

Significance of microbialites, calcimicrobes, and calcareous algae in reefal framework formation from the Silurian of Gotland, Sweden

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Abstract

The structure of stromatoporoid–tabulate coral reefs from the Mid- to Upper Silurian of Gotland includes complex microbialite and algal framework fabric.

Non-skeletal microbialites show variable fabrics, structures, and morphologies ranging from largely non-laminated, peloidal, irregular masses to well-laminated stromatolite crusts, indicated by convex upwardly oriented overgrowth structures, trichome-like arrangement of peloids and intergrowth with skeletal calcimicrobes and metazoans. Non-skeletal microbialites contribute to framework formation during different stages in the Högklint reef development as well as in the marginal, or flanking beds of stromatoporoid–coral patch reefs in the Tofta Formation. In addition to non-skeletal microbialites, calcimicrobes (mainly *Rothpletzella*) and coralline algae (*Graticula gotlandica*) substantially contribute to framework formation in reefs from the Högklint and the lower Hamra Formation. Depending on the occurrence pattern and abundance of microbialites, calcimicrobes, and calcareous algae, four framework types can be differentiated based on the environmental setting. Type (1)—a tabular stromatoporoid and non-skeletal microbialite framework, characteristic for lower and intermediate parts of the Högklint reefs, developed in slightly deeper, lower energy, fully marine conditions. Type (2)—a graticulacean-microbial/calcimicrobial framework, typically developed in the upper and top parts of the Högklint reefs, marking shallow, moderate to highly agitated water. Type (3)—a stromatolite–*Coenites* framework, being part of the reef development in the Tofta Formation. Stromatolites formed in sheltered, partly restricted parts of stromatoporoid–coral patch reef complexes. Type (4)—a stromatoporoid–calcimicrobial framework, forming relatively small reef bodies in the lower Hamra Formation, situated in a highly agitated, very shallow, open marine environment.

These examples indicate that microbial crusts, calcimicrobes, and graticulacean algae were more important contributors to framework formation in Silurian metazoan reefs than previously thought.

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1. Introduction

Early lithifying microbial crusts are a major prerequisite for the growth of many ancient metazoan reefs with pronounced relief. These microbes provide binding and

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framework formation within and around the metazoans (e.g., Leinfelder et al., 1993, 1996; Wood, 1999, 2000). For example, the significance of microbial crusts has been documented for many Jurassic reefs (Leinfelder et al., 1993; Schmid, 1996; Leinfelder and Schmid, 2000; Leinfelder et al., 2002). Microbial crusts appear to have been more widespread in fossil reefs than in reefs today, especially prior to the Cretaceous (Webb, 1996), perhaps due to high carbonate supersaturation ocean states from the Cambrian to the Cretaceous. The apparent decline in abundance of microbial crusts from the Cretaceous onwards may be a result of the relatively reduced saturation state of seawater, which may in turn be related to the massive radiation of calcareous plankton such as coccoliths in the Cretaceous (Knoll et al., 1993). However, microbial crust formation in extant reefs has hitherto not been in the focus of modern reef research, and its occurrence may be largely underestimated (e.g., Reitner et al., 1996). Microbial and calcimicrobial crusts also play an important role in metazoan reef formation in the Palaeozoic (e.g., Pratt and James, 1982; Soja, 1991; Webby, 1994; Wood, 1999). Silurian reefs frequently yield microbialite and calcimicrobial textures and fabrics (Soja, 1991; DeFreitas et al., 1993; Soja and Antoshkina, 1997; Antoshkina, 1998; Soja et al., 2000). With regard to Silurian reefs from the isle of Gotland, with their well-known spectrum of different reef types (Manten, 1971; Riding, 1981), only a few non-skeletal microbialite features within reefs have been reported since the pioneering work of Rothpletz (1913) and Hadding (1941). Although calcimicrobes are regarded as frequent constituents of the reefs, they are rarely studied as they relate to reefal framework formation. Frameworks in Silurian reefs from Gotland were described by several authors (Kershaw, 1981; Riding, 1981; Watts, 1981; Watts, 1988; Kano, 1989; Watts and Riding, 2000), but usually interpreted as framed by metazoans. Exceptions to this widespread opinion include works by Riding and Watts (1981), and Watts and Riding (2000). These authors mentioned calcareous algal, partly calcimicrobial frameworks that form a relatively thin band (generally 0.3–0.6 m, max. 3 m) at the top of the Högklint reefs (e.g., ‘coral-algal facies’ or ‘algal reef crest’). Frameworks and reefal facies have rarely been illustrated using light microscopical analysis of thin sections.

Hadding (1941, 1950, 1959) first recognized non-skeletal microbial crusts and their significance in Gotlandian reefs. He described flocculent or dense structures with partly ‘faint stratification’ within the interstitial muddy groundmass. This author interpreted these structures as calcareous algae that closely resemble ‘Spongiostromata’ and envelops reefal organ-

isms and often forms the bulk of large parts of a reef. Already Hadding considered these types of ‘algae’ as being of greater importance in reefal framework formation than previously thought. However, this important aspect was largely neglected in subsequent studies (Manten, 1971; Watkins, 1979; Riding, 1981; Watts, 1988; Riding and Watts, 1991; Watts and Riding, 2000). Only Cherns (1982) described small organic buildups composed of stromatolites within the Eke Formation, and inferred that, in a shallow subtidal to intertidal environment, small stromatolite domes grew in scalloped hollows of irregular, sculptured karstic erosion surfaces. Moreover, Calner (2005a,b) detailed columnar stromatolites from the Eke Formation in the context of extinction events.

This paper assesses the role of microbial and algal biota in reef growth based on examples from the Högklint, Tofta and Hamra Formations of Gotland. We show that (a) binding non-skeletal microbial crusts (peloidal microbialites) frequently occur in Silurian Högklint reefs, and play a noticeable role in reef shape and formation, (b) graticulacean algae (formerly assigned to the solenoporaceans, now referred to the corallinaceans by Brooke and Riding, 1998) occur in much higher abundance and are of greater importance in framework formation within the Högklint reefs than previously thought, (c) non-skeletal stromatolites, typically associated with branching tabulate corals (*Coenites*, cf. Utgaard, 1983), contribute to bioherm formation in the Tofta Formation, and (d) stromatoporoïd–calcimicrobial frameworks represent a typical feature of small patch reefs within the lower Hamra Formation (‘algal limestone’ sensu Manten, 1971).

In this paper we use the term calcimicrobes, which is still debated among palaeontologists. According to James and Bourque (1992), this term includes a wide variety of enigmatic microencrusts, often with uncertain or even entirely unknown affinities. We are aware of the fact that this term, used in a strict sense, implies a bacterial or cyanobacterial nature of the organisms. However, since this term is commonly used by palaeontologists (e.g., Wood, 1999; Copper, 2002), we follow the terminology of the above-mentioned authors and use the term calcimicrobes in its broadest sense for microencrusts with distinct skeletal features (e.g., *Rothpletzella*, *Renalcis*-group fossils, *Hedstroemia*, *Wetheredella*) regardless of their systematic affinities.

2. Localities, material and methods

The study areas are located in the Mid- to Upper Silurian succession of Gotland, Sweden. Focussing on

biohermal reef structures, we studied patch reefs from three different formations at four localities. Case study I includes reefs from the Höglint Formation (early Wenlock) at Galgberget 2 and Brissund 4, north of Visby. Case study II focuses on a patch reef complex at Digerhuvud on the west coast of Fårö. This bioherm belongs to a limestone succession formerly attributed to the Höglint Formation, but now placed in the Tofta Formation based on new conodont and lithostratigraphic data (Figs. 1 and 2; Calner et al., 2005). Case study III comprises small initial patch reefs from the lower Hamra Formation (late Ludlow) that are situated at the base of the succession at the Hoburgen 2 locality at the southern tip of Gotland ('algal limestone' sensu Manten, 1971).

Samples were gathered from all accessible parts of the reefs. The facies of the reef structures was deduced from polished slabs and thin sections to determine zonation pattern and framework type. Detailed field

observations provided additional data on the overall zonation pattern and faunal composition of the reefs.

The locality descriptions below follow the system established by Laufeld (1974b). Locality details are given in Laufeld (1974b), and Jeppsson and Jerre (in manuscript, copy available at Allekvia field station, Gotland, and from the senior author). Digerhuvud 2 and Brissund 4 represent new localities.

Digerhuvud 2: 6432615 1694875 (CK 8760 2775); 6850 m NNW of Fårö church, Topographical map sheet 66E Fårösund, Geological map sheet Aa 180 Fårö; rauk area at the NW coast of Fårö, ca. 1250 m SE of the northwesternmost point of Digerhuvud (see Fig. 9); Upper Tofta Formation (sensu Calner et al., 2005); access (i.e. sampling) only allowed with written permission of the 'Naturvårdsenheten' at 'Länsstyrelsen, Visby' (natural preserve).

Brissund 4: 6402275 1653925 (CK 4445 0060); ca. 7100 m SW of Martebo church. Topographical map

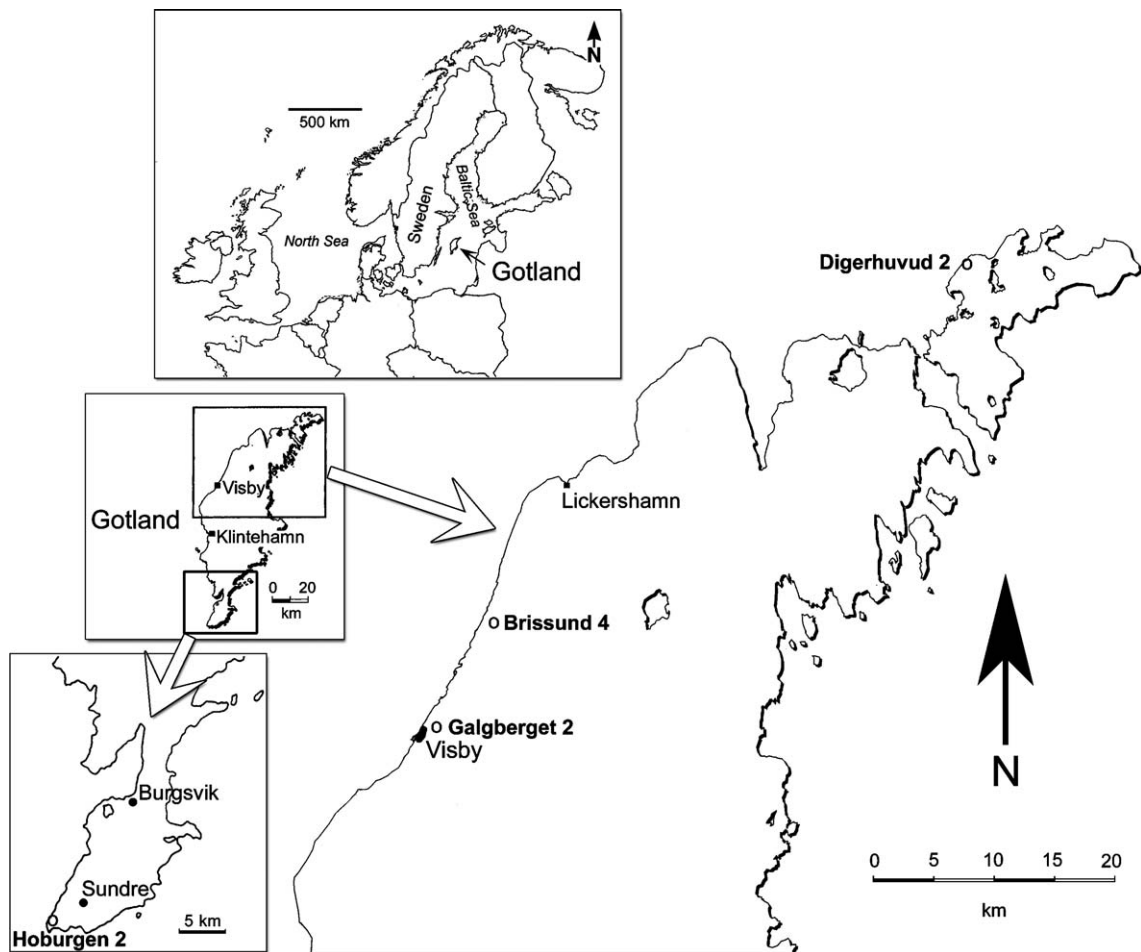


Fig. 1. Sketch map of Gotland, showing the study localities.

