Bryozoan-rich stromatolites (bryostromatolites) from the Silurian of Gotland and their relation to climate-related perturbations of the global carbon cycle

ANNA LENE CLAUSSEN* (iD), AXEL MUNNECKE* and ANDREJ ERNST†

*GeoZentrum Nordbayern, Fachgruppe Paläoumwelt, Friedrich-Alexander-Universität Erlangen-Nürnberg, Loewenichstraße 28, Erlangen, D-91054, Germany
(E-mail: anna.lene.claussen@fau.de; axel.munnecke@fau.de)
†Institut für Geologie, Universität Hamburg, Bundesstr. 55, Hamburg, D-20146, Germany
(E-mail: andrej.ernst@uni-hamburg.de)

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ABSTRACT

Bryozoan–stromatolite associations (bryostromatolites) formed conspicuous reef structures throughout the Sheinwoodian (Wenlock) to Ludfordian (Ludlow) stratigraphy on Gotland but have not been described so far. They are mainly composed of encrusting bryozoans forming a complex intergrowth with porostromate and spongiostromate microbes and are different from the abundant stromatoporoid–coral–algal reefs with respect to their composition. In the bryostromatolite different growth stages can be identified. The observed succession can be taken as evidence for cyclic environmental changes during reef formation. Stenohaline reef-dwelling organisms, such as echinoderms, sponges, corals and trilobites, indicate fully marine salinities. Ten localities exposing bryostromatolites were discovered. Individual bryostromatolites are small with few decimetres up to one metre in size, and occur solely in shallow marine areas. Common features of these reefs on Gotland are cauliflower-like growth, a high bryozoan diversity, a high abundance of phosphatic fossils and components such as bryozoan pearls and inarticulate phosphatic brachiopods, enhanced bioerosion, *Palaeomicrocodium* crusts, vadose silt and gypsum pseudomorphs. The high abundance of *Palaeomicrocodium*, as well as the alternation with other crust-forming contributors, suggest that it could have been formed directly at the palaeo-sea surface, probably in times of minor but high-frequency sea-level fluctuations. Vadose silt and pseudomorphs after gypsum in reef cavities indicate subaerial exposure shortly after reef growth. The high amount of phosphatic components indicates a high nutrient input, probably by dust. All bryostromatolites were formed in times of strongly elevated $\delta^{13}C$ values. The unusual combination of sedimentological and palaeoecological features, as well as their occurrence exclusively during strong positive $\delta^{13}C$ excursions, are evidence that the bryostromatolite development responded to climatic/oceanographic changes, which may have played an important role in reef control.

Keywords *Palaeomicrocodium*, phosphate, reef, stable carbon isotopes, subaerial exposure.

INTRODUCTION

The Silurian sequence on Gotland (Sweden) is well-known for its abundant and very well-preserved reefs (Manten, 1971). Numerous publications deal with different reef types, from small decimetre/metre-sized patch reefs up to biostromal reefs of kilometre size (Manten, 1971, Riding,

1981), or reefs formed in deeper water (Calner *et al.*, 2000; Berkowski & Zapalski, 2018). For many years the Silurian was considered a completely calm and stable period. During the last twenty years, however, researchers have challenged this assumption by documenting several strong positive δ^{13}C excursions. On Gotland, the Ireviken, Mulde, Linde and Lau excursions were discovered (Samtleben *et al.*, 1996, 2000; Munnecke *et al.*, 2003; Calner *et al.*, 2004), with the Lau excursion being the strongest short-lived positive δ^{13}C excursion of the whole Phanerozoic (Munnecke *et al.*, 2003).

In 2015 a new reef type was discovered in the Sheinwoodian Hangvar Formation which was unknown on Gotland so far (Ernst *et al.*, 2015). This study presents the first facies description of this reef type from Gotland, which might be called bryolith (Scholz & Krumbein, 1996) or bryostromatolite (Palinska *et al.*, 1999). Palinska *et al.* (1999) and other authors used the term bryostromatolite to describe recent bryozoan-rich stromatolites from Coroong Bay in Australia. Because the term bryolith is also used for bryozoan rolling stones, the counterpart to algal rhodoliths, the term bryostromatolite is used here in order to avoid confusion.

Besides Palaeozoic reef builders such as stromatoporoids and corals, the bryostromatolites are composed of abundant encrusting bryozoans and microbial carbonates, giving the reef a cauliflower-like appearance. Three new bryozoan genera were described from the bryostromatolite mentioned above (Ernst *et al.*, 2015) and the samples show evidence for the oldest deep-boring bivalves (Claussen *et al.*, 2019), altogether indicating an unusual environmental setting.

The purposes of the present study are: (i) to assess the nature of bryostromatolite associations in relation to the environments in which they occur, characterize their reefal structures, and thus to attempt to understand the controls on their growth in the Silurian settings of Gotland; and (ii) to compare the bryostromatolites on Gotland with literature reports of their occurrence elsewhere, in order to find general trends in controls on their growth.

GEOLOGICAL SETTING

Gotland represents an exposure of a huge carbonate complex formed in the Baltic Basin during the Silurian (Hede, 1960; Manten, 1971; Calner *et al.*, 2004). Different reef stages were developed during the lower Silurian lower Visby Formation

(upper Telychian) to the upper Silurian Sundre Formation (late Ludfordian) (Hede, 1960; Manten, 1971; Samtleben *et al.*, 1996). The sediments attain an overall thickness of approximately 500 m and are subdivided into 14 formations (Calner *et al.*, 2004). The oldest (Telychian) sediments crop out on the north-western coast of the island and the youngest (Ludfordian) in the south (Fig. 1).

MATERIALS AND METHODS

Material

Six bryostromatolite occurrences were discovered on Gotland during a field trip in 2018. Four additional occurrences were found in 2019. The ten localities are: Högklint (located at the Visby Viewpoint), Nors Stenbrott, Hällagrund, Nyan, Lau Backar, Bote 2, Botvide, Hallsarve 1 and Hallsarve 2, and Hoburgen (Table 1, Fig. 1).

Methods

Thin sections
For this study thin sections were prepared and investigated with a Zeiss Imager.M2m microscope, equipped with an Axiocam MRc 5 camera, and a Zeiss Axio Zoom.V16 binocular microscope, equipped with an Axiocam 506 colour camera (Carl Zeiss AG, Oberkochen, Germany). The images were processed with the program Zen core v2.6. In total 223 thin sections were studied from material taken during the fieldtrips in 2018 and 2019 and from additional material from the diploma thesis of Oswald (2010) as well as from the microfacies teaching collection of the GeoZentrum Erlangen (Table 1)

To extract phosphatic fossils, samples SNS from Nors Stenbrott and SN8 from Nyan were dissolved with 10% acetic acid. Images of the received fossils were processed with the program Zen core v2.6 in combination with the Axio Zoom.V16 binocular microscope. A single specimen of sample SN8 was selected and investigated using scanning electron microscopy (SEM) at the Friedrich-Alexander University Erlangen-Nuremberg. For this the sample was glued on a stub, sputter-coated with gold and photographed with a VEGA 2 XMU TESCAN SEM (Tescan Analytics, Fuveau, France).

Quantification
For quantification of the material, the areas covered by the constituents in the thin sections were calculated with Adobe Photoshop® CS6 by
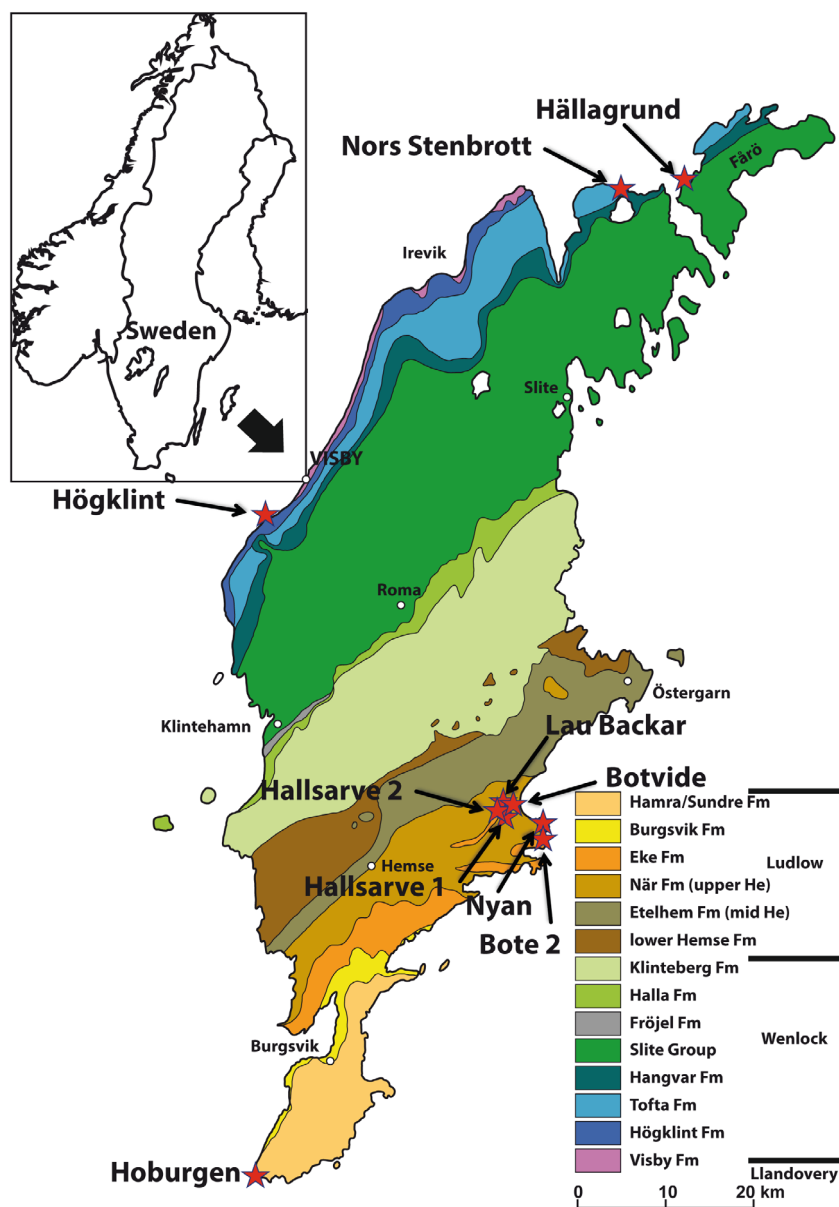
Fig. 1. Geological map of Gotland (after Calner *et al.* 2004), investigated localities are indicated by red stars.

measuring the exact outline of each component. With this method the exact amount of calcite produced by every component was determined. The measured components/constituents were: corals, sponges, bryozoans, porostromate microbes (i.e. with remnants of calcified tubes), spongiostromate microbes (i.e. without organic or 'cellular' microstructures), *Palaeomicrocodium* (see section *Microbial carbonates*), echinoderms, tentaculitoid worms, brachiopods, ostracods, allochthonous sediment, calcite spar and borings (see section *Microfacies results*). The terms porostromate and spongistromate microbes are used in a purely descriptive sense and have

no meaning with respect to taxonomy (see discussion in Monty, 1981). In total 60 thin sections were analysed to quantify the components.

The standard error of the mean is calculated by dividing the standard deviation by the square root of the number of measurements. This error is indicating the accuracy of the measurements. The used formula is $\sigma = \frac{\sigma}{\sqrt{n}}$, σ is the standard deviation and n the number of measurements.

Stable carbon isotopes

For chemostratigraphic purposes the isotopic compositions of some samples were measured. With a hand-held drill micrite and – when

Table 1.   List of all samples and thin sections included in this study; GZN = GeoZentrum Nordbayern Friedrich-Alexander University Erlangen-Nuremberg.

Locality / GPS position	Formation	No. thin sections	Additional samples
Högklint / 57°36′00.3N 18°12′05.7E	Högklint Formation, Lower Sheinwoodian	24	17 × AM427a to AM427-16 (collection GZN)
Nors Stenbrott /57°55′09.0N 18°55′19.1E	Tofta Formation, Lower Sheinwoodian	16	2 × Z19A and X5A from Oswald (2010)
Hällagrund / 57°55′33.4N 19°02′56.2E	Hangvar Formation, Lower Sheinwoodian	11	–
Nyan / 57°16′33.2N 18°42′21.7E	Eke Formation, Ludfordian	49	–
Lau Backar / 57°17′14.9N 18°38′20.5E	Eke Formation, Ludfordian	33	5 × AM300-1 to AM300-5 (collection GZN)
Bote 2 / 57°15′28.3N 18°42′39.4E	Eke Formation, Ludfordian	15	–
Botvide / 57°17′44.9N 18°39′04.4E	Eke Formation, Ludfordian	21	–
Hallsarve 1 / 57°17′16.8N 18°38′45E	Eke Formation, Ludfordian	19	–
Hallsarve 2 / 57°16′53.1N 18°38′24.4E	Eke Formation, Ludfordian	14	–
Hoburgen / 56°55′20.5N 18°7′43.8E	Hamra Formation, Ludfordian	21	–

possible – brachiopod shells were drilled. The carbonate powders were reacted with 100% phosphoric acid at 70°C using a Gasbench II connected to a ThermoFisher Delta V Plus mass spectrometer (ThermoFisher Scientific, Waltham, MA, USA). All values were reported in per mil relative to V-PDB (Vienna Pee-Dee Belemnite). Reproducibility and accuracy were monitored by replicate analyses of laboratory standards calibrated by assigning $\delta^{13}C$ values of +1.95‰ to NBS19 and −47.3‰ to IAEA-CO9 and $\delta^{18}O$ values of −2.20‰ to NBS19 and −23.2‰ to NBS18. Reproducibility for $\delta^{13}C$ and $\delta^{18}O$ was ±0.07 and ±0.05 (1 standard deviation), respectively.

RESULTS

Bryostromatolites in the field

Bryostromatolite reefs can be identified in the field by their characteristic shape. Their surfaces have a typical cauliflower-like appearance (Figs 2 and 5A) that is developed in every available direction, even downward (Fig. 2A). The reefs are small, a few decimetres up to 1 m in height, but they can extend for several tens of metres horizontally. Their distribution is patchy and they are only slightly elevated in the field, for example at Bote 2 (Fig. 2F). Allochthonous sediments were deposited in between the different reef bodies. In most cases, the reefs are surrounded by coarse-grained, poorly sorted reef debris. In Nors Stenbrott the bryostromatolite is surrounded by well-sorted shoal deposits (Ernst *et al.*, 2015). Thin sections from every bryostromatolite are displayed in Figs 3 and 4.

Microfacies results

Quantitative composition and diversity
The method for quantifying components is displayed in Fig. 5 and the results in Fig. 6 for all localities individually. The bryostromatolites are

Fig. 2. Bryostromatolite samples in the field showing characteristic cauliflower-like growth: (A) sample from Nors Stenbrott, pen diameter = 1 cm; (B) sample from Nors Stenbrott, Estwing rock pick hammer length = 33 cm, width = 18.5 cm; (C) sample from Nyan, Estwing rock pick hammer length = 33 cm, width = 18.5 cm; (D) sample from Hällagrund, thumbnail width = 1.5 cm; (E) sample from Lau Backar, pen diameter = 1.5 cm; (F) outcrop of Bote 2, the bryostromatolite reefs (arrows) are slightly elevated compared to the surrounding sediments.
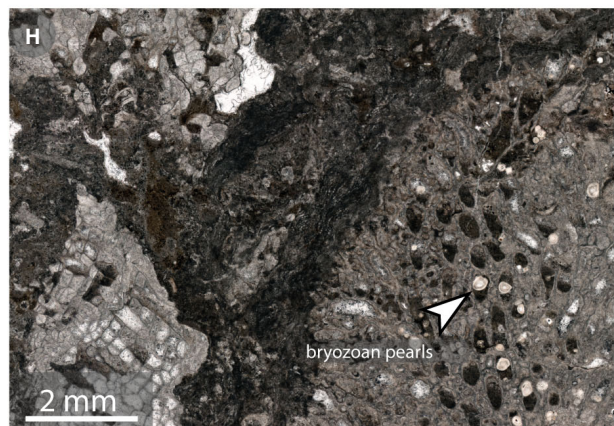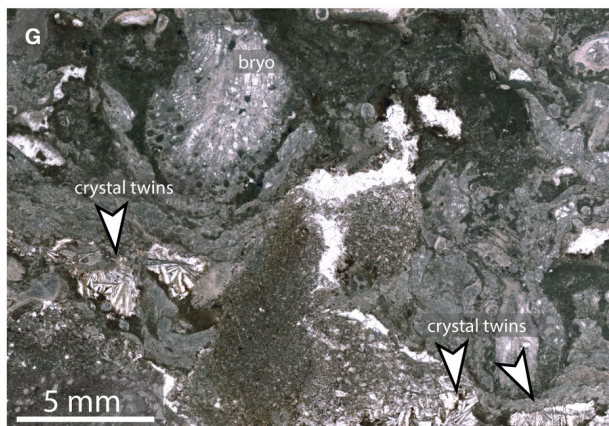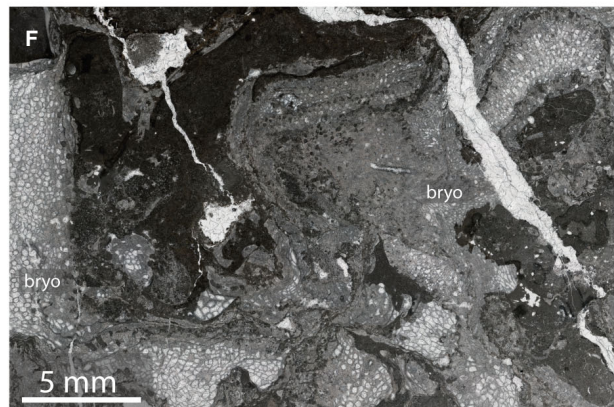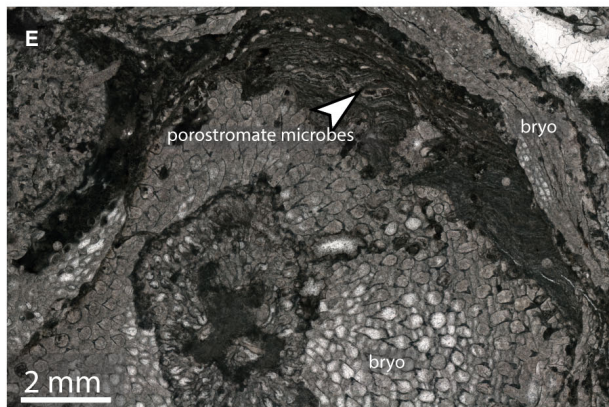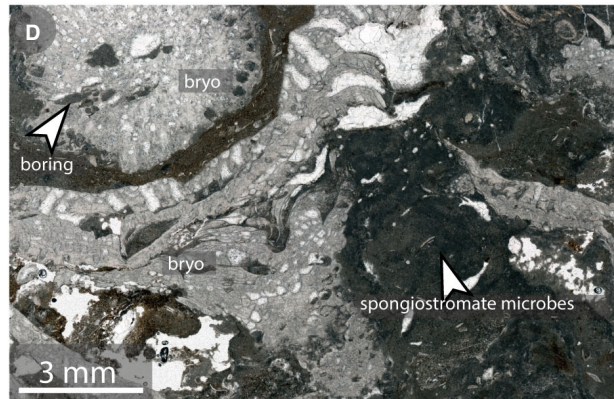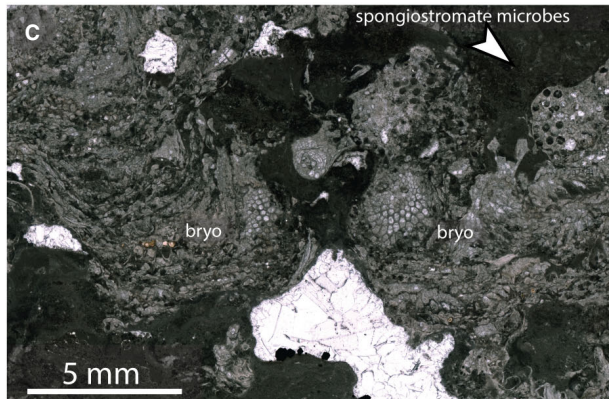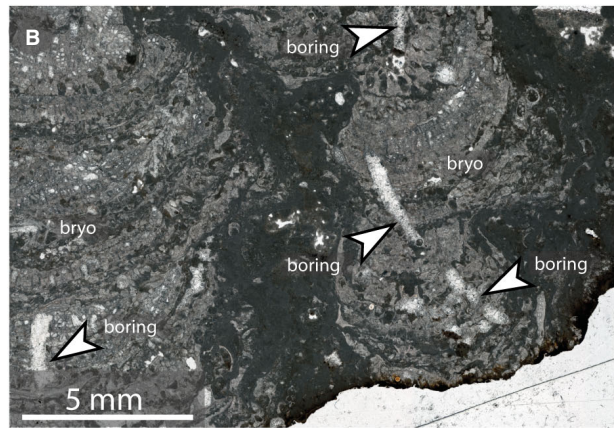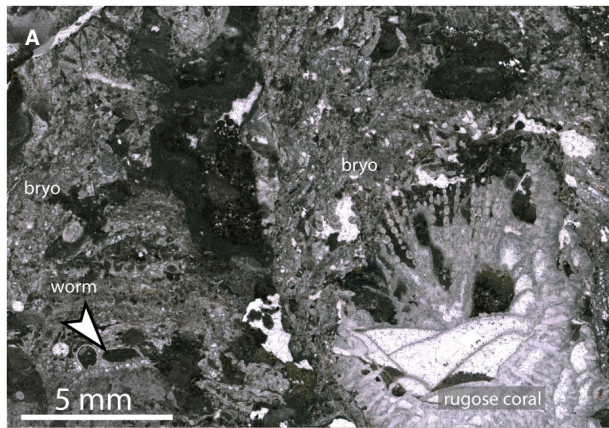
Fig. 3. Example of thin sections of the investigated bryostromatolites Högklint, Nors Stenbrott, Hällagrund, Hällgrund 2, Botvide, Nyan and Lau Backar. Main components are highlighted with arrows: (A) thin section from Högklint (SHOj) with a rugose coral, microconchid worm and bryozoans; (B) thin section from Nors Stenbrott (SNS1-12) with bryozoans and borings (arrows); (C) thin section from Hällagrund (SHG1f), highlighted are spongiostromate microbes (arrow) and bryozoans; (D) thin section from Hallsarve 2 (SHL2r2) with spongiostromate microbes (right arrow), bryozoans and borings (left arrow); (E) thin section from Botvide (SBT19f) with bryozoans and porostromate microbes (arrow); (F) thin section from Nyan (SN1-2) with bryozoans; (G) thin section from Lau Backar (SLB18-2k) with bryozoans and cross-shaped crystal twins (arrows); (H) thin section from Hallsarve 1 (SHL1t2) showing bryozoan pearls in a *Favositella interpuncta* colony; abbreviation bryo = bryozoan.

