SOME ECOLOGICAL ASPECTS OF MODERN FRESH-WATER STROMATOLITES IN LAKES AND STREAMS OF THE CUATRO CIENEGAS BASIN, COAHUILA, MEXICO

BY

BARBARA MADDEN WINSBOROUGH, B.A., M.S.T.

DISSERTATION

Presented to the Faculty of the Graduate School of
The University of Texas at Austin
in Partial Fulfillment
of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

THE UNIVERSITY OF TEXAS AT AUSTIN

May, 1990

SOME ECOLOGICAL ASPECTS OF MODERN FRESH-WATER STROMATOLITES IN LAKES AND STREAMS OF THE CUATRO CIENEGAS BASIN, COAHUILA, MEXICO

APPROVED BY

SUPERVISORY COMMITTEE:

Bassett Maguire Jr

Robert L. Folk

Eric R. Pianka

Richard C. Starr

Keith Young

ACKNOWLEDGMENTS

I am indebted to my parents for instilling in me an appreciation for learning and to my husband Philip for his untiring patience, encouragement and help with field logistics. Participation in this interdisciplinary program in the Division of Biological Sciences has allowed me the opportunity to interact with an inspiring and eclectic dissertation committee. My co-chairmen, Drs. Bassett Maguire, Jr. and Robert L. Folk provided the breadth of expertise necessary to accomplish this research. Other members of my committee, Drs. Eric Pianka, Keith Young, and Richard Starr were generous in providing their special expertise. Dr. Al Fischer first made me aware of the potential significance of the Cuatro Ciénegas deposits and convinced me that they were worthy of detailed investigation. My enthusiasm for this research was sustained over some rough times by the support and encouragement of Dr. Stjepko Golubić of Boston University. Funding for field work was provided in part by Sigma Xi, and by a grant from the Division of Biological Sciences of the University of Texas. Assistance in resolving diatom taxonomy problems came from a Jessup-McHenry Fellowship to the Academy of

Natural Sciences of Philadelphia.

Field and lab work were carried out over eleven years, and many people have assisted me in various aspects of the research. I am particularly grateful to Srs. Pepe Lugo Guajardo, Manuel Gonzalez Ramos, Roberto Arredondo, Jose Castañeda M. and Lic. Antonio Palacios Villareal of Cuatro Ciénegas. Drs. Robert Stallard and Richard Murnane, of Princeton University, collected and analyzed the 1983 water chemistry samples. Dr. Alan Pentecost (King's College) identified the Gongrosira and also made some water chemistry measurements. Bob White provided fluent spanish interpretation when critical and Jacob-Sebastian Seeler made the photon fluence measurements and cultured cyanobacteria from the stromatolites. Michael Hein aided in resolving diatom taxonomy problems. Dr. Richard Starr cultured and identified the Chroodactylon ramosum, Dr. Bassett Maguire, Dr. Jim Wee and Betsy Maxim helped with the protozoan identifications, and Dr. Richard Forrester (USGS, Denver) identified the ostracods. This work benefited very much from information collected with the help of John Hendricks, and SCUBA divers Drs. Chris Caran and Bassett Maguire Jr., Jerry Johnson, Alice Puig, Mark

Morsheimer, Don Seitz, Greg Irwin and Ted Kennedy. Michael Starcher made the mineralogical x-rays. Dr. George Ward wrote the fortran program to calculate distance measurements between stromatolite diatom associations at the different sites. Dr. Richard Rezak of Texas A&M University contributed the atomic absorption analysis of Cuatro Ciénegas soil material.

ABSTRACT

The ecology of freshwater stromatolites and related microbial deposits forming in a spring-fed desert basin, including their community architecture, physical, and mineralogical characteristics are described. Four stromatolite types are distinguished. Type 1 laminated stromatolites and oncoids, produced by _Homoeothrix balearica_ and _Schizothrix lacustris_, have a surface pattern of small horizontal lobate ledges or micro-terraces. Type 2 stromatolites and oncoids, constructed by _Gongrosira calcifera_, cyanobacteria and diatoms, form bulbous laminated cushions at the ends of branched digitate elements. Type 3 stromatolites are large, and globose, with a non-laminated sinuously-incised surface pattern resulting from the growth of _Dichothrix bonetiana_, _Schizothrix lacustris_, _Cyanostylon_ sp., and diatoms. Type 4 laminated, domed stromatolites result from the sequential growth of _Scytonema mirabile_, _Schizothrix_ cf _affinis_, and diatoms.

These types grow in habitats that differ in light intensity, current, depth, amount of detrital sediment and lithification rate. Water chemistry, similar at all

sites, is dominated by calcium sulfate, with lesser amounts of sodium, magnesium, and chloride. The precipitated low-magnesian calcite is modified by sheaths and stalks that leave biogenic imprints on the crystals. Calcite shape is further modified from the euhedral habit by lattice growth distortions due to poisoning by magnesium or sulfate.

All stromatolite types have a vertically-differentiated microbial mat community, which represents variations on the upright-radial colonial growth pattern. It consists of algae, cyanobacteria, bacteria and benthos, and includes at least one microorganism that precipitates calcite. A firm substrate is essential for development of this architecture. The diverse, motile, stromatolitic micro- and macro-benthos community is adapted to rapid carbonate accumulation. Of these, the macro-benthos including chironomids, amphipods, worms, mites, insects, and snails are the most potent modifyers of mat fabric.

Diatoms are abundant and diverse in the stromatolite mat and often preserved in the lithified structure. They clearly play a role in mat formation and diagenesis, and their associations, along with the cyanobacteria, are

used to assess the similarity of the various stromatolite types. Dissolution of diatom frustules is correlated with presence of authigenic quartz crystals in the lithified stromatolite matrix.

TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

Figures Page

Tables

Chapter 1. INTRODUCTION

1.1. Nature of Stromatolites and Goals of This Investigation

The word stromatolite is an english translation of stromatolith, a term used first by E. Kalkowsky in 1908 to describe laminated nonmarine carbonate deposits in northern Germany. The term "stromatolite" as used here refers to lithified, frequently laminated, organo-sedimentary structures built by microbial communities through the processes of sediment trapping and binding and/or of carbonate precipitation (Winsborough and Golubić, 1987). This definition is essentially the same as the definition of cryptalgal structures made by Aitken, (1967), which was adopted by Monty (1976). The terms "blue-green algae and bacteria" (referring to the constructive agents) are replaced here by the more inclusive term "microbial Communities", expanding the concept of a microbe thus to include a diverse community of plants and animals. Gerdes and Krumbein (1987) also use the term microbial community for stromatolites produced by diverse microecosystems which include not only those cyanobacterial and fungal components that are preserved due to their extracellular sheaths, envelopes and capsules, but those other associated phototrophs and anaerobic heterotrophs which regulate the physico-chemistry of a mat system. In summary, "stromatolites represent the accrued products produced by the dynamic interaction of microbes and sediment" (Awramik, 1984). New or redefined terms describing biogenic structures similar to stromatolites include "cryptalgal sedimentary rocks" and "thrombolites" (Aitken, 1967 and Kennard and James, 1986) and "microbialites" (Burne and Moore, 1987).

Stromatolites and related microbial accretions constitute a major part of the lithofacies (rock units) in some of the lakes and streams of the Cuatro Ciénegas Basin. They include several kinds of laminated, lithified, biogenic formations with specific characteristics related to their morphology and genesis. These different morphologies and the nature of their microbial populations reflect physical settings that differ primarily in the intensity of light, nature of current, and exchange rates and availability of water. Also variable is the nature, source, quantity, and lithification rate of the accreted sediment.

Four macroscopically distinctive types of stromatolitic structures are presently forming in different spring- and stream-systems within the Cuatro Ciénegas Basin. The ecology of these microbial structures and the organisms associated with them is the subject of this investigation. This study has 3 goals. The first is to describe the water chemistry, habitat, macrostructure, community composition, architecture, fabric, and microstructure of the four types of stromatolites. The second is to identify the relationship between the organisms associated with stromatolitic growth, the nature of the lithified structure, and the relative influence of biological and environmental factors over stromatolitic morphogenesis. The third goal of this investigation is to describe the role of diatoms in the growth of fresh-water stromatolites. From this information it may be possible to construct a model of Cuatro Ciénegas stromatolitic habitats, which can be used to compare the Cuatro Ciénegas stromatolites with modern non-marine and marine stromatolites in other parts of the world and serve as a modern analog with which to compare fossil non-marine stromatolites. The unique and outstanding advantage of this study is the opportunity to examine a variety of living stromatolitic types from one area and relate the similarities and differences of these separate types to the mineralogical product which may ultimately be preserved in the geological record.

Diatoms have been shown to play a role in stromatolite growth (Winsborough and Seeler, 1986). In some instances, diatoms may represent a major portion of the algal biomass of a stromatolite at Cuatro Ciénegas. Clarification of their role in stromatolitic growth under specific environmental conditions will aid in interpreting the paleoenvironmental conditions associated with diatom-bearing stromatolites. Although cyanobacteria (blue-green algae) are sometimes preserved in the lithified structure they are not particularly useful in interpreting paleoenvironmental conditions as they have broad ecological ranges and many taxonomic problems. Diatoms on the other hand are good indicators of environmental conditions because their population structure (number and kinds of species present) is sensitive to ecological changes, and their identification and taxonomy are reasonably straightforward. If they are preserved in the stromatolites they would be useful as paleoecological indicators.

1.2. Importance of Cuatro Ciénegas Stromatolites

The Cuatro Ciénegas stromatolites are important because of their occurrence in diverse habitats within a geographically restricted area. This makes them potentially very useful in the study of environmental and biological control of stromatolitic community structure, morphology, preservation, and diagenesis. The basin is thus a natural laboratory for the study of stromatolitic colonization, growth and syndepositional diagenesis. The input from this research should be very useful in the interpretation of fossil, freshwater, stromatolitic paleoecology and biostratigraphy. This study also extends the known geographical distribution and ecological range of modern, fresh-water stromatolites.

The study of stromatolite ecology is by nature a multidisciplinary enterprise. Biologists traditionally emphasize the relationship between stromatolitic microorganisms and their immediate environment, including succession, the distribution of oxygen, and carbonate precipitation and dissolution by specific organisms. Geologists on the other hand are more interested in the mechanisms of carbonate precipitation, stromatolitic preservation-potential, and the paleoenvironmental significance of the organisms preserved in the stromatolites. The International Geological Correlation Program 163, "Stromatolites," begun in 1987, is the most recent and broad-based international effort to investigate the biostratigraphical and environmental significance of stromatolites and other microbially derived organosedimentary structures through space and time. It is anticipated that the results of this study will contribute to this effort by providing additional evidence that certain stromatolitic forms can be related to discrete, biotic associations and environmental constraints, permitting world-wide comparisons of stromatolites formed under similar and different environmental settings.

Microscopic study of the stromatolites in the field, under natural conditions, is the only practical approach from the standpoint of the necessity of studying the structures alive to observe them with their original integrity intact. In this way the major stromatolitic biota are identifiable (preservation of some of the species that make up the stromatolite community is very difficult). The role of microbenthos, macrobenthos, and fish, in sediment modification at the stromatolite surface and in the interior of the structures can be observed in the field. The community architecture of the different stromatolitic types will be characterized by quantitative and semi-quantitative methods of informational analysis, including measures of diversity, and distance.

1.3. Occurrence of Stromatolites

Stromatolites are found in marine, hypersaline, brackish, and freshwater settings. They have been produced throughout much of earth's geologic history. They first appeared about 3,500 million years ago and were the most conspicuous and among the most abundant fossils until the end of the Proterozoic, about 570 million years ago (Awramik, 1984). With the evolution of higher plants and metazoans, stromatolitic formation has declined, and become restricted to particular settings which, (while precluding extensive colonization by other types of vegetation), provide an input of carbonate, silicate, or occasionally other minerals, and support the growth of a set of specific micro-organisms that can outcompete higher plants, interact with these minerals and produce a permanent structure called a stromatolite.

The distribution of modern, marine stromatolites includes shallow (photic zone) subtidal, intertidal and supratidal habitats, hypersaline bays, mud flats and sabkhas; and arctic to tropical temperature-regimes. Freshwater stromatolites form in a wide variety of habitats both sub-aerial and aquatic. They form in carbonate-rich lakes and streams, thermal and cold seeps and springs, saline lakes, algal calcareous marshes, sinkholes, and on wet walls and ice floes. Because of their long temporal and broad ecological distribution, the literature on stromatolites is voluminous and spans the biological and geological disciplines. Walter (1976) and Monty (1981) provide extensive bibliographies.

1.4. Description of the Cuatro Ciénegas Basin

1.4.1. Geographic Setting

The Bolson de Cuatro Ciénegas (Fig. 1.4.1-1), at 26^{0} 59' north and 102^{0} 04' west, is a small intermontane desert valley about 30 km north to south and 40 km east to west (Minckley, 1969). It is located just east of the eastern edge of the Coahuila Platform in the western edge of the Sabinas Basin in central Coahuila, Northeastern Mexico (Humphrey, 1956). The basin floor has an elevation of 740 m and is bounded on all sides by mountains, the tallest reaching an elevation of over 3000 m above the basin floor. No perennial surface streams enter the basin and only a small canal carries water out toward the east. The Cuatro Ciénegas Basin is one of only two large desert spring systems on the North American Continent whose rich biota is characterized by high rates of endemism, the other is Ash Meadows in Nye County, Nevada (Almada-Villela and Contreras-Balderas, 1984).

