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TAPHONOMY OF MODERN MARINE BAHAMIAN MICROBIALITES

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ABSTRACT

Extensive study of modern Bahamian stromatolites has resulted in a comprehensive model for their formation. Modern Bahamian thrombolites—microbial deposits with a mottled, clotted fabric—have not, however, received the same degree of study. Current models link the Bahamian thrombolites with the presence of a mixed-bacterial-and-metaphyte benthic ecosystem, whereas stromatolite formation is linked with an almost exclusively bacterial benthic ecosystem. By focusing on the preserved fabrics of several specimens, including an entire column 1.5 meters tall, we have developed a new model for the genesis of the clotted, thrombolitic fabric. Our findings demonstrate that variations in the amount and style of penecontemporaneous diagenesis, rather than differences in surficial benthic ecosystems, are the predominate cause of the disparate carbonate fabrics present in the Bahamian microbialites examined. More specifically, the irregular, clotted fabric that characterizes the thrombolites is the result of remodeling a precursor fabric. This remodeling is caused by physical and metazoan disruption, penecontemporaneous micritization, secondary cementation, and localized carbonate dissolution. This new model of syndepositional remodeling of a laminated fabric to a well-cemented, clotted one may be applicable to some ancient thrombolites.

INTRODUCTION

The discovery of extensive modern stromatolites, first in Shark Bay, Western Australia (Logan 1961; Playford and Cockbain 1976) and later in the Eleuthera Bight (Dravis, 1983) and the Exuma Islands of the Bahamas (Dill et al., 1986; Reid et al., 1995), inspired numerous studies on modern microbial carbonates. Investigations in these modern systems have resulted in valuable new concepts about the genesis of fossil microbial deposits. The Bahamian stromatolites are of special interest as analogues of fossil examples; they are thoroughly lithified columns up to two meters tall and are forming in waters of oceanic salinity (Dill et al., 1986; Reid et al., 1995). Although all of the Bahamian microbial carbonates were initially described as stromatolites—i.e., laminated microbial structures—further studies revealed large variations in the internal fabrics of the columns. Internal morphology varies from well-laminated to irregular, clotted, and mottled fabrics (Dill, 1991; Macintyre et al., 1996; Feldmann and McKenzie, 1998). The columns composed predominately of mottled fabrics were termed thrombolites (Macintyre et al., 1996; Feldmann and McKenzie, 1998), which is the term used to describe common Paleozoic microbial reefs characterized by a clotted fabric (Aitken, 1967). Many of the Bahamian microbial columns, however, contain both stromatolitic (laminated) and thrombolitic (clotted) fabrics. It is, therefore, preferable to use the term microbialite, which was introduced by Burne and Moore (1987) to describe all microbially mediated structures with relief.

There has been considerable progress in understanding the origin and lithification of laminations in Bahamian microbialites, notably the elucidation of the roles of filamentous and boring cyanobacteria during initial cementation processes (Golubic and Browne, 1996; Macintyre et al., 2000; Reid et al., 2000; Visscher et al., 2000; Andres et al., 2006). There is still limited understanding, however, of the formation of the Bahamian thrombolitic fabric. Most of the research on Bahamian thrombolitic microbialites has focused on observations of benthic ecosystems, with limited examination of the mottled carbonate fabric (Riding et al., 1991a, 1991b; Macintyre et al., 1996; Feldmann and McKenzie, 1998). It has been proposed that the thrombolitic fabric develops when an algal rather than a cyanobacterial benthic ecosystem is dominant (Feldmann and

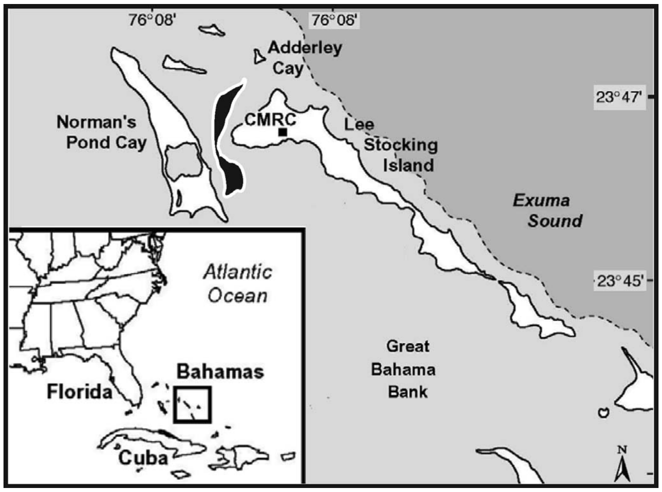

FIGURE 1—Map of the study area (modified from Hu and Burdige, 2007). The black area outlines the distribution of microbialites in Adderly tidal channel; CMRC = Caribbean Marine Research Center.

FIGURE 2—Microbialite macrostructure; underwater view of a group of microbialites surrounded by moving sand dunes; arrow indicates columnar microbialite AC-1.

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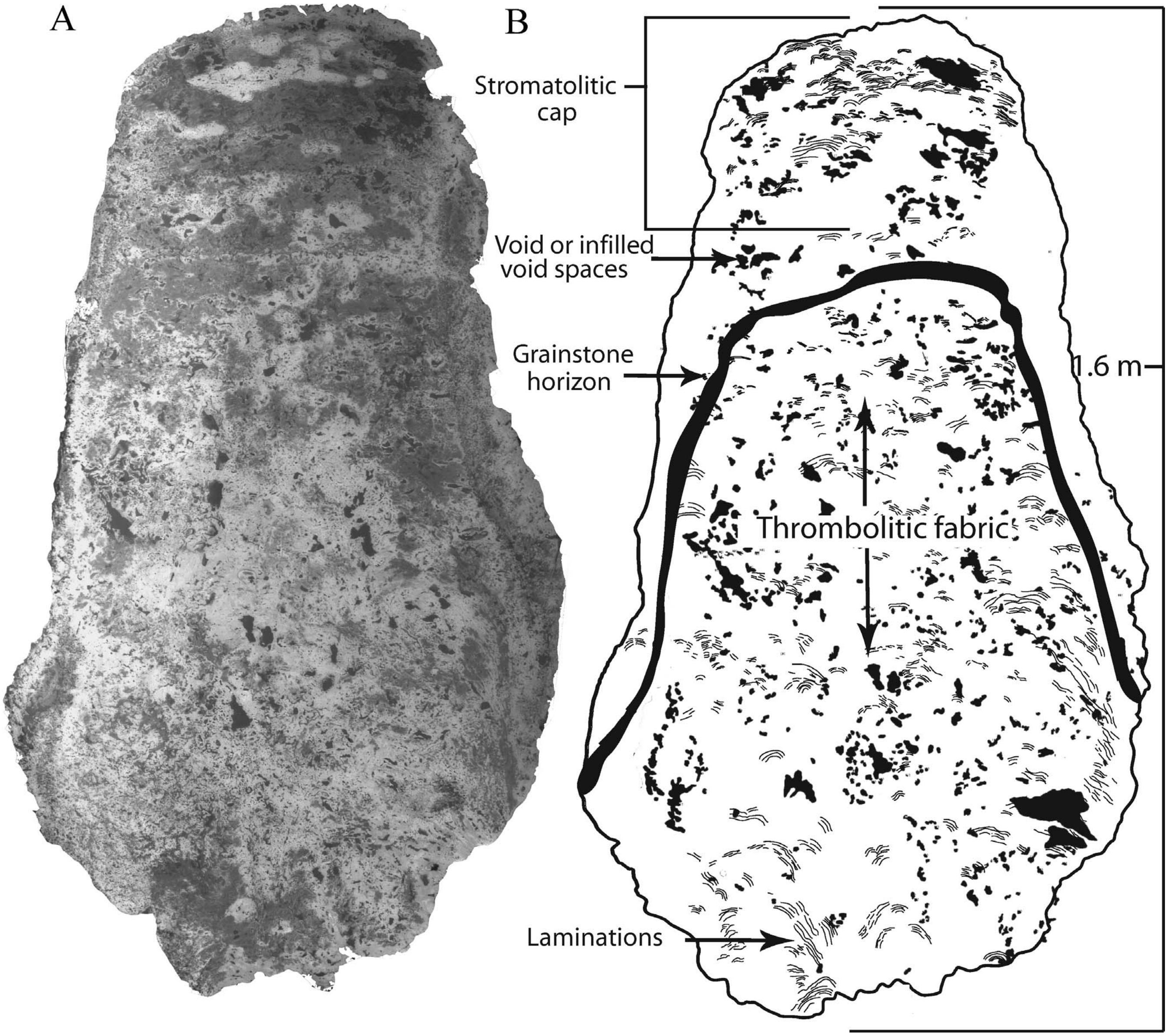

FIGURE 3—Distribution of fabrics in the AC-1 microbialite. A) Polished section impregnated with pigmented epoxy resin; variations in resin darkness (patchy coloration) are result of variations in porosity: more porous areas are darker and lighter areas more cemented. B) Distribution of laminations, vugs (solid masses), and the narrow boring-rich skeletal-grainstone horizon (solid curved band).

McKenzie, 1998). The framework components of the thrombolitic fabric are thought to be calcified filaments of the green alga (Chlorophyta) *Ostreobium* sp., with clots formed by spores of the chlorophyte *Acetabularia* sp. (Feldmann and McKenzie, 1998). Testing this model and other possible explanations for the formation of the thrombolitic microbialites requires a more intensive study of the carbonate fabrics.

This report is based on study of a suite of representative specimens, including a complete 1.5-m-tall columnar specimen (AC-1), and several smaller, serially sectioned Bahamian microbialites (AC-2–AC-5). Together, these specimens offer a special opportunity to characterize a variety of microbialite fabrics. From our findings, we propose a new model for the genesis of the thrombolitic fabric. The model results from detailed descriptions and interpretations of the microbialite fabrics in the context of our observations and of published descriptions of the benthic communities and physical processes. We propose that the thrombolitic fabric is the result of a taphonomic remodeling of a precursor fabric; this remodeling is caused by physical and metazoan disruption, penecontemporaneous micritization, secondary cementation, and localized carbonate dissolution.

MATERIALS AND METHODS

Five microbialites were serially sectioned and their surfaces impregnated with pigmented epoxy resin. The degree of epoxy impregnation serves as a qualitative proxy for porosity and permeability because penetration is controlled by connectivity of pores, which is a function of the amount of intergranular cement. In addition, the basic mesostructural features of more than 40 other slabbed subtidal and intertidal Bahamian microbialites were examined. The specimens illustrated here are stored in the Comparative Sedimentology Laboratory Collection at the Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Florida.

