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**A MICROBIALITE/ALGAL RIDGE FRINGING REEF COMPLEX,
HIGHBORNE CAY, BAHAMAS**

BY

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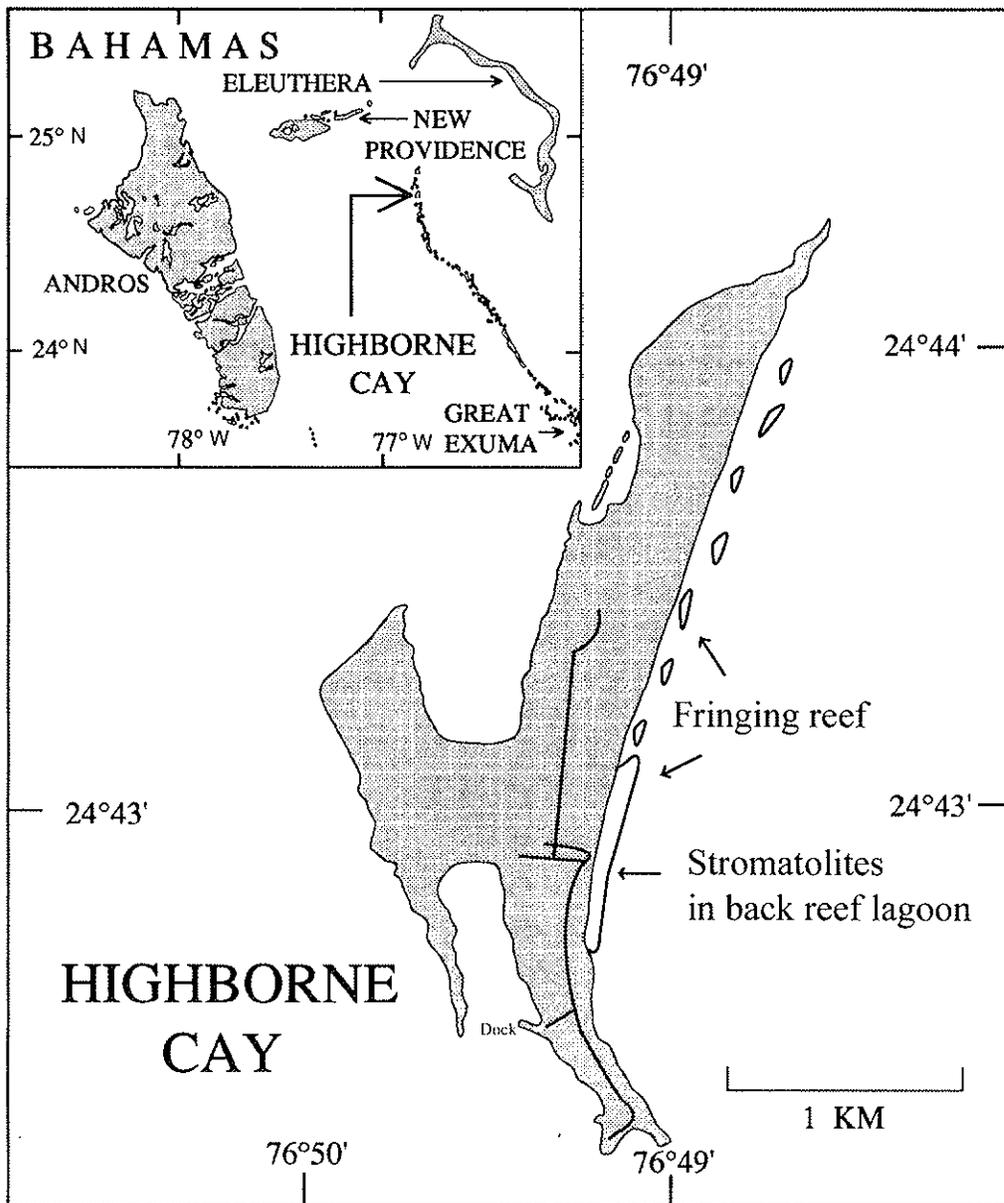


FIGURE 1. Map showing the location of Highborne Cay, Bahamas; stromatolites form in the southernmost kilometer of a microbialite/algal ridge fringing reef complex along the east shore.

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ABSTRACT

Microbial deposition plays an important role in the construction of a present-day fringing reef complex at Highborne Cay, Bahamas. This reef consists of an algal ridge that grades shoreward to a back reef lagoon with a diversity of microbial buildups. Intertidal stromatolites and thrombolites form tabular mounds several meters in diameter and up to a meter thick in the nearshore zone. Shallow subtidal stromatolites form ridges and columnar heads up to half a meter high in the sandy lagoon. A tufa-like rock forms ridges at the bases of some of the thrombolites. The algal ridge is composed mainly of the branching crustose coralline alga, *Neogoniolithon strictum*, which, until recently, was not known to form algal ridges. The coralline algae are commonly coated with micritic crusts of possible microbial origin. This unusual reef is an ideal system for geomicrobiological studies.

INTRODUCTION

Laminated microbial deposits known as stromatolites have a unrivalled geologic history dating back more than 3 billion years and ranging to the present day. Modern stromatolites forming in waters of normal marine salinity were first discovered in the Schooner Cays on the northeastern margin of Exuma Sound (Dravis 1983). Subsequently, marine stromatolites have been mapped at numerous locations throughout the Exuma Cays, on the western margin of Exuma Sound (Dill et al. 1986; Dill 1991; Reid and Brown 1991; Reid et al. 1995). Stromatolites in most of these examples occur as columnar buildups in tidal channels. However, at two locations, Stocking Island and Highborne Cay, stromatolites form as part of a fringing reef complex. In addition to stromatolites, these fringing reefs incorporate an unusual algal ridge system (Steneck et al. 1997). The growth history of the stromatolite-algal ridge reef complex at Stocking Island was studied by Macintyre et al. (1996). The present paper describes the reef zonation at Highborne Cay. The Highborne Cay reef includes some of the best laminated stromatolites in the

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FIGURE 2. Fringing reef along the east shore of Highborne Cay; line marks the location of the transect shown in Figure 3.

HIGHBORNE REEF PROFILE

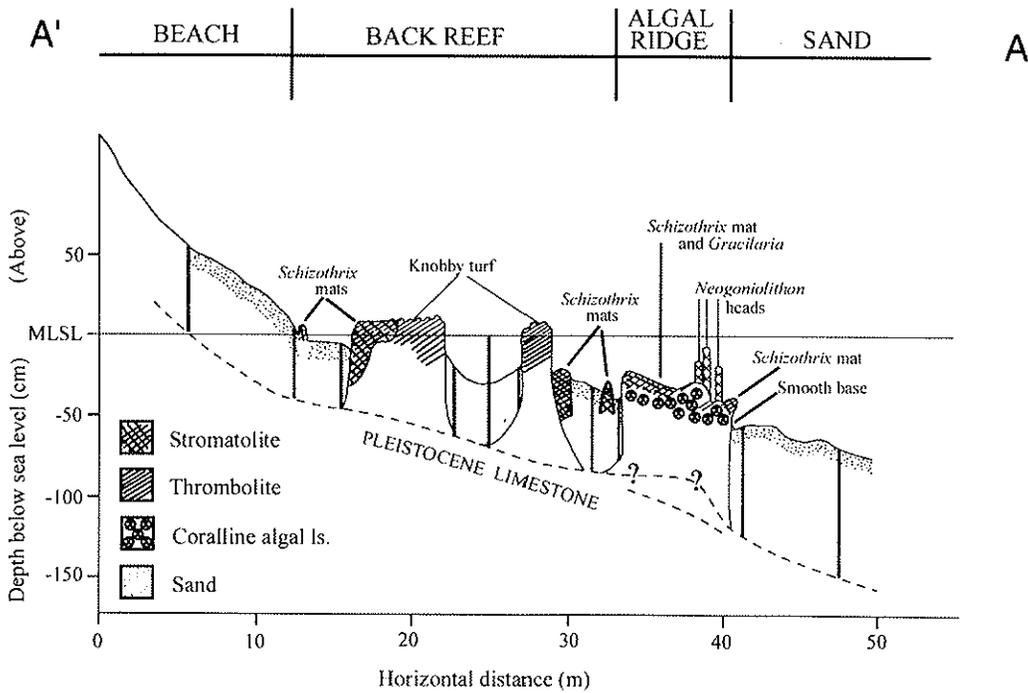


FIGURE 3. Transect across the fringing reef, along line A-A' as shown in Figure 2; vertical lines mark the location of probe holes made to estimate depth to Pleistocene.