The landscape of the Cuatro Ciénegas Basin includes a broad flat basin floor or "barrial" consisting of fine carbonate and evaporitic sediments which gives way to the alluvial fans rimming the steep to vertical canyon slopes of the Sierra San Marcos and surrounding ranges. Springs and seeps reaching a density of 12-15 per km^2 emerge along the distal margin of these alluvial fans, especially those of Sierra San Marcos. This fan-apron, which is one kind of a "bajada" is composed of poorly sorted gravels and clays washed down from the steep canyons characteristic of the area. Most of the springs are warm (up to 35^{0}C), but springs and seeps as cool as 19^{0}C are also found. Some of the springs have nearly constant water temperatures throughout the year, whereas others vary between 19 and 35^{0}C. The springs vary in size from small shallow marsh seeps to deep spring-fed lakes and streams. Some springs are permanent, some dry out gradually, and some, as the water table drops, reverse their flow and then drain the lake they had been feeding. Preliminary water chemistry analyses (Minckley and Cole, 1968, Murnane and Winsborough, in prep.) indicate that the spring waters are dominated by Ca^{++} and SO_4^{--}. Stromatolites occur in all of the habitats described above.

The mean annual air temperature at Cuatro Ciénegas is 23^{0}C (Morafka, 1977), with air temperature ranging from below 0^{0}C in winter to over 44^{0}C in summer (Marsh, 1984). The annual rainfall is less than 200 mm, over half of that occurring in September (Garcia et al., 1975). Episodic rains occur at all times of the year, however. This arid climate with highly seasonal rainfall provides the setting for a flat basin filled with a facies-mosaic of evaporitic minerals. Stromatolites represent only part of a much larger and more complex suite of habitats in which a spectrum of carbonate and evaporitic minerals from gypsum to bloedite and epsom salts precipitate. Cyanobacterial or bacterial mats, sometimes thick and luxuriant, can be found in each of these evaporitic settings, but they do not produce stromatolites.

The vegetational zones within the basin consist of grasslands, aquatic and semi-aquatic habitats, a gypsum dune zone, a transition zone between grasslands and bajadas, desert scrub, chaparral, oak-pine and oak woodlands and montane conifer forests (Pinkava, 1984). With regard to aquatic and associated riparian vegetation in the basin, Meyer (1973) described an open water aquatic plant association, a riparian association along stream margins, a marshy spring association, and an association found at the margins of lakes and ponds. The open water vegetation association includes the water lotus (Nymphaea ampla DC.), pondweed (Potamogeton nodosus Poir. in Lamarck), widgeongrass (Ruppia maritima L.), muskgrass (Chara spp. and Nitella spp.), bladderwort (Utricularia sp.) and horned pondweed (Zannichellia palustris L.). The riparian association, found along stream banks and around springs includes sedges (*Scirpus olneyi* Gray, *Eleocharis rostellata* Torr., *E. cellulosa* Torr., *Schoenus nigricans* L. and *Cladium jamaicense* Crantz.). Marshy springs support sedge beds comprised of *Carex prenglei* L. H. Bailey, *Dichromena colorata* (L.) Hitch., *Eleocharis rostellata*, *Fimbristylis spadicea* (L.) *Vahl*. and *Scirpus olneyi*. Meyer's lake and pond margin plants include mixed stands of sedges and cattail (*Typha domingenesis* Pers., and occasionally ash (*Fraxinus* sp.), mesquite (*Prosopis glandulosa* Torr. var. *torreyana* [L. Benson] M. C. Johnston), willow (*Salix* sp.) and seepwillow (*Baccharis glutinosa* Pers.). There are 25 species of birds (Contreras-Balderas, 1984) and 66 species of amphibians and reptiles of which 10% are endemic (McCoy, 1984).

1.4.2. Stratigraphy and Paleoecology

Late Paleozoic tectonics produced fine-grained chlorite, sericite and muscovite schists with a lesser amount of phyllitic marble and phyllitic quartzite, indicating that the area has undergone low-grade metamorphism (Barcelo-Duarte, 1983). These rocks are considered part of the interior zone of the Ouachita

Belt, which extends southward into Mexico (ibid). Sedimentation during the early Cretaceous in Northern Mexico occurred in embayments and gulfs bordering a series of islands and peninsulas, and produced carbonate, evaporite, and terrigenous rocks (Flores Espinoza, 1989). Deposited on a weathered late Triassic basement of calc-alkalic plutonic rocks, possibly near a plate boundary, (Padilla y Sanchez, 1982)), and a Jurassic section of 1750 m of conglomerate (Mc Kee _et al_., 1984), are a series of basal Cretaceous sedimentary deposits representing marine inundation of the area. The Cretaceous sedimentary sequence begins with a section of Neocomian fanglomerates about 1000 m thick exposed along the western base of Sierra San Marcos, for a distance of about 50 kms (Mc Kee _et al_., ibid). As described by Jones et al. (1984) this basement of arkose is covered by lagoonal carbonates and tidal flat evaporites (Padilla Fm.) followed by a prograding, marine-margin suite of sediments that represent fluvial, overbank, beach bar, and shallow-water shelfal facies (La Mula Fm.). On this was deposited 200-600 m of gypsum and dolomitic sediments of the La Virgin Formation, interpreted as a coastal lagoon or sabkha system (Barcelo-Duarte, 1983), and then shelf carbonates of the Cupido Fm., followed by dark, clay-rich shales of the overlying deeper-water La Pena Fm. A measured section on the east side of the Cuatro Ciénegas Basin (Charleston, 1973) includes these Lower Cretaceous formations. East of the present Cuatro Ciénegas Basin, in the area of the Jurassic-Cretaceous Sabinas Basin, deposition continued throughout the Late Cretaceous, where a series of transgressions and regressions took place (Cenomanian), followed at the beginning of the Turonian by terrigenous sedimentation which continued for the remainder of the Cretaceous (Flores Espinoza, 1989); but in Late Cretaceous rising land masses in western Mexico began to provide fine, terrigenous sediment to the area, deltas prograded in an easterly direction and mud and organic matter accumulated in these deltaic cycles, later to be buried to form shale and coal (Barcelo-Duarte, 1983).

One investigation of modern and fossil arboreal and Compositae pollen sequences in the Cuatro Ciénegas Basin, suggests that an ecologically equivalent if not identical vegetation to that now present, has occupied the floor of the basin since mid-Wisconsin time (Meyer, 1973). Meyer's support of this interpretation is based on the presence of a highly endemic flora and a lack of geologic evidence for large Pleistocene lakes in the area, and he suggests that the "aquatic and terrestrial habitats of the valley lowlands remained stable environments throughout the Quaternary, regardless of fluctuations in regional climate". Meyer did find trends in the pollen record which suggest that the regional climate was cooler and perhaps more moist during the last Pluvial than at present, becoming progressively warmer and drier during late-Pluvial time. The presence of inactive but uneroded stromatolites peripheral to several of the present lakes, travertine dams on the dry desert floor, and dry lake bed sediments capping active springs, support the idea that in the recent past these lakes were at least slightly larger than at present, and several meters deeper. The construction of canals has lowered the water level in many of the lakes and depleted the water supply in the marshes (Almada-Villela and Contreras-Balderas, 1984). No lacustrine bench marks have been found around the perimeter of the basin suggesting significantly higher lake levels in the past, but these may have been obscured by current erosion and depositional processes.

1.4.3. Structure and Tectonics

The late Paleozoic tectonic history hypothesized for this part of northern Mexico is related to an arc-trench system which resulted from subduction of the South American plate under the North American plate (Jones et al, 1984). The western margin of the Cuatro Ciénegas basin defines the eastern edge of the Coahuila Island, a distinct structural feature of Late Jurassic-Early Cretaceous paleogeography, bounded on the north by the San Marcos fault (McKee et al., 1984). This paleotectonic element is essentially a massif, at least the eastern edge of which is held up in part by Late Triassic granites which may be related to an ancient, later aborted, Triassic spreading center (Young, 1983). The Coahuilan Island was uplifted and deformed by block faulting (Upper Jurassic) which also formed the Sabinas Basin, a graben-like trough adjacent to the Coahuila island to the east. The Coahuilan Island, Sabinas Basin, and Tamaulipas Peninsula, (which encloses the Sabinas Basin on the north and east sides), are major paleotectonic elements which influenced the distribution and types of sedimentary deposits during most of the Mesozoic (Flores Espinosa, 1989). The topographically high Coahuila Island was inundated, along with the

Sabinas Basin, during the Cretaceous. The Sabinas Basin, a northwest-southeast elongate basin about 200 miles long and 60-75 miles wide, contains a virtually uninterupted sequence of Upper Jurassic to Upper Cretaceous rocks (Weidie, Wolleben and McBride, 1978). The deposition of Cretaceous shallow water carbonates, clastics and evaporites is a reflection of the proximity of the Sabinas Basin to the Coahuila Peninsula (Island) and the thick sequences of evaporites indicate that the basin was restricted (ibid).

The valley of Cuatro Ciénegas is part of the Ridge and Basin Province (Humphrey 1956), also called the Coahuila Marginal Folded Belt of the Sierra Madre Oriental (Weidie and Murray, 1961). Between 80 and 40 m.y. ago, (late Cretaceous-Eocene) during the Laramide Orogeny, the Sierra Madre Oriental in Northern Mexico underwent folding and thrust faulting (Coney, 1976). The present landscape is the result of this folding which produced broad synclines separated by sharp, narrow, asymmetrical anticlines. A mechanism suggested for the production of this landscape is gravity sliding over a decollement, due to the presence of a impermeable unit (evaporites) over a permeable unit with abnormal fluid pressure (Jurassic sands and gravels) allowing sliding over a gentle slope (Barcelo-Duarte, 1983). Weidie _et al._, (1978) suggest that uplift and erosion has continued to the present day as evidenced by the dissected alluvial fans and bajadas of the region. In the arid climate of the present, the land is characterized by internal drainage that has converted the valleys into broad alluvium-filled intermontane basins (Barcelo-Duarte, 1983).

Central to the presence of the Cuatro Ciénegas springs is the Sierra San Marcos, a faulted, overturned, anticlinal mountain composed of the lower and middle Cretaceous rocks described in 1.4.2. The Sierra San Marcos represents a section of the westernmost bordering element of the Sabinas Gulf against the margin of the Coahuila Peninsula (Humphrey, 1956). The northernmost part of the range, protruding from the south, nearly bisects the basin (refer back to Fig. 1.4.1-1). Almost the entire west flank of the anticline has been eroded away (Kellum, et al, 1936). Running through the crest of the range is the northwest-trending San Marcos Fault. This fault is part of a model of wrench-fault tectonics including left-lateral transcurrent motion associated with the effect of continental collision (Longoria, 1985). Longoria proposes that the wrench fault system is responsible for deformation of the Mesozoic sedimentary succession in northeastern Mexico and that the San Marcos fault represents a Miocene reactivation of an older fault. Evidence for older movement along the fault comes from Padilla y Sanchez (1982) who include the San Marcos Fault in the Sierra Mojada-China Lineament with left-lateral strike-slip movement occurring during the Late Paleocene-Early Eocene. This continuous history of activity on the fault suggests that there could have been springs in this general vicinity for a geologically long time.

Chapter 2. METHODS

2.1. Analyses of Biological Components

Small portions of living surface mat from the various biogenic structures were removed, and, without lifting them out of the water, examined and dissected in the field to obtain qualitative information about the community structure of the plants and animals associated directly with the stromatolites. Reflected and transmitted lights were used with dissecting, bright field, fluorescence, and phase-contrast microscopes (lights were powered by a portable generator).

Phytoplankton grab samples were collected in 1 liter Nalgene bottles and later concentrated. Zooplankton were collected by pouring 36 liters of water through a standard plankton net and bucket assembly. Qualitative and semi-quantitative samples of benthic sediment were collected with a 9x9 inch (23 x 23 cm) Ekman Dredge. Stromatolite cores were recovered using either a battery-powered hole saw coring bit or a set of brass cork borers. Routine collections were preserved in 3% formaldehyde or paraformaldehyde. Material collected for

SEM was treated with gluteraldehyde (8% aqueous), dehydrated in an ethanol/water dilution series and critical point dried. Samples for thin sections were dehydrated and embedded in Spurr Low Viscosity Resin. Cyanobacteria, diatoms, protozoa, and micrometazoa were examined in the field and some were also cultured in the lab for further study. Samples of problematic taxa were sent to a number of specialists who cultured and identified specific microorganisms (please see acknowledgments).

