The role of endolithic cyanobacteria in the formation of lithified laminae in Bahamian stromatolites

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ABSTRACT

The microboring activity of endolithic cyanobacteria plays a major role in the formation of the dominant lithified laminae in modern marine stromatolites in the Exuma Cays, Bahamas. These stromatolites are composed primarily of fine-grained carbonate sand that is trapped and bound by the filamentous cyanobacteria *Schizothrix* sp.. Periodic introduction of coccoid endolithic cyanobacteria *Solentia* sp. during hiatuses in stromatolite growth associated with very low rates of sedimentation results in the formation of lithified horizons, 200–1000 μm thick. These layers consist of micritized grains that are welded together at point contacts. The micritization is caused by extensive microboring and carbonate precipitation within boreholes concurrent with endolithic activity. Grain welding occurs when boreholes cross from one grain to another at point contacts. Thus, microboring destroys original grain textures but, at the same time, plays a constructional role in stromatolite growth by forming lithified layers of welded grains. These lateral bands of fused carbonate grains help to stabilize and preserve the stromatolite deposits.

Keywords Endolithic cyanobacteria, lithification, micritization, stromatolites.

INTRODUCTION

Stromatolites are laminated sedimentary structures formed by the binding, trapping and lithification action of microbial communities (Kalkowsky, 1908; Awramik, 1984; Ginsburg, 1991). They have an unrivalled geological history that extends back 3·5 billion years (Schopf, 1983). Recent discoveries of modern stromatolites in open-marine environments in the Exuma Cays, Bahamas (Fig. 1; Dravis, 1983; Dill *et al.*, 1986; Reid & Browne, 1991; Reid *et al.*, 1995) provide a unique opportunity to study the processes responsible for the formation of these long-lived microbial deposits.

Studies to date have emphasized the role of the filamentous cyanobacterium *Schizothrix* in the growth of Exuma stromatolites (Browne, 1993;

Reid *et al.*, 1995; Macintyre *et al.*, 1996; Golubic & Browne, 1996; Seong-Joo *et al.*, 2000; Golubic *et al.*, 2000). Initial growth of Exuma stromatolites is controlled by the binding action of *Schizothrix* filaments, which results in the accretion of carbonate sand grains. Intermittent periods of lithification produce distinct banding patterns in these stromatolites. The major lithified laminae are typically about 1 mm thick and are particularly well displayed on saw-cut surfaces (Fig. 2).

Ongoing studies in the Research Initiative on Bahamas Stromatolites (RIBS) Program are investigating biogeochemical processes of lithification in Exuma stromatolites. As a contribution to this programme, the present paper shows that periodic introduction of endolithic cyanobacteria to the bound sediment community results in the formation of lithified layers of micritized sand grains
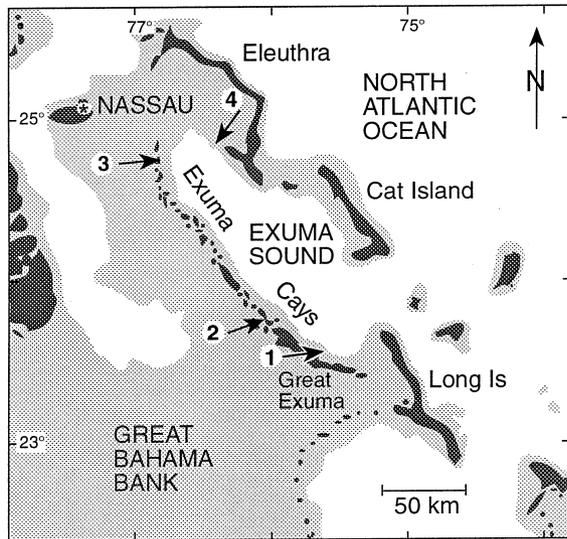
Fig. 1. Map showing the locations of stromatolite sites on the margin of Exuma Sound, Bahamas. 1. Stocking Island (Reid & Browne, 1991; Macintyre *et al.*, 1996); 2. Lee Stocking Island (Dill *et al.*, 1986); 3. Highborne Cay (Reid *et al.*, 1995); and 4. Schooner Cays (Dravis, 1983).
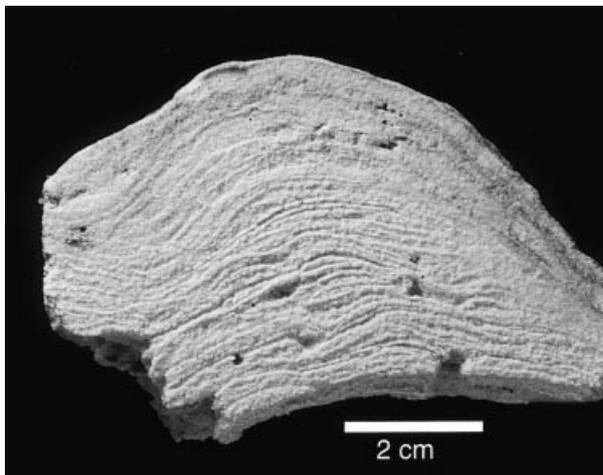

