

INTERGROWTH OF BRYOZOANS WITH OTHER INVERTEBRATES IN THE LATE PRIDOLI OF SAAREMAA, ESTONIA

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Abstract: Nine invertebrates intergrew with bryozoans in the latest Pridoli of Saaremaa, Estonia, namely: cornulitids (*Cornulites baranovi* and *Conchicolites* sp.), hydrozoans, rugosans (*Tryplasma* sp. and *Entelophyllum* sp.), *Anoigmaichnus*, microconchids (*Tuberoconchus wilsoni*), unknown tubicolous organisms and unknown soft-bodied organisms. The most common host of endobionts was *Fistulipora przhidolensis*, but trepostomes also participated in symbiotic associations. Solitary rugosan-cystoporate and hydrozoan-cystoporate associations were common in the Pridoli of Saaremaa, while other cases of intergrowth are rare. The rugosan-cystoporate, hydrozoan-cystoporate, hydrozoan-trepostome and *Anoigmaichnus*-cystoporate associations most likely were not a result of accidental intergrowth, whereas other associations presumably resulted from accidental intergrowth of two organisms. New data from the Pridoli of Saaremaa indicate that the Pridoli probably was not a time of lowered symbiosis levels in the regional ecosystem. Symbiosis levels in the Pridoli of Baltica were comparable to those in the Ludlow and Early Devonian worldwide.

Key words: Symbiosis, bioclaustrations, cystoporates, trepostomes, rugosans, hydrozoans, cornulitids, microconchids.

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INTRODUCTION

Among the best examples of long-term, biological interactions between different organisms in the fossil record are endobionts bioimmured (i.e. embedded) in the living tissues of host organisms (Taylor, 1990). Bioclaustrations are often formed around the soft-bodied parasitic (Zapalski, 2007, 2009; Baliński and Yuanlin, 2010; Zapalski and Hubert, 2011; Rogers *et al.*, 2018) and commensal (e.g., Scrutton, 1975; Ślowiński *et al.*, 2020) organisms in the skeletons of their hosts. Embedded cornulitids, tabulates and rugose corals differ from the original bioclaustrations, defined by Palmer and Wilson (1988), in having their own skeleton. Animals that live in close proximity could often grow into one another to form fused skeletons, which differ from simple encrustation in that the skeletons overlap

each other (Tapanila, 2008). The fully intergrown organisms provide the best evidence of symbiosis of the taxa involved (Tapanila, 2008). Symbiosis is here viewed as any type of a long-term and close, biological interaction between two different organisms, be it parasitic, commensalistic or mutualistic.

Rugose corals are common and diverse in the Pridoli of Saaremaa, Estonia (Kaljo, 1970). The eastern Baltic late Silurian bryozoan fauna has been studied in detail (Kopajevich, 1968, 1971, 1975; Astrova, 1970; Astrova and Kopajevich, 1970; Pushkin *et al.*, 1990). However, only a few symbiotic associations between bryozoans and other invertebrates have been described from the Pridoli of Baltica (Vinn and Wilson, 2010; Vinn *et al.*, 2020, 2021).

Solitary rugosans and the cystoporiferan bryozoan *Fistulipora przhidolensis* Kopajevich, 1990 formed a symbiotic association in the Kaugatuma Formation (early Pridoli) of Saaremaa, Estonia (Vinn et al., 2020). The *syn vivo* nature of the latter association was indicated by the complete intergrowth of both organisms and the perpendicular orientation of the rugosans to the bryozoan growth surface (Vinn et al., 2020). There were one to seven endobiotic rugosans per *Fistulipora* colony in the Kaugatuma Formation. The lack of malformations and decrease in the size of bryozoan zooids near the rugosans indicate there were no strong negative effects of the rugosans on the bryozoan in the Kaugatuma Formation. Vinn et al. (2020) suggested that the rugosans probably benefited from their association with the bryozoan, which served as an anchor to stabilize them in hydrodynamically active waters, and the bryozoan may have benefited by protection against some types of predators. The rugosan-bryozoan associations of the Kaugatuma Formation were most likely mutualistic (Vinn et al., 2020). In addition to the rugosan-bryozoan association, *Cornulites* sp.-*F. przhidolensis* formed a symbiotic association recorded in the Kaugatuma Formation in Saaremaa, Estonia. The symbiotic nature of the latter association is indicated by intergrowth of both organisms. Vinn et al. (2021) described cornulitids as completely embedded within the cystoporiferan bryozoan colony, leaving only their apertures free on the growth surface of the bryozoan. Vinn et al. (2021) suggested that this association could have been slightly harmful to *F. przhidolensis* as *Cornulites* sp. may have been a kleptoparasite.

This paper: 1) describes in detail the intergrowth between bryozoan hosts and other invertebrates from the latest

Pridoli (late Silurian) of Saaremaa, Estonia; 2) assesses the palaeoecology of endobiont-cystoporiferan and endobiont-trepostome associations; and 3) discusses symbiotic interactions in the Pridoli of Baltica.

