Modern Marine Stromatolites of Little Darby Island, Exuma Archipelago, Bahamas: Environmental Setting, Accretion Mechanisms and Role of Euendoliths

R. Pamela Reid, Jamie S. Foster, Gudrun Radtke, and Stjepko Golubic

1 Introduction

The search for modern stromatolites was initiated by geologists in an attempt to understand the processes that governed the Earth for about five sixths of the history of Life. Entire land- and seascapes dominated by stromatolites are rare in the modern world of plants and animals. Modern stromatolites were first encountered under extreme environmental conditions, such as the hypersaline ponds of Hamelin Pool, Shark Bay (Logan 1961; Reid et al. 2003). Discovery of stromatolite formation under normal sea water conditions in Schooner Cays and at Lee Stocking Island in the Bahamas (Dravis 1983; Dill et al. 1986) was therefore, of particular significance. These stromatolites grow under peculiar conditions of sand transportation along tidal channels, and accrete primarily through the trapping and binding of sand grains. Similar stromatolites were later encountered at a variety of locations throughout the Exuma Cays (Reid et al. 1995); those in the shallows of a wave-exposed coast at Highborne Cay (Reid et al. 1999, 2000) generated a number of publications dealing with production and decomposition of organic matter, lithification of microbial mats, and successions, interactions and seasonal distribution of microbial communities [reviewed by Stolz et al. (2009)].

R.P. Reid (✉)

Marine Geology and Geophysics, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Cswy, Miami, FL 33149, USA
e-mail: preid@rsmas.miami.edu

J.S. Foster
Department of Microbiology and Cell Science, University of Florida, Gainesville, FL 32611-0700, USA, Space Life Sciences Lab, Kennedy Space Center, Merritt Island, FL 32899, USA

G. Radtke
Hessisches Landesamt für Umwelt und Geologie, Rheingaustr. 186, 65203 Wiesbaden, Germany

S. Golubic
Biological Science Center, Boston University, 5 Cummington Street, Boston, MA 02215, USA
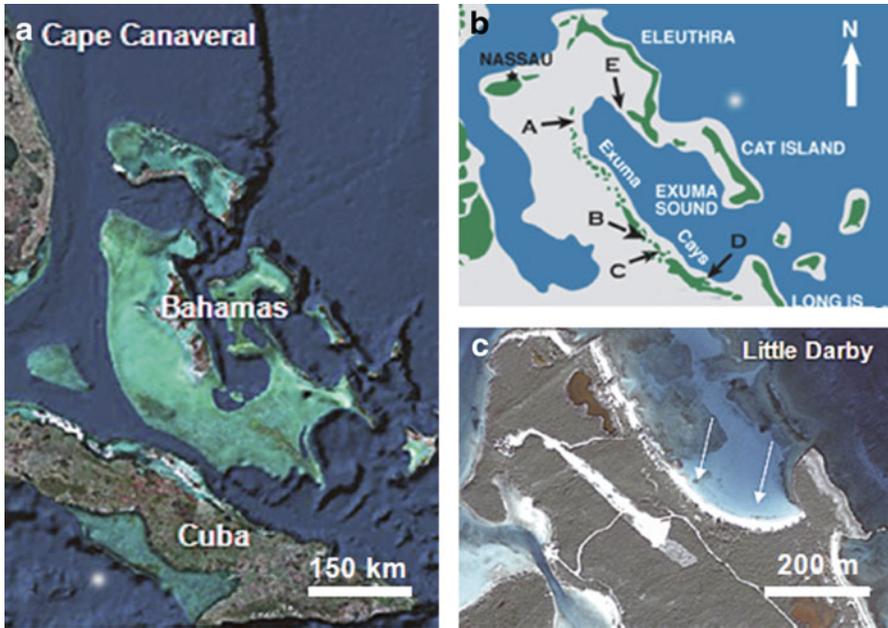
Fig. 1 Geographical location of Little Darby Island and stromatolites. (**a**) Google Earth image of Bahamas platform. (**b**) Diagrammatic map of the location of stromatolites found within the Exuma archipelago. Highborne Cay (A); Little Darby (B); Lee Stocking Island (C); Stocking Island (D); and Schooner Cays (E). (**c**) Google Earth image of the stromatolite beach on the north east coast of Little Darby Island. *Arrows* point to the major clusters of actively accreting stromatolites

In this paper, we present new observations on subtidal stromatolites, in a North-Northeast-exposed sandy bay of Little Darby Island, Exuma Archipelago, Bahamas (Fig. 1). The data, which represent initial results from the first science expedition at the new Little Darby Research Station, focus on the dynamics of stromatolite accretion and the role of euendolithic microorganisms in stromatolite formation.