Fig. 2. Well-developed lithified layers stand out in relief on a saw-cut surface of a stromatolite from Highborne Cay.

that are welded together at point contacts. These layers provide major structural support for stromatolites. Recognition of endoliths as agents of stromatolite construction is significant, as microborers are traditionally considered to be destructive agents of biological erosion (Golubic & Brown, 1996; Perry, 1998). Additional microbial processes, such as photosynthetic production and sulphate reduction, which are also important in the lithification of Exuma stromatolites, are discussed elsewhere (Pinckney & Reid, 1997; Visscher *et al.*, 1998; 1999).

Stromatolite microstructure

Exuma stromatolites consist predominantly of well-sorted, fine carbonate sand (125–250 μm); grains are skeletal or lithic fragments, which commonly have oolitic coatings (Browne, 1993; Reid *et al.*, 1995; Macintyre *et al.*, 1996). Calcified filaments are present in some intertidal stromatolites (Reid *et al.*, 1995; Feldmann, 1997) but, for the most part, cyanobacterial filaments in Exuma stromatolites are uncalcified and are not preserved.

The very prominent lithified horizons in Exuma stromatolites (Fig. 2) have distinctive petrographic characteristics (Reid & Browne, 1991; Browne, 1993; Reid *et al.*, 1995; Macintyre *et al.*, 1996). They typically consist of a micrite crust, 20–50 μm thick, which overlies a layer of micritized sediment grains, 200–1000 μm thick (Fig. 3). The uppermost surfaces of grains in this micritized layer are extensively pitted and, in some cases, the grains are truncated. Micritized grains are cemented at point contacts by aragonite crystals (<1 μm in size) and, with increased lithification, the boundaries between micritized grains disappear as grains appear to 'weld together' (Macintyre *et al.*, 1996, p. 236). The overlying micrite crusts are sometimes encrusted by *Ostreobium*, crustose coralline algae and foraminifera (Reid *et al.*, 1995; Macintyre *et al.*, 1996). The encrusters indicate that these horizons have formed during a hiatus in the growth of the
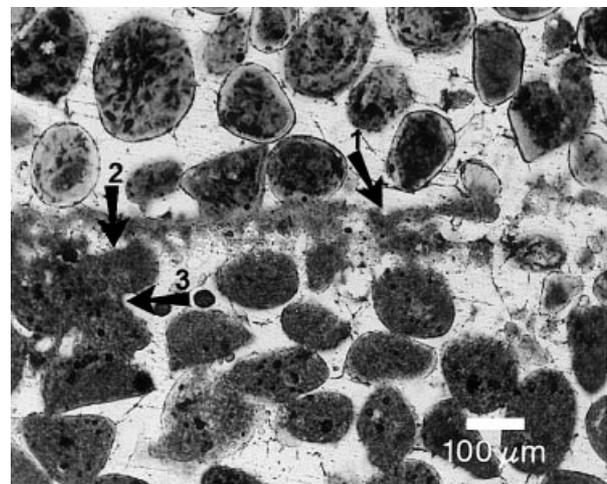

Fig. 3. Photomicrograph (plane polarized light) illustrating the characteristic features of lithified layers in Exuma stromatolites. Note the micrite crust (arrow 1), which overlies a band of micritized grains; some of the uppermost micritized grains are truncated by extensive microboring (arrow 2). Also note how many of the micritized grains coalesce or weld together at point contacts (arrow 3). Sample from Highborne Cay.

stromatolites at a time when the surface was exposed on the sea floor.