GEOLOGICAL BACKGROUND AND LOCALITY

During the latest Pridoli, the palaeocontinent of Baltica was located in equatorial latitudes (Melchin et al., 2004; Torsvik and Cocks, 2013). A shallow epicontinental sea covered the SW part of Saaremaa Island (i.e. Sõrve Peninsula) and was characterized by a wide range of tropical environments and diverse biotas (Hints, 2008). Nestor and Einasto (1977) established a basic facies model for the Baltic Silurian basin from Llandovery to Pridoli. They described five depositional environments: tidal flat/lagoonal, shoal, open shelf, basin slope, and a basin depression. The first three environments formed a carbonate shelf, and the last two a deeper basin with fine-grained siliciclastic deposits (Nestor and Einasto, 1997). On Saaremaa Island, the uppermost Pridoli strata contain shallow to deeper shelf carbonate rocks, rich in shelly faunas. The only uppermost Pridoli exposure in Estonia is Ohesaare cliff, on Saaremaa Island (Fig. 1). The Ohesaare cliff is about 600 m long and up to 4 m high (Fig. 2). The total thickness of the section is 3.5 m, whereas the thicknesses of individual beds are variable throughout the outcrop (Hints, 2008). The characteristic intercalation of thin-bedded limestones and marlstones is exposed at the Ohesaare cliff. The material studied originates from the clay-rich beds at the base of the cliff, on