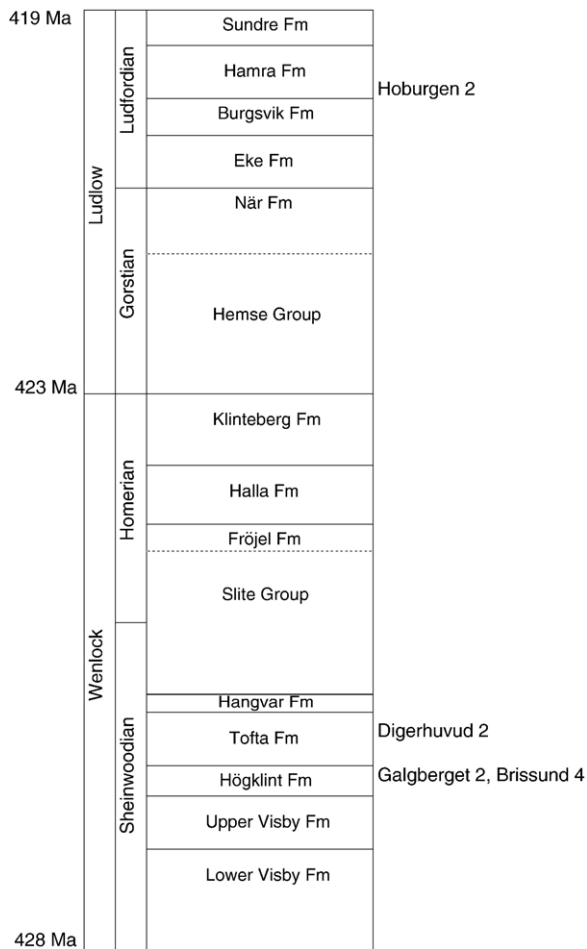


Fig. 2. Stratigraphic column of the Silurian succession in Gotland with positions of the study localities (modified after Calner et al., 2004).

sheet 66C Tingstäde, Geological map sheet Aa 183 Visby and Lummelunda; raised sea cliff ca. 150 m west of road 149. Access to the locality is from the road to Krusmyntagården, ca. 100 m NE from the crossways, where the road to Krusmyntagården turns to the NW; Högklint Formation.

Galgberget 2: CJ 3951 9335; ca. 1250 m NNE of Visby Cathedral. Topographical map 66A Visby, Geological map sheet Aa 183 Visby and Lummelunda. Cliff section north of the gallows at Galgberget. Situated immediately NE of, and opposite to a wooden stairway, with path and stone step at the base of section; Högklint Formation; further references: Watkins (1979), Neuman and Kershaw (1991), Riding and Watts (1991).

Hoburgen 2: 6312937 1641360 (CJ 2517 1252); ca. 3750 m WSW of Sundre church. Topographical map sheet 56A Hoburgen, Geological map sheet Aa 152

Burgsvik. Lower part of the cliff section, ca. 200 m SW of Hoburgsgubben. Hoburgen 2 comprises the NW-facing cliff NW of the path and the talus material and SE of the beach rubble. Samples were taken immediately south of a prominent block close to sea level (see Fig. 11). The entire locality is seen inside the beach rubble and below the steep main cliff (at the base of which the path runs) in Fig. 212, Manten (1971) (the hillock shown in Manten's figure is not Storburg); lower Hamra Formation; selected further references: Jux (1957), Fig. 2 (drawing of the cliff, Hoburgen 2 is located at the extreme right), Böger (1968, pp. 130–131), Laufeld (1974a,b), Stel and DeCoo (1977), Neuman and Kershaw (1991).

3. Case study I: Högklint reefs at Galgberget and Brissund—non-skeletal microbialite and red algal frameworks

Case study I was carried out in the Högklint Formation at Galgberget 2 and Brissund 4. Both localities exhibit Högklint patch reef development. According to Watts and Riding (2000), Högklint reefs reveal a zonation pattern with four successive growth stages (stage 1: Axelsro reefs; stage 2: Halysitid/laminar stromatoporoid frame; stage 3: domical stromatoporoid/algal cluster frame; stage 4: cyanobacterial-algal reef crest). Important contributions to reefal framework development by microbialites or red algae occur within different zones of the reef development. Our own observations relative to the composition and structure of the reef growth stages differ from the zonation pattern suggested by Watts and Riding (2000). Microbialites and red algae are organized into two framework types.

3.1. Framework type 1: tabular stromatoporoid non-skeletal microbialite frames—composition, structure, and distribution pattern

Non-skeletal microbialites within this framework type amount to 10–30% of the total rock volume, and grow as irregular, partly laminated peloidal masses between and on reef-building metazoans (e.g., stromatoporoids, tabulate corals, bryozoans; Figs. 3A, B and 4A–E, G, H). Interstitial spaces are filled with bioclastic carbonate mud, which partly exceeds the microbial crusts in volume, preventing the formation of frameworks in some areas. Non-skeletal microbialites within this framework type exhibit (a) a peloid-bearing, dense micritic fabric, or (b) a peloidal, sparitic, partly clotted fabric. Both types show gradual transitions. Although

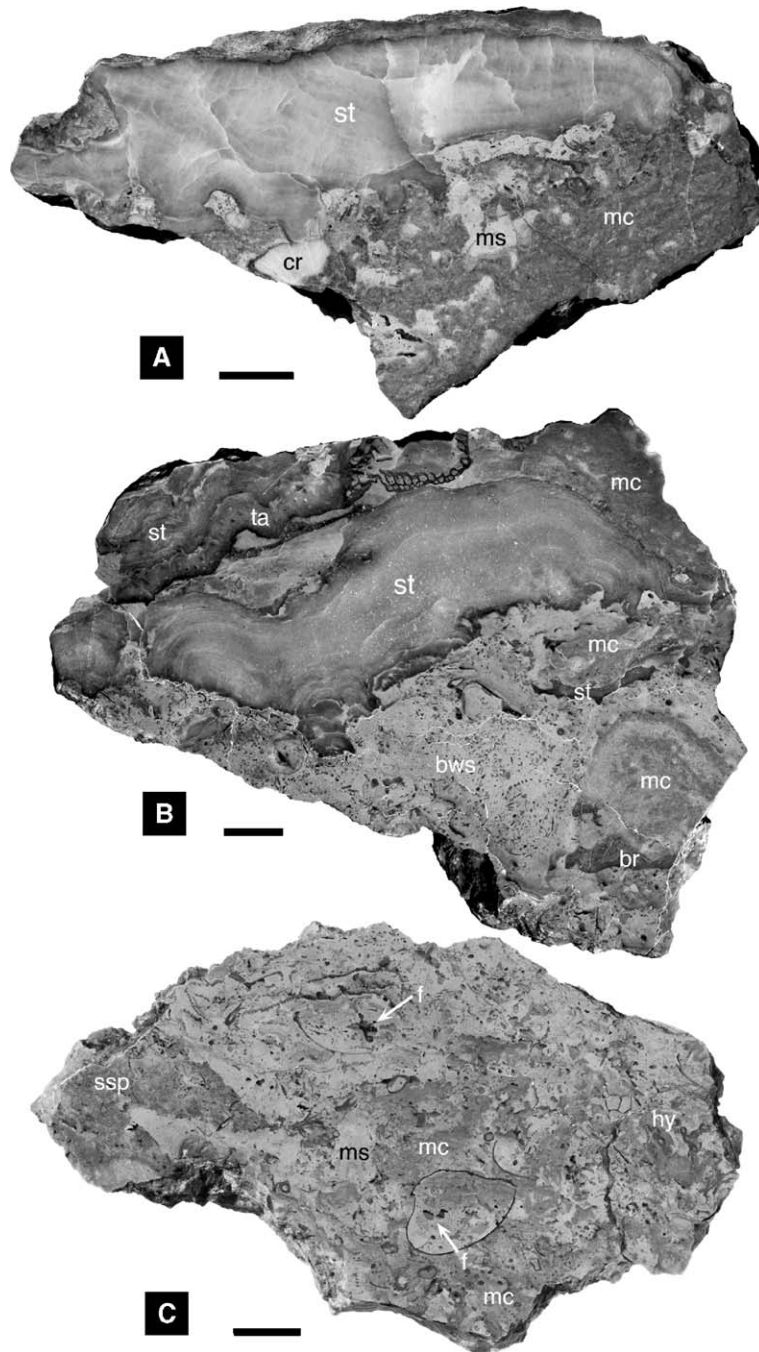
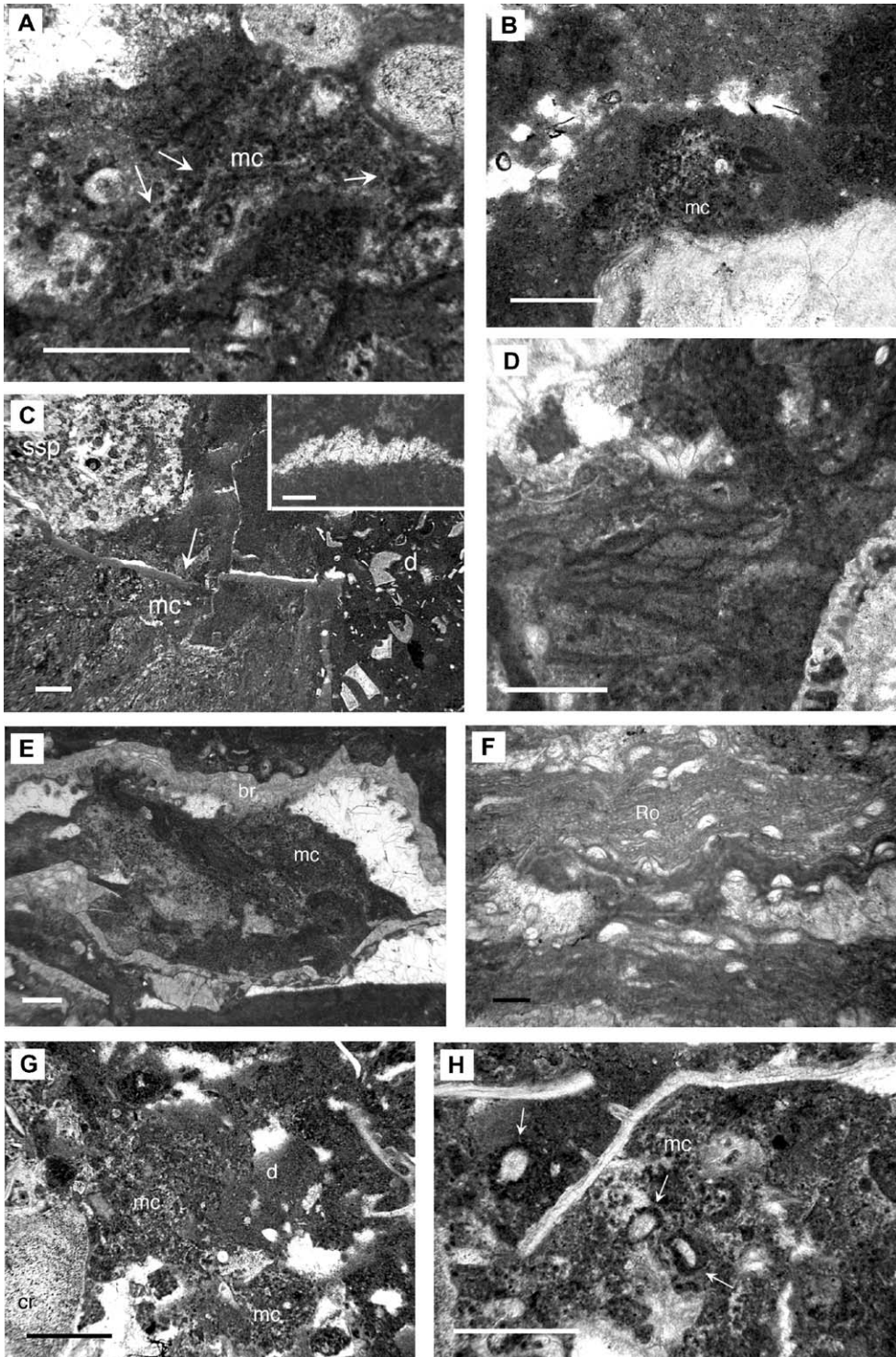


