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; Słowiński 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 cystoporate 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 cystoporate 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-cystoporate 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 (Melehin 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/lagoon-al, 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
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 *Entophysyllum* (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 *Bainbridia*, thus an “auloporid-like” organism, likely a hydrozoan. Their external look is similar to members of Trachypsammiidae, 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 zoooid 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 cornulid 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 *Conchicollites* 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 (Kläamann, 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; Musabelli and Zatoń, 2018; Zatoń and Wrzolek, 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., *Spongophyloides* aff. *nikiforovae*, *Entophysyllum articulatum*, *E. pseudodiant hus*, *Cantrillia eichwaldi*, *Gyalophyllum ex gr. angelinii*), bryozoans (nine species), crinoids (two species) and trilobites (five species; Kläämann, 1970; Nestor, 1990; Pushkin et al., 1990; Mötus and Hints, 2007, Márs and Nestor, 2014). In the Pridoli of Saarmema, *Tryplasma* and *Entophysyllum* were the most common rugosans (Kaljo, 1970, 1997). Most solitary rugose corals were libersessile 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
Intergrowth of bryozoans with other invertebrates

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. Entelophyllium 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. Conchiculites 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* bioclaustations 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 solitary 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 biocl Clawuation, 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 Ohesaare 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 bioclaustrations 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 bioclaustrations per colony in the Ordovician trepostomes, while Silurian cystoporates contain up to ten times more bioclaustrations. It is possible that the Anoigmaichnus organisms became more abundant over time. Alternatively, different parasites inhabited the Ordovician Anoigmaichnus bioclaustrations 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 Tuberoconchus 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 bioclaustrations. 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, rare cases of biotic associations with stromatoporoids (Vinn and Wilson, 2010, 2012; Vinn et al., 2020) and cystoporate bryozoans (this study; Vinn et al., 2018) occur 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 bioclaustrations 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 biostratigraphic, 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. Cystoporate *Fistulipora* formed symbiotic associations with rugosans (mostly with *Tryplasma*, rarely with *Entelophyllum*), cornulitids (*Cornulites* and *Conchicolites*), *Anoigmaichnus*, microconchids (*Tuberoconchus wilsonti*), 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.

Acknowledgements

Financial support to O. V. and U. T. was provided by Estonian Research Council Grants (IUT20–34 and PRG836). We are grateful to G. Baranov, Department of Geology, Tallinn University of Technology, for digital photographing of the specimens and Mare Isakar for access to the Tartu University collections. We are also grateful to Dr. Mikolaj K. Zapalski for help with hydrozoan taxonomy. Błażej Berkowski and an anonymous reviewer are thanked for their helpful remarks and comments, which helped to improve the final version of the manuscript.

REFERENCES

Astrova, G. G., 1970. Nodye ciluriske i rannedevonskie mshanki tsistoporapota i trepostomata Estonii i Podolii. In: Astrova, G. G. & Chudinova, I. I. (eds), *Novye vidi mshanok i korallow*. Nauka, Moscow, pp. 7–22. [In Russian.]

Astrova, G. G. & Kopajevich, G. V., 1970. Bryozoa. In: Kaljo, D. (ed.), *The Silurian of Estonia*. Valgus, Tallinn, pp. 130–140. [In Russian, English summary.]

Baliński, A. & Yuanlin, S., 2010. Tubular shell infestations in some Mississippian spirilophous brachiopods. *Acta Palaeontologica Polonica*, 55: 689–694.

Berkowski, B., Jakubowicz, M., Belka, Z., Król, J. J. & Zapalski, M. K., 2019. Recurring cryptic ecosystems in Lower to Middle Devonian carbonate mounds of Hamar Laghdad (Anti-Atlas, Morocco). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 523: 1–17.

Hill, D., 1981. *Treatise on Invertebrate Paleontology*. Part F. *Coelenterata. Supplement 1. Rugosa and Tabulata*. Volume 2. The Geological Society of America and the University of Kansas, Boulder, Colorado, and Lawrence, Kansas, pp. F379–F762.

Hints, O., 2008. The Silurian System in Estonia. In: Hints, O. Ainsaar, L., Männik, P. & Meidla, T. (eds), *The Seventh Baltic Stratigraphical Conference. Abstracts and Field Guide*. Geological Society of Estonia, Tallinn, 46 pp.

Kaljo, D., 1970. Rugose corals. In: Kaljo, D. (eds), *The Silurian of Estonia*. Valgus, Tallinn, pp. 125–130. [In Russian, English summary.]

Kaljo, D., 1997. Rugose corals. In: Raukas, A. & Teedumäe, A. (eds), *Geology and Mineral Resources of Estonia*. Estonian Academy Publishers, Tallinn, pp. 223–224.

Klaamann, E., 1970. Ohesaare Stage. In: Kaljo, D. (eds), *The Silurian of Estonia*. Valgus, Tallinn, pp. 297–300. [In Russian, English summary.]