2 Environmental Setting of Little Darby Stromatolites

Large fields of stromatolitic structures are distributed, parallel to the beach, at a depth ranging from 1 to 2 m (Fig. 2a). Some of these structures are standing alone in the sand; others coalesce into reef complexes (Fig. 2b–f). Sand is transported by the waves, whereby the stromatolites acted as obstacles, which modify the turbulence and sand transport. During the recent study in September 2009, the upper surfaces of many stromatolites, about 30–50 cm above ground were within the range of periodic sand supply during windy days. They were covered by active microbial mats and showed different degrees of induration. Soft microbial mats
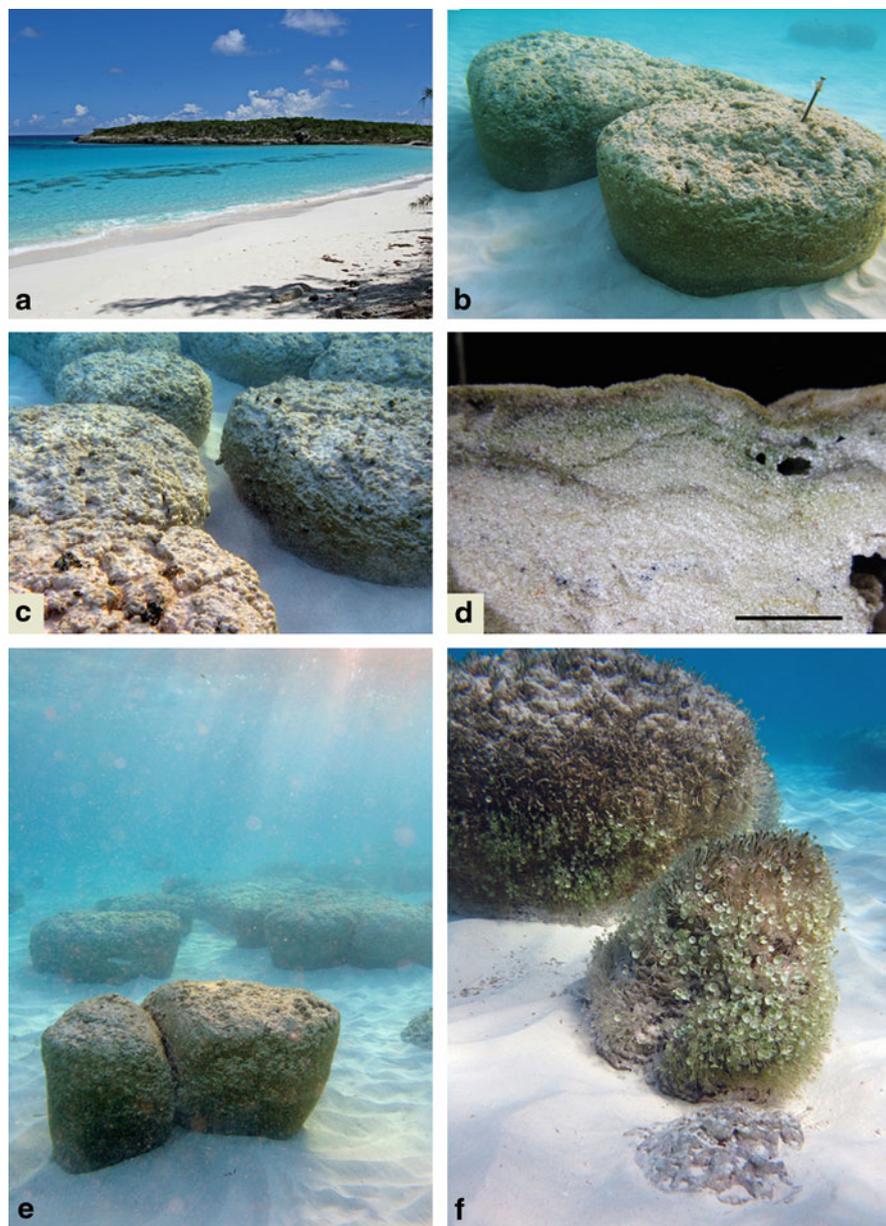
Fig. 2 Stromatolitic structures of the Little Darby Cay, Exuma archipelago, Bahamas. (**a**) The field of subtidal, shallow water stromatolites (*dark areas* in front of the beach). (**b**) Two stromatolites monitored for their accretion rates, note the upward expansion of the structures and zonal coloration of their lateral walls. The nail in upper right is 7 cm long. (**c**) Upper surface of the stromatolites with 5–10 cm diameter domes where active accretion takes place. Stromatolite upper left is 60 cm wide. (**d**) Vertical section through the mat on the upper surface of a stromatolite,

were comprised of sheathed filaments of oscillatoriacean cyanobacteria of the genus *Schizothrix* with incorporated sand grains. These mats, studied earlier at Stocking Island (Reid and Browne 1991), Lee Stocking Island (Browne 1993; Feldmann and Mackenzie 1998) and Highborne Cay (Reid et al. 2000) formed small domal protuberances 1–5 cm in diameter (Fig. 2b, c) on top of Little Darby stromatolites by trapping and binding of sediment particles combined with upward and radial movement of *Schizothrix* trichomes. A vertical section through such protuberances (Fig. 2d) indicated that the vertical accretion of the mat shifts laterally, on a centimeter scale, depending on the combination of local sand supply and cyanobacterial response in movement and growth. During periods of calm weather the accumulation of cyanobacterial biomass produced translucent horizons, which in deeper layers became obscured by sand grain compaction. Lateral shifts in accretion include and slightly favor stromatolite margins, resulting in the gradual widening of the active upper surface, the flat appearance of the stromatolite tops, and the conical outline of stromatolite profiles with overhang side walls. The side walls did not appear to trap significant amounts of sediment; they were covered by different microbial populations than the stromatolite upper surfaces and accordingly were colored differently (Fig. 2e). The bases of these stromatolites were in frequent contact with moving sand ripples, thus exposed to abrasion by moving sands. The surfaces of stromatolites on the more easterly side of the beach were overgrown by macro-algae, predominantly by *Batophora* and *Acetabularia* (Fig. 2f). Other stromatolitic structures in the studied fields were buried in the sand, and some were exposed and colonized by dark colored coating, the black coloration contrasting with the white of the carbonate sand (Fig. 2f, lower right).