Fig. 3. Höglint reefs at Galgberget 2 and Brissund 4, tabular stromatoporoid non-skeletal microbialite framework (type 1), polished slabs: (A) tabular stromatoporoid–microbialite framestone, dark grey non-skeletal microbialites (mc) show marked irregular reticulate morphology and cloudy, partly clotted appearance. Light grey sediment is allochthonous carbonate mud (ms), cr=crinoid, st=tabular stromatoporoid; Brissund 4 (sample no. BRI 4), scale bar: 1 cm; (B) tabular stromatoporoid–microbialite boundstone/framestone, microbialites (mc) show clear convex upwardly oriented overgrowth structures on bryozoan (br) or stromatoporoid (st) remains, especially at the right margin of the slab, bws=bioclastic wackestone, ta=tabulate coral; Galgberget 2 (sample no. GAL 1/1), scale bar: 1 cm; (C) muddy siliceous sponge (ssp)–halysitid tabulate coral (hy) floatstone/boundstone; dark grey portions represent irregular peloidal microbial crusts (mc), light grey areas are composed of detrital mud (ms), which reveal fenestral fabric (f), probably due to burrowing organisms; Galgberget 2 (sample no. GAL 1/2), scale bar: 1 cm.

the origin and nature of non-laminated peloidal crusts is still a matter of debate, our case studies provide strong evidence in support of their microbial nature. Crusts

commonly reveal peloids in rows, and thus suggest trichome-like arrangement. Peloids are variable in size, ranging from 25 to 80 μm (maximum 125 μm , e.g., Fig.



4A–E, G, H). They display an irregular shape, well-rounded to angular. The crusts form (a) convex, upwardly oriented, flat and domal encrustations (Fig. 3B), or (b) connective irregular clusters between reef metazoans (Figs. 3A and 4D, G). Comparable structures were described from the Höglklint Formation as ‘floculent masses’ (Hadding, 1959). The term ‘Spongostromata’ (von Pia, 1927) refers to almost identical structures, which encompass not only non-laminated peloidal overgrowth structures, but also spherical aggregates (e.g., oncoids) and additional elements such as fine tubes and ?algal threads (cf. Hadding, 1959; Johnson and Konishi, 1959).

Locally, the microbial fabric contains irregular stromatolite cavities. Some of the cavities show pronounced scalloped outlines, which are indicative of sponge boring activity and hence early lithification (Fig. 4C—insert; cf. Schmid et al., 2001). Early lithification of microbialites is also indicated by syndimentary fractures that are restricted to microbialitic zones and do not affect the adjacent allochthonous sediment (Fig. 4C).

Calciomicrobes (e.g., *Wetheredella* sp., *Rothpletzella gottlandica*, *Rothpletzella munthei*) occur as thin crusts on different metazoans, but only in low abundances. *Wetheredella* sp. forms encrustations on metazoans (siliceous sponges, stromatoporoids), preferentially on the undersides. *Wetheredella* is characterized by juxtaposed to adherent and encrusting prostrate masses of unbranched tubes with an internal diameter of 60–170 μm . Walls are relatively thick (25–35 μm), perforated by round pores normal to the surface. Our material from the Höglklint Formation closely resembles *W. silurica* (Wood, 1948), except for a slightly larger tube diameter in our form. The systematic position of *Wetheredella* remains unresolved: it has been suggested that it represents an alga, a cyanobacterium or a foraminiferan. Therefore, following Riding and Soja (1993), we regard it as a problematic

organism. In most cases, *Wetheredella* is closely associated with *R. gottlandica* (Fig. 4F), a putative cyanobacterium (cf. Wood, 1948; Riding and Soja, 1993). Tangential sections show the typical radial branching of the filaments. Transverse sections reveal longitudinal as well as transversely cut threads, the latter appearing beaded (cf. Wood, 1948). They measure 25–35 μm in average external tube diameter; similar dimensions have been indicated by Wood (1948). In rare instances, the external diameter reaches 40–45 μm . Compared to *R. gottlandica*, *R. munthei* is much less abundant (see also Rothpletz, 1913). Where present, *R. munthei* is closely associated with *R. gottlandica*. *R. munthei* shows considerably smaller dimensions than those seen in *R. gottlandica*, with an average external tube diameter of only 15–20 μm . Riding and Soja (1993), who studied *Rothpletzella* from the Silurian of the Alexander terrane, Alaska, regard *R. munthei* and *R. gottlandica* as conspecific based on the gradual transition in size. However, our material from the Höglklint reef facies reveals two distinctly separated diameters, and thus suggests that they represent two species.

The macrobenthic assemblage of this framework type is characterized by tabular stromatoporoids, tabulate corals, bryozoans, and crinoids. Stromatoporoids and corals alone did not account for framework formation. Open frameworks only developed in association with non-skeletal microbialites. Siliceous sponges also occur in this framework type. This facies is often characterized by a low density of the macrofaunal elements and intensive development of non-skeletal microbialites (Fig. 3C).

Non-laminated, non-skeletal microbial crusts represent a common feature of the Höglklint patch reefs. These crusts seem to be irregularly distributed within the reefs, independent from the vertical faunal and floral zonation established by Watts and Riding (2000). This pattern may be obscured by the occurrence of detached

Fig. 4. Höglklint reefs at Galgberget 2 and Brissund 4, tabular stromatoporoid non-skeletal microbialite framework (type 1), thin sections: (A) irregular peloidal microbial crust (mc) showing peloids in rows and a bushy substructure (arrows), Brissund 4 (sample no. BRI 7/5), scale bar: 1 mm; (B) convex upwardly oriented peloidal microbialite (mc) encrusting a tabulate coral, Galgberget 2 (sample no. GAL 1/6), scale bar: 1 mm; (C) dense micritic to peloidal microbialite (mc) encrusting a siliceous sponge (ssp). Early diagenetic fracture (arrow) penetrating only sponge and microbialite is indicative for selective early lithification; d=crinoidal wackestone/floatstone, scale bar: 1 mm; insert shows stromatolite cavity within microbial crust. The scalloped roof surface is most likely due to sponge boring activity, scale bar: 0.5 mm, Galgberget 2 (sample no. GAL 1/1); (D) dense microbial crust (mc) in between skeletal metazoans showing faint lamination, Galgberget 2 (sample no. GAL 1/4), scale bar: 1 mm; (E) complex cavity with ?bryozoans (br), which lived as crypts encrusting the roof of the cavity. On broken fragments of the ?bryozoans peloidal microbialites (mc) developed, Brissund 4 (sample no. BRI 7), scale bar: 1 mm; (F) *Rothpletzella gottlandica* crust (Ro) with scattered bubbles of *Wetheredella* sp., Brissund 4 (sample no. BRI 7), scale bar: 0.2 mm; (G) peloidal microbial crust (mc) developed on a crinoid remain (cr), growth cavities are geopetally filled with detrital mud (d), Galgberget 2 (sample no. GAL 1/9), scale bar: 1 mm; (H) microbial crust (mc) associated with terebellid worm tubes (arrows), Galgberget 2 (sample no. GAL 1/9), scale bar: 1 mm.

blocks of various sizes in different stages of reef development. However, non-skeletal microbial crusts occur in different reef facies types and faunal associations, with the most massive crusts developing in frameworks that are rich in tabular stromatoporoids and tabulate corals. This framework type predominantly occurs in more basal and central parts of the Höglint reef limestones at Brissund 4 and Galgberget 2 (Figs. 7 and 8), and most likely corresponds to the growth stage 2—‘halysitid-laminar stromatoporoid reef zone’ sensu Watts and Riding (2000), although the suggested zonation pattern of Watts and Riding (2000) is not clearly visible at Brissund 4 and Galgberget 2.

At the Galgberget 2 locality this may be due to the allochthonous block formation, which is indicated by chaotic geopetals. On the other hand, at Brissund 4, almost all geopetals in slabs and thin sections suggest in-situ boundstone fabric, and thus contradict the occurrence of growth stages proposed by Watts and Riding (2000) (cf. Figs. 7 and 8).

3.2. Framework type 2: graticulacean-microbial/calci-microbial frames—composition, structure, and distribution pattern

Graticula gotlandica is the most important constituent in this reefal framework type; the algal thalli amount to 40–70% of the total rock volume (Fig. 5A–E). Brooke and Riding (1998, 2000) revised *Solenopora gotlandica* Rothpletz, 1908 and placed the species to the genus *Graticula*, family Graticulaceae (Corallinales, Rhodophyta). This extends the stratigraphic range of coralline algae from the Lower Cretaceous to the Lower Silurian, and possibly to the Ordovician (Brooke and Riding, 1998), and results in an enormous stratigraphic gap. In the Caradoc and Ashgill of Eastern Canada, similar forms are present (e.g., Verulam Formation, Ontario; Copper, pers. commun.).

The gross morphology of *G. gotlandica* ranges from laterally joint columns, branches or pillars, to mushroom- or umbrella-like skeletons. Irregular, lumpy and laterally joint knobs are also common. Cauliflower-shaped individuals, up to 10 cm high, are relatively rare. The quadratic, sometimes elongate cells are 20–30 µm wide and 25–35 µm long (Fig. 6F–H). Cross partitions in adjacent filaments are well-aligned, contrasting with all other genera conventionally placed in the Solenoporaceae (cf. Brooke and Riding, 1998). *G. gotlandica* displays two different preservational states, (a) excellent preservation with clearly visible cellular structure of the skeleton, or (b) poor preservation

with a largely recrystallized skeleton and hardly any cellular structure recognizable (Fig. 5A, C). The borderline between these two preservational states is always sharp. In thin section, transitions within a single thallus can be observed, which demonstrate that both types belong to the same organism (Fig. 6F). Poorly preserved specimens are far more abundant than well-preserved individuals. Recrystallization and neomorphism often led to the complete destruction of the skeletal structure, typically along a zone that parallels the surface of the algal thallus. In such diagenetic irregular molds, crystal silt or peloidal wackestones/packstones frequently accumulate as geopetals, due most probably to an early diagenetic meteoric overprint (Figs. 5C and 6H).

Additional constituents within this framework type are non-skeletal peloidal microbialites and calcimicrobes, including the abundant *R. gotlandica*, *Hedstroemia* sp. and subordinate *R. munthei*, *Wetheredella* sp., and *Renalcis*-group organisms.

Non-skeletal peloidal microbialites in this framework type correspond to the microbialite fabric in framework type 1. Peloids range in size from 25 to 75 µm (maximum 135 µm) and exhibit irregular shapes. They are frequently arranged in trichome-like rows. Microbialites typically form connective clusters between graticulacean alga and may display faint stromatolitic lamination (Figs. 5A, B and 6 C, D); they are often found in association with *R. gotlandica* (Fig. 5A). Generally, *R. gotlandica* forms calcimicrobial crusts of variable thickness (ranging from 0.1 to 2 mm) on *Graticula* and reef-building metazoans (stromatoporoids and corals; Figs. 5A and 6E).

