RECENT FRESH-WATER LACUSTRINE STROMATOLITES, STROMATOLITIC MATS AND ONCOIDS FROM NORTHEASTERN MEXICO

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ABSTRACT

Stromatolites, stromatolitic mats and oncoids are forming in two adjacent lakes (El Mojarral East and West) located in the desert basin of Cuatro Ciénegas, Coahuila, Mexico. Characteristic of the stromatolites and stromatolitic mats is a surface pattern of offset, horizontally oriented, outwardly projecting ledges produced by the calcifying cyanobacterium *Homoeothrix balearica*, in conjunction with the uncalcified cyanobacterium *Schizothrix lacustris*. In areas of low light and hence reduced carbonate accretion, endolithic cyanobacteria obscure the boundary between newly precipitated carbonate above and bedrock below. Fish and a diverse and abundant benthic animal population are associated with these biogenic structures. Fish alter the lamination pattern through grazing activities; the microbenthos have little effect on the integrity of the lamination. Diatoms are well preserved in the stromatolites and oncoids under certain conditions and dissolved in other situations. Quartz crystals are present in inverse proportion to the quality of diatom preservation.

INTRODUCTION

Stromatolites and related microbial accretions constitute a major part of the littoral lithofacies in spring-fed lakes and streams of the Cuatro Ciénegas Basin, Coahuila, Mexico. Their habitats range from deeply shaded settings near the bottom of lakes and streams where the current is rapid, to shallow, well-illuminated less energetic current conditions. Several different and distinct stromatolite morphologies are presently forming (Winsborough and Seeler, 1986, Winsborough and Golubic 1987, Winsborough,

1990). In El Mojarral, the lake system described here, stromatolites and stromatolitic mats develop with a characteristic lobate ridged growth pattern, produced primarily by the activity of a distinct and vertically differentiated microbial community. Oncoids, built by the same microbial community as the stromatolites, but lacking well-developed ridges also form.

SETTING

The Cuatro Ciénegas Basin is a small desert valley of about 1200 km² enclosed by mountains of the Sierra Madre Oriental of Coahuila, Northeastern Mexico. The northern tip of Sierra San Marcos, protruding from the south, almost bisects the basin (Fig.1).

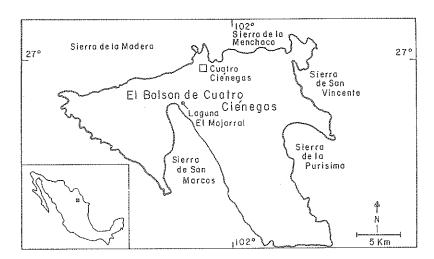


Figure 1 : Location map of the Cuatro Ciénegas Basin, Coahuila, Mexico, showing El Mojarral lakes.

This mountain is a faulted anticline composed of Cretaceous shallow water marine limestone, dolomite, and gypsum. The steep to vertical canyon slopes of Sierra San Marcos are rimmed by alluvial fans, which give way to a flat desert floor (elevation 740m). The mean annual air temperature is 23 °C (Morafka, 1977); annual rainfall is less than 200 mm, over half of that occurring in September (Garcia et al, 1975). This arid climate with highly seasonal rainfall provides the setting for a flat basin filled with a facies mosaic of evaporitic minerals.

Springs and seeps (reaching a density of 12-15 per $\rm km^2$) emerge along the distal margin of the alluvial fans. Most of the springs are warm (up to 35° C), but springs as cool as

19°C are also found. Some of the springs have nearly constant water temperatures throughout the year, whereas others vary between 19 and 35°C. The springs range in size from small shallow marsh seeps to deep spring-fed lakes and streams. Some springs are permanent, some dry out gradually, and some reverse their flow and then drain the lake they had been feeding. The spring-fed lakes and streams at Cuatro Ciénegas, in which stromatolites and oncoids are forming, are all very similar in their water chemistry. The cations are dominated by calcium, sodium, and magnesium while the most abundant anions are sulfates, followed in much less abundance by carbonates and chlorides. What is distinctive about these waters is that, for water with so little chloride, they have unusually high levels of sulfate relative to alkalinity. The water in which these stromatolites form is different in chemistry from stromatolite locations in other parts of the world because it is fresher than that found in a playa or brackish setting and has a greater amount of total dissolved solids than most fresh-water lake and stream examples (Winsborough, 1990).

The El Mojarral system is typical of several Cuatro Ciénegas spring-lake systems as is the growth pattern of their stromatolites and related microbial accretions. Laguna El Mojarral West (westernmost lake) appears to be the primary spring source for it and the adjacent lake, El Mojarral East. The lakes are about 200 m apart, connected by a shallow surface stream (and possibly by subsurface conduits). Extensive marshlands to the west contribute to surface and probably subsurface inflow. El Mojarral West is a roughly constant level, spring-fed lake about 13 m wide, 48 m long, and 1 to 5 m deep. Water temperature varies only about 7 degrees annually, between 28° and 35°C. Physical and chemical characteristics of El Mojarral West are summarized on Table 1. The lake appears to have been partly formed by the collapse of sections of roof

Mg	109.4	Zn	0.0047	Ca	372.7
Cd	0.0004	Na	142.5	Pb	not detected
K	8.0	Ni	0.0026	SO_4	1373.7
Co	0.0001	Cl	102.8	Fe	0.0040
Alk	164.8	Mn	0.00005	Sr	12.7
Cu	0.0033	Si	18.3	TDS	2283
F	2.7	pН	7.1	NO_3	6.8
Cond.	2800 µmhos	PO_4	0.003	Elev.	720 m
Size	14x48 m	Depth	0.5-6 m	Water T	33.3°C
Current	variable	1			

Table 1: Chemical and physical characteristics of Laguna El Mojarral (West), Cuatro Ciénegas, Coahuila, Mexico. Water samples collected July 1983. Analyses by R. Murnane, Princeton University. Data in mg/l unless otherwise specified.

covering a subterranean watercourse, thus it is technically a sinkhole. Water inflow is in the north end of the sinkhole near the bottom, at a depth of about 4.5 m. It comes

through a horizontal cave tunnel, which is passable for about 3 m. Another tunnel in the sinkhole bottom, at the opposite end, carries water out, presumably to El Mojarral East. In contrast to the sinkhole, El Mojarral East is about 50 m wide, 200 m long and 0.5 to 2 m deep. It has a firm, indurated carbonate bottom, in places largely devoid of loose sediment. Water inflow is primarily the surface stream at the west end, from El Mojarral West. The lake has an outflow channel on the east side that flows into the Rio Mesquites, a stream a few hundred meters to the east of El Mojarral. The Phragmites marsh associated with El Mojarral contributes so much particulate organic matter that, in still, marginal areas the sediment that accumulates is largely dark, organic, anoxic. copropelic mud (gyttja). Soft, white carbonate mud, of an undetermined thickness. covers parts of the sinkhole and lake bottoms. On these unconsolidated muds there is no development of microbial mats or stromatolites. Aquatic vegetation associated with the shallow margins of these lakes includes the sedge Eleocharis, the macroscopic alga Chara, the bladderwort Utricularia and the water lotus Nymphaea. Stromatolites were found only in El Mojarral West, oncoids only in El Mojarral East, and stromatolitic mats in both lakes.

METHODS

Some of the living surface mat from the various biogenic structures was removed from the lake, and, while keeping it submerged in lake water, examined and dissected in the field to obtain qualitative information about community structure. Preliminary examination of fresh material was carried out using dissecting microscopes and compound microscopes equiped with brightfield and phase contrast optics (the lights were powered by a portable generator). Material was routinely fixed in 3% formaldehyde or gluteraldehyde in environmental water. Cyanobacteria, diatoms, protozoa, and micrometazoa were later cultured in the lab for further study. Microscopy of field collected material was performed in the laboratory either as whole mounts or on gently decalcified samples (3% HCl) and preserved as semi-permanent slides mounted in glycerol.

DESCRIPTION OF MICROBIAL DEPOSITS

Stromatolites and stromatolitic mats

Along the shallow margin of the sinkhole, stems and roots of sedges, rushes and grasses frequently become cemented into a porous, calcareous travertine sometimes called "tufa". Eroded pebbles of this travertine are eventually distributed in the lake by water currents. The surface of this material as well as snails, discarded cans and bottles, and fragments of dead vegetation are colonized by a specific set of microorganisms responsible, under favorable conditions, for formation of stromatolites oncoids and stromatolitic mats.