3 Accretional Processes in Little Darby Stromatolites

In stromatolites of Little Darby Island, which are similar to those studied at Lee Stocking Island and on Highborne Cay, the accretion takes place within a soft mat along the upward turned surfaces of the stromatolite structures (Fig. 2c). Two components are essential in the process of stromatolite accretion: (a) the presence of the *Schizothrix* mat and (b) the flux of carbonate sand grains supplied by waves or currents. The cyclicity of wind and wave turbulence is marked by pulses in sand supply to the stromatolites and is recorded in fine, mm scale lamination (Fig. 3a).

Fig. 2 (Continued) showing domes of active accretion with a lateral displacement over time. Darker layers comprised of exopolymers of *Schizothrix* mat mark the pauses in sediment supply during calm weather conditions. Scale bar is 1 cm long. (**e**) Groups of stromatolites coalescing into coherent reefs (*background*) with two units showing color zonation on lateral walls. Note the irregular rippling of sand due to interference of wave action around stromatolitic mounds. (**f**) Stromatolites sheltered from sand supply are overgrown by algae. The unit in the center is overgrown mainly by *Batophora* on the top and by *Acetabularia* on its sides. The stromatolitic structure on lower right is re-emerging after having been buried by sand
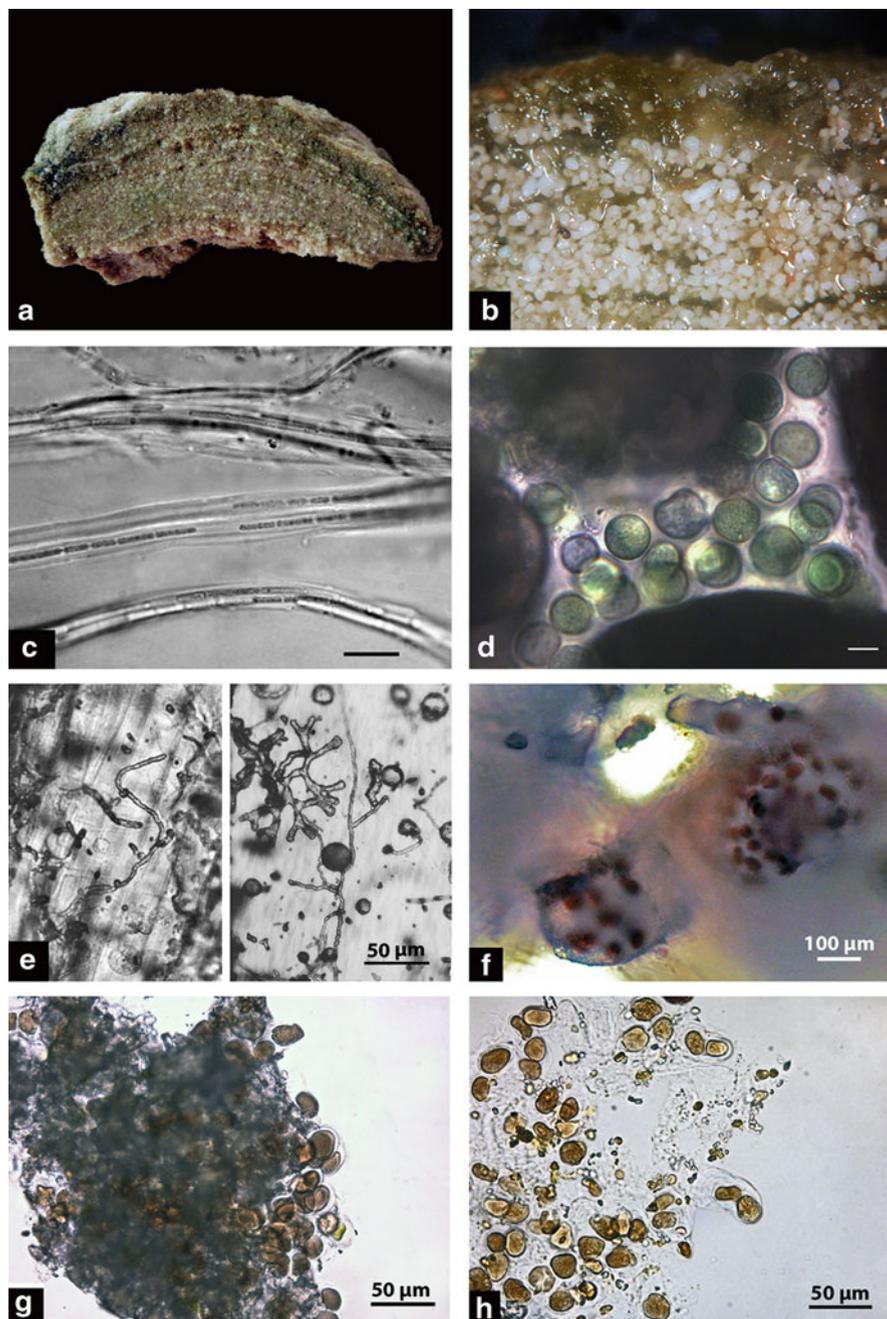
Fig. 3 Early stages in action and solidification of the *Schizothrix* mat responsible for the accretion of stromatolites on Little Darby Cay. (**a**) Section of a domal unit from the upper surface of stromatolites, note the change in the size of entrapped sand grains from layer to layer reflecting the

Gliding trichomes of *Schizothrix*, the primary producer, remain on top of the structure (Fig. 3b) and move upward with stromatolite accretion.

