GROWTH HISTORY OF STROMATOLITES IN A HOLOCENE FRINGING REEF, STOCKING ISLAND, BAHAMAS

IAN G. MACINTYRE\(^1\), R. PAMELA REID\(^2\), AND ROBERT S. STENECK\(^3\)

\(^1\) Department of Palaeobiology, MRC 125, National Museum of Natural History, Smithsonian Institution, Washington D.C. 20560 U.S.A.
\(^2\) Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149 U.S.A.
\(^3\) Department of Oceanography, University of Maine, Darling Marine Center, Walpole, Maine 04573 U.S.A.

ABSTRACT: A stromatolite and algal ridge reef complex 2.1 m thick fringes the east coast of Stocking Island, Exuma Cays, Bahamas. This reef was established on a Pleistocene calcarenite terrace about 4500 yr B.P. Stromatolites, which occur in back-reef and reef-flat zones, are up to 1 m thick and were constructed by cyanobacterial-dominated communities. Study of the growth history of these stromatolites, ranging in scope from facies analyses to details of microfabric construction, presents new perspectives on stromatolite formation.

Lithologies identified in eight cores from across the Stocking Island reef complex, together with plots of 13 radiocarbon dates in relation to a Bahamian sea-level curve, indicate that this reef began as an intertidal vermetid gastropod buildup. Subsequent flooding of the Pleistocene terrace allowed the branching coralline alga Neogoniolithon strictum to overgrow the vermetids and eventually form an emergent algal ridge about 1500 years ago. Shifting sands accumulated in the lee of this ridge and excluded most benthic communities and herbivores, thereby promoting growth of cyanobacterial mats that formed stromatolite builds up. With a decrease in wave energy over the last 500 years, possibly due to the growth of offshore patch reefs, the urchin Echinoaster lucter colonized the algal ridge. Resultant biocorrosion by this urchin destroyed the emergent part of the ridge and is now undercutting the seaward edge of the stromatolite builds up.

Lamination in the Stocking Island stromatolites results from early lithification processes in cyanobacterial mats, possibly in response to biogeochemical changes in the mats during hiatuses in sediment accretion. These processes, which create partially indurated laminae with a distinct microstructure, involve precipitation of thin micritic crusts, intense microboring along a surface below this crust, micritization of sediment grains, and precipitation of point-contact cement between micronized grains. Introduction of turf algae to the cyanobacterial mat community disrupts formation of the lithified laminae, thereby inhibiting stromatolite development.

INTRODUCTION

Laminated sedimentary structures known as stromatolites, which are produced by sediment trapping or precipitation by microorganisms, principally cyanobacteria (definition modified from Walter 1976), are the oldest known macrofossils (Schopf and Walter 1983) and are still forming in modern environments. A major role of stromatolites through much of Earth history has been one of reef building. For 3 billion years during the Precambrian, stromatolites formed impressive reefs that rivaled or exceeded Phanerozoic reefs in size (Grotzinger 1988). Stromatolites continued to contribute to reef construction during the Paleozoic (e.g., Atkin 1988; Newell et al. 1953; Playford and Cockbain 1969; Wolf 1965; Smith 1981; Kahle 1994) and into the Mesozoic (e.g., Bosellini and Rossi 1974). Until recently, they were thought to have disappeared from the reef environment by Cenozoic time (Monty 1973; Gebelein 1976). A discovery at Stocking Island, Exuma Cays, Bahamas (Reid and Browne 1991) documented the first occurrence of stromatolites in a modern reef. In addition to stromatolites, biota in this reef include a complex assemblage of coralline and other macroalgae, corals, hydrocorals, urchins, and reef fish. The reefal setting of the Stocking Island stromatolites distinguishes them from previously reported modern marine stromatolites in the Bahamas (e.g., Dravis 1983; Dill et al. 1986), which occur as isolated or coalesced columnar structures that are not part of a reef complex.

During the past three years, we studied the biology and geology of stromatolites in the Stocking Island reef and elsewhere in the Exuma Cays in an attempt to identify patterns and processes of stromatolite development and to evaluate the role of stromatolites in Holocene reef construction. A variety of stromatolite localities throughout the Exuma Cays were mapped (Reid et al. 1995) and ecological factors controlling the distribution and abundance of Stocking Island stromatolites were investigated (Steneck et al. 1993 and work in progress). In addition, physiological responses of stromatolitic mats at Stocking Island to experimental manipulations of light and water chemistry were determined to identify variables controlling microbial community structure and function (Pinckney et al. 1995). In this paper, we examine growth patterns of stromatolites in the Stocking Island reef to identify when and how the stromatolites formed in relation to other reef-building organisms and to changing sea levels. Our analyses range from broad studies of facies development through time, to detailed examination of stromatolite microstructure.

SETTING

The Exuma Cays (Fig. 1A) are bordered on the west by Great Bahama Bank, where water depths are less than 10 m. To the east they are fringed by a shelf, 1–2 km wide and as much as 40 m deep. The shelf edge (Fig. 1B) marks a precipitous drop to depths of 2000 m in Exuma Sound. Surface waters in Exuma Sound and on the bank margin have a salinity of 36–37 ppt and are supersaturated with respect to aragonite and calcite (Droxler et al. 1988; L.M. Walter, unpublished data 1994). Winds are predominantly south and southeast trades. Tides are diurnal and have an average range of about 1 m.