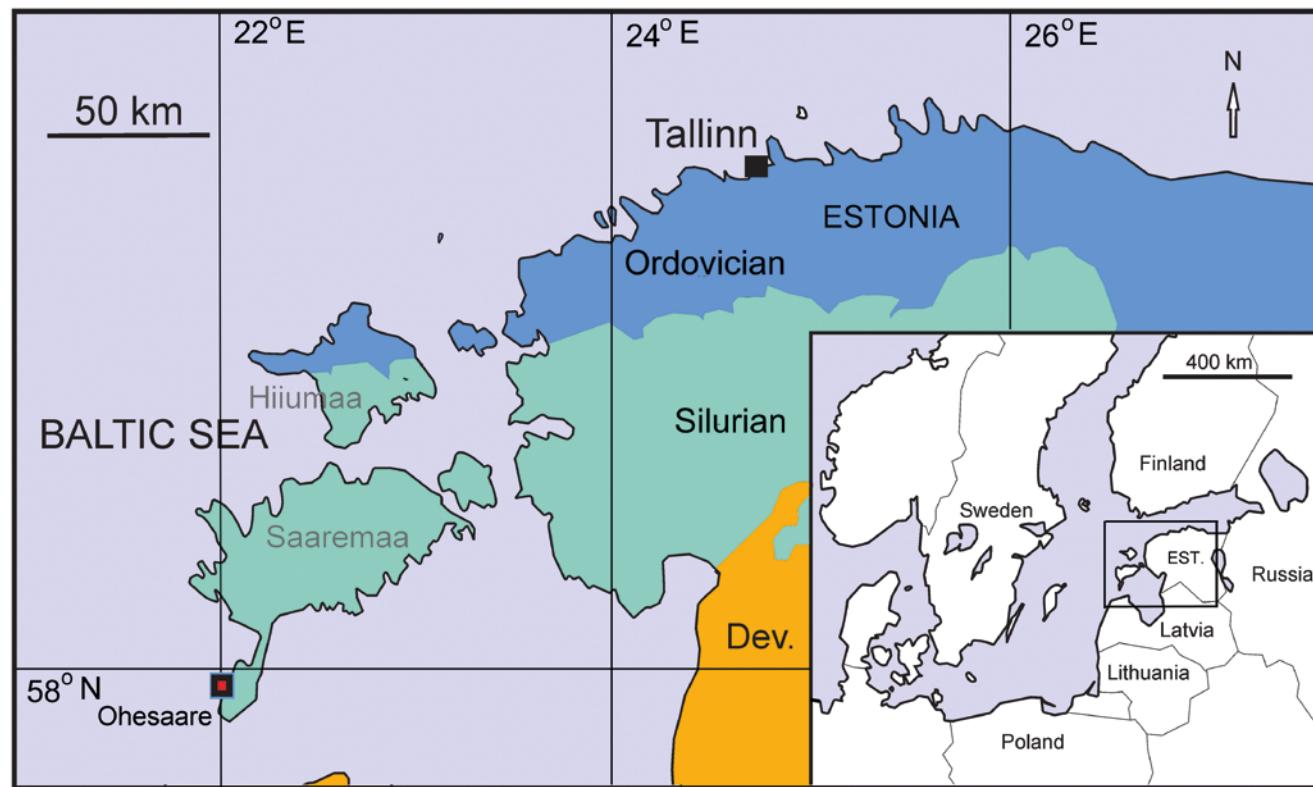


Fig. 1. A map showing the sampled Ohesaare cliff. Abbreviations: Dev. – Devonian

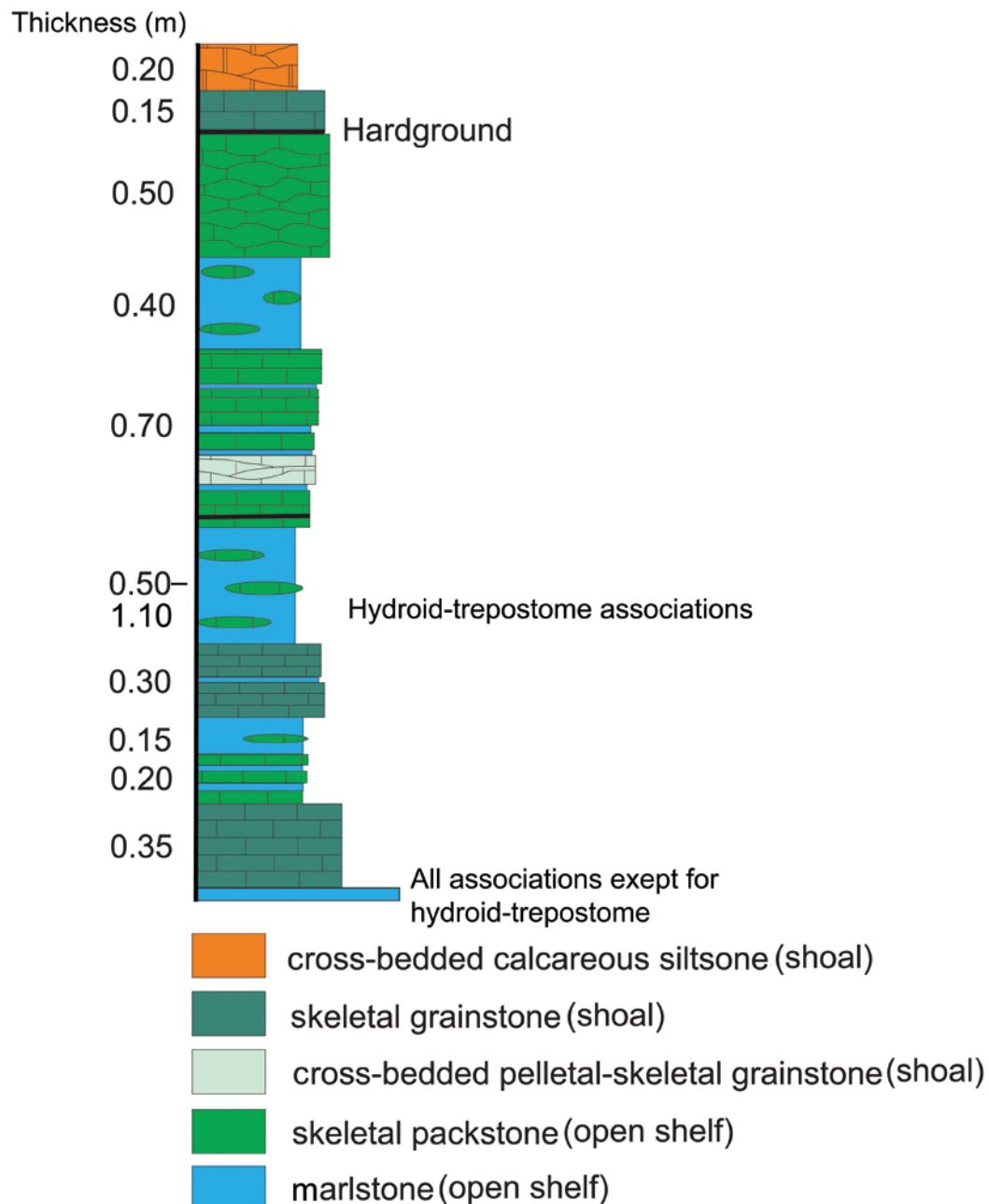


Fig. 2. Section of the Ohesaare cliff (Ohesaare Formation). Modified after Nestor (1990) and Vinn and Wilson (2010).

the modern sea floor (mostly rugosans in bryozoans) and from marlstones, exposed above the cliff's base (mostly hydrozoans in bryozoans).

MATERIAL AND METHODS

A large collection of fossils from Pridoli of Saaremaa was searched for the intergrowth of different invertebrates. The collections of the Department of Geology, Tallinn University of Technology (GIT) and University of Tartu, Natural History Museum and Botanical Garden (TUG), contain about 500 bryozoans from the Ohesaare Formation (uppermost Pridoli, Silurian). Ninety-eight bryozoan specimens from the Ohesaare contained bioclaustrated organisms. All specimens studied were photographed with

a Canon EOS5DS R digital camera and a Leica Z16 APO zoom microscope system. The dimensions of both bioclaustrated organisms and the bryozoans were obtained from calibrated photographs. Fifty-eight colonies were sectioned and one colony, containing hydrozoan specimen, was serially sectioned.

RESULTS

Small cystoporate colonies of irregular shape from the Ohesaare Formation are often intergrown with the other invertebrates. Many cystoporate bryozoans seem to be conspecific with *Fistulipora przhidolensis* Kopajevitch, 1990 in Pushkin *et al.* (1990). The size and shape of the apertures, as well as their radial arrangement around maculae, are

typical for this species. These bryozoans are highly variable in colony shape: sheet-like, dome-shaped, encrusting, often multi-layered. Kopajevich in Pushkin *et al.* (1990) noted that this species encrusts rugosans, crinoids and brachiopod shells. Other studied cystoporate specimens also probably belong to *Fistulipora*, but could represent different species.

Intergrowth of *Fistulipora* (cystoporate) with the other invertebrates is common in the Ohesaare Formation. Intergrowths of the other invertebrates with trepostomes are rare ($N = 5$) and occur only with hydrozoans. *Fistulipora* was most often fully intergrown with the solitary rugosans *Tryplasma*, markedly less with hydrozoans, and most rarely with cornulitids and *Anoigmaichnus*. There are 47 cystoporate colonies that contain endobiotic solitary rugosans (*Tryplasma*) (Fig. 3A, B); one colony is intergrown with *Entelophyllum* (Fig. 3C). There are one to twelve solitary rugosans per single, infested cystoporate colony (mean 3, $sd = 2.3$, $N = 46$). All rugosans are oriented more or less perpendicular to the growth surface of the bryozoans. The growth surface of cystoporate colonies is often elevated around the apertures of endobiotic rugosans. There is no obvious reduction in zooid sizes (though not tested statistically) or any malformations in cystoporate morphology associated with the endobiotic rugosans. Rugosans are always embedded within the cystoporates to the edge of their apertures. Only one rugosan is completely overgrown by *Fistulipora*. The diameter of rugosans within the same cystoporate colony is variable from 1.1 mm to 7.6 mm ($N = 61$, mean 3.3 mm, $sd = 1.63$). There is no obvious pattern in the location of rugosans within the bryozoan colony. They do not form groups and are not concentrated in certain colony regions. Most of the rugosans have relatively thin walls. A sectioned specimen (GIT 403-195) shows that some rugosans have great length inside the bryozoan colony and relatively constant diameter (Fig. 3B). Rugosans seem to lack any orientation within the bryozoans. The orientation of the fossula also seems to vary among the *Tryplasma* specimens within the bryozoan colonies.

