

# Stromatolite-Thrombolite Associations in a Modern Environment, Lee Stocking Island, Bahamas

MARK FELDMANN

*Institut für Geologie und Paläontologie, Georg-August-Universität Göttingen, Goldschmidtstrasse 3, D-37077 Göttingen, Germany*

JUDITH A. MCKENZIE

*Geological Institute, ETH Zentrum, CH-8092 Zürich, Switzerland*

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*Columnar buildups found in a tidal channel off Lee Stocking Island, Exuma Cays, Bahamas, have been interpreted as modern giant stromatolites growing in a subtidal normal marine environment. However, these organically formed columns reveal three discernible internal structures: (1) prokaryotic stromatolites comprised of alternating layers of coarse-grained ooids and peloids, and fine micrite that formed exclusively by microbial activity; (2) eukaryotic stromatolites comprised of microbially-induced micritic layers alternating with detrital layers accumulated, bound, and cemented by eukaryotic algae; and (3) thrombolites displaying irregular, clotted fabrics and formed by microbes, algae, and metazoans. Phanerozoic thrombolites, in contrast, have been interpreted as unlaminated stromatolites constructed by cyanobacteria. Eukaryotic organisms overgrow all of the columns at present. Thus, the contemporaneous formation of prokaryotic stromatolites, eukaryotic stromatolites, and thrombolites under identical conditions within the present environment appears unlikely.*

*We suggest that the prokaryotic stromatolites represent forms that began to develop in an intertidal setting with the Holocene flooding of the Great Bahama Bank. The thrombolites, however, began to form under the present, normal-marine subtidal conditions. The eukaryotic stromatolites represent intermediate forms between prokaryotic stromatolites and thrombolites. There is evidence for a gradual change from stromatolite to thrombolite reefs associated with rising sea-level. With the deepening, there would have been a decrease in salinity, an increase in energy, and possibly an increase in nutrient supply; all factors that favor thrombolite growth. We propose that the co-existing stromatolites and thrombolites found off Lee Stocking Island did not grow contemporaneously, but reflect a response to changing environmental controls with changing sea-level.*

## INTRODUCTION

Since Dravis (1983) found the first high-relief stromatolites in a high-energy, oolitic sand environment on Eleuthera Bank, north of Exuma Sound, Bahamas, and Dill et al. (1986) described "giant" subtidal stromatolites in the vicinity of Lee Stocking Island, Exuma Cays, Bahamas, numerous other locations of stromatolites in the Exuma Cays have been recognized (Reid and Browne, 1991;

Reid et al., 1995). Intertidal stromatolites occur in a few localities (Reid and Browne, 1991; Feldmann, 1995; Reid et al., 1995; MacIntyre et al., 1996), but most known Bahamian stromatolites occur in subtidal settings, such as tidal channels and sandy embayments (Dravis, 1983; Dill et al., 1986; Griffin, 1988; Dill, 1991; Browne, 1993; Feldmann, 1995; Reid et al., 1995). These stromatolites are commonly interpreted as modern structures that accreted subtidally in a normal marine environment following the Holocene transgression. The Lee Stocking columns designated as subtidal stromatolites actually show a variety of internal structures that range from stratiform laminations, typical of stromatolites, to irregularly clotted structures with no recognizable lamination that are better described as thrombolites.

Over the past few decades, many authors have attempted to refine Kalkowsky's (1908) original definition of the term stromatolite: "Stromatolites are organogenic, laminated, calcareous rock structures, the origin of which is clearly related to microscopic life, which in itself must not be fossilised". He described stromatolites with great care and, unfortunately or fortunately, subsequent redefinitions and re-descriptions have not led to a better understanding of these structures (see Krumbein, 1983). Thus, defining stromatolites remains controversial (Ginsburg, 1991). In order to distinguish between laminated and non-laminated microbialites, Aitken (1967) introduced the term thrombolites for "non-laminated cryptalgal bodies characterized by a macroscopic clotted or spongy fabric."

In this study, we distinguish between three types of microbialites that occur in the subtidal environment of Lee Stocking Island: (1) prokaryotic stromatolites, the finely laminated structure of which has been entirely constructed by prokaryotes, (2) eukaryotic stromatolites, the coarse lamination of which has been formed by prokaryotes and algae, and (3) thrombolites, the irregularly clotted structure of which has been built by prokaryotes, algae, and metazoans. We use structural, biological, and environmental considerations to develop a model that explains the co-existence of stromatolites and thrombolites and the distinct features that led to their growth in the modern environments around Lee Stocking Island, Bahamas (Fig. 1). This model, based on changing environmental conditions, may reflect the evolutionary trend from stromatolites, which were abundant in the Proterozoic, to thrombolites, which were widespread during Paleozoic time.

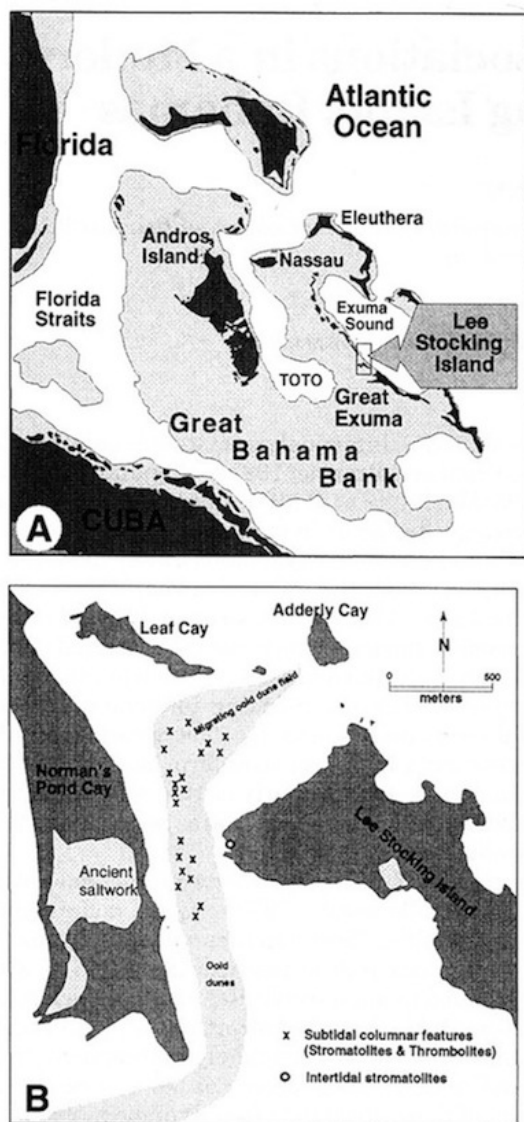


FIGURE 1—Map of the Bahamas. (A) The geographic relation of the Great Bahama Bank and the deep platform reentrants of Exuma Sound and Tongue of the Ocean (TOTO) is shown in relation to the study area. (B) Location of the columnar subtidal features (stromatolites and thrombolites) within the migrating sand dune field in the channel north and west of Lee Stocking Island and the intertidal stromatolites at the northwestern end of the island. Modified after Dill (1991).

#### LOCATION AND SETTING OF COLUMNAR BUILDUPS

This study was carried out near Lee Stocking Island (Fig. 1), where giant subtidal columnar stromatolites were first reported (Dill et al., 1986; Griffin, 1988; Kendall et al., 1990; Dill, 1991; Riding et al., 1991; Browne, 1993; Feldmann, 1995). These subtidal columns occur within a migrating ooid-sand dune field where reversing tidal and wind-driven currents, with velocities up to 1.5 m/s, flow across depositional sites twice daily. The salinity varies from 37‰ during flood tide to over 40‰ during ebb tide (Kendall et al., 1990; Dill, 1991). The buildups occur in water depths from 3 to 8 meters and reach heights of up to 2 meters. Episodically, the columns are covered by migrat-

ing sand dunes, protecting them from grazing and boring organisms and physical stress. If columns are uncovered, they can become overgrown by organisms such as macroalgae, sponges, and corals. In general, the columns appear rounded from the polishing effect of suspended sand particles carried in the turbulent waters.

