



Scale dependent diversity of bryozoan assemblages in the reefs of the Late Ordovician Vasalemma Formation, Estonia

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The reefs of the Vasalemma Formation, late Sandbian, Late Ordovician, of northern Estonia contain an exceptional rich and abundant bryozoan fauna. They are an example of contemporaneous bryozoan-rich reefs known from around the world, representing the peak diversification interval of this group during the Ordovician. The global Ordovician bryozoan diversification was associated with a decrease in provinciality, a pattern known from other skeletal marine metazoans of this period. The diversification is associated with climatic cooling and increasing atmospheric and sea water oxygenation. However, the mechanisms that led to the bryozoan diversification are poorly known. Here we estimate the bryozoan richness (α and γ diversity) and turnover (β diversity) at the level of samples, reefs, and formations in the Vasalemma Formation and in contemporaneous reef limestone occurrences of the Baltoscandian region. The resulting richness and turnover values differ among the three observational levels and hence are scale dependent. A consistent pattern with lowest between-reef turnover and relatively high between-sample turnover could be detected, reflecting high small-scale (within reef) heterogeneities in lithology and original bryozoan habitat. This is consistent with published work, in which evidence has been presented for small-scale substrate heterogeneity as the most important diversification driver of the Ordovician brachiopod diversification in the Baltoscandian region. The fact that reefs and their local substrate are strongly organism moderated environments sheds light on the potentially important ecosystem engineering role of organisms, such as bryozoans, for the Ordovician diversification. □ *Diversity partitioning, richness, Baltica, bryozoan reefs, reef clustering.*

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Bryozoan skeletons are a major component of the reefs of the Vasalemma Formation (Sandbian, Late Ordovician) in northern Estonia. The Vasalemma reefs, with their high bryozoan abundance and richness, can be seen as typical for the time interval.

In reefs of Middle and early Late Ordovician age, bryozoans commonly dominate the preserved skeletal fauna, particularly in eastern Laurentia (see Webby 2002 for a review), but also elsewhere (e.g. Hong *et al.* 2018). Bryozoans built, together with pelmatozoans, corals, and stromatoporoids, reef-forming consortia (e.g. Cuffey 2006; Kröger *et al.* 2017) that probably influenced reef distribution patterns and the regional facies distribution at seascape scale level (e.g. Kröger & Penny 2020).

Bryozoans diversified rapidly during the Ordovician in various marine benthic environments (e.g. Taylor & Larwood 1990; Taylor & Ernst 2004;

Ernst 2018). The peak of the diversification occurred during the Sandbian (Tuckey & Anstey 1992; Ernst 2018). However, global Ordovician bryozoan provinciality patterns show that provinciality decreased steadily from the Early Ordovician (Floian) into the Katian, being the lowest in the mid Katian (Tuckey 1990; Taylor & Ernst 2004; Buttler *et al.* 2013). Provinciality is an important factor influencing the diversity dynamics of bryozoans during the Ordovician with significant effects both on extinctions and originations (Anstey 1986; Tuckey & Anstey 1992). The rising global biodiversity during the Middle – Late Ordovician, therefore, results from processes other than differentiation at the level of bioprovinces. The acme of Ordovician bryozoan reefs and peak bryozoan diversification coincided with the time interval that records the steepest diversity increase of the Great Ordovician Biodiversity Event

(GOBE, Rasmussen *et al.* 2019) and with a massive global expansion of metazoan reefs (Webby 2002).

Although bryozoans comprise only a minor component of the Ordovician skeletal marine fossil record, their role in the diversification process as important ecosystem engineers should not be underestimated (see e.g. Kröger *et al.* 2017). In modern reefs bryozoans are known to create complex framework habitats that enhance biodiversity (Lombardi *et al.* 2014; Wood *et al.* 2012). Reef sites, therefore, potentially were crucial environments not only for the diversification of bryozoans at global scale but also for many other skeletal metazoans. The conditions that

supported and constrained bryozoan richness within reef environments can give important information about the processes that drove this diversification.

The reefs of the Vasalemma Formation are exposed in active and abandoned limestone quarries in northern Estonia (Fig. 1). Two of us (BK, UT) have conducted geological and palaeontological research in these quarries for decades, and at the Estonian Geological Collections there is a wealth of material available for analysis. Here we document and review the available bryozoan-related data with the aim, of obtaining a better overview about the facies-dependent and area-dependent heterogeneity of the fauna.

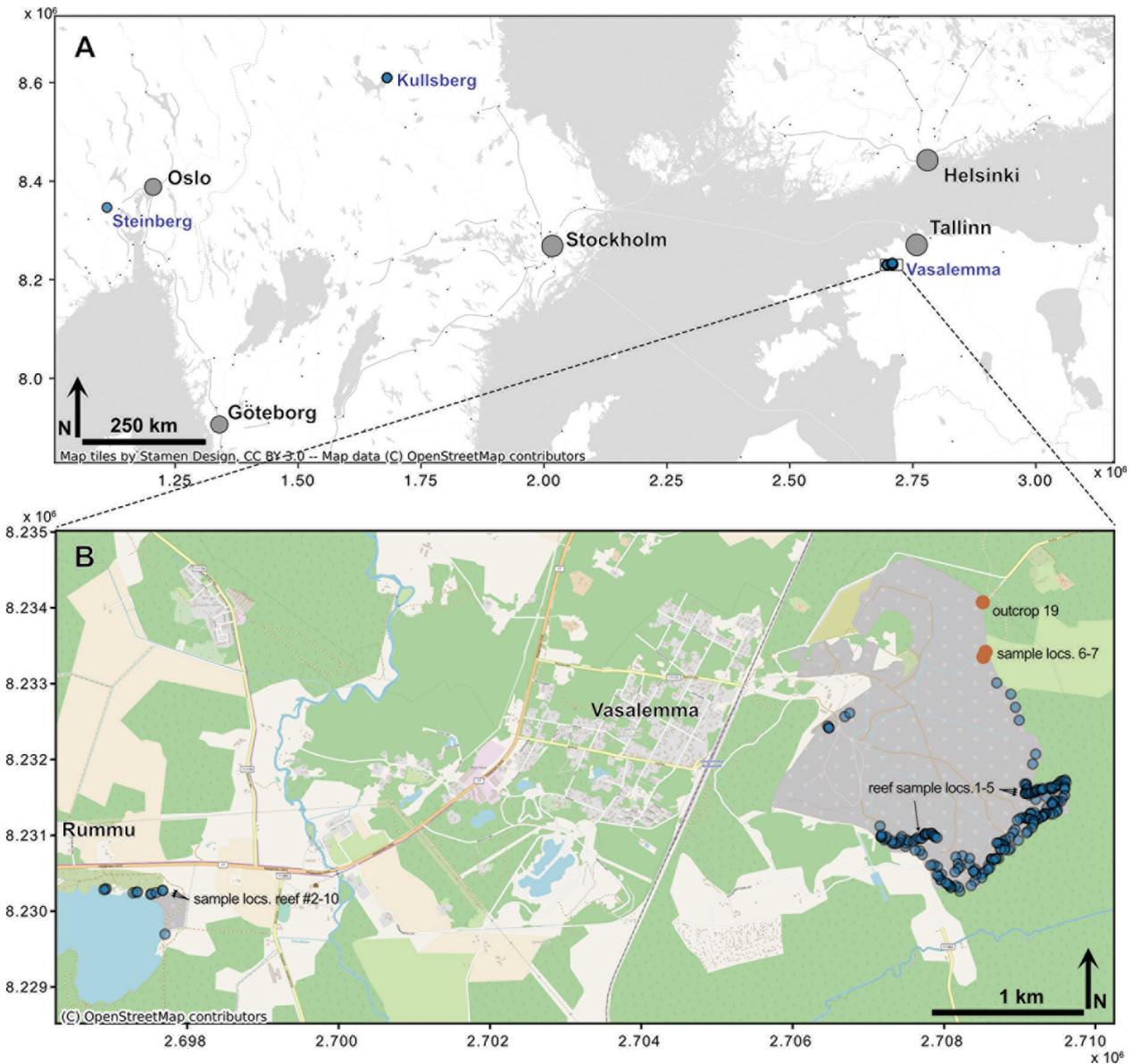


Fig. 1. Maps of sample localities. A, blue circles mark sampled localities. Kullberg: Kullberg quarry, Dalarna, Sweden, Kullberg Formation, late Sandbian; Steinvik: Steinberg, Sandsvær-Eiker district, Norway, Steinvik Formation, early Katian; Vasalemma: Vasalemma area, Estonia, Vasalemma Formation, late Sandbian. B, detail of Vasalemma area, northern Estonia. Blue circles mark reef sites. Red circles mark non-reefal sample localities. Locs., localities. Coordinate system: Web Mercator.