Stromatolites are distributed on a shallow, broad, marginal shelf area that covers part of one end of the sink, and on the sides and bottom of the sink where the current is sufficient to carry away the fine silts, clays, and organic debris, leaving a firm substrate. The sediment covering most of the shelf consists of a poorly-sorted, sand-sized mixture of living and dead snails (mostly *Mexipyrgus churinceanus* Taylor with some *Euboria bella* Conrad and *Mexistobia manantiali* Hershler) and small carbonate pebbles. In addition to isolated individual stromatolites, stromatolitic mats up to 1.5 cm thick, build up on exposed bedrock and any other solid substrate both in El Mojarral West and El Mojarral East.

Macroscopic features of stromatolites and stromatolitic mats

The stromatolites are irregularly rounded in shape. Some are short and others are taller than they are wide. Typical examples reach up to about 20 cm in diameter, and are usually a bit wider than tall. Figure 2 shows the outline, internal and external appearance of a typical stromatolite. Stromatolitic mats up to 1.5 cm thick build up on

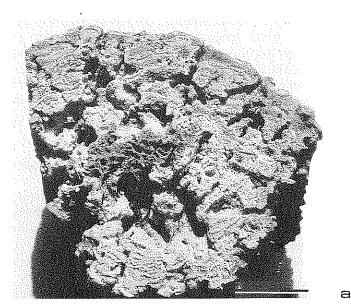


Figure 2: Internal view of typical stromatolite from El Mojarral West, showing ridged appearance of surface, and laminated interior. Scale bar = 2 cm.

exposed bedrock and any other solid substrate. Both the free-standing stromatolites and the stromatolitic mats lithify rapidly, often requiring a hammer and chisel to collect the entire thickness of the living part of the mat. In the case of both biogenic structures the surface is contoured with a constant, regular, repeating growth pattern as seen in Figures 2 and 3. Small, horizontally projecting ridges resembling tiny ledges or terraces are distributed regularly over most or all exposed surfaces. The ledges are lobate and project outward from the stromatolite and stromatolitic mat surface over a distance of about 2 mm. The ledges have an upper surface that is variably convex, leading to a horizontally convex outer rim. The lower side of the projection is variable in shape and sometimes exhibits partial "peeling" (see Monty, 1972) which lifts the projection slightly, shearing it away at the base. Over the surface of the stromatolite or stromatolitic mat these ridges are usually arranged in an offset pattern somewhat similar to that of roof shingles. Well developed ridges are remarkably regular in size and convexity (Fig.3a). When growing vertically, they are radial-campanulate in shape (Fig.3b). In older deposits the ridges fuse horizontally, and form long anastomosing "tuning fork" patterns (Fig.3c).

A general view of the internal pattern of the stromatolite laminae can be seen in Figure 2. Cross-sections through a stromatolite mat, cut parallel to growth (Fig.4a,b) shows, in greater detail, the typical lamination pattern present on the stromatolites and stromatolitic mats. The pattern consists of a series of light-colored, palisade-like layers of porous carbonate, alternating with dark green (or pink-purple) unencrusted organic-rich layers. The thickness of the laminae is not the same everywhere; it varies with the nature and growth rates of the individual organisms. Within the major calcite-rich layers there are sometimes up to about 6 thin carbonate-rich laminae approximately 0.2 mm apart separating sequential organic-rich laminae.

Community architecture of stromatolites and stromatolitic mats from well-lit habitats

By community architecture we mean the lamination and three-dimensional arrangement of the microbial contents. The surface layer of the stromatolites and mats found in well-lit areas is built by photosynthetic cyanobacteria and algae. Differentiation of this layer through time leads to alternation between zones dominated by the rivulariacean Homoeothrix balearica Bornet and Flahault and zones consisting of Schizothrix lacustris A.Braun; another Schizothrix sp. characterized by a slightly thicker trichome and a thinner less diffluent sheath has been recognized but not identified (Fig.5 a,b). Below this come pink-purple layers consisting primarily of empty Schizothrix sheaths surounded and/or inhabited by unidentified flexuous filamentous purple photosynthetic bacteria (Fig.5c), and occasional clusters of Chromatium sp. (not shown). In places this pink-purple layer extends almost to the surface of the mat, indicating an elevation of the redoxcline. The mat thus shows a classical vertical zonation with a surficial layer of

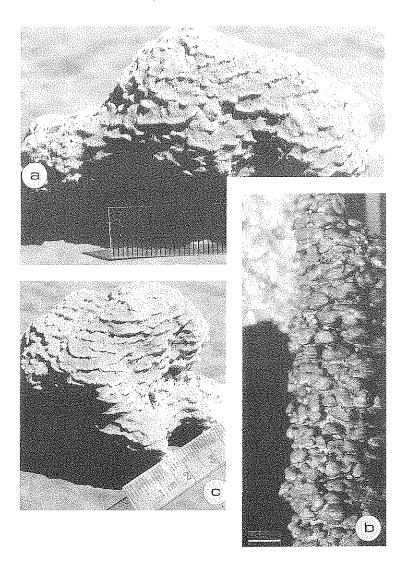


Figure 3: a) b); c) El Mojarral Stromatolites developed around substrates projecting in shallow (0.5 m) areas note well developed ridge patterns. a) & b) general view of mature stromatolites with elongate, sometimes anastomosing ridges. a) & b) scale bars in cm and mm. c) overgrowth of mushroom or campanulate shaped cushions built by *Homoeothrix balearica* around a dead plant stem. This structure will eventually topple over as the stem inside rots away then it will become a potential nucleus for future stromatolite development. Scale bar is in cm.

oxygenic photosynthesizers (cyanobacteria, diatoms and other algae) overlying a reduced layer of anoxygenic photosynthesizers and dissimilatory sulfate reducers. A high rate of sulfate reduction is indicated by the odor of these sediments.

Under high light conditions the brownish appearance of the mat surface is due to the sheath pigmentation of H. balearica filaments, while under low light conditions (such as near the underwater cave mouth and on the underside of stromatolites) these filaments take on a dark purple color due to increased accumulation of phycoerythrin in

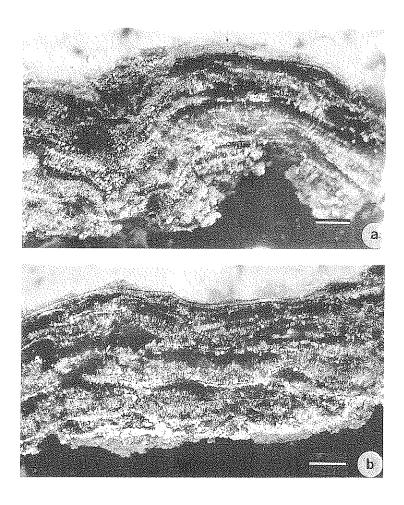
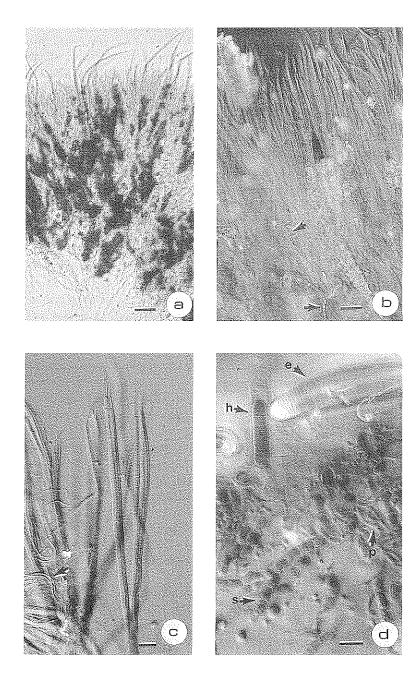


Figure 4:a); b) Sections through the actively growing stromatolitic mat showing the alternation of light colored carbonate-rich and dark colored organic-rich laminae comprising a vertical sequence from bedrock to present growth surface. Scale bar = 1 mm.