Nineteen bryozoan colonies contain hydrozoans; several are found in *Fistulipora* ($N = 6$) and in trepostomes ($N = 5$). Their pattern of budding suggests either *Cladochonus* or *Bainbridgia*, thus an “auloporid-like” organism, likely a hydrozoan. Their external look is similar to members of Trachypsammidae, also a hydrozoan family (but in the Treatise (Hill, 1981) they are classified as tabulates) (Stasińska, 1982; Zapalski *et al.*, 2018; Berkowski *et al.*, 2019). Hydrozoan specimens are fully embedded within the *Fistulipora* and trepostome colonies. Hydrozoan apertures are free of encrustation on the growth surface of a bryozoan colony. There are no obvious reductions in zooid sizes (though not tested statistically) or any malformations in cystoporate morphology associated with the endobiotic hydrozoans (Fig. 3D–F).

Seven cornulitids, presumably *Cornulites baranovi*, are partially to completely embedded within a *Fistulipora* colony (Fig. 3G). In completely intergrown specimens, only their apertures are free on the growth surface of the bryozoan, except for one specimen, the aperture of which is overgrown by a bryozoan. There is a maximum of two cornulitids per bryozoan colony. The bryozoan surface is not

elevated around the cornulitid endobiont. The cornulitids are oriented nearly perpendicular to the growth surface of bryozoan. There are no obvious reductions in zooid sizes (though not tested statistically) or any malformations in cystoporate morphology associated with the endobiotic cornulitids. One *Conchicolites* sp. specimen (GIT 403-177) is also partially intergrown with a cystoporate colony (Fig. 3H).

A single *Tuberoconchus wilsoni* specimen is embedded in a *Fistulipora* colony, having only its aperture free of bryozoan encrustation (Fig. 4A).

Four *Fistulipora* specimens show multiple *Anoigmaichnus* bioclaustrations (Fig. 4B, C). There are ten to forty *Anoigmaichnus* apertures on the growth surface of each *Fistulipora* colony. The apertures including the rim are 0.4 to 0.7 mm wide. The size and rounded to slightly oval shape of the apertures and the longitudinal section of bioclaustration closely resemble those of *Anoigmaichnus odinsholmensis*. The distribution of *Anoigmaichnus* apertures on the *Fistulipora* colonies appears to be random.

Four *Fistulipora* specimens have unknown bioclaustrations with elevated apertures on the bryozoan growth surface. The bioclaustrations have a conical to irregular shape in longitudinal section (Fig. 4D).

Six *Fistulipora* colonies are overgrown by a tubicolous organism. The overgrown tubes are dark in color and have smooth exterior and interior (Fig. 4E, F).

DISCUSSION

Paleoenvironment and associated fauna

The lowermost beds at Ohesaare cliff represent a normal-marine, deep carbonate platform environment with a muddy bottom between the fair weather and storm wave bases (Klaamann, 1970). The Ohesaare mud was rich in clay probably derived from nearby dry land. The soft bottom was colonized by an abundant and diverse shelly fauna that served as benthic islands for hard substrate encrusters (for other examples see e.g., Zatoń and Borszcz, 2013; Zatoń *et al.*, 2017; Musabelliu and Zatoń, 2018; Zatoń and Wrzołek, 2020; Zatoń *et al.*, 2020). Ohesaare *Fistulipora* colonies often were encrusted by rugosans, auloporids, microconchids, *Anticalyptraea* and cornulitids. A few colonies show signs of bioerosion. The Ohesaare soft bottom community includes abundant, large bivalves (*Grammysia obliqua*), tentaculitids (four species), abundant brachiopods (eight species), tabulates (at least four species), rugosans (*Tryplasma* sp., *Spongophylloides* aff. *nikiforvae*, *Entelophyllum articulatum*, *E. pseudodianthus*, *Cantriallia eichwaldi*, *Gyalophyllum ex gr. angelini*), bryozoans (nine species), crinoids (two species) and trilobites (five species; Klaamann, 1970; Nestor, 1990; Pushkin *et al.*, 1990; Mōtus and Hints, 2007; Märss and Nestor, 2014). In the Pridoli of Saaremaa, *Tryplasma* and *Entelophyllum* were the most common rugosans (Kaljo, 1970, 1997). Most solitary rugose corals were liberossessile in the Silurian of Baltica and are characterized by initial attachment to a small sediment grain, but subsequently becoming recumbent on a soft substrate (Neuman, 1988). In contrast, *Tryplasma* and also likely