Diatoms were cleaned of organic matter for taxonomy by oxidation with H_2O_2 and $K_2Cr_2O_7$, followed by treatment with HCl to remove the carbonates. Selected duplicate samples were cleaned with CH_3COOH and HNO_3 to investigate the effect of different acids on the diatom silica. Permanent slides were made by mounting the cleaned material in Hyrax resin. A count of 500-2000 cells, at 1500x, was done on each sample to determine the composition of the diatom flora. Chlorox (sodium hypochloride 3% in water) digestion was used to remove the organic matter from the carbonates, in order to observe biogenic imprints left in the mineral fabric.

To investigate the amount of photosynthetic activity taking place in the water column at Pozo Azul, in addition to the collection of routine phytoplankton samples, productivity was measured by the oxygen method. A light-dark bottle study was done using water taken from the upper meter of the water column, and incubated for an exposure time of four hours (noon to 1600). Dissolved oxygen was measured using a YSI Dissolved Oxygen Meter.

A Catherwood Diatometer was used to observe the nature of short term colonization on glass surfaces. Artificial stromatolites, constructed of cast cement hemispheres pegged to flat rectangular bases were set out in the water to observe long-term growth characteristics. These were cast of neat portland cement pegged with square plastic tubing into bases of the same cementing material. After presoaking in distilled water for several days to remove any toxins, sets of two or four hemispheres were put out in areas where stromatolites were currently forming. These structures were recovered and replaced at intervals throughout a 15 month period. Growth rates were measured by a variety of means. In the Rio Mesquites, a stromatolite and several oncolites were dipped in suspensions of synthetic graphite: H.P.N. grade 239 (petroleum coke graphitized to 99% carbon graphite), and replaced in the stream, for a six month period. Portions of the labeled bioherm were recovered at 6 month and one year intervals.

2.2. Analyses of Physical And Chemical Components

The lakes were surveyed with a plane-table and alidade. The base-line maps used are the Mexican government survey maps: Comision De Estudios Del Territorio Nacional (CETENAL) 1;50,000 scale geologic, soils, and topographic maps. Current measurements were made with a Teledyne-Gurley Price meter and by floating a drogue of near neutral density in the water and timing its progress over a measured distance. This was repeated several times for an average current value. Dissolved oxygen was measured with a YSI Model 34 D.O. Meter. Total dissolved solids was measured with a Cole Parmer Model 141-61 Dist 2 ATC Dissolved Solid Tester, and conductivity with a Cole Parmer Model 141-63 Dist 4 ATC Dissolved Solid Tester. pH was measured with pH paper and various meters including duplicate Cole Parmer pH meters used together. Water and air temperatures were made with a mercury bulb thermometer and an Omega Model HH-6 Digital Thermometer. Salinity, Conductivity and

Temperature were measured with a Beckman RB3 Solubridge Conductivity Meter, and a YSI Model 33 S-C-T Meter. Optical salinity was also estimated using an American Optical Hand Refractometer.

Estimates of photon fluence rate at Pozo Azul were obtained with a Li-COR Quantum Meter. Spectroradiometry measurements using blue, red, yellow, and green filters, were made on two occasions, two years apart, along a 13 m vertical profile over the deepest part of the lake. A canoe attached to a fixed line across the lake was used to maintain position.

Water samples for major element analysis were filtered through a 0.45um millipore filter and stored in the dark in a linear polyethylene (LPE) bottle previously leached with hot distilled water; samples for trace element analysis were filtered through a 0.4um nucleopore filter, stored in a HNO_3/HCL leached LPE bottle, and acidified with 2ml of 6N HCL per 250ml of sample, to arrest biological activity. CO_2 was measured in the field by standard titration methods.

Magnesium, calcium, strontium, and sulfur were measured using ICP emission spectrophotometry. Sodium and potassium were measured with AA spectrophotometry. Colorimetric methods were used to measure silica (Strickland and Parsons, 1968), phosphate (Strickland and Parsons, ibid) and nitrate (Gardner et al., 1976). Samples for the analysis of plant nutrients were filtered through a glass fiber filter, stored in an HCl leached glass bottle and acidified with HCl. Alkalinity was measured using Gran titration techniques. Chloride and flouride were measured using ion specific electrodes. Metal analyses were done using ICP emission spectrophotometry after preconcentration using ion-exchange resins following the technique of Kingston et al. (1978).

Analyses of stromatolite mineralogy included use of compound and petrographic microscopy, scanning electron microscopy (SEM) and energy dispersive x-ray, and x-ray diffraction. Slabbed stromatolites were stained with Feigl's solution to detect aragonite; and with Alizarin Red S and Potassium Ferrocyanide to detect the presence of calcite, iron and dolomite. Thin sections provided the basis of fabric and microstructure descriptions. A cover slip was cemented on the thin sections with Hyrax, a resin with an index of refraction of 1.71. This produces adequate contrast between opal and mounting medium for the diatoms to be seen more easily.

Stromatolite samples were subjected to a variety of chemical treatments in an effort to extract biological information with the least disruption to non-carbonate physical integrity. Treatment with EDTA was the most gentle method of carbonate removal. Dilute acetic acid was also effective.

Diversity and evenness were measured using MVSP a multivariate statistical package for the IBM PC (Kovach, 1986). Stromatolite associations were determined by calculating relative abundance of principle organisms associated with each stromatolite type. A fortran program was written to calculate distance values between the four stromatolite diatom associations.

Chapter 3 Results

Four distinct stromatolite morphologies, based upon variations in overall shape, surface features, community structure, and/or nature of cementation, are distinguished in the Cuatro Ciénegas Basin. These morphologies are often found in more than one locality among the lakes and streams of the basin but their best development is expressed at the sites chosen. These sites regularly produce structures characteristic of the type. Each of the sites described is associated with a discrete spring-fed aquatic system with its own unique physical and biogeochemical characteristics. These systems are geographically isolated from each other and are treated as discrete systems, although there may be subsurface hydrologic connections between them.

Site descriptions include the general habitat associated with the stromatolites; and the macrostructure, community composition and architecture, fabric and microstructure, of each type. By <u>macrostructure</u> is meant the overall shapes and large-scale structures that make up the stromatolite deposit. <u>Community composition and architecture</u> includes the biota associated with the stromatolites, and the spatial arrangement of the dominant elements. This expression is used in preference to community structure because the latter has a more specific definition in ecological literature. _Fabric_ refers to internal spatial properties of these structures such as the development of layering and lamination, and _microstructure_ refers to the microscopic characteristics of the internal properties (Monty, 1976).

Following the description of individual stromatolite sites, the results of the water chemistry analyses, mineralogical composition, physical measurements, and biological investigations are presented. Biological studies include productivity measurements, colonization studies, growth rate experiments, and observations on metazoan interactions.

3.1. Description of Type 1 Stromatolites and Related Microbial Deposits: The El Mojarral System

3.1.1. Habitat

As described in Winsborough _et al_. (in press, 1990)

El Mojarral is an extensive marsh system emerging a short distance from the distal margin of an alluvial fan on the northeastern corner of Sierra San Marcos. The El Mojarral system is typical of several Cuatro Ciénegas spring-lake systems as is the growth pattern of the stromatolitic and related microbial accretions within it. Laguna El Mojarral (West) appears to be the primary spring source for it and two adjacent lakes connected by shallow surface streams (and possibly by subsurface conduits). Extensive marshlands on the western (uphill) side of the lake contribute to surface and probably to subsurface inflow. El Mojarral is a roughly constant-level, spring-fed lake about 13 m wide, 48 m long, and 1 to 5 m deep (Fig. 3.1.1-1A,B). Water temperature varies annually between 28° and $35^{\circ}C$. Physico-chemical measurements made at El Mojarral are presented on Table 3.1.1-1.

The lake appears to have been partly formed by the collapse of a section of roof covering a subterranean watercourse, thus it is technically a sinkhole. Water inflow is in the north end of the lake at the bottom, at a depth of about 5 m. It comes through a small, horizontal cave tunnel. Another tunnel in the lake bottom, at the opposite end, carries water out, presumably to the nearby lakes. It may be no more than a few hundred years since the present lake was marshland, or a much larger and shallower playa lake. This could be the reason why there are no large and extensive multi-generation stromatolites in this lake. They have just not had time to form.

The marsh associated with this lake system contributes so much particulate organic matter that, in quiet marginal areas of the lake, where there is least current, the sediment that accumulates is largely dark organic anoxic copropelic mud (gyttja). Soft white carbonate mud, of an undetermined thickness, covers other parts of the lake bottom. On this mud there is no development of microbial mats or stromatolites, however, clasts of a lithified version of this material appear to form the nuclei of some oncoids. Aquatic vegetation associated with the shallow margins of the lake includes the sedge <u>Eleocharis</u>, the macroscopic alga <u>Chara</u>, the bladderwort <u>Utricularia</u> and the water lotus <u>Nymphaea</u>. The lake is bounded by a <u>Phragmites</u> marsh and then dry desert on the topographically lower distal margin, away from the inflows.

3.1.2. Lake Stromatolites

Along the margin of the lake, stems and roots of sedges, rushes and grasses sometimes become cemented into a porous, calcareous tufa. Eroded pebbles of this tufa are eventually distributed in the lake by water currents. The surface of this material as well as snail shells and fragments of dead vegetation are colonized by a specific set of microorganisms responsible, under favorable conditions, for stromatolite formation.

Stromatolites are distributed on a shallow, broad, marginal bench or shelf area that covers part of one end of the lake, and on the sides and bottom of the lake, where the current is sufficient to carry away the fine silts, clays, and organic debris. The loose sediment covering most of the shelf consists of a poorly-sorted sand-sized mixture of snails and their shells (mostly *Mexipyrgus churinceanus* Taylor with some *Euboria bella* Conrad and *Mexistiobia manantiali* Hershler, and small pebbles.

3.1.2.1. Megascopic Features

The stromatolites are irregular in shape, often somewhat flattened, with rounded contours (Fig. 3.1.2.1-1). Typical examples reach up to about 0.5 m in diameter, are usually quite a bit wider than tall, and often have concave or hollow bottoms. In addition to isolated individuals, stromatolites form as extensive, up to 1.5 cm thick, fleshy encrustations that build up on exposed bedrock, often overlying visible gaps ("bubbles") that may lift the crust from the bedrock. In both instances, the external morphology of the stromatolite mat is a surface contoured with a constant, regular, repeating growth pattern as seen in Fig. 3.1.2.1-1. Small, horizontally projecting ridges resembling tiny ledges or terraces are distributed regularly over most or all of the mat's surfaces. The ledges are lobate and project outward from the stromatolite surface about 2 mm. The ridges 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. 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. When growing vertically, they are radial-campanulate in shape. In older deposits the ridges fuse horizontally, and form long anastomosing "tuning fork" patterns. In some cases, well-developed horizontal lineation is superimposed on an older growth pattern at a different angle, indicating that the structure had been tilted at one time.

In macroscopic appearance, a section through the stromatolite mat, cut parallel to growth, usually reveals a series of light-colored, palisade-like layers of porous carbonate, alternating with dark green (or pink-purple) unencrusted layers (Fig. 3.1.2.1-2). The thickness of the stromatolite mat 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.

3.1.2.2. Community Architecture

The alternating carbonate-rich and organic-rich layers of the mat are due to the differential calcification activity of the cyanobacteria responsible for their construction. Palisade-like tubular or fused-tubular porous carbonate encrustations occur around the tapering filaments of the rivulariacean <u>Homoeothrix balearica</u> Bornet & Flahault (Fig. 3.1.2.2-1A,B). This produces the light-colored layers in Fig. 3.1.2.1-2; while the unencrusted dark green layers in the same figure are dominated by <u>Schizothrix</u> <u>lacustris</u> A. Braun (Fig. 3.1.2.2-1C) and another unidentified <u>Schizothrix</u>. The unidentified one is characterized by a slightly thicker trichome (2 um, as opposed to about 1 um for <u>S. lacustris</u>) and a thinner, less diffluent sheath. Occasionally monocrystalline calcitic encrustations occur as thin tubes surrounding the sheaths of <u>Schizothrix</u> sp. (Fig. 3.1.2.2-1B), however, the bulk of the carbonate is precipitated around the filaments of <u>Homoeothrix balearica</u>. The pink-purple layers consist primarily of empty <u>Schizothrix</u> sheaths surrounded and/or inhabited by unidentified flexuous filamentous purple photosynthetic bacteria, and occasional clusters of <u>Chromatium</u> sp. 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 vertical zonation similar to that of marine microbial mats (see Cohen and

Rosenberg, 1989) with a surficial layer of oxygenic photosynthesizers (cyanobacteria 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 stromatolite surface is due to the sheath pigmentation of H. balearica, whereas under low light conditions, such as near the cave mouth and on the underside of stromatolites, these filaments take on a dark purple color due to increased accumulation of phycoerythrin in the cells and reduced pigmentation in the sheath. 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., *Cocconeis placentula* Ehr. and *Achnanthes* spp. are epiphytic on the *Homoeothrix* filaments, whereas others, especially *Cymbella* spp. and *Brachysira vitrea* (Grun.) Ross form dense clusters among the pockets and crevices on the irregular mat surface.