The predominant mat-forming organism is *Schizothrix gebeleinii* (Fig. 3c); with highly motile gliding trichomes bundled inside exopolymer sheaths (see Golubic and Browne 1996). Minor components consist of other rapidly gliding organisms belonging to cyanobacterial genera *Schizothrix*, *Oscillatoria*, *Spirulina* as well as gliding anoxygenic bacteria of the *Chloroflexus*-type. Molecular signatures of this group has been noted in the stromatolites of Highborne Cay (Foster and Green 2010). During times of wave turbulence, sand particles stick to the mat, gradually burying the cyanobacteria. The latter respond by positive phototaxis, gliding out of their sheaths and maintaining maximum biomass on the top of the structure. These young filaments contain single trichomes, which later duplicate by fragmentation and glide next to each other forming bundles in the common sheath (Fig. 3c). The "mature", i.e. multitrichomous filaments form during calm periods when cyanobacterial biomass accumulates without incorporation of sand (Fig. 3b). The principal primary product contributions are exopolymer sheaths of *Schizothrix*, which are left behind several mm deeper in the mat, and become subject to degradation by organotrophic bacteria as shown for the Highborne stromatolites (Decho et al. 2005) which includes anaerobic respiration via sulfate reduction (Baumgartner et al. 2006). Additional primary production occurs in sheltered interstitial spaces between the entrapped grains, which invite secondary settlement and growth of coccoid cyanobacteria of the genus *Aphanocapsa* producing soft EPS embedded colonies (Fig. 3d).

The second component, consisting of entrapped and thus stabilized sand grains have their own biological history. Prior to incorporation into stromatolites, they were part of mobile, shoaling sand dunes with their own interstitial microflora and fauna, and with a substantial contribution by phototrophic euendoliths (Wild et al. 2006; Tribollet et al. 2010). Shoaling ooids and other carbonate sand particles are bored by a specialized assemblage of euendolithic cyanobacteria, which are able to settle and persist in a highly mobile substrate, experiencing profound and rapid changes in availability of light and nutrients. That assemblage is dominated by species of the cyanobacterial genera *Hyella* (Al-Thukair and Golubic 1991a, b; Al-Thukair et al. 1994) and *Cyanosaccus* (Lukas and Golubic 1981). This

Fig. 3 (Continued) coeval wave energies. (**b**) Detail collected during calm weather resulting in accumulation of sand-free Schizothrix biomass. (**c**) *Schizothrix gebeleinii*, dominant organism in the mat. Note the elongated cells and the characteristic presence of more than one trichome bundled within the common sheath of filaments. Scale bar is 10 μm. (**d**) Soft mats of *Aphanocapsa* sp. developing in the interstices between sand grain the entrapped in the mat. Scale bar is 10 μm. (**e**) Microborings found in particles of calcareous sands surrounding stromatolites. Sand particles are bored prior to entrapment into stromatolites. (**f**) Growth burst of the euendolithic cyanobacterium *Solentia sanguinea* in sand grains following entrapment and stabilization. Note that some cells are in focus on the surface of the grains. (**g**) Crushed sand grain from **f** releasing *Solentia*. (**h**) Colony of *Solentia* upon dissolution of entrapped sand grain by dilute HCl

assemblage is very different from euendoliths inhabiting solid substrates, such as coastal limestone and coral reefs (Radtke et al. 1996, 1997b; Radtke and Golubic 2010). Thus, sand particles are pre-bored by the time they are incorporated in the mats (Fig. 3e), but only a minute proportion of those borings are inhabited by live and active euendoliths.

4 Grain Stabilization Results in a Shift in Euendolith Composition

Ecological conditions for euendoliths undergo a major change after the grains are entrapped and stabilized in stromatolitic structures, resulting in a population explosion of *Solentia sanguinea* (Fig. 3f). *Solentia sanguinea* has been earlier isolated in culture from ooid sand grains off the Lee Stocking Island and from the Arabian Gulf, but is exceedingly rare in free sand grains (Golubic et al. 1996). The growth of the organism is apparently stimulated when the substrate is stabilized as by entrapment in stromatolites or in culture on agar. Similar mass development of *Solentia* has been observed in Highborne Cay stromatolites (Reid et al. 2000; Stolz et al. 2009: fig. 4d). In the stromatolites of Little Darby Island, *Solentia* occurred both on the surfaces of the entrapped sand grains, and bored into the grain's interior (Fig. 3g), with cells penetrating at the end of long gelatinous stalks (Fig. 3h). Development of endolithic blooms of *Solentia* coincides with the process of mat lithification.