the cells and reduced sheath pigmentation. Packed among the upright cyanobacterial filaments and often attached to them is a thick gel-bound zone composed primarily of diatoms, testate and other protozoans, annelids, ostracods, harpacticoid copepods, tiny snails, insect larvae, calcite crystals, and fecal pellets (primarily from snails and fish). Toward the base of this layer, calcite crystals and fecal pellets become more densely packed. Occasionally, colonies of Gongrosira calcifera Krieger are found beneath the uppermost layer, sometimes attached to filaments of H. balearica. Diatoms such as Gomphonema intricatum var. vibrio (Ehr.) Cl. (also called G. angustum Agardh), Cocconeis placentula Ehr. and Achnanthes spp. are epiphytic on the Homoeothrix filaments, whereas others, especially Cymbella spp. and Anomoeoneis vitrea (Grun.) Ross form dense clusters among the pockets and crevices on the irregular mat surface. The diatom population in a well developed stromatolite mat dominated by *Homoeothrix* balearica consists of about 5 very commonly occurring species and about 30 less common taxa. The most common species are as follows. 1. Denticula kuetzingii Grun., 2. Cymbella cesatii (Rabh.) Grun. ex A.S., 3. Denticula elegans Kütz., 4. Achanthes affinis Grun., and 5. Gomphonema intricatum var. vibrio. There is a spatial component to the distribution of different diatom species as there is to the cyanobacteria. D. kuetzingii is sometimes motile, attaches by a mucilage pad, or forms gelatinous masses which are distributed throughout the mat. C. cesatii may attach by a short stalk, but is also able to crawl quite rapidly, and is commonly seen among the loose carbonate particles as well as associated with colonies of the protozoan Ophrydium cf versatile (O.F.M.). D. elegans often forms dense mucilaginous colonies between the filamentous cyanobacteria, whereas A. affinis lives adpressed to the sediment. G. intricatum var. vibrio attaches to other plants with long branching stalks, allowing access to the uppermost parts of the mat where nutrients and light may be more available. These species are all alkaliphilous forms, characteristic of temperate to warm spring-fed streams and ponds with high conductivity water, and prefer or are indifferent to moderate water current. Small diatoms, such as Achnanthes affinis, Anomoeoneis vitrea, Cocconeis placentula, and Amphora spp., and the much larger Epithemia Ehr Kütz, are to be found living in crevices of the mat or as early colonizers of freshly deposited calcite layers. Achnanthes and Cocconeis produce a mucilage pad that leaves a thick bas-relief impression of the cell on the carbonate.

Community architecture of stromatolitic mats from low-light habitats

The general community architecture described above for the well-lit sinkhole stromatolites applies also for the stromatolitic mats lining the deeply-shaded vertical ledge leading to the mouth of the inflow cave. Indeed, there is a continuity of the community architectures from the stromatolites and multilayered stromatolitic mats to these thin surface communities. Thus, with increasing depth (i.e. reduced light) the thickness of the surface encrustation diminishes to about 0.7 mm, and a different suite of cyanobacteria is found in the sub-surface layer. *Homoeothrix* and *Schizothrix* still predominate in the surface layer, at times foundtogether with patches of *Lyngbya*



kuetzingii Schmidle, Gongrosira and the rhodophyte Adouinella sp. However, at the base of the filaments a diverse community of the coccoid chroococcalean and pleurocapsalean cyanobacteria takes over. Examples include Pleurocapsa minor Hansg. em. Geitler, Cyanostylon microcystoides Geitler, and various members of the genera Chlorogloea, Aphanocapsa, Synechococcus, Synechocystis, and Microcystis. Exact determination of these small-celled taxa (1-5 µm diam. cocci) was impossible due to the mixed nature of these populations and each taxon's patchy distribution. Primary cultures on agar media routinely yielded up to a dozen different forms as judged by cell size and colony morphology, but in no case was it possible to correlate cultured cells definitively with the feral material from which it was inoculated. Such low light communities, whose pigmentation is dominated by phycoerythrin, have been termed "red-colored deep water biocoenoses" ("rotbunte Tiefenbiocoenose", see Kann and Sauer, 1982), and are characteristic of low-light habitats of clear, hard-water lakes.

In places where the low light level permits only patchy and reduced growth of the filamentous forms (*Homoeothrix, Schizothrix, Gongrosira, Adouinella* and *Lyngbya*), a 0.1-0.2 mm deep zone of endolithic cyanobacteria penetrates the bedrock below the coccoid forms described above (Fig.5d). It is dominated by *Plectonema terebrans* Bornet & Flahault, *Iyengariella endolithica* Seeler & Golubic (Seeler and Golubic 1991) and another undescribed stigonematalean endolith (Seeler and Golubic unpublished data). These changes in community architecture along the light gradient in El Mojarral West are summarized diagrammatically in Figure 6.

Microstructure and calcification processes of stromatolites and stromatolitic mats

Within the actively growing part of the mat of both stromatolites and stromatolitic mats (up to 10 mm or more in thickness) calcite is precipitated in the vertical-radial masses of *Homoeothrix* filaments to form calcified laminae. The stromatolitic mats consist of an alternation of carbonate-rich and organic-rich laminae. These laminae show a palisade-like pattern made of tubular or fused-tubular carbonate encrustations (Fig.5a) made of rounded to loaf- shaped crystals about 10 μ m wide (Fig.7b). Successive layers of calcified *Homoeothrix*-dominated laminae are usually interrupted or separated by thin,

Figure 5: a); b); c); d) a) Micrograph of the top layer of El Mojarral stromatolite mat showing dark calcitic encrustations surrounding tapering filaments of *Homoeothrix baleairca* among *Schizothrix lacustris*. Scale= $50~\mu m$; b) Detail showing encrusted *H. balearica* filament on lower right, dark area represents filament emerging from encrustaion. Note thin monocrystalline calcitic tubes precipitated around *Schizothrix* sp. filaments (arrows). Scale= $20~\mu m$; c) *Schizothrix lacustris* exhibiting typical branching of filament. Note also filamentous purple bacteria among *Schizothrix* sheaths (arrow). Scale= $10~\mu m$. d. Resin-embedded and decalcified thin section through cyanobacterial and diatom community from mouth of the inflow cave. Note *Eunotia* cf. *maior* (c) and *H. balearica* (short filament, h) on the surface and endolithic undescribed stigonematalean cyanobacterium (s) and *Plectonema terebrans* (p) below. Scale= $10~\mu m$. (a) = plane transmitted light; b), c), d) = Nomarski differential interference contrast.)

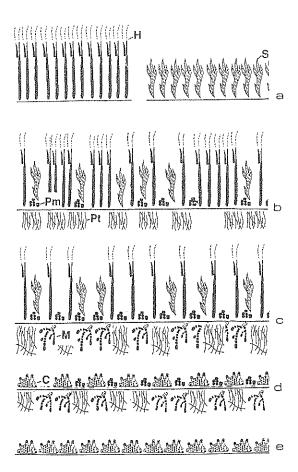


Figure 6: a); b); c); d); e) Profile diagram showing cross-sections of cyanobacterial communities encountered down the depth and light gradient of El Mojarral West illustrating transitions from the high-light surface community a) to the shaded low-light community at depth e). The horizontal line in each cross-section separates the epilith zone (above) from the endolith zone (below). Only representative taxa are included. H = Homoeothrix balearica, S = Schizothrix lacustris, Pm = Pleurocapsa minor, Pt = Plectonema terebrans, M = Mastigocladus-like and Iyengariella endolithica stigonematalean endoliths, C = Chlorogloea sp. and other coccoid epiliths. a) Multi-layered stromatolitic mats consist of alternating Homoeothrix and Schizothrix-dominated laminae, diagrammed here as only a single layer. b) Single epilithic layer from intermediate depth with endolith zone consisting exclusively of Plectonema terebrans. c) More shaded than community in "b)" with the addition of stigonematalean endoliths and exhibiting sparser epilithic growth. d) Deeply shaded mat in which filamentous epiliths have been replaced by coccoid forms. e) In the lowest light regions of the inflow cave only a thin epilithic surface layer of coccoid cyanobacteria (e.g. Chlorogloea sp.) remains.

relatively fine laminae of precipitated material, consisting of cloudy, tightly packed masses of calcite crystals; these sometimes surround Homoeothrix filaments, extending through from the layer beneath. The organic-rich laminae are dominated by the two Schizothrix species reported above. Occasionally monocrystalline calcite encrustations occur as thin tubes surrounding the sheath of the unidentified Schizothrix species (Fig.5b). The surface layers of Homoeothrix balearica and Schizothrix lacustris are thickest on and beneath the crests of the ridges such as illustrated on Fig.4. Carbonate crystals also nucleate upon diatom stalks and the surface of gelatinous spherical envelopes produced by diatoms. In the protected environment of the gel produced by cyanobacteria and diatoms, clusters of sparry calcite crystals with a radial fan-like growth habit develop. A comparable example of in situ mineralization in the shape of spherulitic fans takes place in the mucilage surrounding Scytonema, in the supratidal freshwater cyanobacterial mats illustrated by Monty and Hardie (1976, p. 454, Fig.4h). Calcite is also precipitated in long, plate-like crystal masses around the filaments of Gongrosira, producing hard patches of calcite among the more loosely distributed grains surrounding the cyanobacteria. The crystal morphology associated with Gongrosira is the same as that described and illustrated in Golubic and Fischer, (1975). Micrite and micro-sparitic calcite cement (Fig.8), fills some of the cavities as lithification proceeds. These low-magnesian calcite crystals appear as deformed "gothic arch" and "edge-guttered" calcite (Folk, Chafetz, and Tiezzi, 1985) perhaps due to the poisoning effect of the sulfate ion on the calcite crystal lattice. Crystal size of cement ranges from 2 to >30 um.