Wetheredella sp. also belongs to the microencruster association of this framework type. The form frequently occurs with *R. gotlandica* encrusting lithoclasts, metazoans (stromatoporoids, tabulate corals), and algae (Fig. 6E). In addition to isolated tubes within *Rothpletzella* crusts, *Wetheredella* locally occurs in the form of larger encrusting aggregates of tubes. Similar to the tubes of *Wetheredella* found in framework type 1 they reveal an internal diameter of 60–170 µm and possess relatively thick walls (25–35 µm).

Hedstroemia is a subordinate but regularly occurring element in this framework type. It is frequently associated with graticulacean red algal facies, encrusting metazoans and algae. In some instances, *Hedstroemia* occurs as isolated structure in the groundmass (Fig. 6B). *Hedstroemia* is characterized by oval to roundish masses composed of ramifying tubes in a radial arrangement. Tubes in longitudinal section may show a sinuous irregular morphology. In transverse section,

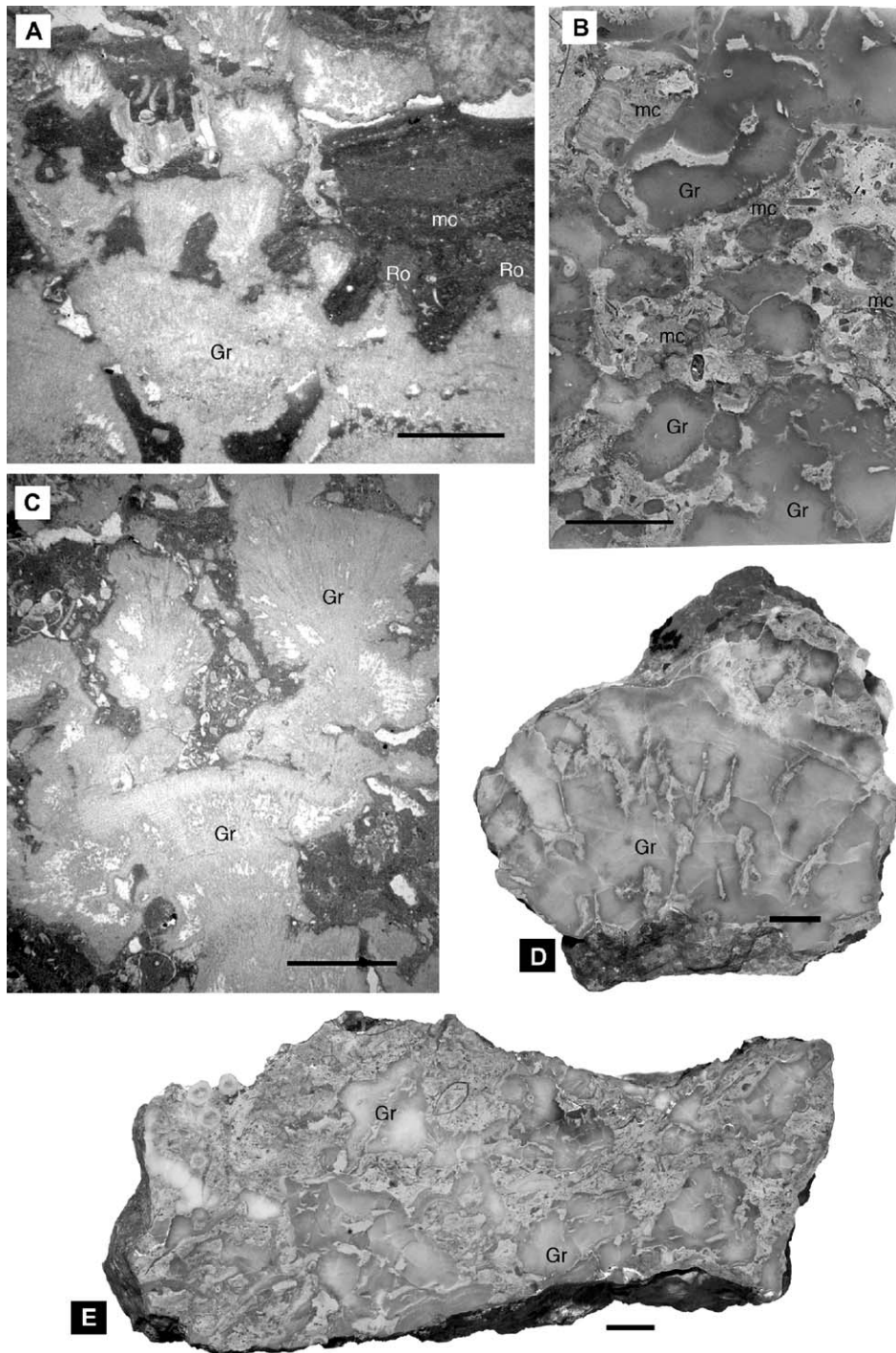
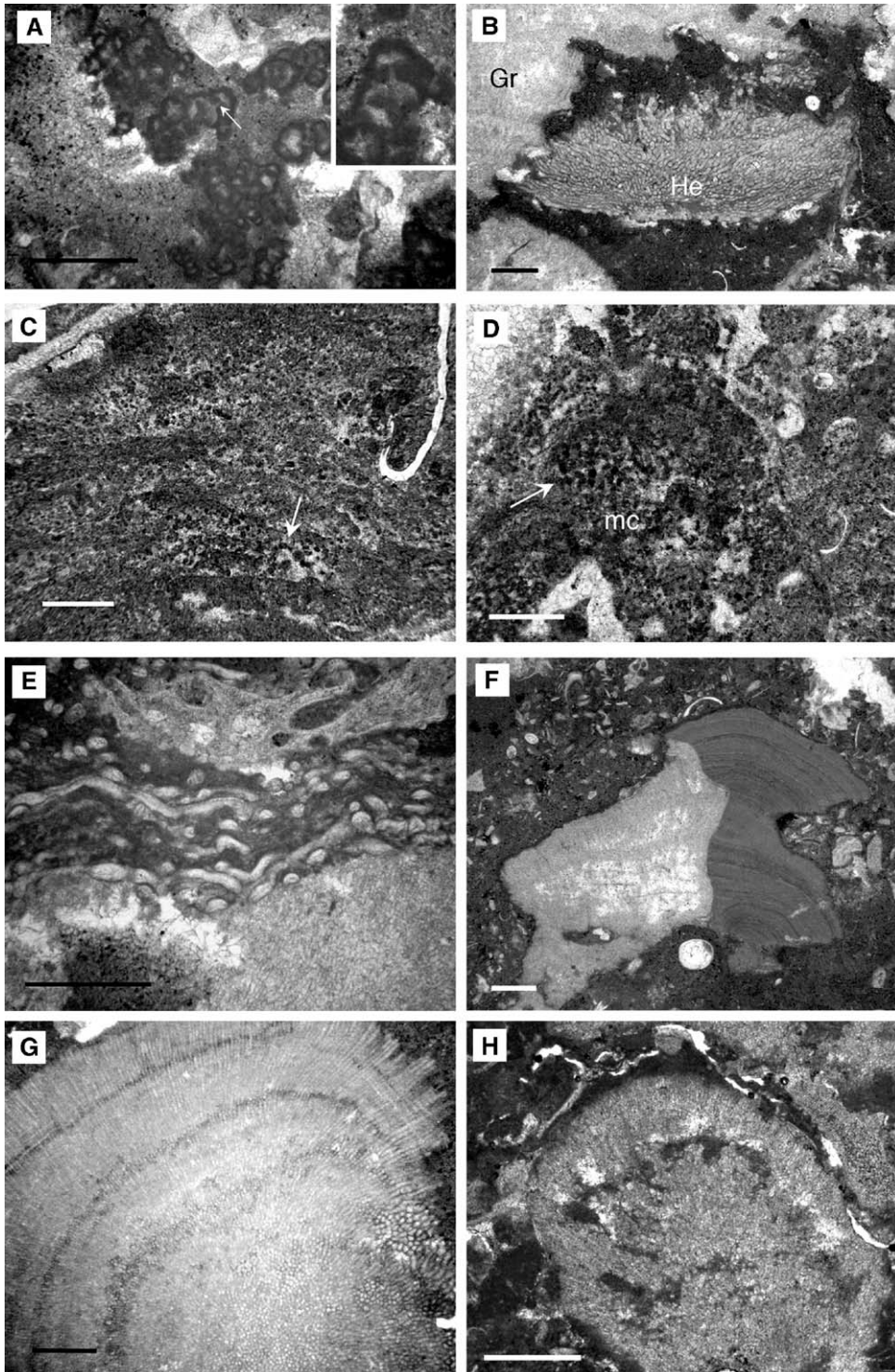


Fig. 5. Höglint reefs at Galgberget 2 and Brissund 4, Graticulacean-microbial/calcimicrobial framework (type 2): (A) *Graticula* thallus (Gr) with cauliflower-like morphology, finger-like branches; note thin *Rothpletzella* crusts (Ro) overgrown by non-skeletal microbialite (mc), thin section; Brissund 4 (sample no. BRI 13), scale bar: 1 cm; (B) polished slab with *Graticula* (Gr) framework, dark grey portions represent mixed *Rothpletzella* non-skeletal microbialite crusts (mc), light grey areas composed of detrital mud; Brissund 4 (sample no. BRI 18/1), scale bar: 1 cm; (C) *Graticula* framework with *Graticula* (Gr) exhibiting cauliflower-, pillar-, and mushroom-shaped growth. Groundmass composed of bioclastic wackestone/floatstone, thin section; Galgberget 2 (sample no. GAL 3/2), scale bar: 1 cm; (D) *Graticula* (Gr) framestone with laterally linked red algal pillars, polished slab; Galgberget 2 (sample no. GAL 2), scale bar: 1 cm; (E) *Graticula* (Gr) framestone/rudstone, polished slab; Galgberget 2 (sample no. GAL Top), scale bar: 1 cm.

the tubes display their polygonal, partly rounded outlines and diameters between 70 and 125 μm , and thus matches the dimensions indicated by Johnson and Konishi

(1959). Riding and Soja (1993) assumed that *Hedstroemia* belongs to the rivulariacean cyanobacteria, while Johnson and Konishi (1959) regarded *Hedstroemia* as a



codiacean green alga. However, the occurrence of a dark microcrystalline wall structure contradicts the latter interpretation. Riding and Watts (1981) and Watts and Riding (2000) regarded *Hedstroemia* as an important element in the graticulacean-cyanobacterial reef crest that occurs in the topmost part of the Höglint reefs. At least in the Höglint reef examples described here, graticulacean-dominated frameworks also occur well below the reef top and are not particularly rich in *Hedstroemia*.

Renalcis-type microfossils occur only sporadically in the reefal limestones of the Höglint Formation. Their scarcity indicates that they represent an accessory element among the encrusting microorganisms with almost no importance in reefal framework formation. This observation corroborates results from the Alexander terrane, SE Alaska, where *Renalcis*-type microfossils also play a minor role in reefal frameworks, contrasting with occurrences in Cambro-Ordovician reefs (Soja and Riding, 1993). Nevertheless, they are part of the microencruster association at Galgberget 2, and worth being mentioned since they are well-preserved and reveal a heretofore unknown morphological detail (see below). Renalcoid microfossils form cloudy aggregates of variable size, depending on the number of chambers or ‘bubbles’, with diameters up to 2.3 mm. The chambers vary from less than 40 to 180 μm (without wall) in maximum diameter. The walls range in thickness from less than 30 to 75 μm , with a normal range between 40 and 60 μm . The inner side of the micritic wall consistently reveals V-shaped clefts (cf. Riding and Watts, 1983). Usually, the individual chambers are not interconnected, but in one individual a short but discrete canal occurs between two chambers (Fig. 6A). Our material resembles the forms attributed to *Renalcis* cf. *tuberculatus* by Riding and Watts (1983). An assignment to *Shuguria*, a foraminiferan (cf. Loeblich and Tappan, 1988), is ruled out based on thicker walls and the occurrence of chambers with a low width to height ratio in the latter taxon. However, the

existence of connections between individual chambers strongly suggests a foraminiferal nature for the renalcoid microfossils considered here, and, at the same time, contradicts the interpretation of *Renalcis* as a cyanobacterium (Riding and Soja, 1993). Since the material shows a close relationship to both *Renalcis* and the related, poorly defined genus *Izhella* (cf. Riding and Watts, 1983), we assign our specimens to the *Renalcis*-group. Based on the striking morphological similarities between *Izhella* and *Renalcis*, it seems likely that both genera are synonymous.