mainly composed of bryozoans and microbes with varying abundances. The percentages of bryozoans range from 28 to 43% (Fig. 6). For understanding bryostromatolite growth, the porostromate and spongiostromate microbial carbonates were measured separately. Porostromate microbes contributed 0 to 14% and spongiostromate microbes 14 to 46%. Palaeozoic reef builders like corals and stromatoporoids were present, but in most samples were less abundant. In Nors Stenbrott and Botvide corals make up about 20% of the reef. Rugose corals and tabulates were both observed. The bryostromatolites from Lau Backar and Hoburgen show high abundances of auloporids (Tabulata). In contrast, sponges were only of importance at Högklint. In the bryostromatolites mainly lithistid sponges (Fig. 7A) but also scarce keratose sponges (Fig. 7B) were observed. Stromatoporoids (Fig. 7C), however, are rare and were only counted in thin sections from bryostromatolites of Nors Stenbrott and Hoburgen. The associated fauna in the bryostromatolite consists of echinoderms (Fig. 6),

tentaculitoid worms (Figs 3A and 6), such as microconchids and cornulitids, brachiopods (Fig. 6) and ostracods (Fig. 6). Allochthonous sediment is present but not in high abundance. Additionally, boring traces were counted but excluded from the total counts because the borings, cutting through different components or sediments, were produced after the bioeroded components were early lithified but at a time when the reef was still growing, proven by reef dwelling organisms that subsequently lived in the boring trace (Claussen *et al.*, 2019) and by traces overgrown by bryozoans and/or microbes.

Bryozoans

Palaeozoic bryozoans mainly belong to the class Stenolaemata, which is subdivided into Cyclostomata, Cystoporata, Trepostomata, Cryptostomata and Fenestrata. All stenolaemates with the exception of Cyclostomata are classified in the Superorder Palaeostomata (Ma *et al.*, 2014a). The order Cyclostomata, however, was
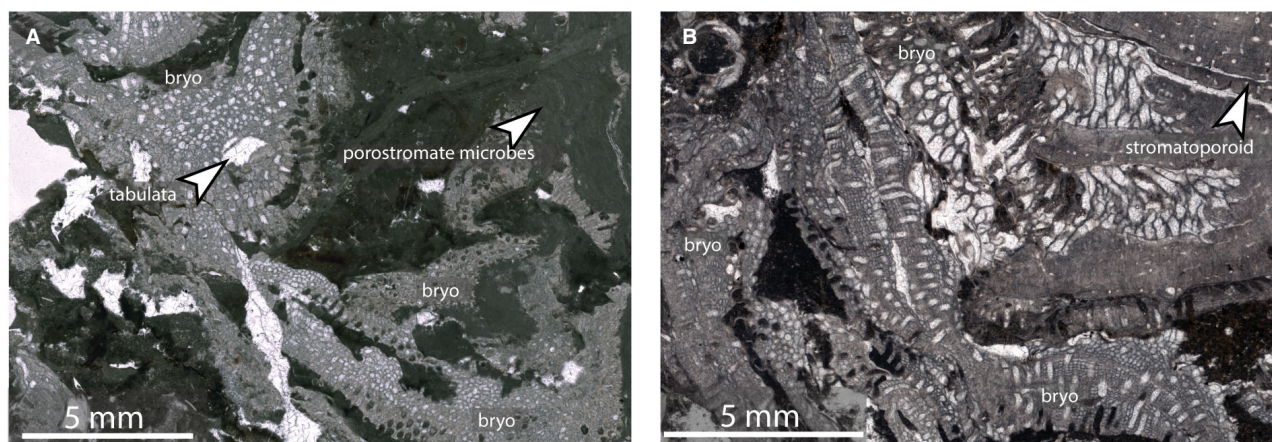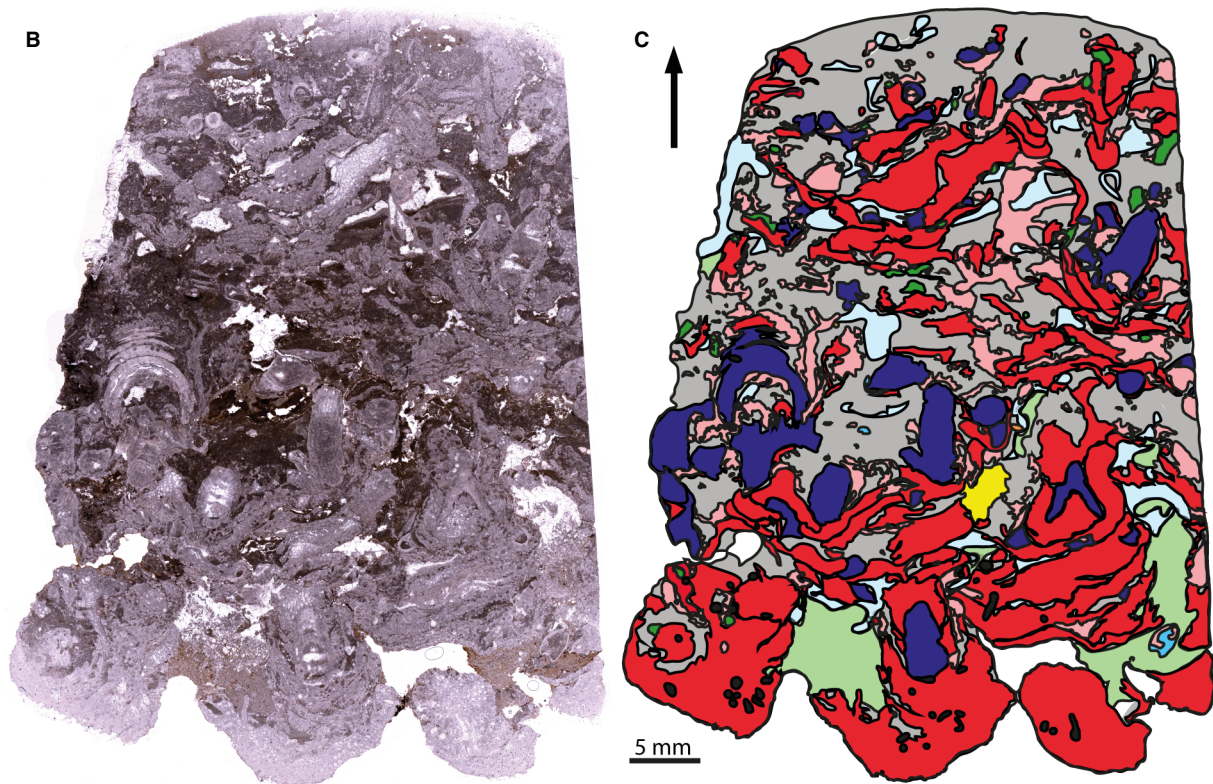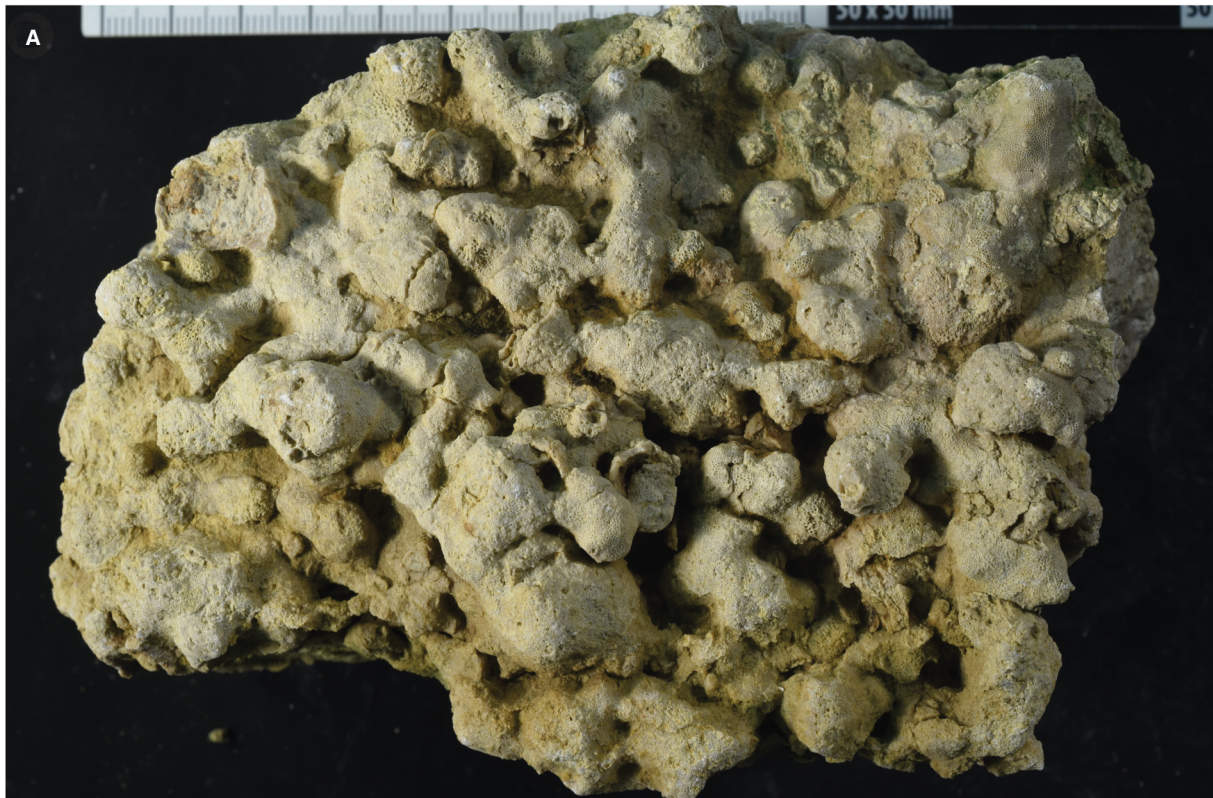

Fig. 4. Example of thin sections of the investigated bryostromatolites from Bote 2 and Hoburgen. Main components are highlighted with arrows: (A) thin section from Bote 2 (SB2-3j) with porostromatate microbes (right arrow), bryozoans, and an endobiontic tabulate (left arrow); (B) thin section from Hoburgen (SHB1) with bryozoans and a stromatoporoid (bryo = bryozoan).

Fig. 5. Sample from Lau Backar in (A), thin section of the same sample in (B) and with coloured components in (C): (A) cleaned sample from Lau Backar SLB18-3 with well-developed cauliflower-like surface; (B) thin section SLB18-3i with downward directed growth, the cauliflower-like surface is facing downward; (C) redrawn thin section to highlight the different contributors of the bryostromatolite, cauliflower-like surface is mainly formed by bryozoans.

rare in Palaeozoic communities and radiated mainly in the Mesozoic. Only one species of cyclostomes has been found in the examined assemblages from Gotland. In total 42 different bryozoan species were identified in the bryostromatolites (Fig. 8), eleven of them were described by Ernst *et al.* (2015) from Nors Stenbrott.

Seven species can be assigned to the order Cryptostomata, thirteen species to the order Cystoporata, eight species to the order Fenestrata, and thirteen species belong to the order Trepostomata. The ranges of the species are displayed in Fig. 8. Twelve species are restricted to Wenlock bryostromatolites, and sixteen species are restricted to

