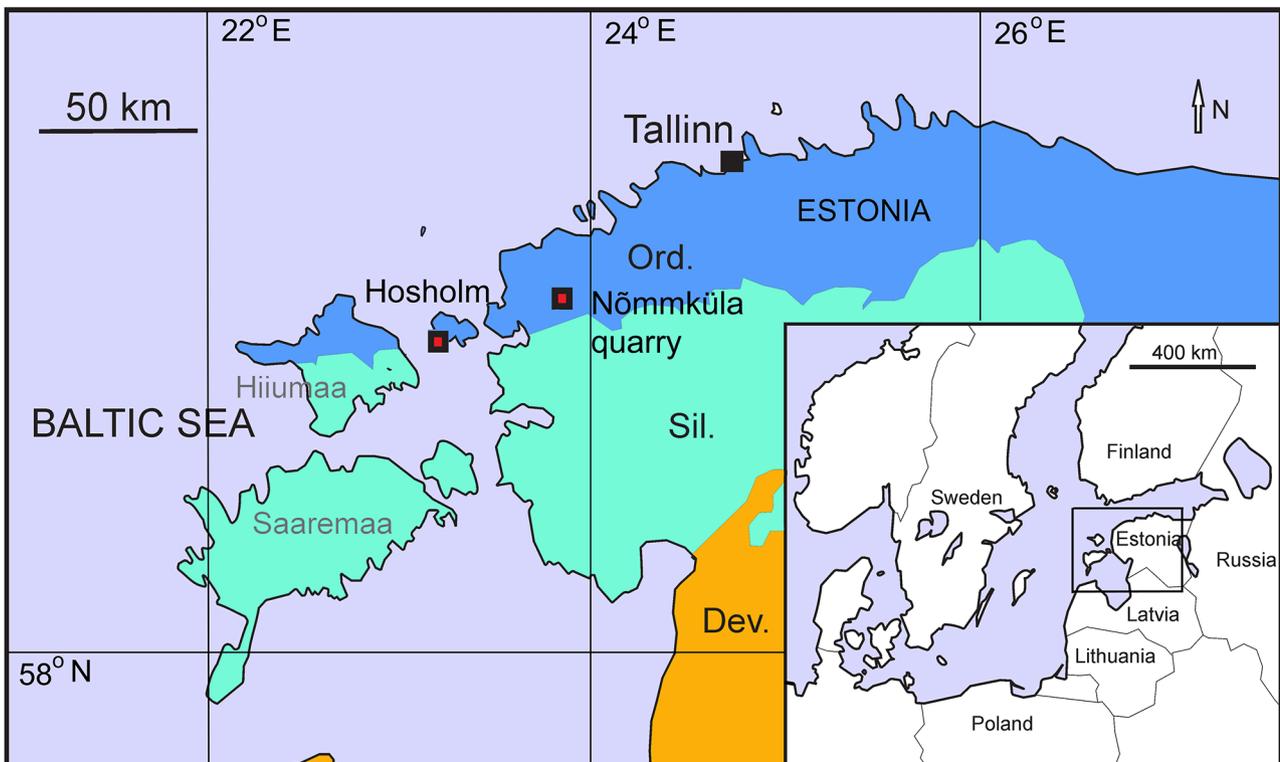

**Figure 1.** Location of Nõmmküla quarry and Hosholm, NW Estonia.

(Figures 2A–B, 3A–B). The bioclaustrations of most *Chaetosalpinx* specimens (N = 10) are in cross-section. A single specimen is visible in an oblique section. The shafts of bioclaustrations are filled with translucent sparite. Moreover, their walls are formed by the host coral. The diameters of individual bioclaustrations are inconstant, with diameters along minor axis ranging from 0.16 mm to 0.66 mm (N = 11, mean 0.41 mm, sd = 0.16 mm). The sections have oval to circular outlines. Two bioclaustrations have a somewhat asymmetrical outline. A single bioclaustration has a flattened or even slightly concave side. All bioclaustrations are located precisely between larger septa about midway from the center to the external wall of the rugosan. The growth lines of rugosans around the shafts are bent so that they follow the shape of the shafts. Most bioclaustrations are concentrated on the side of rugosan opposite to the fossula. The bioclaustrations are tentatively assigned to *Chaetosalpinx siberiensis*? because of their cylindrical shape and dimensions. However, usually *Chaetosalpinx* representatives are very regularly roundish, except for *Chaetosalpinx rex*, which is lenticular in cross section (Tapanila, 2005). Some of our bioclaustrations are atypical in having somewhat irregularly shaped cross sections and could belong to a new cecidospecies, but more specimens have to be collected before the formal description. The elongated oval sections are due to oblique sectioning through the tubular shafts.