We compare these data with our own new data from the roughly time-equivalent reefs of the Steinvika Formation, Norway, and the Kullsberg Formation, Sweden.

The aim of our analysis was also to complement knowledge about spatial heterogeneity of other bryozoan-rich Ordovician reefs (e.g. Mingan Formation, Quebec: Penny *et al.* 2020) and to help to better reconstruct the processes of the diversification of Ordovician bryozoans.

Material and methods

Our report reflects a compilation of results from multiple years of field work with changing research questions as main objectives. This poses a challenge to the analysis, because, the data are a puzzle of different research methods, reflecting changing research questions, sampling situations and practices.

The reef coordinates were recorded with a handheld GPS device in 07/2010 and 07/2020 along the then existing quarry walls in the Vasalemma quarry (Fig. 1B) and in 05/2018 in the Rummu quarry (Fig. 1B). The point counts in the Vasalemma quarry outcrops have been taken with the method described by Kröger *et al.* (2014a) and the point counts taken in the Rummu quarry with the method described by Kröger *et al.* (2017). In Kröger *et al.* (2014a), the point-counts only included the skeletal elements and not the limestone matrix, and lithologies were not distinguished into well delimited and mapped types. This limits comparability of the lithology data between the Rummu and Vasalemma quarries.

Seventeen thin sections were studied from the Vasalemma quarry and 25 from the Rummu quarry (= 42 thin sections from the Vasalemma Formation). The thin section samples were taken in 2019 from the Kahula Formation near outcrop 'waterfall' (V7: N 59.245°, E 24.331°), from the echinoderm grainstone facies of the Vasalemma Formation (V1: N 59.233°, E 24.333°), and from reef core facies in the southeastern part of Vasalemma quarry (V2 and V3: N 59.233°, E 24.334°; V4: N 59.236°, E 24.339°; V5: N 59.235°, E 24.339°), and in 2018 from Rummu reefs #8 (N 59.230°, E 24.227°), #9 (N 59.230°, E 24.227°), and #10-#11 (= reef figured in Kröger *et al.* 2014a, fig. 9a, 14; N 59.230°, E 24.227° (see Fig. 1B, and Kröger *et al.* 2014ba).

The samples from the Kullsberg quarry in Sweden were collected in May 2019 from five reef positions within the quarry (Kul-1: N 60.931°, E 15.099°, Kul-2: N 60.930°, E 15.0999°, Kul-3: N 60.938°, E 60.938°, Kul-4: N 60.930°, E 15.101°, and Kul-5: N

60.930°, E 15.101°). The material from the Steinvika Formation at Steinberg road cut, Drammen municipality, Norway, was collected in September 2017, from three reef localities (St-1: N 59.761°, E 9.984°, St-2: N 59.760°, E 9.984°, and a third locality without GPS coordinates a few tens of meters away from St-1, and St-2). The collected material included series of fist-sized rock fragments from which serial thin section were made, both in the plane of bedding and perpendicular of it.

In total, 222 thin sections were made from the Kullsberg samples, and 200 thin sections were from the Steinberg samples (size of the thin sections: 24 × 48 mm, and 50 × 50 mm). The advantage of bryozoans as modular organisms is that they can be identified even in small fragments. Bryozoan fragments were counted considering their size and position within the serial thin sections. Small bryozoans such as *Kukersella borealis* Bassler, 1911, with branch diameters of less than 0.5 mm were usually regarded as separate fragments in each thin section, whereas larger colonies cut in several serial thin sections, were counted as single colony.

The maps (Fig. 1) were produced with Python (Version 3.9.15) packages matplotlib (Version 3.6.2) and contextily (Version 1.2.0) using OpenStreetMap and tiles from OpenStreetMap.de and Stamen providers. The point pattern of the reef coordinates was analysed, and the G-test was conducted with Python (Version 3.9.15) package pointpats (Version 2.2.0). The G-test is a maximum likelihood statistical significance test and tests if empirical data fit a theoretical expectation (McDonald 2014). Here we computed the G-function for the empirical nearest neighbour distances and replications under a completely spatially random process. The cumulated distribution against distance shows differences between the empirical and random point pattern. The pattern is clustered when the cumulative curve of the nearest neighbour distance accumulates faster than under random expectation and slower, when the pattern is dispersed (Ripley 1979).

For the cluster analysis of the point-counts and thin section bryozoan counts we used the package vegan (Version 2.5-7) (Oksanen *et al.* 2013) of the R-statistical computing software (Version 4.0.4). Before clustering we normalized the samples, i.e., made margin sum of squares equal to one. We used the Bray-Curtis dissimilarity index throughout for computing dissimilarities among samples.

The richness estimates of the alpha diversities (α , within sample diversity) and gamma diversities (γ , total diversity of all samples) were calculated as a coverage standardised, extrapolated Hill number ($q = 0$) using the function iNEXT (Version 2.0.2.) of the

package iNEXT (Hsieh *et al.* 2016). The beta diversity (β , between sample diversity) was calculated by two methods: as proportional species turnover (β_{pt}), which is $1-(\alpha/\gamma)$; and using the method suggested by Cardoso *et al.* 2014), where β -diversity (our β_j) is measured as edge-length difference in trees resulting from hierarchical cluster analysis. With this method edge-length is a measure of the similarity between the clusters. We used the method of Cardoso *et al.* (2014) to allow for a better comparability with other studies. We calculated 95% confidence interval (ci) from the mean. For an estimation of the total number of species and genera known from the Vasalemma Formation we additionally queried the Database of the Geoscience Collections of Estonia (SARV, <https://fossilid.info> at 08.02.2023).

The material illustrated are stored in the collections of the Museum of Evolution, Uppsala University (PMU), Natural History Museum Oslo (prefix PMO), and of Tallinn Technical University (prefix GIT). The non-illustrated thin sections from Vasalemma and Rummu quarries used in this study are stored in the GIT. Supplementary data can be downloaded from <https://doi.org/10.5281/zenodo.7835245>.

Geological setting

The Vasalemma Formation of northern Estonia is found in the East European Craton, which, during

the Early Palaeozoic, formed the Baltic Palaeobasin of the Baltica Palaeocontinent (see e.g. Cocks & Torsvik 2005). During the Middle and Late Ordovician the region was part of the northern shallow shelf of the Baltic Palaeobasin, with a coastline probably situated further north toward the Finnish mainland and the center of the basin directed toward the south in direction of Latvia and Lithuania (e.g. Poprawa *et al.* 1999). Because of the relatively central position on the East European Craton, the Ordovician sediments of the area were very little affected by diagenetic processes and its fossil content and sedimentary record is pristinely preserved (e.g. Ainsaar *et al.* 2010).

