

# Bahamian giant stromatolites: microbial composition of surface mats

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**Abstract** – Subtidal columnar stromatolites up to 2.5 m high near Lee Stocking Island in the Exuma Cays, Bahamas, have surface mats approximately equally composed of algae and cyanobacteria. The stromatolites are composed of fine-medium ooid and peloid sand. This sediment is supplied to the growing stromatolite surfaces by strong tidal currents which lift grains into suspension and sweep migrating dunes over the columns. The algae include an unidentified filamentous chlorophyte, and numerous diatom species mostly belonging to *Mastogloia*, *Nitzschia* and *Navicula*. The dominant cyanobacteria are two oscillatoriacean species, both probably belonging to *Schizothrix*. Trapping of sediment is mainly effected by the unidentified chlorophyte which is veneered by epiphytic diatoms. Grains are bound into a mucilaginous mat composed of diatoms and cyanobacteria. Cyanobacteria alone would not be able to trap and bind coarse sediment so effectively in this environment. In being coarse-grained and having a significant eualgal component to their mats, these stromatolites are similar to subtidal columnar stromatolites at Shark Bay, Western Australia. The Lee Stocking stromatolites are physically stressed by high velocity tidal currents and mobile sediment. The Shark Bay stromatolites are stressed by hypersalinity. In both cases stress deters grazers, encrusters and bioeroders. These coarse-grained eualgal stromatolites contrast with micritic and predominantly prokaryotic stromatolites of most Recent marine environments, and are not analogues for most pre-Phanerozoic stromatolites. They appear to be a response to changing stromatolitic mat components in the Cenozoic.

## 1. Introduction

Examples of modern marine subtidal stromatolites at Shark Bay, Western Australia (Logan, Hoffman & Gebelein, 1974; Playford & Cockbain, 1976), together with those discovered in the Bahamas (Dravis, 1983; Dill *et al.* 1986; Shinn, 1987), have attracted attention as potential analogues for pre-Phanerozoic stromatolites (Logan, 1961; Dill *et al.* 1986). The subtidal Shark Bay columns, however, possess coarser grain size (0.5–2.0 mm) and poorer lamination than most Proterozoic (for example see Bertrand-Sarfati & Moussine-Pouchkine, 1985) and Archaean stromatolites, and this difference may be due to the presence of an important algal component in addition to cyanobacteria in their surface mats (Awramik & Riding, 1988). The size of grains trapped by stromatolites depends not only on sediment availability and fluid dynamics, but also on the size and phenotypic characteristics of the organisms that build the mat.

The subtidal columnar stromatolites in the Bahamas are composed of coarse-grained sediment (0.1–2 mm) (Dravis, 1983; Dill *et al.* 1986; Shinn, 1987), and are

also known to have mats containing algae in addition to cyanobacteria (J. A. West *in* Awramik & Riding, 1988, p. 1328). Here we report details of mat composition in the ‘giant’ Lee Stocking stromatolites and show that algae constitute approximately one-half the volume of microbes in surface mats studied. An as yet unidentified filamentous chlorophyte 50–70  $\mu\text{m}$  in diameter, together with diatoms which produce copious mucilage, appear to be the major microbes responsible for stromatolite construction by trapping coarse grains.

The importance of algae and the coarseness of the sediment support the view that modern subtidal columnar stromatolites like those forming in the Bahamas and Shark Bay are distinct from the fine-grained, well-laminated, prokaryote-dominated stromatolites widespread in many Recent carbonate tidal flat environments, and also are distinct from most Proterozoic stromatolites (Awramik & Riding, 1988). This challenges the widely held view (Logan, 1961; Dill *et al.* 1986) that Bahamian and Shark Bay examples are general analogues for pre-Phanerozoic columnar stromatolites, and it suggests that the