The margin of Exuma Sound is an area of unusual stromatolite abundance. The first modern lithified stromatolites in water of normal marine salinity were discovered in the Schooner Cays, on the northeast edge of the Sound (Dravis 1983). Subsequently, stromatolites have been found at numerous locations, both subtidal and intertidal, throughout the Exuma Cays (Fig. 1A; Dill et al. 1986; Dill 1991; Reid and Browne 1991; Reid et al. 1995). Although stromatolites at most of these sites occur as isolated structures, at two localities (Stocking Island and Highborne Cay, Fig. 1A), they occur with other reef-building organisms as integral parts of laterally extensive fringing reefs.

Stocking Island, the study site, is approximately 2 km east of Georgetown, Great Exuma Island (Fig. 1B). The reef complex, which lies along the windward, east coast, is about 50 m wide and extends for about 3 km. There are scattered patch reefs 100–200 m seaward of the fringing reef.

METHODS

Surface samples from the Stocking Island reef were collected in 1992 and 1993; the reef was drilled in spring 1992. Cores 54 mm in diameter were recovered from 8 drill holes along a transect across a well developed section of the reef (Plate 1A) with a hand-operated hydraulic drill (Macintyre 1978). The deepest core hole was 2.41 m, and core recovery was excellent—commonly 100% in all but the uppermost, poorly lithified stro-
stromatolitic sections. Several short 30 cm cores were also drilled to place sediment maps in the reef. In addition to cores, surface samples were collected with hand saws and chisels in all reef zones, particularly at the tops of core holes with poor recovery.

Over 125 petrographic thin sections were prepared from core and surface samples. Surface samples of stromatolite, both untreated and treated with 5% sodium hypochlorite to remove organic tissue, were mounted on aluminum stubs, gold-palladium plated, and examined with a Hitachi S-570 scanning electron microscope.

Carbonate mineralogy was determined by standard X-ray diffraction techniques with Cu Kα radiation (Milliman 1974). Distribution of argonite and Mg calcite was determined by staining thin-section stubs with Feigl's solution (Friedman 1959) and Clayton yellow (Winland 1971), and making peels of stained surfaces.

It was difficult to obtain material from the Stocking Island reef for radiocarbon dating because of the abundance of marine cement and reworked skeletal debris. Using a dental drill, we removed cement surrounding and/or within several pieces of coral, hydrocoral, and gastropods for skeletal analysis; in other cases we analyzed bulk samples of lithified sediment and/or skeletons. Eight 14C dates were determined by standard techniques by Beta Analytic Ltd., and five small samples were dated by the particle accelerator (AMS) technique by the Lawrence Livermore National Laboratory. Dates are reported as radiocarbon years before 1950 A.D., conventionally termed "before present" (B.P.), using a Libby half-life of 5568 yr and a modern standard based on 95% of the activity of the National Bureau of Standards oxalic acid. No corrections were made for the DeVries effect, reservoir effect, or for natural isotopic fractionation.

The term "micrite" as used in this paper refers to carbonate crystals < 4 μm in size, following Folk (1974). "Micritization" is used in the sense of Alexanderson (1973) to refer to the alteration of a preexisting fabric to a micritic texture by changes in crystal size or shape and/or by the destruction of an ordered crystal arrangement.

RESULTS

Surface Zonation

The Stocking Island reef complex can be subdivided into three standard reef zones: back reef, reef flat, and fore reef; the fore reef includes coralline algal and pinnacle subzones (Plate 1A; Fig. 2). Each zone has a different degree of intertidal exposure and is characterized by a distinct biological community. Autothrophic assemblages include microbial mats dominated by filamentous cyanobacteria and algal turf (Sneek Steneck 1988), which is a mixed assemblage of diminutive algae, including prokarystic microalgae (cyanobacteria) and eukarystic filamentous algae, as well as corticated macroalgae. Herbivory is highest in the fore reef and essentially nonexistent in the back reef (Steneck et al. 1993).

Although the back-reef zone is typically exposed for 3–4 hr during each low tide, surfaces do not dry out completely, because they are occasionally washed by waves. Surfaces in the back reef are generally covered by soft or crusty, knobby microbial mats dominated by the filamentous cyanobacterium Schizothrix (Fig. 3A). On an initial visit to the reef site (Nov. 1989), gelatinous putulites of Navicula-like diatoms were also abundant (Reid and Browne 1991), but these have not since been observed. Other algae, such as Batophora australis, are common in subtidal channels in the back reef.

The reef flat is exposed for 5–6 hr at low tide, but is also continually washed by waves. Surfaces of the reef flat are generally uneven and hard. Mats in shoreward areas are light orange and are dominated by cyanobacteria, mainly Schizothrix, with minor Lyngbya spp., Oscillatoria sp., Phormidium sp., Calothrix sp., and Gloeocapsa sp.; scattered turf algae such as Cladophora macrorhiza, Laurenzia papillosa, and Eremosphaera verruculosa are also common (Fig. 3B). In addition to microbial covers forming hard surfaces, small patches of thin Schizothrix mats occur in depressions on the reef flat and coat walls of channels that cut through the reef flat. The seaward part of the reef flat is dominated by macroalgae, commonly with
an understory of *Schizothrix* sp. and sand; the turf community consists of macroalgae including phaeophytes (*Dictyota* sp., *Lobophora variegata*), chlorophytes (*Acetabularia calyculus*, *Batophora oerstedii*, *Cladophoropsis macrorhiza*, *Dictyosphaeria cavernosa*, *Erdosmis verticillata*), and rhodophytes (*Laurencia papillosa*).