This generally loose fabric changes gradually downward, toward the interior of the mat, to more rigidly packed sheaths of *Homoeothrix* surrounded at first by loose anhedral, then tighter interlocking coarser crystals (see Fig.10, next section). This internal pattern of change in the crystallographic habit represents gradual crystal growth concomitant with bacterial degradation of the organic components of the mat. Some filaments in the interior of the mat may become coated by closely packed fine-grained calcite crystals (micrite). This collection of carbonate fabrics may represent various stages in the syndepositional and early diagenetic processes that take place during growth of the surface mat. The moldic porosity may be altered to a denser fabric as the holes are filled with cement.

In some cases the decomposed remains of *H. balearica* and *S. lacustris* produce fenestrae, (cf. Monty, 1976 and Monty and Mas, 1981). Particularly in the low-light stromatolitic mats, such interstices may be secondarily filled with growth of *Plectonema terebrans*, other cyanobacteria of the LPP type (*Lyngbya-Plectonema-Phormidium*, see Rippka *et al*, 1979), the chroococcalean *Cyanostylon microcystoides*, or they may remain open and eventually become lined with sparry calcite cement.

Whereas the stromatolite microfabric is largely the consequence of *in situ* calcite precipitation, there is evidence of detritus incorporation into the structures. Sediment consisting primarily of snails, shell fragments, fecal pellets, micrite and sparite grains is episodically trapped and bound into the surface community. Fish activity, for example, often stirs up clouds of fine sediment, which settles on the nearby stromatolites.

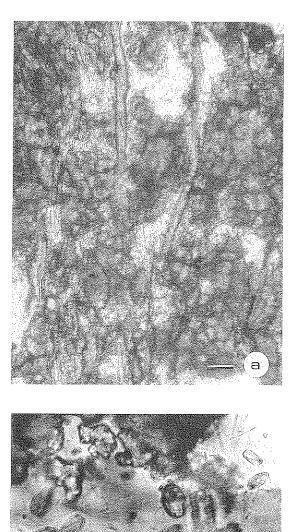


Figure 7: a); b) Micritic and rounded spar crystals photographed in situ from the surface of an actively growing stromatolite mat; a) Crystals attached to the surface mucilage of Homoeothrix balearica filaments; b) Crystals associated with diatom mucilage. Scale bars = $10 \, \mu m$.

Oncoids

Macroscopic features of oncoids

Spherical to subspherical oncoids (Fig.9a) are found in scattered areas along the margin of El Mojarral East in water depths of 0.5 to 2 m, where the bottom is hard, and the current is sufficient to remove material smaller than a pebble. The average diameter of the oncoids observed is about 10 to 20 cm. The most concentrated deposit occurs along the initial 25-50 m or so of a broad outflow stream that leads to the Rio Mesquites. The flat floor of the stream is almost covered with a layer of oncoids. The oncoids show a well-laminated cortex composed of alternating layers of dense, light colored carbonate-rich laminae and porous, darker, organic-rich laminae (Fig.9b). This lamination pattern is essentially indistinguishable from that of the stromatolites described above. The nucleus may be a calcite pebble, snail shell, or piece of organic debris. The material that forms the nuclei of the oncoids is variable in porosity and microstructure. Some pebbles consist of an unlaminated snail-fragment biosparite beneath the laminated cortex. Others are composed of fragments of marsh travertine or calcified *Chara*.

The oncoid surface is usually slightly wavy or lumpy, with round holes 1-2 mm wide distributed somewhat unevenly over the surface (Fig.9a). These holes are lined with living microorganisms. The holes are the external expressions of irregularly shaped channels and chambers oriented roughly perpendicular to the growing surface; they extend at varying distances, often more than 1 cm into the interior of the oncoid, and frequently reach or even penetrate the nucleus. These channels appear to be maintained by the activities of the associated benthos.

Community architecture of oncoids

The organisms responsible for construction of the oncoids are *Schizothrix* and *Homoeothrix*, producing a rhythmic depositional pattern similar to that of the stromatolites. The surface of the oncoids lacks the ledges, and has an overall lumpy appearance produced by tufts of *Homoeothrix*. The cyanobacteria, diatoms and other eukaryotic algae are the same species as those found on the stromatolites. Channels and interior chambers in the oncoid cortex are lined with microbial growth, and the underlying carbonate is bright green for a thickness of almost a millimeter due to the extensive activities of endolithic cyanobacteria (principally *P. terebrans* and other LPP forms). These cavities in the stromatolites show decreased *Homoeothrix* growth. Detrital material, particularly fecal pellets, partially fills some holes.

Microstructure and calcification processes of oncoids

Oncoid Iaminae consist of alternating dense carbonate-rich, and porous organic-rich

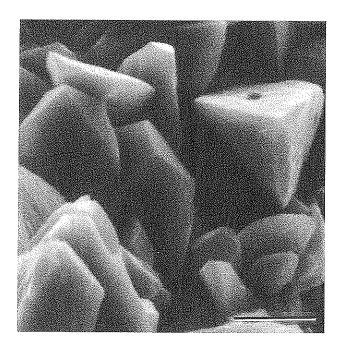


Figure 8: SEM view of cavity-lining micritic and microsparitic cement in cortex of stromatolite. Crystal irregularities such as ragged faces, bezeled or guttered edges and corners, pits in the center of faces and arched curves are common. Scale bar = 5 µm.

layers as do the stromatolites, but the laminae are generally somewhat thinner, tighter and more compact. They also do not exhibit secondary internal Schizothrix growth to the same degree as do the stromatolites. In thin section Homoeothrix filaments are clearly evident in growth position, to a distance of more than a cm into the cortex of oncoids (Fig.10a). Micritic calcite indicates what was formerly the surface of the cyanobacterial filament as seen in Fig.10b. The sheath cavity has been filled with micrite. Some organic matter (possibly last remains of the original sheath) appears as thin black linings (arrows, Fig. 10b). In addition to the micrite described above, interlocking fringes of isopachous sparry calcite crystals fill voids between Homoeothrix filaments in Fig.10b. Carbonate particles (including snail shells) smaller than 5 mm diameter are usually bored by Plectonema terebrans and other LPP forms (sensu Rippka et al, 1979) to such an extent as to constitute a cohesive organic matrix even when all carbonate is dissolved away with acid. Other cyanobacterial endoliths contributing to carbonate boring in oncoids include the undescribed stigonematalean depicted in Fig.5d and at least three new species of Hyella (J.-S. Seeler and S. Golubic, unpublished).



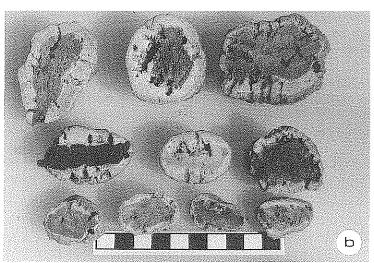


Figure 9:a); b) a) External view of oncoids. Note undulating surface pattern and scattered holes leading to internal chambers; b) Oncoids sawn open to illustrate laminated cortex, and unlaminated nuclei. Scale bars in cm.

Imperfectly formed bipyramidal quartz crystals (Fig.11) are found in oncoids as well as occasionally in stromatolites. These crystals range in size from about 4.5 x 8.2 µm to 20.0x62.5 µm. An authorhthonous origin for the quartz crystals is supported by the presence of colorless filaments trapped in some of them (Fig.11, lower left crystal, with arrows). In the residues of porous internal structures of stromatolites with alternating thin, dense, and thick, sparsely calcified laminae, there are large numbers of well preserved diatoms and fewer quartz crystals. In thinly-laminated oncoids and stromatolitic mats from the deeply shaded areas, there are few diatoms preserved in the insoluble residue and numerous quartz crystals. These preliminary observations show an inverse relationship between the number of diatoms preserved in a structure and the number of quartz crystals in the residue. This suggests that diatom opal, which resembles silica gel (Krumbein and Werner, 1983), is being dissolved to feed the growth of quartz crystals precipitating locally in the mat.