5 Lithification of Bahamian Stromatolites

Lithification of modern stromatolites is one of the processes that link the genesis of these structures with their historic record. The timing of the process appears essential even for the definition of the stromatolite concept (e.g. Krumbein et al. 2003). Stromatolite-forming microbial mats experience early lithification. Two closely coupled components drive carbonate precipitation within microbial mats: (1) changes in the ion activity product $Ca^{2+} \times CO_3^{2-}$ and (2) the organic matrix in which the minerals nucleate (e.g. Pentecost and Riding 1986; Reitner 1993; Dupraz and Visscher 2005). Activity of CO_3^{2-}, which determines the saturation index of $CaCO_3$ minerals in many natural systems, is affected via pH and alkalinity changes by microbial metabolism, such as photosynthesis or sulfate reduction, and environmental parameters. The organic matrix of extracellular polymeric substances (EPS), which embed the microbial communities, is the physical location where carbonate minerals nucleate and grow. Fresh EPS typically binds cations (e.g. Ca^{2+}), thereby inhibiting CaCO3 precipitation. Precipitation results when degradation of the EPS reduces this inhibition and releases previously bound Ca^{2+}, or by oversaturation of the cation-binding capacity (Braissant et al. 2007). Microbial activity is ultimately responsible for EPS production and degradation leading to mineral precipitation.

In Bahamian marine stromatolites, active accretion by *Schizothrix* mats is punctuated by thin horizons of carbonate precipitates and cemented grain layers, as documented on vertical sections through stromatolites (e.g. Reid et al. 2000: fig. 4). Studies at Highborne Cay indicate that thin micritic crusts form in surface biofilms with abundant heterotrophic bacteria and high rates of sulfate reduction (Visscher et al. 2000; Andres et al. 2006). Precipitation of aragonite within the biofilm forms a micritic lamina, which caps the underlying ooids. The high level of carbonate saturation of the interstitial waters in and around Bahamian stromatolites allows minor changes in pH to trigger precipitation, which makes it difficult to distinguish among, abiotic, biogenic and organogenic causes of calcification. In theory, several microbial metabolic activities operating in actively accreting stromatolites may act as triggers of precipitation. Highborne Cay studies suggest, however, that heterotrophs play a more direct role in crust precipitation than previously assumed (Visscher et al. 2000; Andres et al. 2006).

The cemented grain layers that punctuate *Schizothrix* trapping and binding are characterized by an abundance of *Solentia sanguinea*. *Solentia* tunnels through grains, leaving bore holes filled with EPS. Aragonite precipitation within the EPS results in micritization of the grains and, when tunnels cross between grains, welds the grains together. This process forms a well-cemented layer (Macintyre et al. 2000; Reid and Macintyre 2000; Reid et al. 2000). The crystallization pattern of carbonate precipitate observed in the *Solentia* borings complies with the texture of the EPS stalks of this organism (Reid and Macintyre 2000). The compliance of mineral arrangement with the organic template offered by specific EPS product illustrates the principle of organo-mineralization (Trichet and Défarge 1995; Reitner et al. 1995). Precipitation within the *Solentia* layers indicates that carbonate precipitation may be an integral part of the activity of euendoliths, which dissolve carbonate in the process of boring and re-deposit it elsewhere as suggested by Kobluk and Risk (1977a, b), Schneider and Le Campion-Alsumard (1999) and Garcia-Pichel (2006).

6 Post-accretional Transformations of Stromatolites

The existence of stromatolites as actively growing submarine structures in modern environments is a rarity, and attention typically focuses on accretion. However, as noted above, stromatolitic structures that became sheltered from sand supply enter extended non-accretional periods. At Little Darby Island, these sheltered structures were overgrown by algae, mainly by *Acetabularia* and *Batophora* (Figs. 2f and 4a), becoming practically indistinguishable from any carbonate hardground under the same setting. This observation confirms the importance of sand supply as one of the essential components of stromatolite growth. Although some entrapment of sand grains among the thalli of macroalgae is inevitable, there is no evidence of stromatolite accretion by macroalgae as proposed by Awramik and Riding (1988). Other processes contributing to the diagenetic history of stromatolitic structures include micro- and macroborings and secondary encrustations that may ultimately
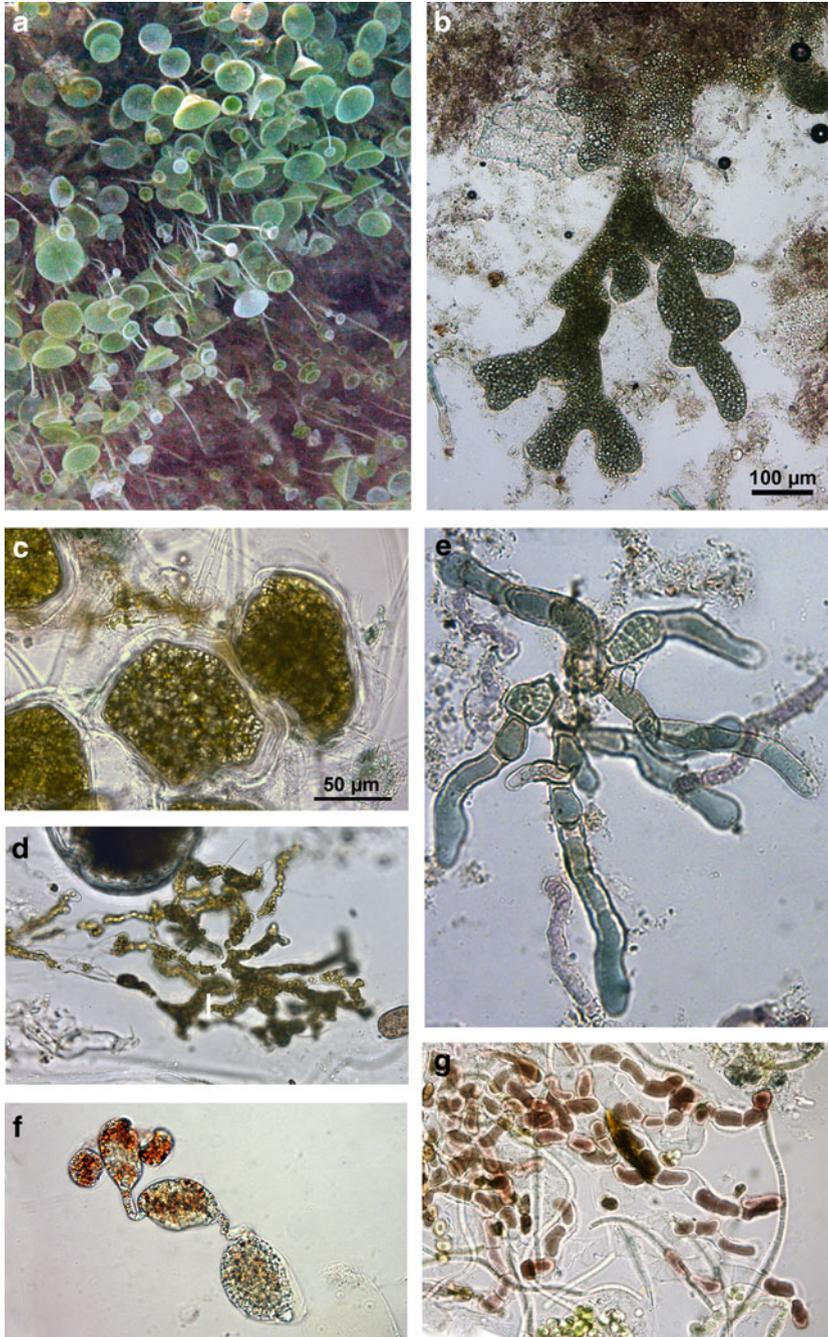
Fig. 4 Assemblages of epi- and endoliths following stases in stromatolite accretion. (**a**) A population of *Acetabularia* overgrowing the side of a stromatolite (detail of Fig. 2f). (**b**) The euendolithic rhizoid of *Acetabularia* in growth position, extracted by acid treatment of the crust.