The fore reef is almost entirely subtidal. Waves break in the shoreward part of the fore reef, which is designated the coralline/echinoderm subzone (Fig. 2). The surface of this subzone is extensively pitted by excavations by the echiurenid *Echinometra lucunter*, which feeds on drift algae and tends to concentrate near the mean low tide level. Large populations of this active bioracer are rapidly undercutting the inner part of the fore reef and cutting back into the seaward edge of the reef flat (Fig. 3C). Branching forms of the coralline alga *Neogoniolithon strictum* are also common in this subzone, particularly on the emergent tops of columnar mounds, with up to 0.5 m of relief, at the inner limits of the fore reef (Fig. 3C). Diverse macroalgae form turfs throughout the fore-reef, including, in order of decreasing abundance, *Erdosmis verticillata*, *Cladophoropsis macrorhiza*, *Laurencia oblonga*, *Neogoniolithon strictum*, *Dictyota* sp., *Dasyycladus vernacularis*, *Colpomenia sinuosa*, *Dasya bailiwiana*, *Caulerpa* spp., *Paragoniolithon typica*, *Dictyosphaeria cavernosa*, *Anadyomene stellata*, *Peyssonnelia* sp., *Gracilaria cylindrica*, *Padina pavonica*, *Jania canariaca*, *Wrangelia penicillata*, *Spyridia filamentos* and *Sargassum* sp. The first four species of this list constitute nearly 75% of the macroalgae. Small colonies of corals and hydrocorals are also common in the fore reef, particularly at the seaward limits of the coralline/echinoderm zone (Fig. 3D). The most abundant of these is *Millepora complanata*, but *Siderastrea radians*, *Siderastrea siderea*, *Diploria clivosa*, *Porites porites*, and *Porites astreoides* are also common.

Seaward of the coralline/echinoderm subzone, the sea floor drops to a depth of 4 m and the bottom is characterized by numerous pinnacles and ridges rising up from a sand-swept, smooth rocky floor (Fig. 3E). This area was designated as the ‘‘pinnacle subzone’’ of the fore reef. The ridges are perpendicular to the shoreline and are commonly composed of a series of blade-like pinnacles, which generally have a shoreward inclination. Most of these pinnacles have smooth hard surfaces; several also have rough, slightly bulbous caps, with scattered growths of macro-algae (including *Sargassum* sp. and *Caulerpa* sp.), and *Schizothrix* mats (Fig. 3E).

**Internal Structure**

Cores indicate that the Stocking Island reef is up to 2.1 m thick and was established on a terrace of Pleistocene limestone (Fig. 2). Caliche crusts, a leached appearance, and root casts in the Pleistocene limestone enabled easy recognition of the Holocene/Pleistocene contact in the field. In thin section, the Pleistocene limestone is characterized by blocky, sparry, calcite mosaic cement, which allowed identification of lithoclasts of this limestone in the overlying Holocene reef.

**Reef Facies**

Five facies were identified in core material recovered from the Stocking Island reef: stromatolite, branching coralline algal, encrusting coralline algal, vermetid, and calcarenite facies (Fig. 2).

**Stromatolite Facies:** The stromatolite facies is a zone of microbial deposits, many of which show macroscopic lamination and are accordingly designated ‘‘stromatolites’’. This facies is a major component of the back-reef (Holes 5 and 8 and uppermost Hole 6; Fig. 2) and reef-flat zones (Holes 1, 3, and 4; Fig. 2); over 1 m of stromatolite was recovered in Hole 1.

Layering in the stromatolites is defined mainly by differential lithification; laminae are most readily observed in sawed slabs from the upper sections of the buildups, where preferentially indurated layers 1–3 mm
Fig. 3.—Photographs showing surface biota in each reef zone. A) Knobby *Schizothrix* mat in back reef. B) Hard microbial mat with dwarf turf algae on seaward part of reef flat. C) Contact between reef flat and fore reef. Turf-covered, seaward edge of reef flat has been undercut by the urchin *Echinometra lucunter*. Abundant growths of *Neogoniolithon strictum* occur at the inner edge of the fore reef (arrow). D) Outer edge of coralline/technoderm zone showing *Millepora complanata* (M), *N. strictum* (N), and *Porites porites* (P) on an extensively bored substratum covered with macroalgae and anemones. E) Fore-reef pinnacles; most have smooth erosional surfaces, a few have bulbous caps covered with crustose corallines and other macroalgae.
Fig. 4.—Scanning electron micrographs of micritic horizon in a stromatolite. A) Microbially mediated upper surface with micritic crust bridging grains; note that intense microborings along this surface truncate the tops of grains. B) Point-contact aragonite cement between micritized grains.

thick stand out in relief on cut surfaces (Plate 1B). These layers are commonly disrupted by cavities, typically 1 cm or more in diameter, created by sponges, molluscs, worms, and other boring organisms (Plate 1B).