Underwater observations and petrographical analysis of hand samples reveal that many of the columns lack internal laminations but are irregular, massive structures. Obviously, the simple external morphology of the columns is not sufficient to identify them as stromatolites. The columns occurring in the present subtidal setting reveal three discernible internal structures (Fig. 2A–F) each associated with distinct biological assemblages.

Recently-formed stromatolites have been found in the intertidal and uppermost subtidal zone of a small, very shallow bay at the northwestern end of Lee Stocking Island (Fig. 1B). They are protected in this bay from the strong tidal currents moving back and forth in the channel separating Norman's Pond Cay and Lee Stocking Island. These stromatolites grow upward to form columns of a few centimeters on wave swept debris, most commonly on conch shells (Fig. 3). Occasionally, they are covered by sand, which is provided by wave action.

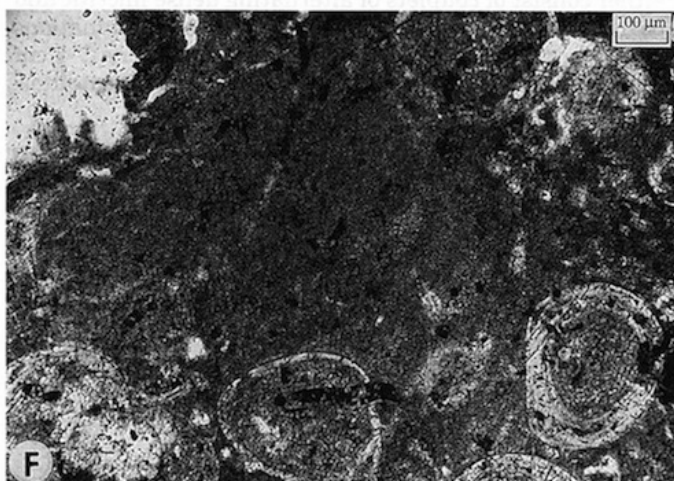
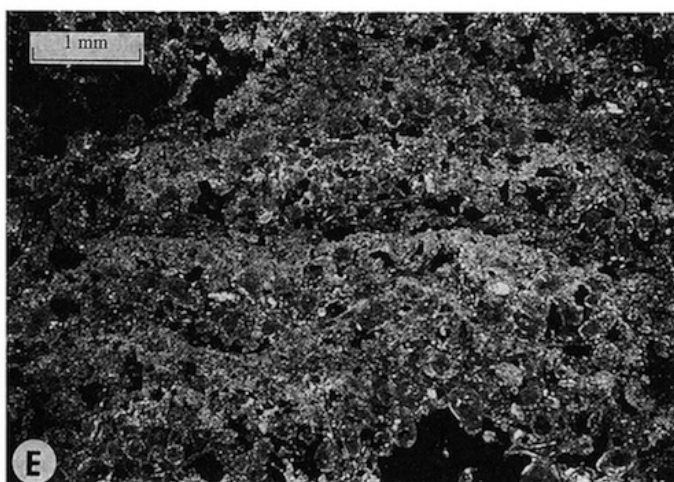
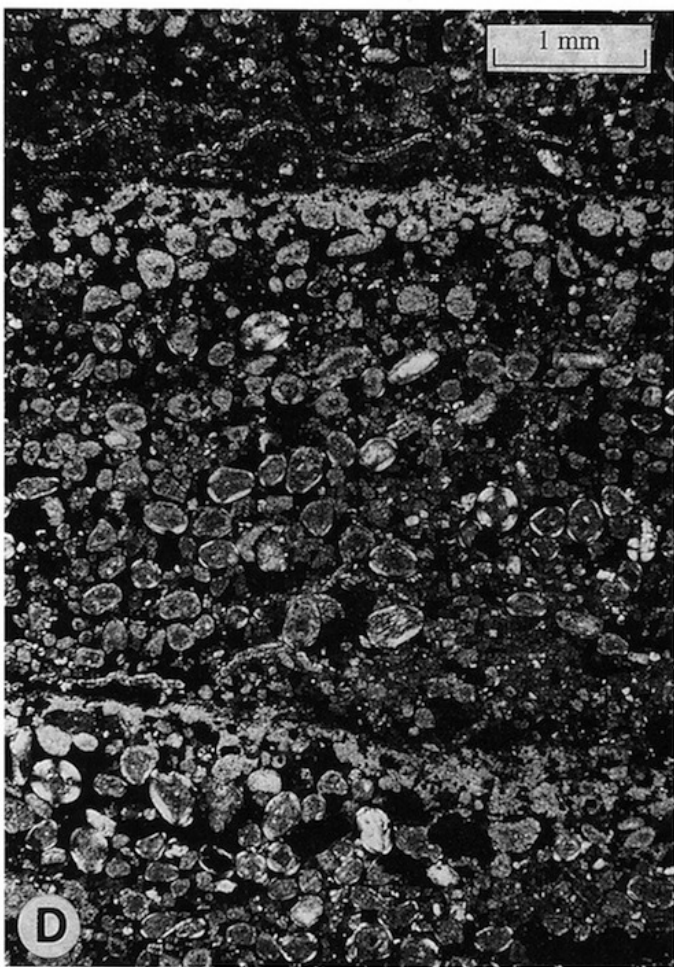
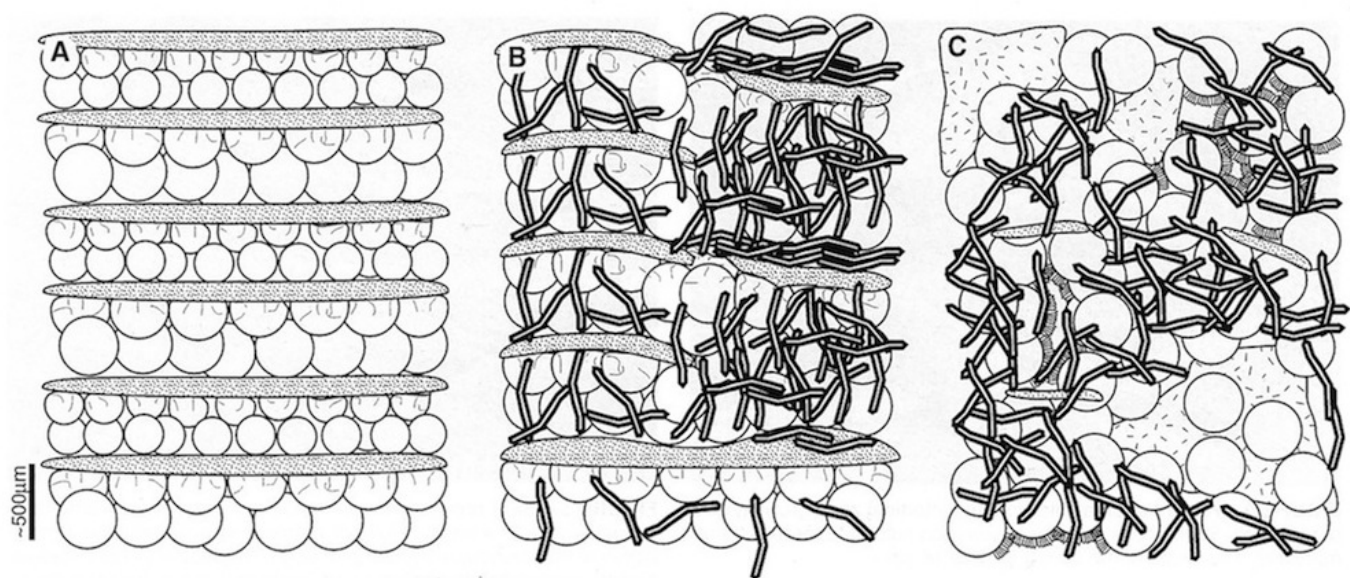
#### STRUCTURAL FEATURES OF COLUMNAR BUILDUPS