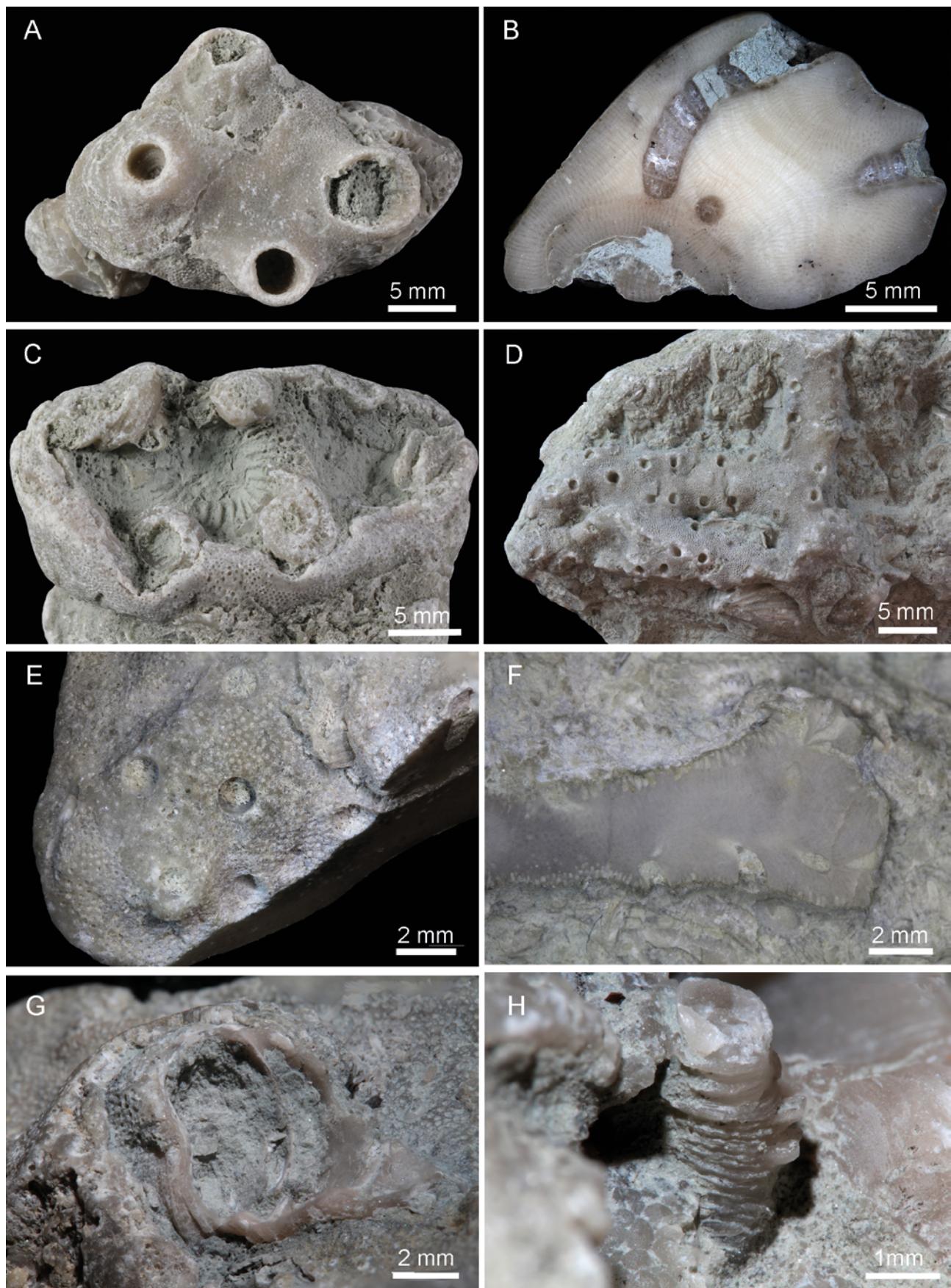


Fig. 3. Intergrowth of bryozoans with other invertebrates from the Ohesaare Formation (upper Pridoli), Ohesaare cliff, Saaremaa Island, Estonia. **A.** *Tryplasma* sp. in cystoporate *Fistulipora* (GIT 403-200). **B.** Longitudinal section of *Tryplasma* in *Fistulipora* (GIT 403-195). **C.** *Entelophyllum* sp. in *Fistulipora* (GIT 403-201-1). **D.** Hydrozoans in trepostome colony (GIT 403-416). **E.** Hydrozoans in *Fistulipora* (GIT 403-190-2). **F.** Longitudinal section through hydrozoans in bryozoan colony (GIT 403-418). **G.** *Cornulites baranovi* in *Fistulipora* (GIT 403-218-7). **H.** *Conchicolites* partially intergrown with *Fistulipora* (GIT 403-177-1).