Thin sections (Plate 1C, D) reveal that the stromatolites have a characteristic microfabric, in terms of both grain size and microstructure. They are composed predominantly of well-sorted fine sand (125–250 μm), which contrasts with the poorly sorted, fine sand to gravel-size sediment in internal cavities of the stromatolites and on the adjacent sea floor. The fine stromatolitic sand consists mainly of rounded micritic grains, some of which have relict skeletal or biotic textures, with about 5–10% clearly recognizable skeletal grains—mainly molluscs, corals, coralline algae, benthic foraminifera, and echinoderm fragments. Many of the grains have superficial oolithic coatings. Mg calcite filaments (20 μm in diameter) of the green alga Ostreobium and small, sometimes branching, aragonitic filaments (5–10 μm in diameter), probably representing cyanobacteria, are common in the interstitial spaces of some samples, particularly those from the reef flat. More typically, however, cyanobacterial filaments in the stromatolites are calcified and are not preserved. The fine-grained texture of the stromatolites is identical to that found in living Schizothrix mats in the back reef and on the reef flat.

The indurated layers that stand out in relief on cut surfaces of partially lithified stromatolites (Plate 1B) from upper sections of the reef, as well as the crusty surfaces of many living Schizothrix mats, appear in thin section as “micritic horizons”. The petrographic features of these micritic horizons are subtle but distinct, and once recognized can be used to identify stromatolitic deposits in deeper, well-lithified portions of the reef. These horizons typically consist of two components: micritic crusts and an underlying layer of micritized sediment grains that are truncated along a surface of intense microborings (Plate 1C, D; Fig. 4A). The micritic crusts occur as thin, subhorizontal layers of aragonite, 20–40 μm thick, which bridge grains (Plate 1D), extend laterally for several centimeters, and are commonly encrusted by organisms such as Ostreobium, coralline algae, and foraminifera. Intense microborings immediately below the crust truncates and/or destroys grains (Fig. 4A, Plate 1D), in some cases leaving only remnants of grains that may be difficult to distinguish from the micritic crusts. The zone of grain micritization, typically 200–1000 μm thick, extends well below the densely microborred surface (Plate 1D), and consists of aragonitic grains (generally with few microborings; Fig. 4A) that have lost all evidence of their original texture. These grains have a gray-brown color in plane-polarized light that contrasts markedly with unaltered grains and/or their oolithic coatings, which typically appear golden brown (Plate 1C, D). Equant and needle-shaped aragonite crystals, both < 1 μm in size, form point-contact cement between adjacent micritized grains (Fig. 4B). With increasing precipitation, the boundaries between micritized grains and cement become indistinct and grains appear “welded” together.

Subsequent to early formation of indurated layers, the entire stromatolite is progressively hardened with depth by submarine lithification. Micritic aragonite and Mg calcite, commonly with peloidal textures, are precipitated in interstitial spaces and other cavities. In addition, acicular aragonite rim cement (crystal length 10–20 μm) forms on poorly sorted cavity infillings. Well-lithified stromatolites from Hole 1 also show extensive precipitation of detrital Mg calcite (5–10 μm crystals) rim cement.

Well-laminated stromatolites can grade laterally or vertically to crudely laminated and unlabeled microbial deposits within the stromatolite facies; these deposits are especially common on outer sections of the reef flat and in the inner fore reef, where present-day surfaces are dominated by turf algae. Some of the poorly layered deposits result from pervasive boring and infilling of stromatolite, others are original, unlaminated microbial buildups. The latter, which have a clotted macroscopic fabric, are designated as “thrombolites”, following Feldmann (1995). It is often difficult, at best, to distinguish between the reworked stromatolites and thrombolites.

Both of these poorly layered structures are typically poorly sorted, with an abundance of medium and coarse sand and even gravel-size sediment that is commonly fringed with acicular aragonite. In addition, both structures may contain patches of sediment with the characteristic stromatolite microstructure: fine sand with micritic horizons. A diagnostic feature of many of the thrombolites is an abundance of large calcified algal filaments (25–100 μm) (Plate 1E) and/or irregular holes representing space originally occupied by turf algae. In some thrombolites, the calcified filaments make
framework structures, which may disrupt the continuity of intermixed mictic horizons (Plate 1E).

Branching coralline algal facies: This is the major facies of the fore reef (Fig. 2), forming most of Hole 2 and short cores drilled for sediment traps in the coralline/echinoid zone. It is also present in the back reef, below the stromatolite facies in Holes 6 and 8 (Fig. 2). The facies is characterized by branched skeletons of Neogoniolithon strictum (Fig. 5A). In some samples, N. strictum is mainly in growth position; in other samples, broken fragments of this skeleton form calcirudites.

This facies also includes encrusting coralline algae (e.g., N. strictum in an unbranched form, N. accretum, N. moricae, Paragoniolithon sp., Lithoporella atlantica, Lithophyllum intermedium, Porolithon pachydermum, and Turpinodera spp.) and Peyssonnelia sp. Algal skeletons are commonly encrusted by the foraminifer Homotrema rubrum (Fig. 5B), worm tubes, vermetid gastropods, and Ostreaebium sp. In addition, the skeletal framework is filled with poorly sorted sediments of fine sand to gravel size and consisting mainly of fine to medium, rounded mictic grains that commonly have superficial oolithic coatings and relict skeletal and lithoclastic textures. Skeletal grains in the matrix, which range from sand to gravel size, include molluscs, encrusting coralline algae, porcelainous benthic foraminifera, and lesser proportions of Halimeda, echinoderms, corals, Homotrema and worm tubes; fragments of Pleistocene limestone are also common. This facies is well indurated by submarine lithification. Mictic Mg calcite precipitates, commonly with peloidal textures, are abundant in interstices and other cavities. In addition, rim cement is also common, with acicular aragonite (10–20 μm) dominant in the fore reef and denteate Mg calcite (5–10 μm) dominant in the back reef. Both rim cements can, however, be found in samples from either zone and may coexist in the same sample.