In order to frame this description into a temporal perspective it should be noted that the reported distribution 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 daily, periodic, seasonal, or accidental changes in the environmental parameters. For example, Monty (1976) reports 3 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 process leads to vertical accretion of mat.

The second type of lamination is *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, ibid).

Through time, population dynamics or micro-environmental changes produce an alternation between *Homoeothrix*- and *Schizothrix*-dominated laminae. The result is a stratigraphic sequence where *Schizothrix* grows alone for a while making the sculptured ridges, until conditions change favoring the growth of more *Homoeothrix* at the surface.

The general community architecture described above for the lake stromatolites applies also for the surface encrustations lining the low-light vertical ledge leading to the mouth of the inflow cave. Indeed, there is a continuity of the community architectures from the thick-layered lake stromatolites and multilayered fleshy encrustations to the thin surface communities of the cave stromatolites (Section 3.1.3.). Thus, with increasing depth (i.e. reduced light) the thickness of the surface encrustations diminishes and a different suite of cyanobacteria is found in the sub-surface layer. *Homoeothrix* and *Schizothrix* still predominate in the surface layer, at times found together with patches of *Lyngbya kuetsingii* Schmidle, *Gongrosira* and the rhodophyte *Adouienella 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, *Spirulina* sp., and various members of the genera *Chlorogloea*, *Aphanocapsa*, *Synechococcus*, *Synechocystis*, and *Microcystis*. Exact determination of these small-celled taxa (1-5 um 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 innoculated. 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 100-200 um deep zone of endolithic cyanobacteria penetrates the bedrock below the layer of coccoid forms described above (Fig. 3.1.2.2.-1D). It is dominated by *Plectonema terebrans* Bornet & Flahault and an undescribed stigonematalean endolith tentatively identified as *Herpezonema* (Fig. 3.1.2.2.-1D) as determined by culture studies (J.-S. Seeler and S. Golubić pers. comm., 1990). At the mouth of the inflow cave this community then grades into the cave stromatolite community (see section 3.1.3 below).

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 *Nitzschia denticula* Grun., *Cymbella cesatii* (Rabh.) Grun. ex A.S., *Denticula elegans* Kütz., *Achanthes affinis*

Grun., and Gomphonema intricatum var. vibrio. There is a spatial component to the distribution of different diatom species as there is to the cyanobacteria. N. denticula 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 asociated 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 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, Brachysira vitrea (Grun.) Ross and Cocconeis placentula Ehr. and Amphora spp. and the much larger Epithemia argus (Ehr.) Kütz. are to be found living in crevices of the mat or as early colonizers of freshly deposited calcite layers. <u>Achnanthes</u> and <u>Cocconeis</u> produce a mucilage pad that leaves a thick bas-relief impression of the cell on the carbonate.

An uneven growth pattern is produced by fish grazing which appears to be responsible for removing patches of the stromatolite mat. It is not uncommon that one side of a stromatolite will be cleaned of much surface growth, while the other side is relatively undisturbed. The down-current side is more heavily grazed thus selective mat removal and ultimate stromatolite shape may be due to the effent of current on the feeding habits of the fish. The presence of areas completely abraded by the feeding activities of fishes (they are covered by groups of parallel, tooth-produced grooves) suggests that at least the surface portions of some of the El Mojarral stromatolite communities are significantly affected by the feeding behavior of some of the fish.

Preliminary evidence also suggests that there may be more subtle activities of smaller animals that might have important effects on stromatolite dynamics and structure. For example, one small stromatolite (about 3 x 6 cm) collected from about 2 dm below the air-water surface, had a sectional structure consisting of a fairly hard 0.7-0.8 mm surface palisade layer of calcium carbonate surrounding upright trichomes of H. balearica which extended to about 1 mm above the surface on the ridges and only a small fraction of that in the micro "valleys" between ridges. Below this there were several alternating layers consisting primarily of Homoeothrix or densely tangled Schizothrix lacustris separated by carbonate-rich layers, and then a thicker, denser, and harder layer of carbonate which formed the interior non-living part of the stromatolite. Flagellate protozoans, including bodonids, the euglenoid Petalomonas, and a colorless euglenoid were present in this typical stromatolite mat sample, along with the ciliates Cinetochilum, Aspidisca, Spirostomum, Litonotus, Cyclidium, Vorticella and an unidentified hymenostome. Small snails, particularly Mexypyrgus churinceanus, and small ostracods were also present. Additional species seen after some stromatolites were cultured (in the water in which they had been living) for a week included 3 more colorless flagellates, 6 amoebae (in the broad sense), 2 hypotrichs and 3 other ciliates, 4 rotifers, 1 neorhabdocoel, 1 gastrotrich and an unknown number of species of nematodes.

The protozoans *Euglena* sp., *Bodo* sp. and *Aspidisca* sp., and bdelloid rotifers are frequently observed in stromatolite and oncoid mat samples. Ostracods identified from sediment in and immediately around the stromatolites include *Physocypria* n. sp.(?), *Darwinula stevensoni* (Brady & Robertson 1870), *Limnocythere floridensis*? Keyser 1976, *Cyprideis salebrosa* Van Den Bold 1963, *Pseudocandona* sp. aff. *P. antilliana* Broodbakker 1983, *Cypridopsis vidua* (Mueller 1776); all are eurythermic or thermobiontic, small, narrow "aquifer species", usually associated with spring pools as well as the subsurface (R.M. Forester, pers. comm. 1987).

3.1.2.3. Fabric and Microstructures

Within the actively growing part of the mat (up to 10 mm or more in thickness) calcite is precipitated between the vertical-radial masses of *Homoeothrix* filaments. Sequential layers of these encrusted *Homoeothrix* filaments are usually interrupted or separated by thin, relatively hard layers of precipitated material, consisting of cloudy, tightly packed masses mainly of 10 um calcite crystals, sometimes surrounding

Homoeothrix filaments extending through from the layer beneath (Fig. 3.1.2.3.-1). Monty and Mas (1981) interpret a similar lamination pattern as resulting from the periodic growth of a simple population dominated by a filamentous cyanobacterium, with a micritic rind marking the end of a growth phase. In contrast, our example exhibits a species-specific difference in the degree of calcification, where the alternating laminae are a consequence of alternating populations.

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.

At the growing surface (synoptic profile), Homoeothrix filaments are surrounded by loose micrite (1-5 um), and rounded to loaf-shaped crystals of fine spar (5-30 um), resulting in palisade-like patterns (Fig. 3.1.2.3-1). This carbonate also adheres to, or nucleates upon diatom stalks and the surface of gelatinous 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 (Fig. 3.1.2.3-2). Spar-sized calcite cement (Fig. 3.1.2.3-3) 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. A comparable example of <u>in situ</u> mineralization in the shape of spherulitic fans takes place in the mucilage surrounding <u>Scytonema</u>, 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 <u>Gongrosira</u> producing hard patches of calcite among the more loosely distributed grains surrounding the cyanobacteria. The crystal morphology associated with <u>Gongrosira</u> is the same as that described and illustrated in Golubić and Fischer, (1975).

This generally loose fabric changes gradually downward, toward the interior of the structure, to more rigidly packed sheaths of Homoeothrix surrounded at first by loose anhedral, then tighter interlocking coarser crystals. 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). Fig. 3.1.2.3-4 shows a calcite cast (biogenic imprint) of an unidentified filament that was removed by chlorox. 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.

The surface layers of Homeothrix balearica and Schizothrix lacustris are thickest on and beneath the crests of the ridges. In some cases the decomposed remains of these organisms produce fenestrae, where the gap in the rock framework is larger than the grain-supported interstices (cf Monty, 1976 and Monty and Mas, 1981). Particularly in the stromatolites lining the ledge leading into the cave, 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.

3.1.3. Cave Stromatolites

3.1.3.1. Megascopic Features

At the lip of the inflow cave, in the bottom of El Mojarral (West) on the north side, the regular terraced pattern of lake stromatolites described above grades into manganese and iron-rich carbonate stromatolitic deposits. The cave walls and floor are presently coated with a layer of metallic black to reddish-gray iron and manganese oxide 1-2 mm thick. External surfaces in the cave are irregular, with scattered projections, many of them sharp. Projections range from small regular "flutes" to larger, sharper growths up to 2 cm tall. At the mouth of the cave where the current flows around the upper edge, fairly regular and symmetrically undulating fluted laminae form with the lines representing the crests oriented parallel to current. This succession of parallel ridges at the surface of the stromatolites results from the thickening of carbonate laminae under the crests. Botryoidal clusters of opaque oxide minerals (up to 1 mm in diameter) coat the surface of these densely lithified, thinly laminated, presumably biogenic calcareous structures (Fig. 3.1.3.1-1).

In sawn sections, internal features consist of a combination of continuous and discontinuous concentric laminations and irregularly-shaped clots 1-3 mm in diameter. Laminae are sharp in outline and alternate between dense, fine-grained fabric and a clear, coarse-grained one. Well-defined laminae of metallic oxides occur irregularly in the interior of the carbonate deposit as well.

3.1.3.2. Community Architecture

The photosynthetic organisms comprising the stromatolite mat form a thin layer consisting primarily of the cyanobacterial community described in Section 3.1.2.2. above and diatoms, with isolated areas colonized by patches of <u>Homoeothrix</u> and <u>Adouinella</u>. Filament length of <u>Homoeothrix</u> and <u>Adouinella</u> is reduced significantly due to the prevailing low light conditions. A large part of the surace mat is covered with a densely distributed coating of the diatom Eunotia cf maior, that forms chains up to 10-20 cells long. These are attached directly to the metallic substrate and are often encrusted with tiny metallic grains. A much smaller percentage of the surface is covered with the adnate diatom Cocconeis placentula which also becomes encrusted with the metal deposit and buried. Homoeothrix is attached to the hard substrate and coated with small epiphytic diatoms, mainly Achnanthes, and metallic grains.

3.1.3.3. Fabric and Microstructure

Generally iron and manganese are transported together by underground water in a reduced state (as free ions or bound to organics). They may oxidize spontaneously in the vicinity of the river mouth or be bound on the sheaths of cyanobacteria or on bacterial walls where they are oxidized (see Nealson, 1983). When crushed, the botryoidal mineral clusters on the stromatolite surface consist of aggregates of small spherical red-orange grains about 1 um wide. EDX shows that they contain iron and manganese at a ratio of aproximately 2:1 (Fig. 3.1.3.3-1). These oxides are sometimes found encrusting cyanobacterial sheaths (Fig. 3.1.3.3-2) and diatoms.

Internally these stromatolites contain thin carbonate laminae about 0.1-0.5 mm thick (Fig. 3.1.3.3.-3A). These are of two kinds, a cloudy or opaque micrite layer that appears dark in plane transmitted light, and a more translucent and lighter colored layer of clear spar. Short sub-parallel sheets of opaque micrite are scattered throughout the interior of the structure (see arrows in Fig. 3.1.3.3-3A). Rim cements made up of individual calcite crystals up to 100 um in length line hollow cavities within the stromatolites. Filling the interstices and cavities are clots or irregular deposits of well-defined sub-spherical to ovoid cloudy or "turbid" fine-grained peloids 75-200um in diameter (Figs. 3.1.3.3-3B,C). Some of these are probably fecal pellets, others may have a bacterial origin similar to the internally formed bacterial pellet origin suggested by Monty (1965, 1967, 1972), and Chafetz (1986). Some peloids are surrounded by multiple generations of alternating clear spar and dark, turbid micritic rims, often showing meniscus-like connections between peloids at grain contacts. These connections are marked by arrows in Fig. 3.1.3.3-3C. Cements may completely fill primary porosity as in this figure. The presence of dense colonies of cyanobacteria correlates with dissolution of metallic oxides altering the morphology of the laminae. The surface in these areas is also concave suggesting a net loss of material.

3.1.4. Coated Pebbles and Oncoids

3.1.4.1. Megascopic Features

Pebbles and snail shells, which, together with fecal pellets, make up the bulk of the unconsolidated sediment, are often covered with bright green microbial laminae consisting of LPP-type cyanobacteria and tufted surficial patches of Homoeothrix, Schizothrix, coccoid cyanobacteria, diatoms and micrite. Carbonate particles (including snail shells) smaller than 5 mm diameter are usually bored by Plectonema terebrans and other LPP forms to such an extent as to constitute a cohesive organic matrix even when all carbonate is dissolved away with acid. Other endoliths include the above-mentioned stigonematalean (please refer back to Fig. 3.1.2.2-1D) and at least three new species of Hyella (J.-S. Seeler and S. Golubić, pers. comm. 1990).

Thickening of the surface of the pebbles to become the cortex of an oncoid begins with the establishment of colonies of Homoeothrix thus initiating the rhythmic precipitation of carbonate laminae. There is a continuum in the increasing ratio of cortex to nucleus diameter from coated pebbles to oncoids.