Exuma Cays. Consequently, this island was selected as the primary field site for a multidisciplinary investigation of geomicrobiological processes forming lithified micritic laminae in modern marine stromatolites. This project, which involves participation of approximately 12 investigators from ten institutions in the US and Europe, is known as the Research Initiative on Bahamian Stromatolites, or RIBS project. In addition to stromatolites, a variety of other microbial deposits are abundant in the Highborne Cay reef, including thrombolites, micritic crusts and tufa-like deposits; these microbialites have not been studied in detail and await investigation.

Highborne Cay is a small island near the north end of the Exuma Cays (Fig. 1). Formed predominantly by Pleistocene aeolianite limestone, the island consists of two curvilinear ridges, 2 to 4 km long and trending north-south; the two ridges coalesce in the middle of the island, giving a maximum width of about 1 km. A fringing reef extends along a beach on the eastern margin of the island, facing Exuma Sound. A shelf, with an average depth of 10-20 m, extends 1-2 km offshore; at the shelf margin water depths increase rapidly to greater than 1000 m in Exuma Sound.

Surface waters of Exuma Sound have a salinity of 36-37 ppt and are saturated with respect to both aragonite and calcite (Droxler et al. 1988). Intermittent south and southeastern tradewinds dominate this area (Adey 1978); large ocean swells are rare. Tides are diurnal and have an average range of about 1 m.

REEF DESCRIPTION

The fringing reef along the eastern margin of Highborne Cay is about 2.5 km long. It is best developed in the southernmost kilometer of the beach, where it is 30 to 50 m wide, has 0.5 to 1 m of relief, and shows distinct zonation: an algal ridge colonized dominantly by macroalgae grades shoreward to a back reef lagoon of microbial buildups (Fig. 2). A transect across this southern section, measured perpendicular to the shore using a level line and probe, is shown in Fig. 3. Further north along the beach, the back reef zone of microbial buildups is lacking and the reef becomes a discontinuous algal ridge.

Back Reef

The back reef zone is comprised of carbonate mounds in a sandy lagoon. Surfaces of these mounds are colonized by two distinct types of microbial mat: smooth mats (Fig. 4A) and knobby turf (Fig. 4B); carbonate sand grains are abundant in both mat types. The biologic composition of the smooth mats will be described in detail by Prufert-Bebout et al. (in prep.); these mats are dominated by the filamentous cyanobacterium *Schizothrix* sp., but also include a variety other cyanobacteria, bacteria and microalgae, such as *Oscillatoria* sp., *Microcoleus* sp., *Phormidium* sp., an endolithic coccoid cyanobacterium *Solentia* sp., and diatoms. The knobby turf is composed dominantly of tufts of the cyanobacterium *Dicothrix* (Figs. 4B), but also includes microalgae, such as *Cladophoropsis* sp. and *Ernodesmus* sp., as well as macroalgae, such as *Batophora* sp. Diatoms and *Batophora* show seasonal variability, with higher numbers occurring in warm summer months. Likewise the prokaryotic mat community shows some seasonal

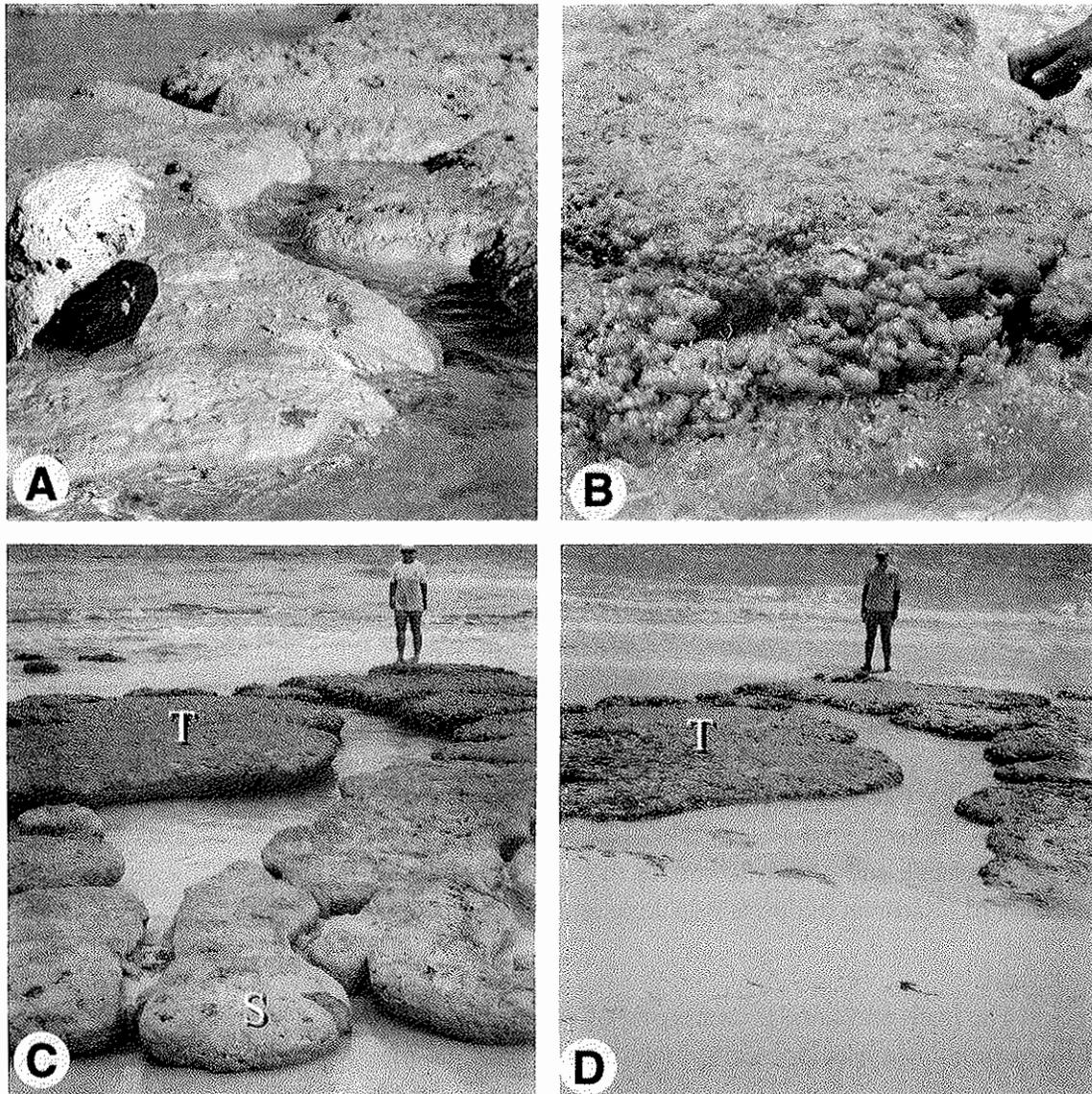


FIGURE 4. (A) Smooth *Schizothrix* mat on the surface of an intertidal stromatolite; hammer head on left is 12 cm long. (B) Knobby turf on the surface of an intertidal thrombolite, or cauliflower head. (C) Light colored *Schizothrix* mat on intertidal stromatolites (S) in foreground grades to knobby turf on thrombolites (T). (D) The same view as in (C), but beach sand is covering the nearshore stromatolites.

variability (Prufert-Bebout et al. in prep.). *Schizothrix* mats are dominant on surfaces that are frequently buried and uncovered by shifting sand; knobby turf dominates exposed mounds that are rarely, if ever, buried (Figs 4C, 4D).

Sawed sections through the back reef mounds reveal two distinct types of internal structure: some buildups have distinct layering (Fig. 5A), whereas others have clotted irregular fabrics, with abundant borings made by molluscs, worms and sponges (Fig. 5B). The layered deposits are typically colonized by *Schizothrix* mats, whereas the unlayered deposits have a surface mat of knobby turf. Similarities between the textures and microstructures of the mounds and the overlying mats, as outlined below, argues that the mounds were constructed by communities equivalent to the present-day mats. Thus, the layered deposits are termed stromatolites, and the mounds with clotted fabrics are designated thrombolites. Because of their knobby appearance, the thrombolites are also referred to as "cauliflower" heads.