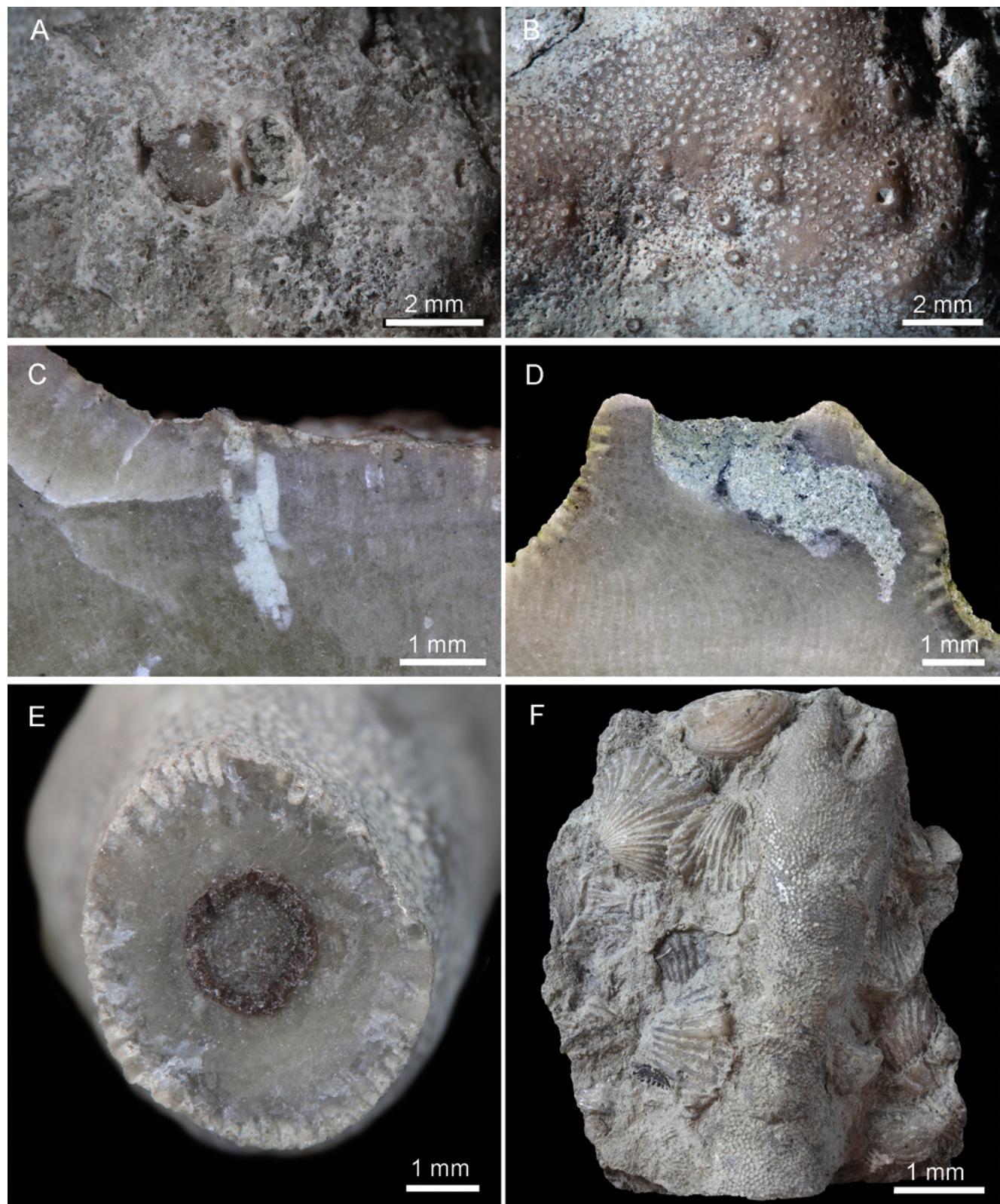


Fig. 4. Intergrowth of bryozoans with other invertebrates from the Ohesaare Formation (upper Pridoli), Ohesaare cliff, Saaremaa Island, Estonia. **A.** *Tuberoconchus wilsoni* partially intergrown with *Fistulipora* (GIT 403-368-1). **B.** *Anoigmaichnus* bioclaustrations in *Fistulipora* (TUG 1307-42-1). **C.** Longitudinal section through *Anoigmaichnus* in *Fistulipora* (TUG 1307-42-2). **D.** Unknown bioclaustration in *Fistulipora* (GIT 430-236). **E.** Unknown tubicolous organism in *Fistulipora* (GIT 403-62). **F.** Unknown tubicolous organism, overgrown by *Fistulipora* (GIT 403-62).

Entelophyllum were fixosessile. Traces in the *Cruziana* ichnofacies were common on the Ohesaare sea floor. Larger nektonic predators were represented by several species of fish and five species of nautiloids (Klaamann, 1970). The bryozoan morphology indicates that colonies were often overturned by storm waves. It is likely that the *Fistulipora* colonies lived under moderate sedimentary stress, caused by storm events and significant clay sedimentation.

Tryplasma-Fistulipora association

Rugosans and *Fistulipora przhidolensis* Kopajevich, 1990 in Pushkin *et al.* (1990) formed a symbiotic association, as indicated by complete intergrowth of both organisms and the perpendicular orientation of rugosans to the bryozoan growth surface. The same association appears earlier in the Pridoli of Saaremaa in the Kaugatuma Formation (Vinn *et al.*, 2020). According to Neuman (1988), *Tryplasma* represents fixosessile rugosans that could grow only on a hard substrate. It seems that walls of endobiotic *Tryplasma* are not markedly thinner than the walls of free-living *Tryplasma* specimens. Thin walls have been recorded in rugosans that lived within Silurian tabulates (Sorauf and Kissling, 2012). The exact process of larval recruitment in *Tryplasma* is not certain, but probably the dead spots of the bryozoan colony were infested. Characteristics of this association are similar in the Kaugatuma and Ohesaare formations, despite somewhat different sedimentation environments. Kaugatuma examples of the association inhabited shallower and hydrodynamically more active waters than the Ohesaare ones. Presumably, this association had a distribution from shallower, nearshore to deeper, offshore regions of the carbonate platform. It has been assumed that this association was beneficial for the rugosans and their bryozoan hosts, and that their relationship may have been mutualistic (Vinn *et al.*, 2020). The latter opinion also is supported by the fact that rugosans could achieve a relatively great length and thus grow for a long time within the bryozoan colony, without being overgrown by the host bryozoan. There is no morphological evidence that endobiotic rugosans caused any harm to the cystoporate colony. The association was probably not accidental (Vinn *et al.*, 2020). Some rugosans in the association have thin walls and such thin or absent walls of solitary rugosans have been previously described by Sorauf and Kissling (2012) from the Silurian, but they grew within the colonies of favositid corals. The symbiosis with bryozoans was not obligatory for the rugosans as in some cases they seem to have grown solitarily before the bryozoan encrustation as epibionts on *Fistulipora*. It is likely that the association with rugosans was not obligatory for *Fistulipora*, as this cystoporate occurs in large numbers without rugosan endobionts in the Ohesaare Formation.