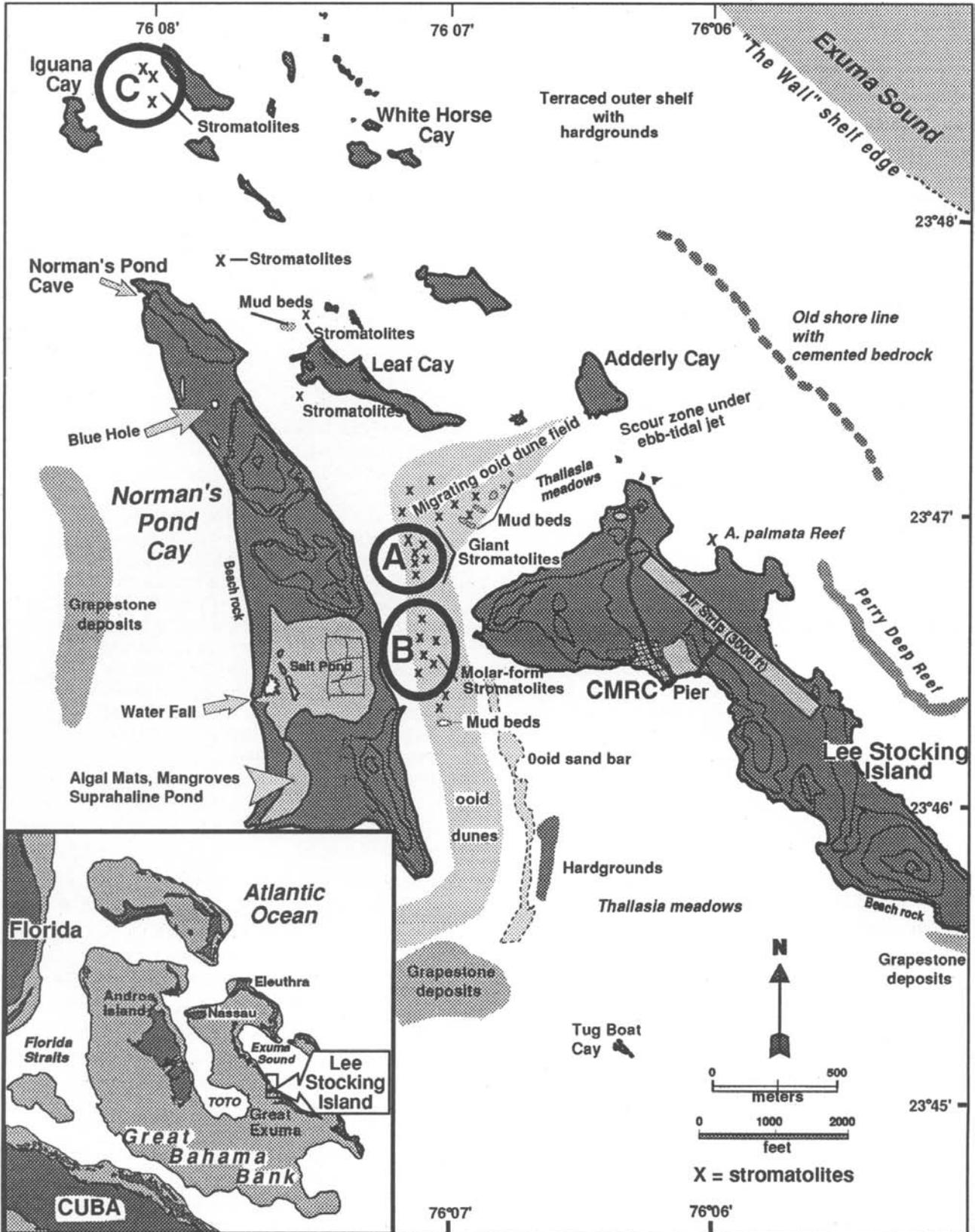


Figure 1. Location map showing sample sites. Sites A and B are in Mail Boat Channel. Site C is in Iguana Cay Cut.



Figure 2. Steep-sided columnar stromatolites, site A, Mail Boat Channel.

microbial community responsible for these Recent coarse-grained stromatolites is of relatively young geological age.