Fig. 6. Component quantities per locality; (A) Högklint, quantification for five thin sections; (B) Nors Stenbrott, quantification for seven thin sections; (C) Hällagrund, quantification for five thin sections; (D) Hallsarve 2, quantification for six thin sections; (E) Botvide, quantification for five thin sections; (F) Nyan, quantification for five thin sections; (G) Lau Backar, quantification for seven thin sections; (H) Hallsarve 1, quantification for eight thin sections; (I) Bote 2, quantification for five thin sections; (J) Hoburgen, quantification for seven thin sections; legend below; *y* – axis is percentage; error bars are displaying the standard error of the mean, calculated by the standard deviation divided by the square root of the number of measurements.
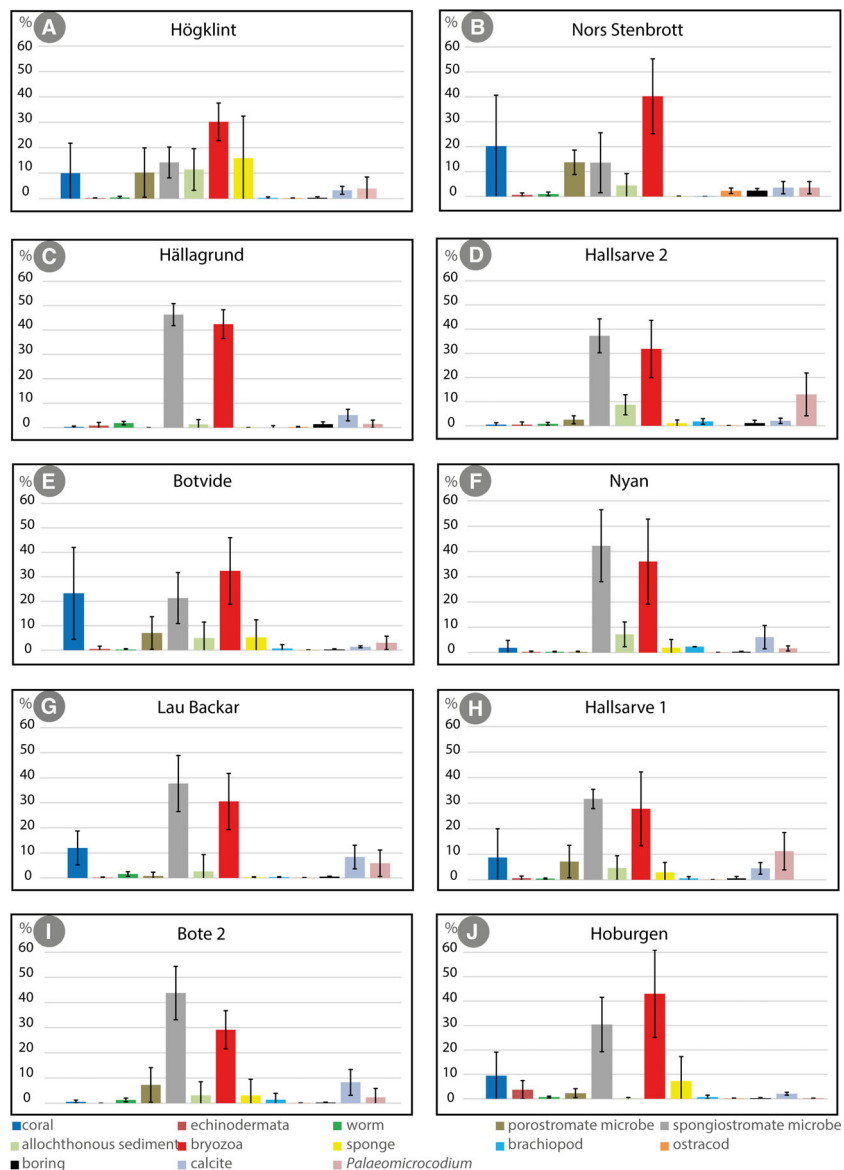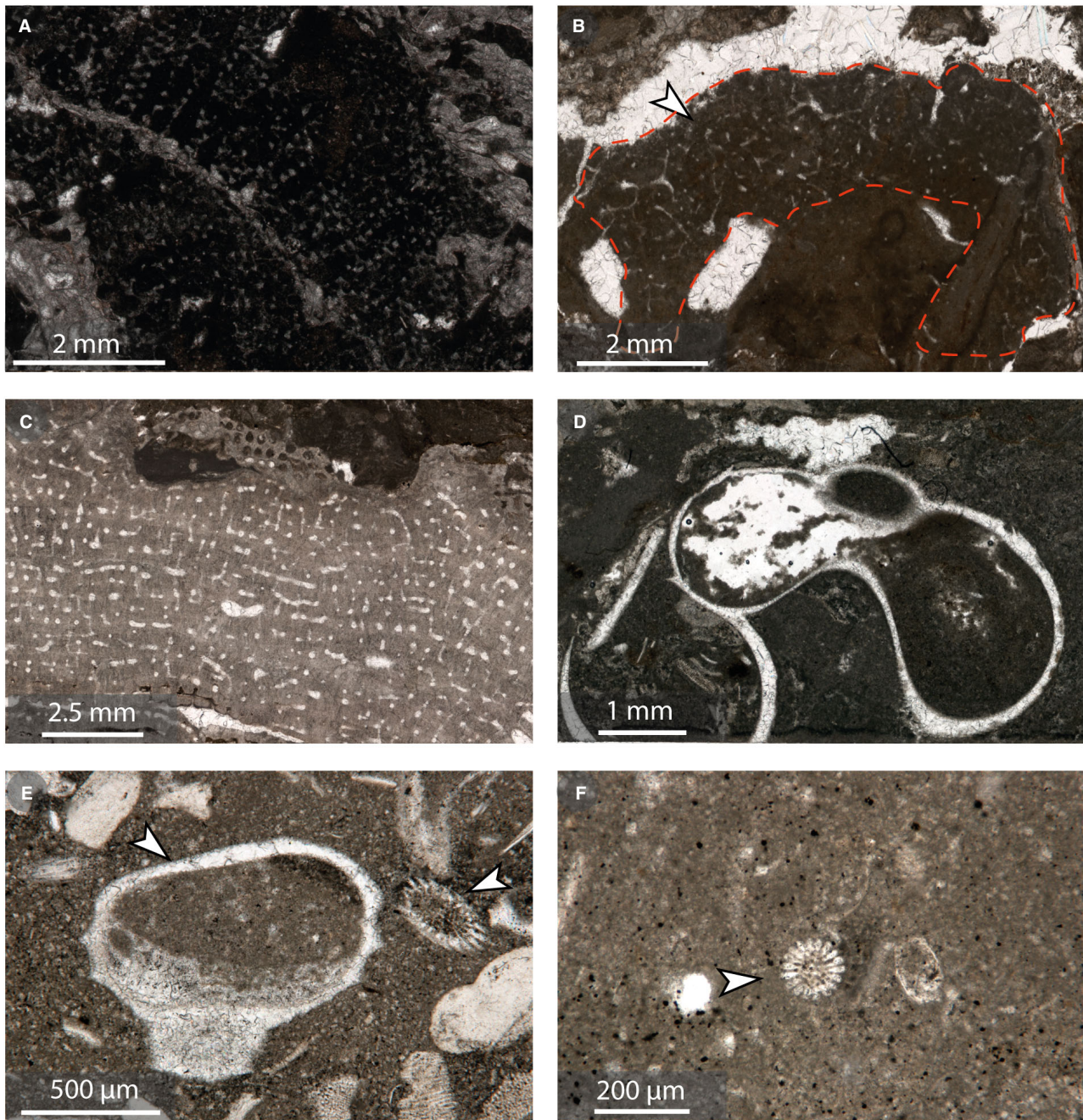
Fig. 7. Different components inside the bryostromatolites: (A) regular mesh-like spicules of lithistid sponges from Högklint; (B) remnant of soft keratose sponge (arrow; cp. Luo & Reitner, 2014; Luo, 2015) preserved in bryostromatolites from Botvide, red dotted line indicating the outline of the sponge; (C) stromatoporoid from Hoburgen; (D) recrystallized, originally aragonitic gastropod shell from Nyan; (E) recrystallized gastropod and characteristic star-like section through echinoid spine, both indicated with arrows; (F) characteristic star-like section through an echinoid spine.

bryostromatolites from Ludlow. Fourteen species have been recorded for both times. The studied bryozoans develop various growth habits: encrusting, branching or ramose, fenestrate and massive (Fig. 8). Encrusting forms are dominant in the bryostromatolites. Branching or ramose growth forms are less abundant in Högklint, Nors Stenbrott and Hällagrund but more important in

Stratigraphic range

	Högklint Högklint Fm	Nors Stenbrott Tofta Fm	Hällagrund Hangvar Fm	Hallsarve 2 Eke Fm	Botvide Eke Fm	Nyan Eke Fm	Lau Backar Eke Fm	Hallsarve 1 Eke Fm	Bote 2 Eke Fm	Hoburgen Hamra Fm
Cyclostomata										
Corynotrypa sp.						————				
Cryptostomata										
Metadictya sp.						————				
Nematopora sp.					———————————					
Orthopora sp.1 cf. worsleyi				———————————————————————————						
Orthopora sp.2				————————————————— - - - - - ————						
Orthopora sp.3						———————— - - - ————————				
Ptilodictya lanceolata				—————————————						
Saffordotaxis sp.			————————————————————————————————————							
Cystoporata										
Acantholunaria expansa	———————————									
Buskopora sp.1				————————————————————————————————						
Buskopora sp.2			————————— - - ————————————————————							
?Buskopora sp.3	——— - - - - - - - - - ———————————————————									
Ceramopora lindstroemi				— - - - - - - - ———————————— - - - ————————						
Ceramoporella sp.		———————————————		— - - - ——————— - - - ———						
Curvipora monostylata		—————————————————————								
Favositella interpuncta		——————————— - - ———								
Fistulipora corticea		—————								
Hennigopora sp.1		——								
Hennigopora sp.2		—————								
Physallidopora sp.				————————————————————————————————						
Cystoporata sp.										————
Fenestrata										
"Arcanopora" sp.	———————									
?Filites sp.			————————— - - ——————— - - - ——————— - - - - —————							
?Prolixicella sp.		———————————————— - - - ———								
Ramipolypora toernqvisti	———————————————									
?Reteporina sp.	——— - - - - ———————————————————————————————————————									
Schischcatella sp.		—————————————————								
Semicoscinium sp.										————
Unitrypa sp.										————
Trepostomata										
Amplexopora sp.										————
Asperopora aspera	———									
Eostenopora peculiare	—————————————————									
Eridotrypa sp.						——————————— - - ———————				
Hallopora varians		———————————————								
?Heterotrypa sp.								————		
Leioclema sp.										————
Leptrotrypa enodis		————————————————————— - - - ———————								
Leptrotrypa perforata		—————————————								
?Loxophragma sp.		——————— - - — ———————————————————————								
?Orbipora sp.				— - - ———————————— - - - - - ——— - - - - ———						
Stellatotrypa hirsuta		—————————								
Trematopora sp.			—————————							
Total	14	19	15	13	15	20	16	16	12	19

Growth types ☐ massive ☐ fenestrate ☐ encrusting ☐ branching/ramose

—— present
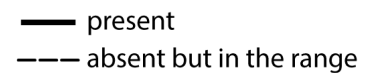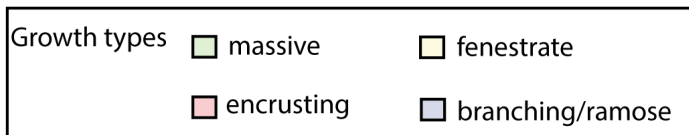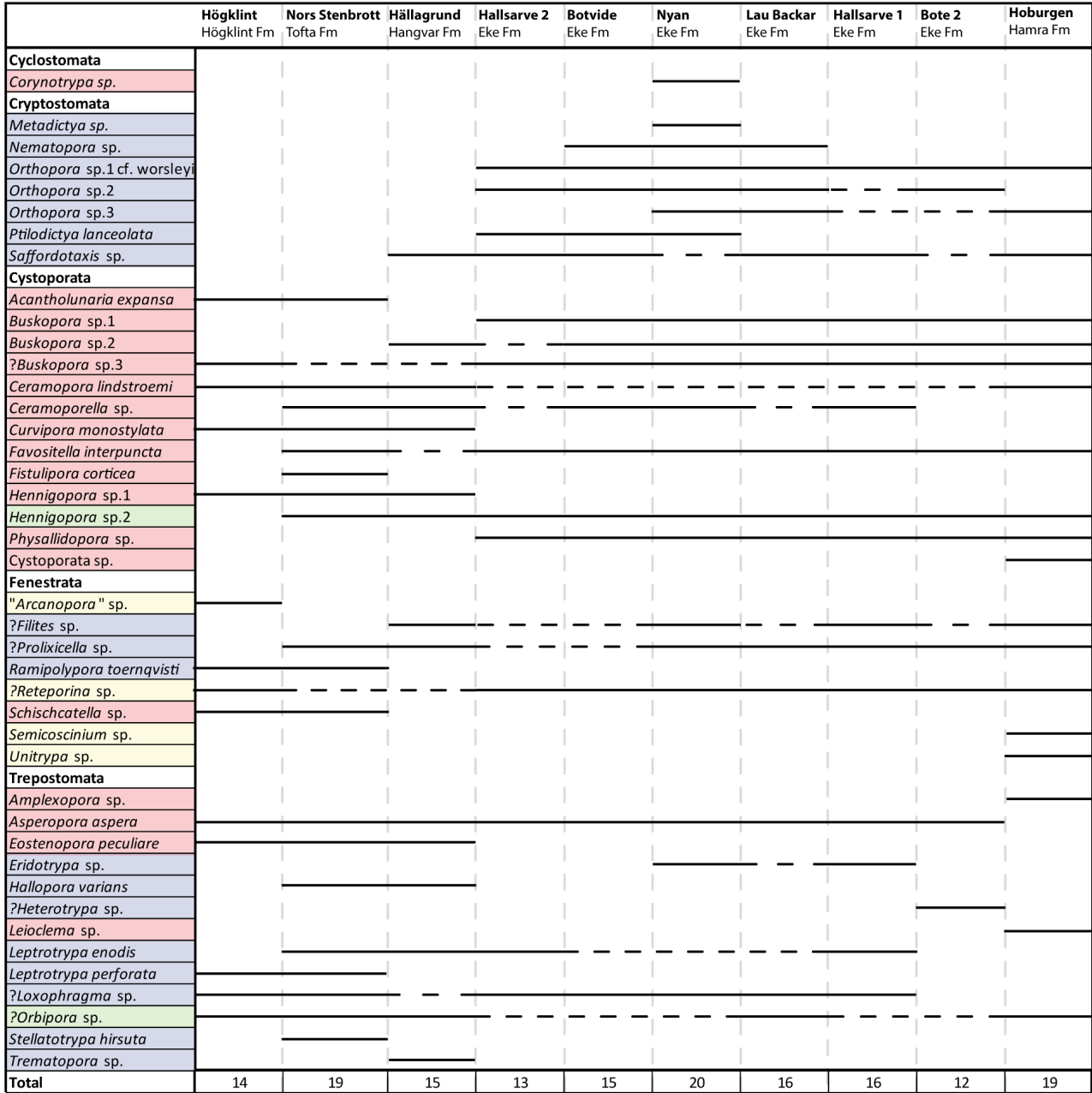– – – absent but in the range

Fig. 8. Bryozoan species ranges for the investigated bryostromatolites with observed growth forms. The observed growth habit of every species is indicated with colours on the left-hand side of the range chart.
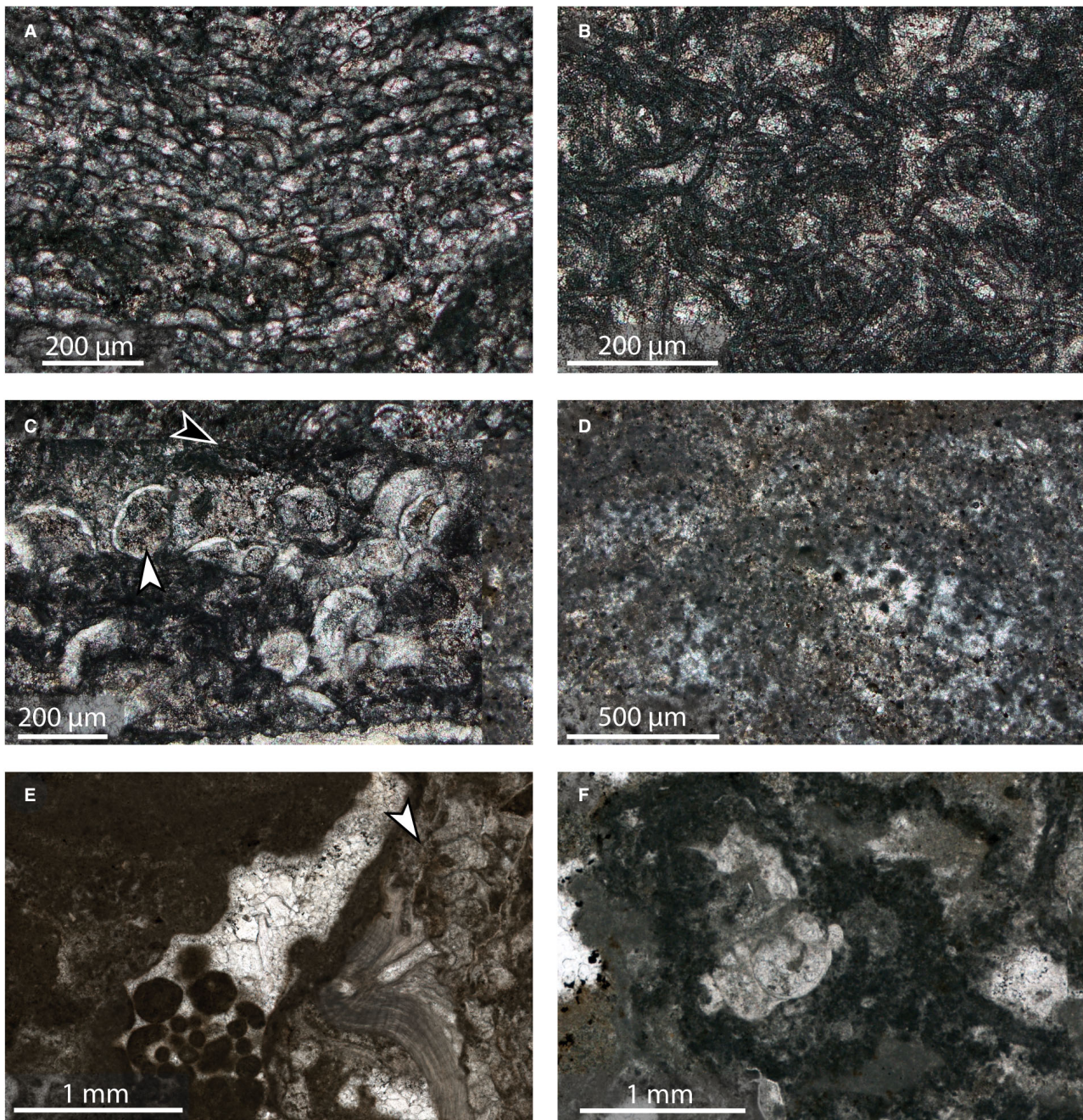
Fig. 9. Different porostromate and spongiostromate microbes observed inside bryostromatolites: (A) *Rothpletzella* sp. from Bote 2; (B) *Girvanella* sp. from Högklint; (C) *Allonema* sp. with *Rothpletzella* sp. from Lau Backar; (D) peloidal micrite from Lau Backar; (E) large peloids inside a cavity created in the interspace between bryozoan fingers (arrow pointing to a finger), sample SHOj from Högklint; (F) clotted spongiostromate microbial layers that cover other components, sample from Nors Stenbrott.

Hallsarve 2, Botvide, Nyan, Lau Backar and Hallsarve 1. Massive and fenestrate bryozoans are less abundant in every bryostromatolite. The detailed taxonomy behind the species identification will be included in an upcoming paper.