Oncoids are unattached accretions distinguished from stromatolites by multiple laminae which occur as concentric layers of varying thickness completely surrounding a nucleus. Spherical oncoids occur in shallow areas of El Mojarral (East) (about 0.5 m deep) where the bottom is hard, and the current is sufficient to remove material smaller than a pebble. The maximum diameter observed is about 10 cm. Larger structures become stationary as their weight precludes further movement by currents. The oncoid surface is usually slightly wavy or lumpy, with round holes 1-2 mm wide distributed somewhat unevenly over the surface (Fig. 3.1.4.1-1A). 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, that extend 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 represent primary gaps in the fabric, enlarged and maintained by the activities of the associated benthos.

The nucleus may be a calcite pebble, snail shell, or piece of organic debris. The material that forms the nuclei of the coated pebbles and 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 tufa or Chara. 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. 3.1.4.1-1B). This lamination pattern is essentially indistinguishable from that of the stromatolites described above. Oncoids that remain stationary do develop the characteristic ledged surface pattern, and when they are moved, a new set of ledges with the same pattern forms, superimposed over the old one, but at a sharply different angle to the former, as the growth pattern adjusts to the new orientation.

3.1.4.2. Community Architecture

The organisms responsible for construction of the oncoids are Schizothrix and Homoeothrix, producing a rhythmic depositional pattern similar to the stromatolites. The surface of the oncoids lacks the ledges, and has an overall lumpy appearance produced by tufts of Homoeothrix. The diatoms, cyanobacteria and bacteria are the same species as those found on the stromatolites, however the diatom population is very heavily dominated by Cymbella cesatii (up to 95%). 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.

One square cm of a coated pebble from the shallow ledge was watched for 15 minutes with a dissecting scope. In this time and space, 3 small chironomid larvae, one rotifer (a large bdelloid), and 2 harpacticoid copepods were seen, and all appeared to be feeding. An additional sample of a multi-layered portion of a stromatolite mat (collected about 2 to 3 dm under the water surface growing on hard bedrock) was torn to small pieces with dissecting needles. The piece used was 0.7 x 2.0 x 0.8 cm, and it was dissected in a water volume of 15 ml. This material was then mixed and a 1 ml sample placed in a Sedgwick Rafter cell. Larger micro-benthos were counted under a dissecting microscope and calculations give estimates of the following numbers per cm^3 of this stromatolite: 532 nematodes, 43 large ciliates, and 14 small ciliates. These estimates are low, as there still were small pieces of stromatolite in which more of these (and other organisms) no doubt were hiding.

3.1.4.3. Fabric and Microstructure

Oncoid laminae consist of alternating dense carbonate-rich, and porous organic-rich layers as do the stromatolites, but the laminae are generally somewhat thinner, tighter and more compact (Fig. 3.1.4.3-1). They also do not exhibit secondary internal Schizothrix growth to anywhere near 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. 3.1.4.3-2). Micritic calcite crystals appear to indicate what was formerly the surface of the cyanobacterial filament. The interior of the sheaths has been replaced with micrite and the original wall material is gone. Some organic matter (possibly last remains of the original sheath) appears as thin black linings to the lower right hand side of central filament and lower left hand side of filament to the right of center in the photo. Carbonate cements include patterns consisting of rows of micrite crystals on the surface of sparry calcite (Fig. 3.1.4.3-3) similar to those illustrated by Pursell (1985, p. 43).

Imperfectly formed, prismatic, bipyramidal quartz crystals (Fig. 3.1.4.3-4) are found in small dense oncoids as well as in the stromatolites described from the cave area. These crystals range in size from about 4 x 8 um to 20 x 63 um. An authigenic origin for the quartz crystals is supported by the presence of colorless cyanobacterial (or fungal) filaments trapped in some of them (Fig. 3.1.4.3-4, 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 cave stromatolites with a dense fabric, such as in the vent area, there are few diatoms preserved in the insoluble residue and numerous quartz crystals. These preliminary observations would accordingly indicate 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.

3.2. Description of Type 2 Stromatolites: The Rio Mesquites System

3.2.1. Habitat

About 1.5 km north of the tip of Sierra San Marcos a spring emerges from an opening at the base of a 2 m tall vertical wall, and flows east-southeast. This is the rheocrene of the Rio Mesquites. A rheocrene is a spring of fairly limited area, that discharges directly into a stream. A significant velocity of flow, alarge quantity of water and a fairly constant temperature are also characteristics. The overburden above the spring vent is an indurated snail-rich sediment, in some places a snail coquina, representing an ancient lake bed. Downstream from the spring, the Rio Mesquites flows as a shallow stream about a meter deep and one to several meters wide, for about 2 kms. Along the margins of this part of the stream there are beds of <u>Chara</u> and other aquatic vegetation. After its first 2 km the stream morphometry changes to a narrow sinuous course, about 2-8 m wide and 1.5-2.5 m deep and turns gradually south where it continues roughly parallel to the margin of the Sierra San Marcos (Fig. 3.2.1-1A). The Rio Mesquites flows a few kilometers to the east of the El Mojarral system and reportedly receives some water from this source.

The flow is swift for the next 3 or 4 km of the stream course, (between 0.4 and 0.6m/sec) in the narrow parts. Along the lower part of this stretch several side streams, carrying water from nearby spring-fed ponds, add to the main flow (Fig. 3.2.1-1B). The stream broadens considerably shortly after these additions, decreasing in velocity as well, because of the greatly enlarged surface area (Fig. 3.2.1-1B). The lower part of the stream could be called Laguna Mesquites as it has more of the characteristics of a lake than a stream (Fig. 3.2.1-1C). Two narrow streams enter a marsh at the downstream end of this section and carry water for about 8 km to where part of it enters a canal and the rest flows into a sinkhole. The owner of the Rio Mesquites, Sr. Roberto Arredondo, reports that water from the sinkhole flows east underground, across the basin, and is the water source which maintains a system of large brackish-water lakes on the east side of the basin called Las Playitas.

Minckley (1969) suggests that the origin of the Rio Mesquites may be the result of headwater foundering of an actively-flowing aquifer system, producing a linear tortuous channel. The presence of extensive dry travertine deposits and associated lacustrine facies in the vicinity of and slightly higher than the present spring, support the idea of an earlier, large spring-fed lake at the site of the present source of the Rio Mesquites. Ground water flow patterns in the basin are such that the present course may represent an antecedent solution passage adopted by the current flow regime.

Although the water level in the Rio Mesquites is essentially constant, except after heavy rains when it spills over its banks, there is almost no woody vegetation other than the occasional Mesquite tree. A dense broad marsh borders the river on its west side, and the east side, except for a narrow rim of marsh plants, consists of dry sparsely vegetated desert dotted with ancient, eroded gypsum sand dunes. The sides of the stream are straight or undercut in many places. Direct light reaches the narrow parts of the streambed for only a short period each day. Where current is swift the bottom is scoured of fine material, whereas in areas where the current is deflected by stromatolites and embayments soft organic-rich sediment accumulates. Rooted macrophytes, including Eleocharis and Nymphaea colonize these refuges. Physico-chemical measurements of the Rio Mesquites are presented in Table 3.2.1-1.

3.2.2. Megascopic Features

Both stromatolites and oncoids are forming in the Rio Mesquites. Because the growth pattern and organisms characteristic of these structures are indistinguishable except for overall shape they are discussed together.

Stromatolites and oncoids are hard, lithified structures with a characteristic morphology. Elliptical to somewhat elongate stromatolites several meters long and over a meter high are attached to the sides and bottom of the stream. Their tops often have raised rims and depressed or eroded centers filled with unconsolidated sediment, small pebbles and oncoids (Fig. 3.2.2-1). The sides are often vertical or taper inward toward a narrow base. They form at all depths and are distributed from the beginning of the narrow sinuous part of the river to the lacustrine segment.

Sub-round to round oncoids as large as 0.3 m in diameter are common in the swift narrow parts of the stream, and cover the bottom in some places. They are distributed in lag piles sorted with respect to oncoid size. Smaller oncoids form piles in the upper reaches of the stream and the size of the oncoids generally increases with distance downstream. Oncoids are often quite heavy because they are densely cemented, but also very porous, due to their growth form. Stromatolites and oncoids consist of rounded, knob- or nubbin-like, digitate projections surfaced with growths of botryoidal (or bulbous) cushion-like algal colonies about 1-3 mm in dia. (Fig. 3.2.2-2 A,B,C). With increasing distance downstream the projections coalesce into a more solid surface with very few deep channels between projections. Figure 3.2.2-2 C illustrates the range of morphological variation of Rio Mesquites oncoids. The oncoids begin as fragments of laminated tubes up to about 4 cm in dia. which form around exposed plant roots and stems (Fig. 3.2.2.-2 A,B). These tubes eventually fall to the stream bottom, move downstream with the current and continue to grow. The overall color of the stromatolites is green.

Growth of the stromatolites and oncoids is in a sinuously-outward, dendritically-branched pattern of hard, smoothly rounded, branched-cylindrical, tightly intertwined projections, creating an open, regular surface whose interstices are filled with cases and tubes of larval insects, ostracods, snails, living and dead Chara, fecal pellets, plant fragments and debris. Internally, discontinuous layering is evident in sawn sections within the individual projections. These layers appear as light colored, clear carbonate-rich somewhat arcuate bands separated by darker, iregular-shaped opaque areas. Figure 3.2.2-3 shows a typical oncoid cut in half. Note the discontinuous appearance of the major elements due to the convoluted nature of their growth.

3.2.3. Community Architecture

Rather than a hierarchy of organisms distributed in thick discrete layers, as in El Mojarral, the stromatolite community is compressed into a thin (1-2mm) mat covering the surface of the projections. The stromatolites and oncoids characteristic of the Rio Mesquites are built by an association consisting predominantly of the green alga *Gongrosira calcifera* (Fig. 3.2.3-1) that is responsible for the overall shape and green color, with a lesser contribution by the cyanobacteria *Homoeothrix balearica*, *Schizothrix lacustris*, *Cyanostylon microcystoides*, and diatoms. *Homoeothrix* and *Schizothrix* are distributed among the *Gongeosira*, with the *Homoeothrix* sheaths as well as diatoms providing the brown color. Associated with the *Homoeothrix* are coccoid forms resembling *Aphanocapsa*, and *Synechococcus*. *Cyanostylon* is also present within the carbonate encrustations of *Gongrosira*. At the base or neck of the nubbins of *Gongrosira*, *Plectonema* sp., *Cyanostylon* and an LPP type occur.

Diatoms are common on the upper surface of the mat and in the deep crevices between the spherical cushions of Gongrosira colonies. The uneven surface provides microhabitats for over thirty species of diatoms, mostly epiphytic and epilithic forms. On the actively growing Gongrosira cells, where calcification has not taken place, the acidophilous diatom Eunotia sp. is common, whereas on the carbonate encrusted surfaces the dominant species are often the alkaliphilous diatoms Amphora katii Selva and Denticula elegans. In addition, Gomphonema intricatum var. vibrio with its long branching stalks forms gelatinous masses up to several mm in diameter in cavities protected from direct current. Epithemia argus is a very large, closely-adnate diatom that is conspicuous on the upper surface even though actual numbers are relatively low. In the lithified interior of the mat dense accumulations of diatoms are preserved (please see Fig. 3.2.4-2), but there is scant evidence of good cyanobacterial preservation.

The Homoeothrix appears to prefer carbonate substrates for attachment rather than new Gongrosira growth, in contrast to the diatoms, although this may be a matter of differential colonization rates rather than substrate preference. Bacteria are present in the lower layers of the Rio Mesquites surface mat but the purple sulfate-reducing species are only locally obvious. In the lithified interior of the digitate structures, horizons of calcified bacteria are preserved in the cemented calcite matrix (Fig. 3.2.3-3 A,B).

The most commonly observed benthic microoganisms associated with the stromatolites and oncoids are cryptomonads, oligotrichs (Halteria sp.), euglyphids, dipterans, elmid beetles, ostracods and snails. Most of the benthos are found in the soft sediment filling the interstices and on the undersides of oncoids. Snails, which are distributed throughout the structures, include Nymphophilus minckleyi Taylor, N. acarinatus Hershler, Mexistlobia manantiali Hershler, Durangonella coahuilae Taylor, Coahuilix hubbsi Taylor, C. landyei Hershler and Mexipyrgus churinceanus, All are species endemic to the Cuatro Ciénegas Basin. In quiet areas of the stream, colonies of Ophyridium versatile attaches itself to the surface of oncolids and stromatolites, forming colonies up to 3 cm wide.

A cube about 1 cm on each side was sawn from the surface of an oncoid (collected 28 April, 1986) from 1.5

m stream depth and disaggregated. The material was diluted with water, examined, at 30 x magnification, and the benthos enumerated. With the exception of small protozoans, which were not counted due to poor preservation, the animals observed include 1 cladoceran, 3 rotifers (Keratella sp.), 12 harpacticoid and 2 cyclopoid copepods, 1 plecopteran larva, 28 dipteran larvae (Chironomidae), 8 dipteran larvae (Heleidae), 3 ephemeropteran larva, 47 elmid larvae and 2 adults, 1 dobson fly (Corydalus sp.), one caddis fly (Hydropsychidae), 4 brown water mites, 1 nematode, 1 flatworm (Dugesia?), 46 ostracods belonging to at least 4 different species, 3 amphipods (Hyalella sp.), and 18 snails (7 Coahuilix hubbsi, 2 Coahuilix landyei, 2 Nymphophilys acarinatus, 4 Durangonella coahuilae, 3 Mexistiobia manantiali).