Non-skeletal microbialites and calcimicrobes considerably contribute to framework establishment by forming connective clusters between algae and metazoans such as stromatoporoids, tabulate corals (mainly syringoporoids), crinoids, ostracodes, trilobite remains, and brachiopods (Fig. 5A, B). *G. gotlandica*, together with microbial and calcimicrobial crusts, forms a tight framework; the groundmass in-between is composed of bioclastic mud (Fig. 5A–E).

This framework type usually occurs in the upper and topmost parts of the Höglint patch reefs (cf. Riding and Watts, 1981). Although sampling was not possible over the entire thickness of the reefs, the lithostratigraphic range of our samples clearly indicates that red algae (*G. gotlandica*) are abundant already far below the top of the reefs. This, however, contrasts with results presented by Riding and Watts (1981) and Watts and Riding (2000), who regarded the algal zone as a thin layer capping the reefs, usually not more than 0.3 to 0.6 m thick (Riding and Watts, 1981). At Brissund 4, these algae already occur in the tabular stromatoporoid–tabulate coral zone. They form tight in-situ frames at least 4 m below the top of the reef body (Fig. 5A, B). Since the reef facies is largely composed of in-situ boundstone fabrics, graticulacean frameworks are apparently more prominent in the Höglint reefs than previously thought. At Galgberget 2, graticulacean in-situ frameworks also occur at least 4 m below the top of the reefs. A few large *Graticula*

Fig. 6. Höglint reefs at Galgberget 2 and Brissund 4, Graticulacean-microbial/calcimicrobial framework (type 2)—algae, calcimicrobes and microbialites; thin sections: (A) cluster of *Renalcis* (cf. *R. tuberculatus*). Note linkage of at least two chambers by a discrete canal (arrow, see also insert with close-up) hinting at a foraminiferal nature, Galgberget 2 (sample no. GAL Top''/2), scale bar: 1 mm; (B) *Hedstroemia* sp. (He) and *Graticula gotlandica* thallus (Gr), Galgberget 2 (sample no. GAL Top'''), scale bar: 1 mm; (C) laminated peloidal microbial crust with peloids locally arranged in curved rows (arrow), Galgberget 2 (sample no. GAL Top2), scale bar: 1 mm; (D) convex upwardly oriented peloidal microbialite with peloids in rows (arrow), pointing to trichome-like arrangement, Galgberget 2 (sample no. GAL Top'4), scale bar: 1 mm. (E) *Wetheredella* sp. and *Rothpletzella gotlandica* encrusting *Graticula* thallus, Galgberget 2 (sample no. GAL Top''/3), scale bar: 1 mm; (F) *G. gotlandica*, thallus fragment showing the two preservational states of the alga. On the left strongly altered, recrystallized state, on the right non-recrystallized, well-preserved algal structure, Galgberget 2 (sample no. GAL 2/2), scale bar: 1 mm; (G) *G. gotlandica*; longitudinal (upper left) and transverse section (lower right), Galgberget 2 (sample no. GAL 2/2), scale bar: 0.5 mm; (H) strongly recrystallized *Graticula* with dissolution zone running parallel to the surface of the alga. Note micritic internal sediment; Brissund 4 (sample no. BRI 13), scale bar: 1 mm.

specimens from the Högklint reefs are up to 20 cm thick and 30 cm in diameter, forming massive digitate structures resembling *Gymnosolen* (P. Copper, personal samples). Reworked graticulacean frameworks within fallen or broken blocks occur even at lower levels in the reef succession (cf. Watts and Riding, 2000) (Figs. 7 and 8).

4. Case study II: Tofta reef at Digerhuvud—*Coenites*-bearing stromatolite framework

At the Digerhuvud rauk field (rauk: erosional rock remnant) in the northwestern part of Färö (Fig. 1), rauks appear to represent erosional remnants of larger patch reef complexes with particulate inter-reef

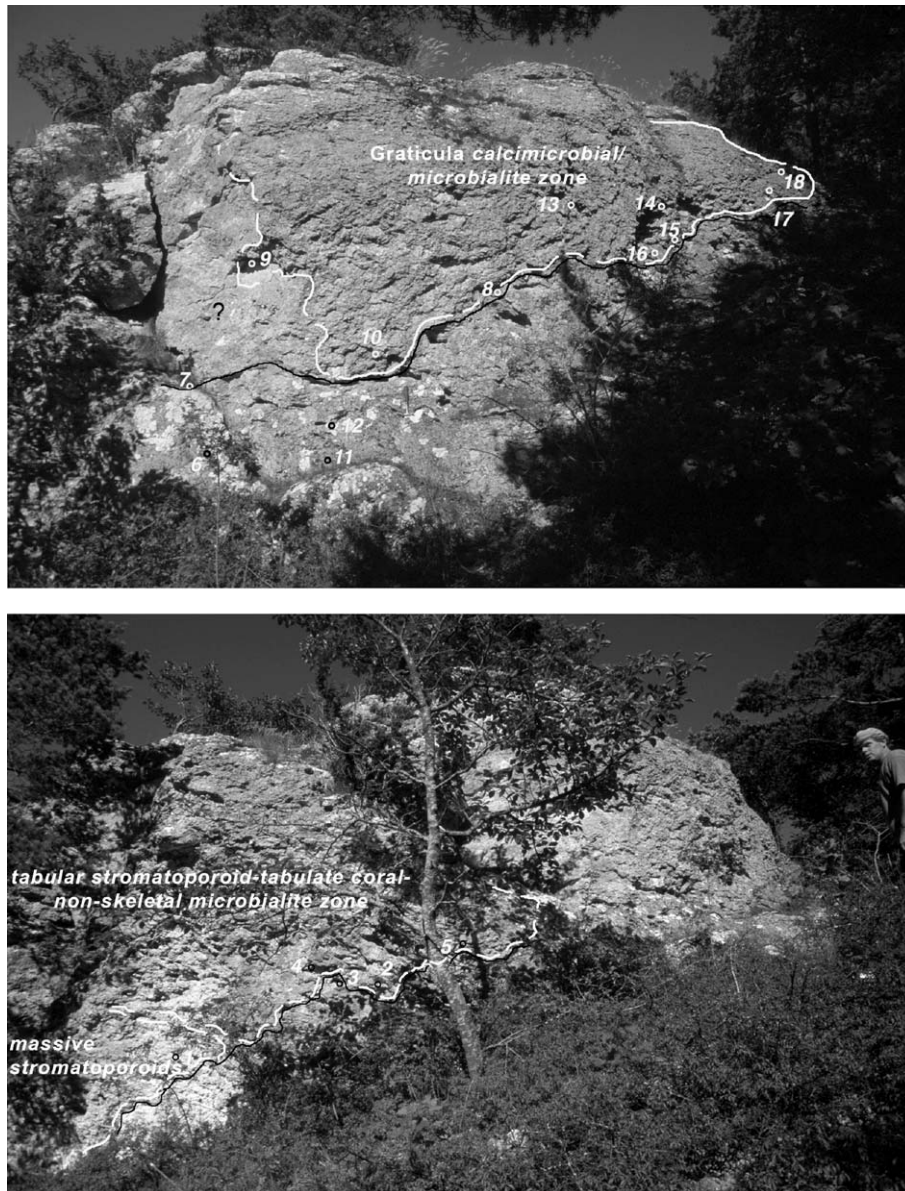


Fig. 7. Högklint reef at Brissund 4; field photographs reveal the lower and upper parts of the reef with approx. overall height of ca. 10 m. The base of the reef is not exposed, but major parts of the reef are shown. Note the early onset of *Graticula* framestone facies. Although large allochthonous block formation has to be taken into account (see Watts and Riding, 2000), all geopetals in the section point to in-situ preservation. Fine black line marks the boundary between reef and non-reef facies. Numbers indicate sample localities (sample nos. BRI 1–18).

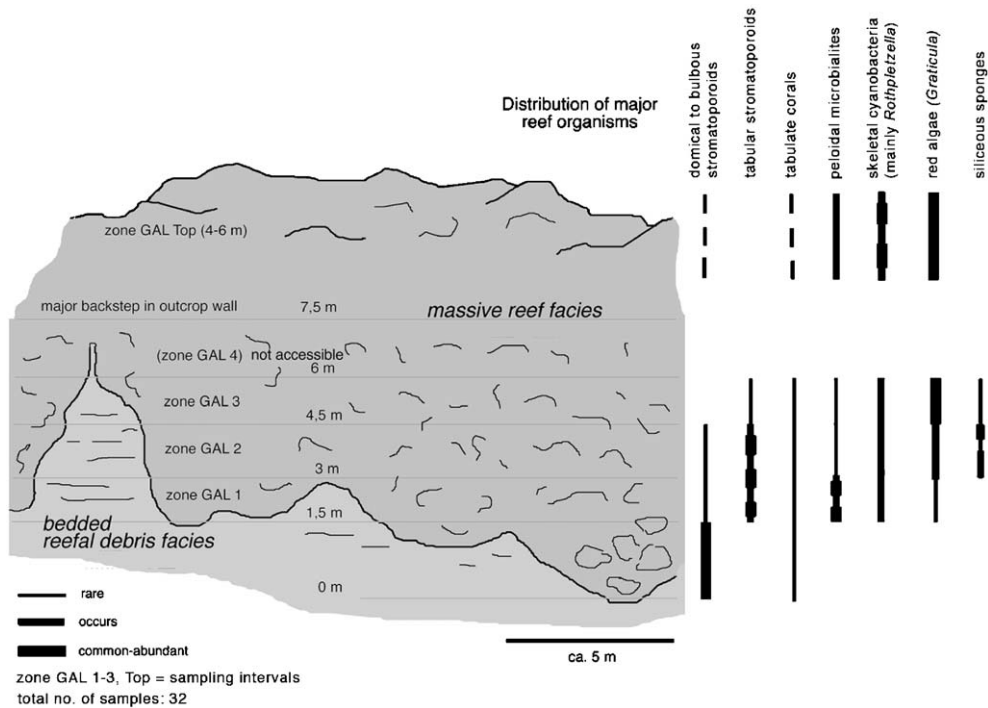


Fig. 8. Högklint reef at Galgberget 2; simplified sketch of the outcrop with sampling zones and overall zonation pattern of main reefal organisms. Geopetals in slabs and thin sections point to partial allochthonous block formation. Zonation pattern is quite similar to Brissund 4 locality.

sediments. This succession is tentatively attributed to the Tofta Formation (Calner et al., 2005). The development of the metazoan-bearing stromatolites is intimately related to the formation of stromatoporoid–coral patch reefs (Fig. 9).

4.1. Framework type 3: *Coenites*-bearing stromatolites—composition, structure, and distribution pattern

The microbialites are developed in the upper marginal part of the patch reefs, and frequently



Fig. 9. Patch reef with marginal development of *Coenites* bearing stromatolites (framework type 3), Tofta Formation, Digerhuvud 2, Fårö; 1—reef core facies with thick tabular to domical stromatoporoids, cerioid-phaceloid rugose and massive to delicate ramose tabulate corals embedded in debris-rich groundmass and dense micritic clusters and scattered stromatolites; 2—reef flanking beds: massive stromatoporoid limestones interfingering with reefal debris rudstones; 3—*Coenites*-bearing stromatolites interfingering with stromatoporoid flanking beds.