The carbonate mineralogy of bulk samples was determined using X-ray diffraction (XRD) with a PANalytical X'Pert PRO X-ray diffractometer operated at the Stable Isotope Laboratory of the Rosenstiel School of Marine and Atmospheric Sciences. Samples for XRD analysis were crushed and examined under a stereomicroscope using reflected light to check for metazoan or coralline algal particles. Samples without

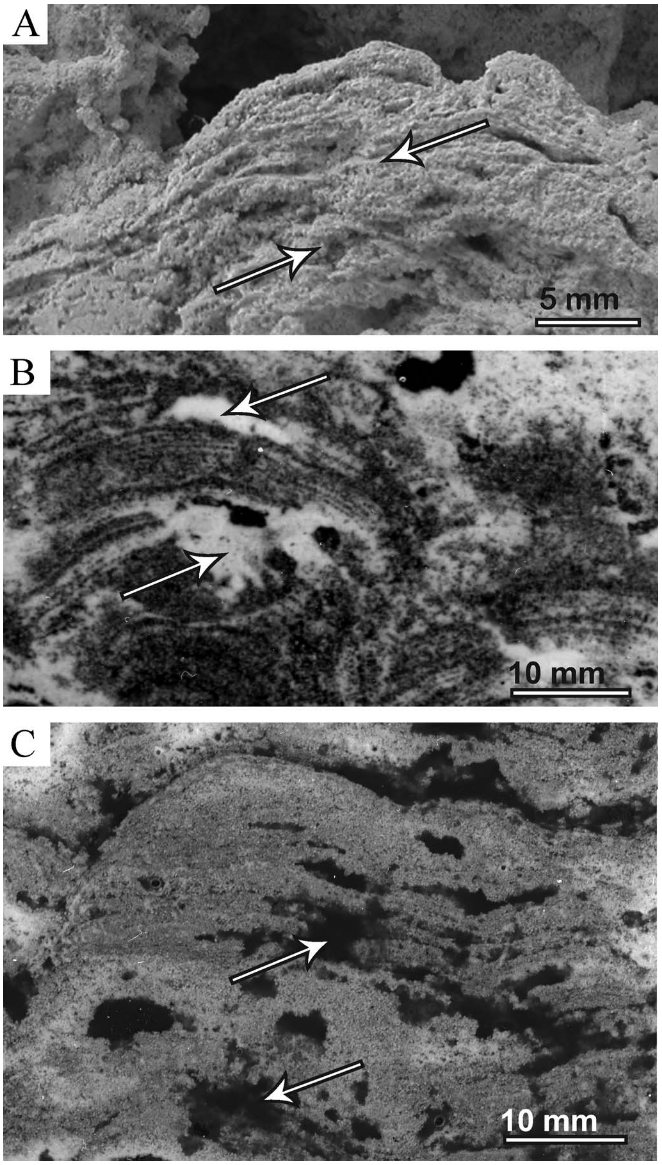

FIGURE 4—Stromatolitic fabric mesostructure (all photos are of vertically oriented sections in reflected light); there is limited cement deposition outside the laminae. A) Well-laminated hemispheroid (etched in 5% HCl for 30 seconds) that contains vugs truncating laminations (arrows). B) Framework of distinct laminations truncated by vugs now filled with pigmented epoxy (black areas) and fine-grained internal sediment (arrows). C) Poorly defined laminations truncated by variably shaped voids (black areas).

particles of invertebrate skeletons or eukaryotic algae were ground in an agate mortar and spiked with calcium fluoride as an internal standard.

Observations and interpretations of microstructure genesis are based on the study of 58 thin sections (50 mm by 75 mm, 30 μm thick). Thirty-four of these are from the columnar microbialite AC-1. Fine-scale microstructure of fractured surfaces and thin sections etched with weak hydrochloric or acetic acid received a palladium coating and were examined using an FEI/Philips XL30 environmental scanning electron microscope (E-SEM) with an Oxford L300QI-Link ISIS EDS in the University of Miami, Department of Geology. The use of electron dispersive spectroscopy (EDS) provided carbonate mineralogy at the micron scale.

Shells of boring bivalves from the AC-1 microbialite were ^{14}C-dated, using standard accelerator mass spectrometry techniques at the National Ocean Sciences Accelerator Mass Spectrometry Facility at Woods Hole Oceanographic Institute, Massachusetts.

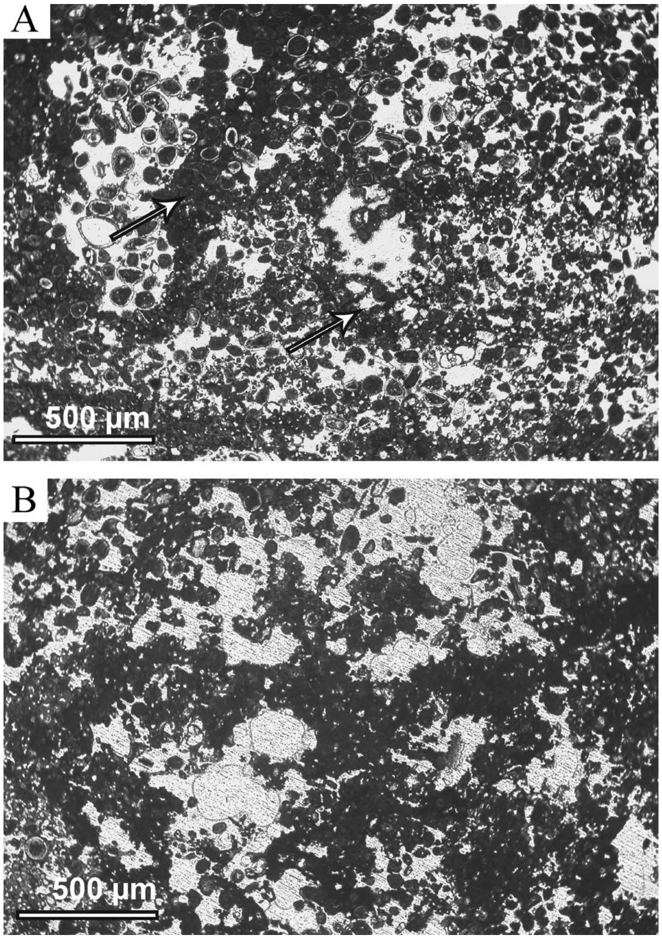

FIGURE 5—Vugs in the stromatolitic fabric (all photos of vertically oriented sections under plane-polarized light). A) Small vugs truncating laminations, likely caused by burrowing; cements developed preferentially around the margins of the vugs (arrows). B) Irregularly shaped, horizontally inclined vugs in a weakly laminated fabric; vugs may have formed through bioturbation or be depositional irregularities.

Microbialite Location and Environment

Subtidal Bahamian microbialites are found at numerous sites in the Exuma Island chain (Reid et al., 1995). Studied samples were collected from the field of columnar microbialites originally described by Dill et al. (1986) in Adderly Channel (Fig. 1) near Lee Stocking Island. The channel connects open-ocean waters of Exuma Sound with those of Great Bahama Bank to the west. As a result, the salinities are typically 37‰ (Dill, 1991), only slightly above that of Exuma Sound. Periodically, the more saline and warmer waters from Great Bahama Bank flood the Adderly Channel during the ebb tide (Dill, 1991).

The microbialites in Adderly Channel are confined to an oolitic sand bar, <5000 m long and <500 m wide at depths of 5–10 m. The bar is ornamented by a series of sand waves 1–2.5 m high (Dill et al., 1986). These waves move seaward and bankward with the tidal currents, periodically covering and uncovering the microbialites during a single year (Dill, 1991).

The heights and morphologies of the columnar microbialites are variable. Heights range from a few centimeters to 2.5 m, but most are 1–1.5 m tall. Isolated columns are the most common external form, but there are bioherms made up of coalesced microbialites. Some columns have an equate form, as seen from above, but most are elongated parallel to the incoming tidal current (Dill, 1991). This asymmetry is similar to some fossil microbialites interpreted as developing in high-energy environments (Hoffman, 1967, 1976). The large columnar microbialite AC-1 was

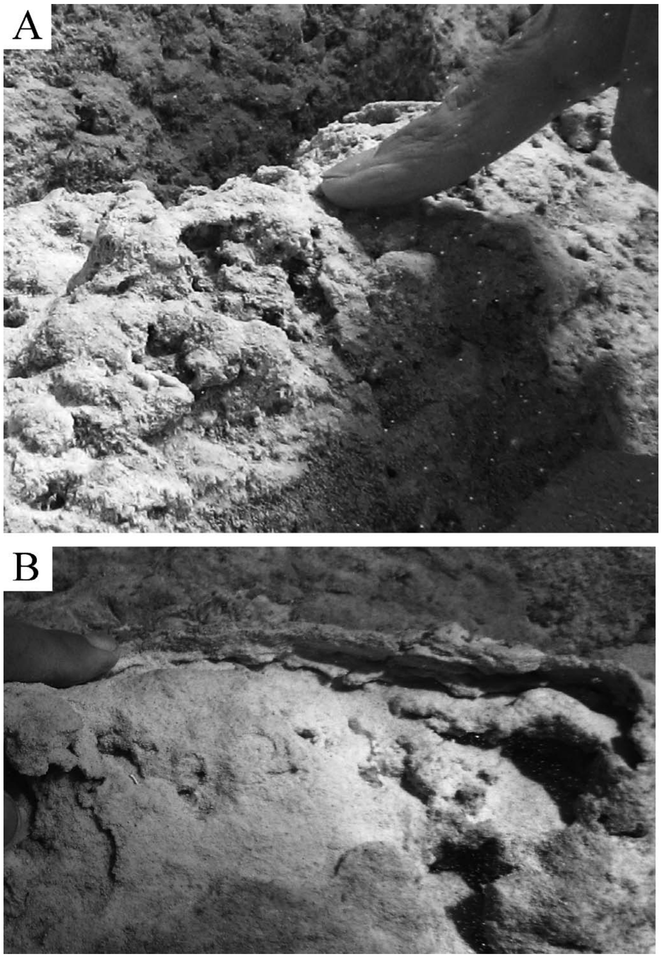

FIGURE 6—Erosional features in semilithified microbialites. A) Disruption on the exposed surface of a friable microbial mat, probably caused by fish grazing or physical erosion; finger (1 cm across) for scale. B) Physical erosion of a stromatolitic hemispheroid.

collected from the terminal section of an elongated bioherm (Fig. 2) at a depth of ~8 m.