One transverse section of *Kenophyllum subcylindricum* (GIT 83-25) from the Pirgu Regional Stage (Katian) contains
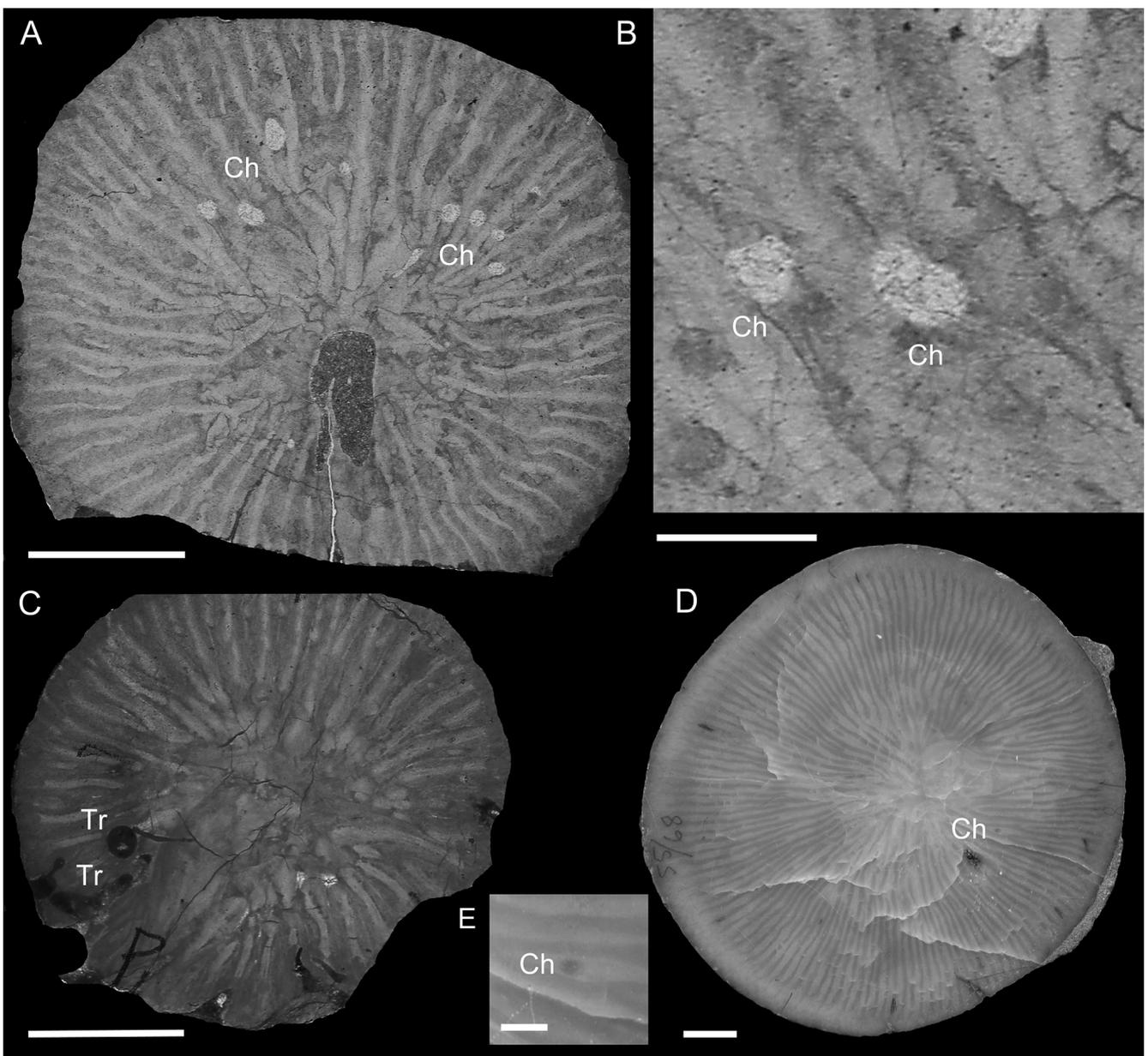
Figure 2. *Kenophyllum subcylindricum* from the Katian of NW Estonia. **A**, multiple *Chaetosalpinx siberiensis* (Ch) in transverse section from Vormsi Regional Stage (Katian) (GIT 80-8). **B**, same as (A), detailed view. **C**, *Trypanites* isp. borings (Tr) from Pirgu Regional Stage (Katian) (GIT 