STUDY AREA AND METHODS

Stromatolite samples were collected from Highborne Cay at the north end of the Exuma chain (Fig. 1, locality 3). As at Stocking Island in the southern Exumas (Macintyre *et al.*, 1996), Highborne Cay stromatolites are located in the lee of a fringing algal ridge (Reid *et al.*, 1995). Thin sections of Highborne Cay stromatolites were examined and photographed with a petrographic light microscope. These sections were then etched for 2 s in 0·35 M acetic acid and coated with gold/palladium for examination with a Hitachi S-570 scanning electron microscope (SEM). The combination of light microscope and SEM observations on the same thin sections allowed direct comparison of petrographic and SEM analyses of individual grains.

In addition to samples collected in the field, indurated crusts formed during the cultivation of stromatolite microbes were also examined in the laboratory. Washed and sterilized loose sediments (ooids) from Highborne Cay were sprinkled onto the surface of five sea-water–agarose plates. Small pieces (approximately 1 mm in diameter) were excised from lithified layers in a Highborne stromatolite, and one fragment was placed on each sediment–agarose plate. These lithified fragments contained an abundance of the photosynthetically active, endolithic coccoid cyanobacterium *Solentia* sp. The inoculated plates were incubated at 25 °C on an 18-h light/6 h dark cycle for a 2-month period. Newly developed crusts formed during this experiment were thin sectioned and examined with light and scanning electron microscopes.

RESULTS

Scanning electron photomicrographs of etched thin sections of Highborne Cay stromatolites show that micritized grains in lithified layers, which have cryptocrystalline grey textures in plane polarized light (Fig. 3), are extensively bored by an endolithic microbe. This microborer forms bore holes 5–10 μm in diameter, with a number of characteristic features. (1) The boreholes are infilled with fibrous aragonitic crystals <1 μm in length; these crystals form banded patterns across the boreholes (Fig. 4), indicating
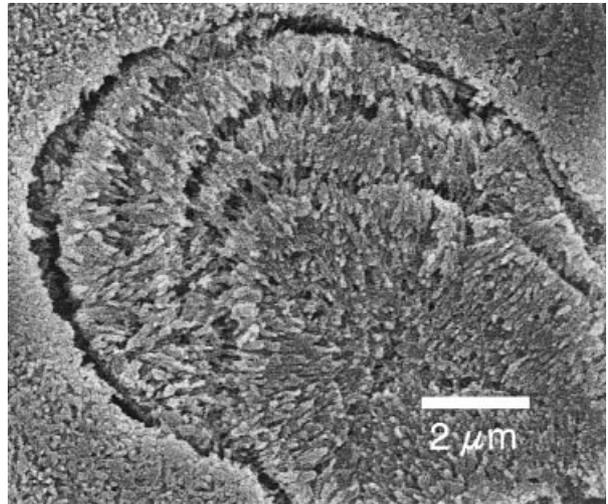

Fig. 4. Scanning electron micrograph of an etched thin section of a micritized grain formed in the laboratory. Detail of a cyanobacterial microboring with concurrent fibrous and banded minimicrite (>1 μm) infill.

that the holes are filled progressively as the endolith bores. (2) The endolith takes great care to preserve original grain boundaries (Fig. 5a); incomplete grain margins and open holes are rare, except for pits at the tops of the uppermost grains in the micritized layers. (3) Boring and filling starts at the outer edges of a grain and eventually penetrates the entire grain; repeated boring of rapidly infilled boreholes progresses to a stage of complex textural patterns, in which it is impossible to detect individual filled borings (Fig. 5b). The result of this microboring activity is the formation of micritized grains that maintain their original surface outlines but, internally, exhibit complex patterns of infillings, which completely destroy and replace original grain textures (Fig. 5). Infilled boreholes also penetrate the micritic crusts, which overlie the micritized grains.