DEFINITIONS

In the discussion of results below, the terms stromatolite and thrombolite are not used to describe the Bahamian microbialites; instead, the term microbialite is used with the modifier stromatolitic or thrombolitic to describe a structure or a section that is generally laminated or generally clotted, respectively. The term fabric is used to refer to the morphology and composition of a section of microbialite. Our use of fabric encompasses several scales of observation; different fabrics contain distinct mesostructures and microstructures. Following Shapiro (2000), the term mesostructure is used to describe features visible at the hand-sample scale (cm scale) and microstructure for features visible using a light microscope (mm scale). In this study, the term fine-scale microstructure is used to refer to features visible using an electron microscope (micron scale).

The Adderly Channel microbialites contain three fabrics: a stromatolitic fabric, a thrombolitic fabric, and a skeletal grainstone. These fabric types were defined based on their mesostructural characteristics, but they also contain distinct microstructures. The framework of the stromatolitic fabric is almost exclusively distinct or poorly defined laminations. This can be the predominant fabric in both large (>1 m tall) and small microbialites. The thrombolitic fabric contains patchy laminations, a clotted appearance at the mesostructural scale, and an abundance of vugs and sediment-filled vugs. The skeletal grainstone is characterized by areas with abundant sponge and bivalve borings in a cemented grainstone. The mesostructure and microstructure of each of these microbialite fabrics is described below and illustrated with examples from the AC-1 microbialite unless specified otherwise.

RESULTS

Stromatolitic Fabric Mesostructure

Distinct laminations are the predominant framework components of the stromatolitic fabric; cementation is generally minimal and largely confined to grain contacts within the laminations. The stromatolitic section on top of the large columnar AC-1 microbialite, which is the only section of the microbialite with a predominantly laminated fabric, is an example of this minimal cementation. The resulting high porosity is evidenced by the darker color produced by the pigmented-epoxy impregnation (Fig. 3A).

There are numerous disruptions of the laminations in the stromatolitic fabric, indicating significant post-depositional modification. Small vugs that crosscut laminations are the most obvious evidence of this disruption (Figs. 4A–C). Many of these are circular and range in diameter from 0.5 to 3 cm on vertical sections through microbialites (Fig. 5A). Vertical sections through the microbialites also reveal elongated vugs, some of which are sinusoidal. The elongated and circular vugs are likely caused by burrowing metazoans. Rare, distinct vertical tubes have been observed, and these may be the molds left by the common alga *Batophora* spp. Groups of laminations are also commonly truncated by irregularly shaped vugs (Figs. 4C, 5B). These could be metazoan burrows, depositional irregularities, or spaces formerly occupied by algae. Larger elongate voids (several centimeters in both width and length) are formed by boring bivalves and are found in most of the Adderly Channel and previously described Bahamian microbialites (Macintyre et al., 1996; Andres et al., 2006).

The margins of laminations are commonly truncated, which could be caused by mechanical erosion or fish grazing. Truncated laminations are visible on the tops of most microbialites (Figs. 6A–B). Our field observations indicate that the disruption occurs after the initial cementation (i.e., lamination formation), but while the microbialites are still highly friable and the semilithified material can easily be broken by hand. The above-described forms of disruption, where concentrated, result in the formation of an area of discontinuous laminations with porous and irregularly packed grains.

Stromatolitic Fabric Microstructure

Three types of lamination couplets were observed. In the most common type, laminae of closely packed, cemented, and micritized sand-sized ooids, superficial ooids, and peloids alternate with uncemented grains. The sand grains in micritized laminations are on average 153 μm in apparent diameter ($n = 200$), while the grains in the relatively uncemented laminations average 143 μm ($n = 200$). In the second type of couplet, the denser laminae are composed of pure micrite. The micrite laminations can also be found directly above the micritized laminae, forming the third type of lamination couplet. These microstructures are similar to those found in well-documented intertidal Bahamian stromatolites from Highborne Cay (Reid et al., 2000).

Thrombolitic Fabric Mesostructure

The thrombolitic fabric has two framework components. The first is isolated areas of discontinuous and indistinct laminations (Fig. 7A). These laminations are surrounded by (and intergrade with) the other framework element, which consists of dense clusters of sand grains and cements, herein termed clots. The margins of the indistinct laminations are commonly truncated and embayed by irregularly shaped clots. Framework components surround less-cemented sand grains or vugs (Fig. 7). Most clots connect to laminae, but some occur as isolated masses, which range

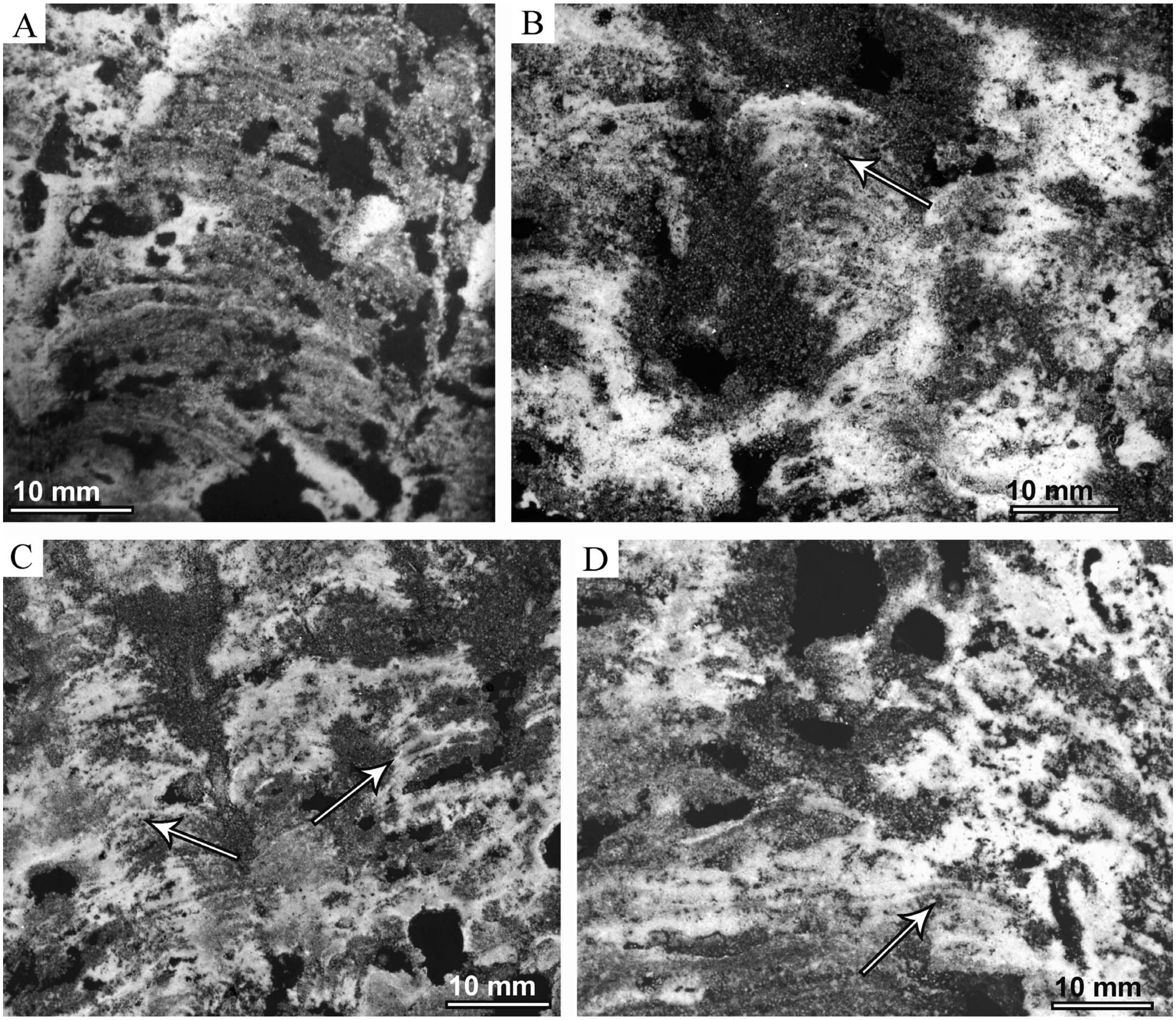

FIGURE 7—Thrombolitic fabric mesostructure; C–D are specimen AC-2 (all photos in reflected light). A) Faintly laminated fabric with abundant vugs (black irregular masses) and clotted areas on margins of laminations (white irregularly shaped masses). B) Small hemispheroid with indistinct and truncated laminations (arrow) grading laterally into clotted fabric, all surrounded by uncemented sand grains (dark areas). C) Faint clots with irregular borders forming around network of patchy laminations (arrows indicate indistinct, patchy laminations); dark areas are uncemented sand grains. D) Mixed laminated and clotted fabric; microclotted and indistinct laminations (arrows) are directly associated with heavily cemented, clotted areas; dark areas are abundant vugs.

from 500 μm to several centimeters in diameter. Clot morphology varies from irregular polylobate or amoeboid to roughly circular masses (Figs. 8A–B) without a preferred orientation.

Clot distribution is highly variable. There are progressions from distinct laminations to indistinct and microclotted laminations and to anastomosing clots within an area of several square centimeters. In some instances, the core of a microbialite may have a pervasive clotted fabric (Fig. 9B), while the outer parts have only limited clots that occur primarily around the margins of voids (Figs. 9A, C). The distribution of clots between surfaces of successive serial sections, even a centimeter apart, is not continuous (Figs. 9C–D). Clot distribution does not correlate with inferred growth horizons (Fig. 9).

Decimeter-scale vugs are also a prominent component of the thrombolitic fabric. Some of these larger vugs truncate laminations, indicating that they formed after sediment accumulation. The complex morphologies of most of the vugs (e.g., Fig. 3A), indicate they are not the result of a single stage of metazoan burrowing or boring. The majority of these larger vugs are partially to completely infilled with internal sediment, which is typically either laminated mud or silt-sized sediment with geopetal features or coarser sand.

Thrombolitic Fabric Microstructure

In most cases, aggregates of closely packed grains become thoroughly cemented to produce the dense, clotted areas visible at the mesostructural scale (Fig. 10). Grain-density maps show that there is a general correlation between closer packing and cementation (Figs. 11A–B). Packing also appears to affect cement morphology; micritic cements develop preferentially between closely packed grains, whereas interstitial fibrous aragonite splays predominate in more porous areas (Figs. 11A–B). James and Ginsburg (1979) reported a similar relationship of packing and cement morphology from syndepositional cement on the reef wall in Belize. Extensive cementation can develop in densely packed areas around laminations (Fig. 11A).