obscure the original accretional features. Such structural modifications may lead to formation of thrombolitic textures when viewed in section or in outcrop (Planavsky and Ginsburg 2009).

The extended stasis provides new opportunities for the settlements of epi- and endoliths alike, resulting in an increase in diversity and complexity of the resident microboring community apparently at the expense of *Solentia,* which is rarely encountered in these samples. Prominent are algae, including eukaryotic euendoliths, especially *Acetabularia* (Fig. 4a) and its euendolithic rhizoids (Fig. 4b) formerly misidentified as *Ostreobium brabantium* (see Radtke et al. 1997a). The hardened surfaces are often paved by large polygonal chlorophyte cells with chaetae (Fig. 4c), rhizoids of *Batophora oerstedtii*, euendolithic networks of the siphonal chlorophyte *Ostreobium quekettii* (Fig. 4d). Among cyanobacterial euendoliths dominant are various species of *Hyella,* which have not been observed anywhere else (Fig. 4e). In addition, Conchocelis stages of a local marine red alga are occasionally observed (Fig. 4f).

The accretion of every stromatolitic structure observed in the Little Darby field is localized to cm sized areas always on the upward surfaces of the structure. The sides of the stromatolites are stationary and firmly cemented. They are externally coated by different mat types (including *Leptolyngbya* spp.) and, under these mats, harbor a highly diverse community of epilithic and euendolithic phototrophs, an assemblage comparable to that found on structures with extended stasis.

The lower parts of the stromatolite side walls are covered by dark, almost black veneer which is locally abraded, and show patches of white carbonate (Fig. 1f, bottom right). These lower parts of the stromatolites and sometimes the entire structure are occasionally completely covered by sand. The stress imposed by light deprivation and exposure to repeated abrasion by sand prevents the growth of most algae and other epilithic organisms, and exerts selective pressure on euendoliths as well. Under the conditions of sand-erosion pressure and repeated covering and uncovering by sand, the euendolithic assemblage has reduced diversity and may be dominated by *Solentia sanguinea* (Fig. 4g).

7 Dynamics of Stromatolite Formation

The dynamics of microbial mats operate at different spatial and temporal scales. Stromatolite accretion at Highborne Cay results from a cycling between three different mat types on the stromatolite surface, with each subsurface layer representing a former surface mat (Reid et al. 2000). Similar dynamics appear to be important in the stromatolites of Little Darby Island.