Continued microboring results in a welding or coalescence of micritized grains. This fusion occurs when endoliths cross grain boundaries at lightly cemented point contacts (Fig. 6a). Rapid infilling of boreholes penetrating adjacent grains results in the formation of a rigid framework of micritized grains (Fig. 6b).

Crusts formed during laboratory experiments exhibit many of the same features as those observed in field samples (Fig. 7). During a 2-month period, coccoid cyanobacteria in a 1-mm-diameter inoculum generated progeny that colonized surrounding grains. Grain penetration by these endolithic microbes resulted in the
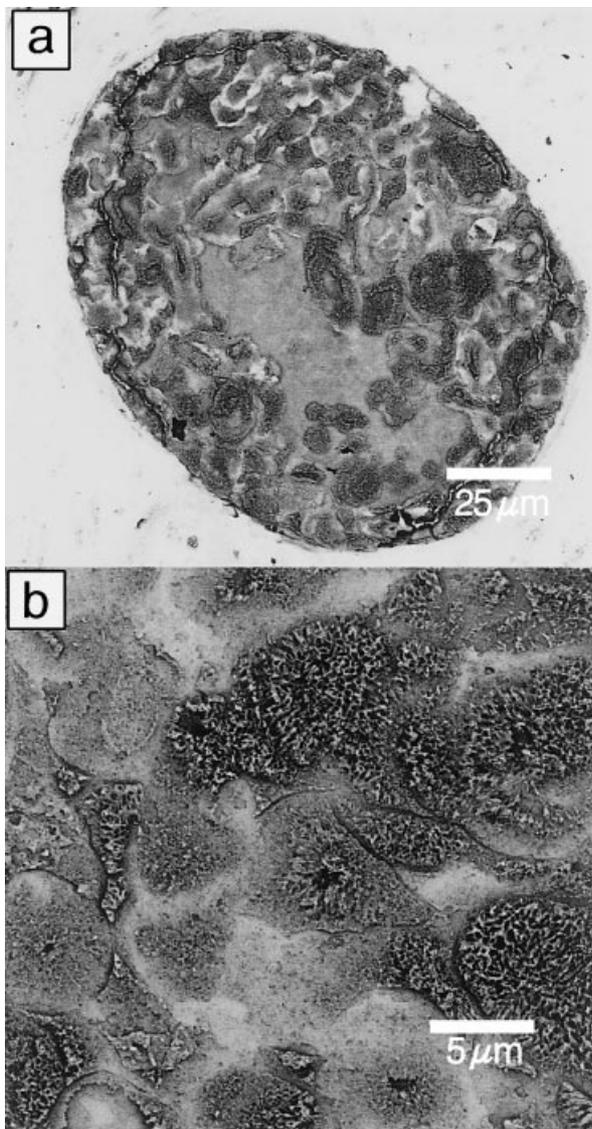
Fig. 5. Scanning electron micrographs of etched thin sections of micritized grains from a Highborne Cay stromatolite showing extensive microboring and concurrent filling of boreholes. (a) This grain is completely microbored except for a small patch in the interior; note that the grain margins are almost completely intact. (b) Higher magnification view showing that multicyclic boring/infilling has completely replaced the original texture of this grain with a fibrous micritic infill.

fusion of loose grains into lithified crusts, one or two grains thick, with diameters of about 2 cm. Virtually no loose grains remained in any of the five replicate plates after the 2-month period. Like the field samples, laboratory-generated crusts consist of extensively microbored, micritized grains that are fused at point contacts by infilled boreholes that cross grain boundaries (Fig. 7). In a few places, thin laminae of micrite were also precipitated above the micritized grains. A feature that differentiates laboratory and field samples is the presence of well-developed acicular rim cements, 1–5 µm in length, which coat grains in the laboratory crusts (Fig. 7).