Results from combined litho-, bio-, and chemostratigraphy allow for a high-resolution stratigraphical correlation of the strata of the Vasalemma Formation across Baltoscandia (Meidla *et al.* 2023, see also Kröger *et al.* 2014ab). The strata can be age constrained as latest Sandbian Stage, belonging to the uppermost Keila East Baltic Regional Stage, and correspondingly to the uppermost Dalbyan Scandinavian Regional Stage (Meidla *et al.* 2023; Nielsen *et al.* 2023, Fig. 2)

The Vasalemma Formation is preserved in a c. 20 km long E-W stretched belt with a N-S extension of c. 5 km. Toward the north, the extension of the formation is partly limited by an erosional front. Its western, southern, and eastern extension are relatively well known from drill core sections and surface outcrops (Kröger *et al.* 2014a). Hence, the Vasalemma

| Epoch | Stage | Regional Stage | | Lithostratigraphy | | | | Regio. Stage | | |
|-----------------|----------|----------------|--------------|-------------------|-----------------|----------|------------------|--------------|-----------|------------|
| | | Scandinavia | Baltic | Norway | | Sweden | northern Estonia | Baltic | | |
| | | | | Oslo area | Skien-Langesund | Siljan | | | | |
| LATE ORDOVICIAN | Katian | Ka4 | Jerrestadian | Pirgu | Grimløya | Herøya | Johnstorp | Moe | Pirgu | |
| | | Ka3 | Moldään | Vormsi | Venstøp | Venstøp | Fjäckå Shale | Kõrgesaare | Vormsi | |
| | | | | Nabala | | | Saunja | Nabala | | |
| | | | | Rakvere | | | Paekna | Rakvere | | |
| | | | | Oandu | | | Rägavere | Rakvere | | |
| | Sandbian | Ka1 | Keila | Solvang | Steinvika | Freberga | Moldå Lst | Hirmuse | Oandu | |
| | | | | Nakkholmen | | | Skålberg Lst | | Vasalemma | |
| | | Sa2 | Dalbyan | Haljala | Frognerkilen | Fossum | Kullberg Lst | Kahula | Haljala | |
| | | | | | Arnestad | | | | | Skagen Lst |
| | | | | | Dalby Lst | | | | | |

Fig. 2. Regional stratigraphical scheme of early Late Ordovician strata of Baltoscandia with reefs (marked with asterisks). Lithostratigraphical units are formations if not otherwise marked. Subdivisions in Stage column are Ordovician time slices (after Bergström *et al.* 2009). Compiled from Owen *et al.* (1990), Calner *et al.* (2010), Meidla *et al.* (2023), Nielsen *et al.* (2023). Lst, Limestone. Regio., Regional. Numbers give Million years ago. Grey fields are sedimentary hiatus.

Formation forms a relatively narrow belt of an up to 15-m-thick pelmatozoan grainstone with concentrations of patch reefs in its central areas. Three regions with reef concentrations are known from surface outcrops: the area around the Vasalemma settlement (Vasalemma quarry); the area south of the Rummu settlement (abandoned Rummu quarry); and an area east of the Tuula village (Kröger *et al.* 2014a, fig 5C). Where preserved, the echinoderm grainstone and reef facies of the Vasalemma Formation laterally grades into the time equivalent skeletal grainstone of the Saue Member of the Kahula Formation.

The reefs are up to c. 10 m thick and up to 50 m wide and their cores are formed by a matrix rich boundstone (50–80% matrix), with abundant echinoderms, bryozoans, and receptaculitids as main skeletal components (Kröger *et al.* 2014a). Three end-members have been distinguished within the variation of the skeletal components of the reef-cores: a bryozoan boundstone; an echinoderm boundstone with *Hemicosmites* as main skeletal component; and a bryozoan-receptaculitid-microbial boundstone (Kröger *et al.* 2014a).

Associated with the reef cores are commonly pockets, preserving locally restricted siliciclastic (marl, silt), microbial limestone facies with concentrations of cephalopods (see Kröger & Aubrechtová 2017) and well-preserved echinoderms (e.g. Rozhnov & Jefferies 1996).

The Vasalemma reefs are nearly time equivalent to the mud mounds of the Kullberg Formation, Dalarna, central Sweden (Ebbestad & Högström 2007; Nielsen *et al.* 2023) and the reefs of the Steinvika Formation, Oslo region, southern Norway (e.g. Harland 1981) (Fig. 2). Both areas represent, together with the reefs of the Vasalemma Formation, a first peak occurrence in reef development on the Baltica Palaeocontinent. The Kullberg reefs are composed of massive stromatolitic limestone with flanks of skeletal wacke-, pack-, and grainstone with pelmatozoans as main components (bryozoans are locally abundant), and are interpreted as representing relatively deep neritic depositional environments (e.g. Calner *et al.* 2010; see Kröger *et al.* 2016 for a review). The reefs of the Steinvika Formation are more comparable to the Vasalemma Formation reefs with respect to the depositional environment.

The Steinvika Formation (Harland 1980) is mainly composed of limestone alternating with mixed limestones and siliciclastics. The formation as a whole is 41.4 m thick in its type area in Langesund. The Steinberg road cut of the Drammen municipality, is within the Eiker-Sandsvær district (Harland 1980), which is too poorly known at present for any formal

subdivision or estimate of thickness to be made. Local bioherms with calcareous algae, stromatoporoids, echinoderms and corals are developed in its type area in Steinvika, within the lowermost Bunes Member, Skien-Langesund district (Harland 1980). Trilobites and graptolites in the Steinvika Formation, indicate an Early Katian age, within the *Dicranograptus clingani* graptolite zone. The type area in Steinvika, near Langesund is thermally metamorphosed by Permian intrusions. Bryozoans here are rare, and usually recrystallized, neomorphosed into sparitic calcite.

The reefs of the Steinvika Formation formed on local shoals and banks of pelmatozoan grainstone (Kröger *et al.* 2016, and references therein). The reef cores differ from that of the Vasalemma Formation, in having a higher percentage of skeletal material, and tabulate corals are a common element (Kröger *et al.* 2016, and references therein). Their palaeogeographical position was closer to the edge of the Törnquist Palaeo-Sea at the modern SW edge of the Baltica Palaeocontinent.

Results

Composition of the bryozoan assemblage

The bryozoan fauna of the Vasalemma Formation is diverse and abundant but never has been studied in detail and in its entirety. Bassler (1911) described 43 species, including also re-descriptions of taxa established earlier by Eichwald (1829, 1840, 1854, 1855, 1860) and Dybowski (1878). Some taxa were described by Soviet and Russian researchers (e.g. Modzalevskaya 1953; Lavrentjeva 1990; Gorjunova & Lavrentjeva 1993).

Männil (1959) in his unpublished dissertation documented 67 species for the Keila horizon in Estonia. He erected many new species which are not valid (*nomen nudum*) according to International Rules of Zoological Nomenclature, because Männil (1959) is an unpublished work. Pushkin (1987, 1990) re-erected some of the Männil's species to make them valid, among them also species from Vasalemma (e.g. *Ceramopora vasalemmica* Männil & Pushkin in Pushkin, 1990).

The bryozoans of the Kullberg Formation are well known among fossil collectors but have never been studied in detail. Spjeldnaes (1984) erected a new species, *Cyclophaenopora (Nematotrypa) robusta* from the Kullberg Formation of the Amtjärn quarry, and Ernst (2012) described a new species *Inconobotopora intricata* from the same locality. Bryozoans from the Steinvika Formation have not been previously documented.