Fig. 4 (Continued) (**c**) Puzzle shaped chlorophyte cells with tubular bristles lining the surfaces of the walls. The scale in **c** is valid for **d–g**. (**d**) *Ostreobium quekettii* the most common euendolith under low light conditions. (**e**) *Hyella* sp., probably a new species. (**f**) Conchocelis stage of a bangialean rhodophyte. (**g**) *Solentia sanguinea* in erosion stressed base of a stromatolite

The soft mat is dominated by *Schizothrix*, which is responsible for trapping of sand and a vertical growth of local domes (=Type 1 mat of Reid et al. 2000). In the process, trichomes of *Schizothrix* move to the mat surface leaving significant amounts of their photosynthetic product, their empty EPS sheath behind to bacterial consumers. Both layers moved upward in the process of the accretion of the stromatolitic structure, interrupted by short pauses in sedimentation. These pauses are marked by biofilm development and corresponding precipitation of thin micritic crusts (=Type 2 mats). Extended stasis in stromatolite accretion is accompanied by changes in microbial euendolith composition. The changes feature a population increase of *Solentia* – first in the entrapped sand particles, and later from grain to grain over calcified bridges (=Type 3 mat). During these extended pauses in accretion, the stromatolite hardens. The endolith diversity also increases over time (Stolz et al. 2009) and may involve removal and truncation of bored grains by grazers, together with the resident euendoliths. The resumption of stromatolite accretion starts another cycle in mat development, incorporating the truncated grains as a horizon within the stromatolite (Reid et al. 2000). This cyclicity involves alternation of the accretionary phase with mat types 1, with sorter or longer stationary phases resulting in mat types 2 and 3 respectively. A vertical sequence of this cyclicity is historical and in vertical petrographic section it is evident as a stratigraphic record.

Accretional periods may be interrupted by much longer periods of stasis, which permit profound changes in microbial composition and an overgrowth by algae and animals. Similar interruptions may be caused by burial of stromatolites in the sand. In the deep tidal channels of the Lee Stocking Island, where sand moves passing stromatolites in massive dunes, both burial and deprivation of sediment supply tend to occur cyclically, leaving accretion as limited "windows of opportunity" (Golubic and Browne 1996; Seong-Joo Lee et al. 2000). In the case of Little Darby, local sheltering of some stromatolites from sediment supply can result in long periods of stasis with algal overgrowth, whereas burial of stromatolites may take place during major storms.

References

Al-Thukair AA, Golubic S (1991a) Five new *Hyella* species from the Arabian Gulf. Algological Studies 64:167–197

Al-Thukair AA, Golubic S (1991b) New endolithic cyanobacteria from the Arabian Gulf. I. *Hyella immanis* sp. nov. Journal of Phycology 27:766–780

Al-Thukair AA, Golubic S, Rosen G (1994) New euendolithic cyanobacteria from the Bahama Bank and the Arabian Gulf: *Hyella racemus* sp. nov. Journal of Phycology 30:764–769

Andres MS, Sumner DY, Reid RP, Swart PK (2006) Isotopic fingerprints of microbial respiration in aragonite from Bahamian stromatolites. Geology 34:973–976

Awramik SM, Riding R (1988) Role of algal eukaryotes in subtidal columnar stromatolite formation. Proceedings of the National Academy of Sciences of the United States of America 85:1327–1329

Baumgartner LK, Reid RP, Dupraz C, Decho AW, Buckley DH, Spear JR, Przekop KM, Visscher PT (2006) Sulfate reducing bacteria in microbial mats: Changing paradigms, new discoveries. Sedimentary Geology 185:131–145

Braissant O, Decho AW, Dupraz C, Glunk C, Przekop KM, Visscher PT (2007) Exopolymeric substances of sulfate-reducing bacteria: Interactions with calcium at alkaline pH and implication for formation of carbonate minerals. Geobiology 5:401–411

Browne KM (1993) Lamination in Recent Bahamian Subtidal Stromatolites: Origin and Lithification. Unpublished PhD dissertation, University of Miami, Coral Gables, pp 296

Decho AW, Visscher PT, Reid RP (2005) Production and cycling of natural microbial exopolymers (EPS) within a marine stromatolite. Palaeogeography, Palaeoclimatology, Palaeoecology 219:71–86

Dill RF, Shinn EA, Jones AT, Kelly K, Steinin RP (1986) Giant subtidal stromatolites forming in normal saline waters. Nature 324:55–58

Dravis JJ (1983) Hardened subtidal stromatolites, Bahamas. Science 219:385–386

Dupraz C, Visscher PT (2005) Microbial lithification in marine stromatolites and hypersaline mats. Trends in Microbiology 13:429–438

Feldmann M, Mackenzie J (1998) Stromatolite thrombolite association in a modern environment, Lee Stocking Island, Bahamas. Palaios 13:201–212

Foster JS, Green SJ (2010) Microbial diversity in modern marine stromatolites. In: Tewari V (ed) Cellular Origin, Life in Extreme Habitats and Astrobiology: Stromatolites. Springer, Berlin, in press

Garcia-Pichel F (2006) Plausible mechanisms for the boring on carbonates by microbial autotrophs. Sedimentary Geology 185:205–213

Golubic S, Browne KM (1996) *Schizothrix gebeleinii* sp. nov. builds subtidal stromatolites, Lee Stocking Island, Bahamas. Algological Studies 83:273–290

Golubic S, Al-Thukair AA, Gektidis M (1996) New endolithic cyanobacteria from the Arabian Gulf and the Bahama Bank: *Solentia sanguinea* sp. nov. Algological Studies 83:291–301

Kobluk DR, Risk MJ (1977a) Micritization and carbonate-grain binding by endolithic algae. American Association of Petroleum Geologist Bulletin 61:1069–1082

Kobluk DR, Risk MJ (1977b) Calcification of exposed filaments of endolithic algae, micrite envelope formation and sediment production. Journal of Sedimentary Petrology 47:517–528