Microbial carbonates

The bryostromatolite reefs are composed not only of diverse bryozoans but also of different microbial carbonates. On average one-third of
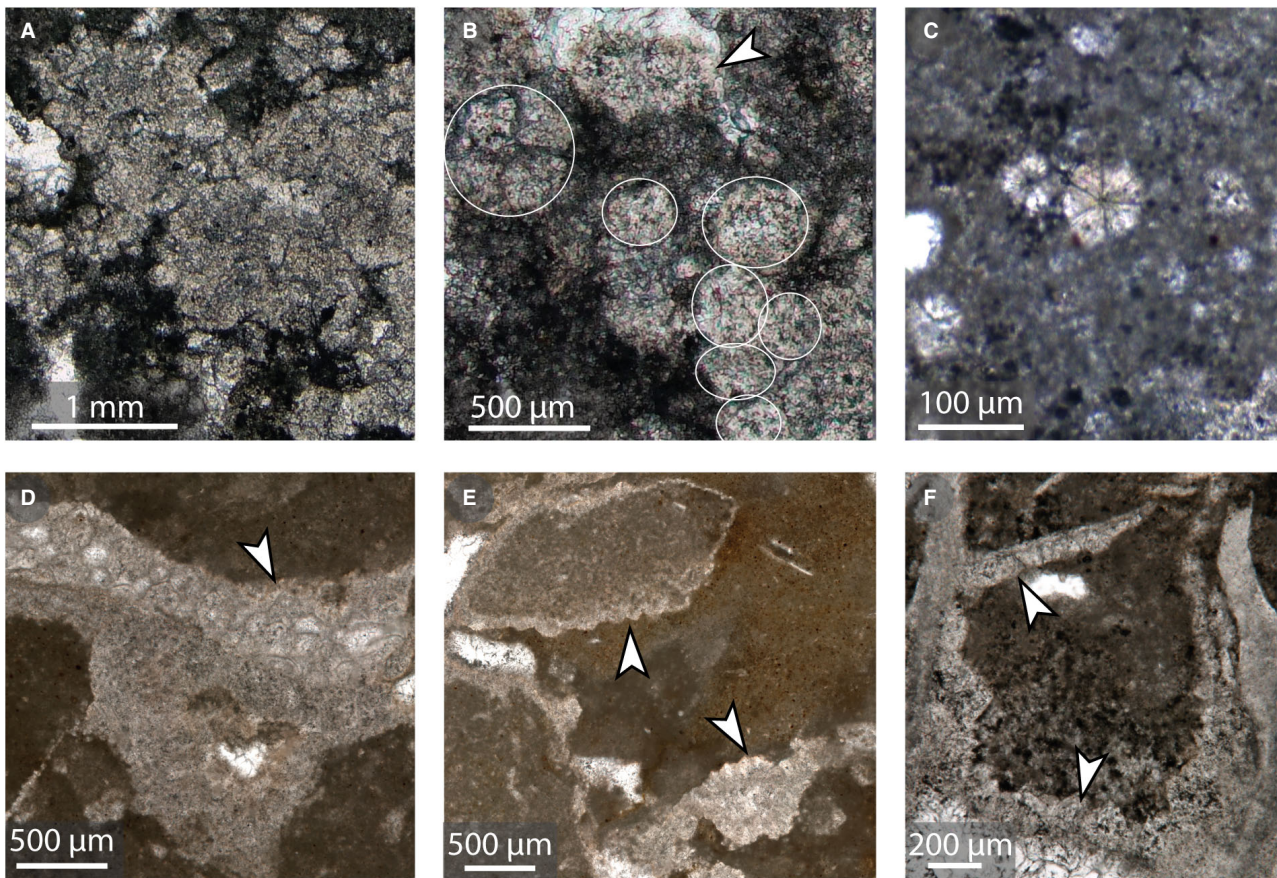
Fig. 10. Observed growth habits of *Palaeomicrocodium* (A) to (F): (A) crusts composed by spheroidal *Palaeomicrocodium* from Hallsarve 1; (B) crust with highlighted (circle) spheroidal *Palaeomicrocodium* from Hallsarve 1, note that the crust in the upper part (arrow) was growing inside a pore; (C) characteristic rosette-shape from Nors Stenbrott; (D) bryozoan (arrow) growing on top of a *Palaeomicrocodium* crust in Hallsarve 2; (E) root-like association of granular crusts composed of *Palaeomicrocodium* – the left side is granular, while the right side is composed of more spheroidal forms from Hallsarve 2, both indicated with arrows; (F) *Palaeomicrocodium* as early cement-like structure (arrow) inside a tabulata from Nors Stenbrott.

each reef's material (Fig. 6) is composed of microbial carbonates formed by calcified microbes. Two different 'groups/classes' of microbial carbonates are observed: porostromate microbes and spongiostromate microbes. The porostromate microbes have a clear tubular structure. They are present in moderate abundances and are related to cyanobacteria (Flügel, 2004), and were therefore light-dependent. They produced autochthonous crusts of a millimetre up to few centimetres in thickness. Species composing these crusts are *Rothpletzella* sp. (Fig. 9A and C) and *Girvanella* sp. (Fig. 9B). *Allonema* sp. (Fig. 9C) is also commonly observed in these crusts; its systematic position, however, is debated (Jarochowska & Munnecke, 2014; Wilson & Taylor, 2014; Jarochowska *et al.*, 2016).

Spongiostromate microbial crusts have a higher abundance (Fig. 6). They produced dark clotted coats (Fig. 9F), peloidal clotted sediments (Fig. 9D), or peloids in cavities (Fig. 9E). In contrast to porostromate microbes, they do not show any microstructures and appear dark or even black in thin sections.

Another noteworthy and common structure is *Palaeomicrocodium* (Mamet & Roux, 1983). It is cement-like and present in almost every bryostromatolite on Gotland. The habit of *Palaeomicrocodium* is variable (Fig. 10A to F). It can form single prismatic rosettes (Fig. 10C) as well as clusters composed of spheroidal (Fig. 10A and B) to granular translucent (Fig. 10D and E) or fibrous crusts. It can form complex three-dimensional structures that
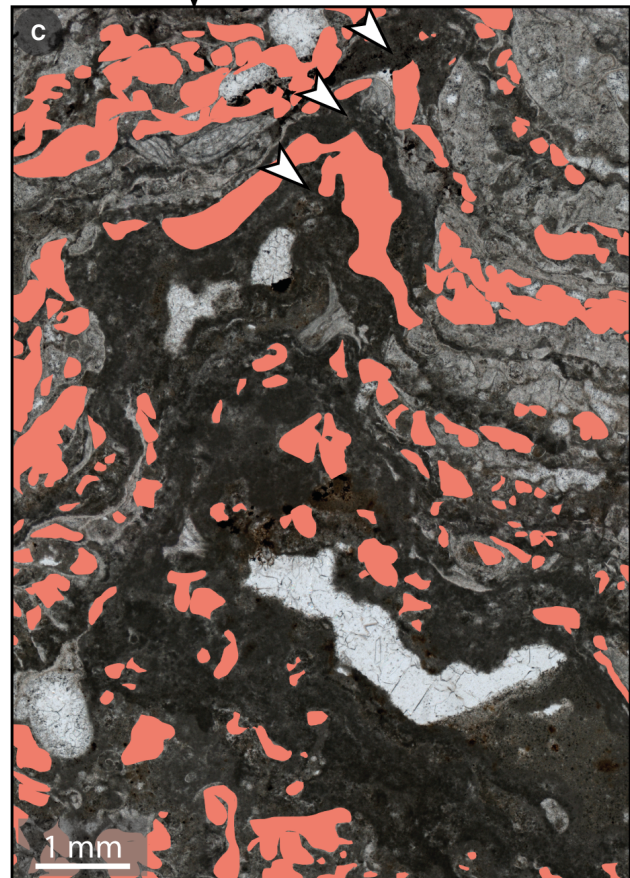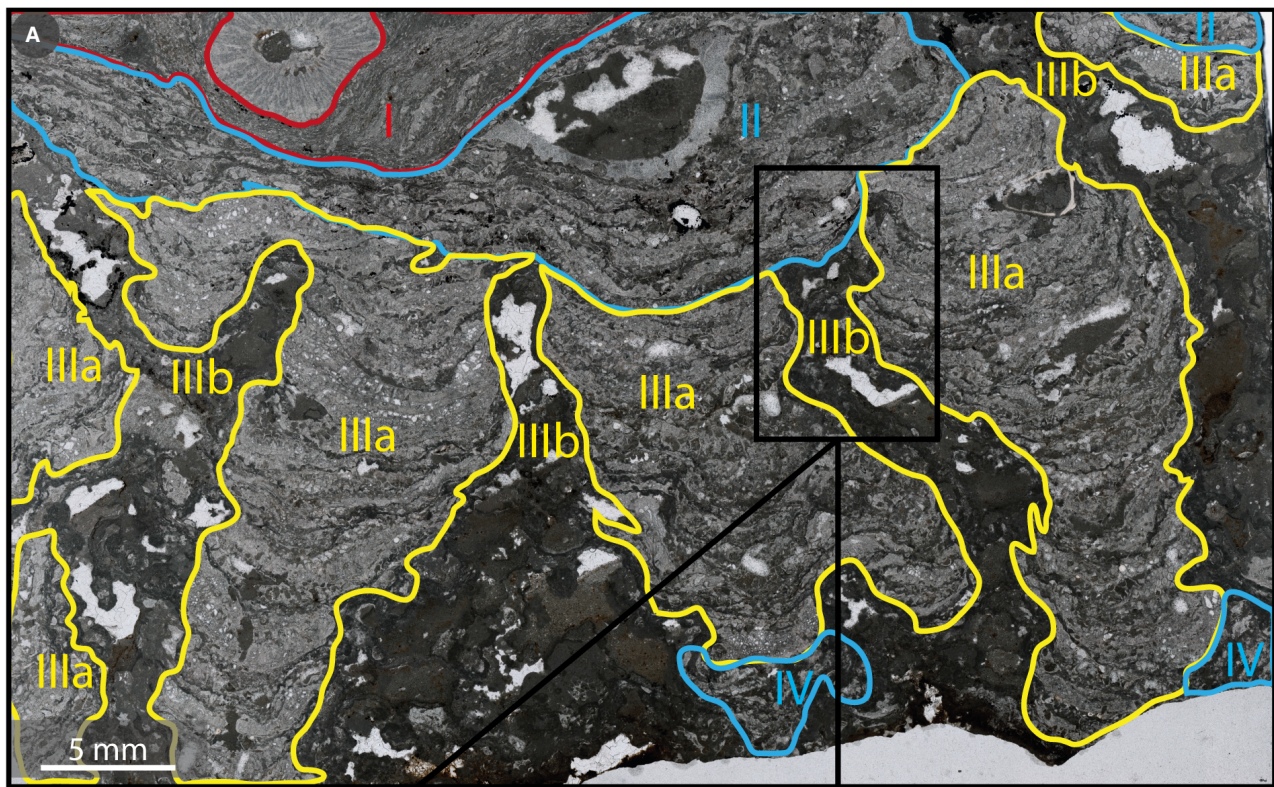
Fig. 11. Bryostromatolite growth succession in SNS1-4 in (A) and *Palaeomicrocodium* distribution highlighted in an area from the sample above (B) and (C): (A) different associations during the bryostromatolite growth succession highlighted on the sample SNS1-4 from Nors Stenbrott in different colours, labelled with I, II, IIIa, IIIb and IV; (B) area of the thin section from above; (C) same area with *Palaeomicrocodium* crusts highlighted with red colour, arrows pointing to spongiostromate microbial layers to highlight the alternation with *Palaeomicrocodium*.

appear in thin sections like translucent root-like or vesicular crusts (Fig. 10E). Some spheroids show a zonation with darker areas in the centre. *Palaeomicrocodium* can occur inside microbial carbonates (Fig. 5), in pores, or as a crust attached to corals (Fig. 10F), bryozoans or other components. In some cases, the bryozoans used *Palaeomicrodium* as a substrate (Fig. 10D). It is present in all bryostromatolites and can contribute significant amounts to the reef. In the bryostromatolites from Hallsarve 1 and Hallsarve 2, more than 10% of the volume of these reefs were composed of *Palaeomicrocodium*. Its origin is under debate: some authors (Mamet & Roux, 1983; Mamet & Préat, 1985) have assigned it to algae or cyanobacteria, while Antoshkina (2014) interpreted it as structures created by early lichens (see *Discussion* section below).

Bryostromatolite growth succession

The investigation of the microfacies revealed three different associations of microbes and/or bryozoans in the reefs. A sample from Nors Stenbrott (Fig. 11A) was chosen to highlight the different stages of growth. These are: thick porostromate multilayers (I, Fig. 12A and B), thin bryozoan layers alternating with clotted spongiostromate microbes (II, Fig. 12C and D), and finger-like bryozoan multilayers, growing in every direction (IIIa, Fig. 12E and F; Table 2). The interspaces between the fingers were filled by spongiostromate microbes (IIIb, Fig. 12G and H). These described associations are abundant, but not all of them can be found in every bryostromatolite, and their succession can also vary (Table 3).

Other biogenic components and structures

An overview about the presence, absence and, respectively, the abundance of the features per locality is given in Table 4.

Epifaunal organisms
In addition to reef building organisms also remnants of mobile epifaunal organisms can be found in all bryostromatolites. Characteristic recrystallized former aragonitic gastropod shells (Fig. 7D and E) can often be observed in the thin sections. Also, characteristic star-like microstructures of echinoid spines are common features (Fig. 7E and F).

Bioerosion
Bioerosion is a common feature in the Silurian bryostromatolites on Gotland. Traces of boring organisms are especially abundant at Nors Stenbrott, Hällagrund and Hallsarve 2, but are also present in the bryostromatolites from other localities. Various boring structures of different thicknesses can be found (Fig. 13A and B), penetrating different substrates. Also, borings could be observed that were drilled through components as well as sediment. In some borings reef-dwelling organisms could be observed, like sponges, or bioclasts (Fig. 13B). Generally, they are more abundant in bryozoan fingers than in crusts. Some of the larger borings from Nors Stenbrott contain bivalves (Oswald, 2010; Claussen *et al.* 2019), which presumably produced the boreholes themselves and did not occupy pre-existing boreholes, while other boreholes were occupied by nestling lingulid brachiopods.

Cystoidea
In the bryostromatolite from Nors Stenbrott unusual echinoderms are abundant. They are globular in shape, but have a huge opening at the basal area, where they are attached directly to the hard substrate (Fig. 14C to G). No specimen possessed a stem, but the specimens had specialized attachment plates, which grew broader in diameter at the direct attachment to the substrate (Fig. 14C to G). All observed specimens showed a similar helmet-like growth and they possessed a spiral-like ornamentation due to the arrangement of their ambulacral plates (Fig. 14A and B). This characteristic shape was produced by the diploid cystoid *Celticystis gotlandicus* (Angelin, 1878) (Regnéll, 1945; Bockelie, 1979). Their only observed occurrence in this study is in the bryostromatolites from Nors Stenbrott.
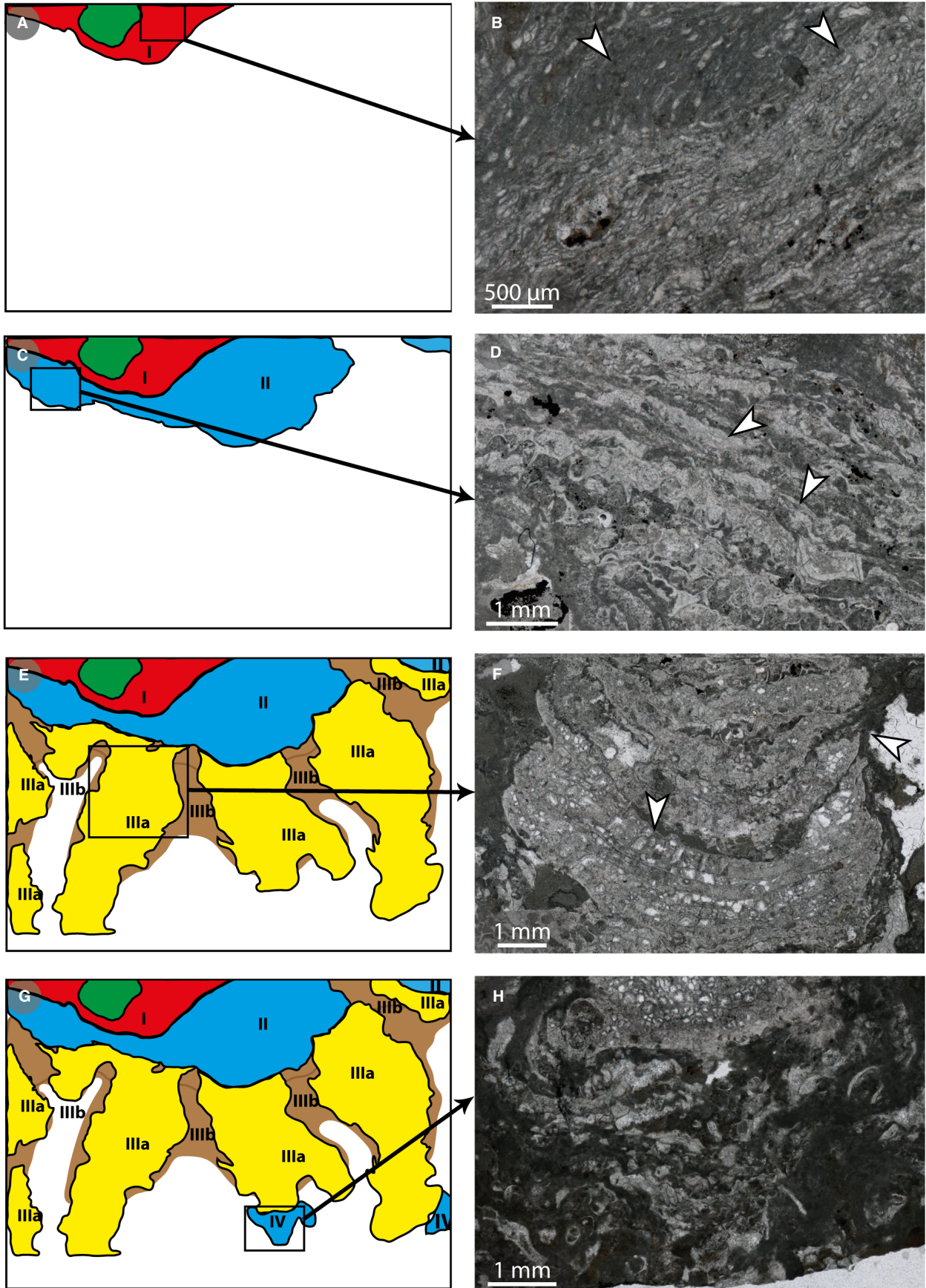
Fig. 12. Sequence of growth shown step by step for sample SNS1-4 (see Fig. 11A for overview), different layers are indicated by arrows, on the left side the drawing is shown whereas on the right side thin section details are displayed: (A) stage I shows the formation of a porostromate crust during the microbial optimum (Fig. 17); (B) example of stage I in thin section, arrows indicating different stages during the growth of the porostromates; (C) stage II is composed of alternating thin layers of bryozoan and microbial crusts; (D) thin section of stage II, arrows are pointing to thin bryozoan layers; (E) stage III is dominated by bryozoans, here thick bryozoan crusts are formed (IIIa), but at the same time also spongiostromate microbes (IIIb) started to grow in the interspaces between the stage IIIa fingers; (F) example of a bryozoan stage IIIa bryozoan finger with spongiostromate crust (stage IIIb) surrounding it (right arrow); (G) the conditions changed back to more hostile conditions, alternating bryozoan and microbial crusts are developed (stage IV); (H) the termination of the bryozoan fingers by thin layered bryozoans and spongiostromate coating.

Endobionts and epibionts

Often the bryostromatolites show intense intergrowth by other organisms. The bryozoans themselves showed often epibiontic activity, either by forming of new layers on themselves (secondary or self-overgrowth), or by colonies overgrowing existing ones of either the same or a different species. Additional to this, other organisms interacted with the bryozoan community. Epibiontic and endobiontic activity can be recognized commonly in the bryostromatolites. Palaeozoic tentaculitoid microconchid worms (Fig. 13E) can be found attached on bryozoan crusts or on other associated organisms. Other epibiontic organisms besides microbes are corals (for example, auloporids), brachiopods (for example, Craniida), sponges and echinoderms. Furthermore, some corals were forming intergrowths with bryozoans. In many cases, they were observed to be embedded in the bryozoan skeletons of the massive growing cystoporate *Hennigopora* sp. 2 (Fig. 13C and D). Rounded or tube-like structures with septae, possibly syringoporid corals or *Chaetosalpinx* bioclausations (Fig. 13C and D), can often be observed inside nearly all specimens from the Eke and Hamra bryostromatolites. The calcitic skeletons of *Hennigopora* as well as of the syringoporid show structural distortion (Fig. 13C and D).

Ostracods

Some pores in the reef framework are filled with ostracods. They can be numerous, and are often stacked (Fig. 13F), but some pores contain only single specimens. This feature was observed in all bryostromatolites.