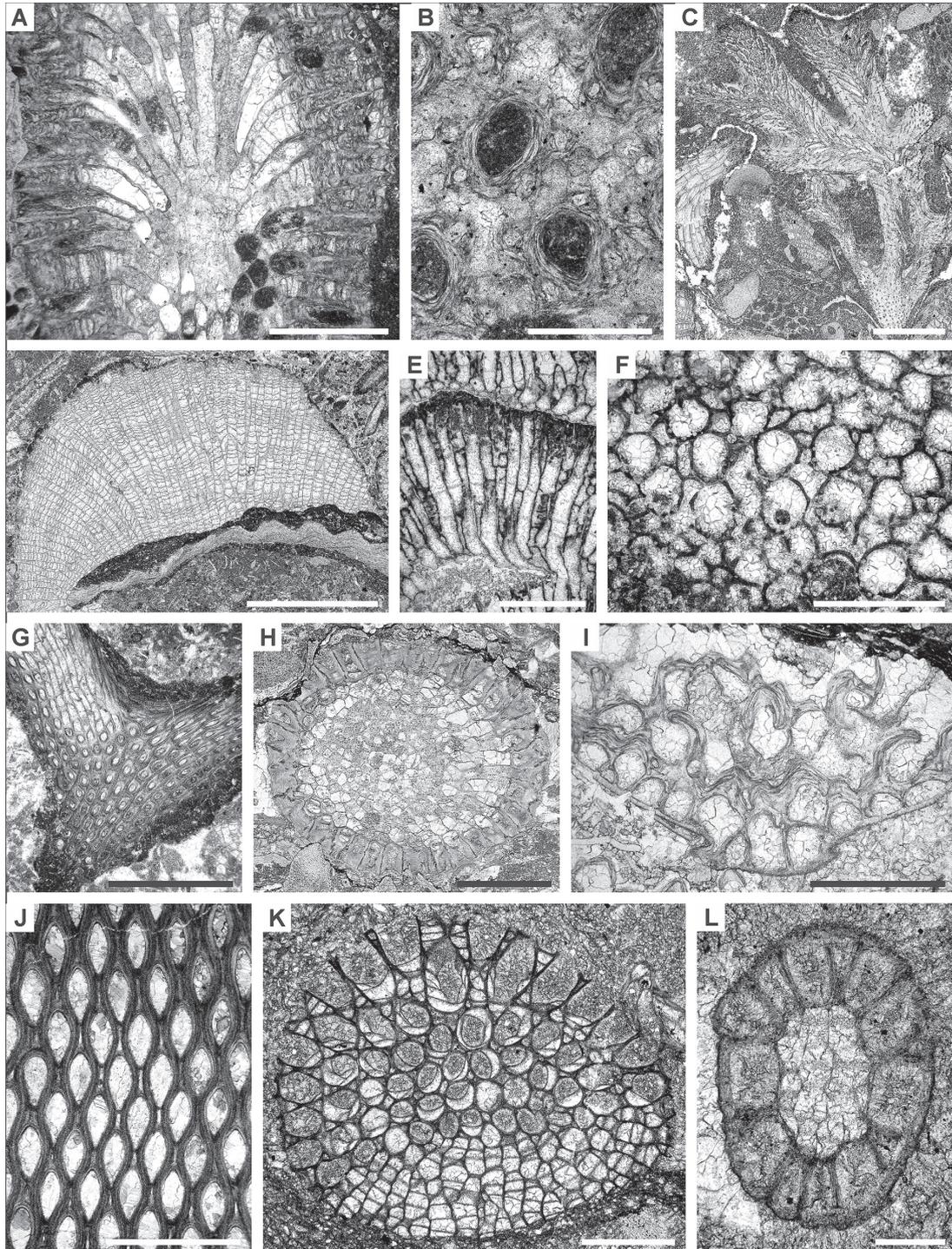


Fig. 3. Bryozoans in thin sections from reefs of late Sandbian-early Katian age from Baltoscandia. A, B, *Dittopora colliculata* (Eichwald, 1856), reef R9, lithology 4, Rummu quarry, Vasalemma Formation (A, longitudinal section; B, tangential section); C, *Pseudohornera bifida* (Eichwald, 1860), sample GIT 825-36c, Vasalemma quarry, Vasalemma Formation; D, *Orbignyella germana* Bassler, 1911, longitudinal section of a massive colony, sample GIT 825-37i, Vasalemma quarry, Vasalemma Formation; E, F, *Ceramopora massalis* Männil, 1959 (*nomen nudum*), Vasalemma quarry, Vasalemma Formation (E, longitudinal section, sample GIT 825-38a; F, sample GIT 825-38b, tangential section); G, *Ptilotrypa prima* Lavrentjeva in Gorjunova & Lavrentjeva, 1993, from sample GIT 825-39d, Vasalemma quarry, Vasalemma Formation; H, *Hemiphragma panderi* (Dybowski, 1878), transverse section of the branch, sample PMU 39555/1, Kullberg quarry, Kullberg Formation; I, *Anolotichiina laciniatus* (Eichwald, 1860), sample PMU 39499/1, Kullberg quarry, Kullberg Formation; J, *Astrovidictya sparsa* Lavrentjeva, in Gorjunova & Lavrentjeva, 1993, tangential section, sample PMU 39634/1, Kullberg quarry, Kullberg Formation; K, *Prasopora esthonica* Modzalevskaia, 1953, sample PMO 222.307, Steinrika Formation, Steinberg road cut; L, *Kukersella borealis* Bassler, 1911, sample PMO 222.319, transverse section of the branch, Steinrika Formation, Steinberg road cut. Scale bars 5 mm (D), 2 mm (A, C, E, G, H), 1 mm (F, I, J), 0.5 mm (B, K), and 0.2 mm (L).

The thin sections from these collection sites, analysed here, reveal a high bryozoan richness and abundance. The total number of species found reaches almost 100, many represented by numerous fragments. We also detected a large range variation in colony size: trepostome species such as *Diplotrypa abnormis* (Modzalevskaya, 1953), *Homotrypa similis* Foord, 1883, and *Mesotrypa egena* Bassler, 1911 developed large and macroscopically well recognisable colonies. Similarly, cryptostomes like *Proavella proava* (Eichwald, 1840) or *Ptilotrypa prima* Lavrentjeva in Gorjunova & Lavrentjeva, 1993 grew to large sizes with robust colonies (Fig. 3G), as well as cystoporates, e.g. the massive species *Ceramopora massalis* Männil (1959, nomen nudum) (Fig. 3E, F), and the branched *Constellaria varia* Ulrich, 1893.

Phylloporine and cryptostome bryozoans developed reticulate and cribrate colonies, which could reach sizes of 20 cm. However, these colonies are often composed of thin branches fused together, or are thin, leaf-shaped, and therefore very fragile, e.g. *Chasmatopora furcata* (Eichwald, 1854), *Ennalopora ulrichi* (Bassler, 1911), *Graptodictya delicata* Männil in Gorjunova & Lavrentjeva, 1993, and *Trigonodictya cyclostomoides* (Eichwald, 1855).

Numerous fragments of such colonies are found in debris between the larger bryozoans (Fig. 3). Additionally, many branched species (mainly rhadomesine cryptostomes, but also trepostomes and the cyclostome *Kukersella borealis* (Bassler, 1911) (Fig. 3L), produce small colonies with branch diameters less than 0.5 mm, e.g. *Moyerella francisca* (Bassler, 1911), *Ottoseetaxis indubius* Gorjunova, 1985, *Nematopora ovalis* Ulrich, 1890, and *Batostomella cf. tenuis* (Ernst & Key, 2007). The richness of such 'interstitial' bryozoans is locally very high and it cannot be estimated macroscopically.

A significant number of species produced encrusting colonies, which can be thin (less than 1 mm in thickness), unilamellar or form relatively thick masses (5–10 mm in thickness), often multilayered. Such encrusting species are represented by cystoporates and trepostomes, e.g. *Crepipora uxnormensis* (Bassler, 1911), *Ceramopora cf. spongiosa* Bassler, 1911, *Minutolunaria rhombica* (Bassler, 1911), *Orbignyella germana* Bassler, 1911, and *Revalopora revalensis* (Dybowski, 1878) (Fig. 4B). The latter is a quite common species, which developed encrusting sheets, both unilamellar and multilayered (Fig. 3B). This species has remarkable maculae consisting of radially arranged ribs.

Most of the species we found in the Vasalemma, Kullberg and Steinvika formations are widely distributed in Katian sediments of the Baltoscandian

region. However, some species are also known from contemporary sediments of Laurentia: *Anaphragma mirabile* Ulrich & Bassler, 1904, *Balticopora tenuimurale* (Ulrich, 1893), *Constellaria varia* Ulrich, 1893, *Homotrypa similis* Foord, 1883, *Nematopora ovalis* Ulrich, 1890, *Parvohallopora dumalis* (Ulrich, 1893), *Stigmatella claviformis* (Ulrich, 1893). *Constellaria varia* Ulrich, 1893 has even been recorded from the Sandbian of Argentina (Ernst & Carrera 2012).

Intra- and inter-reef facies heterogeneity

The reefs of the Vasalemma Formation (Fig. 5) are strongly clustered (Figs. 6B), with a median nearest neighbour distance of c. 25 m. In the Vasalemma quarry the reefs have a median thickness of 4 m (1st–3rd quantiles: 2–5 m, n = 75) and a median diameter of 6 m (1st–3rd quantiles: 4–10 m, n = 82).

In the Rummum quarry we distinguished 11 lithologies (Table 1). The facies mosaic at the level of individual reefs is highly varied (Fig. 7). When comparing reef core lithologies of different reefs at Rummum, a moderate variability in skeletal content is apparent (55–71%). Areas with a variable content of echinoderm-roots and encrusting bryozoans occur (Table 2, Fig. 8) but well distinguishable reef types (e.g. one group clearly dominating the reef core) could not be detected.