Entelophyllum-Fistulipora association

Entelophyllum and *Fistulipora* formed a symbiotic association, as indicated by the almost complete intergrowth of both organisms and the perpendicular orientation of the rugosan to the bryozoan growth surface. Similar associations of colonial rugosans with bryozoans have not been described previously. There are no obvious morphological differences between free-living and endobiotic

Entelophyllum colonies. The present authors assume that *Entelophyllum* larva settled on a dead spot in *Fistulipora* colony. The occurrence of only one intergrown specimen in the collection indicates that *Entelophyllum* seldom settled on living bryozoans, which differs from solitary *Tryplasma*. Non-intergrown *Entelophyllum* are common fossils in the Ohesaare Formation. Apart from differences in the selection of substrate, the authors presume that the palaeoecology of this association was similar to that of the *Tryplasma-Fistulipora* association.

Hydrozoan-Fistulipora association

The *syn vivo* nature of this association is indicated by the full intergrowth of both organisms and by the fact that the hydrozoan apertures were not encrusted by the bryozoan. *Fistulipora* occur independently in Ohesaare Formation and this association was not obligatory for bryozoans. However, hydrozoans are not known to occur independently of bryozoans in the Ohesaare Formation and the association with the bryozoan may have been obligatory for them. Alternatively, this could have been a preservation issue. The bryozoans greatly enhance the preservability of the hydrozoans. Hydrozoans may have benefited from the hard substrate, provided by the cystoporate colony. There is no evidence that hydrozoans caused any malformations in cystoporate colonies. Hydrozoans as predators probably did not interfere with the feeding of the host bryozoan, as the feeding methods of hydrozoans and bryozoans were different; hydrozoans kill their food with nematocysts and all bryozoans are filter feeders. Hydrozoan-cystoporate associations have not been described previously, but Devonian fenestrate bryozoans contained the budding tubes of the soft-bodied, colonial epibiont, called *Caupokeras* (McKinney, 2009). These tubes are similar to those of extant hydroids and they represent a symbiotic relationship between the host fenestrate bryozoans and the epibiotic hydroids (McKinney, 2009).

Hydrozoan-trepostome association

The full intergrowth of trepostomes with hydrozoans and the fact that hydrozoan apertures were never encrusted by the bryozoan is characteristic to a *syn vivo* association. Similar trepostomes occur independently in the Ohesaare Formation and this association was probably not obligatory for the bryozoan. There is no evidence that hydrozoans caused any malformations in trepostome colonies. The palaeoecology of this association was similar to that of the hydrozoan-*Fistulipora* association. Similar hydroid-trepostome associations have been described from the Emsian of Spain (Suárez Andrés *et al.*, 2020b).

Cornulites-Fistulipora association

Both *Cornulites baranovi* Vinn and Toom, 2020 and *Fistulipora* occur independently in the Ohesaare Formation and this association was neither obligatory for the bryozoan, nor for the cornulitids. There is no morphological evidence that fully or partially intergrown cornulitids caused any harm to the cystoporate colonies. Cornulitids may have benefited from the hard substrate provided by the cystoporate colony. They may have also interfered with the feeding

of the host bryozoan, as both were filter feeders. Cornulitids in similar associations have been interpreted as kleptoparasites (Vinn *et al.*, 2020). The smaller number of intergrown cornulitids, as compared to rugosans, could be explained by the somewhat chance nature of this association.

Conchicolites-Fistulipora association

The partial intergrowth of *Fistulipora* with *Conchicolites* sp. indicates a symbiotic association. The smaller number of intergrown *Conchicolites*, as compared to *Cornulites*, could be explained by their different substrate preferences. *Conchicolites* may have preferred to settle on non-living hard substrates. There are no previous reports of *Conchicolites*-bryozoan symbiosis, but endobiotic *Conchicolites* has been described from Late Ordovician tabulates of Estonia (Vinn and Mõtus, 2012). It is not known whether *Conchicolites hosholmensis* was an obligatory coral symbiont, or if it occurred as encrusters on biogenic and abiogenic substrates, as well. The relatively thin walls of *C. hosholmensis* could be interpreted as indicating obligatory symbiosis (Vinn and Mõtus, 2012). In contrast to the *Conchicolites*-tabulate association, the *Conchicolites-Fistulipora* association probably was accidental.

Anoigmaichnus-Fistulipora association

Anoigmaichnus is a bioclaustration, formed by a living bryozoan colony around a worm-like infesting organism (Vinn *et al.*, 2014). Several species of *Anoigmaichnus* have previously been described from the Middle and Late Ordovician of Estonia. The specimens of the present authors from the Ohsaare Formation extend the known stratigraphic occurrence of *Anoigmaichnus* from early Katian (Vinn *et al.*, 2018) to latest Pridoli. The palaeoecology of Ordovician *Anoigmaichnus*-bryozoan associations has been studied in detail and most likely these bioclastrations belonged to bryozoan parasites (Vinn *et al.*, 2014, 2018). On the basis of the morphology of the apertures and longitudinal sections, the authors envision the ecology of *Anoigmaichnus-Fistulipora* association to have been somewhat similar to the *Anoigmaichnus odinsholmensis-Mesotrypa bystrowi* (Darriwilian) (Vinn *et al.*, 2014) and *Anoigmaichnus odinsholmensis-Mesotrypa expressa* (Katian) (Vinn *et al.*, 2018) associations. However, the Ordovician analogues occurred in trepostome bryozoans and the Pridoli records belong to cystoporates. Moreover, there are at the most four *Anoigmaichnus* bioclastrations per colony in the Ordovician trepostomes, while Silurian cystoporates contain up to ten times more bioclastrations. It is possible that the *Anoigmaichnus* organisms became more abundant over time. Alternatively, different parasites inhabited the Ordovician *Anoigmaichnus* bioclastrations in trepostomes.