3.2.4. Fabric and Microstructure

At the mat surface the Gongrosira colonies are often coated with small carbonate grains, fecal pellets, mucilage, and adnate diatoms. The primary fabric of the stromatolites and oncoids, however, consists of macroscopic, sinuous, upright, outward-radially-dendritic tubes of dense light-colored compact micrite-sized calcite crystals. These irregular-shaped calcite crystals between the Gongrosira cells are mostly 4-8 um wide (Pentecost, 1988). The tubes often show thin lamination (see Fig. 3.2.2-1). In thin sections cut perpendicular to growth, the bulbous projections exhibit thin discontinuous laminae irregular in length and thickness, and often interrupted by patches of cloudy micrite or pieces of debris. Pentecost (ibid) measured ill-defined, concentric laminations 25-100 um apart in the oncoids. Some of this lamination may be the result of episodic cementation on the surface of voids within the part of the structure exposed to flushing by carbonate-laden water. Other laminae may be produced by changes in the rate of Gongrosira growth in contrast to the amount of sediment accumulated by the mucilage of cyanobacteria and diatoms. In thin section, 3 sizes of cyanobacterial filaments are visible, sometimes in growth orientation, in the lithified structure. The tubes are either replaced by micrite, or in some instances the original organic material remains, surrounded by micrite or sparry calcite. These filaments represent species of Schizothrix and Homoeothrix.

As the growing dendritic structures become infilled with fecal pellets, ostracods, snails, and debris this muddy material becomes lithified along with the rest of the structure and is identifiable as irregular pockets of mottled, peppery grey, cloudy, material. Fragments of Chara are often incorporated as well. Some of the infilling material consists of small fecal pellets in various stages of induration from loose aggregates to well-cemented rock. Spar crystals line the interstices as cementation proceeds (Fig. 3.2.4-1A). Diatom tests are well-preserved in the interior of the oncoids and stromatolites. Fig. 3.2.4-1B is an SEM view of the interior of a piece of oncoid, broken in half to show the interior. A significant amount of the material is composed of diatom tests. A long chain of Fragilaria cells still attached to each other can be seen in the upper part of the photo. Bacteria are also preserved in the oncoids. Fig. 3.2.4-2A,B shows a different part of the surface shown in the previous photo. Bacteria that appear to be calcified are cemented in sheets or plates about the thickness of one bacterium. The resultant fabric of the Rio Mesquites stromatolites and oncoids is thus a laminated biomicrite with clotted infillings.

3.3. Description of Type 3 Stromatolites: Los Pozos Azules

3.3.1. Habitat

Los Pozos Azules is a cluster of deep lakes fed by a spring-marsh system located near the southern end of the Cuatro Ciénegas basin, on the east side of Sierra San Marcos. These lakes represent the most massive and extensive accumulations of stromatolites in the basin. Out of a total of more than 60 springs shown on the CETENAL map in the vicinity of Pozos Azules (Fig. 3.3.1-1), there are at least eight lakes containing stromatolites. The lakes are highly variable in their morphometry. The Pozos Azules are a somewhat linear series of sinkholes (Fig. 3.3.1-2A). They are bounded by a desert with sparse vegetation on the west side, between them and a large alluvial fan at the base of Sierra San Marcos. A marsh borders the lakes on the east side. The two deepest lakes explored are about 100 m apart, 13 m deep, and have steep, often vertical to undercut sides.

The largest sinkhole, called Pozo Azul, is rounded, 13 m deep, and about 48 x 62 m in dia. (Figs. 3.3.1-2B, and 3.3.1-3). It is triangular in plan view, and irregularly funnel-shaped in profile, with a broad flat shallow shelf on one side, dropping off vertically to the bottom, and a more gradual slope on the other two sides. The water level is almost constant, rising about 0.5 m after heavy rains as a result of runoff from the surrounding desert floor. The lake is fed by spring vents located near or at the bottom. The water temperature at the surface varies seasonally from 19.9^{0} to 32^{0}C. Pozo Azul has an outflow stream which carries water toward the east side of the basin, and another surface channel which connects it with the other lake of similar morphometry. The sediment flooring the shallow areas is a pale gray carbonate mud, with dark golden patches of diatom mat. This carbonate mud overlies darker sulfate-rich muds. No measurable current could be detected in the lake. Macroscopic vegetation consists of a large variety of marsh plants, particularly Phragmites sp., sedges, rushes and the saltgrass Distichlis spicata (L.) Greene along the margins; and in the lake submerged Nymphaea leaves surround the stromatolites. Physico-chemical measurements of Pozo Azul are presented on Table 3.3.1-1).

3.3.2. Megascopic Features

The stromatolites that occur in the well-illuminated areas of Pozo Azul consist of individuals up to a meter tall and broad, frequently tapering downward to a narrower base (Fig. 3.3.2-1A,B,C,D). Dome-shaped forms, many of which resemble young campanulate mushrooms Fig. 3.3.2-1A,B), grow on the shady sides and bottom, and in stacks along the vertical walls (Fig. 3.3.2-1C). These have a "draped" appearance, when the sides grow outward without making direct contact with the substrate. Pendulous structures hang down from under overhanging ceiling. There are no emergent stromatolites, they appear to cease their upward growth when within about 20 cm of the water surface, while continuing to expand laterally. A shallow cluster of linked and stacked stromatolites is shown in Fig. 3.3.2-2 A,B. The stromatolites also form massive reef-like deposits (bioherms). The largest deposit covers an entire vertical wall from the surface of Pozo Azul to the bottom, and extends laterally for about 30 m. These large composite structures result when many individuals grow adjacent to and on top of each other.

Stromatolite growth in the shallow areas of Pozo Azul begins with the development of a thick diatom mat (Fig. 3.3.2-3A). A portion of diatom mat growing on the sediment surface becomes thick and encrusted with grains of calcite and various microorganisms. The mat increases in surface relief and swells to a crenulate shape as gases accumulate beneath. Filamentous cyanobacteria colonize the crenulate surface and mat cementation progresses to the extent of producing a hardened surface. This vertical component enhances the current-baffling effect, increasing the ability of the community to remove fine sediment from the water column. The third dimension of this structure becomes more pronounced, raising it from the surrounding sediment, as it thickens and grows into the characteristic rounded shape of the stromatolite (Fig. 3.3.2-3B). Material in all stages of this early growth have been collected at the same time from shallow marginal areas in water about a meter deep.

On a large scale, the stromatolites have an overall evenly-rounded bulbous shape; they are without irregular projections other than the occasional _Chara_ or _Utricularia_ plant. The surface texture is that of granular silt, and the color is yellowish gray. The surface pattern is produced by rounded, bulbous to cauliflower-shaped growths (Fig. 3.3.2-4A) that cap the surface of irregular or convolute, vertically oriented plates up to about 2 cm thick, constituting columnar structural elements (Fig. 3.3.2-4B). These columns are separated by deeply incised often narrow sinuous channels averaging about 1-2 cm deep (but occasionally extending as much as 5 cm into the interior of the structure, as shown in Fig. 3.3.2-4B. The result is a sinuously-incised pattern which in plan view is similar to that on the surface of a brain. The size of this pattern is variable from one stromatolite to another, but is rather constant over the surface of an individual. Some stromatolites have a fine pattern with surface features about 3-5 mm wide and channels about 2 mm wide. Others have a coarser pattern with surface features 1-2 cm wide and channels about 1 cm wide. In vertical profile, untreated fragments of the columns of some stromatolites show laminae about 7 mm apart, discernable as shallow cuspate projections of slightly more erosion resistant horizons (indicated by arrows on Fig. 3.3.2-4B). The stromatolites accumulate material rapidly at the surface but are slow to become cemented. The surface mat, to about 2-3 cm within the structure, is often friable and so delicate that it easily crumbles when touched. In sections cut parallel to growth the mat is poorly laminated, with different layers sometimes visible as different colored bands.

There are two morphologies found in the deep parts of Pozo Azul that are distinctive. Along the wall in the deeper part of Pozo Azul, thin, lithified, tabular structures up to a meter long and sometimes as broad, and 0.25-0.35 m thick, project outward and slightly upward from a horizontal plane. These structures have a surface texture which varies with the amount of light exposure. In contrast to the typical stromatolites, the framework of these stromatolites is one of a dense, solid pale to dark colored calcite, with many large (1-3 cm) elongate-oval holes passing completely through the stucture (Fig. 3.3.2-5). In sawn section, the surface mat is thin (about 1-2 mm) with indistinct banding, evident as subtle color changes, sometimes visible in the interior. Surrounding these deep structures is a light olive grey micritic marly ooze. Where there is very little light such as up under overhangs, a black uncalcified cyanobacterial mat may blanket the sediment surface (and the sediment under this mat may be very soft).

Another distinctive stromatolite facies grows on the outer vertical faces of walls, where light is low and indirect. These structures project from the wall on one or more short, cone-shaped bases or stalks which expand to a faintly laminated, irregular-shaped, shallow-concave, foliose top with curled-up edges resembling an ear or the jelly fungus Tremella (Fig. 3.3.2-6A,B). These stromatolites reach 10-20 cm in diameter, at the top. The surface of these auriculate growths is pale golden green, and rather smooth, with an incised surface pattern of tiny teeth marks made by grazing fish. The curled-up edges may result from an ongoing process called syneresis- "The spontaneous separation or throwing off of a liquid from or by a gel or flocculated colloidal suspension during aging, resulting in shrinkage..." (Bates and Jackson, 1980).

3.3.3. Community Architecture

The Pozo Azul stromatolites that occur in the well-illuminated areas of the lake are soft and friable for a depth of one to several cm. The open surface pattern allows light penetration, frequent exchange of pore water and ready egress for protozoans and other small grazers into the upper portion of the stromatolites. The mat surface is patchy in the distribution of different organisms, with colonies of filamentous cyanobacteria projecting from some areas and thick deposits of diatoms filling other areas. The living mat extends to a depth of about 5 mm. In the upper 0-1 mm, epiphytic diatoms, and detritus are attached to the as yet uncalcified sheaths of Dichothrix bonetiana Geitler (Fig. 3.3.3-1). Schizothrix lacustris predominates around the Dichothrix and at the upper surface on the less well-illuminated parts of the structures. Rhizoclonium sp., a chlorophyte, and the rhodophyte Chroodactylon ramosum (Thwaites) Hanse are locally conspicuous at the surface. From 1-3 mm carbonate grains and microorganisms are packed between calcified sheaths of living Dichothrix. In this layer the coccoid cyanobacterium Cyanostylon microcystoides is common, along with Nodularia sp., Merismopedia sp., Chroococcus sp., Schizothrix lacustris., Johannesbaptisia sp., Pleurocapsa minor, Spirulina sp., Tolypothrix sp., Chlorogloea sp, Hyella sp., Oscillatoria sp., and Gloeothece sp. The chlorophyte Gongrosira calcifera is also present at this level. Below 3 mm no more large filamentous cyanobacteria were found alive, but smaller filaments, particularly *Schizothrix*, coccoid forms and diatoms were abundant among the more densely packed grains. The diatom assemblage is diverse but clearly dominated by *Mastogloia* spp. *Brachysira* spp. and *Denticula elegans* Kutz.

The low-light concave foliose structures are colonized at the surface by *Schizothrix lacustris* and a larger *Schizothrix*, about 2-3 um wide, that forms pulvinate cushions. There are also abundant diatoms, particularly *Amphora katii* and *Epithemia argus*, and coccoid cyanobacteria, including an LPP form and endoliths. All of these organisms are embedded in a thick mucilage that is extremely difficult to disaggregate.

The tabular stromatolites from near the bottom of the lake contain mostly *Cyanostylon*, *Gongrosira* and diatoms. *Utricularia* sp. and *Beggiatoa* sp. form long filaments that sometimes drape over the surface of these stromatolites. Less well-lit surfaces are patchy in the distribution of organisms. Some areas are carpeted with a dense coating of *Cocconeis placentula* Ehr., others with gelatinous colonies of sponges. Beneath the surface community, dense populations of endolithic cyanobacteria color the structure pale green.

Common at the surface of well-illuminated stromatolites is the dinoflagellate *Peridinium inconspicuum* Lemm., and testate protozoans, including *Euglypha* sp. and *Quadrigula* sp. In live material protozoans including *Vorticella* sp., chytrids, *Euglena* sp., *Euglypha crenulata* Wailes, 1912, *Aspidisca* sp., *Bodo* sp., *Difflugia crassa* Cash, 1909 and other small flagellated protozoans were observed as well. Also present in live material were cladocerans, including *Alona* sp., rotifers, cyclopoid and harpacticoid copepods and their nauplii, nematodes, the oligocheate *Lumbriculus inconstans* Smith, the foraminiferan *Ammonia beccarrii* (d'Orbigny), and the glass shrimp *Palaemonetes suttkusi* Smalley 1964.