Highborne Cay stromatolites and the overlying *Schizothrix* mats are composed primarily of well-sorted fine sand (125-250 μm), consisting mainly of peloidal grains with superficial oolitic coatings. Grains in surface mats are bound by cyanobacterial filaments; these filaments are, however, typically not calcified and are not preserved at depth. Lamination in the stromatolites is defined by differential lithification: layers are most visible in sawed sections, where lithified horizons, typically 0.5 to 1 mm thick, stand out in relief on cut surfaces (Fig 5A). Lamination in surface mats is reflected in variations in color and hardness: crusty to hard gray/green layers with high biomass alternate with soft white grain layers with low biomass (Fig. 5C). The gray/green layers contain an abundance of the endolithic cyanobacterium, *Solentia* sp. (Macintyre et al. in prep.; Prufert-Bebout et al. in prep.). In thin section, indurated layers in the stromatolites and *Schizothrix* mats appear as micritic horizons with characteristic features (Fig. 5E): they consist of a micritic crust, typically 20-40 μm thick, which commonly overlies a layer of micritized carbonate grains, 200-1000 μm thick. The micritized grains are often truncated along their upper surfaces and are cemented at point contacts. With increasing micritization, grain boundaries become indistinct and grains appear welded together.

Size distributions of grains within the stromatolites were compared with bottom sediment from the back reef lagoon using a Coulter particle size analyzer (Model LS200). Three samples of poorly indurated stromatolite were disaggregated by soaking for 24 hours in 5% sodium hypochlorite to remove organics. Grains in these stromatolites and three samples of lagoonal sand (Fig. 6) show distinct differences in size. The stromatolites have mean grain sizes of 160-175 μm , and are significantly finer than the lagoonal sediments, which have mean grain sizes of 300-350 μm . In addition, the stromatolites contain 1-2 % material coarser than 400 μm , considerably less than found in the lagoonal sand (12-15 %). In contrast, the fine fraction (< 100 μm) forms an average of 10 % of the stromatolites, but is insignificant in the lagoonal sediment. These differences indicate that *Schizothrix* mats selectively trap and bind fine sand; they exclude grains larger than 400 μm , but include fine material from the water column that is winnowed out of the lagoonal sediment. In addition to trapped sediment, the fine fraction in the stromatolites includes

micrite precipitated within the stromatolites.

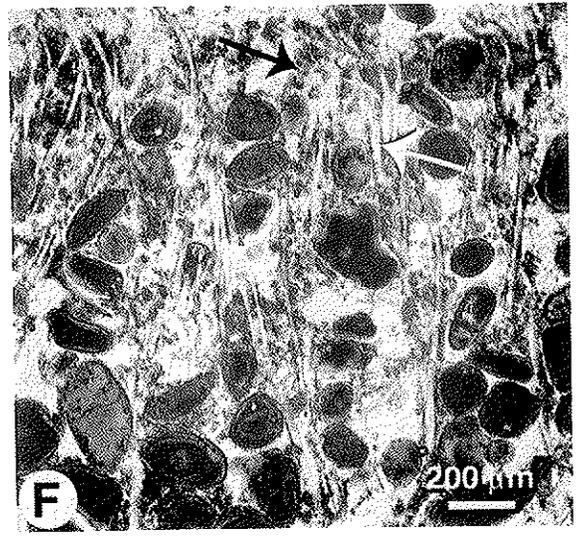
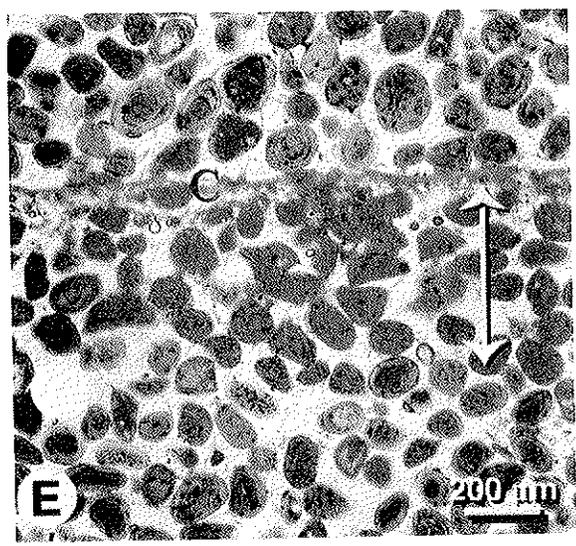
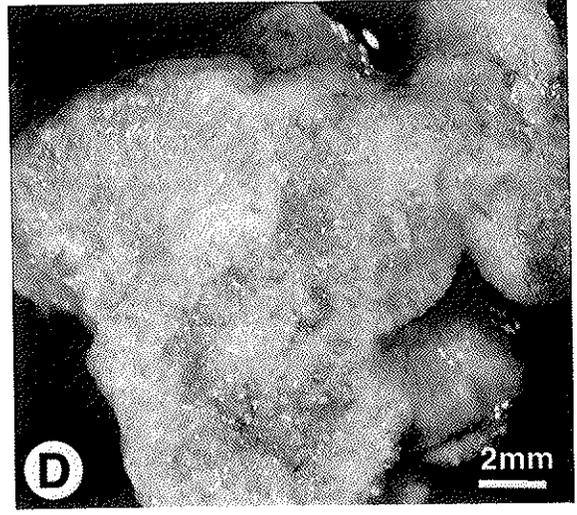
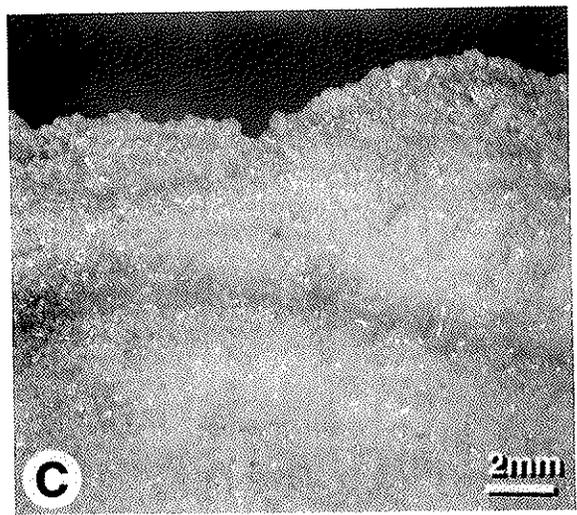
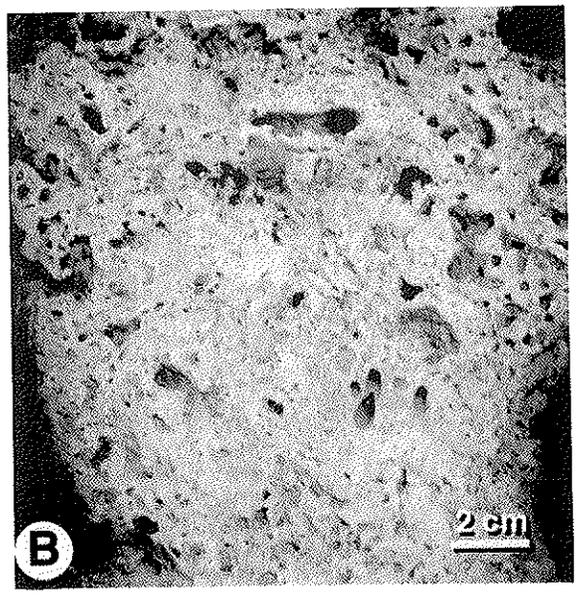
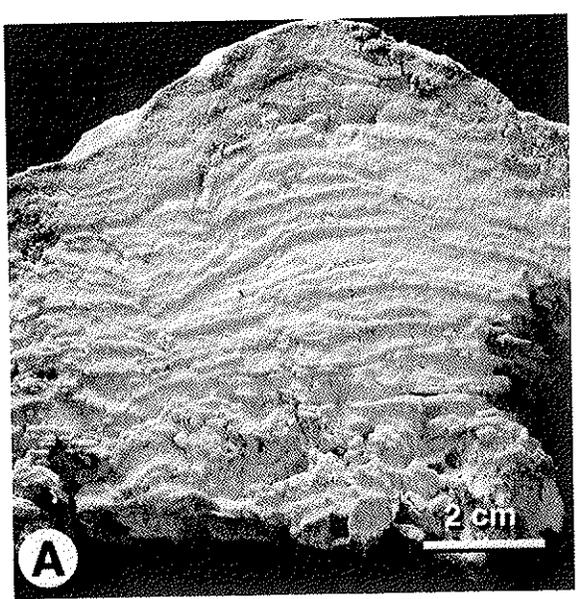
At periodic intervals, stromatolite-forming *Schizothrix* mats may be colonized by turf or macroalgae, such as *Batophora* or *Gracilaria*. Episodes of eukaryotic colonization are evident in cross sections through the stromatolites, as decayed roots and holdfasts leave horizons of open holes. Sediment within these eukaryotic horizons is typically less well sorted, coarser grained, and more porous than that accreted by *Schizothrix* mats.