##### Prokaryotic Stromatolites

Prokaryotic stromatolites are herein considered to be laminated buildups, the structure of which does not indicate an impact by eukaryotic organisms on its formation. Prokaryotic stromatolites occur as columnar buildups (Fig. 4) with laminations constructed of alternating, dense calcium-carbonate micrite and coarse detritus (Fig. 2A, D). The micritic layers can be up to 250  $\mu$ m thick. Empty tubes, 2–6  $\mu$ m across and 30–50  $\mu$ m long, are occasionally observed in the micrites (Fig. 5) and are probably filament molds of cyanobacterial origin. Other remnants of organic structures were not detected within the micritic layers. Carbonate grains incorporated into the micritic layers, in contrast to the grains of the alternating clastic layers, are commonly heavily bored, truncated, and micritized.

The clastic layers consist mainly of ooids, peloids, and less abundant bioclasts. These layers can exceed 1 mm and are very porous. The grains within each detrital layer are poorly sorted, and average grain size varies from layer to layer. In coarse-grained layers, the average grain size is 150–200  $\mu$ m, compared to the finer-grained layers, that have an average grain size of about 100  $\mu$ m (Fig. 2D). The upward transition from a clastic layer to a micritic layer is commonly gradual, whereas the contact between the micritic layer and the overlying detrital layer is generally sharp. Very rarely, calcified filaments of the chlorophyte *Ostreobium* are found in the clastic layer. These organisms, however, are too sparsely distributed to have a major impact on structural development.

The layers of prokaryotic stromatolites generally occur as parallel laminations, having a convex-upward structure that encompasses the entire columnar buildup (Fig. 4). Diameters of such columns are up to 25 cm. Prokaryotic stromatolites are weakly lithified and show minimal signs



**FIGURE 2**—Fabric elements in stromatolites and thrombolites. (A–C) Simplified illustration showing the structural elements in (A) a prokaryotic stromatolite consisting of alternating micrite and detrital layers, (B) a eukaryotic stromatolite revealing undulose laminations caused by increasingly irregular accumulation and binding of detritus by eukaryotic algae and, (C) an irregularly structured thrombolite with micritic clots, calcified algal filaments, and inorganic isopachous cements forming the framework. (D–F) Thin-section photomicrographs illustrating the structural elements depicted schematically in A–C. (D) shows a prokaryotic stromatolite with couplets of alternating layers of dense micrite and coarse detritus, in which the grains directly underlying a micritic layer are commonly heavily micritized. (E) shows an eukaryotic stromatolite revealing an undulose laminated structure. This fabric amplifies laminations that were formed by a combination of cyanobacterial and eukaryotic algal activity. *Ostreobium* is dominant in the framework cementation of the detrital layer. (F) shows a boundary between a micritic clot and a detritus-rich sediment pocket in a thrombolite.





FIGURE 3—Recent stromatolite from the intertidal zone growing on a conch shell. Such shells are a very common substrate for these stromatolites. The width of the conch shell is 16 cm.

of destruction by organisms. The grains are preferentially cemented by micrite at grain contacts. Inorganic cements of acicular aragonite forming isopachous rims around detrital components were not observed. The presence of tunicate spicules approximately 40  $\mu\text{m}$  across is a prominent feature of pore spaces in the detrital layers (Fig. 6). A morphologic comparison of these spicules with tunicate spicules described from the Great Bahama Bank (Purdy, 1963) indicates that they are apparently the product of the tunicate species *Didemnum candidum*.

#### Eukaryotic Stromatolites

Eukaryotic stromatolites are herein considered to be laminated buildups, the structure of which indicates an influence of eukaryotic organisms on its formation. They either consist of couplets of alternating dense micritic and coarse detrital layers and reveal undulose laminations (Fig. 7), or they are composed of digitate columns 1–5 cm in diameter. In contrast to the prokaryotic stromatolites,



FIGURE 4—Columnar prokaryotic stromatolite grown on a *Calianassa* burrow showing convex-upward laminations that encompass the entire columnar buildup. Scale bar unit = 1 cm.

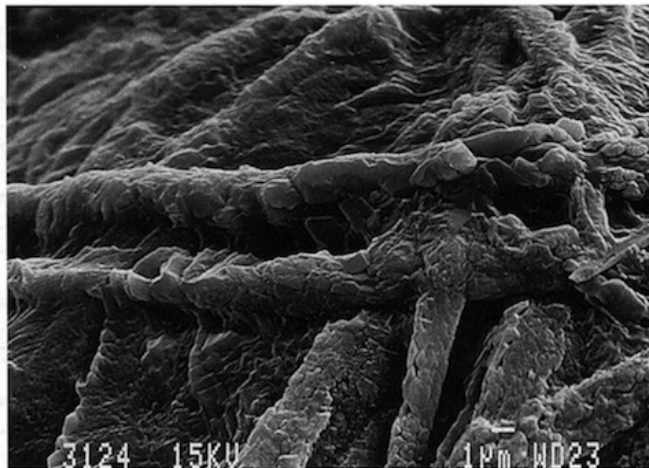


FIGURE 5—SEM photomicrograph showing a mold of a filamentous cyanobacteria in a micritic layer of a prokaryotic stromatolite. Precipitation of rhombohedral crystals probably took place in the extracellular sheath surrounding the cellular part (trichome) of the cyanobacteria.

these columns contain abundant calcified filaments of the alga *Ostreobium*. This alga is important as a binding agent and framework-builder in the detrital portions overlying micrite layers and between digitate columns. The *Ostreobium* filaments are about 25  $\mu\text{m}$  across and appear in thin sections as brown outlines rimmed by high-magnesium calcite. *Ostreobium* filaments have been described as important agents in the development of hardgrounds (Dravis, 1979) in Recent reefs in Bermuda (Schroeder, 1972), and in stromatolites from other Bahamian locations (Dravis, 1983). Such filaments frequently overlie the microbial micrite layer (Fig. 2E). Carbonate grains are often heavily bored by *Ostreobium*. Clastic portions are generally poorly sorted with grain sizes of 50–400  $\mu\text{m}$ . Detritus commonly accumulates preferentially in *Ostreobium*-rich zones, resulting in a less well-laminated fabric. The textural pattern of these buildups appears to be microbially-(cyanobacterially-) induced with well-cemented algal

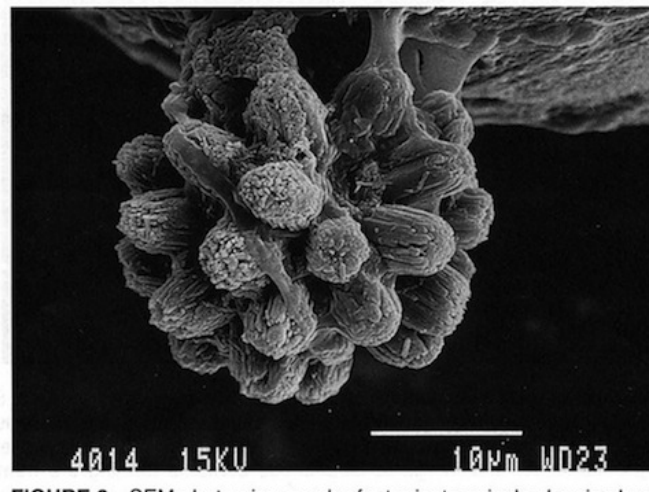


FIGURE 6—SEM photomicrograph of a tunicate spicule showing bundled aggregates of aragonite growing outward to form a rosette-shaped body. Such spicules are a common feature of prokaryotic stromatolites.