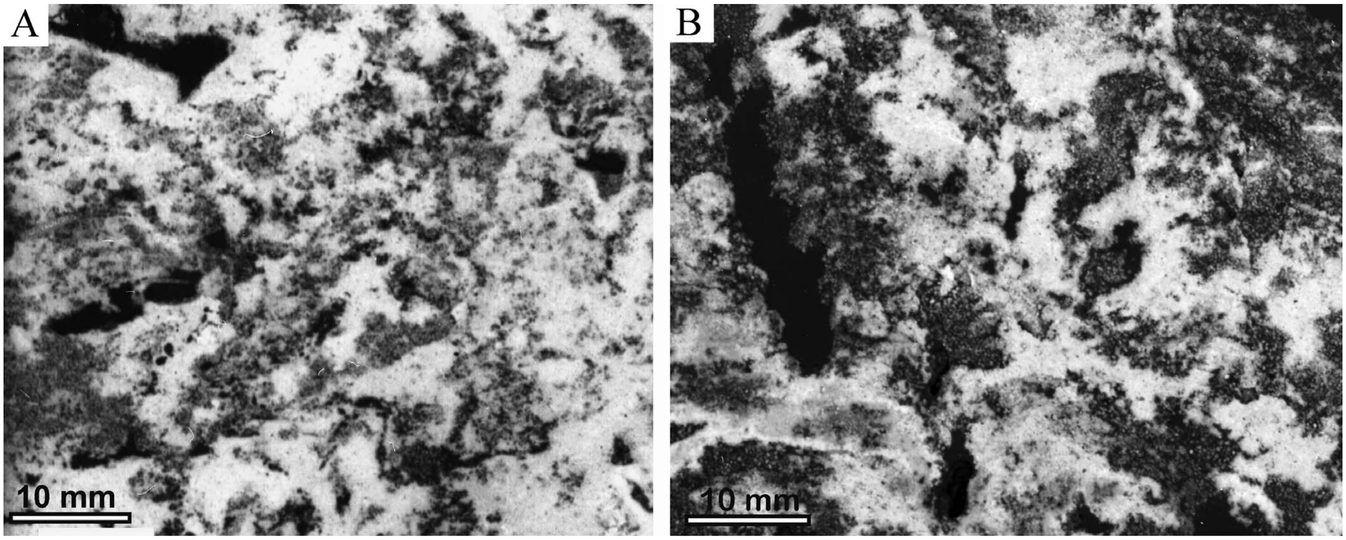

FIGURE 8—Thrombolitic fabric mesostructure in reflected light. A) Discrete clots grading into a massive clotted fabric (right) (specimen AC-2). B) Series of interconnected and roughly circular clots.

FIGURE 9—Serial sections (A, C, E) from a small microbialite (specimen AC-2) and corresponding clot distribution maps (B, D, F), showing that heavily cemented, clotted areas have a highly variable distribution. Clotted fabric is limited on the edges (A, E) and pervasive in the center of the microbialite (C). Distance between A and C is ~7 cm and 1.2 cm between C and E.

There has been significant crystal alteration and recrystallization as well as secondary cementation in the majority of the clotted areas. Within these clots, individual peloids can be so altered that grain boundaries are barely discernable (Fig. 12A). The resulting grains are irregularly shaped, have jagged margins, pitted surfaces, and are associated with substantial post-alteration cements (Fig. 12B). Patches of altered grains viewed using SEM etched thin sections do not have intragranular borings characteristic of micritization mediated by endolithic cyanobacteria (Macintyre et al., 2000; Reid and Macintyre, 2000) (Figs. 13A–B). Cement crystals are also altered. For instance, fibrous aragonite in the micritized areas often has indistinct crystal faces, pitted surfaces, or crystals that are fused to adjacent crystals (Fig. 14B).

The combination of XRD and SEM-EDS reveals that high- and low-magnesium calcite cements developed preferentially in clotted areas. Calcites are found in areas with abundant recrystallization features, such as those described above (Figs. 14A–B). Calcite has not been observed in the surficial microbial community using either SEM-EDS or XRD analysis (XRD data not shown). Non-acicular crystals have EDS spectra that lack a strontium peak and have a small but noticeable magnesium peak; these are interpreted as low-magnesium calcite (Fig. 14B). Low-magnesium calcite peaks appear in XRD spectra of bulk samples from clotted areas that do not contain noticeable coralline algae or metazoan fragments, which supports our interpretations of the EDS spectra. Magnesium calcites have variable morphologies, but are easily recognizable by a large, distinct magnesium peak in the EDS spectrum (Fig. 14A). The aragonite crystals are typically acicular and contain a strontium peak in the EDS spectrum.

Rarely, the clotted areas visible at the mesostructural scale are composed of peloids with high internal porosity that are surrounded by cements (Fig. 15). Although these clots form discernable masses, they appear to have formed around the adjacent sand grains (Fig. 15A). The relationship of the clots to the surrounding grains implies a cavity-filling origin. These porous peloids are significantly smaller than surrounding sand grains (Fig. 15B). The peloids are typically surrounded by micrite or fibrous aragonite cement (Fig. 15C). Individual peloids are composed of randomly oriented acicular needles or clusters of micrite and acicular crystals, and may be allochthonous sediment or an *in situ* precipitate (Fig. 15C). As originally noted by Dill et al. (1986), these sediments are typically rich in high-magnesium calcite and are found well below the surficial benthic community (typically <0.5 m).

In rare instances, metazoans aid in the formation of a clotted fabric. An agglutinating foraminifer, on which taxonomic work has not been

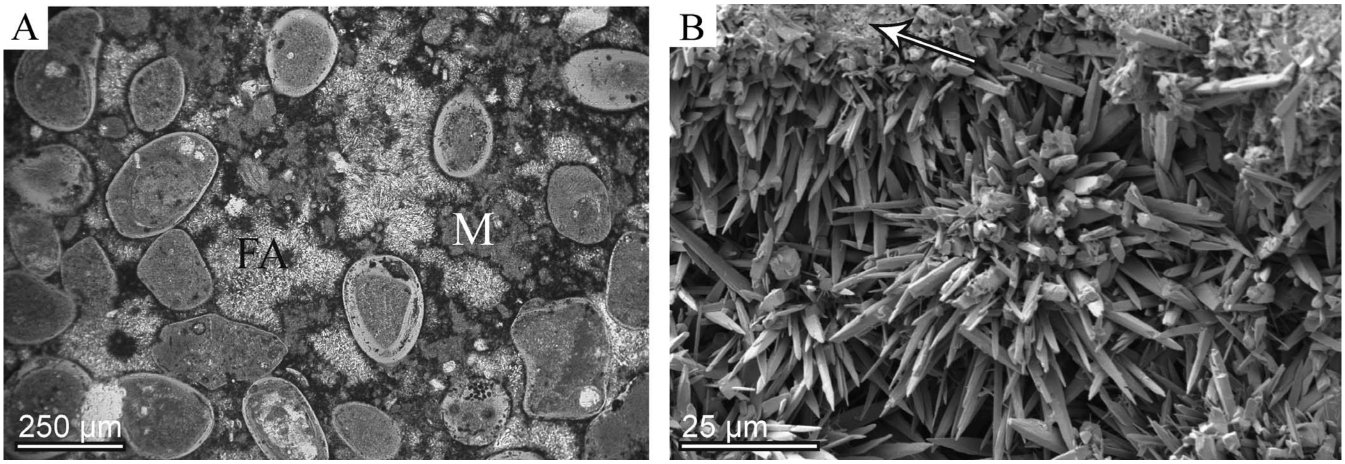

FIGURE 10—Cement microstructure. A) Peloids encased by micritic (M) and more abundant fibrous aragonite (FA) cements (plane-polarized light). B) Fine details of a fibrous aragonite cluster; the aragonite is acicular and has well-defined crystal faces, underlain by micritic cement (arrow) (SEM of a fractured surface).

conducted (Browne, 1993), leads to formation of millimeter-sized grain aggregates. Abundant agglutinating foraminifera can lead to the formation of a microclotted mesostructure. The foraminifera are rare (Browne, 1993), however, and were found in less than half of the thin sections examined. Clusters of calcareous worms have also been observed in the clotted fabric. Worm tubes truncate sand grains, indicating a boring habit. Uncommon *Ostreobium* carbonate tubules typically occur in areas with calcareous worms and agglutinating foraminifers.

Cement deposition is not limited to clots, and fibrous aragonite occurs sporadically in areas of unclotted sand. Together, the selective cementation that forms clots and the sporadic deposition of fibrous aragonite cements in unclotted sand produce a fully lithified limestone.

Mesostructure and Microstructure of the Bored Skeletal Grainstone

Bivalve shells and cemented sand grains that have been heavily bored by sponges are the primary components of the bored skeletal grainstone (Fig. 16A). In the AC-1 microbialite, the grainstone is limited to a thin horizon that separates the large core of thrombolitic fabric from the stromatolitic cap (Fig. 3). The relative concentration of sponge borings in this horizon varies considerably without any apparent trend. Most of the bivalves are themselves boring species, indicating a multi-generational fabric, and fragments of bryozoans, corals, foraminifera, and gastropod shells are a minor component of the fabric (Fig. 16B). There is extensive early diagenetic cementation as well as multiple stages of boring. The grainstone typically occurs as a thin horizon, but also occurs as the predominant fabric.