A comparison of point counts of macroscopic skeletal elements in the reef-cores shows significant differences between the Rummum and Vasalemma quarries (Table 3, Fig. 9). These mainly reflect differences in the relative abundance of bryozoans and in the presence / absence of receptaculitids and sole-noporans, which are both abundant in Vasalemma. In Rummum these elements are relatively rare, and bryozoans are commonly dominant (Kröger *et al.* 2014a, Table 2–3). We also noted that patches dominated by edrioasteroids are more common in the Rummum reefs.

The Rummum and Vasalemma quarries differ also with respect to the taxonomic content of the bryozoan assemblages (Fig. 10A): at Vasalemma erect bryozoan species are more abundant, among them branched cystoporates (e.g. *Anolotichiina crassimuralis* (Bassler, 1911), *Constellaria varia* Ulrich, 1893), trepostomes (*Dybowskites hispidus* Gorjunova, 2005, *Homotrypella cribrosa* Bassler, 1911, *Parvohallopora dumalis* (Ulrich, 1893)), cribrate and branched cryptostomes (*Eichwaldictya laminata* Lavrentjeva, 1990, *Proavella proava* (Eichwald, 1840), *Ottoseetaxis indubius* Gorjunova, 1985). Moreover, the assemblages of the Vasalemma quarry differ from those of the Rummum quarry in the presence of dome-shaped massive species

in the former such as *Mesotrypa orientalis* Bassler, 1911 and *Esthoniopora subsphaerica* (Bassler, 1911).

Notably, the inter-reef differences of the bryozoan assemblages at Rummu and Vasalemma, are low when compared with the differences between the two quarries (Fig. 10A). The inter-reef dissimilarities generally are also lower than the dissimilarities between facies units (compare Fig. 10A, B). This pattern cannot be replicated when comparing bryozoan growth forms (see Fig. 10C, D).

Diversity

A total of 140 bryozoan species belonging to 81 genera are known from the Vasalemma Formation (both from the collections at SARV and from our own thin sections). The extrapolated species richness for the total Vasalemma Formation, based on our thin section counts is 63. At each reef site we estimated on average 36 species, and 25 in each sample (Fig. 11). In the Vasalemma Formation the proportional turnover

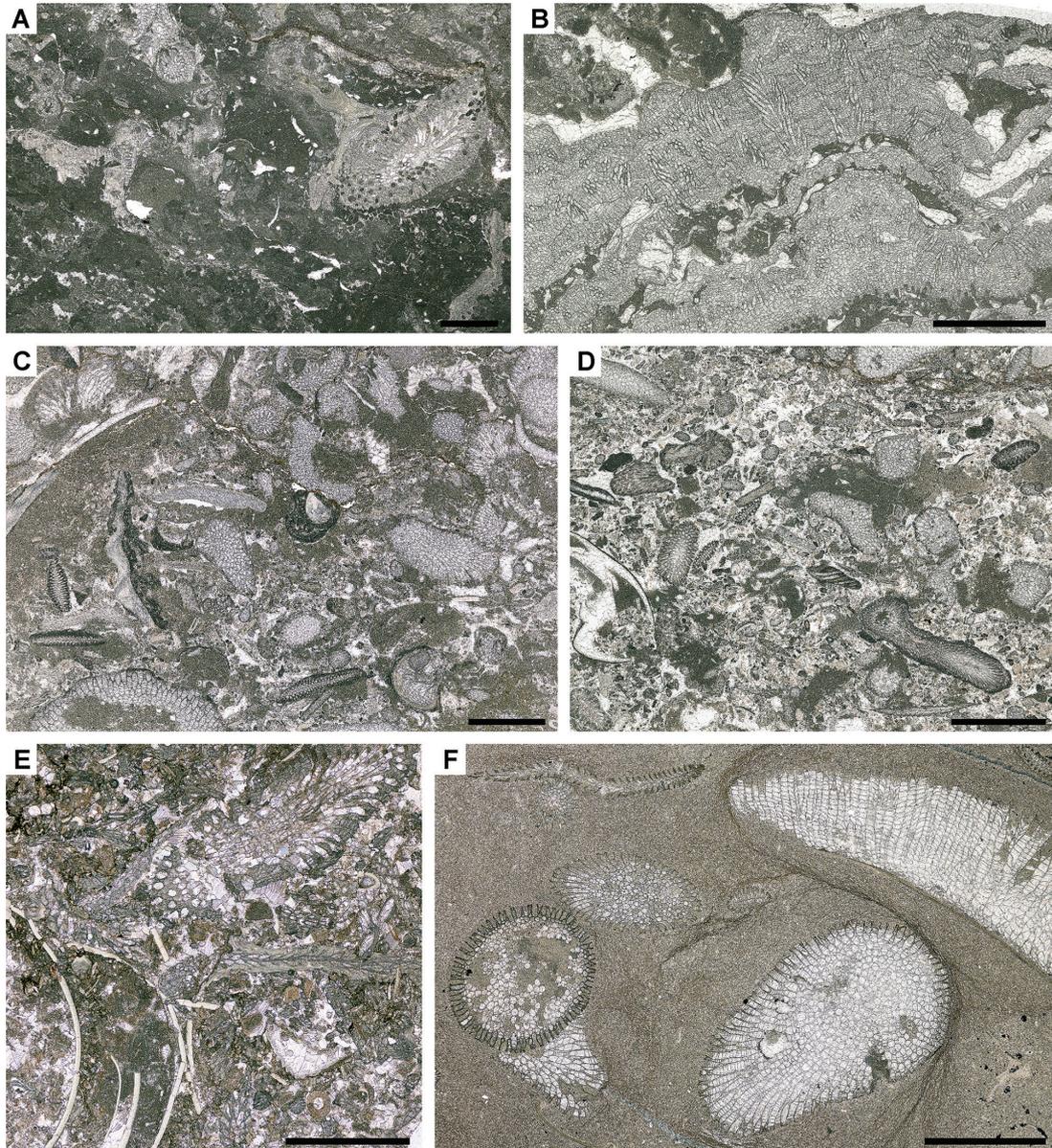


Fig. 4. Examples of bryozoan rich microfacies from reefs of late Sandbian-early Katian age of Baltoscandia. A–D, Vasalemma Formation, northern Estonia. A, *Dittopora colliculata* (Eichwald, 1856) in the middle right; B, from reef R9, lithology 5, Rummu quarry with multiple layers of *Revalopora revalensis* (Dybowski, 1878); C, D, sample GIT 825–40d (C), GIT 825–39k, Vasalemma quarry Vasalemma; E, sample PMU 39480, Kullsborg quarry Kullsborg, Kullsborg Formation, Dalarna, Sweden with *Dybowskiites orbicularis* (Modzalevskaya, 1953) in the top right; F, sample PMO 222.251, Steinvik Formation, Steinvik road cut, Norway, with diverse trepostome and cryptostome bryozoans. Scale bars 5 mm.



Fig. 5. Outcrop situation of reefs in the Vasalemma quarry, northern Estonia, Vasalemma Formation, late Sandbian. Height of the quarry wall is approximately 5–7 m.