Grazers and predators associated with stromatolites, stromatolitic mats and oncoids

There is a varied and numerous benthic fauna associated with these biogenic structures, relying on them for shelter and food. In a typical mat from a well-lit area of the sinkhole the benthos usually includes amoebae, flagellate protozoans, euglenas, ciliates, rotifers, neorhabdocoels, gastrotrichs, nemerteans, nematodes, harpacticoid copepods, flatworms, chironomid larvae, small snails, ostracods, water mites and amphipods. Nematodes are very common in the interstices of the mat, and because of their size and numbers appear to disturb the softer laminae as they move through them. The thin, deeply shaded stromatolitic mats do not exhibit significant benthic fauna. In addition to the invertebrates, several species of fish graze on the stromatolites and related structures, leaving groups of parallel, tooth-produced grooves on the stromatolite surface sometimes removing entire patches of mat growth, exposing the greenish-white calcite interior.

DISCUSSION

Abundance of stromatolites, stromatolitic mats, and oncoids

Stromatolites are distributed in El Mojarral West in water from 0.5 to 4.5 m depth. Their distribution is limited primarily by the availability of an appropriate substrate and adequate current which prevents burial by detrital sediment. Their abundance has diminished over the years due to vandalism, and excessive siltation. The stromatolitic mats are extensive in distribution in both El Mojarral East and West and relatively undisturbed. From experiments using artificial substrates, the growth rate of stromatolites and stromatolitic mats is estimated to be on the order of several mm or more per year. The distribution of oncoids is very current dependent and large numbers are concentrated only in the outflow area of El Mojarral East.

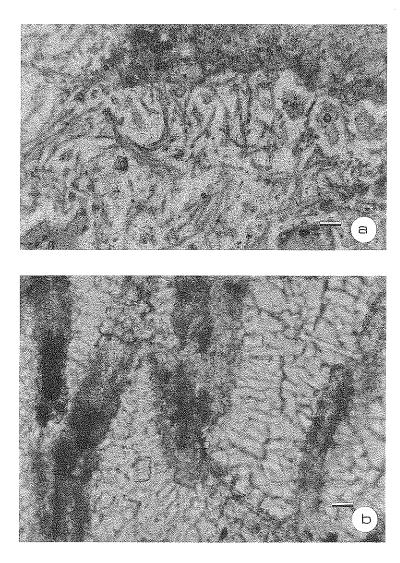


Figure 10: a) Thin section 1 cm into interior of oncoid cortex showing Homoeothrix filaments in growth position. Scale= 50 μm ; b) Closer view showing micritic calcite at position of former filament surface. Note interlocking spar-calcite crystals between filaments. Scale= 10 μm .

Factors controlling lobate ridged surface morphology

The structure of the El Mojarral stromatolites and stromatolitic mats is primarily the consequence of *in situ* precipitation of carbonate, rather than trapping and binding of detrital sediment particles by its constituent microbiota. Both biological and physical factors play a role in the morphology of the ridged pattern of stromatolites and stromatolitic mats. The offset pattern of small lobate ridges or micro-terraces characteristic of El Mojarral stromatolites and stromatolitic mats appears to be produced by the regularly spaced, upright intermingled, closely bound growth habit of *Homoeothrix* combined with a steady water current which prevents the accumulation of detritus. The algae on the surface appear to grow in such a way as to maximize light and nutrient absorption; the result is enhanced growth on the outer and upper surfaces which leads to the formation of the ledges. Each such ledge forms a "canopy" which shades the area directly around and beneath it.

Similar patterns of ridges or terraces are observed in modern non-marine stromatolites in various parts of the world. At Yellowstone, microterraced crusts are the most ubiquitous small-scale feature (Pursell, 1985). These crusts are described as quasi-horizontal microterraces with a raised rim (0.5-1.33 cm high) and a small irregular "basin" or depression (1.3-2.5 cm wide) behind the smooth microcrystalline calcium carbonate rim. Pursell (1985) found that cuts perpendicular to the microterraced surface show a composition of dendritic crystals oriented with their main axis perpendicular to the substrate. Similar structures called anastomosing ridges, with a "torn-tissue" texture, have been described from steeply sloping rimstone faces in a stream in Dyfed, South Wales (Braithwaite, 1979). Gomes (1985) described tabular "crinkled stromatolites" from Wondergat Sinkhole in the Western Transvaal of South Africa, the pattern of which, from illustration and description, appears to be similar in size and shape to that at El Mojarral.

Another term that may refer to the same type of pattern is "ridge and furrow structure" R. Riding, pers. comm. 1986). Monty (1972) discusses and illustrates lineations called ridges on pinnacle-bearing stromatolites subjected to water currents driven by persistent trade winds, at Andros Island in the Bahamas. Another interpretation of ridges, suggested by Casanova (1986) who studied similar Plio-Pleistocene lacustrine stromatolites in the Gregory Rift Valley of Tanzania and Kenya, is that they represent a regular succession of ripples or ridges induced by the development of a microbial community which is at its climax condition. His illustrations (Casanova, 1986, plates 50-54) resemble the most mature examples at El Mojarral (Fig.3b), where the ledges have anastomosed into continuous ridges. The structure of the El Mojarral mats has not changed significantly in the decade we have been observing them, which may suggest some degree of long term stability. Dixit (1984) refers to Pleistocene lacustrine ridged oncoids from Lake Manyara in Tanzania as having "peaked ridges formed by laminae having a cuspate profile". His conclusion regarding the formation of the ridges was that the "laminae of these oncolites are clearly not formed by binding of carbonate detritus by the mucilaginous filaments of

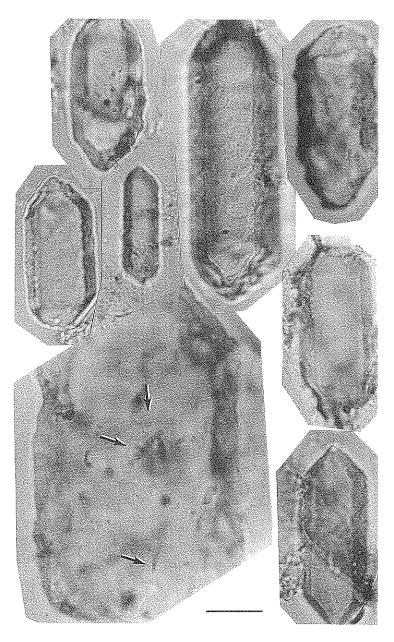


Figure 11 : Quartz crystals liberated by acid treatment of lake stromatolite mats. Note filaments in crystal on lower left (see arrows). Scale bar = $10~\mu m$.

algae...they appear to be formed either by the inorganic precipitation of calcium bicarbonate...or by biological precipitation because of the photosynthetic activity of algae".

Although conventional wisdom holds that oncoids are associated with agitated conditions providing regular or constant movement of the structures, oncoid movement such as rolling or flipping has not yet been observed at El Mojarral. Large oncoids do sometimes develop a rudimentary ridged pattern and some with a ridged pattern exhibit sharply juxtaposed growth orientations. The ledges always form close to horizontal in each of the sequential growth periods, suggesting that movement of at least the larger oncoids is episodic in nature rather than continuous or regular. This same observation was made by Jones and Wilkinson (1978) who recognized that their large oncoids were overturned infrequently.

Lamination in well-lit settings

In order to frame the description of the mat architecture into a temporal perspective it should be noted that the reported distribution or dominance of the microbiotic components is not static. Population dynamics is, as discussed by Monty (1973), a basic parameter controlling not only the formation of laminated fabric but also the development of particular biodiagenetic features throughout the mat. He distinguishes 2 types of lamination patterns in microbial mats. The first is historical lamination resulting from the succession of the alternating microbial populations at the surface of the mat following diurnal, periodic, seasonal, or accidental changes in the environmental parameters. For example, Monty (1976) reports three different types of laminated fabrics built by the same two cyanobacteria, each heavily calcified, or not, depending on slight environmental changes in the same setting. This lamination The second type of lamination is process leads to vertical accretion of mat. instantaneous or biological stratification resulting from the in-depth distribution of successive specialized microbial populations occupying specific zones and niches along steep physico-chemical gradients; this "metabolic" stratification, superimposed on the historic lamination, contributes to the diagenesis of the mat and moves upwards following their accretion (Monty, 1976).