In contrast to the laminated stromatolites, Highborne Cay thrombolites and the overlying knobby turf have an irregular microstructure (Figs 5B, 5D). The knobby surface mats are comprised of radiating tufts of filaments with entrapped carbonate sand (Fig. 5D). Thin sections show that the mats and thrombolites consist of calcified filaments (10 to 100 μm in diameter), abundant micrite and carbonate grains (Fig. 5F). Size distributions of sediment in these mounds have not been analyzed, but the grains appear less well sorted and coarser (medium sand-size) than in the stromatolites.

Stromatolites and thrombolites at Highborne Cay form buildups of a variety of shapes and sizes (Fig. 7). Stromatolites occur as both intertidal and subtidal mounds. Intertidal stromatolites form in the nearshore beach zone (Fig. 3) where, as mentioned above, they are alternately buried and uncovered (Figs. 4C, 4D). These stromatolites grade seaward to intertidal thrombolites, which are rarely, if ever, buried (Figs. 4C, 4D). The thrombolites are prominent features of the Highborne Cay reef: they are about a meter in height and are subaerially exposed for 3 to 4 hours twice daily at low tide. Commonly protruding from beach sand at the water's edge at low tide, the thrombolites form large, tabular mounds, that may be several meters in diameter (Figs. 3, 7A); these large mounds are typically constructed by the coalescence of smaller mounds.

Thrombolites also form intertidal columns in the lagoon between the algal ridge and the nearshore tabular mounds (Figs. 3, 7A). Subtidal stromatolites are also present in this lagoon, commonly forming ridges, 20-30 cm in height, perpendicular to the shoreline (Fig. 7B). In other parts of the lagoon, subtidal stromatolites form individual heads and

FIGURE 5. Internal structures of microbial buildups and surface mats in the back reef lagoon. (A) Cut section through a well laminated stromatolite-- lithified layers about 1 mm thick stand out in relief. Sample 8/98NS8TRd. (B) Cut section through a thrombolite with an irregular, clotted structure-- open bore holes are abundant. Sample SI-92-c. (C) Cross section through a *Schizothrix* mat; the gray/green layer at 2-3 mm depth is hard; white grain layers above and below are soft. Sample 8/98NS8TRc. (D) Cross section through knobby turf composed of *Dicothrix* filaments and carbonate grains-- crusty patches are dispersed throughout the knob. Sample 8/98NSc. (E) Thin section photomicrograph showing the characteristic microstructure of lithified laminae in stromatolites and *Schizothrix* mats: a micritic crust (c) overlies a layer of micritized sand grains (arrow), which are welded together at point contacts. Thin section 6/97NS8f. (F) Thin section photomicrograph showing the characteristic microstructure of thrombolites and knobby turf: calcified filaments (white arrow) and irregularly dispersed micritic precipitates (black arrow) are abundant. Thin section 8/98NSc.



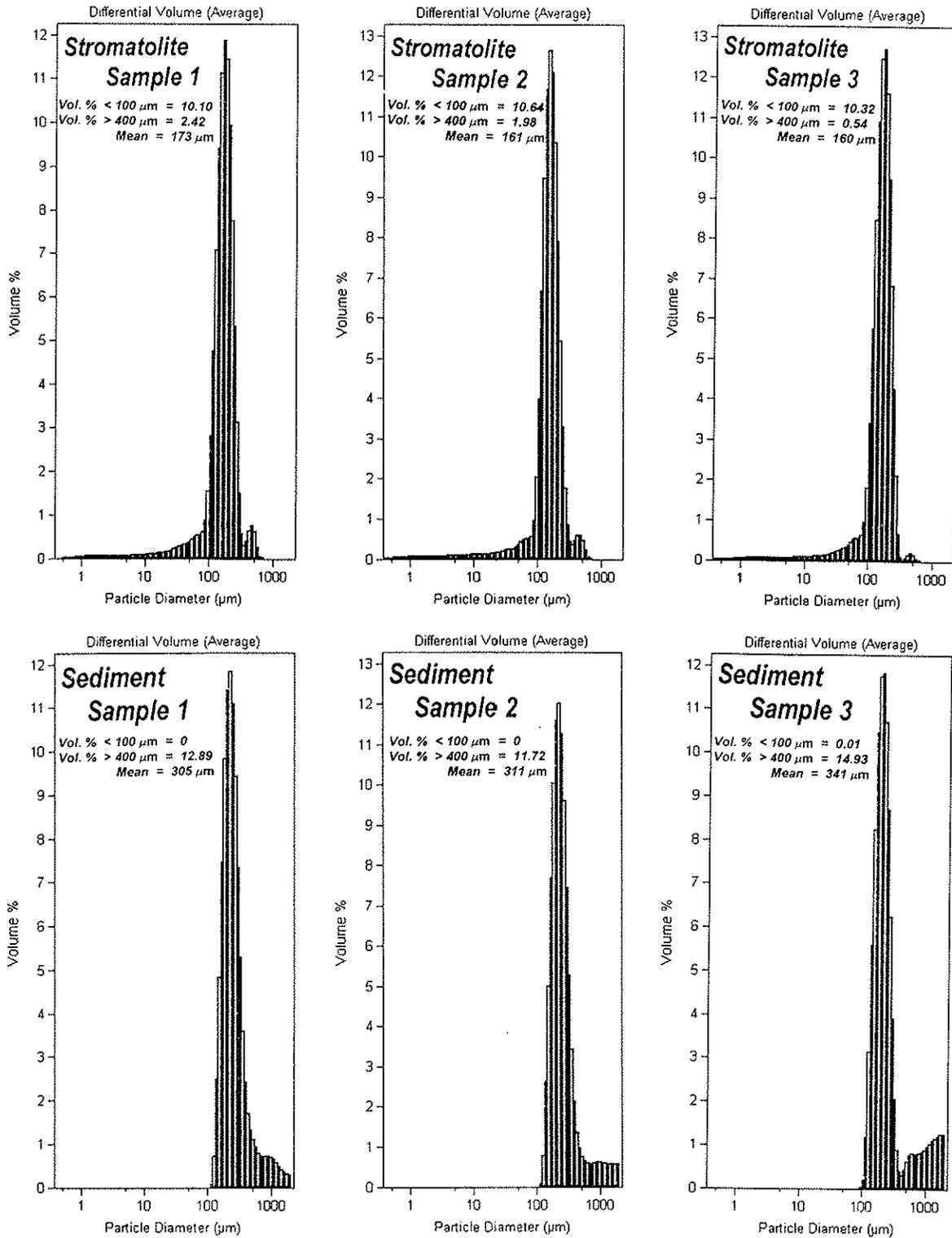


FIGURE 6. Histograms comparing grain-size distribution patterns in three subtidal stromatolites and three sediment samples from the back-reef lagoon.