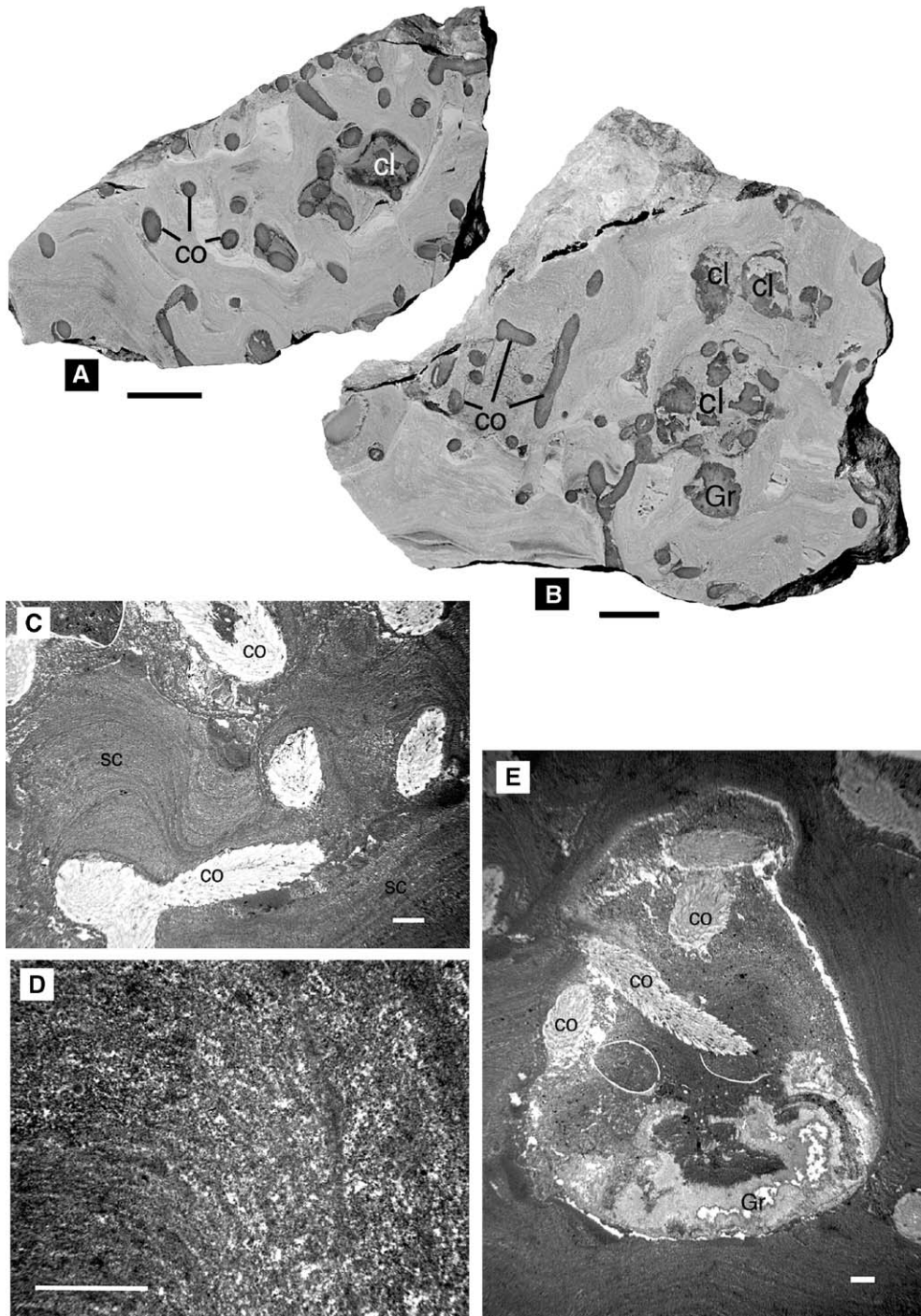


Fig. 10. *Coenites*–stromatolite framework (type 3) from the Tofta Formation—polished slabs (A, B) and thin sections (C–E): (A) dense, well-laminated stromatolite enveloping plasticlasts (cl) and *Coenites* branches (co), Digerhuvud 2 (sample no. DIG 2), scale bar: 1 cm; (B) dense stromatolite bearing plasticlasts (cl) and common *Coenites* branches (co) as well as *Graticula* remains (Gr), Digerhuvud 2 (sample no. DIG 4), scale bar: 1 cm; (C) microscopic structure of dense peloidal stromatolites (sc). Note pillar-like overgrowth structures on *Coenites* branches (co), Digerhuvud 2 (sample no. DIG 3), scale bar: 1 mm; (D) close-up of (C) showing the dense peloidal, well-laminated fabric of stromatolites, scale bar: 1 mm; (E) plasticlast, composed of bioclastic floatstone, co=*Coenites*, Gr=*Graticula*. Note sparite filled shrinkage cracks around the clast, Digerhuvud 2 (sample no. DIG 3/2), scale bar: 1 mm.

associated with tabulate coral debris (*Coenites*). *Coenites* has been interpreted as a branched tabulate coral (Utgaard, 1983; Li et al., 2002; Niko, 2003, 2004). Historically, however, the tabulate coral affinity of *Coenites* was questioned (e.g., Brood, 1970, 1979). It is interesting to note that *Coenites* is also a significant element in the upper part of the Höglint Formation (Höglint c unit) in the Vattenfallet section (cf. Hede, 1960; Jaanusson et al., 1979). *Coenites*-rich strata from this locality are characterized by a high carbonate content, high abundance of peloids, peloidal lithoclasts, and skeletal remains ('*Solenopora*', echinoderms, stromatoporoids and corals).

The non-skeletal stromatolites display a dense to peloidal microstructure with alternating micritic dense laminae and peloidal sparitic coarser grain-supported laminae. Peloids with irregular shape range from well-rounded to angular; the outline is indistinct. Peloids are poorly 'sorted', and show grain sizes between 20 and 100 μm , but most peloids are within a range of 30 to 70 μm . Stromatolites form massive encrustations with irregular growth directions that depend on the substrate and its orientation (e.g., around *Coenites* branches). However, the overall pattern clearly shows the convex upwardly oriented growth of the stromatolites indicative of the organic nature of the crusts (Fig. 10A–D).

Only Hadding (1950) has to date mentioned identical microbial fabrics from the locality Bugenäs, situated on the east coast in northernmost Gotland. These stromatolites probably belong to the Slite Group, although the locality is not exactly indicated. Hadding considered the peloidal stromatolitic crusts as a 'dense mass consisting of irregular layers, which follow the varying form of the substratum, both horizontally and vertically'.

Stromatolites co-occur with *Coenites*, *G. gotlandica*, ostracodes, and brachiopods. They initially form upwardly oriented caps, or finger-like growth forms on *Coenites* branches that are subsequently overgrown by planar massive stromatolites (Fig. 10A–E). *Graticula*-thalli and *Coenites*-*Coenostea* may also occur as part of lithoclasts where *Coenites* and *Graticula* are embedded in recrystallized bioclastic calcareous mud. In some instances, the lower half of the lithoclasts interrupt the stromatolitic lamination, whereas the upper half show enveloping stromatolitic encrustation. Close to the boundary between the enveloping stromatolites and the lithoclasts, the clasts show shrinkage cracks (partly circumgranular), probably the result of differential lithification and/or collapse of the clast sediment (Fig. 10A, B, E). Both shrinkage cracks and the well-rounded shape of the clasts point to a semi-consolidated condition of the lithoclasts, which may therefore be

termed plasticlasts (cf. Flügel, 2004). The poorly consolidated clasts were presumably overgrown by early hardening stromatolitic crusts. Eventually, the deformable surfaces of the 'soft' clasts locally detached from the overlying and encrusting microbial mats, which resulted in spar-filled cavities that parallel the boundary between stromatolites and plasticlasts (Fig. 10E).

The rauk field at Digerhuvud exposes strongly eroded patch reefs with particulate inter-reef sediments. The investigated area at Digerhuvud 2 includes three rauks (Fig. 9). The right rauk exhibits dominant development of the stromatolitic framework type as well as transitions to thick-bedded stromatoporoid beds, whereas the central and left rauk reveal different fabrics and composition. The central rauk represents a reef-core facies, dominated by a fairly high-diversity metazoan-algal association with large domal stromatoporoids, massive and branching tabulate and rugose corals (*Favosites*, *Coenites*, *Acervularia*), and graticulacean algae. The groundmass is usually debris-rich with strongly reworked reef builders, but dense micritic, partly laminated stromatolitic areas also exist. The left rauk displays indistinct but thickly bedded nodular, debris-rich stromatoporoid flank beds. Based on the faunal and facies distribution pattern, along with the bedding plane inclination/orientation, the three rauks were probably part of a larger patch reef with the stromatolitic-tabulate coral framework occurring at the flank of the reef during a late stage of reef development.

The tabulate coral *Coenites* occurs both in central and marginal facies of the patch reefs, and the inter-reef rudstones with hummocky cross-stratification; the latter often are exclusively composed of *Coenites* debris that frequently covers small stromatoporoid–coral patch reefs (e.g., Langhammarshammar at the northernmost tip of Fårö).

5. Case study III: lower Hamra reefs at Hoburgen—stromatoporoid–calcimicrobe framework

Stromatoporoid–calcimicrobial frameworks in the lower Hamra Formation occur in the southernmost part of Gotland, within the so-called 'algal limestone' sensu Manten (1971). This unit forms the base of the Hamra Formation and is intercalated between the underlying oolites or sandstones of the Burgsvik Formation and the overlying Hamra limestones. Reef development in the 'algal limestone' has been described by Munthe (1921), Manten (1971), and Stel and DeCoo (1977) from various other localities in southern Gotland (e.g., Kättelviken, Grumpevik). Our data were obtained

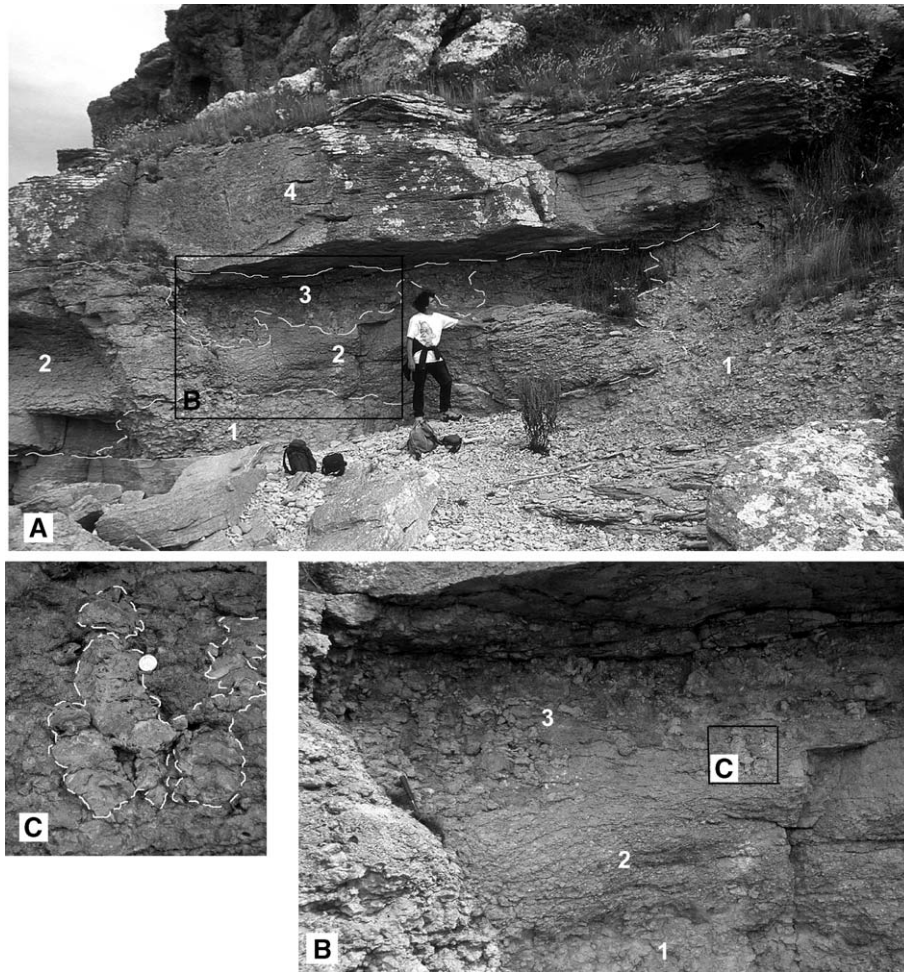


Fig. 11. Reef development in the lower Hamra Formation at Hoburgen 2—stromatoporoid–calcimicrobial framework (type 4): field photographs figure facies assemblage with initial and more mature reef development. (A) General outcrop situation with main facies units, 1: stromatoporoid–calcimicrobial reef facies, 2: detrital coarse-grained crinoid–bioclast–oncoïd facies, 3: coarse-grained crinoid facies with initial stromatoporoid–*Rothpletzella* framestone, 4: crinoid–bioclast grainstone/rudstone. (B) Detail from (A) (numbers refer to (A)). (C) detail from (B) with columnar growth of stromatoporoid–calcimicrobe frames (white dashed line).

from the Hoburgen 2 locality. Close to the present-day sea level, above the Burgsvik oolite/sandstone, the ‘algal limestone’ is exposed and reveals an intimate association of initial stromatoporoid–calcimicrobial reef growth and allochthonous coarse-grained sediment composed of oncoïds and crinoidal bioclastic grainstones/rudstones (Fig. 11).