The alternation of uncalcified, *Schizothrix* dominated laminae with calcified laminae of *Homoeothrix* may thus be considered as an example of "instantaneous" lamination. The local coalescence of *Homoeothrix* filaments at the mat surface results in the formation of sculptured ridges and provides the microhabitat necessary for the growth of *Schizothrix* below. *Homoeothrix* is found in conditions ranging from high light near the water surface to deeply shaded areas near the inflow cave. Hence it appears that *Homoeothrix* is adapted to life in a broad range of light conditions. Under conditions of high light, *Homoeothrix* exhibits the characteristic dark brown sheath pigmentation, while at low light intensities, colorless sheath and increased phycoerythrin pigment production in the cells enhances its ability for efficient light capture. Further, laboratory cultures of this organism have confirmed its ability to undergo complementary chromatic adaptation (*sensu* Tandeau de Marsac, 1977), a low light

physiological response to changes in the spectral quality of light (Seeler, unpublished results). *Schizothrix*, on the other hand, appears only in the sub-surface layer of the mat, where it is shaded by *Homoeothrix*, and thus restricted to a much narrower photic environment than *Homoeothrix*. It therefore appears likely that the alternating lamination of *Homoeothrix* and *Schizothrix* is the consequence of the different ecological responses of these organisms to light.

Calcification process in laminations

The El Mojarral stromatolites and stromatolitic mats exhibit species-specificity with respect to in situ carbonate precipitation. Carbonate precipitation at El Mojarral is strongly light-dependent, therefore suggesting that it is driven by photosynthesis. Carbonate precipitation by Homoeothrix (and not Schizothrix) may be related to the difference in their sheath thicknesses, affecting CO2 diffusion rates to the photosynthetic trichomes. Hence the thicker trichomes (and relatively thinner sheaths) of Homoeothrix cause more severe local CO2 depletion leading to CaCO3 precipitation. The calcite layers separating Homoeothrix laminae are due perhaps to faster accumulation of carbonate on the mat surface during the dry season when the water is most saturated with carbonate; possibly coincident with the end of the growth cycle of Homoeothrix. Pentecost (1987) observed a seasonal pattern of growth in Rivularia haematites (D.C.)Ag. colonies in North Yorkshire, where two different processes of calcification may be operating: when cyanobacterial growth was slow, a dense annual winter zone of calcite precipitation (attributed to nucleation at the sheath surface and possibly from calcite seeds trapped from the surrounding water) accumulated on the surface of the colonies, with much the same appearance as the calcite rinds at El Mojarral. Additionally, he describes a set of narrow calcified summer bands associated with zones of active Rivularia growth and cell division, induced by photosynthesis. Similar sets of thin bands occur between the rinds at El Mojarral. The organization of the lamination in El Mojarral stromatolites, consisting of loose laminae 1-2 mm thick, separated by calcite-rich rinds, resembles the architecture of the lamination of Type 2 oncoids described from Lower Cretaceous (Wealdian) deposits of the Province of Valencia, Eastern Spain (Monty and Mas, 1981). These fossils were built by the superposition of spongious loose laminae produced by populations of a carbonatecoated filamentous cyanobacterium, separated by micritic rinds marking the end of a growth phase.

In another nonmarine cool-water travertine setting, in the Arbuckle Mountains of Oklahoma, a seasonal pattern of alternating sparry, "bushy" layers (spring-summer) and darker micritic layers (fall-winter) was interpreted by Love (1985). This seasonal origin of the laminae was later confirmed by measuring the δ^{18} O and δ^{13} C signatures of seasonally alternating sparry and micritic laminae in the same travertine stromatolites (Chafetz et al., 1991). These authors found significant variations in the stable isotope compositions, particularly the δ^{18} O values between sparry and micritic laminae, with δ^{18} O values higher in the micritic laminae, and δ^{13} C values higher in the sparry

laminae.

An example of succession involving the vertical growth of long thick cyanobacterial filaments through a felt of thinner ones has been documented by Kann (1941) for lacustrine cyanobacterial crusts built by *Calothrix* and *Dichothrix*. Oncoids that occur in Lake Constance are constructed by two cyanobacteria, *Schizothrix*, forming dense layers, and *Phormidium*, *Calothrix*, and/or *Dichothrix* forming spongy layers (Schafer and Stapf, 1978). The sequential layering of *Homoeothrix* produces a vertically-differentiated palisade-type structure which is much like that described by Monty (1972, 1976) for stromatolites in pools of the Fresh Creek area on Andros Island, where long vertical filaments of *Scytonema*, calcified below their growing tips, produce a vertically-oriented feature, and by Monty (1976) for stromatolites from Shark Bay where rapid cementation and incomplete oxidation produce a similar fabric.

Oncoids with a nuclear composition and cortex lamination pattern resembling those of El Mojarral have been reported by Jones and Wilkinson (1978) from marl lakes in Michigan. Stream oncoids with similar calcite grain morphology (but lacking the regular alternation of dense and porous layers) constructed by Gongrosira, Homoeothrix and Phormidium were described by Roddy (1915) and later by Golubic and Fischer (1975) from Little Connestoga Creek in Pennsylvania. Minckley (1963) described a calcareous encrusting community from Doe Run (a stream in Kentucky) consisting of Gongrosira, Phormidium, Schizothrix and diatoms. His oncoids grew around the shells of Goniobasis. El Mojarral coated pebbles with snail nuclei, that develop into irregularly rounded oncoids, are also similar to those described by Weiss (1970) for oncoids forming around Goniobasis snails. An example of fossil lacustrine oncoids that resemble the type of laminated oncoids forming at El Mojarral comes from the Paleogene nonmarine algal deposits of the Ebro Basin in Northeastern Spain (Anadón and Zamarreño, 1981). These oncoids contain radially growing calcified filaments periodically pervaded by concentrically disposed micrite films or disrupted by the invasion of chironomid larvae. Chironomid larvae are sometimes abundant in the interstices of the El Mojarral structures as well.

Impact of fish and other grazers

The assumption has been made that metazoan evolution has caused a decrease in stromatolite distribution in marine strata beginning with the Precambrian/Cambrian boundary, (Awramik, 1971, 1981, 1984). Several authors have even suggested that recent potential stromatolites cannot develop in the presence of grazing and burrowing animals (Garrett, 1970 a,b, Gerdes and Krumbein, 1984). This hypothesis however has been criticized by Monty (1972), Winsborough (1990) and Golubic (1991). The presence of a diverse animal community associated with living, actively growing stromatolites at Cuatro Ciénegas shows that at least some aquatic communities, which appear to be as complex as average fresh-water communities, do not prevent stromatolite or oncoid formation and growth. The vertical channels that are present in oncoids penetrate deep into the structures and allow the circulation of carbonate-rich water to reach the interior, increasing the likelihood of rapid internal cementation.

Movement of benthic animals, particularly amphipods, in these channels enhances water circulation thus contributing in a positive way to stromatolite diagenesis. Fish are responsible for the most extensive damage to stromatolites and stromatolitic mats, (and oncoids to a lesser degree) as they sometimes clear areas a cm or more in diameter thus disrupting the continuity of laminae. An uneven growth pattern produced by fish grazing has been documented by in in-situ colonization experiments, where fish grazing appears to be responsible for removing patches of the mat. Pieces of mat up to a cm in diameter have been removed from the artificial substrate by predation. It is not uncommon that one side of a structure (that which is on the down-current side) will be cleaned of much surface mat growth, while the other side is relatively undisturbed.

Relationship of diatoms and quartz in stromatolites and oncoids

With regard to the disappearance of diatoms, and concomitant appearance of quartz crystals in the interior of some stromatolites and oncoids, the following mechanism is suggested. Dissolution of diatoms in the stromatolite mat may be taking place in the ecological zone where dissimilatory sulfate reduction by bacteria such as Desulfovibrio causes local chemical characteristics to be significantly altered. This would be deep enough into the mat that many of the diatoms present are likely to be dead. After death of the algal cell, the protecting organic coating is degraded exposing unprotected diatom frustules to dissolution; further, removal of metallic complexes may also contribute to these processes (Lewin, 1961). Birnbaum and Wireman (1984) suggest that metabolically-mediated pH changes by Desulfovibrio may significantly influence decomposition of certain silicate minerals due to hydrolysis reactions, and later provide the microenvironment for the nucleation and precipitation of diagenetic silica from a saturated solution. These authors discuss a mechanism by which soluble silica in the form of monosilicic acid, H₄SiO₄, dissociates to H₃SiO₄ - at pH values above 9.7. The initial increase in pH leading to silica dissolution is attributed to the release of ammonia during proteolysis; Desulfovibrio then releases CO2 and sulfide ions, lowering pH and while other cyanobacteria and diatoms, through the production of copious amounts of mucilage, contribute to carbonate precipitation as well as sediment trapping and This microbial community is also responsible for the shaping and In low-light areas, endolithic microstructure of the stromatolite's lamination. cyanobacteria may contribute significantly to net carbonate removal. microhabitats therefore require detailed study of the respective roles (ie. carbonate precipitating or dissolving) of the cyanobacteria enmeshed within the carbonate matrix. It is noteworthy that in such microhabitats carbonate precipitation (principally by Homoeothrix) and carbonate dissolution (by the endoliths below) occur simultaneously, and in close spatial proximity, thus obscuring the boundary between newly accreted carbonate and the bedrock below (cf. Fig.5d, 6b,c). Culture studies have confirmed the carbonate penetrating ability of stigonematalean endoliths (Seeler and Golubic, unpublished).