Microconchid-bryozoan association

Vinn and Wilson (2010) described *syn vivo* association of two microconchids with sheet-like encrusting bryozoans. Here the present authors report an intergrowth of *Fistulipora* with a single specimen of *Tuberocoelchus wilsoni*. However, the discovery of only three bioclaustrated microconchids can be explained by the chance nature of this association. There is no morphological evidence that the bioclaustrated

microconchids caused any harm to the bryozoans. However, microconchids may have interfered with the feeding of the host bryozoan, as they both were filter feeders.

Unknown endobiont-Fistulipora association

Fistulipora colonies contain cavities of unknown endobionts, which at least in their apertural parts are true bioclastrations. The elevated apertures of the cavities may have resulted from spatial competition between the bryozoan host and its endobiont. The cavities may have contained a soft-bodied endobiont, possibly a cnidarian. The lack of malformations in the bryozoan colony indicates that the relationship was not significantly harmful to the bryozoan host. Somewhat similar unknown endobiont cavities have been described from Late Ordovician trepostomes in Estonia (Vinn *et al.*, 2018), but such cavities are not known in cystoporates, other than in *Fistulipora*.

Tubicolous organism-Fistulipora association

Overgrown, tubicolous organisms resemble the tubes of various cnidarians, such as *Byronia*. The growth pattern of *Fistulipora* around the unknown tubes indicates that the tubes probably grew in an upright position on the seafloor during the bryozoan encrustation. It is difficult to speculate on the exact nature of the relationship, but most likely the bryozoan encrustation did not cause much harm to the tubicolous organism. The bryozoan presumably used the tubicolous organism just as a hard substrate, but maybe also to reach a higher tier for filter-feeding. Similarly, bryozoans sought a higher tier for feeding in the Silurian of North America, where they encrusted the vertical stems of living crinoids (Peters and Bork, 1998).

Symbiotic interactions in the Pridoli of Baltica

Four symbiotic associations were described previously from the Pridoli of Estonia (Vinn and Wilson, 2010, 2012; Vinn *et al.*, 2020, 2021). Rugosans are known to form symbiotic associations with stromatoporoids (Vinn and Wilson, 2012) and cystoporate bryozoans (this study; Vinn *et al.*, 2020). In contrast to the Llandovery to Ludlow interval, where rugosans predominantly infested stromatoporoids in the Pridoli, they seem to have preferred cystoporates as hosts. This could be explained by the lower symbiont tolerance of host stromatoporoids in the Pridoli of Baltica, as compared to the symbiosis-prone host stromatoporoids in the earlier Silurian. The Pridoli may have been the time of appearance of symbiosis-prone cystoporate bryozoans, which remained common in the following Early Devonian (Plusquellec and Bigey, 2019; Sendino *et al.*, 2019; Suárez Andrés *et al.*, 2020a). Cystoporate bryozoans also hosted hydrozoans, *Anoigmaichnus*, cornulitids and bioclastrations of unknown endobionts. However, the associations with cornulitids were likely accidental. Likewise accidental were the associations of microconchids and sheet-like bryozoans (Vinn and Wilson, 2010). In contrast, abundant cases of symbiosis of *Fistulipora* with solitary rugosans and hydrozoans and fewer cases of symbiosis with *Anoigmaichnus* may have not been accidental. The hydrozoan-trepostome associations also were probably not accidental in the Pridoli of Saaremaa.

There appears to be a trend of increasing symbiosis records from the Llandovery to the Ludlow in Baltica (Vinn and Wilson, 2016). A rapid increase in the number of symbiosis records from nine in the Wenlock (1.7 records per 1 my) to 28 in the Ludlow (6.7 records per 1 my) may have had a biological cause (Vinn and Wilson, 2016). It could have been a function of the increase in the number of mutualistic taxa that had evolutionary advantages over taxa less amenable to symbiotic relationships (Vinn and Wilson, 2016). However, this trend is not necessarily an evolutionary trend; it may alternatively have been driven ecologically. There may be numerous biases affecting the Silurian symbiosis data from biostratinomic, through diagenetic, to collecting bias (i.e. specimens from more marly beds are easier to collect than those from the lithified pure limestone). On the other hand, marly beds are common throughout the Llandovery-Ludlow section in Estonia and Llandovery; the Wenlock and Ludlow are all relatively well covered with various carbonate rocks. Nevertheless, the extremely low number of previous records of symbiotic associations ($N = 4$) from the Pridoli has been interpreted as an artefact of sampling bias, as there are very few Pridoli outcrops, as compared to those of the Llandovery, Wenlock and Ludlow (Vinn and Wilson, 2016), supported by the eleven associations in the Pridoli of Baltica. New data from the Pridoli of Saaremaa indicate that the Pridoli probably was not a time of lowered symbiosis levels in the regional ecosystem and globally. The symbiosis levels in the Pridoli of Baltica (2.9 records per 1 my) were comparable to those in the Wenlock and probably also the Early Devonian.

CONCLUSIONS

The cystoporate colonies of irregular shape from the Ohesaare Formation (upper Pridoli) are often intergrown with other invertebrates. Cystoporates *Fistulipora* formed symbiotic associations with rugosans (mostly with *Tryplasma*, rarely with *Entelophyllum*), cornulitids (*Cornulites* and *Conchicolites*), *Anoigmaichnus*, micro-conchids (*Tuberoconchus wilsoni*), unknown tubicolous organisms and unknown soft-bodied organisms. Trepostomes formed symbiotic associations only with hydrozoans. Most common is *Tryplasma-Fistulipora* symbiosis in the Ohesaare Formation. There appears to be a trend of increasing symbiosis records from the Llandovery to the Ludlow in Baltica and some decline in the Pridoli, most likely due to sampling bias. The Pridoli symbiosis records are based on few localities, whereas the rest of the Silurian is represented by numerous outcrops.

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