5.1. Framework type 4: stromatoporoid–calcimicrobe frames (Hoburgen, lower Hamra Formation)—composition, structure, and distribution pattern

This framework type reveals an intimate intergrowth of tabular to domical stromatoporoids (mainly

Parallelostroma), encrusting tabulate corals, and thick planar to pillar-like calcimicrobial crusts, the latter sometimes alternating with thin non-skeletal microbial crusts. Domical and bulbous stromatoporoids range from several centimeters to 10–15 cm in diameter, and laminar to tabular individuals are between 1 cm and 3–5 cm thick. The coral fauna is primarily composed of flat, encrusting favositids (e.g., *Favosites forbesi*) and alveolitids (e.g., *Alveolites suborbicularis*) as well as subordinate solitary rugosans. Crinoids (stem and root remains) are locally common. Calcimicrobial crusts are almost exclusively composed of *R. gotlandica* and *R. munthei*; the former taxon is much more common. The external tube

diameter of *R. gotlandica* measures 25–30 μm (rarely up to 40 μm). The tube diameter of the rare *R. munthei* reaches only about 20 μm . Metazoans and calcimicrobes form the bulk (60–80%) of the total

rock volume, with the remaining interstitial space filled with quartz-bearing allochthonous sediments composed of bioclastic grainstones/rudstones or marly mudstones (Fig. 12A–E).

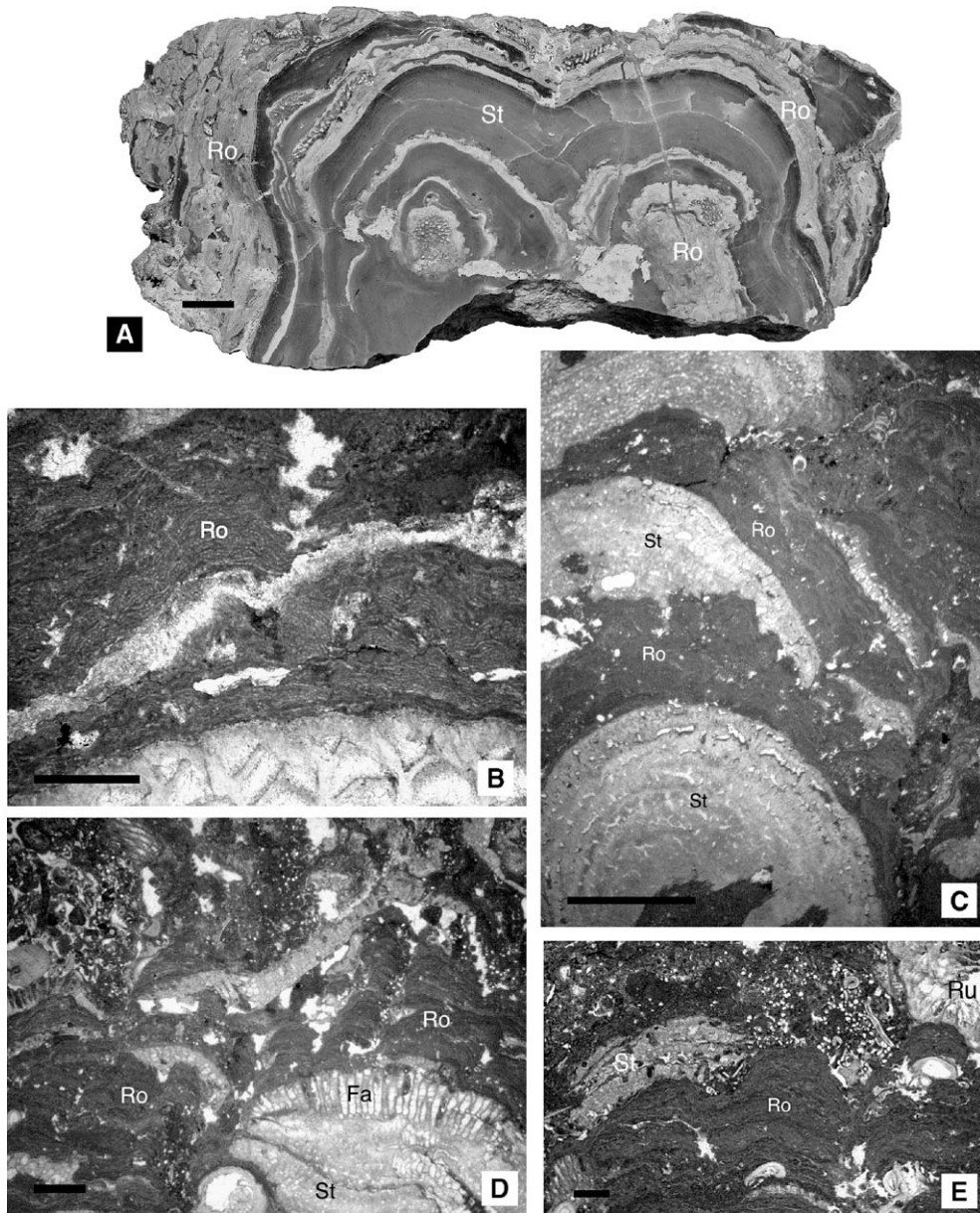


Fig. 12. Stromatoporoid–calcimicrobial frameworks (type 4) from the lower Hamra Formation at Hoburgen 2: (A) polished slab with domical stromatoporoid (St) (?*Parallelostroma*) and abundant *Rothpletzella* crusts (Ro). Note alternating waxing and waning of calcimicrobial crusts and stromatoporoid laminae, Hoburgen 2 (sample no. HOB 8), scale bar: 1 cm; (B) thick *Rothpletzella* crust growing on a rugose coral, Hoburgen 2 (sample no. HOB 2/2), scale bar: 1 mm; (C) alternating growth of domical stromatoporoids and *Rothpletzella* crusts, Hoburgen 2 (sample no. HOB 5), scale bar: 5 mm; (D) multiple framework of intergrowing stromatoporoids (St), tabular *Favosites* (Fa) and irregular, columnar *Rothpletzella* crusts (Ro), Hoburgen 2 (sample no. HOB 2/4), scale bar: 2 mm; (E) bulbous, hemispherical growth of *Rothpletzella* (Ro) encrusted by solitary rugose coral (Ru) and tabular stromatoporoid (St), Hoburgen 2 (sample no. HOB 2/3), scale bar: 1 mm.

6. Environmental setting of framework types and significance in reef development

6.1. Höglint reefs—stromatoporoid non-skeletal microbial to graticulacean microbial/calcimicrobial frameworks (types 1, 2) at Brissund and Galgberget

The reef-bearing Höglint Formation was formed in a shallowing-upward sequence, and the internal succession of the reef also follows this trend (Riding, 1981; Watts and Riding, 2000). Reefs at the Galgberget 2 and Brissund 4 localities display a zonation pattern, which apparently differs from the zonation pattern of the Höglint reefs described by Watts and Riding (2000). Reefs show domical to bulbous stromatoporoids near the base that are progressively replaced by tabular stromatoporoids and tabulate corals, the latter associated with non-skeletal microbialites. Together, they formed an open framework with muddy, bioclastic background sedimentation. The faunal assemblage (stromatoporoids, corals, crinoids) in this stage of the reef development is indicative of a fully marine, relatively low-energy environment. Scattered siliceous sponges occur at Galgberget and other localities in comparable stratigraphic position (e.g., Snäckgårdsbaden, own observations) and suggest slightly deeper water position for at least the early stages of reef development. This accords with Watts and Riding (2000), who state that their corresponding growth stage 2 ('halysitid/laminar stromatoporoid zone') was formed in 20–40 m deep water, most likely below fairweather wavebase. Based on the occurrence of large block formation and steep dips (indicated by geopetals), a moderate to high relief formation was estimated (at least 15 m; Watts and Riding, 2000). This matches observations from Jurassic reefs, which did not form biohermal structures with pronounced relief when non-skeletal microbialites (thrombolites) were absent (Leinfelder et al., 1993). Microbialites appear to be a major prerequisite for the development of reefal framework in mid-Palaeozoic reefs. Moreover, stromatoporoids and many tabulate corals alone are not normally capable of forming large rigid frameworks, resulting in generally low-profile reef structures (cf. Kershaw and Keeling, 1994; May, 1997; Kershaw, 1998; Wood, 2000). According to Kershaw (1998), rigid frameworks are absent in stromatoporoid reefs unless they are bound by microbial crusts. This seems to be the crucial factor for the Höglint reefs. The presence of non-skeletal microbialites assisted in the formation of the high profile during this reef growth stage, as postulated by Watts and Riding (2000). However, muddy sedimentation partly suppressed a

more vigorous growth of the microbialites that would have led to a higher degree of tight framework development. As a result, Höglint reefs at this growth stage were most likely biohermal structures with a pronounced relief, although rigid frames did not develop pervasively. This gave way to early gravitational breakup and large clast formation, even in low to moderate water energy settings (cf. Watts and Riding, 2000).

Using the sequence stratigraphic framework provided in Calner et al. (2004), the development of the Höglint reefs in the lower Wenlock (lower Sheinwoodian) can be assigned to a Highstand Systems Tract. The rapid shallowing-upwards ('catch-up') trend of the reef adds support to this interpretation. Highstand situations are generally characterized by high carbonate production that leads to rapid accumulation of biotrital, calcareous intra- and inter-reef sediments (cf. Schlager et al., 1994), applicable to parts of the Höglint reefs (cf. Watkins, 1979; Watts and Riding, 2000).

The upper part of the Höglint reefs is formed by a graticulacean-microbial/calcimicrobial tight framework. The faunal composition, along with abundant red algae (*Graticula*) and calcimicrobial (mainly *Rothpletzella*, subordinate *Hedstroemia*) crusts, partly associated with non-skeletal microbialites, crinoids, and subordinate stromatoporoids, tabulate and rugose corals, is indicative of a very shallow marine, moderate to high water energy environment. Watts and Riding (2000) estimated a water depth of not more than 5 m, and Riding and Watts (1981) interpreted this zone as an algal reef crest that shares some similarities with modern coralline algal ridges. Compared with the tabular stromatoporoid non-skeletal microbialite framework, the ratio of non-skeletal microbialites to calcimicrobes is much lower. This suggests that calcimicrobes became increasingly abundant towards the top of the reef, i.e. shallow, agitated water, due perhaps to potentially higher wave resistance of rigid, skeleton-secreting microbes compared with microbial communities secreting non-skeletal peloidal carbonate. Riding and Watts (1981) suggested that early marine cements added considerably to the strength of the skeletal framework. Based on our observations, it is likely that the structures described by these authors as 'micritic cement' are identical to the structures that we interpret as formed by benthic microbial communities (non-skeletal microbialites). All meso- and microscopic features of these structures (i.e. heterogeneous peloidal fabric with peloids arranged in rows, convex upwardly oriented overgrowth, connective structures between red algal thalli) are indicative of an organic microbial nature, rather than of inorganic cements.