Errata: Block of text starting on line 28, page 95, with "while other", and ending on line 30, page 96, with "this community", should be moved and inserted after line 28 on page 97, following " structures".

Characteristic of stromatolitic structures at El Mojarral and certain physico-chemically similar lakes in the Cuatro Ciénegas basin is the development of a remarkably constant surface growth pattern of horizontally oriented lobate ridges or ledges. These ridges are linear areas of enhanced cyanobacterial growth and carbonate precipitation. They result from the horizontal coalescence of individual cushions of *Schizothrix lacustris*, capped by the growth and carbonate precipitation of *Homoeothrix balearica*. These two dominant filamentous cyanobacteria exhibit species-specific differences in biogenic calcium carbonate precipitation. Similar terraced or ridged patterns have been described in the literature, from modern and fossil nonmarine stromatolite deposits in various parts of the world.

The stromatolites, mats, and oncoids of El Mojarral display similar internal microstructure and lamination. Differences appear to depend primarily on composition of the biological communities, available light, the kind and amount of grazing, and the amount of internal cyanobacterial and mineralogical growth and diagenesis. Typical oncoids and stromatolites which form in full sun and moderate current, particularly within about 2 meters depth, show a repeated alternation of gelatinous cyanobacteria-rich laminae and dense carbonate-rich ones. In some habitats, the original cyanobacterial or algal material is trapped as inclusions in the lithified structures, in others the mold of the organic material has been filled by calcite.

The surface relief of the structures may also be affected by feeding activities of fish and crustaceans. To a much lesser degree, locomotion and feeding activities of smaller benthic animals such as flat worms, nematodes and dipterans can disrupt the fabric of internal laminae. Some of these animals appear to be important in the maintenance of open vertical and horizontal channels irregularly distributed within the living mat. Our observations suggest that both fish and microbenthos may play important roles in controlling the growth and population dynamics of the algal/cyanobacterial portion of the stromatolite community by affecting the rate and pattern of stromatolite accretion. Fish, in particular, through their feeding activities, disrupt the surface relief, influencing the ultimate shape of the structures. Besides the direct effects of the interactions between the grazers and the stromatolites, predators in this community increasing carbonate alkalinity in the localized environment surrounding the cells. thereby causing precipitation of silica. Stoessell (1992) outlines the overall anaerobic aqueous sulfate reaction of carbohydrates, presumably controlled by Desulfovibrio, in a discussion of the pathways for sulfate-reduced mixing-zone pore-water fluids, under various pore-water geochemical regimes.

An example of the precipitation of silica in oncoids was reported by Schafer and Stapf (1978). They observed the precipitation of quartz in the interior of oncoids forming in Lake Constance and attributed the process to the production of ammonia. They suggest that the silica was dissolved from the abundant diatom tests embedded in the algal fabric, as diatom tests could only be detected within the outer layer of the oncoids. Diatom dissolution and the precipitation of silicate minerals were also linked in a study by Stoffers and Holdship (1975) who found that diatom-poor intervals in a core from Lake Manyara contain abundant quantities of analcine and erionite, and suggest that

these silicates may arise from the dissolution of biogenic silica. Holdship (1976) interpreted the diatom-poor periods as representing a more concentrated hydrochemical environment than the diatom-bearing intervals. Barker (1992) experimentally looked at differential diatom dissolution of Lake Manyara sediments and concluded that the almost complete dissolution of diatoms represents the interaction of specific hydrochemical conditions, with high alkalinity accompanied by undersaturation with respect to silica.

The dissolution of diatoms may be the reason why no diatoms were found in otherwise well preserved oncoids and stromatolites of the Green River Formation (Winsborough, unpublished). The associated biota described by Bradley (1929, 1964) suggests that the habitat was amenable to diatom growth, yet diatoms are notably absent. No diatoms were found associated with the stromatolites of the Pliocene Ridge Route Formation either (Link et al., 1978), although the fauna and flora reported are generally associated with diatoms. In contrast, dense accumulations of well-preserved diatoms are observed in some fossil stromatolites. For example, diatoms are easily recognizable in material from the 6300-8900 yr. old sabkha of Chemchane (Mauritania) (Casanova pers. comm. 1989). The presence or absence of diatoms in fossil biogenic deposits may thus reflect the nature of the biological and chemical conditions present during early diagenesis.

CONCLUSIONS

Microbial structures, which include oncoids, stromatolites and stromatolitic mats are forming in the warm, spring-fed sulfate-rich lakes and sinkholes of the Cuatro Ciénegas They are built by a diverse community of microorganisms, principally cyanobacteria, associated with carbonate precipitation. The stromatolite morphologies presently forming in the El Mojarral Lakes, and the nature of the microbial populations of which they are composed, reflect physical settings that differ primarily in the intensity of light, depth, and possibly current. The community structure of the living surface mat includes a diverse assemblage of both prokaryotes and eukaryotes. Schizothrix and Homoeothrix are responsible for the overall shape of the structures, may influence stromatolites indirectly, perhaps beneficially (see Sterner, 1986) by controlling grazers. Early induration of stromatolitic structures by in situ precipitation of calcium carbonate may be responsible for their preservation in spite of the presence of diverse populations of grazers. In the case of oncoids, actively swimming benthos, such as amphipods, that inhabit the open channels within the oncoids, may actually contribute to rapid cementation by increasing water circulation to the interior of the structures. From our observations of living material, and the lack of benthos- free stromatolites with which to compare, we have no evidence that the smaller animals disrupt stromatolite growth and morphology significantly.

Although never dominant in biomass, the diatoms are by far the most diverse class of stromatophilic eukaryotes at El Mojarral, and are sometimes well preserved in the lithified stromatolites. Many diatom species have autecological preferences or requirements regarding salinity, temperature, pH, nutrient and oxygen concentration,

light intensity, water current and substrate. Careful taxonomic and ecological documentation of the subtle patterns and relationships between modern stromatolite diatoms and their biotic and abiotic environments is a prerequisite to paleoecological analysis. There is evidence suggesting *in situ* precipitation of quartz crystals following dissolution of diatom tests (under certain conditions) during mat growth or early diagenesis. Diagenesis allowing, however, it may even be possible to use the autecological characteristics of diatoms to make interpretations about the specific ecological setting of fossil Cenozoic diatom-bearing stromatolites.

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REFERENCES

Anadón, P. and Zamarreño, I. (1981) "Paleogene nonmarine algal deposits of the Ebro Basin, Northeastern Spain", in C.L.V. Monty (ed.), Phanerozoic Stromatolites, Case Histories, Springer, Berlin Heidelberg New York London Paris Tokyo Hong Kong Barcelona, pp. 140-154.

Awramik, S.M. (1971) "Precambrian columnar stromatolite diversity: reflection of metazoan appearance", Science, 174, 825-827.

Awramik, S.M. (1981) "The Pre-phanerozoic biosphere - three billion years of crises and opportunities", in M.H. Nitecki (ed.), Biotic Crises in Ecological and Evolutionary Time, Academic Press, New York, pp. 83-102.

Awramik, S.M. (1984) "Ancient stromatolites and microbial mats", in Y. Cohen, R.W. Castenholz, H.O. Halvorson (eds.), Microbial Mats: Stromatolites, Alan R. Liss, New York, pp. 59-83.

Barker, P. (1992) "Differential diatom dissolution in Late Quaternary sediments from Lake Manyara, Tanzania: an experimental approach", J. Paleolimnology 7, 235-251.

Birnbaum, J. and Wireman, J.W. (1984) "Bacterial sulfate reduction and pH: Implications for early diagenesis", Chem. Geol. 43, 143-149.