Accumulation Rate

The rate of accumulation of the AC-1 microbialite was estimated by dating the shells of the boring bivalves in the skeletal grainstone horizon below the stromatolitic cap (Fig. 3). Two shells from the bored horizon

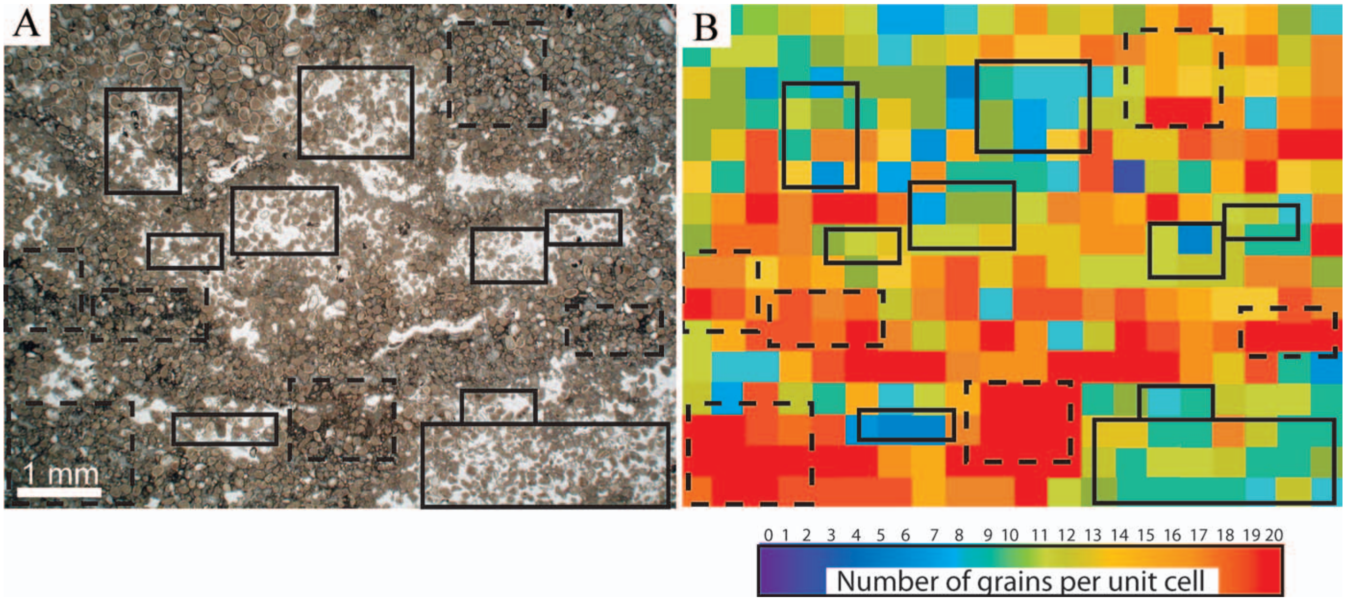

FIGURE 11—Grain-packing control on secondary cement distribution. A) Clotted and faintly laminated fabric with extensive intergranular cement; black intergranular areas contain micrite cement (boxes with dashed line), the grey intergranular areas contain fibrous aragonite cement, and the light intergranular areas lack cements (boxes with solid line) (plane-polarized light). B) Grain-density distribution map of area in A, with dashed and solid boxes the same as in A; colored boxes = number of sand grains/0.5 mm^2; grains were considered part of unit if ≥25% was within the unit boundaries; areas without intergranular cements correlate with less dense grain-packing and areas with micritic cement show a correlation with dense grain-packing.

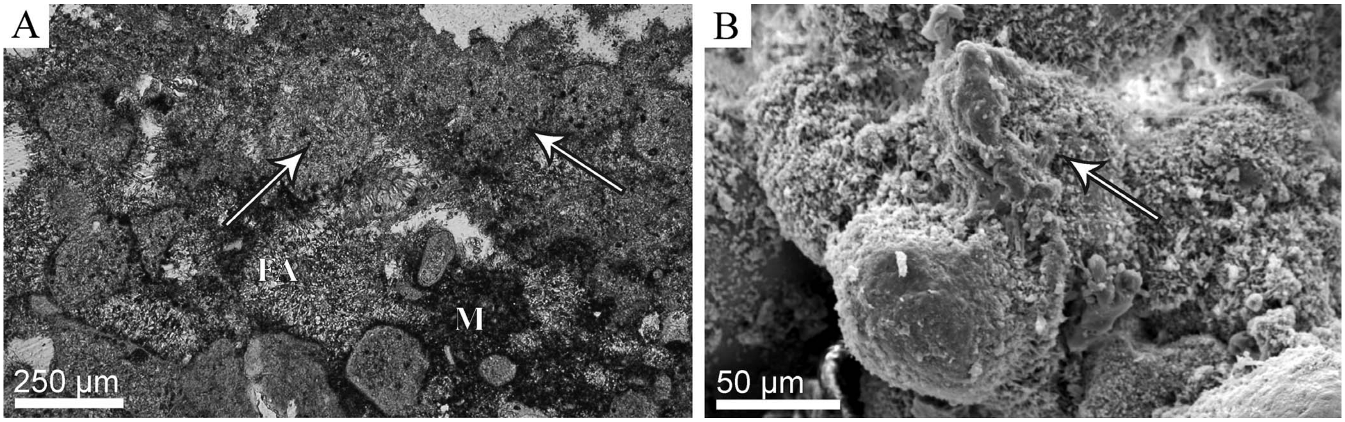

FIGURE 12—Microstructure of extensively micritized, clotted areas. A) Peloids that have been so altered it is difficult to distinguish individual grains (arrows). The grains are associated with micritic (M) and less abundant, fibrous aragonite (FA) cements (plane-polarized light). B) SEM of peloids with pitted, irregular margins (arrow) surrounded by micrite cements. The pitted surfaces of the peloids and irregular grain shape indicate significant early diagenetic modification.

yielded dates of 735 ±35 years and 865 ± 35 years, providing a maximum age for this horizon. Assuming that the growth of the stromatolitic cap was initiated shortly after the younger date, these values indicate accumulation of ~0.33 mm/year. The difference of 130 years between the two dates represents a minimal duration of the hiatus. Microbial mats in which *Schizothrix* predominate can accumulate several millimeters within two weeks (Browne, 1993), indicating there is a large disparity between the potential and actual accumulation rate.

DISCUSSION

Growth Model

Several successive processes create the Bahamian microbialite fabrics, and development of varying fabrics in the microbialites can be grouped into four stages: (1) sediment trapping, binding, and initial lithification; (2) disruption and truncation of the initial fabric; (3) pervasive cementation and clot formation; and (4) late-stage boring (Fig. 17). These processes are generally sequential, but there certainly can be overlap between stages.

The similarity of lamination microstructure between subtidal Adderly Channel microbialites and intertidal stromatolites at Highborne Cay (Reid et al., 2000) suggests similar modes of lamination formation. Macintyre et al. (2000) demonstrated that endolithic cyanobacteria mediate formation of the micritized laminae. Localized sulfate reduction within the biofilm leads to precipitation of aragonitic micrite laminations (Visscher et al., 2000; Andres et al., 2006). Thus, the formation of the stromatolitic laminations is caused predominantly by benthic microbial community stratification and cycling, rather than sedimentary processes (Reid et al., 2000).

The thin micritized and micrite laminations provide some initial stabilization of the microbialites, but they remain highly friable prior to the deposition of extensive secondary cements. During this friable stage, burrows and abundant truncations in laminated fabrics develop both on and below the surface of the microbialites. There is a dense, but largely unstudied, infaunal population in the Bahamian microbialites that is dominated by polychaete worms, nematodes, amphipods, bivalves, and larger crustaceans (Dill, 1991; Shapiro et al., 1995), which probably formed many of the vugs. Erosion of semi-lithified mat material, either during

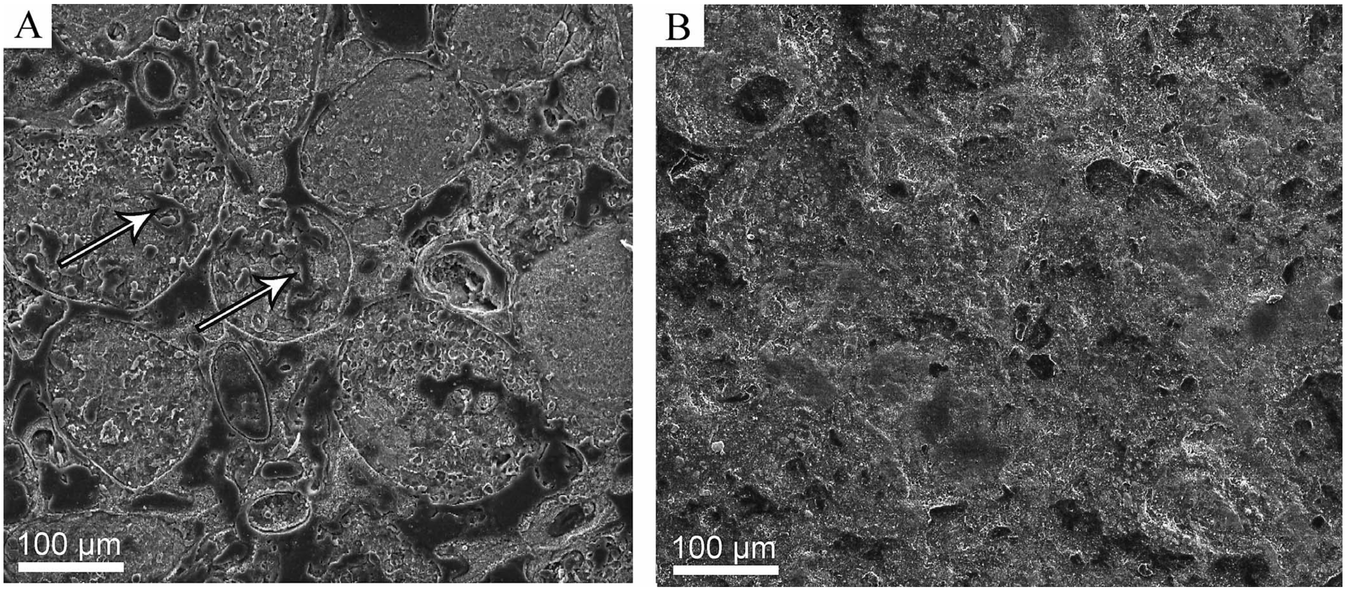

FIGURE 13—Cyanobacteria and dissolution-reprecipitation mediated micritization (secondary electron SEM on acetic-acid etched thin sections). A) Example of cyanobacterial microboring-mediated intergranular and intragranular alteration. The grains contain distinct, cement-filled cyanobacterial borings (arrows), are only joined at contact points and borings, and the alteration is localized to specific sand grains. B.) Example of dissolution-reprecipitation-induced grain alteration. Grains in the altered clump lack discernable borings, the alteration is pervasive rather than localized to individual grains, and grain boundaries are heavily altered. Dissolution-reprecipitation reactions are the dominant form of grain alteration in the clotted fabric.