FIGURE 7—Columnar eukaryotic stromatolite grown on a conch shell shows slightly undulose and visibly coarser lamination than the stromatolite in Figure 4. This relatively coarse lamination forms as a result of higher sand accumulation on the surface due to the trapping activity of eukaryotic algae. Scale bar unit = 1 cm.

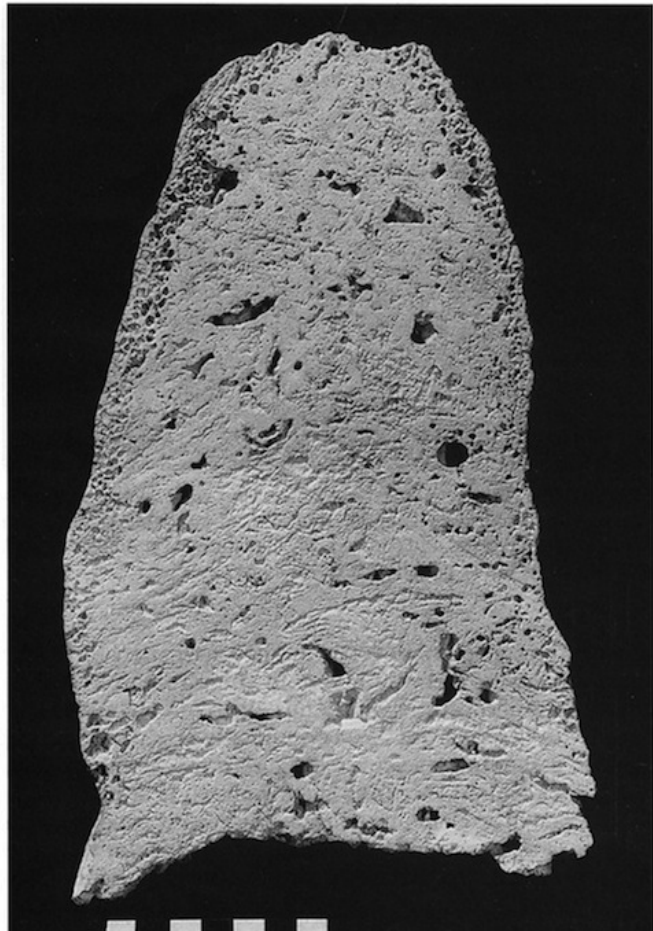


FIGURE 8—Thrombolite revealing a clotted irregular structure and being attacked by numerous borers. This is an example of a modern thrombolite from the subtidal zone in the Lee Stocking tidal channel. Scale bar unit = 1 cm.

framework fabrics, leading to their designation as eukaryotic stromatolites. In addition, acicular aragonite around detrital components can occur in detritus-enriched zones.

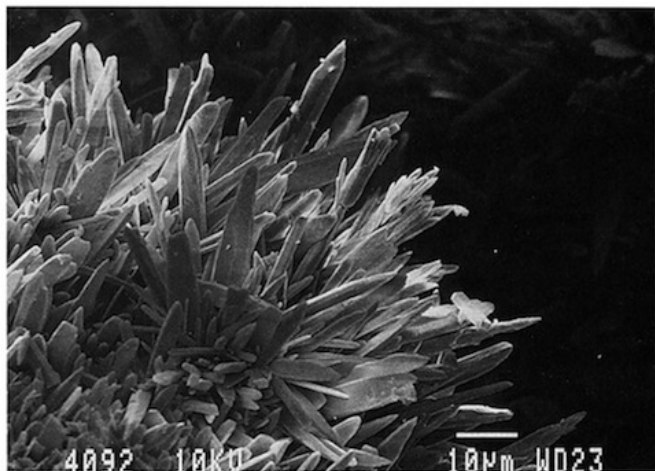
### Thrombolites

Modern subtidal thrombolites from Lee Stocking Island are buildups having no regular laminated structure (Fig. 8). They contain mesoclots that are up to a few millimeters across, have a micritic texture, and are commonly dark colored in thin section (Fig. 2F). Characteristically, they contain calcified filaments of *Ostreobium*. *Ostreobium* filaments occur throughout the examined columns and are the dominant framework builders (Fig. 9). *Ostreobium* filaments have diameters of up to 300  $\mu\text{m}$  but commonly are 20 to 50  $\mu\text{m}$  wide (Schroeder, 1972; Kobluk, 1977; Kobluk and Risk, 1977a, b; Dravis, 1979). Detrital particles are either sparse or absent within the mesoclots, but unbound-sediment pockets between the mesoclots are composed of detrital particles (see Aitken, 1967; Kennard and James, 1986). The detrital particles consist mainly of ooids and minor amounts of well-rounded, frequently well-sorted pebbles and skeletal debris. Grains found in these columns



FIGURE 9—Thin-section photomicrograph of primary binding and cementing by filament calcification of the alga *Ostreobium* in oolitic portions of a thrombolite. The thin micritic rim outlining the filament consists of high-magnesium calcite, whereas the filament interior is void. These filaments have a striking similarity with *Girvanella*, a common agent in Phanerozoic thrombolites usually interpreted as cyanobacteria.





**FIGURE 10**—SEM photomicrograph showing well-developed aragonite needles filling pore spaces. This form of inorganic cementation occurs in thrombolites and occasionally in eukaryotic stromatolites, but was not observed in prokaryotic stromatolites.

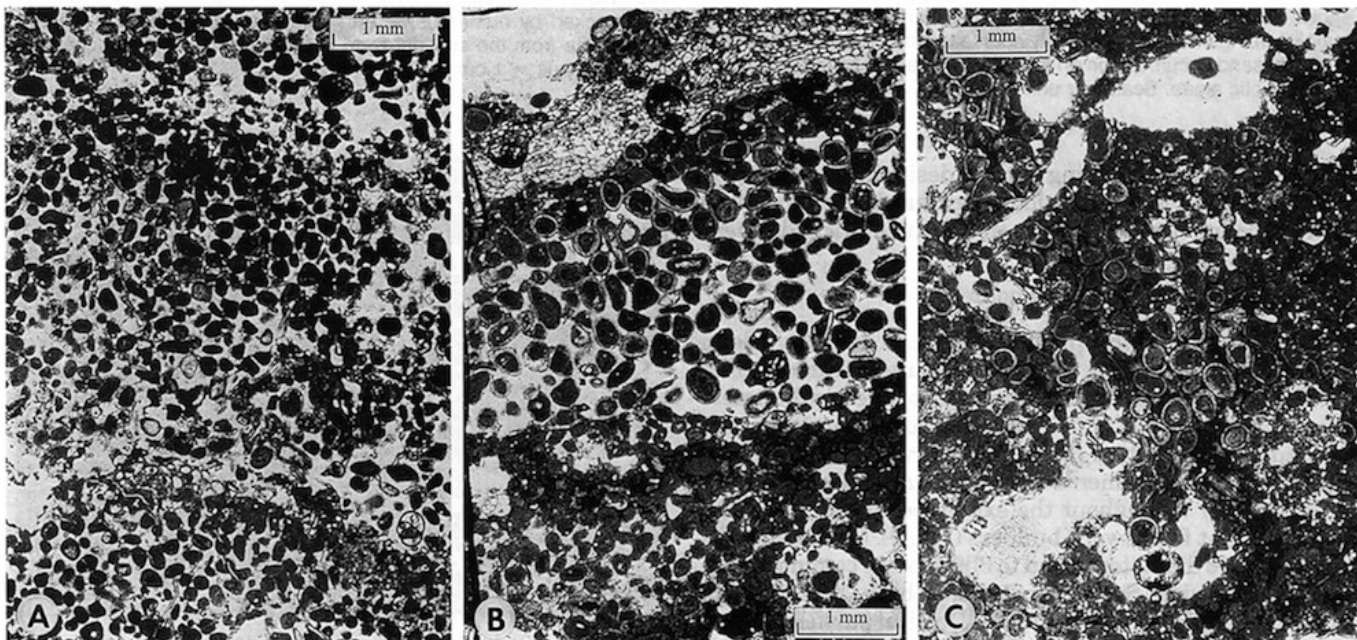
have diameters of up to 400  $\mu\text{m}$ . They are generally larger than the grains forming layers in the stromatolites. Encrustations of coralline algae and calcareous sponges occur repeatedly. Aside from these organically produced binding agents, cements of acicular aragonite are common (Fig. 10). These cements occur as isopachous rims around detrital components. Cements grow as microspar needles, with lengths of up to several tens of  $\mu\text{m}$ , perpendicular from the surfaces to connect adjacent grains. The organically-produced micrite and the inorganic microspar cement bind