## 2. Depositional setting and samples

Near Lee Stocking Island (Fig. 1), columnar stromatolites up to 2.5 m high (Fig. 2) occur associated with subtidal ooid sand dunes in inter-island channels. Tidal currents up to  $150 \text{ cm sec}^{-1}$  sweep in and out of the channels three hours out of every six (Dill *et al.* 1986; Dill, Kendall & Shinn, 1989). Salinity varies between 37.9 ppt during flood tide to over 40.0 ppt during ebb tide (September 1987). In order to study the variability of the sediment and micro-organisms in the microbial mats, we collected a total of 19 mat samples from the tops and sides of 8 columnar stromatolites at three sites in mid-September 1987 (Fig. 1). Sites A and B (at depths of 7 m and 8 m respectively) are in the main channel northwest of Lee Stocking Island (Adderly Cut, also known as Mail Boat Channel), and site C (6.5 m depth) is 2 km to the northwest in Iguana Cay Cut (Fig. 1).

The outer, unolithified portions of the mats (up to 8 mm thick) were collected, stored in sea-water, kept cool, and examined within two days of collection at the Caribbean Marine Research Center (CMRC) on Lee Stocking Island. Preliminary identifications and relative abundance data for microbial components were

based on visual estimates of wet mounts determined with both dissecting and compound microscopes. Aliquots were preserved in a 3% formalin-filtered seawater solution and later re-examined for sediment and microbe composition. Sedimentary characteristics of the microbial mats and channel sand were determined by standard sieving techniques and observation under a binocular microscope. The outermost portions of the mats were investigated in this manner because this part contains the microbial community that trapped and bound the sediment and thus caused stromatolite growth.

## 3. Sedimentology

The grains trapped within the mats are almost exclusively ooids and peloids, with few skeletal fragments. The grains range in size from 0.1 to 2.0 mm and are predominantly fine-medium sand with an average size of  $270 \mu\text{m}$  (eighteen sieved samples). The sediment of the mats is of the same composition as the loose sediment deposited between the columns at all three sites (K. M. Griffin, unpub. M.Sc. thesis, Univ. California, Santa Barbara, 1988). Sediment on the stromatolite surfaces contains 20–33% more fine-grained material than sediment from the channels. The tops of the stromatolites contain approximately 10% more fine-grained sediment than the sides of the columns (Fig. 3).

## Sediment accreted by stromatolites vs. channel sand

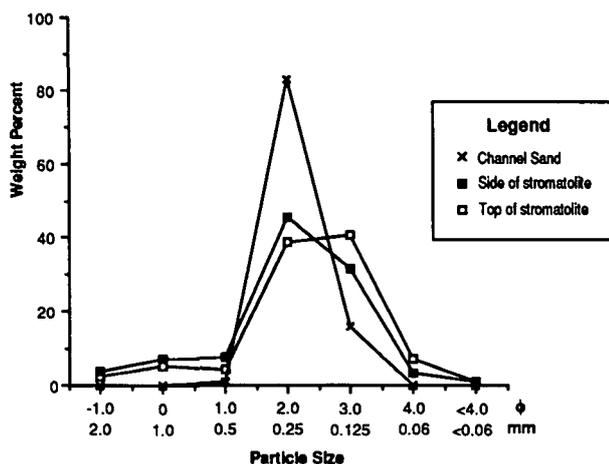


Figure 3. Sediment particle-size distribution of tops and sides of stromatolites and of the channel sands from sites A and B, measured as weight percent from 18 sieved samples.