The remaining space within the algal-microbial/calcimicrobial framework is filled with allochthonous carbonate mud, which does not necessarily contrast the high-energy character of this stage of the Högklint reef development. It is known from modern algal cup reefs that mud is baffled by the algal frame and trapped in interconnected cavities regardless of the overall high-energy conditions (Riding, 1981; Riding and Watts, 1981).

6.2. Patch reefs from the Tofta Formation on Fårö—*Coenites*–stromatolite frameworks (type 3)

The development of the metazoan-bearing stromatolites in the Tofta Formation is intimately related to the formation of stromatoporoid–coral patch reefs.

The impoverished fauna as well as the intensive development of stromatolites are interpreted as a very shallow marine, somewhat restricted environment. Outcrop and spatial distribution of *Coenites* stromatolitic framework suggest growth in sheltered areas between stromatoporoid patch reef complexes. The tabulate *Coenites* was most probably only a subordinate element in the stromatolite environment based on the massive post-mortem overgrowth of *Coenites* fragments by microbial crusts. *Coenites* is not preserved in its habitat of growth, but rather comes from a surrounding setting in the form of fragments of larger colonies. In rare instances, semi-consolidated lithoclasts were shed from adjacent reef facies onto the stromatolite substrate prior to final lithification based on the fact that clasts partly interrupt the stromatolitic lamination with their base. The clasts in turn show overgrowth by microbial crusts. Shrinkage cracks, sometimes with circumgranular outline between clasts and surrounding stromatolites, are suggestive of the collapse of semi-consolidated, relatively soft clasts against enveloping, more quickly lithifying stromatolitic mats. The finely laminated stromatolites formed under relatively low-energy conditions in protected areas. A high-energy environment can be ruled out since breccias, pebble conglomerates, and sedimentary current structures are missing. In modern stromatolitic mats, strong wave action with turbulent high-energy conditions scour and damage potential stromatolitic structures by removing microbial mats and weakly lithified stromatolite layers, and thus inhibit stromatolite growth (Feldmann, 1995; Feldmann and MacKenzie, 1997). Those authors conclude that undisturbed stromatolite formation requires laminar water flow where scouring and reworking is low. These conditions would occur within a shallowing trend induced by relative sea-level fall.

The Digerhuvud examples show several structural similarities to stromatolites described by Chems (1982) from the lower Eke Formation in eastern Gotland where stromatolites are suggested to have developed as small mounds on subaerial exposure and erosional surfaces. The environment was characterized by shallow subtidal low-energy conditions during much of the time of mound growth. Only in the upper levels, intertidal conditions developed, which are demonstrated by desiccation features affecting the upper surface of the mounds (Chems, 1982; Fig. 5D). In contrast to the environmental setting of the Gotlandian stromatolites, there are also reports of stromatolite or microbialite dominated fabric from high-energy, wave swept settings, e.g., from the Silurian of Arctic Canada and Alaska (DeFreitas et al., 1993; Soja et al., 2000). With regard to fabric and microstructure, these stromatolites/microbialites differ considerably from the stromatolites described here in association with early diagenetic cement crusts.

6.3. Patch reefs of the lower Hamra Formation (Hoburgen)—stromatoporoid–calcimicrobe frameworks (type 4)

Tight stromatoporoid–calcimicrobial frameworks characterize the small early growth stage reefs, but are also formed in larger patch reefs and biostromes in the lower Hamra Formation at Hoburgen. The lower Hamra Formation ('algal limestone' sensu Manten, 1971), characterized by oncoids and small stromatoporoid–calcimicrobial patch reefs and biostromes, developed during a transgression (Stel and DeCoo, 1977; Calner et al., 2004) on the Burgsvik mixed sandstone–oolite succession, which is interpreted as a series of storm-dominated offshore bars (Long, 1993). The underlying and surrounding facies with ooids and oncolitic, crinoidal bioclastic grainstones/rudstones is indicative of a high-energy, abrasive environment in very shallow subtidal settings. The high-energy character of the sediments is further substantiated by regular concentric oncoids formed under constant water movement (cf. Stel and DeCoo, 1977). *Rothpletzella*–stromatoporoid associations in high-energy, partly siliciclastic settings have also been described from the Lower Silurian of England (Much Wenlock limestone; Powell, 1991), and the Upper Devonian back reef facies in the Canning Basin reef complex (Wood, 2000). However, *Rothpletzella* stromatolites are also known from low-energy shallow water settings exemplified by a Middle Devonian occurrence in China (Yangshuo, Guangxi province; Bao, 1992). In the Late Devonian Canning Basin reef

complex, *Rothpletzella* co-occurs with *Renalcis* as major frame-building microencruster in a deep-water slope environment (Wray, 1972).

In the reefs from the lower Hamra Formation, *Rothpletzella* crusts and stromatoporoids interfinger and alternate with one another, due most probably to syn-vivo competition for space. High-energy environment with mobile bioclastic lithofacies may have favoured encrustation of stromatoporoids by *Rothpletzella*, since stable firm substrates suitable for colonisation were probably rare (Powell, 1991). In the Högklint reefs and lower Hamra reefs, *Rothpletzella* was the most abundant form of microbial and calcimicrobial organisms in shallow agitated water, whereas non-skeletal microbialites appear to dominate in slightly deeper water with low to moderate water energy. This may be related to a higher rigidity, and hence higher resistance to wave action of the *Rothpletzella* skeletal structure in comparison to the non-skeletal microbialites that consist of diffuse, peloidal calcareous masses.

6.4. Sea-level change and oceanographic circulation pattern

According to the overall oceanographic picture for the Silurian reef-bearing succession of Gotland established by Jeppsson (1990) based on conodont data, reef development in the Högklint, Tofta, and lower Hamra Formation falls into the so-called 'Vattenfallet' and 'Hoburgen Secundo Episodes', which are characterized by more arid climate and salinity stratified ocean at low latitudes that favour the growth of reefs. Based on stable isotope data, this model was later modified by Bickert et al. (1997) using the terms A- and H-episodes for time intervals characterized by arid and humid climate respectively. Apart from the fact that not all episodes of Jeppsson (1990) are documented by changing $\delta^{13}\text{C}$ values, slight differences also exist in the onset of climatic changes (Calner et al., 2004). Shifts between estuarine and anti-estuarine circulation patterns in shallow seas due to precipitation changes are regarded as the main driving process in the modified model. According to the new nomenclature, reef and framework development in the Högklint, Tofta, and lower Hamra Formation fall into the lower Sheinwoodian and the upper Ludfordian A-periods. In addition to arid climate, A-episodes are characterized by anti-estuarine circulation and oligotrophic conditions that favour reef growth (Bickert et al., 1997; Samtleben et al., 2000). Based on the sequence stratigraphic interpretation given by Calner et al. (2004), larger bioherms (e.g., reefs in the Högklint

Formation and upper Tofta Formation) primarily grew during high sea-level stands (late TST and HST) within the arid A-episodes. High sea level accounted for moderate to high accommodation space that allowed for the development of biohermal reef structures with distinct relief. Due to the arid climate conditions, reef growth was not negatively affected by terrigenous influx that would have accounted both for reduced accommodation space and suppressed growth of metazoans, algae and microbial crusts. This scenario characterizes the humid H-episodes, which apparently only allowed for growth of biostromes, level bottom communities, and small patch reefs (cf. Bickert et al., 1997; Sandström and Kershaw, 2002; Munnecke et al., 2003). Reef development here may be related to phases of reduced humidity or pronounced sea-level rises of higher order.

7. Summary and conclusions

- (a) Non-skeletal microbialites in Silurian reefs from Gotland produced different fabrics, structures and morphologies, ranging from largely non-laminated peloidal irregular masses in the Högklint reefs at Galgberget 2 and Brissund 4 (framework type 1) to well-laminated stromatolites from the stromatoporoid–coral patch reefs of the Tofta Formation at Digerhuvud 2 on NW Fårö (framework type 3). The organic nature of the crusts is indicated by convex upwardly oriented overgrowth structures, trichome-like arrangement of peloids and intergrowth with skeletal calcimicrobes and metazoans. Non-skeletal microbialites contribute to framework formation during different stages of the Högklint reef development at Brissund and Galgberget, as well as in the marginal parts or flanking beds of the stromatoporoid–coral patch reefs at Digerhuvud.
- (b) *G. gotlandica*, interpreted as a coralline alga by Brooke and Riding (1998), also formed frameworks in the Högklint reefs (framework type 2). They were supported by non-skeletal microbialites and calcimicrobial crusts (*Rothpletzella*). *Graticula* frameworks dominate the upper parts of Högklint reefs at Galgberget 2 and Brissund 4 and play a more important role in overall Högklint reef growth than previously thought (cf. Riding and Watts, 1981; Watts and Riding, 2000).
- (c) A fourth type of framework is characteristic of initial stromatoporoid–coral patch reefs in the lower Hamra Formation at Hoburgen 2. This type

is predominantly composed of tabular to domical to irregular stromatoporoids, encrusting tabulate corals and thick calcimicrobial *Rothpletzella* crusts.

- (d) The typical zonation pattern of Högklint reefs, as suggested by Watts and Riding (2000), is not clearly visible in the Högklint reefs at Galgberget 2 and Brissund 4. A tabular stromatoporoid–tabulate coral rich interval is superposed on a zone with predominantly massive stromatoporoids. Coralline algal dominated frameworks are not restricted to the caps of the reefs, but also occur 4–5 m below the reef tops. The latter also contrasts with the zonation pattern proposed by Watts and Riding (2000). Those authors described only a thin coralline algae–cyanobacterial capping reef crest with an average thickness of 0.3–0.6 m. The tabular stromatoporoid–tabulate coral zone reveals the most vigorous development of non-skeletal microbialites. This zone largely corresponds to growth stage 2 sensu Watts and Riding (2000) ‘halysitid–laminar stromatoporoid zone’, said to develop a high synsedimentary relief of at least 15 m above the seafloor. The correlation of vigorous microbialite crust development to the formation of high relief reef structures is consistent with observations from Jurassic reef systems where bioherm formation is intimately linked to the flourishing of microbial crusts (Leinfelder et al., 1993; Leinfelder et al., 2002).
- (e) Structural differences in framework types mirror different environmental settings. Framework type (1)—tabular stromatoporoid non-skeletal microbialite frames (Brissund 4, Galgberget 2—Högklint reefs), characteristic for early or intermediate growth stages within Högklint reefs, developed in slightly deeper, low-energy, fully marine water based on the occurrence of siliceous sponges, mud rich allochthonous carbonate matrix, and scattered occurrence of calcareous algae and calcimicrobes. In terms of water depth, we follow Watts and Riding (2000), who reconstructed a water depth of 20–40 m for their growth stage 2, which most likely corresponds to the framework type 1-bearing strata described here. Framework type (2)—graticulean–microbial/calcimicrobial frames (Brissund 4, Galgberget 2—Högklint reefs) is characteristic for the late growth stage of the Högklint reefs that grew in shallow, moderate to highly agitated water, not exceeding 10 m depth (cf. Watts and Riding, 2000). Framework type (3)—stromato-

lite–*Coenites* frameworks (Digerhuvud on Fårö, Tofta Formation) formed in sheltered, partly restricted parts of patch reef complexes. Framework type (4)—stromatoporoid–*Rothpletzella* frameworks were situated in a highly agitated, very shallow open marine environment.

- (f) The Gotland reefs indicate that, during the Silurian (and Palaeozoic), the presence of microbial frameworks considerably affected and supported the formation of many more shallow water metazoan reefs than previously thought.

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