Bradley, W.H. (1929) "Algal reefs and oolites of the Green River Formation", U.S. Geol. Survey Prof. Paper 154-G, Washington, pp. 203-223.

Bradley, W.H. (1964) "Geology of Green River Formation and associated Eocene rocks in southwestern Wyoming and adjacent parts of Colorado and Utah", U.S. Geol. Survey prof. paper 496-A, Washington, pp. 1-86.

Braithwaite, C.J.R. (1979) "Crystal textures of recent fluvial pisolites and laminated crystalline crusts In Dyfed, South Wales", J. Sediment Petrol. 49, 181-194.

Casanova, J. (1986) Les stromatolites continentaux : paleoécologie, paleohydrologie, paleoclimatologie. Application au Rift Gregory. Thesis, Université d'Aix- Marseille II.

Chafetz, H.S., Utech, N.M. and Fitzmaurice, S.P. (1991) Differences in the δ^{18} O and δ^{13} C signatures of seasonal laminae comprising travertine stromatolites", J. Sediment. Petrol. 61, 1015-1028.

Dixit, P.C. (1984) "Pleistocene lacustrine ridged oncolites From the Lake Manyara area, Tanzania, East Africa", Sedimentary Geology 39, 53-62.

Folk, R.L., Chafetz, H.S. and Tiezzi, P.A. (1985) "Bizarre forms of depositional and diagenetic calcite in hot-spring travertines, central Italy". in N. Schneidermann, and P.M. Harris (eds.) Carbonate Sediments, S.E.P.M. Spec. Pub. 36, 349-369.

Garcia, E., Vidal, R., Tamayo, L.M., Reyna, T., Sanchez, R., Soto, M. and Soto, E. (1975) Precipitation y probabilidad de la lluvia en la Republica Mexicana y su evaluation. Comision de Estudios del Territorio Nacional, Instituto de Geografia, UNAM, Mexico.

Garrett, P. (1970a) "Deposit feeders limit development of stromatolites", Am. Assoc. Petrol. Geol. Bull. 54, 848.

Garrett, P. (1970b) "Phanerozoic stromatolites: noncompetitive ecologic restriction by grazing and burrowing animals", Science 169, 171-173.

Gerdes, G., and Krumbein, W.E. (1984) "Animal communities in recent potential stromatolites of hypersaline origin", in Y. Cohen, R.W. Castenholz, H.O. Halvorson (eds.), Microbial Mats: Stromatolites, Alan R. Liss, New York, pp. 59-83.

Golubic, S. (1991) "Modern stromatolites: a review", in R. Riding (ed.), Calcareous Algae and Stromatolites, Springer, Berlin Heidelberg New York London Paris Tokyo Hong Kong Barcelona, pp. 541-561.

Golubic, S., and Fischer, A.G. (1975) "Ecology of calcareous nodules forming in Little Conestoga Creek near Lancaster, Pennsylvania", Verh. Int. Verein. Limnol. 19, 2315-2323.

Gomes, N.A. (1985) "Modern stromatolites in a karst structure from the Malmani Subgroup, Transvaal Sequence, South Africa", Trans. Geol. Soc. S. Afr. 88, 1-9.

Holdship, S.A. (1976) The Palaeolimnology of Lake Manyara, Tanzania: a diatom analysis of a 56 meter sediment core, PhD Dissertation, Duke Univ.

Jones, F.G., and Wilkenson, B.H. (1978) "Structure and growth of lacustrine pisoliths from Recent Michigan marl lakes", J. Sediment. Petrol. 48, 1103-1110.

Kann, E. (1941) "Krustensteine in Seen", Arch. Hydrobiol. 37, 495-503.

Kann, E., and Sauer, F. (1982) Die "Rotbunte Tiefenbiocoenose" (Neue Beobachtungen in osterreichischen Seen und eine zusammenfassende Darstellung), Arch. Hydrobiol. 95, 181-195.

Krumbein, W.E. and Werner, D. (1983) "The microbial silica cycle", in W.E. Krumbein (ed.), Microbial Geochemistry, Blackwell, Oxford, pp. 125-157.

Lewin, J.C. (1961) "The Dissolution of Silica From Diatom Walls", Geochimica et Cosmochimica Acta, 21, 182-198.

Link, M.H., Osborne, R.H. and Awramik, S.M. (1978) "Lacustrine stromatolites and associated sediments of the Pliocene Ridge Route Formation, Ridge Basin, California", J. Sediment. Petrol. 48, 143-158.

Minckley, W.L. (1963) "The ecology of a spring stream- Doe Run, Meade County, Kentucky", Wildlife Monographs 11, 5-124.

Monty, C.L.V. (1972) "Recent algal stromatolitic deposits, Andros Island, Bahamas, Preliminary Report", Geol. Rundschau 61, 742-783.

Monty, C.L.V. (1973) "Remarques sur la nature, la morphologie et la distribution spatiale des stromatolithes", Sciences de la Terre, Nancy, 8, 189-212.

Monty, C.L.V. (1976) "The origin and development of cryptalgal fabrics", in M.R. Walter (ed,), Stromatolites, Elsevier, Amsterdam pp. 193-249.

Monty, C.L.V. and Hardie, L.A. (1976) "The geological significance of the freshwater blue-green algal calcareous marsh", in M.R. Walter (ed.), Stromatolites, Elsevier, Amsterdam, pp. 454.

Monty, C.L.V. and Mas, J.R. (1981) "Lower Cretaceous (Wealdian) blue-green algal deposits of the province of Valencia, eastern Spain", in C.L.V. Monty (ed.), Phanerozoic Stromatolites. Springer, Berlin Heidelberg New York, pp. 85- 120.

Morafka, D.J. (1977) A Biogeographical Analysis of the Chihuahuan Desert Through Its Herpetofauna. W. Junk, the Hague.

Pentecost, A. (1987) "Growth and calcification of the freshwater cyanobacterium *Rivularia haematites*", Proc. R. Soc. London Ser. B 232, 125-136.

Pursell, V.J. (1985) The petrology and diagenesis of Pleistocene and recent travertines from Gardiner, Montana, and Yellowstone National Park, Wyoming. Thesis, Univ of Texas, Austin.

Rippka, R., Deruelles, J., Waterbury, J.B., Herdman, M., and Stanier, R.Y. (1979) "Generic assignments, strain histories and properties of pure cultures of cyanobacteria", J. Gen. Microbiol. 111, 1-61.

Roddy, H.J. (1915) "Concretions in streams formed by the agency of blue-green algae and related plants", Amer. Philos. Soc. Proc., 54, 246-258.

Schafer, A. and Stapf, K.R. (1978) "Permian Saar-Nahe Basin and Recent Lake Constance (Germany): two environments of lacustrine algal carbonates", Spec. Pub. Int. Assoc. Sedimentol. 2, 83-107.

Seeler, J-S. and Golubic, S. (1991) *"Iyengariella endolithica* sp. nov. a carbonate boring stigonematalean cyanobacterium from a warm spring-fed lake: nature to culture". Arch. F. Hydrobiological Studies 65, 399-410.

Sterner, R.W. (1986) "Herbivores' direct and indirect effects on algal populations", Science, 231, 605-607.

Stoessell, R.K. (1992) "Effects of sulfate reduction on CaCO3 dissolution and precipitation in mixing zone fluids", J. Sediment. Petrol. 62, 873-880.

Stoffers, P. and Holdship, S.A. (1975) "Diagenesis of sediments in an alkaline lake: Lake Manyara, Tanzania". Proc. IX th Int. Cong. Sedimentology, Nice.

Tandeau de Marsac, N. (1977) "Occurrence and nature of chromatic adaptation in cyanobacteria", J. Bacteriol. 130, 82-91.

Weiss, M.P. (1970) "Oncolites forming on snails", J. Sediment. Petrol. 44, 765-769.

Winsborough, B.M. (1990) Some ecological aspects of modern fresh-water stromatolites in lakes and streams of the Cuatro Ciénegas Basin, Coahuila, Mexico. Dissertation, Univ of Texas, Austin.

Winsborough, B.M. and Seeler, J-S. (1986) "The relationship of diatom epiflora to the growth of limnic stromatolites and microbial mats", in M. Ricard (ed.,) Proceedings of the 7th international symposium on living and fossil diatoms, Paris, 1984, pp 395-407.

Winsborough, B.M. and Golubic, S. (1987) "The role of diatoms in stromatolite growth: two examples from modern freshwater settings", J. Phycol. 23, 194-201.