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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.

Keywords: Non-skeletal microbialites; Calcimicrobes; Red algae; Reefal framework formation; Silurian; Gotland

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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 organisms 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) stromatoporoid–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 microencrusters, 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 microencrusters 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