Phosphatic components

In addition to the calcitic components, many phosphatic components are observed in the bryostromatolites. The most important ones are phosphatic brachiopods (Fig. 15A to C) and bryozoan pearls (Fig. 15D to H; Table 5). The brachiopods are clearly visible but their taxonomic identities cannot be determined in the thin sections. Therefore, several rock samples from Nors Stenbrott (SNS) and Nyan (SN1) were dissolved with acetic acid in order to extract the phosphatic components, and were imaged under reflected light and SEM (Fig. 15A to C). Craniid and lingulid brachiopods were recovered from the samples from Nors Stenbrott, while the brachiopods from Nyan belong to the discinid *Chynithele vexata* (Barrande, 1879) and to lingulid

Table 2. Average length and average number of single bryozoan layers counted for the bryozoan fingers for every locality. Additionally, the number of counts is displayed.

	Högklint	Nors Stenbrott	Hällagund	Hallsarve 2	Botvide	Nyan	LauBackar	Hallsarve 1	Bote 2	Hoburgen
Average length in millimetres	19.9	19.3	16.9	5.6	7.1	22.4	12.9	11.9	10.6	10.6
Mean number of layers	27	34	19	7	11	22	12	9	8	8
Counted fingers	4	5	21	15	9	12	13	6	10	6

Table 3. Growth succession for every bryostromatolite locality with common, as well as rare contributors, which affect the growth succession, and noticeable remarks.

Localities	Growth succession	Abundant contributors	Rare contributors	Remarks
Högklint Högklint Formation	I, II, IIIa, IIIb	Corals, sponges, porostromates	–	Corals often as substrate, sequence clearly visible, layering in thin sections
Nors Stenbrott Tofta Formation	I, II, IIIa, IIIb	Corals, sponges, porostromates	–	Corals and stromatoporoids as substrate, sequence clearly visible
Hällagrund Hangvar Formation	II, IIIa, IIIb	Spongiostromates, bryozoans	Corals, sponges porostromates	Stage I is absent, no hard substrate, bryozoan fingers directly on spongiostromate
Hallsarve 2 Eke Formation	I, II, IIIa, IIIb	Spongiostromates	–	*Palaeomicrocodium* contributed extensive parts of bryolith, succession sometimes incomplete
Botvide Eke Formation	I, II, IIIa, IIIb	Corals	–	Succession sometimes incomplete, bryozoan fingers rare and short, massive bryozoans instead of fingers
Nyan Eke Formation	I, II, IIIa, IIIb	Spongiostromates, bryozoans	Porostromates	Massive growing bryozoans often initiated growth of bryozoan fingers
Lau Backar Eke Formation	I, II, IIIa, IIIb	Corals, porostromates	–	High amount of primary pores, many different reef-dwelling organisms present like corals or worms
Hallsarve 1 Eke Formation	I, II, IIIa, IIIb	Bryozoans, porostromates	–	*Palaeomicrocodium* contributed extensive parts of bryolith
Bote 2 Eke Formation	I, II, IIIa, IIIb	Spongiostromates	Porostromates	High amount of primary pores, extensive areas with spongiostromate
Hoburgen Hamra Formation	I, II, IIIa, IIIb	Bryozoans	–	Corals and stromatoporoids as substrate, succession sometimes incomplete, fingers with broad base

brachiopods. So far, this species has been discovered in only the bryostromatolites from the Eke and Hamra formations and can be found in various thin sections. The Craniida were observed in only Nors Stenbrott (Table 5).

A high abundance of phosphatic constituents can even be recognized in thin sections inside bryozoan colonies. The species *Ceramoporella* sp., *Favositella interpuncta* (Quenstedt, 1878) and *Hennigopora* sp. 2 include abundant phosphatic pearls. In the specimens of *Ceramoporella* sp. (Fig. 15D) and *Favositella interpuncta* (Fig. 15E) the pearls are relatively large, concentric, have a clear nucleus such as brownish or whitish grains, and are located in the basal areas of the colonies. In contrast, *Hennigopora* sp. 2 has only small phosphatic pearls (Fig. 15F), without obvious concentric layering, which are distributed all over the entire colony.

Some other bryozoan species such as *Ptilodictya lanceolata* (Goldfuss, 1826) and ?*Orbipora* sp. did not produce pearls but have phosphatic linings in the basal parts of their feeding zooids (Fig. 15G and H). This habit can be observed in all bryostromatolites.

Table 4. Bryostromatolite features presence–absence-list with classification into absent, present and abundant. The abundance is depending on the studied component: for bryozoan species abundant means more than five species, for diversity more than 10 species, for porostromate and spongiostromate microbes more than 10 percent, for bioerosion and epibionts more than 1 percent for cauliflower growth, for cyclic growth, for endobionts, for ostracods, for crystal twins and for vadose silt is how often they can be found in thin sections: 0 = absent; 1 = present; 2 = abundant; spongiostr = spongiostromate microbe.

Features	Högklint	Nors *Stenbrott*	Hällagrund	Hallsarve 2	Botvide	Nyan	Lau Backar	Hallsarve 1	Bote 2	Hoburgen	Mentioned in Figure or Table
Bryozoan growth forms:											
Encrusting	2	2	2	2	2	2	2	2	2	2	Fig. 8
Branching/ramose	1	1	1	2	2	2	2	2	1	2	Fig. 8
Massive	1	1	1	1	1	1	1	1	1	1	Fig. 8
Fenestrate	1	1	1	1	1	1	1	1	1	1	Fig. 8
Diversity	1	2	1	2	2	2	2	2	1	2	Fig. 8
Porostromate microbes	2	2	1	2	2	1	1	2	1	1	Fig. 9
Spongiostr. microbes	2	2	2	2	2	2	2	2	2	2	Fig. 9
Cauliflower-like growth	1	2	2	2	1	2	2	2	2	1	Fig. 2
Cyclic growth	1	2	1	2	1	2	2	1	2	1	Figs 11, 12, 17, Table 3
Bioerosion	1	2	2	2	1	1	1	1	1	1	Fig. 13A, 13B
Crinozoa	0	2	0	0	0	0	0	0	0	0	Fig. 14
Endobionts	0	1	0	2	2	2	2	2	2	0	Fig. 13C,D
Epibionts	1	2	2	1	1	1	2	1	2	1	Fig. 13E
Ostracods in pores	1	2	2	1	1	1	2	1	1	1	Fig. 13F
Crystal twin structures	0	2	1	1	1	1	2	1	1	0	Fig. 13G, 13H, 16A–D
Vadose silt	1	2	1	1	1	1	2	1	2	1	Fig. 16E

Cavity fillings

Pores as well as fenestral structures are common in the bryostromatolites. They were often filled geopetally by vadose silt (Fig. 16E) and sometimes by biogenic components, mostly ostracods (Fig. 13F). In some cavities, large twinned crystals are visible, sometimes developed as cross-shaped twins (Figs 13G, 13H, 16A and 16B). Except for the bryostromatolites of Högklint and Hoburgen, these crystal twin structures can be found in every locality (Table 4). Also elongated rhombic and lenticular crystals can be found in these cavities (Fig. 16C and D).

Stable isotope values

The measured stable $\delta^{13}C$ and $\delta^{18}O$ isotope ratios are displayed in Table 6. Without exception, all bryostromatolites are characterized by $\delta^{13}C$ isotope values that range between 3.6‰ and 5.8‰. The background $\delta^{13}C$ isotope value ranged between 0.0 to 2.0‰ during the Silurian (Samtleben *et al.*, 1996, 2000; Bickert *et al.*, 1997; Munnecke *et al.*, 2003; Calner *et al.*, 2004).

INTERPRETATION AND DISCUSSION

All bryostromatolites on Gotland were formed in shallow platform conditions. The high abundance of calcified cyanobacteria is evidence of growth in the photic zone, and the presence of well-washed grainstones surrounding or interfingering with the reefs is an indicator of formation above the wave base. The bryostromatolites are a maximum of decimetres up to 1 m high, but can extend for several tens of metres horizontally. The cauliflower-like growth (Figs 2 and 5A) indicates vertical relief within the reefs of at least several decimetres up to about 1 m. Within protected areas in the reefs, allochthonous bioclastic sediment is preserved.

However, some questions arise: (i) why are reefs of this type comparatively rare – are they really rare, or have they simply not been previously recognized; (ii) what kind of environmental conditions are required to favour this reef type; (iii) why are stromatoporoids, which are common reef builders on Gotland, so rare in these reefs; and, finally, (iv) why are phosphatic components/fossils so abundant?
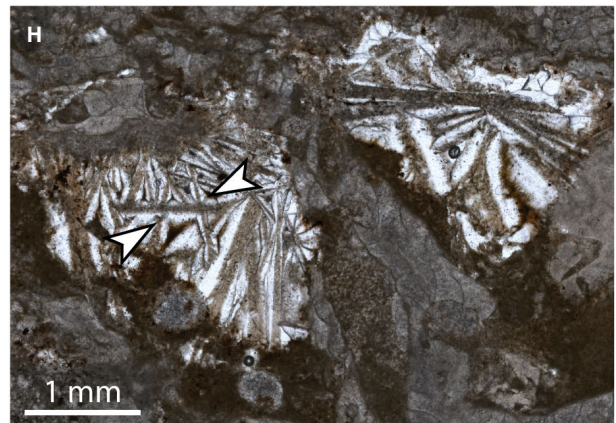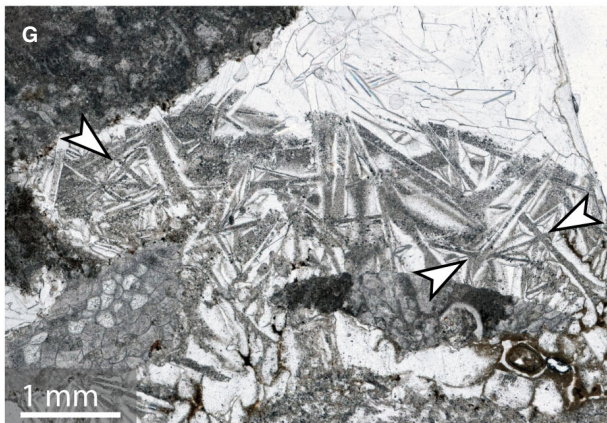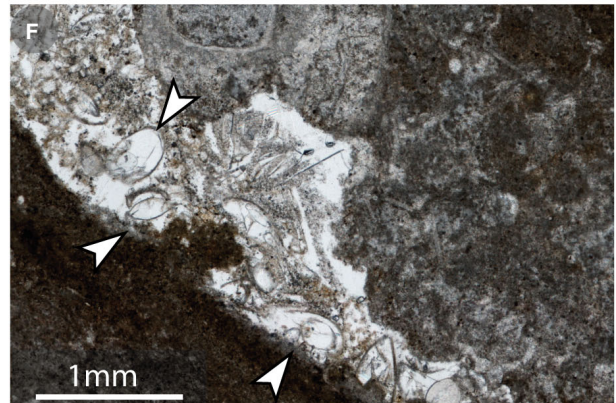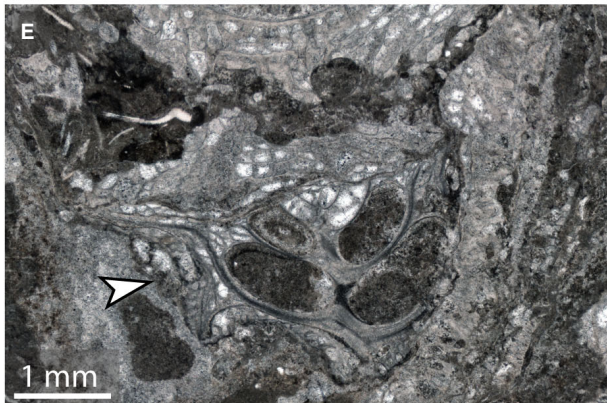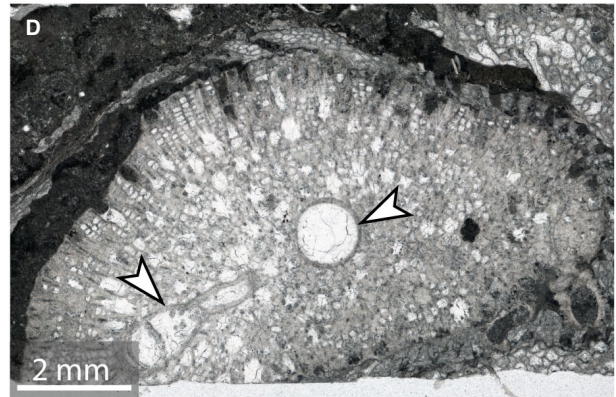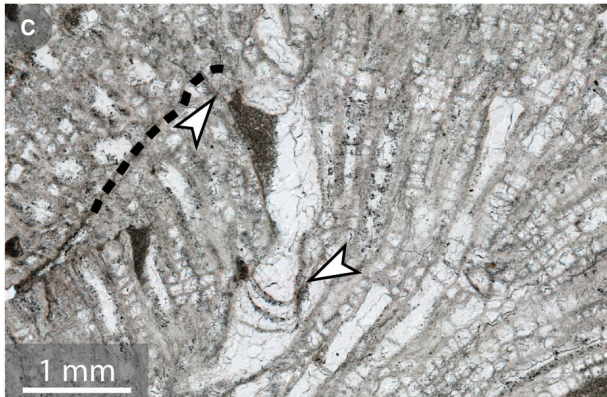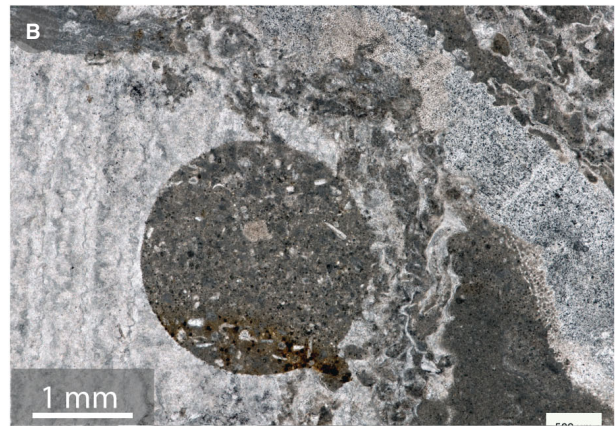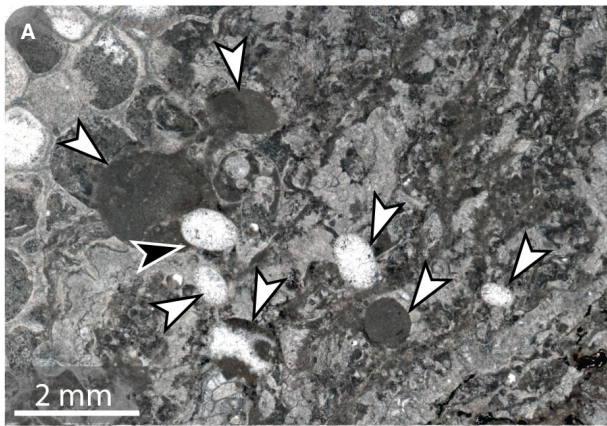
Fig. 13. Characteristic features observed in the bryostromatolites: (A) numerous borings (arrows) inside a bryostromatolite, note that a sparite-filled boring (black arrow) sharply penetrates a micrite-filled boring; SNS1-5 from Nors Stenbrott; (B) large boring inside a rugose coral, X5a from Nors Stenbrott; (C) possible endobiontic tabulate or *Chaetosalpinx*–like bioclaustration inside a *Hennigopora* sp. 2 colony from Nyan SN9, distortion of bryozoan skeleton and endobiont is visible by the thickening and thinning of the specimens (arrows), image rotated, top is oriented to the right; (D) possible endobiontic tabulate or *Chaetosalpinx*–like bioclaustration (arrows) inside a *Hennigopora* sp. 2 colony from Nyan SN7-4, (E) epibiontic microconchid worm with vesicular walls on bryozoan layers in a sample from Nyan SN7-4; (F) ostracods (arrows) in a pore from Lau Backar AM300-1; (G) cross-shaped hemi–bipyramidal twins (arrow) grown in pores of the bryostromatolite, sample AM300-1 from Lau Backar; (H) cross-shaped hemi–bipyramidal twins (arrow) grown in pores of the bryostromatolite, sample SLB18-2k from Lau Backar.

Rigidity of the bryostromatolite reefs

Many reefs on Gotland, especially in the Visby, Högklint, and Hamra formations, are composed of reef builders in a micritic matrix. Many, but not all, of these reefs show clear evidence of synsedimentary slumping, indicating that they did not produce a rigid framework. The bryostromatolites are one of the few exceptions. They formed a rigid, probably, but not necessarily, wave-resistant framework. Both reef builders and sediment have been truncated by boring organisms, which is evidence for very early lithification of the reefs. These hard substrates were heavily occupied by boring organisms. Bioerosion was rare in Palaeozoic reefs; however, the boring trace *Trypanites* occurs in various reef systems and hardgrounds and was presumably produced by worms (e.g. James *et al.*, 1977; Nield, 1984; Taylor & Wilson, 2003). The bryostromatolites, on the contrary, were bored not only by *Trypanites*, but also macroborings, occupied by lingulids or bivalves (Claussen *et al.*, 2019). In addition to boring activity, a large variety of different sessile organisms such as encrusting tentaculitoid worms (Fig. 13E) and cystoids (Fig. 14) were observed. Furthermore, many organisms show an endobiontic mode of life. Endobiontic adaptation means protection for the organism against, for example, predation or water energy. Another possible explanation could be symbiotic adaptation such as: parasitism, where one side was profiting whereas the other was suffering; commensalism, which means that one side was profiting while the other has no gain or loss; or mutualism, where both sides had positive effects from the association (Leung & Poulin, 2008). To examine fossil communities and to study their association is not trivial (Fagerstrom *et al.*, 2000) because in many cases it is hard to prove whether the organisms were alive at the same time. In the bryostromatolite, *Hennigopora* sp. 2 was heavily infested by endobionts. At least half of the observed specimens had the same vermiform tabulate or *Chaetosalpinx*-like bioclaustration (Ernst *et al.*, 2014) inside their colonies. Furthermore, this coral was not observed without the bryozoan colony. The outer walls of the coral are comparably thin (55 μm thick) and have a similar thickness to the autozooidal walls formed by the bryozoan (47 μm thick); for comparison, 37 μm was measured in the bryozoan when the endobiont was absent. This can be taken as evidence for adaptive behaviour. To verify the kind of interspecific relationship it is necessary to prove that the specimens show interactions. The endobiont showed a complex intergrowth with the bryozoan colony, evidence that the colony was structurally influenced by the endosymbiont. The bryozoan specimens tend to overgrow themselves; this commonly observed behaviour is called secondary overgrowth and is a protective behaviour against being buried or encrusted (Palinska *et al.*, 1999, Ernst *et al.*, 2015). The endobionts' growth terminated directly at the surfaces of the specific layers. In one example, distortion for both endobiont as well as bryozoan colony could be observed (Fig. 13C) which can be taken as evidence that this association had existed at the same time as described by Fagerstrom *et al.* (2000).