Encrusting coralline algal facies: In contrast to the facies above, the encrusting coralline facies is distinguished by an abundance of encrusted growth forms of N. strictum (Fig. 5C). N. strictum changes its growth form from branched in open settings to encrusting when mantled by sediment (Steneck et al., in press). This facies is present in the shore zone of the back reef, overlying Pleistocene limestone in Hole 7 (Fig. 2), and forms caps on some of the fore-reef pinnacles. Probing with an air chisel indicated that encrusting coralline algae facies formed the upper half of a large pinnacle 1.8 m tall (Fig. 2).

In addition to encrusting forms of N. strictum, occasional branching forms of this alga are also present. Algal skeletons are commonly encrusted by Homotrema rubrum, tubules of Ostreaebium, and worm tubes. Sediment between the larger skeletons is similar to that in the branching coralline algal facies. Occasional patches of fine sand with horizons of micritized grains and/or mictic grains and/or skeletal grains like those in the stromatolite facies are present in the pinnacle. Micritic Mg calcite precipitates, commonly with peloidal textures, form cavity infillings throughout the encrusting algal facies. The dominant rim cement in both the back reef and the pinnacle is dentate Mg calcite (5–10 μm), with minor aragonite fringe cement (10–20 μm).
TABLE 1.—Radiocarbon dates of Stocking Island core samples

<table>
<thead>
<tr>
<th>Holes</th>
<th>Core 4</th>
<th>Core 5</th>
<th>Core 6</th>
<th>Core 7</th>
<th>Core 8</th>
<th>Core 9</th>
<th>Core 10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth of Recovery (m)</td>
<td>3.70</td>
<td>3.45</td>
<td>3.66</td>
<td>3.64</td>
<td>3.95</td>
<td>2.02</td>
<td>1.00</td>
</tr>
<tr>
<td>Material</td>
<td><em>Gastropod Cucullata sp.</em></td>
<td><em>Hydrocorallus sp.</em></td>
<td><em>Lithocorallus sp.</em></td>
<td><em>H. mollispora sp.</em></td>
<td>Bulk sample of <em>Vermelina</em></td>
<td>Bulk sample of <em>Vermelina</em></td>
<td>Bulk sample of <em>Vermelina</em></td>
</tr>
<tr>
<td>Measured 14C Age (y B.P. ± SD)</td>
<td>3750 ± 70</td>
<td>2370 ± 70</td>
<td>4440 ± 130</td>
<td>2910 ± 100</td>
<td>4270 ± 130</td>
<td>3460 ± 160</td>
<td>1890 ± 80</td>
</tr>
</tbody>
</table>

*Samples analyzed by the accelerator mass-spectrometer technique.*

**Vernedtid facies:** This facies is characterized by an abundance of vernedtid gastropods (Fig. 5D) and overlies Pleistocene limestone at the base of Holes 1, 3, and 4 (Fig. 2). Other framework contributors in this facies include coraline algae, such as *Paragoniolithon* sp. and encrusting forms of *N. strictum*. These skeletons are commonly encrusted with *Ostreobium* sp., *Homotrenia rubra* and, worm tubes. Surrounding and infilling the skeletal framework is a fine to medium sand similar to that in the coralline algal facies. Cavity infillings of precipitated micritic Mg-calcite are abundant. The dominant rim cement is detrital Mg calcite (5–10 μm), but rims of acicular aragonite (10–20 μm) cement are also present.

**Cacareneous facies:** This is a minor facies of the Stocking Island reef, forming the base of the fore-reef pinnacles and patches in the reef flat and back reef (Fig. 2). Composition, grain size, and cement in this facies are similar to those in the coralline algal facies; although coraline algae are not dominant components of the cacarene. Coralline algae in this facies include *N. strictum* and *Titanodera* sp.

**Age of the Stocking Island Reef**

Radiocarbon ages of samples from the Stocking Island reef (Table 1, Figure 2) show some reversals in the core holes, indicating possible redeposition of skeletal fragments. In addition, because several dates represent analysis of bulk samples (Table 1), introduction of marine cements could cause an apparent reduction in age of associated skeletal material.

**Discussion**

**Reef Development**

Despite the difficulties in dating material from the Stocking Island cores, an overall pattern of reef development is suggested by available 14C dates. Comparison of the ages and facies distributions (Fig. 2) with a Bahamian sea level curve (Boardman et al. 1989), suggests the following growth stages (Fig. 6).

**Stage 1. Vernedtid Reef (~ 4500–4000 yr B.P.).**—Reef growth at Stocking Island was initiated on a Pleistocene limestone terrace with establishment of an intertidal vernedtid gastropod assemblage that became a well-developed buildup by about 4000 yr B.P. These gregarious gastropods are noted for forming reef accumulations on intertidal benches or ledges elsewhere (Crossland 1905; Perret and Picard 1952; Kempf and Labore 1968; Saffert 1974). Indeed, a present-day analog of this environmental setting exists ~ 2 km north of our core hole transect at Stocking Island, where the beach gives way to a cliff shoreline and the sea impinges on
exposed Pleistocene limestone with intertidal vermetid accumulations (Fig. 7A).