#### 4. Component organisms

The surfaces of the stromatolites are colonized by a variety of organisms. The macroalgae *Batophora* (Chlorophyta), *Sargassum* (Phaeophyta), and *Laurencia* and *Polysiphonia* (Rhodophyta) are locally conspicuous. *Acetabularia* (Chlorophyta), which is common earlier in the summer, was not abundant when the stromatolites were sampled in September 1987. In some samples from surfaces that have been subject to erosion, the carbonate-encrusted rhizoidal systems of the unidentified siphonaceous chlorophyte are exposed. Colonial hydrozoans, sponges, corals (*Siderastrea*), and calcareous tube worms also live on the stromatolites but do not constitute a significant part of them. In the few slabbed columns studied, worm tubes were found but no corals were observed. Large conchs (*Strombus gigas*) localized in troughs between dunes often form the basal nuclei of stromatolites in the outer part of the channel. One conch has been dated using  $^{14}\text{C}$  and has an age of 480 a B.P. (Dill *et al.* 1986).

The dominant organisms constituting the mats are microscopic algae and cyanobacteria. Three components of this microbiota are present and are frequently mutually associated. These are:

(1) An unidentified filamentous branched chlorophyte (Fig. 4), commonly 50–70  $\mu\text{m}$  (but up to 270  $\mu\text{m}$ ) in diameter), forms a dense felt of recumbent and erect filaments, some of which extend up to 1 cm above the mat surface.

(2) The dominant cyanobacteria are two oscillatoriaceans with well-defined sheaths. One (a *Schizothrix* species) has trichomes averaging 1.5  $\mu\text{m}$  in diameter, and the other (probably also *Schizothrix*) has trichomes up to 7  $\mu\text{m}$  in diameter (Fig. 5). On the tops of columns, and at the mat surface, trichomes are

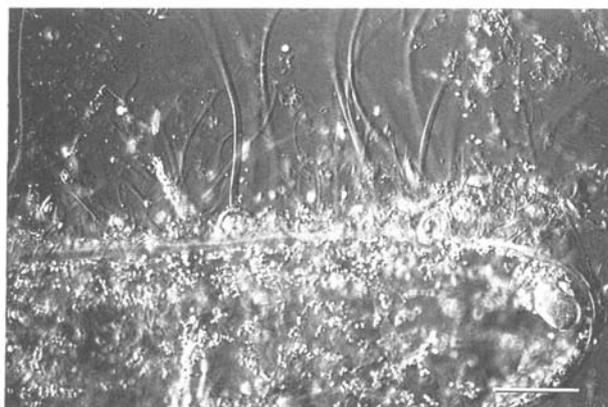


Figure 4. Unidentified filamentous chlorophyte with epiphytic stalked diatoms. Bar scale = 20  $\mu\text{m}$ .



Figure 5. Pink-coloured, relatively large, oscillatoriacean of the mat on the side of a stromatolite column. Bar scale = 10  $\mu\text{m}$ .

blue-green, while at depth ( $\geq 1$  mm) within the mat the trichomes of the larger form are commonly pink. On the sides of stromatolite columns they give a pink colour to the surface mats. These cyanobacteria occur tangled around ooids, epiphytic on the filamentous chlorophyte, and intimately associated with benthic diatoms in gelatinous masses.

(3) Diverse benthic diatoms, commonly associated with the oscillatoriaceans, appear as golden-brown patches among the white ooids. Many are epiphytic on the chlorophyte filaments (Fig. 4), and are attached to the ooids and larger algae by means of mucilaginous secretions in the form of envelopes, strands, stalks, and tubes. Motile forms glide freely over the surfaces of stabilized ooids leaving behind slime trails which aid in binding the ooids. The average number of diatom species present in any sample is 50. *Mastogloia* is the most well-represented genus with 10 species being common, followed by *Nitzschia* and *Navicula*, each with about six species. Individual diatoms range in size from small (4  $\times$  8  $\mu\text{m}$ ) to long and slender (4  $\times$  200  $\mu\text{m}$ ). There are no obvious differences between

the diatom populations on the tops and sides of the stromatolites. Population differences do exist, however, in their preferred microhabitat. Cryptic species are concentrated in pockets and interstices of the bound ooid surface and other species project into the current by means of long stalks and tubes.