grains into a wave-resistant framework, in contrast to the relatively weakly bound, laminated framework of the stromatolites. The irregularly structured thrombolites may contain patches of stromatolitic layering, each a few centimeters in width.

#### Stromatolite-Thrombolite Associations

The columns from Lee Stocking Island show a temporal change from stromatolite to thrombolite structures that can be considered a change in reef type (Fig. 11A–C). This change is facilitated by distinct organisms with distinct environmental requirements.

Structural changes even occur within individual build-ups. Examination of 6 columns sampled in Spring, 1992, from the tidal channel off Lee Stocking Island showed that a single column can contain more than one of the previously described structures with a gradual transition from one to another. One of the samples consists entirely of prokaryotic laminations, whereas another has a prokaryotic base that gradually changes upward into a coarser, eukaryotic structure. Two of the samples have an eukaryotic core that gradually changes out- and upward into a thrombolitic structure; two other columnar samples have irregular structures, locally showing coarse laminations. More finely-laminated structures generally are composed of smaller sized grains. The amount of skeletal debris and borings increases with the transition from stromatolite to thrombolite.



**FIGURE 11**—Thin-section photomicrographs showing gradual structural changes from the core to the surface in a 10-cm-high buildup from the subtidal zone in the tidal channel. (A) The core of the column represents a prokaryotic stromatolite that is weakly lithified with very thin micritic layers. Some *Ostreobium* filaments occur in the detritus-rich parts (center). (B) With increasing distance from the core the laminae are more undulose, the micritic layers are thicker, and eukaryotes occur, as indicated by the sponge fabric overlying the upper micritic layer. This is an example of a common eukaryotic-stromatolitic structure. (C) Towards the surface, the structure of the buildup is thrombolitic; it is irregular, reasonably well lithified, and exhibits micritic clots.

## BIOLOGICAL ASSEMBLAGES

## Tidal Channel

If lithified stromatolites and thrombolites are uncovered by migrating sand dunes and exposed to tidal currents, they can become capped by a microbial mat and overgrown by larger organisms. Observations during dives showed that if a reefal body is overgrown, the stage of overgrowth is related to the length of exposure time or to scouring activity within this high-energy environment. Many of the most recently uncovered column surfaces appear polished; those that protrude just slightly above the water/sediment interface are especially prone to polishing, which can be explained by a higher scouring potential due to higher suspended particle concentrations in the near-bottom water. Surfaces located on the lee side of columns or nearer to the water surface are not as heavily exposed to detrital bombardment and are, therefore, more easily overgrown by organisms.

When column surfaces are freshly exposed, they may be covered by a thin, smooth microbial mat. Surface mats can contain distinct communities of microbes (Riding et al., 1991), but are essentially dominated by the filamentous cyanobacterium *Schizothrix* (Browne, 1993). Other microbes found in the mats are the filamentous cyanophytes *Oscillatoria* and *Spirulina*, coccoid cyanobacteria, and benthic diatoms. The subsurface of microbial mats (~1 mm below the surface) has a different microbial community, dominated by an assemblage of unidentified bacteria, possibly living in an anoxic environment of previously secreted organic material (Feldmann, 1995; Feldmann, 1997).

However, pure cyanobacterial mats that cover entire surfaces of columns were not observed. Instead, cyanobacteria are commonly accompanied by small algae that protrude a few millimeters above the mucilaginous mats. Microbial mats often cover "knobs", which comprise accumulated sand on surfaces forming small mounds of 2 to 3 cm. "Knobs" were often observed growing around a sticky algal filament. Algae are abundant (the number of algae counted within a 7 cm<sup>2</sup> grid on a microbial mat was between 6 and over 100; N = 15) and appear to grow epiphytically on the organic substrate of the microbial community, or on the hard substrate provided by earlier mineralization.

Many columnar surfaces are intensely colonized by green algae, of which *Batophora* is the most abundant. These non-calcifying green algae trap and bind abundant sediment particles, leading to an irregular deposit of detritus on the surfaces. Dravis (1983) reported that *Batophora* is one of the main trappers of sediment grains on stromatolites from Eleuthera. Dill (1991), however, remarked that the occurrence of *Batophora* on the surfaces of the Lee Stocking forms could be a seasonal feature.

*Acetabularia* is another common green alga on column surfaces. It generally colonizes in summer, but not in fall or winter (Dill, 1991). Because *Acetabularia* calcifies, it has potential importance as a framework builder. Some surfaces are predominately colonized by green spheres with diameters of 20–30 µm. The origin of the green spheres has not been definitely determined, but they are considered to be spores of *Acetabularia* (Fig. 12A, B). The

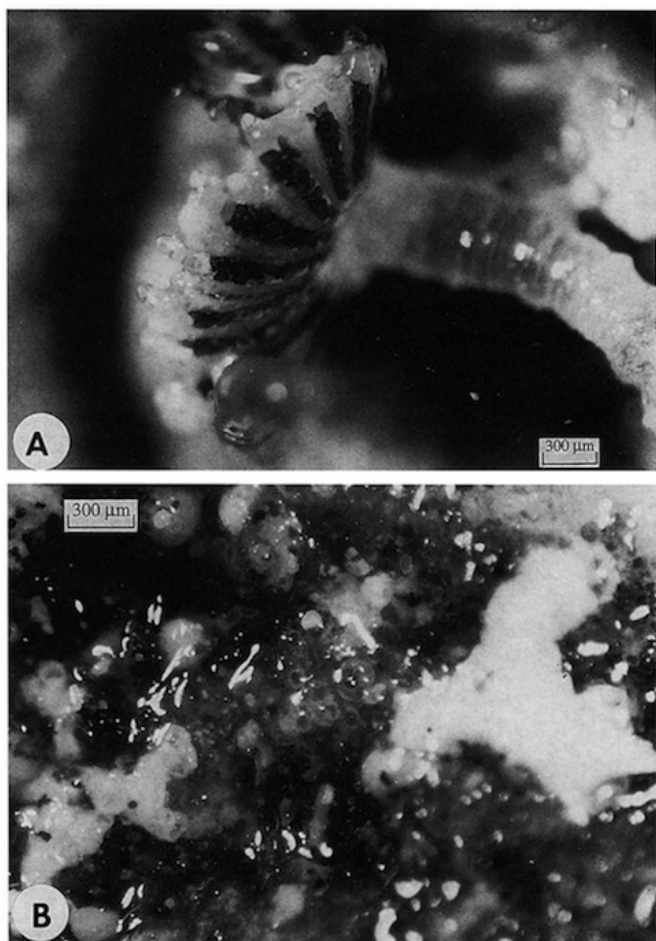


FIGURE 12—Light microscopic views showing an example of calcification by a eukaryotic alga. (A) The calcifying green alga *Acetabularia* is a common constituent on column surfaces. (B) Colonies of green spheres, probably spores of *Acetabularia*, are common calcifying constituents on the surfaces of subtidal buildups forming micritic patches or clots.