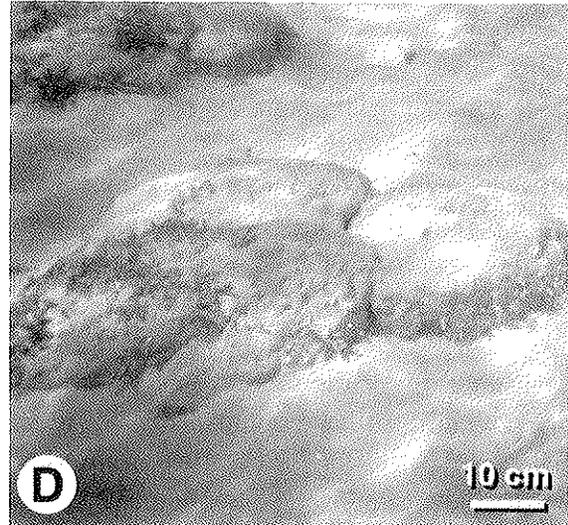
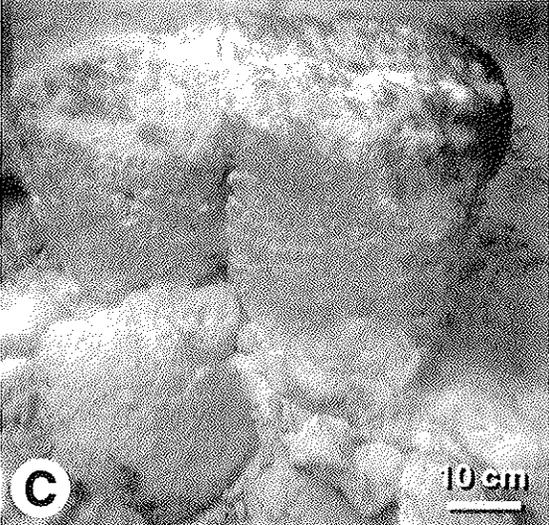
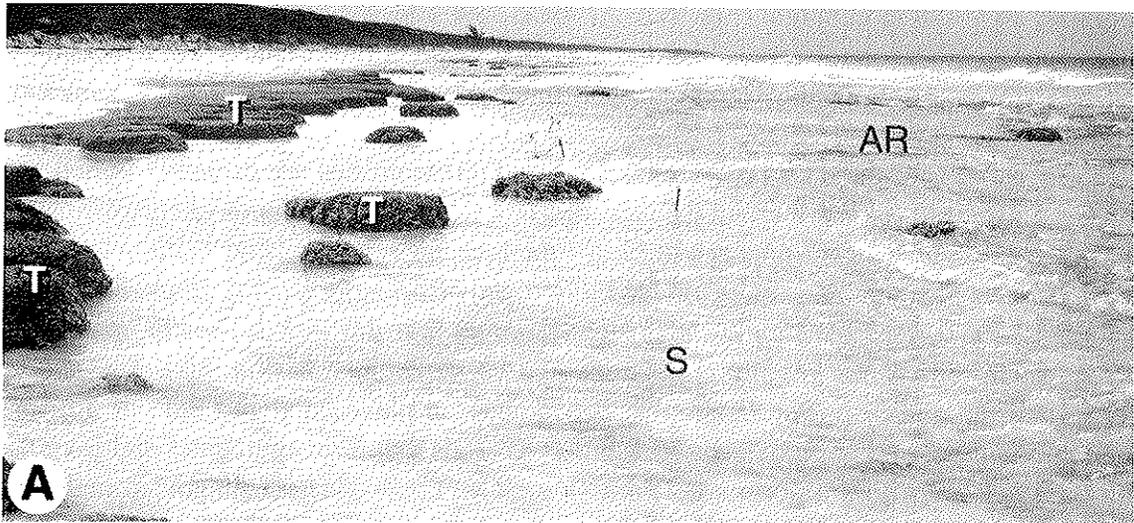
columns, up to 0.5 m in height (Fig. 7C). At mean low tide, the subtidal stromatolites are submerged in 30-50 cm of water. Like the intertidal stromatolites in the beach zone, the subtidal stromatolites in the lagoon are continually buried and uncovered by migrating sand (Figs 7C, 7D).

The bases of the back reef thrombolites and stromatolites are generally buried and consequently little is known about the substrates on which these mounds are growing. We did however, recover what appears to be a tufa forming ridges several centimeters high near the bases of some thrombolites. This ridge rock is extremely porous (Figs. 8A). Thin sections show that carbonate sand grains are rare and that the rock is mostly micrite; in places, the micrite forms knobby projections and vague lamination (Fig. 8B). The micrite has an unusual and distinct petrographic appearance: in plane polarized light, it appears as an intimate mixture of golden and dark brown crystals that form aggregates and irregular clustered masses within a porous network (Fig. 8C). These clusters of golden and dark brown crystals are commonly rimmed with acicular cement (Fig. 8C). Scanning electron microscope (SEM) observations show that the rock consists mainly of filament molds, 3 to 10 μm in diameter, encased in spherulitic clusters of aragonite needles (Figs 8D, 8E). It is therefore tentatively classified as a tufa. Formation of tufa in a subtidal marine environment would, however, be highly unusual, as tufa is typically considered to be a freshwater deposit (Pentecost and Riding 1986). The origin of this ridge rock thus warrants further investigation.

Algal Ridge

An algal ridge, which forms a platform about 10 m wide, forms the seaward margin of the Highborne reef and is the focus of breaking waves (Figs. 3, 9A). Hemispherical heads of the branching crustose coralline alga *Neogoniolithon strictum* dominate the seaward edges of the ridge, forming an emergent lip that is subaerially exposed at extreme low tides (Fig. 9B). These heads, which can be over 50 cm in diameter and 20 cm in height, are among the largest observed for *N. strictum* in the tropical Atlantic and Caribbean. Several species of macroalgae attach to, or become entangled in, the *N. strictum* heads, including *Sargassum* and *Gracilaria*. *Gracilaria* also forms thickets shoreward of *N. strictum*, grading into *Schizothrix* mats at the edge of the platform (Figs. 3, 9C). Patches of *Schizothrix* mat are also present on the seaward lip of the ridge, growing between heads, and sometimes coating, *N. strictum*. The sea urchin, *Echinometra lucunter* has a patchy distribution on the ridge, with an average density of 6 urchins/m²; this is considerably lower than the average density of 55 urchins/m² on the algal ridge at Stocking Island (Steneck et al. 1998).

In the subsurface, the algal ridge consists mainly of dense, well indurated coralline algal limestone. Branches of *N. strictum* are abundant (Figs. 10A, 10C). In addition, *N. strictum* and other coralline algae form platy encrustations, which are commonly intergrown with the foraminifer, *Homotrema rubrum* (Figs. 10B, 10D). Branches of *N. strictum* are often coated with micritic crusts, which may be up to several millimeters thick (Figs 10C, 10E). In thin section, these micritic crusts are similar to the tufa: in plane



polarized light, they appear as intimate mixtures of golden and dark brown crystals forming irregular clusters in a porous network (Fig. 10E). SEM shows that these crusts consist of micritic crystals with a variety of shapes, ranging from granules to platy crystals and needles; these crystals are permeated with holes, less than 5 μm in diameter, which could be filament molds (Fig. 10F). The crusts are of possible microbial origin, but further studies are needed to confirm this interpretation.

DISCUSSION AND CONCLUSIONS

The microbialite/algal ridge complex at Highborne Cay is an unusual and intriguing reef complex. Reef zonation is similar to that at Stocking Island, as described by Macintyre et al.1996. At Stocking Island, an outer ridge constructed primarily by *N. strictum* forms a protected back reef lagoon where conditions are favorable for the development of microbial mounds. Radiocarbon dates indicate that growth of the algal ridge at Stocking Island was initiated about 4000 years ago when the Pleistocene terrace was flooded during the Holocene transgression (Macintyre et al.1996). Maximum reef development at Stocking Is. occurred about 1500 years ago, with the development of an emergent coralline algal lip. For the past 500 years, the Stocking Is. reef has been in a destructive stage, with extensive bioerosion by *E. lucunter* degrading the algal ridge. As *E. lucunter* is considerably less abundant at Highborne Cay (6 urchins/m²) than Stocking Island (55 urchins/m²), bioerosion rates are lower and the Highborne Cay algal ridge has maintained an emergent lip.