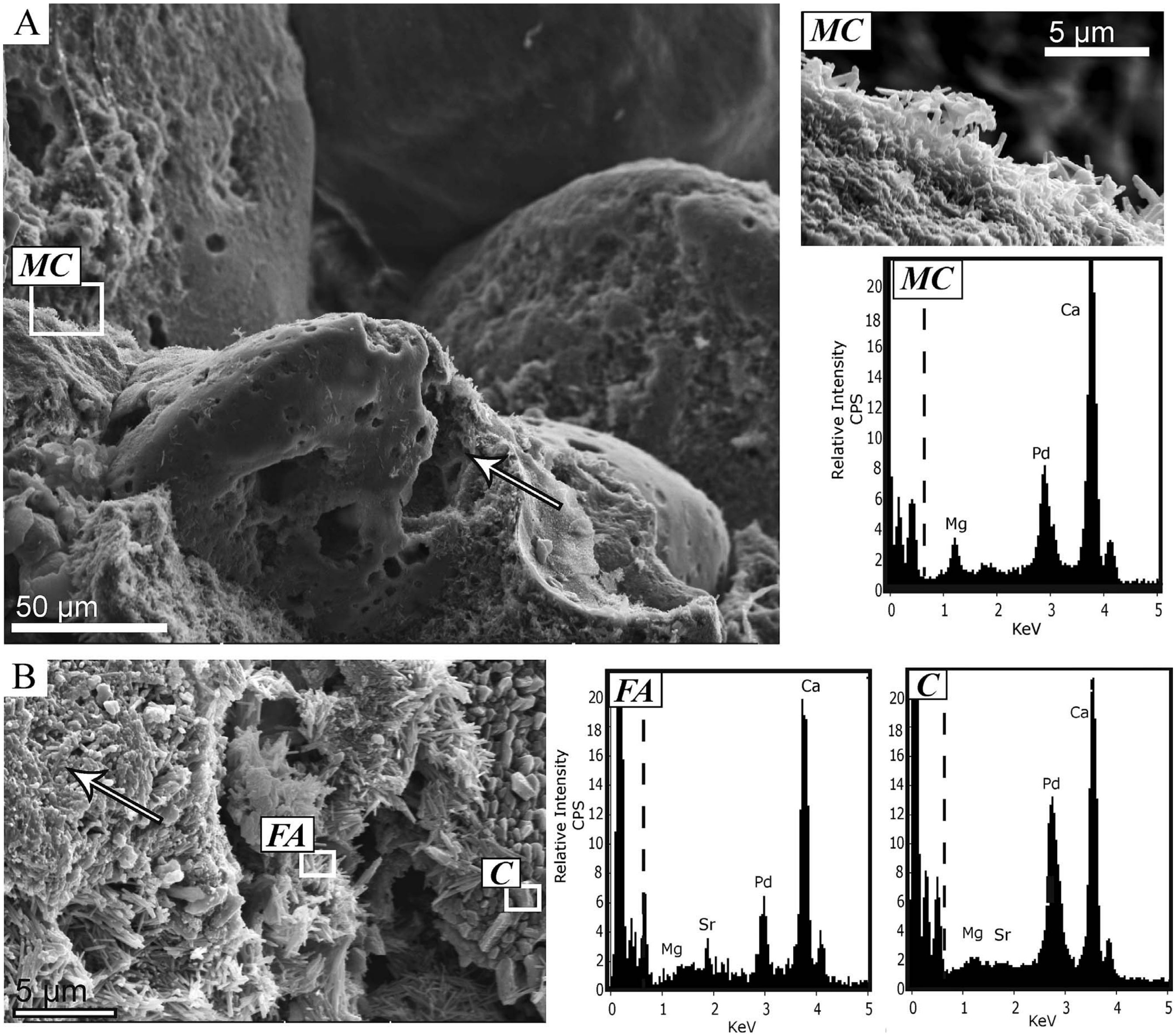

FIGURE 14—Calcite cements (secondary electron SEM on a fractured surface). A) Irregularly shaped, pitted peloid (arrow) surrounded by micritic, high-magnesium calcite cement (left) with higher magnification of boxed area and corresponding EDS spectrum (right); the relatively large Mg peak in the EDS spectrum indicates high-magnesium-calcite mineralogy. B) Blocky, low-magnesium calcite (right) interbedded with aragonite cement that has indistinct, fused crystals (arrow); EDS spectra of boxed areas are shown on the right; the aragonite cement (FA) contains a significant strontium (Sr) peak; the low-magnesium calcite (C) lacks a Sr peak and has only a slight Mg peak.

burial and exhumation by sand waves or through fish grazing, truncates laminations. Large voids that do not resemble burrows may have formed when microbialites are covered by migrating sand waves. This type of void formation is presumably linked with degradation of the stabilizing microbial community and subsequent removal of loose sediment (Lee et al., 2000). Disruption of the initial laminated fabric creates a highly irregular fabric, but does not directly form clotted structures. The presence of algae in a benthic ecosystem dominated by cyanobacteria may also aid in the formation of an irregularly packed and porous fabric.

A major finding of this study is that formation of clots occurs below the growing surface and is not directly related to the surficial microbial community. The lack of a relationship between specific growth horizons (Fig. 9) and the irregularly distributed clotted fabric indicates that clot formation occurs during penecontemporaneous diagenesis, after the initial trapping and binding of the sand grains. The examples of progressive transformation of a laminated to clotted fabric (Figs. 4, 7–8) also supports the interpretation that clot formation is a diagenetic process. This interpretation is consistent with results of previous studies, which did not observe the polylobate cement and micritized clots, which are present in fully lithified samples, in semi-lithified, surficial microbial ecosystems (Dill et al., 1986; Dill, 1991; Riding et al., 1991a; Browne, 1993; Golubic and Browne, 1996). The porous and irregular framework created by lamination disruption is the template for the clotted fabric. Areas of microbialite with closer grain-packing become preferentially cemented. Preferential cementation, micritization, and localized carbonate dissolution and reprecipitation form dense clots, which become framework elements. Significant taphonomic remodeling likely occurs during periodic depositional hiatuses when the microbialites are covered with benthic algae. This new model is consistent with the meticulous observations of Dill et al. (1986) that no accretion occurs when microbialite surfaces are covered by algae. These authors also emphasized the importance of early diagenetic cementation (Dill et al., 1986).

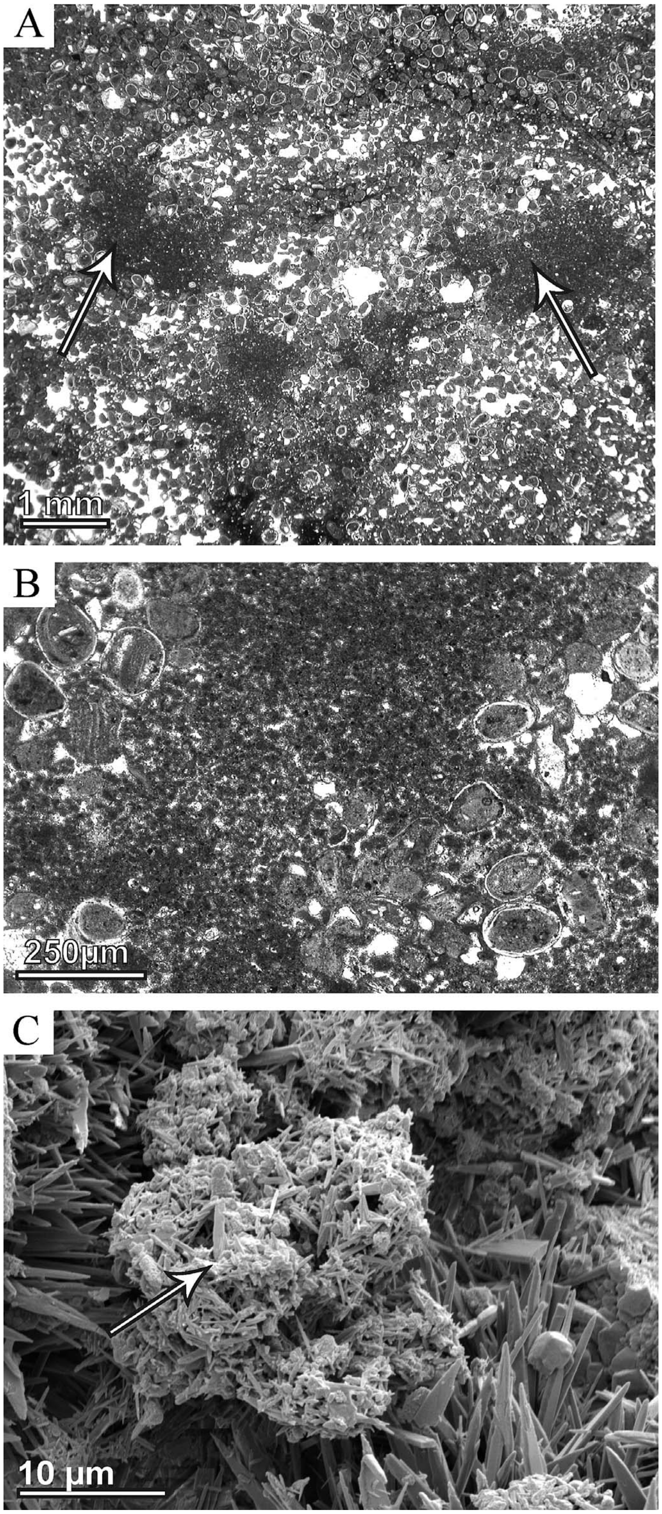

FIGURE 15—Microstructure of peloidal internal sediment. A) Clots made of peloids and cements (arrows) forming around loosely packed, peloidal sand grains suggesting they are vug fillings (thin section under polarized light). B) Detail of internal-sediment peloids and surrounding cement; peloids have less-distinct grain boundaries and are much smaller than surrounding sand grains (thin section under polarized light). C) Internal-sediment peloid (arrow) composed of randomly oriented, bladed aragonite surrounded by fibrous aragonite (SEM of a fractured surface).