A cube about 1 cm on each side was removed July 6, 1986, from the surface of a typical stromatolite at about 1 m depth, and preserved in 5% formaldehyde. It contained 1 rotifer (*Monostyla* sp.), 1 cladoceran, 2 harpacticoid copepods (*Cletocamptus albuquerquensis* (Herrick) 1895)), 1 nematode, 1 oligocheate, 1 water mite

(*Diplodontus despiciens* (Muller), 1 ceratopogonid larva, 2 chironomid larvae, 70 ostracods, 1 elmid beetle larva, 11 amphipods (*Hyalella azteca*), and 15 snails (2 *Nymphophilus minckleyi* Taylor, 1 *N. acarinatus* Hershler, 6 *Mexistobia manantiali* Hershler, 2 *Mexipyrgus churinceanus* Taylor; and 4 *Durangonella coahuilae* Taylor).

A sample from the same area collected in January, 1987. contained a similar benthic assemblage, with the addition of elmid beetle larvae and adults. A comparable section from a stromatolite forming at a depth of 5 meters contained only 22 ostracods, representing at least 4 or 5 species. The benthos in the deep tabular stromatolites is restricted to sponges and an occasional ostracod or chironomid larva. A preserved cube about a cm on a side, cut from the concave foliose stromatolites in June, 1984, contained 1 rotifer, 7 ostracods, and 1 water mite (*Diplodontus despiciens*). The concave surface of these ear-like stromatolites shows evidence of heavy grazing by fish. Fish may also be responsible for keeping the clayey sediment from accumulating around the base of the stromatolites by creating small water currents.

At certain times the surface of some of the shallow stromatolites is completely covered by firmly attached, green gelatinous colonies of the ciliated peritrich protozoan Ophrydium versatile (O.F.M), the cells of which contain dense mutualistic internal algal populations, which appear to be chlorophytes. The globular colonies grow radially on the stromatolites in a hemispherical pattern, from a single small, calcified attachment point at the center of the colony. The Ophrydium cells are anchored by long stalks that pass into the interior. The interior consists of gel containing a diverse community of microorganisms, principly the diatoms Cymbella cesatii, Denticula elegans, Mastogloia spp., Brachysira vitrea; and the coccoid cyanobacterium Gloeothece. Ostracods and snails are also present. These mucilaginous spheres are finely laminated (perhaps daily) with calcite (Fig. 3.3.3-2). The hemispheres may become coated with a thick (up to 3-4 mm) layer of carbonate some of which remains on the stromatolites after degradation of the gelatinous material.

3.3.4. Fabric and Microstructure

The textural composition of the surface of the mat of the shallow stromatolites is determined by the detrital material that adheres to the surface of the stromatolites. This is composed of objects which are similar in size, and fall within the magnitude of about 0.1-1 mm. Most of this material is fecal pellets. Fecal pellets incorporated into the stromatolites range in size from 12.5-50 um in width and 400-875 um in length. There is a major textural distinction between fish feces which are tubular and loosely compacted, with flat, unconsolidated ends; and those pellets of crustacea and snails which are densely compacted, and smoothly rounded ovals with tapering ends. As the fecal pellets degrade, calcite crystals usually 3-15 um dia. are released. The remainder of the detrital component consists of sparry calcite, ostracods, snails, larger testate protozoans such as _Euglypha_, the diatom _Campylodiscus_ and the dinoflagellate _Peridinium inconspicuum_. Projecting through this detritus is new growth of _Dichothrix_, on which calcification first appears as thin rings or bands of micrite about 12 um wide, spaced about 15 um apart, encircling the sheath.

About 1 mm into the surface mat, the _Dichothrix_ sheaths are coated with clusters of loaf-shaped sparry calcite producing a calcite tube about three times as thick as the original sheath. Because of differences in size of the individual spar clusters, the surface of the tube is irregular in thickness. Patches of calcite precipitated by <u>Gongrosira</u> are conspicuously harder to the touch than the sparry tubes surrounding <u>Dichothrix</u>. In thin sections of the outer 2 cm of the surface mat, the tubes are oriented in growth position but incompletely cemented together. Incorporated into the interior of the stromatolite are diatoms, snails, ostracods and sponge spicules, but there is no evidence that the testate protozoans are preserved.

In some samples there are distinct laminae about 2 mm apart at the surface of the stromatolites. In plane transmitted light they consist of a tan porous surface lamina made up of a community of filamentous cyanobacteria and diatoms underlain by a thinner slightly paler and denser lamina characterized by a much greater proportion of carbonates and diatoms to cyanobacteria. This thin laminated pattern is sometimes repeated once or twice but these laminae cannot be distinguished in the interior of the stromatolites. Cementation takes place deeper into the stromatolite, where the tubes and interstices become infilled with sparry calcite cement. In this region, degraded filaments of *Dichothrix* sometimes remain in the calcite tubes. The resulting fabric comprising the interior of the stromatolites is a massive, hard, unlaminated, somewhat opaque sparry calcite.

The concave foliose stromatolites found in the deeper parts of the lakes are fragile to the touch as they consist of a mixture of mucilage and a relatively small amount of carbonate. When fresh they are composed of a groundmass of mucilage in which clusters of sparry calcite are embedded. In the interior of the structure clear crystals of micrite and spar are bound up with massive amounts of degraded fragments of mucilage, and well-preserved diatoms, particularly *Amphora katii*. These structures do not show obvious lamination beneath the color-banded surface mat, which is not surprising in an environment which must vary little from season to season. The carbonates do appear to be stacked in subtly discernable horizontal packets, however, suggesting a periodic shift in the amount of carbonate transported to the structures in comparison to the rate at which the gelatinous material is produced. Internal cements consist typically of spar about 20-30 um wide.

Tabular stromatolites from the deeper parts of the lake are hard and partially cemented with clear spar to within 1-2 mm of the surface. The irregular surface is covered with loosely aggregated anastomosing clusters of irregular-shaped zoned micrite crystals ranging from 2 - 10 um long, but generally 4-6 um long and slightly less wide. These crystals often have an opaque center that appears greenish to dark in plane transmitted light, with a clear rim. Colonies of *Cyanostylon* are often embedded in these clusters, along with the diatoms *Epithemia argus* and *Amphora katii*, LPP type cyanobacteria and *Gloeothece*. Within the porous sparry internal framework, pockets filled with uncemented fecal pellets are common.

3.4. Description of Type 4 Stromatolites: the Garabatal System

3.4.1. Habitat

The Garabatal System covers several square km, and consists of the contracted remnants of a once more extensive spring system on the west side of Sierra San Marcos. Old, dry, vegetated lake beds and eroded dunes border the modern marsh on the east side nearest the mountain. A complex facies mosaic of old and young karst and travertine features are distributed on the basin floor in association with the springs. The name "garabatal" means "scribbles", perhaps after surface features consisting of long, narrow sinuously-linear slit-like openings about 0.2 m wide in the ground that pirate some of the water into subterranean channels. This seasonal spring system is highly variable in the number and location of active springs and the rate of flow over the annual cycle as contrasted with the other systems in the basin. Some springs are small ill-defined seeps, others are spring boils. One stream is fed by a swift rheocrene (Fig. 3.4.1-1). As the water table drops, certain springs cease to flow and some of the streams and lakes dry up. One spring reverses itself and becomes a whirlpool (estival) at times, draining one of the lakes.

The springs feed a network of broad, shallow, hard floored stromatolite-filled streams about a half meter deep, which lead to a series of lakes sometimes connected by shallow streams. Many of the streams and lakes are only intermittently full, but most have stromatolites (Fig. 3.4.1-2A,B). The largest and topographically highest lake, Laguna Garabatal, is sometimes 30 m wide and 2 m deep (Fig. 3.4.1-3A,B) and other times completely dry (Fig. 3.4.1-4A,B). It has a sandy, mostly unvegetated bottom composed of snail shells and carbonate sand grains, and occasionally is covered with a microbial mat. Table 3.4.1-1 contains physico-chemical mesurements of the lake.

Spring water flowing from Laguna Garabatal travels along a shallow, somewhat confined, stream similar to the inflow stream with individual stromatolites, and enters a second lake that is very different in appearance although it is located only about 35 m away. Each wet season this flat-bottomed lake fills to almost a meter deep and about 40 m wide and 80 M long. Soon a dense growth of heavily mineralized Chara covers the bottom. When the lake dries up the chara disintegrates. Tan Chara muds with mud cracks up to a third of a meter deep characterize some areas of the lake. Individual and laterally-linked stromatolites rim the margins of this lake but do not develop on the Chara muds. This Chara lake is connected to a much smaller, deeper pool with a reversing spring in the bottom. The pool is sometimes floored with black, rich mud, Nymphaea plants and sedges, and other times scoured clean, funnel-shaped and several meters deeper.

At high water levels the flow spills out of the Chara lake onto a shallow marsh surface laced with anastomosing travertine dams about 25 cm tall and several meters long. This shallow flow leads into a terminal lake that is often dry but contains the remnants of older travertine ridges, terraces at different elevations, and stromatolites. Other nearby spring-fed streams, with springs in the bottom, and with no surface connection to each other or any other lake, are producing large numbers of stromatolites.

3.4.2. Megascopic Features

Hard, porous, internally laminated, turbinate, stratiform, bulbous, or nodular stromatolites cover most of the available space in the shallow streams, on many of the lake bottoms, and around the periphery of the larger lakes. Best development of tall (nearly a meter) stromatolites is along the north and west margins of Laguna Garabatal, in the areas of maximum current. They are flat-topped, laterially linked domes almost a meter tall and over a half meter wide (refer back to Figs. 3.4.1-3 A,B and 3.4.1-4A,B). The sides are slightly convex to straight with small hard rounded projections representing recent growth. They are sometimes undercut at their base where they may erode to a narrow support. Lake stromatolites develop on a substrate of silty carbonate sand. Stromatolites in the streams are attached to older lithified crusts.

The surface pattern typical of the Garabatal stromatolites, while submerged, consists of tightly packed rounded coalescent cushions about a cm in diameter (Fig. 3.4.2-1). The openings around these cushions produce narrow, vertical, discontinuous pores, up to a cm deep. The cause of these pores has not been determined. They could be related to features caused by escaping gases, as are observed in Italian travertines (R.L. Folk, pers. communication) or the structures may be maintained by the activities of metazoans, or there may be a combination of causes. These holes often become infilled with wind-borne detrital sediment each season after the water level receedes and growth ceases.

3.4.3. Community Architecture

As described in Winsborough and Golubić (1987) Garabatal stromatolites are covered by actively growing layers of microorganisms down to an average depth of about 10 mm. In cross-section, beneath a surface layer of diatomaceous material, laminae can be detected which were built by at least three different microbial communities that succeed each other in colonizing the surface of the stromatolites. Two of these communities, which produce alternating bands with horizontal and vertical fabric, are both built by cyanobacteria. The coarse vertically striated heavily calcified lamina is dominated by _Scytonema_ cf. _mirabile_ (Dillw.) Born. (Fig. 3.4.3-1), and the thin horizontally striated lamina consist primarily of _Schizothrix_ cf. _affinis_ Lemm. The filaments of _Scytonema_ cf. _mirabile_ are predominantly upright, falsely branched and slightly divergent, forming an upward convex layer. The filaments of _Schizothrix_ cf. _affinis_ are prostrate and intertwined. Coccoid cyanobacteria are occasionally observed on the growing layers. Diatoms are interspersed within all of these layers. Many are epiphytic on the upright projecting cyanobacterial sheaths, while others are found further into the mat, attached to or crawling actively on the carbonates. Under conditions of persistent submergence, in the deeper lakes, Gongrosira calcifera becomes a more important component of the community. It precipitates noticeably more dense carbonates in patches beneath the relatively more friable layers produced by the cyanobacteria. This sequence of layers produced by horizontally and vertically oriented cyanobacteria is periodically interrupted by the third type of layering, a pale gray, densely compacted lamina produced almost exclusively by stalk and gel secreting diatoms.

At the beginning of the wet season, the first organisms to appear on the surface of the dried stromatolites are coccoid cyanobacteria and diatoms, followed rapidly by Scytonema that forms small, discrete, rounded to cauliflower-shaped laminated colonies (Fig. 3.4.3.-2A) about 2-5 cm in dia. and 1-3 cm tall. In areas of rapid current these structures eventually coalesce through the development of a continuous mat that covers all submerged surfaces (Fig. 3.4.3-2B). Cementation is rapid and extensive, and the oriented lithified filaments clearly reveal the direction of current.