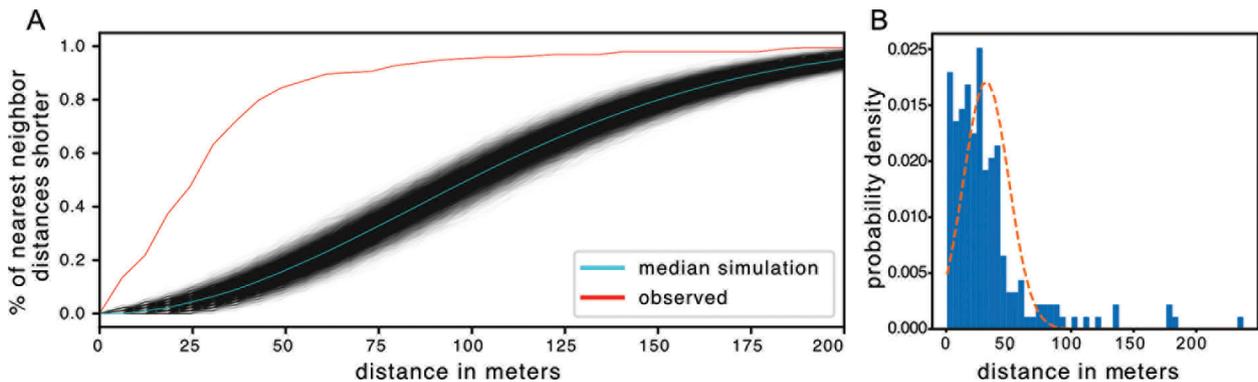


Fig. 6. Spatial distribution of reefs of the Vasalemma Formation. A, plot of the $G(d)$ function, with distance-to-point d on x-axis and fraction of nearest neighbour distances smaller than d on y-axis. Red line: empirical cumulative distribution of nearest neighbor distances of reef of the Vasalemma quarry, turquoise line is mean of simulations, black are 95% confidence interval of simulations, diagram design. after: https://geographicdata.science/book/notebooks/08_point_pattern_analysis.html; B, histogram of nearest neighbour distances of reefs of the Vasalemma Formation, orange hatched line is fitted normal distribution with standard deviation = 18 and mean = 32.

(our β_{pt}) is highest at the sample level and lowest at the reef site level (Table 4, Fig. 12).

Comparisons with samples from the Steinvika and Kullberg formations (Table 4) shows that similar heterogeneity patterns exist in all three formations, with highest heterogeneities at lowest the level of observation and highest richness estimates at the formation level (highest level of observation). The latter can be expected from positive species-area relationships well known in macroecology (e.g. Connor & McCoy 1979).

However, the richness increase from lower level of observation to higher level of observation is not associated with an equal increase in beta diversities. Throughout, our level with highest proportional turnover rates is the level of samples, and at the level of reef sites the β -diversity is lowest. The β -diversity values at sample level are also higher than the turnover between lithologies (see Table 4).

Interpretation

Small scale heterogeneity is most important

In the Vasalemma Formation the per-sample, and the per-locality α -diversities are significantly lower than the total diversity (γ). This is no surprise, because smaller sampling areas and volumes are known theoretically and empirically to contain lower richness (e.g. Connor 1979). Interestingly, however, the lowest β -values occur at our locality (reef site) level. This indicates that inter-reef assemblage heterogeneities were less important in creating the high total richness of the Vasalemma Formation than heterogeneities among samples. Samples from one locality came from different lithologies, and the β -diversity among lithologies, in turn, is also very high in the Vasalemma Formation. Hence, small scale local differences in facies and habitat here are the main contributors to the high total species richness.

Table 1. Macroscopically differentiated lithologies in the reefs of the Rummu quarry, northern Estonia, Vasalemma Formation, late Sandbian.

| Lithology | Description |
|-----------|--|
| Lith. 1 | Argillaceous, silty, yellowish to greenish mud-, to wackestone with predominantly pelmatozoan debris as skeletal components. |
| Lith. 2 | Wavy to flaser bedded, bioturbated wackestone, with echinoderm ossicles and bryozoans as main skeletal components, and with few cephalopods. |
| Lith. 3 | Wavy bedded, bioturbated wackestone with biodebris from encrusting bryozoans as main skeletal component, partly with sheet-like bryozoans in situ. |
| Lith. 4 | Bluish-grey, wavy bedded, partly argillaceous, skeletal wacke-, packstone, with echinoderm roots in situ, edrioasteroids, echinoderm ossicles, partly with birdseyes-structures. |
| Lith. 5 | Silty, finely laminated marl. |
| Lith. 6 | Massive bluish skeletal wackestone, partly with birdseyes-structures, with edrioasteroids, and echinoderm ossicles as main skeletal component. |
| Lith. 7 | Massive pale grey skeletal wackestone with few edrioasteroids and variegated skeletal components, such as echinoderm ossicles, molluscs, and bryozoans. |
| Lith. 8 | Silty marl with tabulate coral and echinoderm roots. |
| Lith. 9 | Marly, intraclastic float- to rudstone, with rounded intraclasts of lithologies 3, 4, 6, 7. |
| Lith. 10 | Massive pale grey skeletal wacke-, packstone with abundant birdseyes structures and clotted fabric, skeletons of edrioasteroids and encrusting bryozoans are abundant. |
| Lith. 11 | Echinoderm grainstone. |

At the regional scale, a gradient in facies and/or habitat differences led to two clearly distinguishable bryozoan assemblage groups. The group comprising the samples of the Vasalemma quarry contained more erect colony-forms, whilst in the Rummu quarry encrusting forms are more common. This difference in bryozoan growth forms is associated with differences in occurrence of other reef forming organisms,

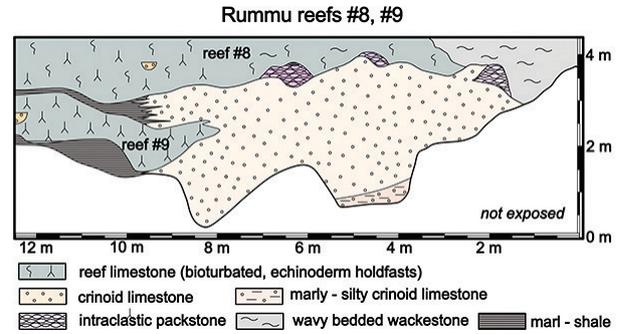


Fig. 7. Vertical facies relations of reefs RR8 and RR9, Rummu quarry, northern Estonia, Vasalemma Formation, late Sandbian.

such as solenoporans and *Receptaculites*, which are more common in the Vasalemma quarry. The spatial setting of the two areas with the reefs of the Vasalemma quarry positioned closer to the palaeo-shore line suggest a lower energy-exposed habitat in the latter. The reefs of the Rummu quarry, in contrast, probably represent a palaeo-position closer to the distal rim of the reef belt. This seascape scale differentiation contributed to the total bryozoan diversity of the Vasalemma Formation, but less so than the small-scale intra-reef facies heterogeneity. A similar β -diversity pattern with lowest values at the level of reef sites is also apparent in our results from the Kullberg Formation, suggesting that small scale facies and habitat heterogeneity was the most important contributor to richness there, too.

At the global scale the Vasalemma reefs probably can be best compared with the bryozoan-rich patch reefs described from the nearly time equivalent Carters Limestone (late Sandbian – early Katian), Tennessee, USA (Alberstadt *et al.* 1974), which also shows a considerably high facies and assemblage differentiation at local level. These reefs are positioned on a palaeo-shelf, similar to the reefs analysed herein. Highly diverse and locally heterogenous bryozoan assemblages are also known from reefs of Rockdell

Table 2. The relative abundance of components in the reef cores of reefs of the Rummu quarry, northern Estonia, Vasalemma Formation, late Sandbian, estimated from macroscopic point counts from outcrops.

| Reef site | Lithology | Total Counts | Matrix | Echino-derm (indet.) | Bryozoan (branched) | Bryozoan (encrusting) | Edrio-asteroid | Recep-taculite |
|-----------|-----------|--------------|--------|----------------------|---------------------|-----------------------|----------------|----------------|
| RR8a | Lith. 3 | 65 | 0.68 | 0.29 | 0.02 | 0.02 | – | – |
| RR8b | Lith. 3 | 66 | 0.70 | 0.23 | – | 0.05 | 0.03 | – |
| RR8c | Lith. 3 | 23 | 0.70 | 0.17 | – | 0.04 | 0.09 | – |
| RR1a | nn | 29 | 0.55 | 0.03 | – | 0.41 | – | – |
| RR1b | nn | 65 | 0.57 | 0.08 | – | 0.32 | 0.02 | 0.02 |
| RR1c | Lith. 10 | 72 | 0.64 | 0.32 | – | 0.04 | – | – |
| RR1d | nn | 76 | 0.71 | 0.16 | – | 0.13 | – | – |
| RR1e | nn | 87 | 0.67 | 0.18 | – | 0.15 | – | – |
| RR2 | nn | 76 | 0.70 | 0.16 | – | 0.14 | – | – |



Fig. 8. Examples of reef core facies exposed in the Rummu quarry, northern Estonia, Vasalemma Formation, late Sandbian. A, area with abundant encrusting bryozoan colonies; B, area with abundant edrioasteroid skeletons; C, area with encrusting bryozoans and echinoderm roots. Same scale in A-C.