Kopajevich, G. V., 1968. O novom rode kriptostomnykh mshanok semeistva Rhinichitidae iz silura Estonii. Moskovskoe Obshchestvo Ispytatelei Priorodory. Byulleten, Otdelenie Geologi, 43: 127–129. [In Russian.]

Kopajevich, G. V., 1971. O rode Diplolecma (Bryozoa) i ego predstavitelvyakh iz siluriiskikh otlozhenii Estonii. *Paleontologicheskih Zhurnal*, 2: 119–123. [In Russian.]

Kopajevich, G. V., 1975. Siluriskie mshanki Estonii i Podoloi (Cryptostomata and Rhabdomesonata). *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, 151: 151–153. [In Russian.]

Märs, T. & Nestor, H., 2014. Stop B11: Ohesaare cliff. In: Bauert, H., Hints, O., Meidla, T. & Männik, P. (eds), *4th Annual Meeting of IGCP 591, Estonia, 10–19 June 2014. Abstracts and Field Guide*. University of Tartu, Tartu, pp. 200–201.

McKinney, F. K., 2009. Bryozoan-hydroid symbiosis and a new ichnogenus, *Caupokeras*. *Ichnos*, 16:193–201.

Melchin, M. J., Cooper, R. A. & Sadler, P. M., 2004. The Silurian Period. In: Gradstein, F. M., Ogg, J. G. & Smith, A. G. (eds), *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge, pp. 188–201.

Möttus, M. A. & Hints, O. (eds), 2007. Excursion B2: Lower Paleozoic geology and corals of Estonia. August 18–22.
In: Excursion Guidebook. 10th International Symposium on Fossil Cnidaria and Porifera. Institute of Geology at Tallinn University of Technology, Tallinn, p. 64.

Musabelli, S. & Zatoń, M., 2018. Patterns of cornulitid encrustation on the Late Devonian brachiopod shells from Russia. Proceedings of the Geologists’ Association, 129: 227–234.

Nestor, H., 1990. Locality 7: 4 Oheesaare cliff. In: Kaljo, D. & Nestor, H. (eds), Field meeting. Estonia 1990. An Excursion Guidebook. Institute of Geology, Estonian Academy of Sciences, Tallinn, pp. 175–178

Nestor, H. & Einasto, R., 1977. Model of facies and sedimentology for Paleobaltic epicontinental basin. In: Kaljo, D. (eds), Facies and Fauna of the Baltic Silurian. Academy of Sciences of the Estonian S. S. R. Institute of Geology, Tallinn, pp. 89–121. [In Russian, English summary.]

Nestor, H. & Einasto, R., 1997. Ordovician and Silurian carbonate sedimentation basin. In: Raukas, A. & Teedumäe, A. (eds), Geology and Mineral Resources of Estonia. Estonian Academy Publishers, Tallinn, pp. 192–205.

Neuman, B. E. E., 1988. Some aspects of life strategies of Early Palaeozoic rugose corals. Lethaia, 21: 97–114.

Palmer, T. J. & Wilson, M. A., 1988. Parasitism of Ordovician bryozoans and the origin of pseudoborings. Palaeontology, 31: 939–949.

Peters, S. E. & Bork, K. B., 1998. Secondary tiering on crinoids from the Waldron Shale (Silurian: Wenlockian) of Indiana. Journal of Paleontology, 72: 887–894.

Plusquellec, Y. & Bigey, F. P., 2019. New data on the intergrowth of Rugosa-Bryozoan in the Lower Devonian of North Gondwana. Carnets de Géologie, 19: 421–437.

Pushkin, V. I., Nekhorosheva, L. V., Kopaevich, G. V. & Yaroshinskaya, A. M., 1990. Przhidolskie mshanki SSSR. Nauka, Moscow, 125 pp. [In Russian.]

Rogers, R.R., Curry Rogers, K.A., Bagley, B.C., Goodin, J.J., Hartman, J.H., Thole, J.T. & Zatoń, M., 2018. Pushing back to the Cretaceous. Acta Palaeontologica Polonica, 63: 271–280.

Složiwski, J., Surmik, D., Duda, P. & Zatoń, M., 2020. Assessment of serpulid-hyroid association through the Jurassic: A case study from the Polish Basin. PLoS ONE, 15(12): e0242924.

Sorauf, J. E. & Kissling, D. L., 2012. Rugosans immersed in Silurian Paleoflavosites; Brassfield Formation (Llandovery) of Ohio. Geologica Belgica, 15: 220–225.

Stasińska, A., 1982. Colony structure and systematic assignment of Cladochomus temutcollis McCoy, 1847 (Hydroidea). Acta Palaeontologica Polonica, 27: 59–64.

Suárez Andrés, J. L., Sendino, C. & Wilson, M. A., 2020a. Coral-bryozoan associations through the fossil record: glimpses of a rare interaction. In: Wyse Jackson, P. & Zágoršek, K. (eds), Bryozoan Studies 2019. Czech Geological Survey, Prague, pp. 157–168.