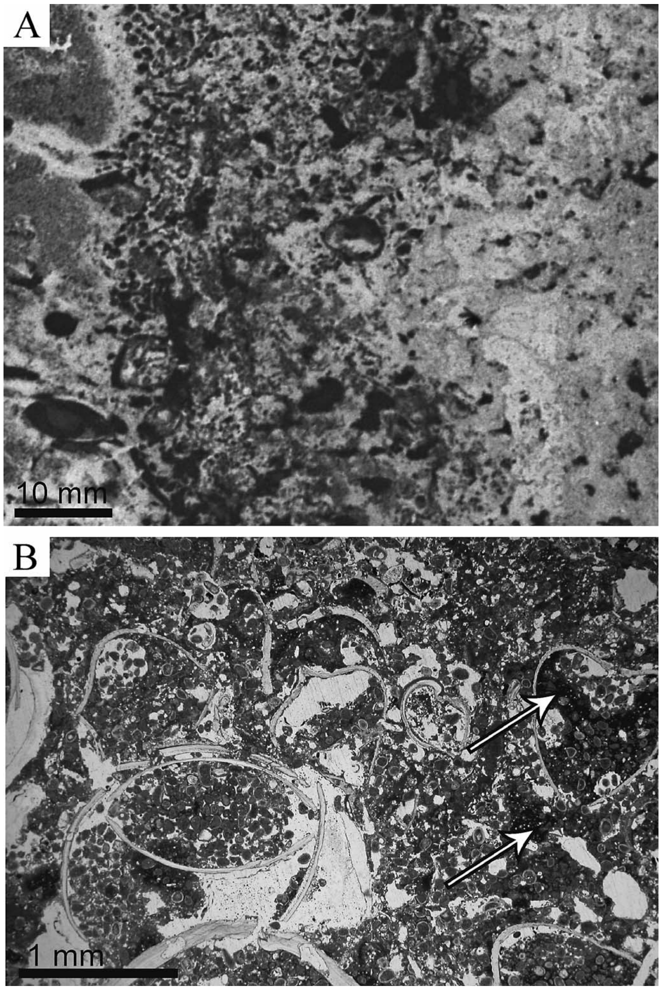

FIGURE 16—Skeletal grainstone mesostructure (A) and microstructure (B). A) Heavily bored grainstone with high concentrations of bivalves (bottom of photo) and sponge borings (top) (taken in reflected light). B) Predominant components in grainstone are fragmented bivalve shells and sand grains with micritic cement (arrows) (plane-polarized light).

The fine-scale microstructures provide additional evidence that clot formation is linked with early diagenetic processes. Numerous features, such as the jagged, pitted surfaces of the peloids, can only be explained through dissolution, requiring pore-water carbonate undersaturation. Abundant cements are directly associated with evidence of dissolution, indicating high levels of supersaturation. The microbialites, therefore, are a highly dynamic geochemical system. Dissolution features must be linked with organic matter remineralization, because Adderly Channel is highly supersaturated with respect to calcite and aragonite. Periodic burial by sand waves creates discrete periods of high heterotrophic microbial activity with relatively low exchange with the overlying water column—circumstances that could produce undersaturated interstitial water. Benthic sulfur cycling (sulfide production during initial stages of microbial sulfate reduction and sulfide oxidation) and aerobic respiration are the most common microbial processes that induce carbonate dissolution in modern carbonate systems (Morse and MacKenzie, 1990; Ku et al., 1999; Hu and Burdige, 2007). There is geochemical evidence for areas of low-magnesium calcite deposition and high levels of aragonite dissolution in the carbonate sand beds near Lee Stocking Island (Hu and Burdige, 2007), and this study provides petrographic evidence of this process occurring in adjacent microbialites. Low-magnesium calcite precipitation is likely induced by high alkalinities in the presence of aragonite and high-magnesium calcite undersaturation and by a reduced Mg/Ca ratio caused

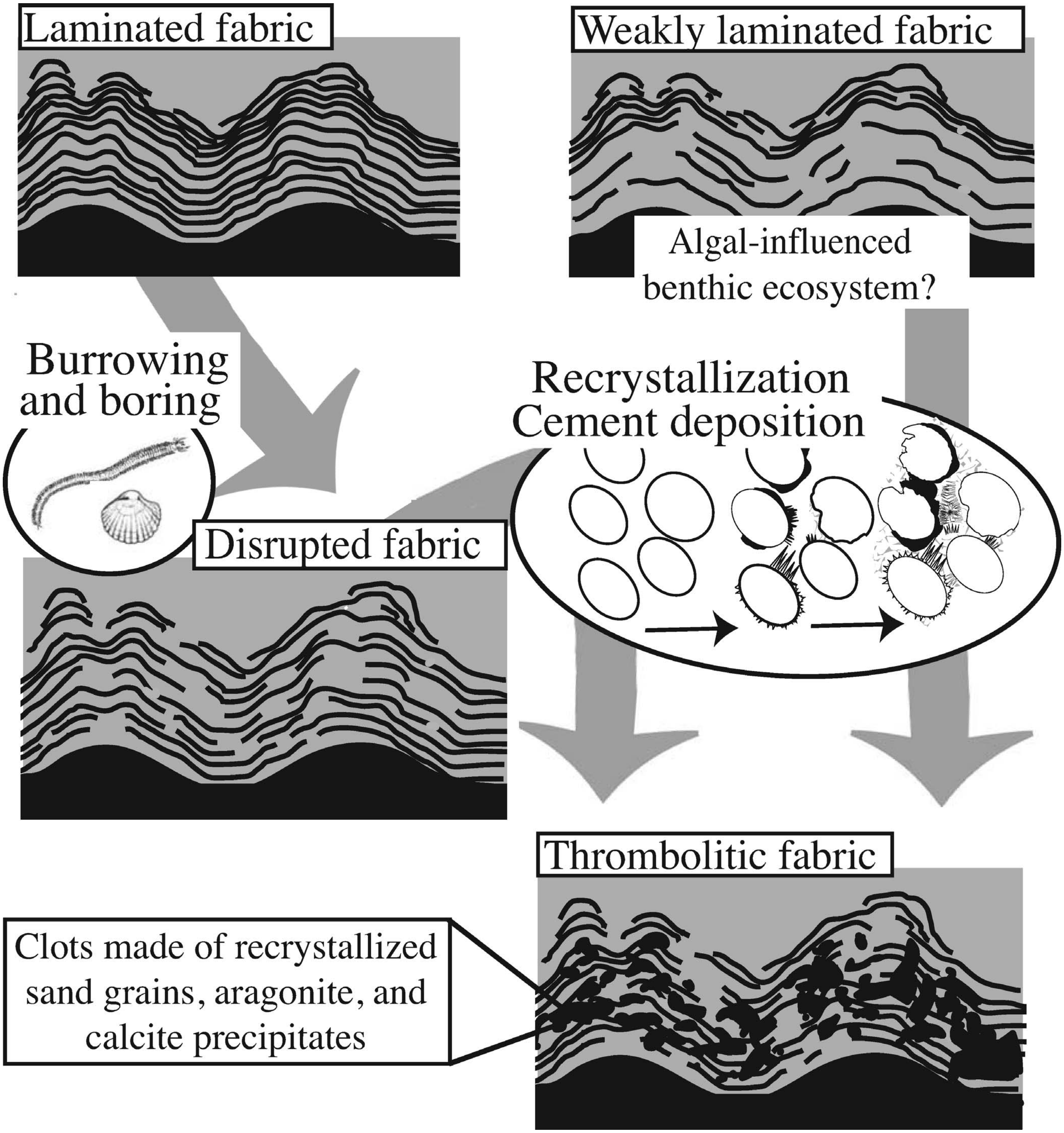

FIGURE 17—Schematic of inferred process in formation of Bahamian thrombolitic fabric, which is characterized by a clotted texture, disrupted laminations, and abundant vugs. The formation of fabric can be thought of as occurring in several stages: (1) sand grains are trapped and bound by a benthic ecosystem and initial cementation occurs, (2) an irregular packed framework is created through physical or biological modification, and (3) extensive secondary cementation and recrystallization occurs. See text for further details.

by aragonite dissolution (see Hu and Burdige, 2007, for further discussion). The precipitation of aragonite and high-magnesium calcite secondary cements are also likely linked with microbial processes, notably sulfate reduction (Morse and MacKenzie, 1990). Without stable isotope analysis of pore waters and cements, however, it is not possible to gauge the degree to which microenvironments of precipitation were shifted from ambient seawater.

During and after secondary cementation, the microbialites are commonly colonized by metazoans and bioeroded. As in other Caribbean carbonate environments (e.g., Choi, 1984), calcareous worms and foraminifera are among the first metazoan colonizers. They can promote the formation of an irregular, mottled fabric. These pioneering metazoans are followed by boring bivalves and sponges as well as encrusting bryozoans. In areas of extensive metazoan bioerosion, the primary microbial fabric is completely overprinted, forming a well-cemented, skeletal grainstone that is rich with borings.

The large, columnar Bahamian microbialite AC-1 offers unique insights into the dynamics of microbialite formation. The variability in fabrics in this microbialite reflects differing degrees of the early diagenetic processes described above. The stromatolitic fabric on the top was formed by cyanobacterial-mediated sediment trapping and binding, initial cementation, early stage bioturbation, and erosion. Later extensive cementation, crystal alteration, and further bioerosion produced the predominant thrombolitic internal fabric. Extensive bioerosion during a substantial hiatus in microbialite growth, produced a single, heavily bored grainstone horizon.

Comparison to Shark Bay Microbialites

Hamelin Pool, a hypersaline embayment in Shark Bay, Western Australia, contains well-studied, abundant, and diverse microbialites with fabrics that are remarkably similar to the Bahamian microbialite fabrics, as Reid et al. (2003) noted. The present study demonstrates the similarity between the unlaminated fabrics present in both these modern microbialites. Specifically, the unlaminated calcarenite and the unlaminated micrite of Reid et al. (2003) have similar microstructures and inferred modes of formation as the thrombolitic fabric described here. Most notably, the unlaminated micrite formed by the partial infilling of pore spaces with secondary cements between laminae of earlier-deposited micrite (Reid et al., 2003). Also, the unlaminated fabric at Shark Bay is extensively micritized, similar to the thrombolitic fabric of the Bahamian microbialites. Unfortunately, due to extensive metazoan overprinting, it is not clear if these microscale processes at Shark Bay can produce mesostructural clotted fabrics similar to those in the Bahamas. The radiocarbon-based estimate of the growth rate of the Adderly Channel microbialites (0.33 mm/year) is also similar to the rate obtained for the Shark Bay microbialites (0.4 mm/year) (Chivas et al., 1990).

Bahamian Microbialites as Modern Analogues

Although the Bahamian microbialites contain clotted structures (Fig. 8), the clots are not directly analogous to the abundant Neoproterozoic and early Phanerozoic thrombolites. Aitken (1967) first coined the term thrombolite for a ‘‘cryptalgal structure related to stromatolites but lacking lamination and characterized by a macroscopic clotted fabric.’’ No Bahamian microbialite has yet been found in which discrete clots are the dominant mesostructural feature as they are in many early Phanerozoic thrombolites. Because thrombolites are defined by their clotted fabric (see Shapiro, 2000 for discussion), we consider it problematic to refer to the Bahamian microbialites as thrombolites. The majority of Bahamian clots contain sand-sized grains as well as authigenic precipitates, whereas the clots in most Neoproterozoic–early Phanerozoic thrombolites are almost exclusively autochthonous.