Table 3. Relative abundance of skeletal components in the reef cores of reefs of the Rummu and Vasalemma quarries, northern Estonia, Vasalemma Formation, late Sandbian, estimated from macroscopic point counts from outcrops. RR1–8, reefs of Rummu quarry, vas_25–26, reefs of Vasalemma quarry.

| Sample | Total count | Echinoderm indet | Bryozoan | Receptaculitid | Tabulate coral | Rugose coral | <i>Solenopora</i> | Edrioasteroid |
|---------------|-------------|------------------|----------|----------------|----------------|--------------|-------------------|---------------|
| RR1 | 45 | 0.69 | 0.24 | – | 0.07 | – | – | – |
| RR1a | 13 | 0.08 | 0.92 | – | – | – | – | – |
| RR1b | 28 | 0.18 | 0.75 | 0.04 | – | – | – | 0.04 |
| RR1c | 26 | 0.88 | 0.12 | – | – | – | – | – |
| RR1d | 22 | 0.55 | 0.45 | – | – | – | – | – |
| RR1e | 29 | 0.55 | 0.45 | – | – | – | – | – |
| RR2 | 23 | 0.52 | 0.48 | – | – | – | – | – |
| RR2a | 25 | 0.32 | 0.52 | – | – | – | 0.16 | – |
| RR3 | 46 | 0.57 | 0.41 | – | – | – | 0.02 | – |
| RR4 | 32 | 0.69 | 0.25 | 0.03 | – | – | 0.03 | – |
| RR6 | 50 | 0.64 | 0.34 | – | – | – | 0.02 | – |
| RR8a | 21 | 0.90 | 0.10 | – | – | – | – | – |
| RR8b | 20 | 0.75 | 0.15 | – | – | – | – | 0.10 |
| RR8c | 7 | 0.57 | 0.14 | – | – | – | – | 0.29 |
| vas_25a | 58 | 0.83 | – | 0.16 | – | – | 0.02 | – |
| vas_25b | 25 | 0.88 | – | – | – | – | 0.12 | – |
| vas_flank_26f | 67 | 0.67 | 0.10 | 0.07 | 0.01 | – | 0.13 | – |
| vas_core_26a | 40 | 0.18 | – | 0.18 | 0.08 | 0.05 | 0.53 | – |
| vas_core_26b | 113 | 0.64 | 0.08 | 0.02 | 0.01 | – | 0.26 | – |
| vas_core_26c | 66 | 0.44 | 0.12 | 0.05 | 0.02 | 0.02 | 0.36 | – |

and Holston formations (late Sandbian), Tennessee, USA (Walker 1973; Ruppel & Walker 1982), which were deposited on palaeo-platform to ramp positions. A scale dependent diversity pattern within the bryozoan assemblages with small scale facies and habitat differentiation being the most important factor for total diversity can therefore be also expected in these reef settings.

Increasing role of within community diversification

The extraordinarily rich bryozoan assemblages of the Vasalemma Formation can be seen as an example of the late Sandbian bryozoan-rich reef faunas, which are known from other low palaeo-latitude settings of that age, such as from eastern Laurentia (Webby

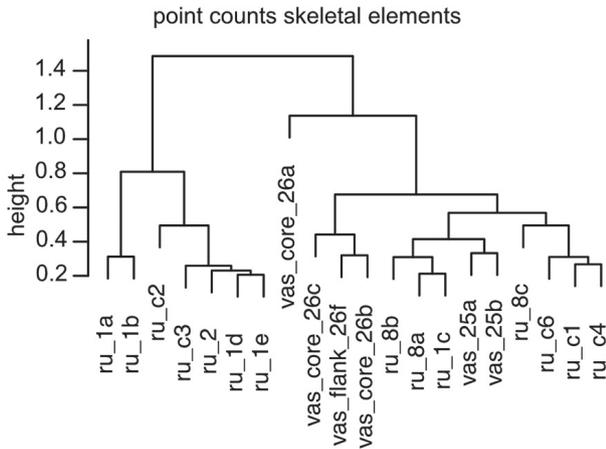


Fig. 9. Cluster diagram of results from point counts of skeletal elements in reef core areas of the reefs of the Rummu quarry (ru) and Vasalemma quarry (vas), northern Estonia, Vasalemma Formation, late Sandbian, using the Bray-Curtis dissimilarity index and the Ward clustering method (Murtagh & Legendre 2014).

2002). The Vasalemma bryozoan assemblages also represent the global Ordovician peak diversification interval of this group (Ernst 2018). The diversification generally is seen as a consequence of global climatic cooling (e.g. Trotter *et al.* 2008; Rasmussen *et al.* 2019; Cocks & Torsvik 2021) and increasing oceanic oxygenation (e.g. Edwards 2019).

However, the actual mechanisms of the diversification are poorly understood (see e.g. discussion in Stigall *et al.* 2019). One of its peculiar features is the generally declining regional disparity (Miller 1997; Hofmann *et al.* 2019; Penny & Kröger 2019), which is also visible in bryozoans (e.g. Tuckey 1990; Buttler *et al.* 2013). The diversification was instead increasingly driven by a rise of within-sample (α), within-community diversity, i.e., below spatial and temporal resolution of the respective analyses (see Hofmann *et al.* 2019; Penny & Kröger 2019). This is consistent with an analysis of early Palaeozoic brachiopod occurrences of the Baltic Basin, where small-scale substrate heterogeneity has been detected as the most important diversification driver (Penny *et al.* 2022). Our results from the Vasalemma Formation support these earlier works.

In this context it is interesting that the Middle Ordovician reefs of the Mingan Formation, (Darriwilian), Quebec, Canada show considerable compositional variation, i.e., high between-reef diversity (β) (Penny *et al.* 2022). A direct comparison of the datasets from the Mingan Islands and the Vasalemma Formation is difficult because between-sample diversity data are not available for the Mingan Islands. The reefs of the Mingan Formation differ additionally in