Microbes and their implications for carbonate saturation, sea-level development and subaerial exposure

Usually, reefal structures with a high abundance of microbial carbonates form in extreme settings and do not exhibit a diverse reef fauna. This, however, is not the case here. The bryozoan community is highly diverse. More than twelve species can be found in every locality (Fig. 8). This indicates a high abundance of free niches or high food availability, or both. The community was composed mainly by encrusting organisms, but also bryozoans with ramose or
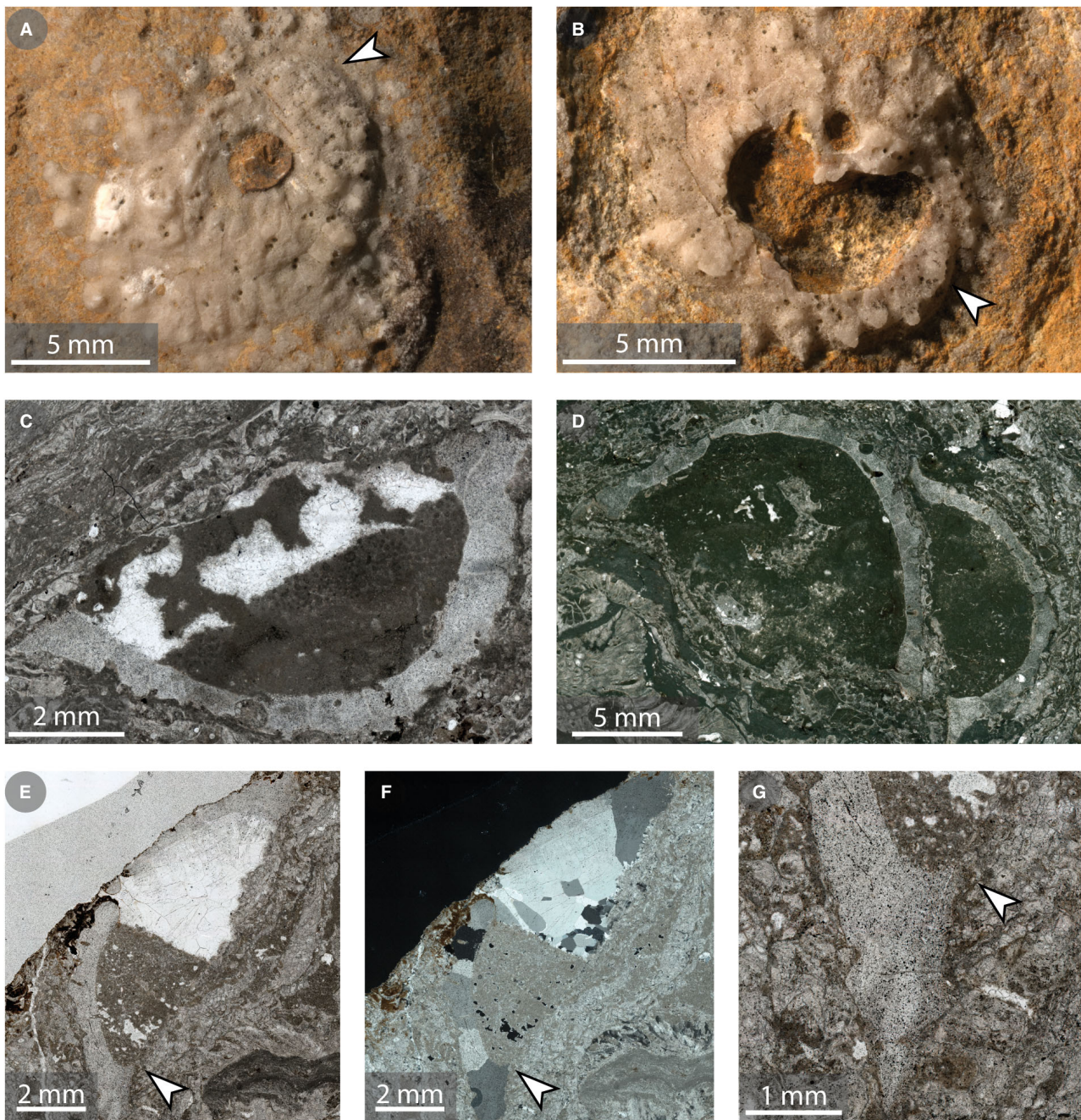
Fig. 14. Echinoderm species *Celticystis gotlandicus* (Angelin, 1878) from Nors Stenbrott: (A) complete specimen on weathered surface, arrows indicating spiral-like ornamentation; (B) complete specimen on weathered surface, arrows indicating spiral-like ornamentation; (C) vertical section through a complete specimen, this specimen grew downward as indicated by the geopetal filling; (D) two complete specimens, one is attached on the other, vertical section; (E) vertical section through a complete specimen, arrow is pointing to the specialized basal attachment plates; (F) same specimen from (E) with polarized light, arrow is pointing to the specialized basal attachment plates; (G) same specimen from (E) with higher magnified specialized basal attachment plates (arrow), note here that the basal plates are directly attached to the bryozoan crusts.

branching forms implying an adaptation to various habitats (e.g. Amini *et al.*, 2004; Taylor, 2005). Within the allochthonous sediments deposited in protected reef habitats, fragments of various reef-dwelling organisms, such as crinoids, brachiopods, bivalves, trilobites,
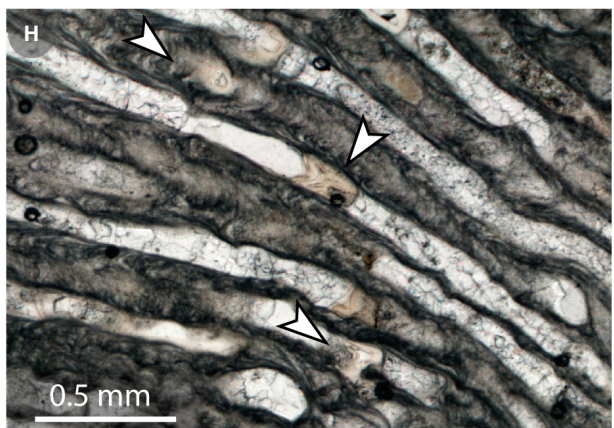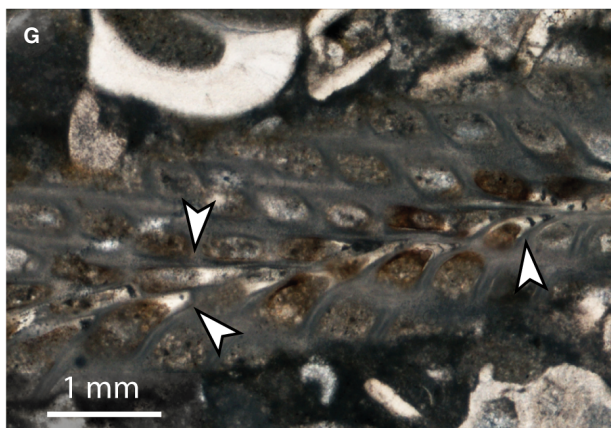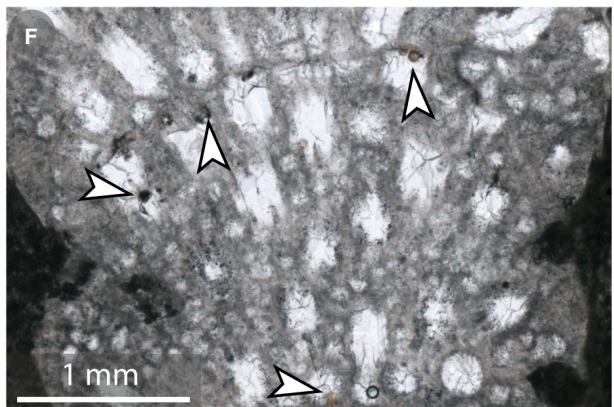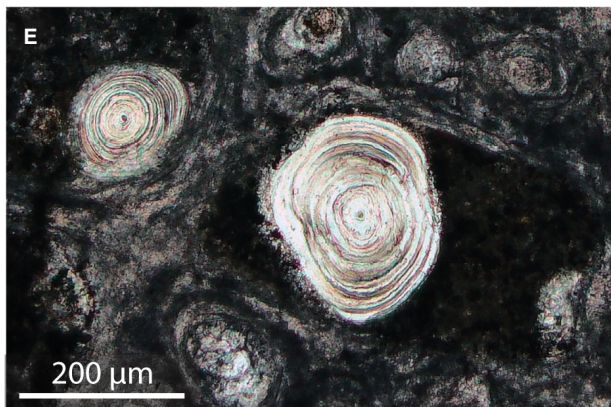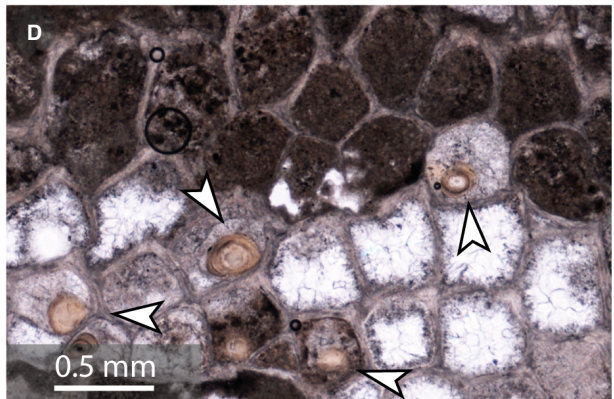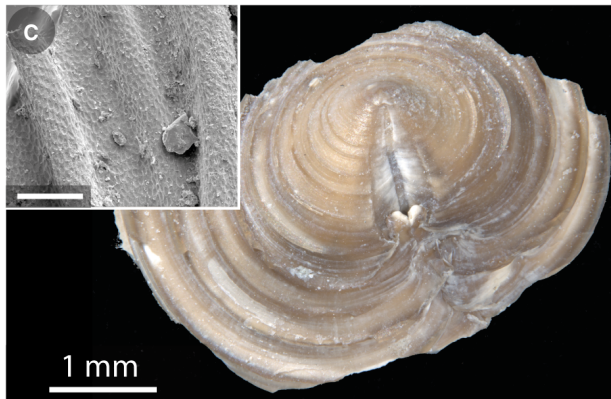
Fig. 15. Phosphatic component from the bryostromatolites: (A) ventral valve of a craniid brachiopod, sample SNS from Nors Stenbrott; (B) broken valve of a lingulid brachiopod, sample SNS from Nors Stenbrott; (C) ventral valve of a specimen of the discinid brachiopod *Chynithele vexata*, sample SN8 from Nyan, the picture in the top left corner is showing a higher magnified part of the shell with characteristic ornamentation taken via scanning electron microscopy (SEM), scale bar = 50 μm; (D) *Ceramoporella* sp. with phosphatic pearls (arrows) sample SN8 from Nyan; (E) *Favositella interpuncta* with phosphatic pearls, sample SHL1t2 from Hallsarve 1; (F) *Hennigopora* sp. 2 with small randomly distributed pearls (arrows), sample SN7 from Nyan; (G) *Ptilodictya lanceolata* with phosphatic linings at the basal part of the feeding zooids (arrows), sample SBT19j1 from Botvide; (H) ?*Orbipora* sp. with phosphatic linings at the basal part of the feeding zooids (arrows), sample SHB1-6 from Hoburgen.

gastropods, sea urchins, ostracods, tentaculitoid tubeworms and corals, indicate a fully marine environment. Calner (2005) argued that the time of high abundance of microbial carbonates in the upper Ludfordian of Gotland represents an 'anachronistic period', i.e. an episode following a minor extinction event. Calner (2005) suggested that the high abundance of preserved microbial structures is the result of a strongly reduced abundance of grazing organisms. There is, however, no indication of any extinction event of grazing organisms in the Ludfordian; in fact, fragments of gastropods and sea urchins are commonly observed in the thin sections (Fig. 7D to F). Some of these epifaunal organisms could have had a grazing mode of life. In the Silurian, echinoids developed more complex jaws and the first lanterns (Kier, 1965) and with this probably adapted to harder food sources. Additional to grazing of algae or biofilms, epifaunal organisms fed on detritus or were predators.

An alternative explanation could be a slight change in the water chemistry. Cyanobacteria precipitate calcium carbonate outside of their cells ('biologically induced') simply by removing CO_2 from seawater by photosynthesis, in contrast to metazoans, which precipitate calcium carbonate inside their cells ('biologically controlled'). A small increase in carbonate saturation of the seawater on the platform therefore would directly facilitate biologically induced calcium carbonate precipitation, resulting in an increased calcification and preservation of microbes. A change in calcium carbonate saturation is, however, difficult to prove. An increase in temperature would lead to a decrease in dissolved gases in the water and, consequently, also to a decrease in dissolved CO_2. Stable oxygen isotope values from diagenetically stable brachiopod shells, however, show an increase at these times (Samtleben *et al.*, 1996, 2000), arguing for cooling rather than

Table 5. Phosphate components presence-absence-list for phosphatic brachiopods and phosphate precipitating bryozoans: 0 = absent; 1 = present.

|	Högklint	Nors Stenbrott	Hällagrund	Hallsarve 2	Botvide	Nyan	Lau Backar	Hallsarve 1	Bote 2	Hoburgen
Phosphatic brachiopods										
Craniida	0	1	0	0	0	0	0	0	0	0
Lingulata	0	1	0	0	0	1	0	0	0	0
Chynithele vexata	0	0	0	1	1	1	1	1	1	1
Pearl forming bryozoans										
Ceramoporella sp.	0	1	1	0	1	1	0	1	0	0
Favositella interpuncta	0	1	0	1	1	1	1	1	1	1
Hennigopora sp. 2	0	1	1	1	1	1	1	1	1	1
Bryozoans with phosphate										
Ptilodictya lanceolata	0	0	0	1	1	1	0	0	0	0
?*Orbipora* sp.	1	1	1	0	0	0	1	0	0	1
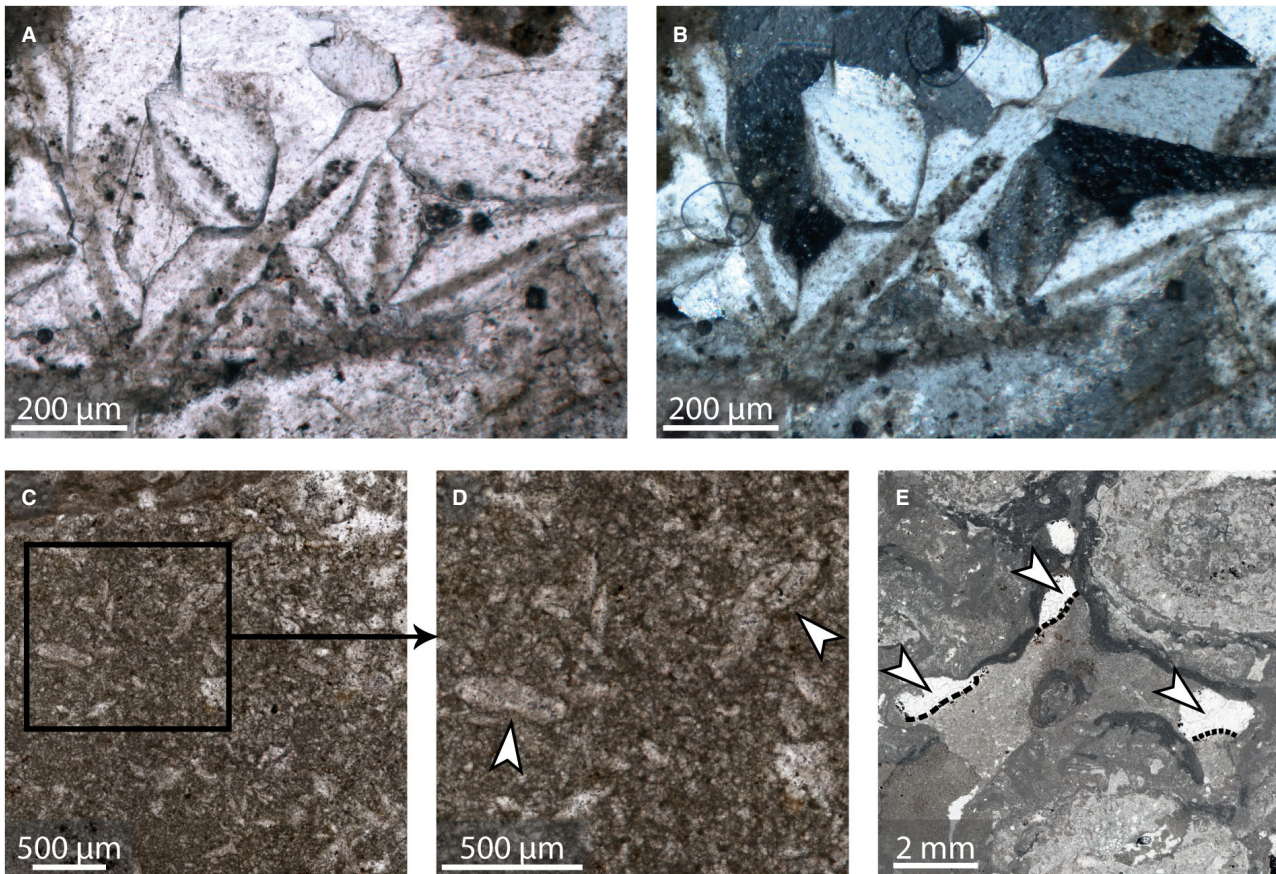
Fig. 16. Characteristic features observed in the bryostromatolites: (A) hemi-bipyramidal twin, sample SLb18-2k from Lau Backar; (B) the same crystal twin from (A) with polarized light; (C) lenticular former gypsum crystals, the crystals have formed directly in fine-grained sediment inside a reef cavity; (D) higher magnified part of (C), arrows pointing to two examples of lenticular gypsum pseudomorphs; (E) vadose silt infilling a pore in the bryostromatolite of Lau Backar SNS1-3, arrows indicating the surface of the geopetally filled cavity.

warming. According to Kozłowski (2015) a high input of aeolian carbonate dust might also have contributed to 'carbonate hypersaturation'. Finally, another option could be a drop in sea level, exposing the shallowest parts of the platforms. Very recently deposited carbonates would be subaerially exposed and dissolved, thereby increasing the calcium carbonate saturation in the epicontinental shelf areas. Such a scenario is supported by the observation of vadose silt in almost every thin section from bryostromatolites. Vadose silt was first discovered by Dunham (1969) and interpreted as indicator for subaerial exposure. This would mean that all bryostromatolites on Gotland formed not only in very shallow water but also during times of fluctuating sea level. For the Eke Formation, subaerial exposure and shallow karstification has been reported in detail by Cherns (1983). Also, the Högklint-

Tofta and Tofta-Hangvar boundaries are characterized by pronounced erosional unconformities (Samtleben *et al.*, 1996; Jeppsson, 2005). Following this hypothesis, the twinned as well as the rhombic to lenticular crystals probably represent pseudomorphs after former gypsum crystals (Cody & Cody, 1988; Warren, 2006). According to their shape the twins can be classified as hemi-bipyramidal twins (Figs 13G, 13H, 16A and 16B) which is a structure that is restricted to gypsum and forms in laboratory studies with the presence of terrestrial humic acids (Cody & Cody, 1988). Together with hemi-bipyramidal twins also rhombic or lenticular gypsum pseudomorphs (Fig. 16D and E) can be found in the cavities. Similar to the hemi-bipyramidal twins they seem to have been crystallized directly inside fine-grained sediment inside a reef cavity. They occur in high abundance in these areas

Table 6. Geochemical data measured in micrite or brachiopod shells for all localities.