Additional common microbial components are other filamentous cyanobacteria (forms resembling *Calothrix*, *Microcoleus*, and *Scytonema*), coccoid cyanobacteria including *Gomphosphaeria* and *Coelosphaerium*, coccoid and colonial chrysophytes, and filamentous chlorophytes and rhodophytes. Protists include flagellate and testate protozoans. Microscopic animals in the microbial community include harpacticoid copepods, spionid polychaetes, cladocerans, nemerteans, nematodes, ostracodes, polyps of hydroids, encrusting bryozoans, and at least two species of sponge.

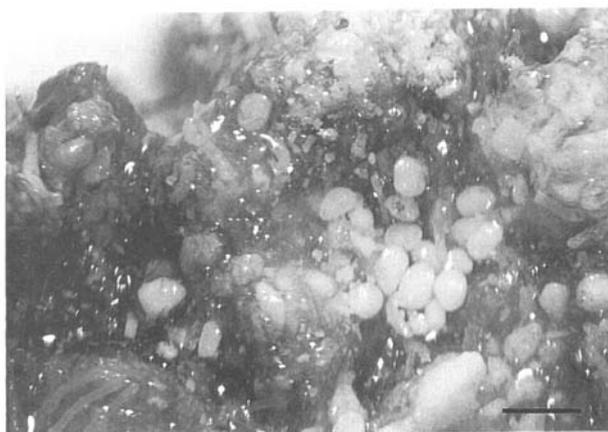


Figure 6. Gelatinous matrix with ooid sand from lower storey of the mat. Bar scale = 200  $\mu\text{m}$ .

Microbial components of surface mats on Lee Stocking Island stromatolites

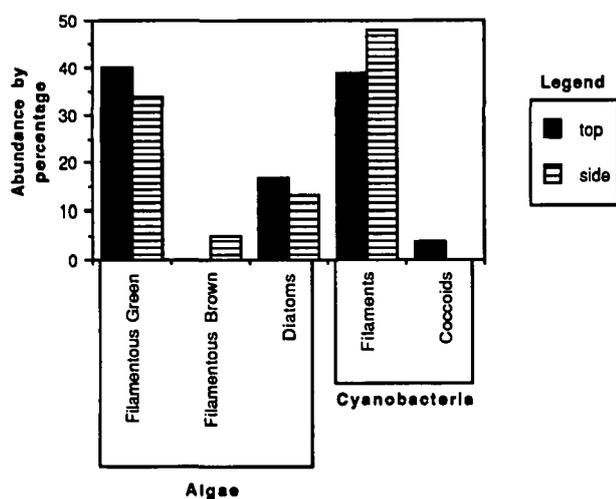


Figure 7. Abundance of microbial components of the surface mats. Percentages calculated from 18 samples collected September 1987.

## 5. Sediment accretion and mat structure

Sediment accretion on the stromatolite surfaces is effected by baffling, caused by the erect growth of the filamentous chlorophyte, which traps grains which then adhere to and are bound into mats by the mucilaginous diatoms and cyanobacteria. The microbial mat can be divided into a two-storey system. The unidentified chlorophyte is, individually, the largest organism in the mat and also the principal sediment trapping agent. Relatively large size and erect growth habit of the chlorophyte are important in determining the structure of the mat. It is rooted in a gelatinous mass of diatoms and cyanobacteria, forming the lower storey, while its erect filaments form an upper storey projecting up to 10 mm above the main microbial mat surface. In the lower storey the filaments and grains provide stable substrate for colonization by epiphytic diatoms and cyanobacteria which form a dense mucilaginous mat (Fig. 6). The chlorophyte filaments create a relatively non-turbulent microenvironment and act as a baffle with the result that sediment is trapped between them. The surfaces of these sand grains are then colonized by benthic diatoms and cyanobacteria and are tightly bound into the lower storey of the mat (Fig. 6). In the upper storey, the same microbial components are present; however, the processes involved are different. The surfaces of the chlorophyte filaments are colonized by benthic diatoms and cyanobacteria (Fig. 4). These epiphytes (which excrete mucilage) appear to trap and bind sediment directly from the water column. The upper storey, therefore, does not form a real mat and the amount of sediment trapped in the upper storey appears to be less than that collecting in the lower storey at the base of the chlorophyte filaments. We have not observed any size differences between the sediment of the upper and lower storeys. Although the microbiotas from the two levels are superficially similar, the lower storey may contain more mucilage-rich coccoid cyanobacteria and the diatoms here may produce more gel. It is possible to recognize a third (and uppermost) storey where colonial hydrozoans, chlorophytes (the unidentified form and others), and rhodophytes produce even higher relief than the aforementioned upper storey. These erect organisms probably assist trapping by baffling sediment which is later bound by the diatoms and bacteria.