Krumbein WE, Brehm U, Gorbushina AA, Levit G, Palinska KA (2003) Biofilm, biodictyon and biomat – biolaminites, ooolites, stromatolithes – geophysiology, global mechanism and parahistology. In: Krumbein WE, Paterson DM, Zavarzin GA (eds) Fossil and Recent Biofilms. Kluwer Acad Publ, Dordrecht, pp 1–27

Logan BW (1961) Cryptozoon and associate stromatolites from the Recent, Shark Bay, Western Australia. Journal of Geology 69:517–533

Lukas KJ, Golubic S (1981) New endolithic cyanophytes from the North Atlantic Ocean: I. *Cyanosaccus piriformis* gen. et sp. nov. Jounral of Phycology 17:224–229

Macintyre IG, Prufert-Bebout L, Reid RP (2000) The role of endolithic cyanobacteria in the formation of lithified laminae in Bahamian stromatolites. Sedimentology 47:915–921

Pentecost A, Riding R (1986) Calcification in cyanobacteria. In: Leadbeater BSC, Riding R (eds) Biomineralization of lower plants and animals. SAS 30, Clarendon, Oxford, pp 73–90

Planavsky N, Ginsburg RN (2009) Taphonomy of modern marine Bahamian microbialites. Palaios 24:5–17

Radtke G, Golubic S (2010) Microbial euendolithic assemblages and microborings in intertidal and shallow marine habitats: insight in cyanobacterial speciation. In: Reitner J, Queric, N-V, Arp G (eds) Advances in Stromatolite Geobiology. Lecture Notes in Earth Sciences 131, Springer, Berlin, pp 213–241

Radtke G, Le Campion-Alsumard T, Golubic S (1996) Microbial assemblages of the bioerosional "notch" along tropical limestone coasts. Algological Studies 83:469–482

Radtke G, Gektidis M, Golubic S, Hofmann K, Kiene WE, Le Campion-Alsumard T (1997a) The identity of an endolithic alga: *Ostreobium brabantium* Weber-van Bosse is recognized as carbonate-penetrating rhizoids of *Acetabularia* (Chlorophyta, Dasycladales). Courier Forschungsinstitut Senckenberg 201:341–347

Radtke G, Le Campion-Alsumard T, Golubic S (1997b) Microbial assemblages involved in tropical coastal bioerosion: An Atlantic-Pacific comparison. Proceedings of the 8th International Coral Reef Symposium 2:1825–1830

Reid RP, Browne KM (1991) Intertidal stromatolites in a fringing Holocene reef complex, Bahamas. Geology 19:15–18

Reid RP, Macintyre (2000) Microboring versus recrystallization: Further insight into the micritization process. Journal of Sedimentary Research 70:24–28

Reid RP, Macintyre IG, Steneck RS, Browne KM, Miller TE (1995) Stromatolites in the Exuma Cays, Bahamas: Uncommonly common. Facies 33:1–18

Reid RP, Macintyre IG, Steneck RS (1999) A microbialite/algal ridge fringing reef complex, Highborne Cay, Bahamas. Atoll Research Bulletin 466:1–18

Reid RP, Visscher PT, Decho AW, Stolz JF, Bebout BM, Dupraz CP, Macintyre IG, Paerl HW, Pinckney JL, Prufert-Bebout L, Steppe TF, DesMarais DJ (2000) The role of microbes in accretion, lamination and early lithification of modern marine stromatolites. Nature 406:989–992

Reid RP, James NP, Macintyre IG, Dupraz CP, Burne RV (2003) Shark Bay stromatolites: Microfabrics and reinterpretation of origins. Facies 49:45–53

Reitner J (1993) Modern cryptic microbialite/metazoan facies from Lizard Island (Great Barrier Reef, Australia) – Formation and concepts. Facies 29:3–40

Reitner J, Gautret P, Marin F, Neuweiler F (1995) Automicrites in a modern microbialite – Formation model via organic matrices (Lizard Island, Great Barrier Reef, Australia). Bulletin de l´Institut océanographique Monaco 14(2):237–263

Schneider J, Le Campion-Alsumard T (1999) Construction and destruction of carbonates by marine and freshwater cyanobacteria. European Journal of Phycology 34:417–426

Seong-Joo Lee, Browne KM, Golubic S (2000) On stromatolite lamination. In: Riding R, Awramik SM (eds) Microbial sediments. Springer, Berlin, pp 16–24

Stolz JF, Reid RP, Visscher PT, Decho AW, Norman RS, Aspden RJ, Bowlin EM, Franks J, Foster JS, Paterson DM, Przekop KM, Underwood GJC, Prufert-Bebout L (2009) The microbial communities of the modern marine stromatolites at Highborn Cay, Bahamas. Atoll Research Bulletin 567:1–29

Tribollet A, Golubic S, Radtke G, Reitner J (2010) On Microbiocorrosion. In: Reitner J, Queric, N-V, Arp G (eds) Advances in Stromatolite Geobiology. Lecture Notes in Earth Sciences 131, Springer, Berlin, pp 243–253

Trichet J, Défarge C (1995) Non-biologically supported organomineralization. Bulletin de l´ Institut océanographique Monaco Spec 14:203–236

Visscher PT, Reid RP, Bebout BM (2000) Microscale observations of sulfate reduction: Correlation of microbial activity with lithified micritic laminae in modern marine stromatolites. Geology 28: 919–922

Wild C, Laforsch C, Huettel M. (2006) Detection and enumeration of microbial cells within highly porous calcareous reef sands. Marine and Freshwater Research 57:415–420