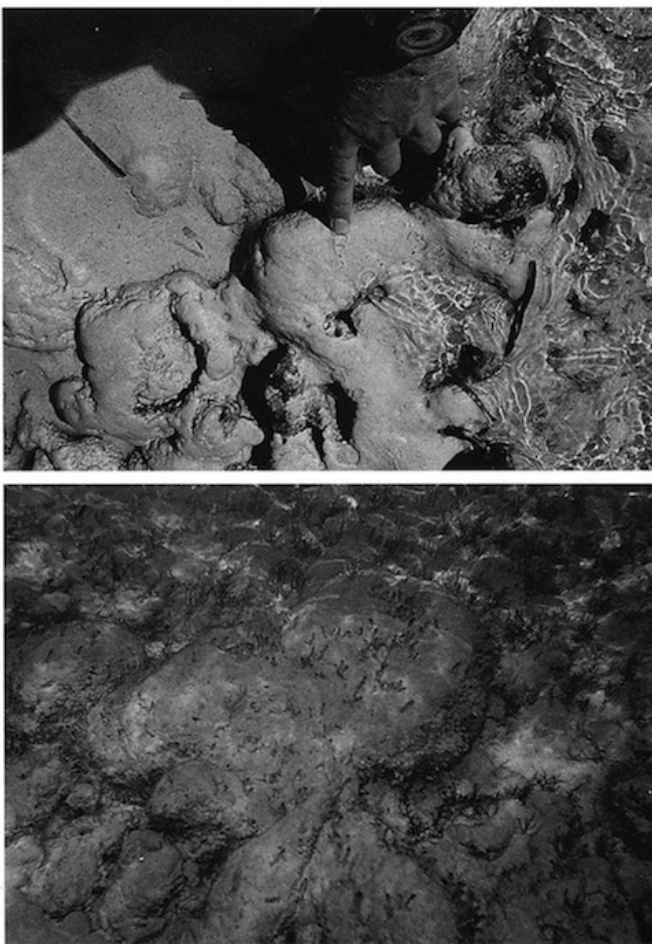
spheres do not actively move over the surfaces, but secrete a gelatinous matrix that becomes calcified. If there is a large colony of these green spheres, a hard micritic, clotty crust develops and cements neighboring unconsolidated grains (Fig. 12B). Green spheres are frequently accompanied by the encrusting alga *Lithothamnion*.

Other algae, such as *Halimeda* or *Penicillus*, and metazoans, such as the boring sponge *Cliona*, which are abundant in the Lee Stocking region, were only occasionally observed on column surfaces. Columns that rarely become buried by migrating sand dunes are overgrown by larger organisms, such as brown algae (*Sargassum*), corals (*Siderastrea*), sponges, and hydrozoans.

## Sandy Embayment

The boundary between the uppermost subtidal and intertidal zone in the shallow bay at the northwestern end of Lee Stocking Island is clearly indicated by a sharp change in surface colonization of presently forming stromatolites (Fig. 13A, B). Surface mats of stromatolites from the uppermost subtidal zone essentially have a similar composi-





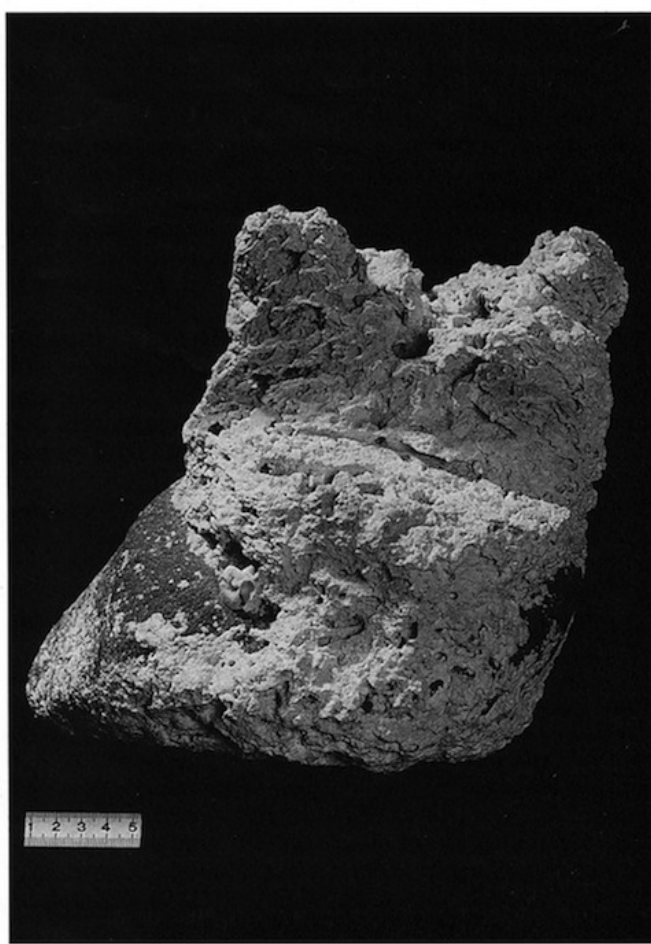
**FIGURE 13**—Stromatolite surfaces recently forming at the northwest end of Lee Stocking Island. (A) Surface of an intertidal stromatolite showing no evidence of colonization by eukaryotic macro-organisms. (B) Surface of a stromatolite from the uppermost subtidal zone (water depth about 10 cm during low tide) colonized by numerous eukaryotic algae (*Batophora* is the most abundant).

tion to the freshly exposed surface mats in the tidal channel. They are colonized by a community consisting of cyanobacteria, of which the most prominent is *Schizothrix*, algae, such as *Batophora* and *Acetabularia*, and benthic diatoms. With increasing water depth, eukaryotic algae become more abundant and metazoans also occur. In contrast, intertidally forming stromatolites are almost exclusively colonized by *Schizothrix*. Macroscopic algae are absent on these surfaces.

#### AGE OF BUILDUPS

The age of the Lee Stocking buildups in the tidal channel is not exactly known. A conch shell forming the base of a 90-cm-high column was dated at  $480 \pm 80$  yr. BP (Dill, 1991). An oncolitic core in another column provided a  $^{14}\text{C}$  age of 3,700 yr. BP (Aalto and Shapiro, 1990). However, in both cases the internal structure of the columns was not determined. Thus, it is not known whether the dates refer to prokaryotic stromatolites, eukaryotic stromatolites, or thrombolites.

Recently a 15-cm-high thrombolite grown on a basaltic



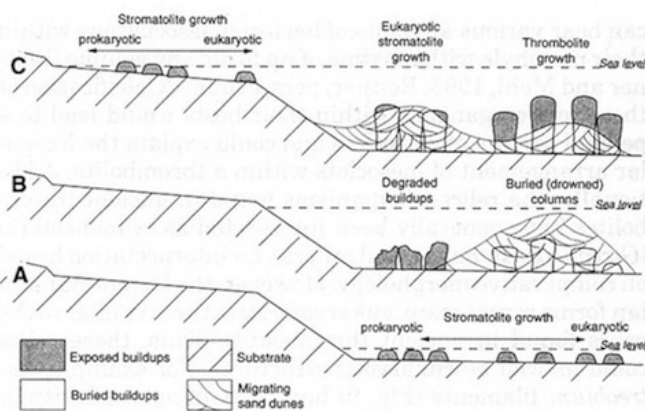
**FIGURE 14**—Thrombolite grown on a basaltic balast stone in the subtidal zone of the tidal channel. Balast stones were deposited between the 17th and 19th Century in association with the saltwork on Norman's Pond Cay (Fig. 1B).

balast stone was found in the tidal channel at a water depth of 7 meters (Fig. 14). Such balast stones were dropped from vessels that came between the 17th and 19th century to Norman's Pond Cay in order to obtain salt from the saltworks. This buildup may demonstrate that thrombolitic structures have preferentially formed in the tidal channel over the last 400 years.