Stage 2. Algal Ridge (~ 4000–2000 yr B.P.)—The Pleistocene terrace and vermetid reefs were flooded during the Holocene transgression. Branching forms of the coralline algae *N. strictum* began to grow at the outer edge of the platform, and spread shoreward over the vermetid buildup. *Neogoniolithon* buildups were also established on inshore elevated Pleistocene areas. In addition, an offshore sand bar formed seaward of the rapidly developing algal ridge.

Stage 3. Stromatolite Formation (~ 2000–1000 yr B.P.)—The *Neogoniolithon* ridge at the outer edge of the terrace caught up with sea level and formed an intertidal lip, reducing wave energy in the back reef. Stromatolites began to form behind the ridge at this time. An analog for this stage of reef growth is the present-day reef at Highborne Cay, where a partially exposed algal ridge provides protection for shoreward growth of stromatolites (Fig. 7B; Reid et al. 1995). In addition to stromatolites, algal buildups dominated by encrusting forms of *N. strictum* formed in localized inshore areas. During this stage, the offshore sand bar became partially lithified, and was differentially eroded to form ridges and pinnacles. Some pinnacles were colonized by encrusting forms of *N. strictum* and *Schizothrix* mats, which formed bulbous caps on some of these structures.

Stage 4. Apex Growth (~ 1000–500 yr B.P.)—The stromatolite and algal ridge reef complex was probably at the apex of its development. A mature *Neogoniolithon* algal ridge at its outer edge allowed inshore stromatolites to flourish, and as they grew up to sea level, individual columns coalesced to form a broad reef flat. Encrusting *N. strictum*, now buried in the back reef, continued to grow on fore-reef pinnacles that were being abraded and scoured by sand.

Stage 5. Reef Degradation (~ 500 yr B.P. to present).—The past 500 years have been dominated by reef destruction. Although stromatolites continued to flourish in the back-reef area, extensive bioerosion has reduced the algal ridge from an emergent intertidal feature to a submerged, subtidal pavement. Bioerosion was accomplished mainly by *E. lucunter*. Urchins may have started to flourish on the reef following a reduction of wave energy caused by development of offshore patch reefs. A similar scenario was proposed for the demise of an algal ridge complex off the southeast coast of St. Croix (Adcy and Burke 1976).

*E. lucunter* is an efficient bioeroder that easily attacks the open network of branching growths of *N. strictum* at Stocking Island. As a result, the algal ridge was rapidly undercut and large pieces were eroded by waves, leading to considerable reduction in relief. *E. lucunter* then began to erode the upper section of the outer edge of the reef flat, exposing the original microbial columnar buildups. Indeed, *E. lucunter* are still actively undercutting the seaward edge of the reef flat at the mean low tide level (Fig. 3C). Present-day rates of bioerosion of this reef suggests that, eventually, much of the upper sections of the stromatolite accumulations at Stocking Island will be destroyed.

### Stromatolite Growth

Our investigation of past and present growth patterns of stromatolites in the Stocking Island reef suggests that they were built by microbial mats dominated by the cyanobacterium *Schizothrix*, that stromatolite laminar formation results from early lithification within these cyanobacterial mats, and that competition for substrate between cyanobacteria and turf algae is an important control on stromatolite formation. Similarities between the textures and microstructures of well-layered, subsurface microbial deposits and those in living *Schizothrix* mats in the reef are evidence for the involvement of these mats in forming the stromatolites. This inference is further supported by detailed studies of the role of *Schizothrix* in construction of subtidal stromatolites at Lee Stocking Island (Browne 1993).

Episodic lithification of sediment agglutinated by the cyanobacterial mats, which creates the laminated fabric of the stromatolites, corresponds to the development of micritic horizons. The characteristic features of these lithified horizons (micrite crusts overlying "welded" micritized grains) are unlike previously known features formed by submarine cementation. To our knowledge, they develop only in cyanobacterial mats. This suggests that precipitation in these horizons is biologically induced. We hypothesize that the micritic horizons form within cyanobacterial mats during hiatuses in sediment accretion. Biogeochemical processes within stable, stratified mats could induce micritization of grains, precipitation of point-contact cements between micritized grains, and precipitation of micrite crusts.

Micritization is a well-known process of carbonate diagenesis that is generally attributed to precipitation of carbonate cements in microborings (Bathurst 1975; Tucker and Wright 1990). It has recently been shown, however, that micritization of shallow-water carbonate grains also occurs by processes of crystal alteration, which involve changes in the size, shape, and, in some cases, mineralogy of these grains (Reid et al. 1992; Macintyre and Reid 1995; Reid and Macintyre 1995). Observations that grains in the micritic horizons of Stocking Island stromatolites are
micritized well below the surfaces of intense micromorbing (Plate ID), together with the paucity of micromorbing in grains below this surface (Fig. 4A), argue that these grains were micritized mainly by crystal alteration rather than by infilling of micromorbing. Crystal alteration could be induced by fluctuating chemical microenvironments within an established mat, which lead to alternating dissolution and reprecipitation. These conditions, possibly in association with carbonate dissolution by micromorphing at the surface of the micritized horizon, could also cause precipitation of point-contact cements between micritized grains.