The microbial mats from the sides and tops of the stromatolite columns were studied in order to determine if there were any substantial differences that might help to explain the high synoptic profile of the columns. Slight differences in the microbial components (Fig. 7) and sediment (Fig. 3) were detected between the tops and sides. These presumably relate to variation in physical factors such as exposure to currents, substrate orientation, and light intensity. They do not appear to be sufficiently different to

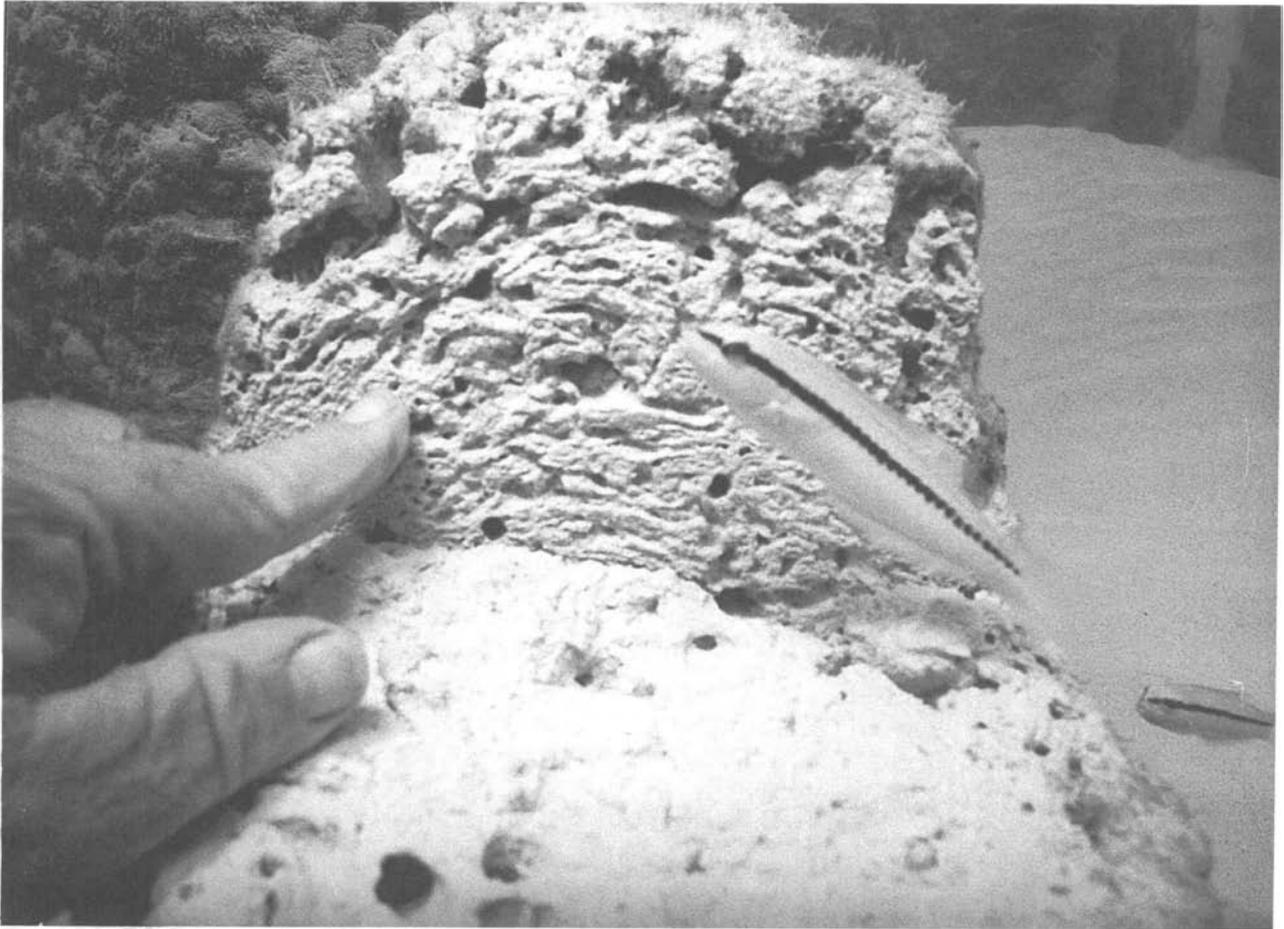


Figure 8. Sawn section of the upper part of the narrow stromatolite column facing the diver in Figure 2. Lamination is conspicuous, but crude. It appears to be non-enveloping. Note the filamentous mat on the uppermost surface, and the presence of internal borings.

explain the morphology of the tall, near vertical-sided, columns (Fig. 2). The columnar forms of some Shark Bay stromatolites can be explained by the scouring of column bases by waves (Logan, Hoffman & Gebelein, 1974) and this commonly leads to bulbous shapes. Bulbous shapes, although well represented in the population of Lee Stocking stromatolites, do not dominate. More commonly, stromatolites have vertical and near-vertical sides (Fig. 2). Domical forms are also common. Where bases of columns are exposed, scouring has occurred and the bases are narrower than the upper parts of columns (Fig. 2). Lamination can be observed on vertical sawn surfaces; it is distinctly developed but the laminae are thick (millimetric scale) and laterally discontinuous (Fig. 8).

## 6. Discussion

The construction of steep-sided columnar stromatolites with high synoptic profile off Lee Stocking island appears to be due in great part to the strong tidal currents which can lift sediment high into the water column and onto the tops of columns, or by the associated dune systems migrating over and burying

them. Cover and re-exposure of individual columns by dune migration takes place over a period of approximately four months (Dill, Kendall & Shinn, 1989). A feature observed in areas of the most active currents is the development of a girdle of younger stromatolites around the bases of some larger stromatolites. These younger stromatolites are less cemented and crumble easily in the hand. Sloping shingle-like protrusions are also present on the flood-current side of large stromatolites. These features grow away from the main core of the column and contain what appear to be crustose coralline algae. These protrusions have not been studied in sufficient detail to determine their origin or the microbial community forming them, although they are common on the larger stromatolite columns.

The dunes that migrate back and forth across the stromatolite fields provide both sediment for accretion and stress to inhibit competitors (Dravis, 1983; Dill *et al.* 1986; Dill, Kendall & Shinn, 1989). Preliminary observations indicate that the composition of the mat varies seasonally and that it is influenced by the time of year when the stromatolite surface is re-exposed by migration of the dune field. The presence of a uniform