#### GROWTH MODEL

The stromatolites from Lee Stocking Island developed preferentially on large clasts, such as conch shells, cemented walls of *Callianassa* burrows, pebbles, and rock fragments. Such debris is found everywhere around Lee Stocking Island, though it commonly accumulates along protected shore lines, where it is deposited during storms. The surfaces of debris deposits are irregular, with gaps and elevations, resulting in a relative relief of several centimeters. If these debris deposits are flooded by rising sea level, the surfaces of single elements may be preferentially colonized by cyanobacteria. This is possible because, in shallow water of a few centimeters, light conditions may be better for growth on the elevated surfaces of the debris deposits than on the surrounding bedrock. During low



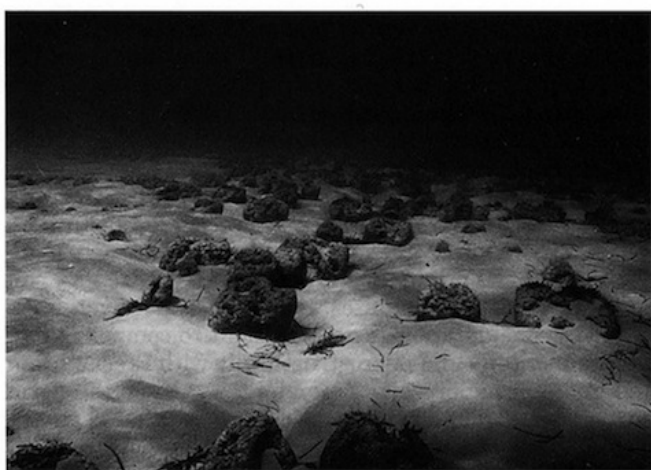


**FIGURE 15**—Illustrative model showing the association between stromatolite and thrombolite growth in the Lee Stocking Island area. (A) Stromatolite growth is promoted with the flooding of a substrate. Prokaryotic stromatolites develop in intertidal zones and prokaryotic stromatolites in shallow subtidal zones. (B) With continuously rising sea level, sand dunes and bars begin to form. If stromatolites become buried under sand dunes, their growth is interrupted and can not keep pace with the rising sea level; thus, they become drowned. If weakly lithified stromatolites become exposed from their protective sand dune cover for a longer period of time, they undergo degradation due to the strong physical stress in the tidal channel. (C) Simplified present day situation in the area of Lee Stocking Island. In the shallow bay, prokaryotic stromatolites form in the intertidal zone and eukaryotic stromatolites form in the uppermost subtidal zone. In the tidal channel, eukaryotic stromatolites form if the column surfaces are freshly exposed from beneath their sand cover. Thrombolites grow above the sand crests.

tide, the colonized surface may even be exposed. Such conditions promote evaporation and the resulting high salinity inhibits colonization by stenohaline organisms.

The cyanobacteria develop microbial mats on the elevated surfaces. From time to time, strong wind and wave conditions lead to deposition of sand layers on the mats. Subsequently, the cyanobacteria must migrate upward towards the light to form new microbial mats. The uppermost clasts of the sand layer become incorporated into the new mats and are bound by microbially secreted organic material. Otherwise, they are unable to serve as a stable substrate for cyanobacterial growth. Within the specific chemical micro-environment of the organic mat, supersaturation with respect to  $\text{CaCO}_3$  can occur, causing micrite to precipitate. A micrite layer could develop in this way (Feldmann, 1997). Additional precipitation induced by the metabolism of the microbes (i.e., photosynthesis or sulfate reduction) can also induce cementation of clasts. With the upward migration of cyanobacteria, organic material of the former microbial mat would be left behind to be microbially decomposed.

If the accumulation of sand layers fixed by microbial mats can keep pace with slowly rising sea level, columns of prokaryotic stromatolites may develop in this high salinity environment. The upper surfaces of the columns would experience intermittent high-salinity conditions due to tidally-controlled exposure, while at the same time, the conditions at the base of the columns would slowly change from intertidal to subtidal. With time, the importance of evaporation would decrease and the water composition would slowly change from predominantly hypersaline to normal marine. Organisms, such as green and red algae,



**FIGURE 16**—Degraded stromatolites at the edge of a migrating submarine sand dune. The columns are overgrown by sea grass and are apparently not growing. They are exposed to physical stress within the strong tidal currents. The water depth is about 6 meters, the height of the columns is about 50 cm.

could colonize surfaces. As sea level continued to rise, the amount of sand produced and transported would increase and stromatolites would be buried under sand bars, inhibiting further growth. At some point, stromatolite growth would be unable to keep pace with rising sea level and the columns would become drowned features in the subtidal environment (Fig. 15).

With the subsequent removal of overlying sand, the exhumed relic surfaces of the stromatolites could be recolonized by a community of organisms, such as cyanobacteria, algae, and metazoans. These organisms would give the surface an irregular topography and more efficiently bind suspended detritus than microbial mats alone. Some of the organisms, such as *Ostreobium*, *Acetabularia*, and coralline algae, are able to calcify, which makes them important framework builders in the subtidal environment. Under these conditions, and depending on the stage of overgrowth by eukaryotes, eukaryotic stromatolites or thrombolites would be formed. The abundance of algae and the type of framework cementation provided by *Ostreobium* are believed to indicate that algae are responsible for the formation of the relatively thick (up to more than 1 mm) detrital layers, such as those found in eukaryotic stromatolites. With increasing time of exposure, algae grow irregularly over the surface; other organisms, such as sponges, occur as well. This provides additional organic matter for subsequent microbial decomposition in the subsurface, resulting in micrite precipitation under certain chemical conditions, such as sulfate reduction. Formation of laminae is inhibited, and irregular structures, such as those found in thrombolites, dominate. However, if stromatolites are insufficiently lithified and exposed to the physical stress of tidal currents over a long period of time, they will be destroyed, as shown by the numerous stromatolite fragments and degraded stromatolites at the edge of sand dunes (Fig. 16).

#### CONTROVERSIES—STROMATOLITE VS. THROMBOLITE

Interpretation of the subtidal Lee Stocking stromatolites is controversial. If subtidal stromatolites are present-

ly forming, they contain, to a significant degree, macroscopic eukaryotic algae that serve as important agents in framework cementation and detritus accumulation. Thus, considering the genetic definitions, which exclusively require formation by microbial growth (Kalkowsky, 1908; Walter, 1976; Krumbein, 1983), these Bahamian stromatolites are not stromatolites *sensu stricto* (see also Awramik and Riding, 1988). Following the descriptive definition, which only requires a layered or laminated structure independent of its origin (Semikhatov et al., 1979), they can be regarded as stromatolites. In this case, however, a descriptive consideration is not sufficient to compare them environmentally and microstructurally with Precambrian and many Phanerozoic stromatolites. Using the term "stromatolite" for all of the subtidal columns found off Lee Stocking Island leads to further misconceptions concerning the environment in which stromatolites grow, the biological assemblage that forms stromatolites, and the fabric by which stromatolites are texturally recognized.