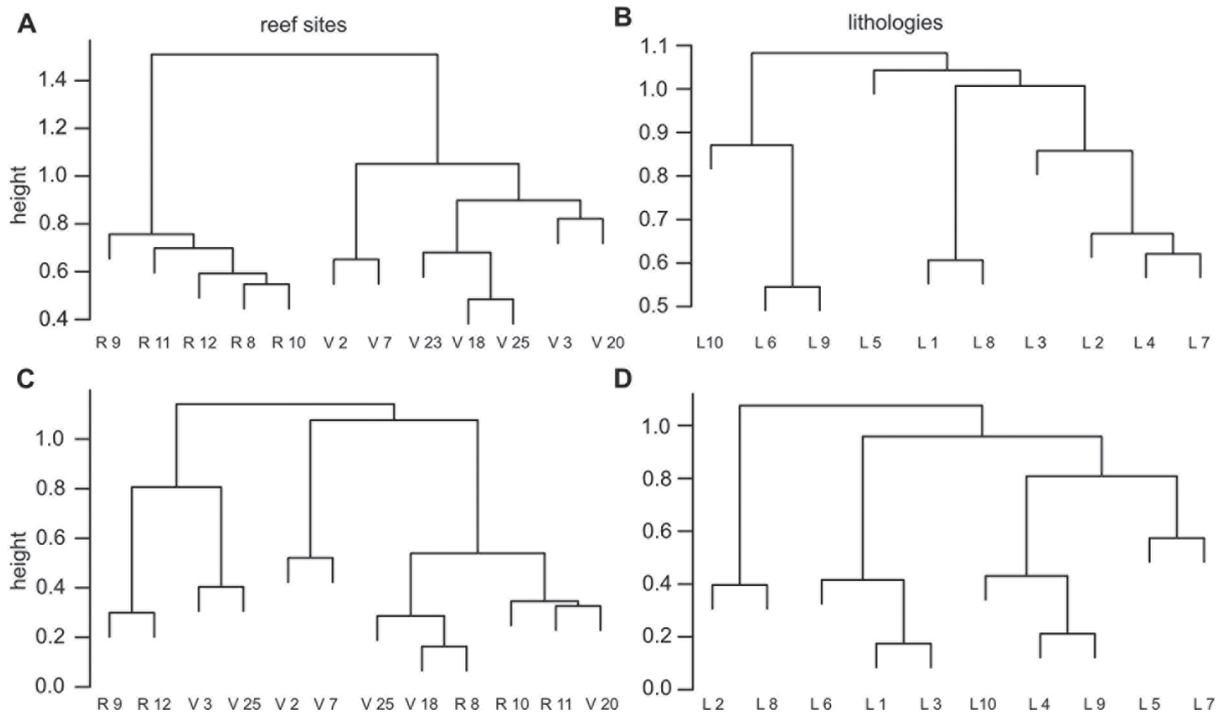


Fig. 10. Cluster diagrams of results from thin section analysis of samples from the Rummu quarry (ru) and Vasalemma quarry (vas), northern Estonia, Vasalemma Formation, late Sandbian, using the Bray-Curtis dissimilarity index and the Ward clustering method (Murtagh and Legendre 2014). A, cladogram of reef sites based on abundance of bryozoan taxa; B, cladogram of lithologies based on abundance of bryozoan taxa; C, cladogram of reef sites based on bryozoan colony forms; D, cladogram of lithologies based on bryozoan colony forms. R8–12, reefs of Rummu quarry; V3–25, reefs of Vasalemma quarry; L1–10, Lithologies of Rummu quarry (see Table 1).

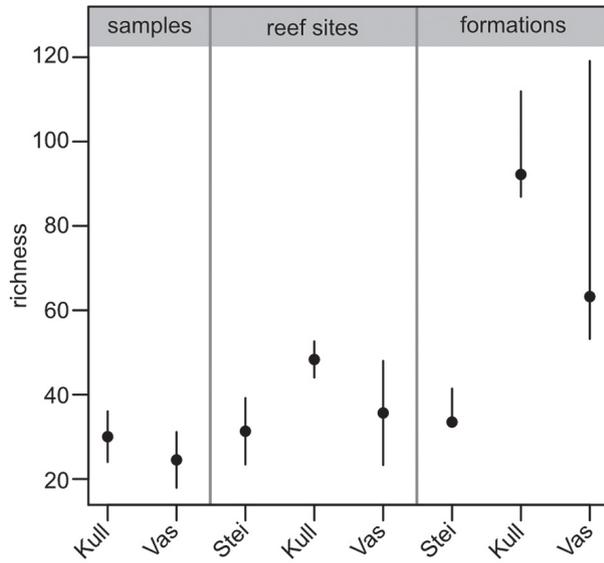


Fig. 11. Estimated bryozoan richness from samples, reef sites, and formations. Kull, Kullsborg Formation; Stei, Steinvika Formation; Vas, Vasalemma Formation. Vertical bars are 95% confidence intervals.

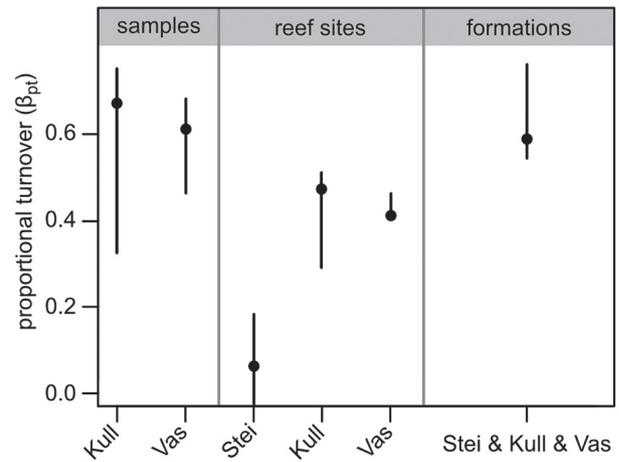


Fig. 12. Proportional turnover (β_{pt}) of bryozoan taxa in-between samples, reef sites, and formations. Kull, Kullsborg Formation; Stei, Steinvika Formation; Vas, Vasalemma Formation. Vertical bars are 95% confidence intervals.

Table 4. Results from diversity estimations from thin section samples of the Steinvika Formation, Norway, Kullsborg Formation, Sweden, and Vasalemma Formation, Estonia. N, number counted; β_{pt} , proportional turnover; β_e , edge-length difference in trees resulting from hierarchical cluster analysis after Cardoso et al (2014); ci, 95% confidence interval.

| Estimate | Steinvika Fm. | Kullsborg Fm. | Vasalemma Fm. |
|----------------------------|----------------------|----------------------|----------------------|
| N observations | 850 | 1243 | 1944 |
| N samples | 3 | 22 | 42 |
| N localities | 3 | 3 | 12 |
| γ | 33 (ci: 33–41) | 92 (ci: 87–112) | 63 (ci: 53–119) |
| Mean α (reef sites) | 31 (ci: 23–29) | 48 (ci: 44–53) | 36 (ci: 23–48) |
| Mean α (samples) | – | 30 (ci: 24–36) | 25 (ci: 18–31) |
| β_{pt} (reef sites) | 0.06 (ci: -0.3–0.19) | 0.48 (ci: 0.29–0.51) | 0.41 (ci: 0.41–0.47) |
| β_{pt} (samples) | – | 0.67 (ci: 0.33–0.76) | 0.61 (ci: 0.46–0.68) |
| β_{pt} (lithologies) | – | – | 0.47 (ci: 0.42–0.64) |
| β_t (reef sites) | 0.38 | 0.14 | 0.30 |
| β_t (samples) | – | 0.43 | 0.48 |
| β_t (lithologies) | – | – | 0.54 |

being more closely spaced (their mean nearest neighbour distance is only 6 m), randomly distributed, and in showing only a weak palaeo-depth segregation (Kröger & Penny 2020). It is therefore not clear if the differences between the Mingan reefs and the Vasalemma reefs represent a general trend or just differences in the specific depositional environment. More generally, it remains an open question if a shift of reef environments from more β -diversity dominated communities (as e.g. the Mingan reefs) toward more α -diversity dominated communities (e.g. Vasalemma

reefs) can be detected within the Ordovician reefs. Finding an answer to this question could also contribute to the open question of whether the increasing role of α -diversity was an effect of an increasing role of organismic moderated habitat differentiation.

Conclusions

The following conclusions can be drawn from this study.

1. The reefs of the Vasalemma Formation (late Sandbian), northern Estonia, occur in a c. 5 × 20 km wide pelmatozoan grainstone belt, have a median diameter of 6 m, a median nearest distance of 25 m, are highly clustered, and contain a rich bryozoan assemblage of 140 species belonging to 81 genera.
2. The Vasalemma reefs are relatively matrix-rich (55%–71%). Bryozoans (up to 32%) and pelmatozoans (up to 32%) are the most important skeletal elements in the reef cores. *Receptaculites*, solenoporans, and locally, tabulate corals are additional skeletal elements in the reefs. The reefs are composed of a highly heterogeneous 3D-facies mosaic, comprising carbonate and siliciclastic elements.
3. Regional differences exist within the formation with respect to the relative abundance of different bryozoan colony forms, receptaculitids and solenoporans, which are interpreted as due to regional differences in water energy levels. However, the between-reef diversity of bryozoans is lower than the between-sample bryozoan diversity, and the between-lithology diversity of bryozoans.
4. The average estimated bryozoan species richness of samples is c. 40% of the total estimated bryozoan species richness of the Vasalemma Formation, and the average richness of a reef site is 57% of the total richness. Given the relatively low in-between reef diversity, it can be concluded that the sample level, reflecting small-scale lithology and habitat heterogeneity, contributes most to the bryozoan diversity in the Vasalemma Formation.
5. A similar pattern can be detected in the time equivalent bryozoan rich reef limestone of the Kullberg Formation of Sweden. Small-scale substrate heterogeneity also has been detected as the most important diversification driver in the Ordovician diversification of brachiopods of the Baltic Basin (Penny *et al.* 2022).
6. The increasing production of small-scale substrate and habitat heterogeneity, moderated through organismal activity, such as that detected in the reefs of the Vasalemma and Kullberg formation, can be seen as an important mechanism driving the diversification during the Ordovician.

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