83-25). **D**, single *Chaetosalpinx siberiensis* (Ch) in transverse section from Pirgu Regional Stage (Katian) (GIT 406-370). **E**, same as (D), detailed view. Scale bars: A, C, D = 5 mm; B, E = 1 mm.
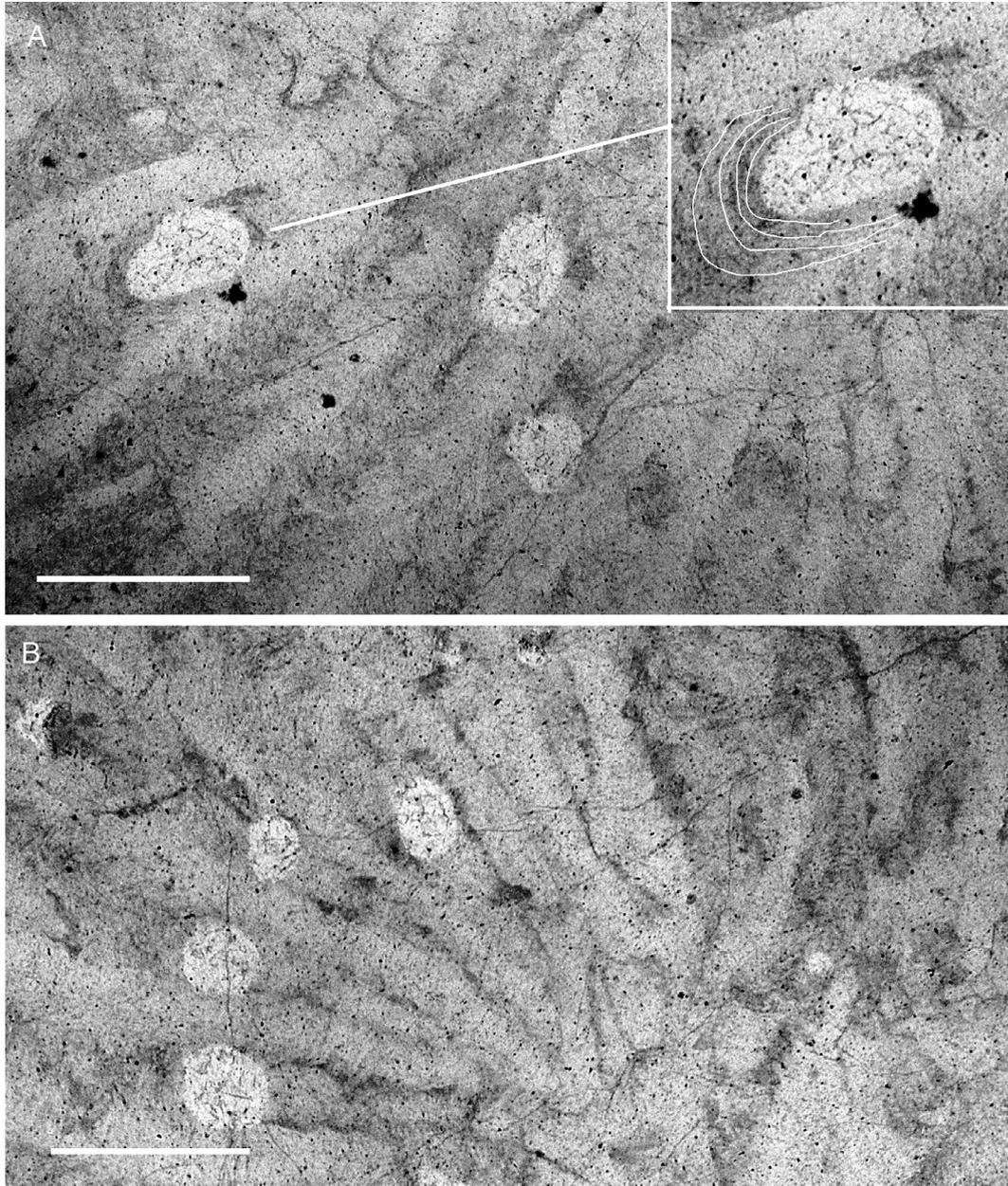
Figure 3. A–B, *Kenophyllum subcylindricum* from the Katian of NW Estonia with multiple *Chaetosalpinx siberiensis* in transverse section from Vormsi Regional Stage (Katian) (GIT 80-8). Scale bars = 1 mm.