Based on cell dimensions and distribution patterns, and on observed morphological characteristics of the sheaths, which show distinct banding patterns, the coccoid endolith responsible for crust formation is identified as belonging to the genus *Solentia*, *sensu* Le Campion-Alsumard *et al.* (1996). More detailed studies of the behaviour and ecology of this endolithic organism are in progress.

DISCUSSION

The presence of endolithic microbes in Bahamian stromatolites has been noted in previous studies (Browne, 1993; Reid *et al.*, 1995; Macintyre *et al.*, 1996; Golubic & Browne, 1996; Feldmann, 1997). The major role that these organisms play in the formation of lithified laminae in these structures has, however, not been recognized. Previous discussions of endoliths in Bahamian stromatolites have focused on the destructive bioerosional role of these microbes (e.g. Golubic & Browne, 1996; Golubic *et al.*, 2000). In addition, based on the smooth grain margins and a lack of open boreholes in most of the micritized grains, it has been suggested that micritization in Exuma stromatolites was primarily a result of recrystallization, rather than filled microborings (Reid *et al.*, 1995; Macintyre *et al.*, 1996).

Results from the present study indicate that lithified layers of micritized grains, which provide major structural support for Exuma stromatolites, are formed by endolithic activity. Observations show that oolitic sand grains, which appear light brown in plane polarized light, are micritized by a process of multicyclic boring and concurrent infilling of boreholes by the coccoid cyanobacterium *Solentia* sp.. With advanced stages of multicyclic boring and concurrent filling of boreholes, the original texture of the grains is completely replaced by fibrous aragonite infilling; the result is alteration to a cryptocrystalline grey texture. Grains are welded together as infilled boreholes cross grain boundaries at point contacts. Welded grains form a rigid framework that plays a critical role in stabilizing and protecting stromatolites from erosion. This microboring and infilling activity by *Solentia* sp. appears to flourish only when this photosynthetic organism
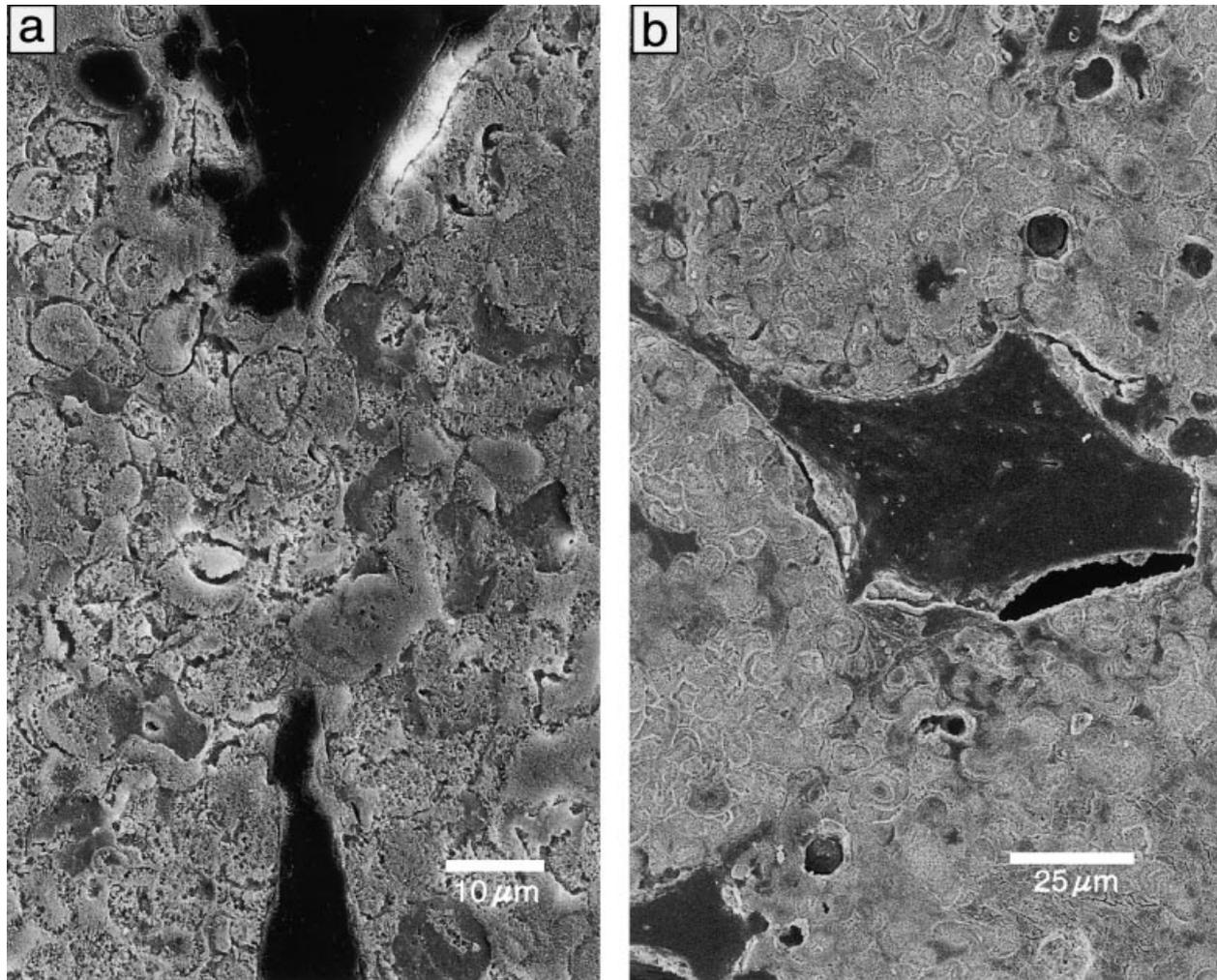
Fig. 6. Scanning electron micrograph of an etched thin section from a Highborne Cay stromatolite showing micritized grains that are welded together at point contacts. (a) Detail of point contact showing how the grains have become welded together during the concurrent filling of microborings by endolithic cyanobacteria as they cross grain boundaries. (b) With the progress of this endolithic cyanobacteria spreading across grain boundaries, a rigid framework of welded grains is formed.