Prior to the discovery of the Stocking Island and Highborne Cay reefs (Steneck et al.1997), algal ridges built by *N. strictum* were unknown. Algal ridges are typically composed of robust coralline algae, which form thick laminar layers that can withstand high wave energy (e.g. Adey 1975; Bosence 1984). Indeed, high wave energy has been considered essential for algal ridge formation, as waves deter parrotfish, which are major herbivores of coralline algae. (Adey 1975 1978; Steneck and Adey 1976). The Exuma algal ridges are unique in many respects. They are formed by a relatively unusual coralline species, *N. strictum*, which had not been reported to build algal ridges. *N. strictum* thrives in environments with relatively low wave energy, high rates of sedimentation and low rates of herbivory, where most ridge-forming algae cannot grow (Steneck et al.1997). Experimental manipulations at Stocking Island, which showed that *N. strictum* is capable of surviving when covered with sediment for at least 100 days, indicate that this alga is adapted to surviving in sediment-dominated environments (Steneck et al. 1997).

FIGURE 7. Microbial buildups in the back reef lagoon. (A) View looking north along the beach. Intertidal thrombolites (T) form tabular mounds in the beach zone and isolated heads in the lagoon, shoreward of the algal ridge (AR). Subtidal stromatolites (S) are present in the foreground; stakes mark the position of study sites for the RIBS project. (B) Ridges of subtidal stromatolites, which trend perpendicular to the shore. (C) Subtidal columnar stromatolites. (D) The same stromatolites as shown in C, but a few days later when the heads are almost entirely covered by sand.

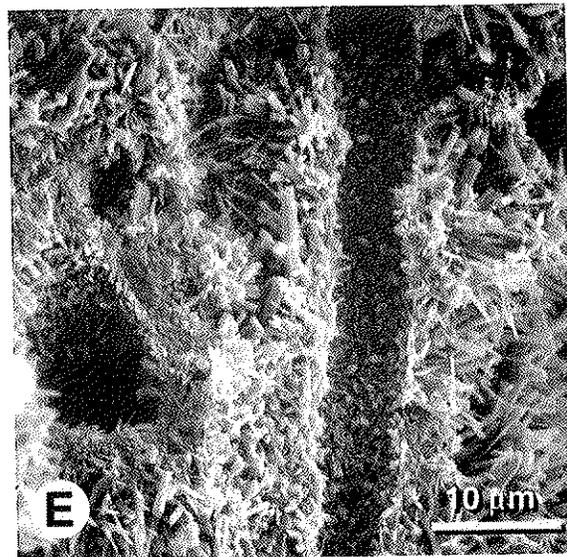
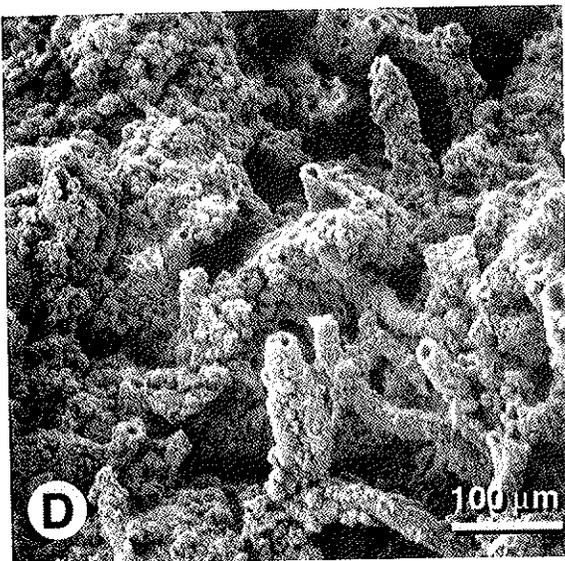
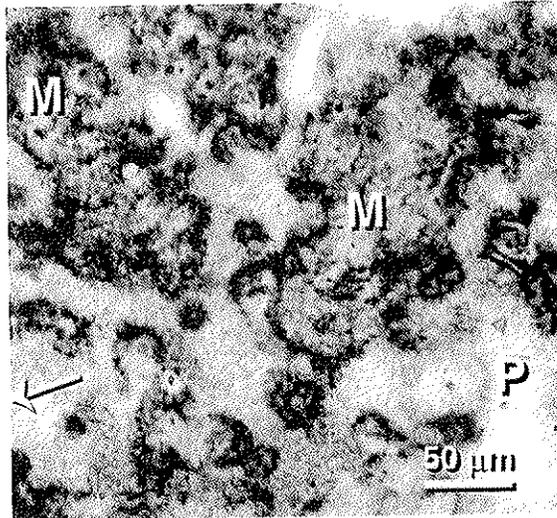
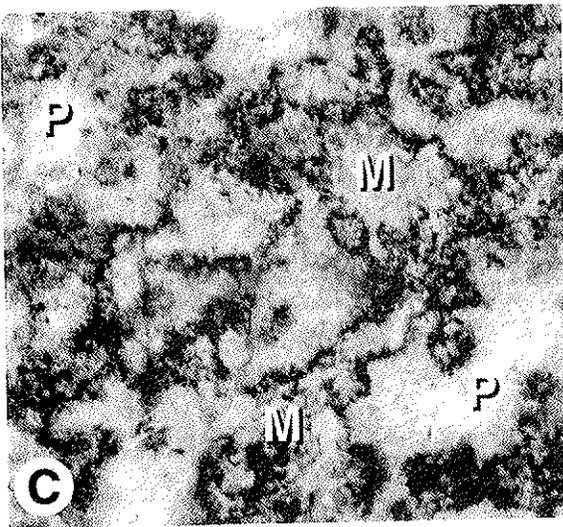
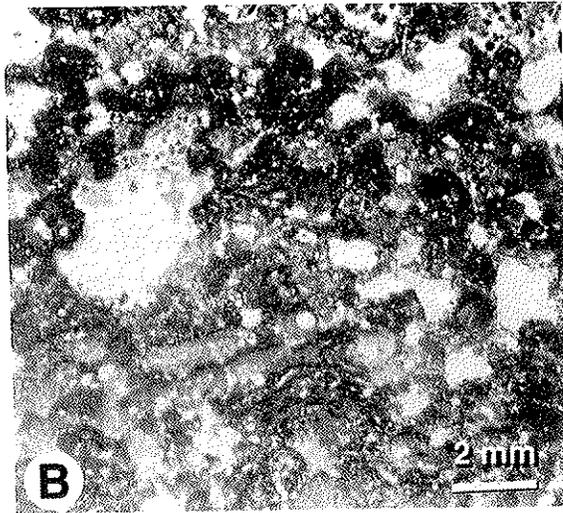
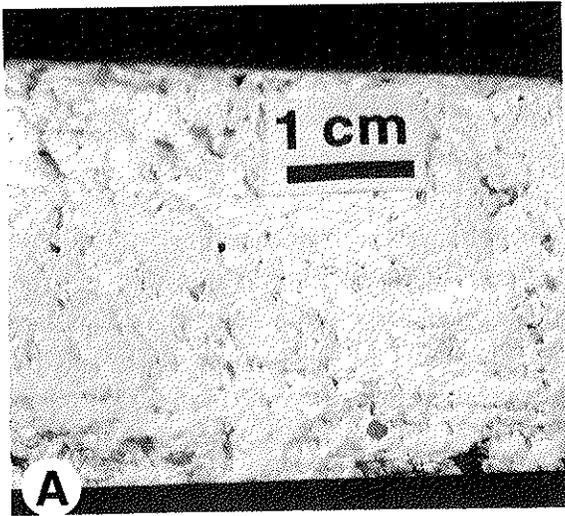
Inherently low levels of parrotfish grazing in reefs along the west margin of Exuma Sound may be important in allowing algal ridge development in this moderate wave energy environment (Steneck et al. 1997).

Growth of stromatolites in the lee of an algal ridge is another unique feature of the Highborne Cay and Stocking Island reefs. As the first known examples of marine stromatolites in a modern reef environment, these structures provide an opportunity to examine ecological controls of stromatolite development. Manipulative experiments conducted by Steneck et al. (1998) showed that stromatolites dominate where species diversity (especially among eukaryotes) and associated ecologic pressures is low. At Highborne Cay and Stocking Is, frequent periods of sediment inundation in the back reef create an ecologic refuge for stromatolites (Steneck et al. 1998). Most eukaryotic reef-dwelling organisms cannot survive or colonize under high sedimentation rates. Turf algae, for example, can survive desiccation and thermal stress on a reef flat, but not the high sedimentation rates of the stromatolite zone (Steneck et al. 1998). In contrast, stromatolite-forming *Schizothrix* mats thrive under conditions of high sedimentation. Although these mats can also grow in other areas of the reef environment, their reef-building contribution is low and their laminated microstructure is lost except in habitats where abiotic stresses maintain an ecologic refuge-- i.e. a refuge from the ecologic pressures of other organisms (Steneck et al. 1998).