multiple *Trypanites* isp. borings with diameters ranging from 0.25 mm to 0.94 mm. The growth lines around the boring do not show any reaction. The borings are filled with dark sediment (Figure 2C).

A single transverse section of *Kenophyllum subcylindricum* (GIT 406-370) from Pirgu Regional Stage (Katian) contains a single shaft of *Chaetosalpinx* with a diameter of 0.66 mm (Figure 2D–E). The sectioned bioclaustration has a slightly oval outline. This bioclaustration is assigned to *Chaetosalpinx* because of its cylindrical shape, and because its walls are formed by the host coral. The bioclaustration is filled with translucent calcite. The bioclaustration is located within a large septum between the external wall and center of the rugosan, slightly closer to the center and close to the fossula.

DISCUSSION

Interpretation of the association

Vertical and sub-vertical shafts in the coral growth surfaces could either be the result of *post-mortem* bioerosion or *syn-vivo* embedment of soft-bodied worms. The latter leaves a bioclaustration in the coral skeleton. Bioclaustrations form only when both host (*i.e.*, substrate) and infesting organism are alive. Therefore, the growth lines of the host coral should show a reaction to the infesting organism. In the case of *Kenophyllum subcylindricum*, growth lines around shafts show a reaction to the infester, indicating that these shafts are bioclaustrations and not the boring (*i.e.*, *Trypanites*). Another specimen of *K. subcylindricum* shows *Trypanites*

isp. in a transverse section, filled with sediment. In contrast, shafts of *Chaetosalpinx* in tabulates from the Silurian of Baltica are almost always filled with translucent calcite (Mõtus & Vinn, 2009). The latter is not a definite indicator of a bioclaustration, but here, combined with changes in the course of growthlines, it lends support to the interpretation of these traces as bioclaustrations. The stereotypic placement of bioclaustrations in the interspaces between large septa is also indicative of *syn-vivo* infestation. On the other hand, one could argue that the skeleton of rugosans is basically composed of theca and septa. Thus, "bioclaustrations" would be expected to be located within skeletal elements, not between them. Without their own wall it is unlikely to have them preserved within the calyx fill. However, the structures described herein are not preserved in the calyx fill, but certainly within the skeletal material. This is because the rugosan calyces are not without a bottom; even between the septa, there is a skeletal floor deeper between them too, and within this skeletal floor, the bioclaustrations were formed. Alternatively, could these structures be artifacts? The answer to this question is most definitely not. Any shafts that could be produced during the diagenetic dissolution of calcite would not have smooth walls.