remains at or near the surface of stromatolites when they are not actively accumulating.

The laboratory studies indicate that the microboring activities of the endolithic cyanobacterium *Solentia* sp. can produce lithified crusts of micritized, welded sediment grains within a 2-month period. Moreover, published descriptions of the behaviour of *Solentia* (Le Campion-Alsumard *et al.*, 1996) provide explanations for the characteristic features of these crusts, including the contrast between open pits of the truncated grains at the surfaces of micritized horizons, and the infilled tunnels and well-preserved grain outlines below the surface (Fig. 3). When a colonizing *Solentia* cell settles on a grain surface, it divides into a proximal cell, which remains in an open pit

just below the grain surface, and an apical cell, which penetrates further into the grain. The proximal cell eventually divides many times, producing baeocytes (small reproductive cells) that are released from the open cavities. Meanwhile, the boring apical cells continue to penetrate into the grains, with concomitant production of nested packets of cup-shaped sheaths. Although not reported by Le Campion-Alsumard *et al.* (1996), *Solentia* sheaths left behind by the advancing microborer appear to be active sites of carbonate precipitation. The banded pattern of the fibrous aragonite within the tunnels (Fig. 4) mimics the 1–2 μm crescent-shaped banded pattern of *Solentia* sheaths. The presence of microborings in some of the micrite crusts that overlie
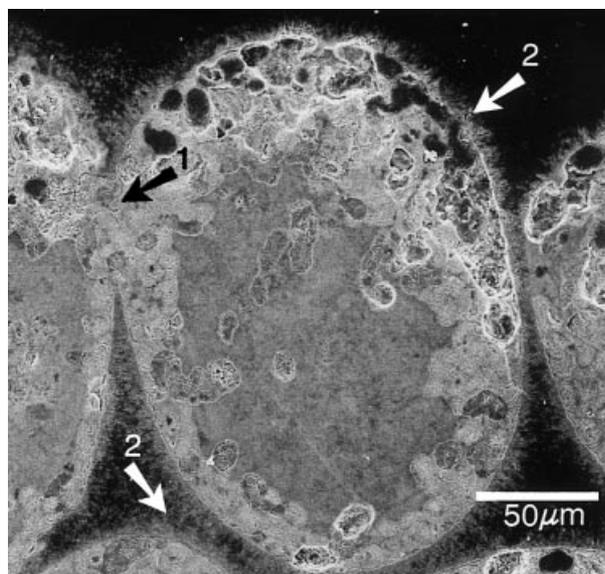
Fig. 7. Scanning electron micrograph of an etched thin section of micritized grains formed in the laboratory. Extensive boring and concurrent filling of boreholes and coalescing of grains at point contacts (arrow 1) are identical to observations seen in the Highborne stromatolites. In contrast, the fibrous aragonite rim cements (arrow 2) were not seen in natural stromatolite samples.