Bryolith occurrence	Reference	Age	Sample material	$\delta^{13}C$ (‰)	$\delta^{18}O$ (‰)
Högklint	This paper	Högklint Formation, Lower Sheinwoodian	Micrite	4.90	−6.78
Nors Stenbrott	Ernst et al. (2015)	Tofta Formation, Lower Sheinwoodian	Brachiopod shell	4.40	−4.20
Hällagrund	This paper	Hangvar Formation, Lower Sheinwoodian	Micrite	4.13	−6.77
Hallsarve 2	This paper	Eke Formation, Ludfordian	Micrite	3.63	−5.40
			Brachiopod shell	3.68	−5.93
Botvide	This paper	Eke Formation, Ludfordian	Micrite	3.85	−6.74
Nyan	This paper	Eke Formation, Ludfordian	Micrite	4.02	−6.27
			Brachiopod shell	4.57	−4.53
Lau Backar	This paper	Eke Formation, Ludfordian	Micrite	4.45	−6.69
Hallsarve 1	This paper	Eke Formation, Ludfordian	Micrite	4.63	−6.44
Bote 2	This paper	Eke Formation, Ludfordian	Micrite	5.83	−6.41
Hoburgen	This paper	Hamra Formation, Ludfordian	Micrite	3.91	−5.63

(Fig. 16C and D). The gypsum pseudomorphs exhibit a clear zonation with dark crystal centres (Fig. 16A and B). Comparable darker zones were also produced in gypsum crystals formed during the Messinian Crisis (Lugli et al., 2010). There, filamentous cyanobacteria were incorporated in gypsum crystals (Panieri et al., 2008, 2010; Lugli et al., 2010). Possibly the origin of the zonation is comparable in the bryostromatolites. The occurrence of the gypsum crystals solely in pores but not inside the sediment indicates their post-depositional nature. Probably hypersaline brines formed in supratidal settings under arid climate conditions and percolated downward through the exposed reefs, as described by Färber & Munnecke (2014) for reefs of the Slite Group on Gotland, and this not only flushed vadose silt and sometimes ostracods into the open pore spaces but also precipitated gypsum in some pores. Also, the finding of Palaeomicrocodium, which, to the authors' knowledge has not been described from Gotland so far, indicates sub-aerial exposure and probably soil formation. According to Košir (2004) and Antoshkina (2014) Palaeomicrocodium first occurs in Ludlow and is a product of symbiosis of soil fungi and the roots of higher plants or possibly lichen. It can be taken as indicator of extreme conditions. Its occurrence is restricted to extremely shallow water with temporal subaerial exposure (Antoshkina, 2014). Antoshkina (2006) used Palaeomicrocodium as evidence for drying periods in Upper Devonian microbial mounds from the Ural Region in Russia in addition to vadose cementation, brecciation and freshwater leaching. In the present studied material Palaeomicrocodium can be observed everywhere in the bryostromatolite reefs. It occurs inside pores (Fig. 10B, arrow) as well as within the microbial cement (Fig. 10C) and it created coatings around several components. If the interpretation by Antoshkina (2006) is correct it would indicate that the bryostromatolite growth was interrupted probably several times by subaerial exposure. This means that the reef-dwelling organisms suffered extreme stress due to exposure and might offer an explanation for the (almost) absence of stromatoporoids, which otherwise are the most common reef builders on Gotland.

Sometimes Palaeomicrocodium was formed directly on top of the bryozoans and corals (Fig. 10E), indicating that the latter were already dead, perhaps due to short-term subaerial exposure. Additionally, in some cases bryozoans used Palaeomicrocodium as a substrate (Fig. 10D), which indicates its role during early lithification of the reefs. Palaeomicrocodium grew mainly inside areas composed of microbial cements (Figs 5, 11B and 11C). Nevertheless, its occurrence seems not to be linked to the abundance of microbial crusts in the bryostromatolites. Palaeomicrocodium is observed in almost

every thin section, which would indicate repeated times of exposure. Such a scenario would favour short-lived species like bryozoans rather than corals and stromatoporoids. The finger length as well as the high number of different bryozoan layers per finger (for example, in Nors Stenbrott the mean number is 34, Table 2) indicates that they grew for several years up to decades before the growth was terminated, excluding an annual (seasonal) exposure.

Cyclic growth succession

On thin section scale, a repeated alternation of porostromate and spongiostromate microbial layers and bryozoan finger-shaped crusts is observed in all bryostromatolites, except in Hällagrund, indicating cyclic reef growth. This small-scale cyclicity is illustrated in Figs 11A, 12 and 17. Three different stages of bryostromatolite growth were identified. The bryostromatolite growth was initiated on upward growing stromatoporoids or corals, in most cases rugose corals, as substrate. In the first association the conditions were obviously hostile for metazoans, so only microbial crusts formed (mostly porostromate). The second association experienced less hostile conditions, and bryozoans were able to form thin crusts. Due to the presence of extensive microbial crusts, mainly spongiostromates, together with the bryozoans, this stage can be interpreted as one of bryozoan tolerance (Fig. 17). The third stage is the formation of bryozoan fingers produced the characteristic cauliflower-like shape of the reef; they performed their growth in every vacant space. Interspaces between the fingers are filled with spongiostromate microbes (Fig. 12, IIIb) by microbial fouling. Their interfingering with the layers of the bryozoan fingers indicates that they formed at the same time. This stage was terminated by re-occurring thin layered bryozoan and spongiostromate coatings. The complete succession from initial to developed stage of the bryostromatolite reef is illustrated artistically in Fig. 18.

In addition, obviously *Palaeomicrocodium* played an important role during the reef succession. This is why it is also highlighted in Fig. 17. *Palaeomicrocodium* structures played a role in nearly every observed growth stage except in the early stages of the bryostromatolite. It is rare at the initial spongiostromate or coral colonies and also in the porostromate crusts, but in all other areas it seems to fill every available space (Fig. 11B and C). Moreover, areas can be observed where *Palaeomicrocodium* is clearly alternating with spongiostromate microbes (Fig. 11C). Because of this, it seems plausible that the assumed reef exposure that caused the formation of *Palaeomicrocodium* crusts were re-occurring, or permanent, during the reef growth. This means that the bryostromatolites were formed in very shallow conditions close to or directly at the palaeo-sea surface.

Implications of the predominantly downward growth

Generally, bryozoans are known to survive in highly stressed environments. An example of this is the growth of bryostromatolites in the brackish
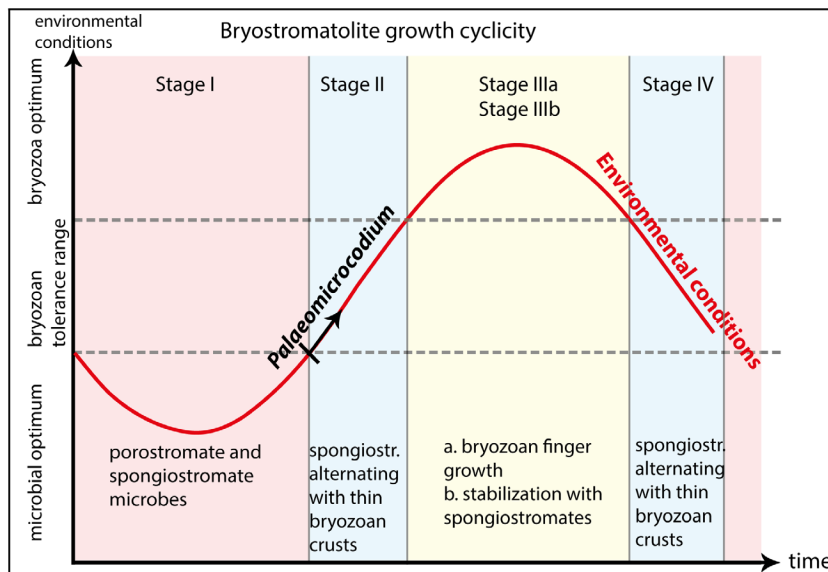

Fig. 17. Schematic drawing of the bryostromatolite growth succession over time with different growth stages. The red curve shows the simplified conditions during reef formation. The y-axis is showing environmental conditions ranging from microbial optima to bryozoan optima, in the middle there is the bryozoan tolerance range, indicated by dashed line, representing that bryozoa were tolerant to the environmental conditions even when they are not optimal; spongiostr. = spongiostromate microbes.
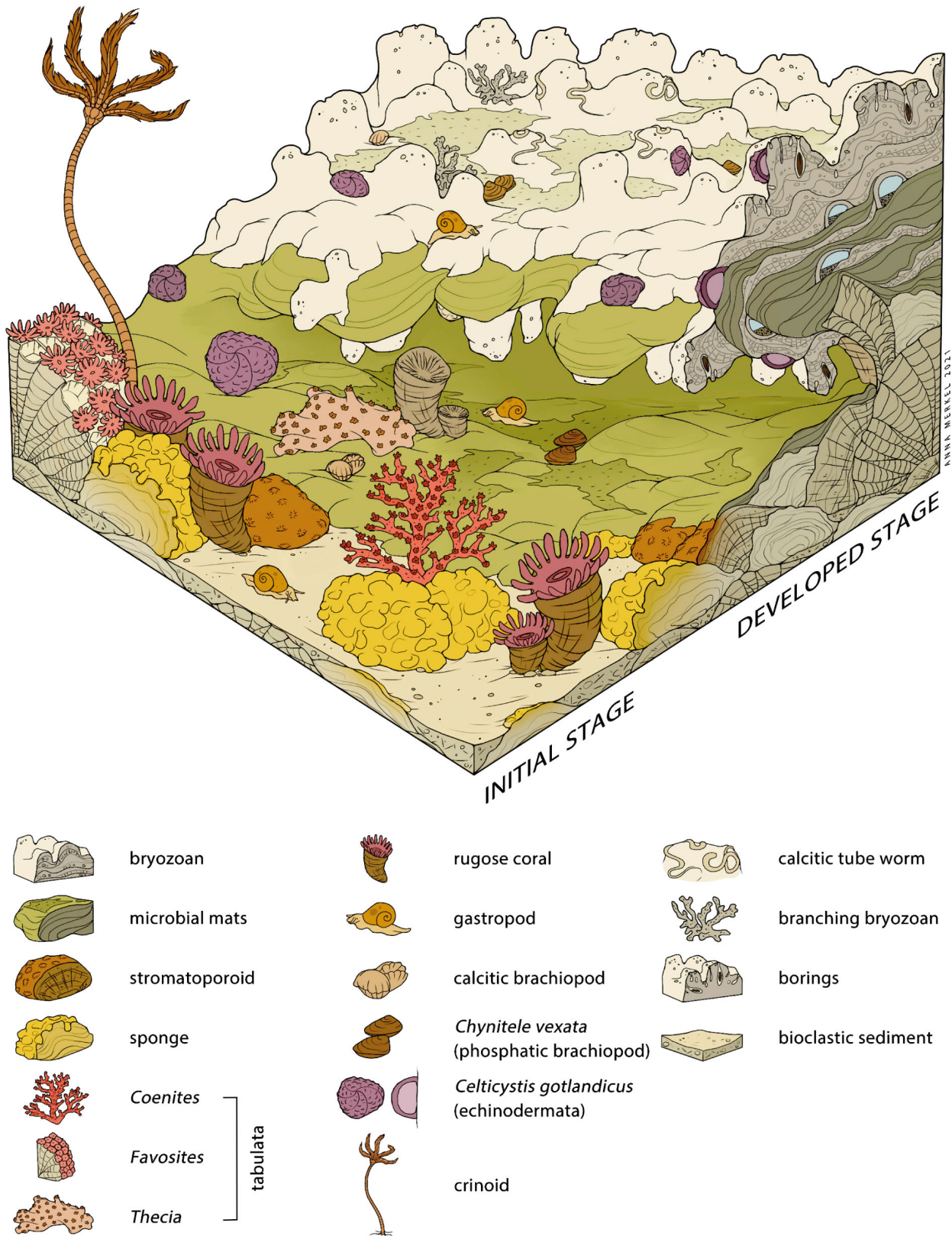
Fig. 18. Artistic reconstruction of a bryostromatolite reef. The front is showing the initial stage of the bryostromatolite, indicated by rugose corals, tabulates, sponges and stromatoporoids. Towards the background it is developing more and more into a bryostromatolite, drawing by Anna Merkel.

inland ponds of Zeeland in The Netherlands (Bijma & Boekschoten, 1985; Harrsion *et al.*, 2021). Stress factors in these environments are low salinity, daily changing saline conditions due to tidal activity, euxinic conditions in the summer, as well as high heavy metal concentrations such as arsenic and titanium (Harrsion *et al.*, 2021). Another modern analogue is the growth of bryostromatolites in Coorong Bay in Australia (Palinska *et al.*, 1999). There, the reefs are formed in lagoons, which are hypersaline to completely dry during summer. Both environments can be characterized as extremely hostile (at least temporarily), but due to seasonal changes in the water conditions the bryozoans are able to grow. Another controlling factor affecting the reef growth is presumably a protective self-over-growth of the bryozoans against microbial fouling (Palinska *et al.*, 1999). In the case of Coorong Bay, freshwater input also promoted the growth of the bryozoan reefs (Palinska *et al.*, 1999). Similar conditions are hard to prove for ancient counterparts. Nevertheless, a cyclicity that influenced the bryostromatolite growth is also visible.

The growth of the bryozoan finger structures is showing similarities to cave deposits in Pleistocene cyanobacterial mounds in Perachora Peninsula in Greece described by Kershaw & Guo (2006), where downward growing coralline algae formed similar finger-like structures (Kershaw & Guo, 2006, Fig. 7A to C) which were surrounded by a mixture of peloidal and laminated micrite. The overall structure of the fingers as well as the infill of peloidal and laminated micrite is similar. Nevertheless, the formation of cavity systems where the structures were developed cannot be supported for bryostromatolites. The bryozoans were possibly filling vacant spaces. More similar are the bryostromatolites with the earliest observed bryozoan reefs from the lower Ordovician (Tremadocian) of China (Adachi *et al.*, 2012, 2013). There, an association of upward growing lithistid sponges with downward or laterally growing bryozoan structures being observed. In comparison with bryostromatolites, stages I and II, together with the coral/stromatoporoid reef core, of the bryostromatolite growth succession, can be interpreted as resembling the lithistid sponge upward-directed growth with subsequent formation of downward growing bryozoan colonies. In the mentioned examples from China and Greece, cryptic habitats were formed, and similar habitats also occurred in the bryostromatolites.

Phosphatic components and their implications

In marine (but also terrestrial) environments phosphorous is a limiting nutrient for primary productivity, and has low concentrations especially in tropical oligotrophic waters. Therefore, phosphatic components are rare in modern reefs, and this holds also for Palaeozoic reefs. In the bryostromatolites, however, several phosphate-precipitating organisms were observed and are comparatively abundant. Not only were phosphatic shelled brachiopods found, but also bryozoans with phosphate in the basal parts of their colonies and pearls. It almost seems like there was an 'oversupply' of phosphorous during times of bryostromatolite growth – but why?

In general, the phosphatic brachiopod *Chynithele vexata* is a very rare brachiopod species. It has been described only from the Prague Basin so far (Mergl *et al.*, 2018). Nevertheless, it occurs in high abundances in the bryostromatolite samples from the Eke Formation (Fig. 15C). Additionally, lingulid and craniid brachiopods were observed (Fig. 15A and B). However, not only phosphatic brachiopods were common; also bryozoan species with the ability to produce phosphatic 'conodont' pearls are abundant (Fig. 15D, E and F). For the bryozoan species *Ceramoporella* sp. and *Favositella interpuncta* the production of fine laminated phosphatic pearls (Oakley, 1966) is a rare but previously recorded habit. However, pearls are also observed for the first time in *Hennigopora* sp. 2, in which the pearls are smaller and randomly distributed inside the colony (Fig. 15F) compared with those of *Ceramoporella* and *Favositella*. The size of these remains is comparable to brown bodies, which are interpreted as remnants of organics (Gordon, 1977). Nevertheless, they are composed of phosphate, so the origin could be different compared to brown bodies. Lindskog *et al.* (2017) critically analysed the origin of different phosphatic micro-spherules including spherules formed by Ceramoporidae. While Oakley (1934) suggested that bryozoan pearls were produced during the life of a colony, and were possibly a digestive by-product like urinary stones due to the differing mineralogy compared to the surrounding colony, Lindskog *et al.* (2017) pointed out that the occurrence of the bryozoan formed spherules seemed to be time-specific because those authors confirmed their occurrence only for Wenlock. Nevertheless, on Gotland the phosphatic pearls were found throughout Wenlock and Ludlow, comparable to Oakley's observation (1934).

Furthermore, in colonies of *Ptilodictya lanceolata* phosphatic linings (Martinsson 1965, Conti & Serpagli, 1988, Ma *et al.*, 2014b) are observed (Fig. 15G). This is a common Silurian bryozoan species, but colonies have been found where these linings are absent (Hennig, 1905; Ross, 1960). Similar remains were found in ?*Orbipora* sp. (Fig. 15H). For ?*Orbipora* sp. this habit is also unknown; however, in this case it is possibly a new species. Such phosphatic linings have been reported previously by Ma *et al.* (2014b) from different Palaeozoic stenolaemate groups. Those authors assumed that the formation of phosphatic linings was caused by environmental as well as biological factors. Comparable to this, Conti & Serpagli (1988) also assumed that the presence of phosphatic components was environmentally driven, maybe caused by elevated phosphorous in the ocean water. The fact that phosphatic pearls were observed in both Ceramoporidae and *Hennigopora* sp. 2, together with the occurrence of phosphatic linings in *Ptilodictya lanceolata* and other species, is evidence that this process could have been linked to the water chemistry, probably due to a plethora of phosphate in the seawater.

Where did all the phosphorous come from? Phosphorus is primarily delivered to the ocean by continental weathering, transported to the ocean via riverine influx (Paytan & McLaughlin, 2007). Enhanced freshwater input can promote bryozoan growth by enhanced nutrient input. However, dilution of shelf water by riverine freshwater would lower the $\delta^{18}O$ composition of the seawater, but the respective deposits on Gotland show heavy $\delta^{18}O$ values (Samtleben *et al.* 1996). In addition, riverine nutrient input usually goes hand in hand with clay input, constricting classical reef growth. However, eutrophic conditions would be in accordance with the high microbial activity as well as the highly diverse bryozoan community that was present in the bryostromatolites. Eutrophic conditions were favourable for bryozoans (Moissette *et al.*, 2007) but probably not for corals and stromatoporoids. Kershaw (1993) compared the occurrence of rugose corals, tabulates and stromatoporoids to modern coral reefs, from this they favoured oligotrophic or mesotrophic conditions.