Paleoecology of the association

The bioclaustrations are located within the rugosan calyx, and such placement would necessitate perforation of the soft tissue, a phenomenon observed in modern coral associations with other organisms, such as larvae of pyrgomatid barnacles perforating the soft tissue of recent scleractinians (Ross & Yamaguchi, 2001; Tapanila, 2005). The infesting organism initially caused damage to the coral's soft tissues and used the coral's resources to build its domicile, resulting in a negative impact. However, our material does not show proof of growth inhibition around the bioclaustrations observed in tabulates (Tapanila, 2005), which would strongly support the notion of a negative effect on the coral. On the other hand, we have studied mostly the transverse sections that do not show growth changes in the vertical direction. The feeding competition between the host rugosan and infesting worms seems unlikely as the worms were likely suspension feeders similar to modern sabellids and serpulids, while rugosans were micropredators. The placement of worms between larger septa in *K. subcylindricum* from Vormsi Stage could be related to the soft-body anatomy of the host rugosan. It is possible that the location between septa corresponded to the areas between the host's tentacles which would have best fitted for a suspension-feeding symbiont. The placement of worms within the coral tentacle would have certainly interfered with its feeding. There was a large number of worms in a single rugosan from the Vormsi Stage. For modern bryozoans, a high density of parasites is often associated with low virulence (Hill & Okamura, 2007). If this trend holds true across colonial animals, high densities of *Chaetosalpinx* infestation could plausibly suggest either the absence of negative impact or low virulence.

The settling worms benefited from having a habitat and, presumably, protection against predators from the host's nematocysts (Zapalski, 2007). Research into contemporary symbiotic polychaete worms has indicated a preference for hosts possessing robust chemical defenses, such as cnidarians (Martin & Britayev, 1998, 2018). This principle likely applied to *Chaetoslapinx* tracemakers as well.

The scenario described above does not align with the currently accepted definition of commensalism (Zapalski, 2007), and we consider that *Chaetosalpinx siberiensis*?-*Kenophyllum subcylindricum* association was parasitic.

Endobionts in the rugosans

During the Ordovician, rugose corals seldom hosted wormlike invertebrates that created bioclaustrations, as previously evidenced only by the presence of *Chaetosalpinx ferganensis* in *Grewingkia canadaensis* from the Katian Bull Fork Formation of Laurentia (Elias, 1986). The *Grewingkia* specimens in the studied collection did not yield any bioclaustrations, which can either be explained by having an insufficient number of studied specimens or more likely that *Chaetosalpinx* occurs only in *G. canadaensis*, which was lacking in our collection. While there is no specific data on rugosan endobionts from the Silurian, the situation probably mirrored that of the Ordovician (Vinn & Wilson, 2021). In the Devonian Period, rugosans harbored a variety of endobiotic symbionts, including worm bioclaustrations such as *Chaetosalpinx ferganensis* and *Helicosalpinx asturiana*, along with potential tentaculitoid tubeworms like *Streptindytes acervulariae* and unidentified paired aperture cavities (Tapanila, 2005; Vinn & Wilson, 2021). The diversity of endobiotic symbionts in rugosans appears to be much lower compared to tabulates, likely due to the worms' preference for living between the small corallites of tabulates. The tabulate architecture may have been more conducive to suspension-feeding worms compared to being situated within the calyx of solitary rugose corals or between large calyces in colonial rugosans, which could have led to greater disturbance.

CONCLUSIONS

Bioclaustrations are extremely rare in the Ordovician rugosans from Estonia. The *Chaetosalpinx* tracemaker, which probably resembled a worm, initially inflicted damage to soft tissues of the coral and utilized the coral's resources to construct its dwelling, leading to a detrimental effect. The symbiotic worms derived advantages from having a domicile and presumably also protection against predators due to the host's nematocysts. The association between *Chaetosalpinx siberiensis*? and *Kenophyllum subcylindricum* was probably parasitic in nature. Literature data and the studied collection of thin sections suggest that *Chaetosalpinx* tracemakers strongly preferred tabulate corals over rugosans as hosts. The tabulate architecture may have been more conducive to suspension-feeding worms compared to being situated within the calyx of solitary rugosans or between large calyces in colonial rugosans, which could have led to greater feeding disturbance.

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