layers of welded micritized grains is evidence that the crust predates microboring activity. Indeed, the concentration of microboring activity in narrow bands below micrite crusts argues that these crusts may act as barriers to the upward migration of baeocytes released by *Solentia*-infested grains in the subsurface.

The well-developed acicular rim cements that formed in the laboratory experiments (Fig. 7), which are not present in field stromatolites, are probably artifacts of the experimental conditions. In contrast to field stromatolites, which have an abundance of *Schizothrix*, the biomass of *Schizothrix* was low to non-existent in the laboratory cultures. It is suspected that the presence of *Schizothrix*-produced organic compounds (calcium-binding exopolymer and organic acids), observed in the field samples, inhibits the formation of rim cements, and experiments are currently being conducted to test this hypothesis. It should be noted that the thin micrite crusts overlying some sand grains in laboratory-generated crust experiments may possibly be artifacts of the experimental conditions. Capillary action in the agar plates, which draws water up between the sediment grains, could have created a locus for precipitation at the air–water interface.

The microboring pattern exhibited by *Solentia* differs significantly from that in classical models

of micritization, which denote precipitation in open boreholes after the death of an endolith and emphasize micritic rims around the edges of microbored grains. Bathurst (1966, 1971) described a process in which endoliths penetrate perpendicular to grain margins, forming incomplete surfaces and finger-like projections leading into the grain interior; these organisms eventually die, leaving empty boreholes that later become infilled with marine cement. Similarly, Alexandersson (1972) stated that no organisms take a direct part in the precipitation of carbonate in boreholes. In contrast, this study has shown that precipitation in *Solentia* microborings is concurrent with endolithic activity and appears to be biologically induced; open boreholes are rare and, although micritization begins at the grain margins, the outer edges of the grains are intact, and grains become totally micritized in a matter of months. Also, Harris *et al.* (1979) observed microborings infilled with aragonite that radiated from the interior of the boreholes in Pleistocene (Florida) and Holocene (Bahamas) ooids, and *Solentia* was identified as one of the endoliths present in these samples. In addition, it has recently been recognized that *Solentia* plays an important role in the micritization of porcelaneous Bahamian foraminifera (Reid & Macintyre, 2000).

Lithification resulting from the welding together of grains caused by endolithic activity is probably not restricted to stromatolites. One possible example in which similar processes might occur is in the formation of 'grapestone' grains, which were first described by Illing (1954) in his classic study of Bahamian sediments. Grapestone aggregates consist of a cluster of grains 'firmly cemented together' (Taylor & Illing, 1969, p. 80) and are 'much bored by endolithic algae and extensively micritized' (Bathurst, 1971, p. 317); both features are typical of welded grains in Highborne stromatolites.

CONCLUSIONS

Well-developed, lithified laminae in Exuma stromatolites are formed by the microboring activity of endolithic cyanobacteria. Microboring of carbonate grains and concurrent infilling of boreholes by *Solentia* sp. are concentrated at specific horizons in the stromatolites. This activity results in the formation of micritized grains that are welded together at point contacts where infilled boreholes cross grain boundaries. These micritized horizons, which develop during a

hiatus in the growth of the stromatolites, form well-indurated layers as the stromatolite accumulates. These layers provide major structural support that helps to preserve the stromatolites from erosion.

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