Suárez Andrés, J. L., Sendino, C. & Wilson. M. A., 2020b. Life in a living substrate: Modular endosymbionts of bryozoan hosts from the Devonian of Spain. Palaeogeography, Palaeoclimatology, Palaeoecology, https://doi.org/10.1016/j.palaeo.2020.109897

Tapanila, L., 2008. Direct evidence of ancient symbiosis using trace fossils. In: Kelley, P. H. & Bambach, R. K. (eds), From Evolution to Geobiology: Research Questions Driving Paleontology at the Start of a New Century: Paleontological Society Short Course, October 4. Paleontological Society Papers, 14: 271–287.

Taylor, P. D., 1990. Preservation of soft-bodied and other organisms by bioimmuration – a review. Palaeontology, 33: 1–17.

Torsvik, T. H. & Cocks, L. R. M., 2013. New global palaeogeographical reconstructions for the Early Palaeozoic and their generation. In: Harper, D. A. T. & Servais, T. (eds), Early Palaeozoic Biogeography and Palaeoecography. Geological Society, London, Memoirs, 38: 5–24.

Vinn, O., Ernst, A. & Toom, U., 2018. Bioclaustrations in Upper Ordovician bryozoans from northern Estonia. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 289: 113–121.

Vinn, O., Ernst, A., Wilson, M. A. & Toom, U., 2020. Symbiosis of rugose corals with the cystoporaceous bryozoan Fistulipora przhidolensis in the Přidoli (latest Silurian) of Saaremaa, Estonia. Palaios, 35: 237–244.

Vinn, O., Ernst, A., Wilson, M. A. & Toom, U., 2021. Symbiosis of cornulitids with the cystoporaceous bryozoan Fistulipora in the Přidoli of Saaremaa, Estonia. Lethaia, https://doi.org/10.1111/let.12385

Vinn, O. & Mõtus, M.-A., 2012. Diverse early endobiotic coral symbiont assemblage from the Katian (Late Ordovician) of Baltica. Palaeogeography, Palaeoclimatology, Palaeoecology, 321–322, 137–141.

Vinn, O. & Toom, U., 2020. New cornulitid from the Oheesaare Formation (late Přidoli) of Saaremaa, Estonia. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 298: 67–73.

Vinn, O. & Wilson, M. A., 2010. Microconchid-dominated hardground association from the late Přidoli (Silurian) of Saaremaa, Estonia. Palaeontologia Electronica, 13.2.9.A.

Vinn, O. & Wilson, M. A., 2012. Epi- and endobionts on the Late Silurian (early Přidoli) stromatoporoids from Saaremaa Island, Estonia. Annales Societatis Geologorum Poloniae, 82: 195–200.

Vinn, O. & Wilson, M. A., 2016. Symbiotic interactions in the Silurian of Baltica. Lethaia, 49: 413–420.

Vinn, O., Wilson, M. A., Mõtus, M.-A. & Toom, U., 2014. The earliest bryozoan parasite: Middle Ordovician (Darriwilian) of Osmussaar Island, Estonia. Palaeogeography, Palaeoclimatology, Palaeoecology, 414: 129–132.

Zapalski, M. K., 2007. Parasitism versus commensalism: the case of tabulate endobionts. Palaeontology, 50: 375–380.

Zapalski, M. K., 2009. Parasites in Emsian–Eifelian Favosites (Anthozoa, Tabulata) from the Holy Cross Mountains (Poland): changes of distribution within colony. In: Königshof, P. (eds), Devonian Change: Cases Studies in Palaeogeography and Palaeoecology. The Geological Society of London, Special Publications, 314: 125–129.

Zapalski, M. K., Berkowski, B. & Klug, C., 2018. Subepidermal Emsian “auloporids” on crinoids from Hamar Laghdad (Anti-Atlas, Morocco). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 290: 103–110.
Zapalski, M. K. & Hubert, B. L. M., 2011. First fossil record of parasitism in Devonian calcareous sponges (stromatoporoids). *Parasitology*, 138: 132–138.

Zatoń, M. & Borszcz, T., 2013. Encrustation patterns on post-extinction early Famennian (Late Devonian) brachiopods from Russia. *Historical Biology*, 25: 1–12.

Zatoń, M., Borszcz, T. & Rakociński, M., 2017. Temporal dynamics of encrusting communities during the Late Devonian: a case study from the Central Devonian Field, Russia. *Paleobiology*, 43: 550–568.

Zatoń, M. & Wrzołek, T., 2020. Colonization of rugose corals by diverse epibionts: Dominance and *syn vivo* encrustation in a Middle Devonian (Givetian) soft-bottom habitat of the Holy Cross Mountains, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 556: 109–899.

Zatoń, M., Wrzołek, T. & Ebbestad, J. O. R., 2020. Patterns of sclerobiont colonization on the rugose coral *Schlotheimophyllum patellatum* (Schlotheim, 1820) from the Silurian of Gotland, Sweden. *Lethaia*, 53: 486–499.