Prokaryotic stromatolites appear to be rare in the subtidal environment of Lee Stocking Island. However, layered structures in which eukaryotic algae function as accumulators, binders, and cementers of sand clasts are the dominant subtidal features. These structures, termed eukaryotic stromatolites, represent an intermediate stage between prokaryotic stromatolites and thrombolites. With increasing surface colonization, control of detritus accumulation, and framework cementation by eukaryotes, such as algae and sponges, growth of a laminated or layered organic structure is inhibited. Hence, irregular clotted structures form, such as observed in the thrombolites.

Aitken (1967) defined thrombolites as "non-laminated cryptalgal bodies characterized by a macroscopic clotted or spongy fabric." His definition was amplified by Kennard and James (1986) who added that mesoclots occurring in thrombolites are a primary microbial feature and that thrombolites contain detrital particles in unbound sediment pockets between mesoclots, but not within mesoclots. In contrast to the examples described by Aitken (1967) and Kennard and James (1986), the Lee Stocking thrombolites have a high detrital content due to the environmental conditions under which they grow; sand production and sediment suspension is high. However, detritus is absent in mesoclots, the typical textural feature of thrombolites (Fig. 2F).

Mesoclots in ancient thrombolites are considered to be composed of microstructures that are attributed to the *in situ* calcification of coccoid or coccoid-dominated microbial communities (Kennard and James, 1986). However, the textures of ancient and modern clots appear to be similar. Thus, the question arises, might ancient thrombolites also be eukaryotic reefs? Although cellular and rimmed lobate microstructures occurring in thrombolitic mesoclots have a striking similarity to calcified cyanobacterial colonies from Laguna Mormona, Baja California (Horodyski and Vonder Haar, 1975; Kennard and James, 1986), there is no evidence from modern environments that pure microbial mats of cyanobacteria and functional bacterial groups (Van Gemerden, 1993) can form clotted thrombolite fabrics. It seems more likely that a symbiosis of metazoans and prokaryotes or calcification of algal agents, such as the spores of *Acetabularia* (Fig. 12B), may lead to the formation of micritic clots. For example, all known sponges

can bear various amounts of bacterial associations within their mesohyle with maxima of up to 60% by volume (Reitner and Mehl, 1995; Reitner, pers. comm.). Calcification of these microorganisms within their hosts would lead to a pelletal texture of mesoclots and could explain the irregular arrangement of mesoclots within a thrombolite. Additionally, the relics of organisms found in ancient thrombolites have generally been interpreted as cyanobacteria (*Girvanella*, *Renalcis*, and others), an interpretation based on comparative morphology. However, the Recent Bahamian forms reveal many eukaryotic structures similar to the relics found in ancient thrombolites. Thus, these relics could as well be eukaryotic structures. For example, *Ostreobium* filaments (Fig. 9) have a striking similarity in size and shape with *Girvanella* (see also Kobluk and Risk, 1977b; Riding, 1977).

The idea that ancient thrombolites might represent eukaryotic reefs, composed of microbes, algae, and metazoans, and not principally unstructured cyanobacterial stromatolites is consistent with the chronological record. Over a time span of about 2 billion years, from the middle Archean to the Neoproterozoic, cyanobacteria formed most, if not all, stromatolites. The oldest thrombolites are described from the Early Paleoproterozoic of the Rocknest Formation, Canada (Kah and Grotzinger, 1992). However, although these structures reveal the defining character of thrombolites (i.e., a clotted texture), they show no evidence of biological origin and, thus, clearly differ from Neoproterozoic/Paleozoic thrombolites. The latter enter the record at about the same time as widespread fossils of eukaryotic algae (Knoll, 1992) and sponge-metazoans (Reitner and Mehl, 1995). Our suggestion that thrombolites are buildups formed by microbes, algae, and metazoans contradicts the speculation of Kennard and James (1986) that the coappearance of calcified cyanobacteria and thrombolites represents a major adaptive evolutionary change in the history of microorganisms in response to the increased grazing and burrowing pressure exerted by the newly evolved metazoans.

Aitken (1967) considered thrombolites to be a subtidal phenomenon, and stromatolites were understood to be exclusively intertidal to supratidal forms. Based on his study of Cambrian stromatolites and thrombolites from the Georgina Basin, Australia, Kennard (1981) interpreted laminated stromatolites as forms which grew in a "highly saline environment, whereas thrombolites develop in agitated and less highly saline waters." The modern Lee Stocking forms may reflect, in a similar manner, distinct environmental conditions for the growth of stromatolites and thrombolites. Although prokaryotic stromatolites occur today in the subtidal channel environment off Lee Stocking Island, an explanation for their formation based only on their present location and environment may not be adequate. At present, eukaryotic organisms overgrow all of the columns, including both stromatolites and thrombolites. Thus, contemporaneous formation of prokaryotic stromatolites and thrombolites under identical conditions within the present environment appears unlikely, as indicated by a thrombolite grown on a balast stone within the last 400 years (Fig. 14). However, environmental changes at the sites of stromatolite formation could provide an explanation for the co-existence of prokaryotic and



eukaryotic stromatolites and thrombolites in the present subtidal environment.

## CONCLUSIONS

The model presented here for the growth of Bahamian stromatolites and thrombolites proposes that the various distinctive internal structures of the columns in the current subtidal environment of the channel off Lee Stocking Island were formed in response to environmental changes (Fig. 15). In essence, the model distinguishes between three members.

- (1) Prokaryotic stromatolites constructed entirely by prokaryotes representing intertidal hypersaline, low-energy conditions currently form in the intertidal zone of the shallow bay at the northwestern end of Lee Stocking Island. Prokaryotic stromatolites found in the subtidal zone of the tidal channel are considered to be "drowned" intertidal stromatolites. Modern sand dunes under normal marine, high-energy subtidal conditions protect these stromatolites from physical stress and bioerosion, and serve an important function for their preservation but do not support their growth. Prokaryotic stromatolites in subtidal areas could not have formed in their current environment, but were probably formed under hypersaline intertidal conditions. The presence of tunicate spicules (Fig. 6) in these structures supports a low-energy model for stromatolite growth (Monniot et al., 1991). Such spicules were also found in Recent intertidally forming stromatolites (Feldmann, 1995).
- (2) Eukaryotic stromatolites that have a laminated framework constructed by prokaryotes and eukaryotic algae currently form in the uppermost subtidal zone and probably in the tidal channel when shortly exposed from beneath their sand dune cover. They represent (a) transitional forms that progressed gradually from intertidal to subtidal conditions, associated with a change in the biological community from cyanobacterial to eukaryotic-dominated (Fig. 13A, B), or (b) subtidal structures that form if surface colonization by eukaryotes is time-limited by periodic burial beneath migrating sand dunes. If they are insufficiently lithified, they undergo, together with prokaryotic stromatolites, strong degradation and destruction when exposed from beneath their protective sand dune cover (Fig. 16).
- (3) Thrombolites currently form in the subtidal zone of the tidal channel. They represent subtidal normal marine, high-energy conditions.

All the subtidal buildups occurring in the tidal channel from Lee Stocking Island are commonly designated stromatolites (Dill et al., 1986; Griffin, 1988; Kendall et al., 1990; Dill, 1991; Riding et al., 1991; Browne, 1993). However, in order to formulate an approach with which to study and understand their formation, a clear definition of the term stromatolite must be delineated. Structural features are commonly representative of a given environment and are therefore useful as key indicators.

Stromatolitic, laminated structures and thrombolitic, irregular, clotted structures are both defined as organosedimentary features but are related to distinctively differ-

ent environments. Thus, in addition to serving as marker horizons within stratigraphic sequences in the Phanerozoic record (Feldmann and McKenzie, 1997), stromatolite-thrombolite associations such as those occurring in the area of Lee Stocking Island have significant potential as useful tools for interpreting paleoenvironments.

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