As recognized by Reid et al. (1995) and Macintyre et al. (1996), lamination in Exuma stromatolites results from periodic formation of lithified micritic laminae within cyanobacterial mats. Introduction of turf algae disrupts the continuity of the flat-lying, stromatolite-forming community and inhibits the formation of laminae, resulting in formation of thrombolites rather than stromatolites (Reid et al. 1995; and Macintyre et al. 1996). At Highborne Cay, stromatolites form in the beach zone and in lagoonal areas where they are continually buried and uncovered by migrating sand. Stromatolites grade into thrombolites where sedimentation rates decrease sufficiently to allow growth of *Dicothrix*, *Cladophoropsis* and other turf algae.

The microbial mats forming Highborne Cay stromatolites are composed almost exclusively of prokaryotic communities (Prufert-Bebout et al. 1999; Pinckney et al. 1995; Pinkney and Reid 1997) and exhibit superb lamination. Ongoing studies in the RIBS project are documenting biogeochemical processes of lithification within these mats. For example, Macintyre et al. (in review) showed that periodic introduction of the coccoid endolith *Solentia* sp. to the *Schizothrix* community during episodes of low sedimentation

FIGURE 8. Tufa-like rock at the bases of some thrombolites; Sample SI-92-132. (A) Hand specimen showing the porous, knobby nature of this rock. (B, C) Thin section photomicrographs in plane polarized light showing that the rock is composed mainly of micrite with pores of varying sizes and shapes. High magnification view in (C) shows that the micrite (M) forms irregularly-shaped clusters of golden and dark brown crystals; these clusters are fringed with acicular cement (arrows) precipitated in open pore space (P). (D, E) SEM photomicrographs showing that the rock is composed almost entirely of filament molds encased in aragonite needles.



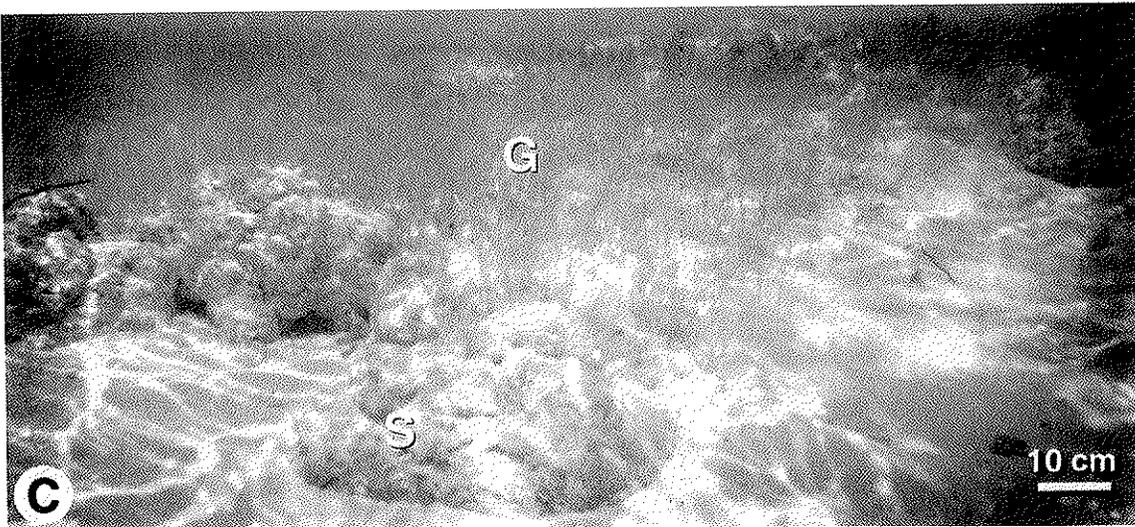
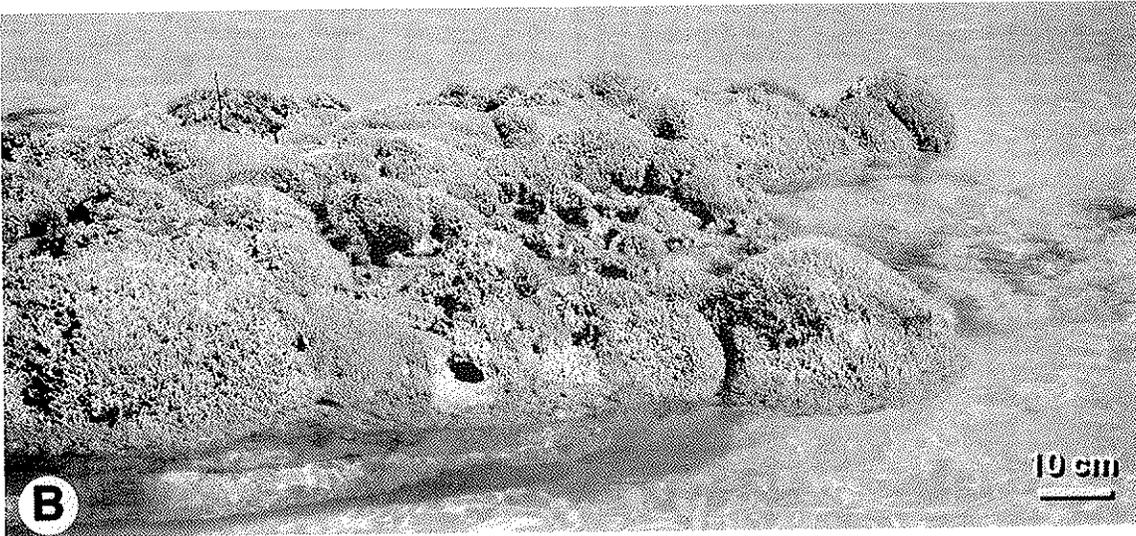
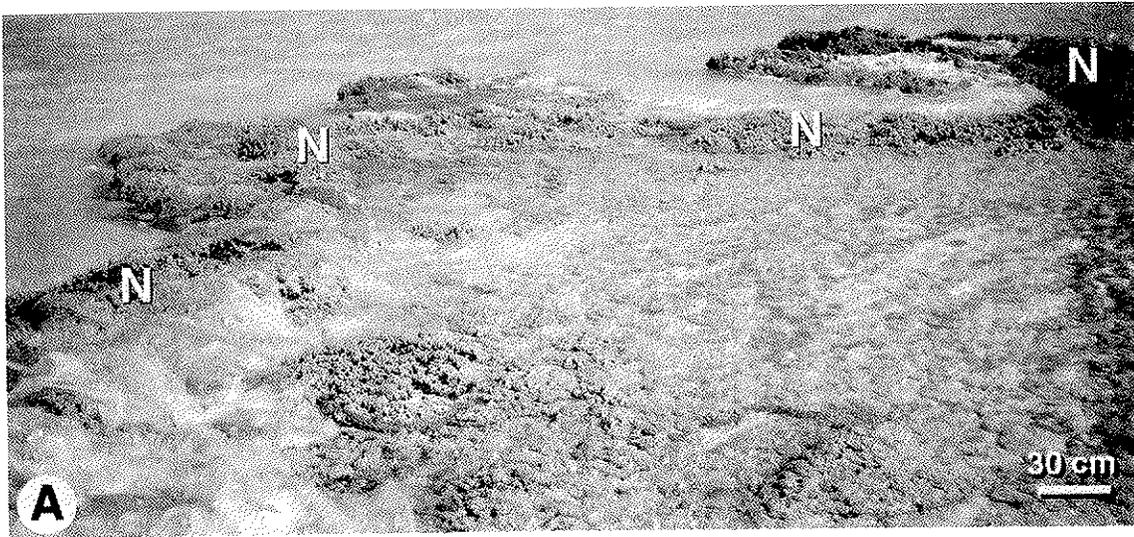
results in formation of lithified layers of micritized grains. In addition, sulfur cycling within the mats is discussed by Visscher et al (1998), who showed that photosynthesis coupled to sulfate reduction and sulfide oxidation is more important than photosynthesis coupled to aerobic respiration in stromatolite lithification. Additional papers documenting stromatolite microstructure, nitrogen cycling, polymer production and degradation etc. are currently in preparation.