Atmospheric deposition through aerosols, volcanic ash and mineral dust can also be an important source of P in the oceans. In this respect it is
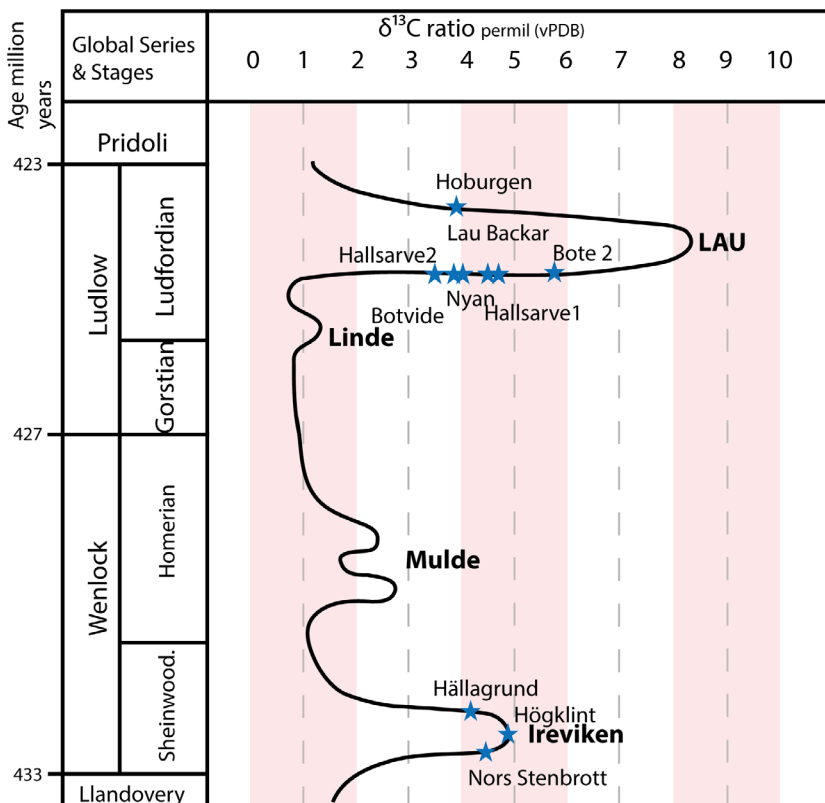

Fig. 19. Measured stable carbon isotope ratios for each bryostromatolite locality from Table 6 plotted on the generalized global $\delta^{13}C$ ratio curve for Gotland, modified after Samtleben *et al.* (1996, 2000), Munnecke *et al.* (2010) and Cramer *et al.* (2011), bold letters for isotope excursions, ages taken from the ICS International Chronostratigraphic Chart v2020/03 (Cohen *et al.*, 2013, updated).

interesting to note that Kozłowski (2015) proposed a strong increase in aeolian influx during the Ludfordian 'Lau' carbon isotope excursion due to a pronounced arid climate in the Baltic area at that time. An arid climate was also proposed by Jeppsson (1990) based on conodont investigations, and by Bickert *et al.* (1997) based on isotopic composition investigations.

Bryostromatolites on Gotland and their relation to the stable carbon and oxygen isotope curve

The Silurian period is characterized by several pronounced positive stable carbon and oxygen isotope excursions proving significant changes of the global carbon cycle (Samtleben *et al.*, 1996, 2000; Kaljo *et al.*, 1997; Wigforss-Lange, 1999; Munnecke *et al.*, 2003; Cramer *et al.*, 2011). The causes of the events are still debated, especially because the amplitudes of the excursions with more than 5‰ in $\delta^{13}C$ (up to more than 10‰) preclude an actualistic interpretation (see review in Munnecke *et al.*, 2010). However, it is interesting to note that all bryostromatolites discovered on Gotland so far show isotope values between +3.5‰ and +6.0‰, and thus belong to the two major isotope excursions – the Sheinwoodian 'Ireviken Excursion' and the Ludfordian 'Lau Excursion'. No bryostromatolites have been reported from sediments of the two smaller isotope excursions on Gotland, the 'Mulde' and 'Linde' excursions (Fig. 19) so far. In order to check whether there is a systematic relationship between the development of bryostromatolites in general and the global carbon cycle, the authors performed a literature survey of Palaeozoic bryostromatolites.

Times of positive $\delta^{13}C$ values in the Silurian are also characterized by high $\delta^{18}O$ values (Samtleben *et al.*, 1996), which have been interpreted as an indication of global cooling or even glaciations (Lehnert *et al.*, 2007). However, if this is correct, it would indicate that the tropical sea surface temperatures dropped by almost 16°C during the Lau Event (corresponding to an increase of $\delta^{18}O_{brach}$ values of 4‰) which is unrealistic (Bickert *et al.*, 1997). Nevertheless, it might be argued that the bryostromatolite reefs are related to a drop in temperature; but in this case, they should occur also in 'warmer times' (i.e. times of low $\delta^{18}O$ values), just in higher latitudes. Because this has not been observed so far, temperature control of these reefs appears unlikely.

Table 7. Literature data of Palaeozoic bryostromatolites and their geochemical data.

| Location	State	Age	Reference	$\delta^{13}C$ (‰)
Fenhsiang Formation	China	Fenhsiang Formation, topmost Tremadocian	Adachi *et al.* (2012)	No data
Mingan	USA	Uppermost Darriwilian	Kröger *et al.* (2017)	No data
Chazy	USA	Uppermost Darriwilian, Chazy Group	Kröger *et al.* (2017)	No data
St Martin Member	Canada	Laval Formation, Chazy Group	Kobluk (1981)	No data
Holston	USA	Holston Formation, under Blackriverian	Walker & Ferrigno (1973)	No data
Chickasaw	USA	Base of Bromide Formation, Lake Member	Cuffey & Cuffey (1995)	No data
Vasalemma	Estonia	Katian GICE	Kröger *et al.* (2014)	1.5–2.0
Ärina	Estonia	Lower Hirnantian	Kaljo *et al.* (2004)	5
Natiscotec	Canada	Hirnantian	Ernst & Munnecke (2009)	6
Beck and Sarle	USA and Canada	Lower Sheinwoodian, early Wenlock, Contact of Irondequoit Member and Rochester Shale Member	Cuffey & Hewitt (1989)	No data
Napoleon Quarry	USA	Sheinwoodian Massie Formation	Thomka & Brett (2015)	No data
Altoona	USA	Latest Pridolian, Keyser Limestone, *Ou. elegans*	Cuffey & Taylor (1989)	No data
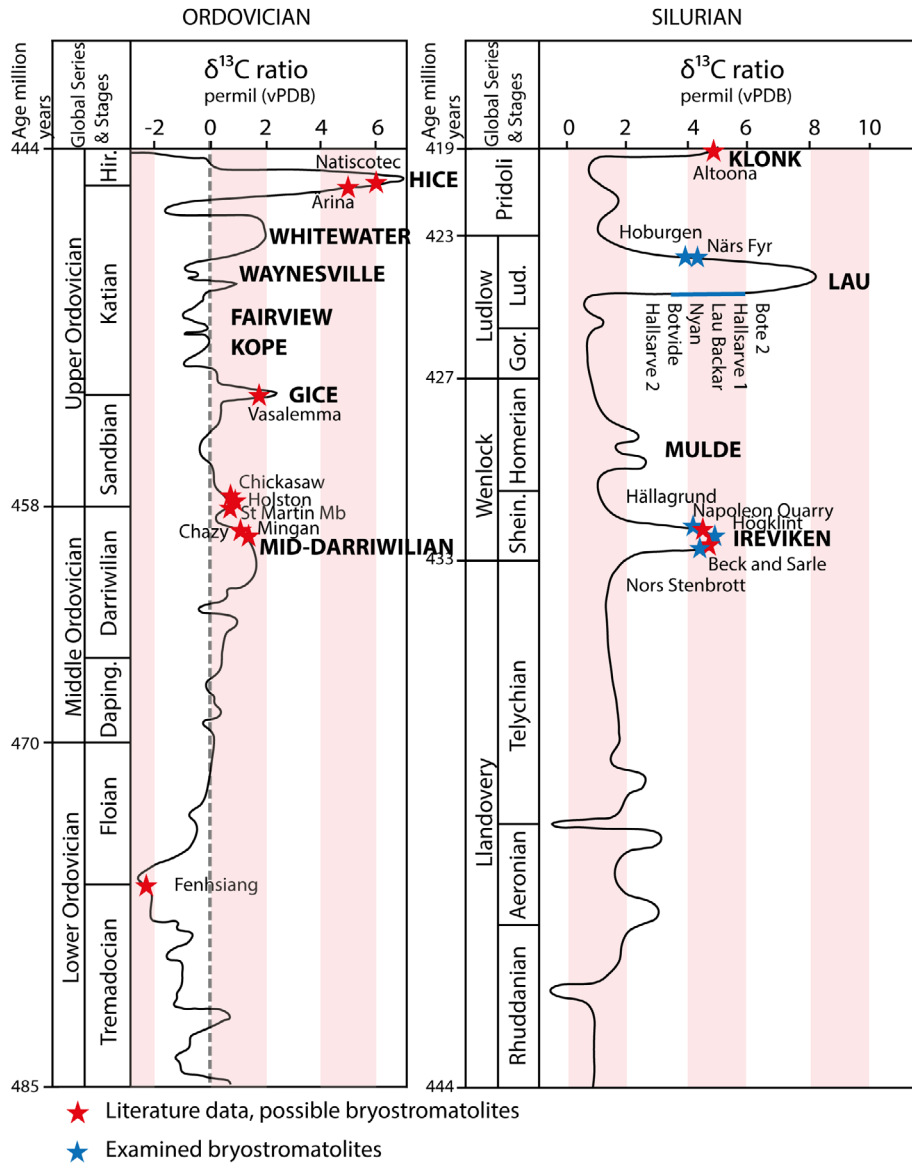
Fig. 20. Measured stable carbon isotope ratios (Table 6) for each bryostromatolite locality from Gotland (blue stars). In addition, bryostromatolites reported in the literature (Table 7) are plotted on the generalized global $\delta^{13}C$ ratio curves for the Silurian (modified after Cramer *et al.*, 2011) and the Ordovician (modified after Bergström *et al.*, 2009), bold letters for isotope excursions, ages taken from the ICS International Chronostratigraphic Chart v2020/03 (Cohen *et al.*, 2013, updated).

Global distribution of Ordovician and Silurian bryostromatolites and their relation to the stable carbon isotope curve

Compared to other reef types, bryostromatolites are rare and volumetrically insignificant. The earliest known bryozoan reefs that also can be taken as bryostromatolites, were the bryozoan–lithistid reefs of the Fenhsiang Formation from the Tremadoc of China (Adachi *et al.*, 2012, 2013). Kröger *et al.* (2017) mentioned four reefs that can be regarded as bryostromatolites for the Ordovician: the late Darriwilian Mingan Reef from Quebec (Canada); the upper Darriwilian Chazy Reefs of Champlain Valley (north-eastern USA); the Katian Vasalemma Reefs (Estonia); and the Hirnantian Ärina Reefs (Estonia). Throughout the American Chazy Group additional reefs were formed that can be taken as bryostromatolites. These reefs are the St Martin
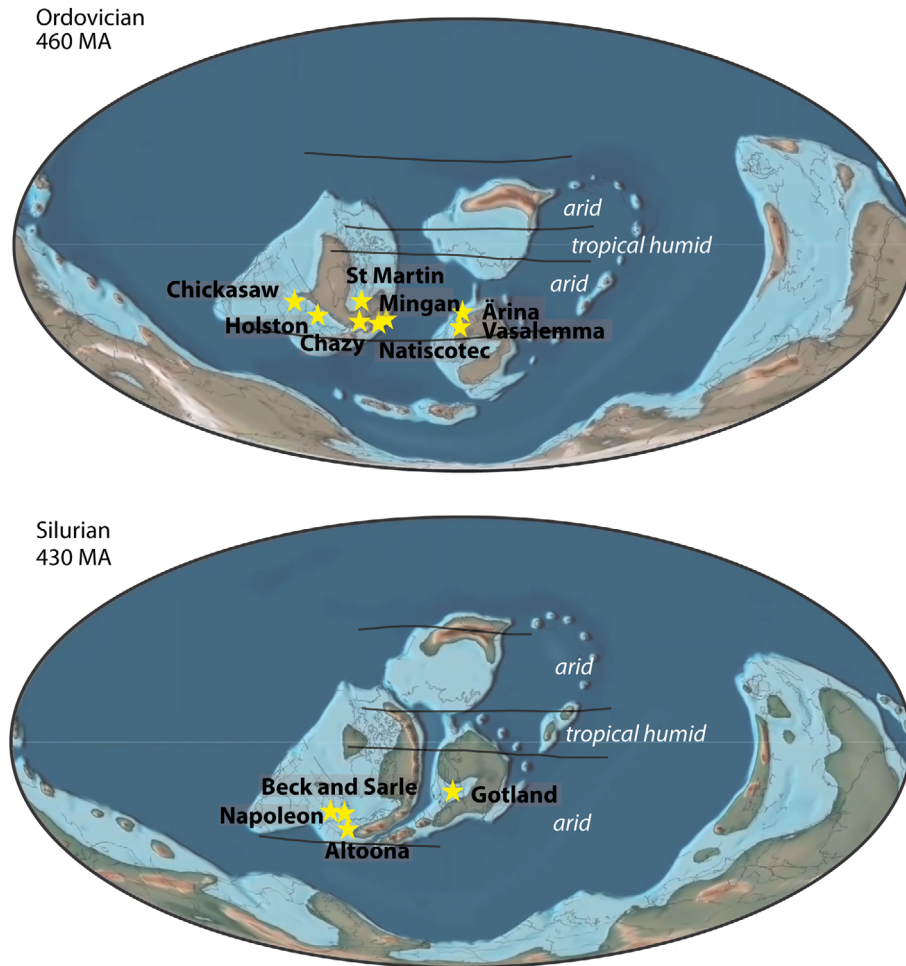
Fig. 21. Palaeogeographic map of the Ordovician and Silurian; bryostromatolite localities are indicated with stars; tropical and arid zones are indicated in the map with lines and italic letters – maps modified after Scotese (2016).

Member reefs from Canada (Kobluk, 1981), the Holston reefs from the Holston Formation of east Tennessee (Walker & Ferrigno, 1973), and possibly the Chickasaw bryozoan reef from the Base of the Bromide Formation of Oklahoma, USA (Cuffey & Cuffey, 1995). In addition, Ernst & Munnecke (2009) described an Ordovician bryostromatolite from the Hirnantian Laframboise Member from the Ellis Bay Formation of Anticosti Island (Canada). For the Silurian, published data are scarce. Cuffey & Taylor (1989) described the Pridolian Altoona Reef of this type from Pennsylvania (USA). Besides this, the lower Sheinwoodian Beck and Sarle reefs of the Niagara Gorge of Ontario and New York (Canada and USA) can be counted as bryostromatolite (Cuffey & Hewitt, 1989). Additional reefs are the microbioherms from the Napoleon quarry of the Sheinwoodian Massie Formation from Indiana (USA)

described by Thomka & Brett (2015). All of these findings (Table 7) as well as those from Gotland were plotted in the global $\delta^{13}C$ chemostratigraphic curves of Bergström *et al.* (2009) and Cramer *et al.* (2011) for the Ordovician and Silurian, respectively (Fig. 20). Although $\delta^{13}C$ values have not been published for all of them, all except the earliest known metazoan reef from the Fenhsiang Formation from the Tremadoc of China (Adachi *et al.*, 2012, 2013) seem to be related to positive carbon isotope excursions (Fig. 20), and they all formed in low palaeolatitudes (Fig. 21). It is interesting to note, however, that none of the known bryostromatolites plots near the palaeoequator but in the arid climate zone south of the equator (Fig. 21). Consequently, it could be argued that arid climate conditions are one of the prerequisites for the formation of the bryostromatolite reefs.

Palaeozoic bryostromatolite reefs were rare and represent an atypical ecosystem. They formed only in extremely shallow water, only in specific time slices characterized by high $\delta^{13}C$ and $\delta^{18}O$ values, and only in arid low-latitude climate zones. Munnecke *et al.* (2003) summarized several sedimentological, palaeontological and geochemical features typical for the most pronounced Cambrian to Silurian isotope excursions. Obviously, the occurrence of bryostromatolites is another feature of these enigmatic excursions. Even though the present work cannot provide a final, convincing, conclusion as to why these bryostromatolites only formed during times of positive $\delta^{13}C$ excursions, it seems obvious that they represent a new type of Otto H. Walliser's 'time-specific facies' (Walliser, 1984a,b, 1986; Brett *et al.*, 2012), which describes the formation of unique facies types in specific short time intervals. The authors hope that this paper will stimulate others to search and to continue the research for these seemingly unspectacular reefs which finally might help to answer the question about the origin of the mysterious Silurian perturbations of the global carbon cycle.

CONCLUSIONS

The conclusions of this study can be summarized as follows:

• For the first time bryostromatolite reefs are described from the Silurian of Gotland. They have a cauliflower-like appearance in the field and consist mostly of porostromate and spongiostromate microbial carbonates and bryozoans.
• On Gotland, bryostromatolites only occur in the Högklint and Tofta formations (Sheinwoodian) and in the Eke and Hamra formations (Ludfordian). They grew in fully marine conditions, and formed a rigid framework and a topographic relief of several decimetres up to about 1 m.
• The bryostromatolites show a relatively high diversity of bryozoans (with up to twenty species in a single reef), a high abundance of reef-building and reef-dwelling organisms, and a surprisingly high abundance of phosphatic constituents.
• Repeated alternations of distinct layers dominated by either porostromate microbes, spongiostromate microbial layers, or encrusting bryozoans indicate cyclic environmental changes.
• Reef growth took place in extremely shallow water. The occurrence of vadose silt and gypsum pseudomorphs in reef cavities indicate subaerial exposure shortly after reef growth.
• The problematicum *Palaeomicrocodium* indicates an extreme environment and, according to Antoskhina (2006), even subaerial exposure. The high abundance and alternation with crust-forming reef-building organisms suggest short phases of subaerial exposure even during reef growth and, therefore, reef growth in extremely shallow water.
• The high abundance of phosphatic components (for example, inarticulate brachiopods, bryozoan pearls and linings) indicates a high input of phosphorous by either rivers or wind. For bryozoan pearls and linings, this hypothesis is supported by several literature studies (e.g. Oakley, 1934; Conti & Serpagli, 1988; Ma *et al.*, 2014b). According to the studies of Kozłowski (2015) in the Baltic area, an aeolian input seems more plausible. This fits the fact that so far, no bryostromatolites have been discovered from the humid equatorial belt.
• Both the bryostromatolites on Gotland and bryostromatolites in the Silurian and Ordovician of other areas occur only in times of elevated $\delta^{13}C$ values, indicating a close link of local bryostromatolite growth and global perturbations of the carbon cycle.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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