We propose that the thin micrite crusts, which typically overlie the layers of micritized sediment grains, represent precipitation within organic films formed at the surfaces of mature mats or precipitation associated with microbial degradation of such films (e.g., Reiner 1993; Kember and Kazmierczak 1993). Observations that these crusts form bridges between adjacent grains, rather than draping over these grains and filling interstitial spaces (Plate ID), are evidence that they were hard at the time of formation; this is supported by the common occurrence of encrusting organisms on the crusts. It is significant to note that the micrite crusts in Bahamian stromatolites are comparable in texture and thickness to crusts in Shark Bay stromatolites (e.g., Monty 1976, fig. 13e), as well as to micritic laminae in some ancient stromatolites. For example, micritic films in a variety of Archean stromatolites are 10-40 μm thick (Walter 1983), and those in some Riphean forms are 30-50 μm (Bartun-Safarli 1976). In addition, Monty and Mas (1981) recognized that thick micritic laminae (200-500 μm) in Cretaceous stromatolites were composed of superimposed micritic films, each about 40 μm thick. These observations are important, because they raise the possibility that biogeochemical processes creating lithified micritic laminae in both modern and ancient stromatolites could be similar. This proposition presents a contrasting point of view to claims that modern marine stromatolites, which are "granny," are inappropriate analogs of ancient stromatolites, which are typically micritic (e.g., Awramik and Riding 1988; Riding et al. 1991a).

Our petrographic observations further indicate that introduction of turf algae to the cyanobacterial-mat community inhibits lamination formation (and thus stromatolite development) because these erect algae disrupt the continuity of the flat-lying cyanobacterial mats, and thereby prevent formation of laterally continuous micritic horizons (Plate IE). The role of eukaryotic algal communities in forming poorly layered or unlayered microbial deposits in the Bahamas has been noted by other authors (Awramik and Riding 1988; Riding et al. 1991a). These authors did not, however, recognize well-laminated Bahamian buildups formed by cyanobacterial mats. In designating all Bahamian microbial buildups as stromatolites, regardless of degree of layering, Awramik and others overlooked the role of cyanobacteria in creating laminated fabrics.

High sediment influx appears to be the major factor excluding turf algae from the present-day back-reef area at Stocking Island, thereby allowing stromatolite formation. This interpretation is suggested by the distribution of biota within the reef complex, which shows a shoreward trend in degree of sediment tolerance ranging from corals (the least sediment-tolerant organisms) to branching coralline algae, encrusting coralline algae, turf algae, and finally Schizothrix-dominated microbial mats (the most sediment-tolerant organisms). It is also supported by reciprocal transplant experiments and sediment-movement data collected in concurrent ecologic studies at Stocking Island, which show low survival of turf algae in the back-reef zone where migrating dunes episodically bury the stromatolites (Steneck et al. 1993). Sediment inundation also prevents invasion of the back-reef zone by grazers and colonization of this area by encrusting biota such as corals and coralline algae (Steneck et al. 1993)—two factors previously cited as important controls on the distribution of Phanerozoic stromatolites (e.g., Garren 1970; Monty 1973).

We therefore propose that sediment stress has played a critical role in the growth history of the Stocking Island reef complex. Sediment-stressed conditions probably first developed in the back-reef area approximately 1500 yr ago, when wave energy in this zone was reduced by emergence of the algal ridge. Sediment accumulations formed in the lee of the ridge, and excluded the settlement and growth of most benthic communities and herbivores; but promoted development of stromatolite-forming Schizothrix mats. In the words of Monty (1973, p. 608), "... when local conditions were such that blue-green algae (cyanobacteria) became temporarily advantaged, they 'bloomed' and originated reef stromatolites". The zone of stromatolite growth at Stocking Island migrated shoreward with rising sea level to remain in the area of actively shifting sand. Older stromatolites in more seaward areas (i.e., the present-day reef flat) were colonized by turf algae when they were no longer inundated with sand, and this new community formed mainly thrombolites.

**Comparison with Other Exuma Stromatolites**

Our observations of stromatolites at numerous localities throughout the Exuma Cays and in the Schooner Cays (Reid et al. 1995) indicate that surface communities, textures, and microstructures of these structures, which typically occur as subtidal columnar buildups, are similar to those of stromatolites in the Stocking Island reef. It is important to note, however, that microbial deposits at most of these sites range from stromatolites to thrombolites.

Although lamination in stromatolites throughout the Exuma Cays results from periodic formation of lithified layers defined by micritic horizons, laminae are typically thinner in stromatolites formed in subtidal environments (e.g., channels near Lee Stocking Island) than in intertidal stromatolites (e.g., many back-reef stromatolites at Stocking Island). In particular, the distance from the top of one micritic horizon to another is ~ 0.5 mm in subtidal stromatolites, compared to ~1-3 mm in intertidal stromatolites. Because of the close spacing of micritic horizons in subtidal stromatolites, most of the grains in these structures are micritized and there is generally no distinct alternation of gray-brown and golden-brown bands, as evident in intertidal stromatolites (e.g., Plate IC).

Our conclusions regarding stromatolite lamination differ from those of previous studies conducted in the vicinity of Lee Stocking Island. We suggest that variations in grain size, alignment of pores, and submicrofibrillar cements (Dill et al. 1986; Griffin 1988; Dill 1991) are insignificant in creating macroscopic lamination. We agree in part with Browne (1993), who concluded that lamination of Lee Stocking stromatolites was defined by laterally discontinuous micritic crusts formed within cyanobacterial mats. We argue, however, that in addition to precipitation of micrite crusts, the formation of lithified laminae in these stromatolite-forming mats involves a "welding" of micritized grains by precipitation of point-contact cements.