level to the tops of the mature stromatolites (Dill *et al.* 1986; Dill, Kendall & Shinn, 1989; Shinn, 1987; K. M. Griffin, Unpub. M.Sc. thesis, Univ. California, Santa Barbara, 1988) and the coincidence between this and the height of the dune crests, suggest that the dune crests determine the growth height of the stromatolites. This can also be related to sediment availability. In areas where the dunes are starved for sediment, they are much lower and their crests farther apart. In these areas the stromatolites are small and, instead of occurring as large individual columns, they often coalesce laterally as 'molar form' (K. M. Griffin, unpub. M.Sc. thesis, Univ. California, Santa Barbara, 1988) stromatolites. Strong currents with suspended sediment also create stress which regulates the benthic grazing organisms and inhibits bioerosion and encrustation by macro-organisms (Dravis, 1983). Nevertheless, there are grazers (fish (Fig. 8), gastropods, worms) which feed on the microbial mats during slack water. This lasts for at least 40 minutes at each change of the tide. These grazing effects have not been quantified or studied in sufficient detail to determine how they modify the columns. Cross-sections of the stromatolites show that they are commonly burrowed and bored by pholads, worms, and other invertebrates (Fig. 8). The borings are cross-cutting and filled with micritic marine cements. The stromatolites are geologically young features, having grown in this Bahamian region only since the last flooding of the bank margin about 4000–5000 years ago. We do not know what long periods of exposure to bioerosion and cementation would do to the internal composition of stromatolites in seas with long-term stability of sea-level.

Apart from the Eleuthera Bahamian stromatolites (Dravis, 1983) which are similar to, but smaller than, the Lee Stocking stromatolites, the only other Recent coarse-grained subtidal stromatolites known are at Hamelin Pool, Shark Bay. The latter are stressed by hypersalinity, rather than dunes, and are supplied with sediment by wave action rather than by tidal currents. Diatoms, large chlorophytes (*Acetabularia*), and other algae are common in addition to cyanobacteria in the subtidal Shark Bay stromatolites (Logan, Hoffman & Gebelein, 1974; Playford & Cockbain, 1976; Awramik & Vanyo, 1986; Awramik & Riding, 1988), but the presence of a small filamentous chlorophyte, analogous to that described here which is so important to the Lee Stocking stromatolites, has not been reported. Nevertheless, both the Lee Stocking and Shark Bay examples of subtidal columnar stromatolites are relatively coarse-grained and contain significant eualgal components in their microbial communities which are believed to be important in trapping sand-size particles. These stromatolites contrast with micritic and predominantly prokaryotic stromatolites of most Recent marine environments, and are not analogues for most

pre-Phanerozoic stromatolites (Awramik & Riding, 1988). Filamentous chlorophytes are likely to have been available as potential elements of microbial mats since Palaeozoic time, or earlier. But diatoms, which appear to be particularly important in trapping and binding the sediment, have only existed since Cretaceous time (Tappan, 1980). Eualgal–cyanobacterial stromatolites may therefore reflect a change in stromatolitic mat components during the past 100 Ma or so, which is a relatively short period in the very long history of benthic microbes.

## 7. Conclusions

Giant Lee Stocking stromatolites are composed of fine to medium sand, are crudely laminated, and have complex microbial communities which are equally dominated by algae and cyanobacteria. They belong to the category of eualgal–cyanobacterial stromatolite recognized by Awramik & Riding (1988). They contrast with micritic, well-laminated, and predominantly prokaryotic, stromatolites typical of most modern marine environments (Park, 1977).

We conclude that the following conditions are necessary for the formation of coarse-grained subtidal columnar marine stromatolites:

- (1) a substantial algal component to agglutinate coarse particles which cyanobacteria alone cannot trap;
- (2) an abundant sediment supply to build the stromatolites;
- (3) stable substrates such as large conch shells and lithoclasts for the inception of stromatolite growth in mobile substrates;
- (4) strong current or wave activity to lift coarse sediment in suspension or in dunes decimetres to a few metres above the substrate to produce large stromatolites;
- (5) stress, either from high velocity tidal currents which cause sediment suspension and dune migration (Bahamas) or hypersalinity (Shark Bay), to deter grazers and bioeroders;
- (6) early cementation to strengthen the columns and repair structural damage by burrowers and borers.

Such stromatolites can be expected to have formed in high-energy environments with suspended coarse sediment and to have had a substantial algal component. Environmental stress to restrict colonizers, bioeroders, burrowers and grazers would only be necessary if these organisms were common at the time of stromatolite formation.

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