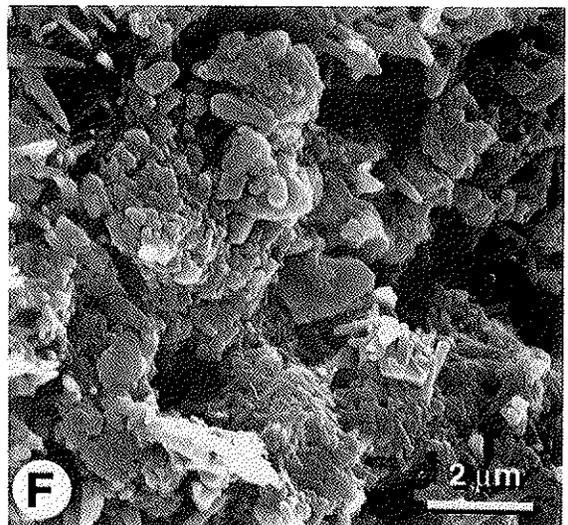
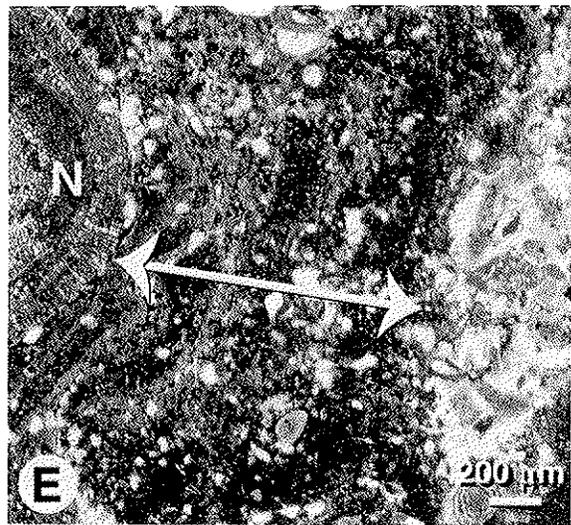
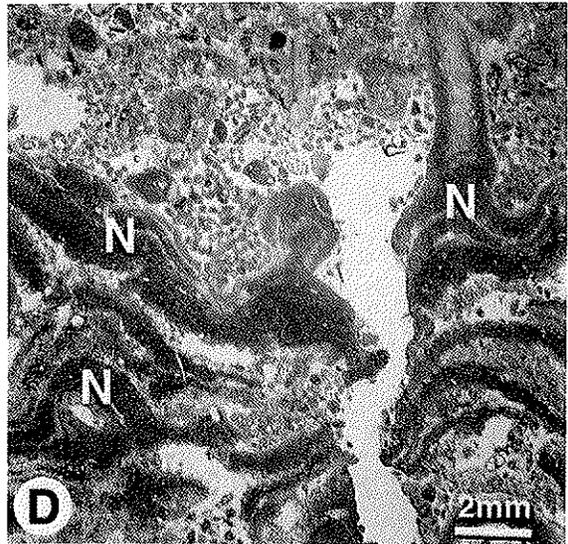
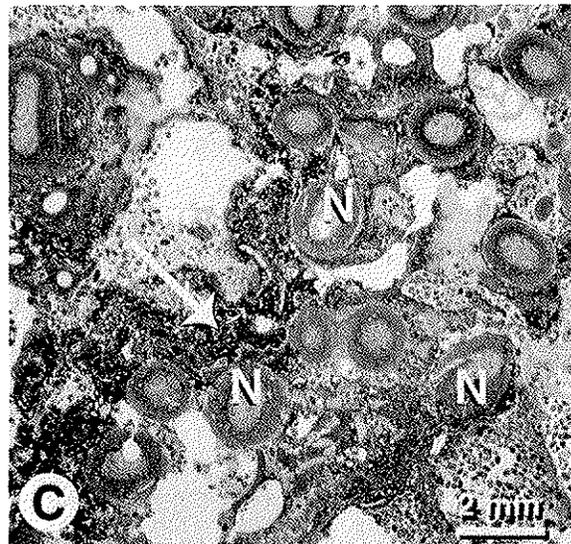
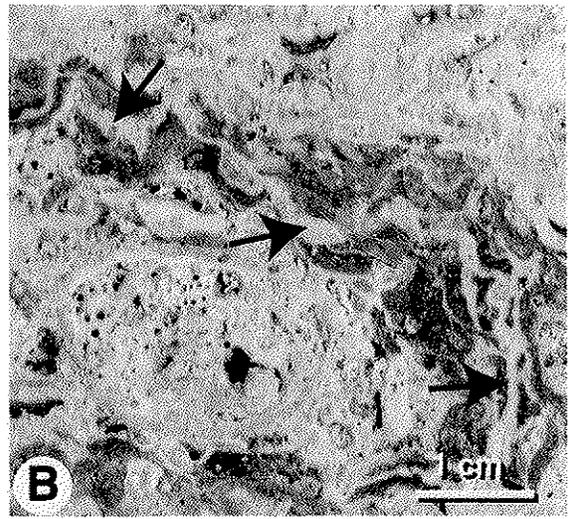
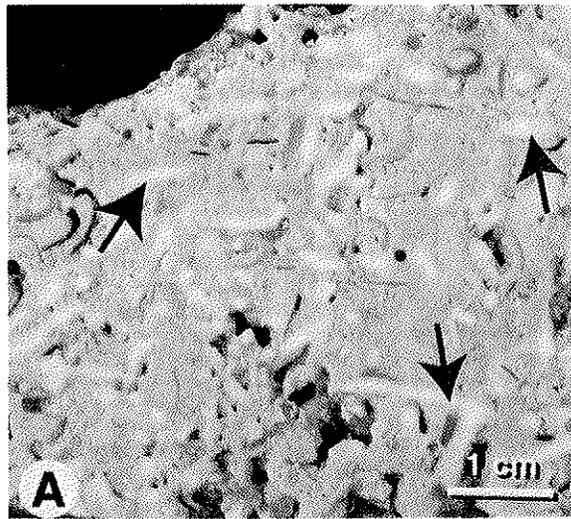
In contrast to the intensive studies of Highborne Cay stromatolites, there have been no detailed investigations of the other microbial deposits within this unusual reef system-- the cauliflower heads, or thrombolites, which form prominent intertidal back reef deposits; the ridges of tufa-like material at the bases of the thrombolites; and the micritic crusts coating coralline algae in the algal ridge. Highborne Cay is indeed a haven for microbial deposition and a natural laboratory that invites further geomicrobiological investigations.

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FIGURE 9. Algal ridge at the seaward edge of the Highborne reef. (A) View looking south across the ridge. Coralline algae limestone forms a platform about 10 m wide; the branched coralline alga, *N. strictum* (N), forms an emergent lip at the seaward edge of this platform. (B) Closer view of *N. strictum* at the platform edge. (C) *Gracilaria* (G) grading shoreward to *Schizothrix* mats (S) at the edge of the ridge.





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- FIGURE 10. Samples from the algal ridge. (A, B) Hand specimens showing *N. strictum* in branched (A, arrows) and encrusting (B, arrows) forms; algal crusts in B are intergrown with the foraminifer *H. rubrum*. (C, D) Thin section photomicrographs in plane polarized light showing the microstructure of branched and encrusting *N. strictum* (N); arrow in C indicates micritic coatings on branches of *N. strictum*. (C, thin section SI-92-56; D, thin section SI-93-125). (E) Higher magnification photomicrograph showing a more detailed view of a micritic crust (arrow) on a branch of *N. strictum* (N); the micrite is an intimate mixture of golden and dark brown crystals with high porosity. Thin section SI-92-56. (F) SEM photomicrograph of a micritic crust; granular, platy and needle shaped crystals are permeated by holes, 1-3 μm in diameter, which may be filament molds Sample SI-92-55.

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