**Reported Occurrences of Stromatolites in Other Holocene Reefs**

Various authors (e.g., James and Ginsburg 1979; Pratt 1982; Riding et al. 1991b; Montagioni and Camoin 1993; Camoin and Montagioni 1994) have used the term "stromatolite" to designate lithified Mg-calcite crusts, which have long been recognized in modern coral reefs (see Macintyre and Marshall 1988). Lamination is, however, uncommon in these crusts, which typically have cloistered peloidal, thrombolitic fabrics. Moreover, recent studies have shown that cyanobacteria, which are photosynthetic and have been considered "sine qua non for stromatolite construction" (Awramik 1991, p. 292), are rare to absent in the cryptic, aphotic environments in which these crusts form (Reiner 1993 and personal communication 1995). These cryptic, micritic crusts are, therefore, in no way comparable to ancient stromatolites. In contrast, stromatolites in the Stocking Island reef, which are macroscopically laminated structures built by cyanobacterial-dominated communities, forming accumulations over 1 m thick in open reef settings, are potential analogs of ancient stromatolites.
SUMMARY AND CONCLUSIONS

Stromatolites are a major structural component of the Stocking Island reef, forming buildups up to 1 m thick. Formation of the reef began about 4500 years ago with the accumulation of vermetid gastropod timbers on an intertidal Pleistocene terrace. With the subsequent flooding of this terrace, the coralline alga Neogoniolithon structure replaced the vermetids and eventually formed an emergent algal ridge about 1500 years ago. Shifting sand accumulated in the lee of this ridge, excluding most benthic communities and termites and promoting the growth of Schizophyllum-dominated microbial mats that formed stromatolites. Extensive bioerosion over the last 500 years, mainly by the archean Echinometra lucunter, has resulted in the destruction of the emergent, intertidal part of the algal ridge and erosion of the outer edge of the stromatolitic reef flat. With the continuous degradation of this reef by echinoids, the poorly lithified, upper sections of the stromatolite buildups could eventually be destroyed.

In contrast to studies reporting that modern marine stromatolites in the Exuma Cays are built by communities of eukaryotic algae (e.g., Awramik and Riding 1985; Kitting et al. 1991a), our findings indicate that microbial deposits at Stocking Island and elsewhere in the Exumas range from well-laminated, prokaryotic structures (stromatolites) to unlaminated eukaryotic buildups (thrombolites). We also argue that macroscopic lamination of the Exuma stromatolites results mainly from biologically induced formation of indurated layers within cyanobacterial mats, rather than from factors such as variations in grain size, alignment of pores, or submarine cements (e.g., Dill et al. 1986; Griffin 1988; Dill 1991). Formation of the indurated stromatolitic layers results in part from precipitation of micritic crusts, as documented by Brown (1993). Additional, previously unrecognized lithification processes within these mats involve a "welding" of micritized grains by precipitation of point-contact cement. Precipitation of this point-contact cement may be induced by micritization. Micritization of grains within the lithified layers is thought to occur by processes of crystal alteration, rather than by microboring, which is confined mainly to the upper surfaces of the micritized layers.

Substrate competition between cyanobacteria and turf algae is identified as an important control of stromatolitic formation based on our observations that lamination formation is disrupted by the introduction of erect turf algae to the flat-lying cyanobacterial mat community. Because algal turf produces thrombolites rather than stromatolites, formation of stromatolites is restricted to areas where environmental factors, such as sediment inundation, limit growth of turf communities. We suggest that competition between turf algae and cyanobacteria could be as important as competition with encrusting bivalves (Monty 1973) or restriction of stromatolites by grazing and burrowing animals (Garrett 1970) in controlling the distribution of modern stromatolites.

Although modern marine stromatolites, which are sandy, have been considered inappropriate analogs for ancient micritic forms (Awramik and Riding 1985; Riding et al. 1991a), our study shows that these structures have a fundamental similarity both are characterized by micritic laminae. Moreover, we propose that in both cases, these micritic laminae could form as a result of biogeochemical processes within cyanobacterial mats.

Finally, we conclude that use of the term "stromatolite" is inappropriate to describe micritic crusts formed within the framework of Holocene reefs, which show limited lamination and are not products of cyanobacterial mats. Although possibly of microbial origin, these crypto crusts are not comparable to ancient stromatolites or stromatolites to Stocking Island reef.

ACKNOWLEDGMENTS

This research was supported by National Science Foundation Grant OCE-9116296 to R.P. Reid and R.S. Steinke. Able field support was provided by T. Miller, M. Luziv, K. Nielsen, A. Palma, R.A. McGreggor, and C. Haxby. Thanks to W. McGreggor, C. Cary, E. Haxby, and the captain and crew of the NRV Calypso for logistical assistance. In addition we are indebted to the following people for their contributions to this study: W.R. Brown and S.G. Braden (SEM); D.A. Dean (thin sections); W.T. Boykins (X-ray diffraction and photography); M.E. Parrish (drilling). We are grateful for stimulating discussions with K.M. Brown and M. Feldmann, who generously shared their knowledge of Exuma stromatolites. Thanks also to S.J. Mazzullo, K.M. Towe, A.H. Cutler, and an anonymous reviewer for helpful suggestions that improved the manuscript.

REFERENCES