Despite important differences between Bahamian and ancient microbialites, the Bahamian examples are useful modern analogues, as they offer insights into the processes occurring in an oceanic microbialite system. Therefore, many of the processes occurring in the Bahamian microbialites are likely applicable to many fossil microbialites. Several factors—including the influence of metazoans and algae, differential cementation, and widespread micritization—can be important in the creation of a single fabric in the Bahamian microbialites and may also have been significant in the formation of ancient thrombolites. The Bahamian microbialites clearly indicate that early diagenetic processes can have strong control over the microbialite fabric, and this factor needs to be considered in future studies of modern and ancient microbialites.

The skeletal grainstone present in the Bahamian microbialites demonstrates the ease with which microbial structures can be overprinted by boring metazoans when accumulation stops. Microbially induced carbonates are a common part of some Quaternary reefs (e.g., Webb et al., 1998; Camoin et al., 1999, 2006) and have been posited to be important in many Phanerozoic metazoan reefs (e.g., Webb, 1998; Shen and Webb, 2005). The ability to detect constructional microbialite fabrics in Phanerozoic reefs is, however, hindered by syndepositional recrystallization (Webb et al. 1998) and, as indicated by Bahamian microbialites, metazoan overprinting. Owing to these taphonomic and diagenetic biases, the importance of microbial carbonates in metazoan reefs is likely underestimated.

CONCLUSIONS

Microbialites from the Adderly tidal channel show a remarkable succession of fabrics linked with remodeling caused by integrated taphonomic processes. The thrombolitic—mottled and clotted—sections of the microbialites have a palimpsest fabric. Surface and subsurface bioturbation and erosion disrupted stromatolitic laminations and created nonhomogeneous packing. Clots developed in this irregular framework through secondary cement deposition and extensive micritization. Closer grain-packing resulted in preferential cementation and micritization, fostering development of the clots. A substantial portion of this micritization was induced by localized dissolution and reprecipitation driven by variable pore-water chemistry rather than by endolithic cyanobacteria. These clots are not directly relatable to a surface ecosystem. When there are significant breaks in accumulation, microbially produced fabrics are completely overprinted, which results in the formation of a boring-rich skeletal grainstone.

The Bahamian microbialites, as the only shallow ocean site of substantial modern microbial reef formation, offer a unique and valuable opportunity to gain insights into the processes that were undoubtedly involved in the formation of many ancient microbialites. The Bahamian analogues clearly demonstrate the need to consider the effect that early diagenetic histories can have on microbialite fabrics, a topic that often escapes discussion.

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REFERENCES

Aitken, J.D., 1967, Classification and environmental significance of cryptalgal limestones and dolomites, with illustrations from the Cambrian and Ordovician of southwestern Alberta: Journal of Sedimentary Petrology, v. 37, p. 1163–1178.

Andres, M.S., Sumner, D.Y., Reid, R.P., and Swart, P.K., 2006, Isotopic fingerprints of microbial respiration in aragonite from Bahamian stromatolites: Geology, v. 34, p. 973–976.

Browne, K.M., 1993, Lamination in recent Bahamian subtidal stromatolites: Origin and lithification: Unpublished Ph.D. Dissertation, University of Miami, Coral Gables, 296 p.

Burne, R.V., and Moore, L.S., 1987, Microbialites: Organosedimentary deposits of benthic microbial communities: PALAIOS, v. 2, p. 241–254.

Camoin, G.F., Gautret, P., Montaggioni, L.F., and Cabioch, G., 1999, Nature and environmental significance of microbialites in Quaternary reefs: The Tahiti paradox: Sedimentary Geology, v. 126, p. 271–304.

Camoin, G., Cabioch, G., Eisenhauer, A., Braga, J.C., Hamelin, B., and Lericolais, G., 2006, Environmental significance of microbialites in reef environments during the last deglaciation: Sedimentary Geology, v. 185, p. 277–295.

Chivas, A.R., Torgersen, T., and Polach, H.A., 1990, Growth-rates and Holocene development of stromatolites from Shark Bay, Western-Australia: Australian Journal of Earth Sciences, v. 37, p. 113–121.

Choi, D.R., 1984, Ecological succession of reef cavity-dwellers (Coelobites) in coral rubble: Bulletin of Marine Science, v. 35, p. 72–79.

Dill, R.F., 1991, Subtidal stromatolites, ooids, and crusted-lime muds at the Great Bahama Bank margin, *in* Osborne, R.H., ed., From Shoreline to Abyss: SEPM, Society for Sedimentary Geology, Tulsa, Oklahoma, p. 147–171.

Dill, R.F., Shinn, E.A., Jones, A.T., Kelly, K., and Steinen, R.P., 1986, Giant subtidal stromatolites forming in normal salinity waters: Nature, v. 324, p. 55–58.

Dravis, J.J., 1983, Hardened subtidal stromatolites, Bahamas: Science, v. 219, p. 385–386.

Feldmann, M., and McKenzie, J.A., 1998, Stromatolite-thrombolite associations in a modern environment, Lee Stocking Island, Bahamas: PALAIOS, v. 13, p. 201–212.

Golubic, S., and Browne, K.M., 1996, *Schizothrix gebeleinii* sp. nova builds subtidal stromatolites, Lee Stocking Island: Algological Studies, v. 83, p. 273–290.

Hoffman, P., 1967, Algal stromatolites: Use in stratigraphic correlation and paleocurrent determination: Science, v. 157, p. 1043–1045.

Hoffman, P., 1976, Stromatolite morphogenesis in Shark Bay, Western Australia, *in* Walter, M.R., ed., Stromatolites: Elsevier, Amsterdam, p. 261–271.

Hu, X.P., and Burdige, D.J., 2007, Enriched stable carbon isotopes in the pore waters of carbonate sediments dominated by seagrasses: Evidence for coupled carbonate dissolution and reprecipitation: Geochimica et Cosmochimica Acta, v. 71, p. 129–144.

James, N.P., and Ginsburg, R.N., 1979, The Seaward Margin of Belize Barrier and Atoll Reefs: Special Publication, v. 3, International Association of Sedimentologists, 191 p.

Ku, T.C.W., Walter, L.M., Coleman, M.L., Blake, R.E., and Martini, A.M., 1999, Coupling between sulfur recycling and syndepositional carbonate dissolution: Evidence from oxygen and sulfur isotope composition of pore water sulfate, South Florida Platform, USA: Geochimica et Cosmochimica Acta, v. 63, p. 2529–2546.

Lee, S.-J., Browne, K.M., and Golubic, S., 2000, On stromatolite lamination, *in* Riding, R., and Awramik, S.M., eds., Microbial Sediments: Berlin, Springer, p. 16–24.

Logan, B.W., 1961, Cryptozoon and associate stromatolites from the Recent, Shark Bay, Western-Australia: Journal of Geology, v. 69, p. 517–588.

Macintyre, I.G., Reid, R.P., and Steneck, R.S., 1996, Growth history of stromatolites in a Holocene fringing reef, Stocking Island, Bahamas: Journal of Sedimentary Research, v. 66, p. 231–242.

Macintyre, I.G., Prufert-Bebout, L., and Reid, R.P., 2000, The role of endolithic cyanobacteria in the formation of lithified laminae in Bahamian stromatolites: Sedimentology, v. 47, p. 915–921.

Morse, J., and MacKenzie, F., 1990, Geochemistry of Sedimentary Carbonates: Elsevier, Amsterdam, 707 p.

Playford, P.E., and Cockbain, A.E., 1976, Modern algal stromatolites at Hamelin Pool, a hypersaline barred basin in Shark Bay, Western Australia, *in* Walter, M.R., ed., Stromatolites: Elsevier, Amsterdam, p. 389–413.

Reid, R.P., and Macintyre, I.G., 2000, Microboring versus recrystallization: Further insight into the micritization process: Journal of Sedimentary Research, v. 70, p. 24–28.

Reid, R.P., Macintyre, I.G., Browne, K.M., Steneck, R.S., and Miller, T., 1995, Modern marine stromatolites in the Exuma-Cays, Bahamas—uncommonly common: Facies, v. 33, p. 1–17.

Reid, R.P., Visscher, P.T., Decho, A.W., Stolz, J.F., Bebout, B.M., Dupraz, C., MacIntyre, L.G., Paerl, H.W., Pinckney, J.L., Prufert-Bebout, L., Steppe, T.F., and Des Marais, D.J., 2000, The role of microbes in accretion, lamination and early lithification of modern marine stromatolites: Nature, v. 406, p. 989–992.

Reid, R.P., James, N.P., Macintyre, I.G., Dupraz, C.P., and Burne, R.V., 2003, Shark Bay stromatolites: Microfabrics and reinterpretation of origins: Facies, v. 49, p. 299–324.

Riding, R., Awramik, S.M., Winsborough, B.M., Griffin, K.M., and Dill, R.F., 1991a, Bahamian giant stromatolites: Microbial composition of surface mats: Geological Magazine, v. 128, p. 227–234.

Riding, R., Braga, J.C., and Martin, J.M., 1991b, Oolite stromatolites and thrombolites, Miocene, Spain: Analogs of recent giant Bahamian examples: Sedimentary Geology, v. 71, p. 121–127.

Shapiro, R.S., 2000, A comment on the systematic confusion of thrombolites: PALAIOS, v. 15, p. 166–169.

Shapiro, R.S., Aalto, K.R., Dill, R.F., and Kenny, R., 1995, Stratigraphic setting of a subtidal stromatolite field, Iguana Cay, Exumas, Bahamas, *in* Curran, H.A., and White, B., eds., Terrestrial and Shallow Marine Geology of the Bahamas and Bermuda: Geological Society of America Special Paper 300, p. 139–156.

Shen, J.W., and Webb, G.E., 2005, Metazoan-microbial framework fabrics in a Mississippian (Carboniferous) coral-sponge-microbial reef, Monto, Queensland, Australia: Sedimentary Geology, v. 178, p. 113–133.

Visscher, P.T., Reid, R.P., and Bebout, B.M., 2000, Microscale observations of sulfate reduction: Correlation of microbial activity with lithified micritic laminae in modern marine stromatolites: Geology, v. 28, p. 919–922.

Webb, G.E., 1998, Earliest known Carboniferous shallow-water reefs, Gudman Formation (Tn1b), Queensland, Australia: Implications for late Devonian reef collapse and recovery: Geology, v. 26, p. 951–954.

Webb, G.E., Baker, J.C., and Jell, J.S., 1998, Inferred syngenetic textural evolution in Holocene cryptic reefal microbialites, Heron Reef, Great Barrier Reef, Australia: Geology, v. 26, p. 355–358.

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