By the end of the "growing season" (which is episodic, rather than associated with a certain time of year) a thick accumulation of white, porous, thinly-laminated densely compacted, diatomaceous material, with a predominantly horizontal fabric, often covers the surface of the structures. This diatom assemblage is characterized by a dominance of *Amphora katii* Selva, *Nitzschia denticula* Grun., *Mastogloia smithii* Thwaites ex Wm. Smith, *Cymbella cistula* (Ehr.) Kirchn., *Brachysira vitrea* (Grun.) Ross., *Mastogloia smithii* var. *lacustris* Grun., *Denticula elegans* Kütz. and *Cymbella norvegica* Grun. Multiple laminae totalling up to 3 cm thick drape stromatolites in certain areas (Fig.3.4.3-3A). This material is composed almost entirely of calcite and diatoms with their extracellular products, and, from the top view, has the appearance of a thin, tenacious, many-layered papery coating (Fig. 3.4.3-3B). The upper surface of this material is covered by a dense layer of live diatom cells upon massive accumulations of gelatinous diatom envelopes and stalks (Fig.3.4.3-4). These diatoms are frequently aligned parallel to water current. Immediately below the surface of the diatomaceous laminae, diatoms are embedded in a porous fabric of polysaccharide sheaths, stalks, and envelopes. The gelatinous material degrades as dewatering occurs within the mat and coagulates into a fiberous mass. The result is a porous trabecular network. Additional papery layers with densely packed diatom frustules and degraded polysaccharide material have been detected in the interior, inactive part of the stromatolites indicating that diatom invasions have reoccurred periodically in the process of stromatolite growth and that they build contiguous laminae i.e. _bona fide_ stromatolitic structural elements.

In addition to this usual assemblage, a vagrant floral element is occasionally contributed to the stromatolite mass, in the following manner. The marsh is floored with loose organic floc which supports the growth of a luxurient ephemeral algal mat composed largely of diatoms and cyanobacteria. During times of rapid spring and seep flow, when marsh productivity is high, fragments of this mat are torn loose by the accumulated gas bubbles underneath, rise to the surface, and are carried by wind and water current to the streams where the sticky material adhers to the stromatolites. This provides an intermittant innoculant to the stromatolites, of a different composition than the predominant stromatolite community, interrupting the orderly development of continuous laminae.

A diverse assemblage of grazers is associated with the stromatolites. Those that are commonly incorporated in the calcified structure include testate protozoans (*Arcella* sp., *Euglypha* sp., *Quadrigula* sp., *Quadruella symmetrica* (Wallich, 1863)), the foraminiferan (*Ammonia beccarrii* (d'Orbigny)), harpacticoid copepods, ostracods, chironomids, water mites, and amphipods (*Hyalella* sp.). Snails are the most conspicuous grazers. They include *Mexistobia manantiali* Hershler, *Nymphophilus minckleyi* Taylor, *Nymphophilus acarinatus* Hershler, and *Eubora bella* Conrad. A sample about 1 cm^3, from the surface of a parially submerged stromatolite, collected June 12, 1984, contained 1 rotifer, 2 harpacticoid copepods, 16 ostracods, 2 chironomid larvae, 1 unidentified pupa, 4 nemerteans (*Prostoma* ?), 14 brown water mites, and 1 fish egg.

3.4.4. Fabric and Microstructure

In cross-section, the surface mat of the stromatolites shows a distinct microstratification (Fig. 3.4.4-1) caused by the superposition of well-defined layers separated by discontinuities. This reflects the rhythmic change in community structure of the active mat. The most abundant lamina, in the sections examined is that produced by Scytonema.

Calcium carbonate precipitates as calcite within the interstices of the polysaccharide network in all types of laminae studied. Within the diatomaceous layers the crystals are distributed as both micrite and microspar, often as clusters surrounding diatom stalks. These crystals have the same peculiar shapes and surface features (Fig. 3.4.4-2) such as curved edges and ragged faces as do those described from the other sites. In addition, calcite crystals of various sizes and fecal pellets are trapped on the surface of these laminae and become attached to the mat by the extracellular products produced by the diatoms. Within Scytonema layers, $CaCO_3$ precipitates around the sheaths of filaments forming closely-packed vertical tubes of laminated calcite up to 1 mm long (Fig. 3.4.4-3). Within Schizothrix layers $CaCO_3$ precipitates first as scattered micrite attached to the sheaths of the microorganisms. The calcite grains increase in size ultimately surrounding the Schizothrix filaments. Calcification increases gradually with increased distance from the stromatolite surface, and the laminae become progressively cemented with sparry calcite.

3.5. Results of Water Chemistry Analyses

The isolated desert basin of Cuatro Ciénegas encompasses an unusual range of aquatic environments. Over a hundred springs and seeps support streams, deep and shallow lakes, and evaporitic playas, and produce a broad suite of mineral precipitates. Samples for water chemistry analysis were collected, not only from the stromatolitic sites, but from as broad a chemical spectrum of aquatic habitats as could be found. The reason for this was to document the range of chemical concentrations in which the Cuatro Ciénegas stromatolites grow. Chemical analyses include the major dissolved cations and anions, nutrients, pH, and dissolved metals (Table 3.5-1). These samples were collected during a three-day period in July of 1983, and during June of 1984. The results of water chemistry analyses for the stromatolite sites discussed in the text are summarized on Table 3.5-2. Field measurements of other physical and chemical parameters also were made opportunistically over an 11 year period.

Two rock types dominate aquifers in the basin: carbonates and sulfates. Ground water in these aquifers therefore carries two characteristic chemical signatures. Waters that originate from calcitic and dolomitic rocks (sites to the north and south of the basin proper) have low sulfate concentrations, high alkalinities, and abundant calcium and magnesium. Waters that originate from rocks composed of gypsum or anhydrite (the majority of sites in the basin) have high sulfate concentrations, relatively low alkalinities, and abundant calcium. The reason for the high sulfate signature is that during lower Cretaceous time the Cuatro Ciénegas area was characterized by shallow coastal lagoons where calcium sulfate salts were deposited, between flooding events which deposited the muds which became the limestone and dolomite. These gypsum facies, alternating with limestone and dolomite, extend as far west as the Sierra San Marcos (Humphrey, 1956).

The stromatolitic lakes and streams at Cuatro

Cienegas are all very similar in their overall water chemistry. The cations are dominated by calcium, with lesser amounts of sodium, and magnesium, while the most abundant anions are sulfates, followed 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 Piper diagram of Cuatro Cienegas surface waters (Fig. 3.5-1) is a graphic illustration of the essential chemical character of the waters. As described by Piper (1944), in the lower triangular diagrams the percentage reacting values of the three cation-groups (Ca, Mg, Na) and the three anion groups (HO_3, SO_4, Cl) are each plotted as a single point according to conventional trilinear coordinates. These points indicate the relative concentrations of the several dissolved constituents of a natural water. They do not show absolute concentrations. The diamond-shaped field in the center shows the overall chemical character of the water by a third single-point plotting at the intersection of rays projected from the lower triangles. The concentration of points in the upper right hand corner indicates that the water type can be discriminated as having secondary (Ca and Mg) salinity (SO_4, Cl,, NO_3) (non-carbonate hardness) which exceeds 50 %, meaning that the alkaline earth cations exceed weak acids (CO_3, HCO_3) and are balanced by strong acids.

The water chemistry of the four stromatolite sites is depicted in absolute concentrations with a rose diagram (Fig. 3.5-2). It is immediately obvious that there is a lot more sulfate in these waters than any other ion. The four sites are very similar in the proportions and amounts of each of the ions, with the exception of alkalinity. El Mojarral has a lower total alkalinity than the other sites.

Once these waters reach the surface, or the near surface, they are concentrated by evaporation. Chloride concentrations are commonly used to gauge the relative amounts of evaporation because chloride is not incorporated in any precipitating minerals until the final stages of evaporation (Eugster and Jones, 1979). All the chemical species in solution become more concentrated as evaporation proceeds until the water is supersaturated with a given phase. Up to this point, there is a constant relationship between a dissolved species and chloride. Generally, calcite is the first mineral that precipitates during evaporative concentration. As evaporation proceeds, calcite will continue to precipitate and chemical species other than carbonate and calcium will become more concentrated. This process will continue until another phase becomes super-saturated or all the calcium or carbonate are removed.

Minerals in the basin's soils and sediments reflect the process of evaporative concentration. In many areas the ground is covered by carbonate crusts. Sediments in brackish lakes, such as Laguna Grande, are composed of gypsum needles, and there are active gypsum sand dunes nearby. Ground water below playas is still being concentrated by evaporation, and can precipitate minerals within playa sediments.

Water temperatures for springs within Cuatro Ciénegas basin are generally close to 30^{o}C with near neutral pH values. Sample CC-14, from a spring whose headwaters are located outside the basin to the north, has a significantly lower temperature (22.6 C) and is one of the least saline waters. Salinities of the springs and streams range between 0.45 and 1.52 ppt and increase as evaporation proceeds. Data from the analysis of the 20 sites listed in Table 3.5-1 are plotted in the following graphs.

An overall gauge of the quality of the chemical analyses presented in Table 3.5-1 is the charge balance calculated with the measured ionic compounds (Fig. 3.5-3). All but the most concentrated samples have a good charge balance. Calcium, magnesium, and sodium are the dominant cations and sulfate is the major anion. The dominance of the sulfate anion produces a relatively unusual water type, as carbonate is the dominant anion in most natural waters. In our water samples, carbonate is the dominant anion in only two samples, both of which are on the edge of the basin.

There is a linear relationship between sodium and chloride concentrations that spans four orders of magnitude (Fig.3.5-4). Sodium and chloride are not precipitated from solution until the final stages of evaporative concentration. This supports the use of chloride as an indicator of high evaporative concentration. Magnesium, sodium, and potassium display conservative behavior except in the most concentrated samples. In contrast, calcium is removed after relatively little concentration, most likely through the precipitation of calcite (Fig.3.5-5). Strontium and flouride show somewhat similar behavior. Strontium is probably incorporated into the precipitating carbonate. Flouride may be removed by flourite precipitation. The behavior of calcium and flouride diverge in the more concentrated samples. This is probably associated with the precipitation of gypsum. Sulfate concentrations diverge from a constant relationship with chloride at the same time calcium concentrations start to decrease dramatically.

At the 3 sites for which we have nitrate and phosphate data, nitrate values range between 5.6 and 6.8 mg/l, and phospate concentrations are 0.002 mg/l to 0.01 mg/l. These may be considered typical early summer nutrient conditions. What was actually measured was the seston fraction, which gives no information about the nutrient levels in the surface mats. Nitrogen is lost from the sediments in the form of N_2 produced during anaerobic decomposition of sediment organic matter, but the interstitial water in sediments usually has a much higher concentration of soluble nitrogen compounds than that of the overlying water and the phosphorous content of the sediments can be several orders of magnitude higher (Wetzel. 1975). Nitrate concentrations are high (50-100 uM) except at the two slightly brackish sites Laguna Grande and Hundido Descanso.

Phosphate appears to be a limiting nutrient in Cuatro Cinegas waters. There are several reasons why the water column values are low. There is inorganic adsorption of phosphate ions to colloidal and sedimenting particulate $CaCO_3$. These insoluble complexes, chelates and salts are coprecipitated with the calcite. Extremely calcareous, hardwater lakes represent a type of maintained oligotrophy in which high calcareous inputs are sustained over long periods of time and reduced productivity is maintained by decreased nutrient availability (Wetzel, 1975). The anomalously high phosphate value at Tierra Falsa, nearly a hundred times higher than all but one of the other sites, results from the nature of the sampling site itself. A hole was dug through black, viscous, sulfate-rich, tar-like sediment, directly beneath the surface of a dry river bed, and the water that filled the hole was used in the analysis. The other site in the basin which had a rather high phosphate value was Hundido Descanso, a small sinkhole lake which has been contaminated by human activity.

Silica concentrations are generally greater than 300 uM. All measured trace metal concentrations are generally less than 10 ppb except Pb in the sample from Hundido Descanzo, CC-17. CC-17 is adjacent to a heavily used dirt road and could be contaminated by the combustion products of leaded gas. Germanium has relatively high concentrations for natural waters and the Ge/Si are much higher than average background values (Froelich et al., 1985; Mortlock and Froelich, 1987), but do not approach concentrations that could inhibit diatom growth (Lewin, 1966).

From the above information, the four stromatolite sites may be described as oligohaline, with salinities of about 1.5 ppm, have total dissolved solids in the range of 2265-2498 mg/l, and are all warm, with a circumneutral pH. They are all fed directly or indirectly by springs located below the surface of the water.

3.6. Mineralogical Composition and Crystal Habit

The mineralogical composition of the stromatolites is the same throughout the study areas. All of the structures described are constructed of low magnesian calcite, in the form of micrite and sparry calcite. X-ray patterns of typical stromatolite material (Fig. 3.6-1) verify this. The magnesium/calcium ratio of the water was calculated for each of the four sites to determine whether magnesium calcite, aragonite or dolomite might be expected to precipitate in addition to calcite. The ratio was 1:2 in all cases, and with the low salinities and temperatures measured at each of the sites, calcite should be favored over aragonite (Folk, 1974, Folk and Land, 1975, Pursell, 1985). Dumbbell-shaped crystals that may be aragonite have been seen in material from Pozo Azul, but they are rare, possibly occurring in what may be an unstable crystal habit, under conditions of particularly rapid degassing.

In the stromatolites, calcite is precipitated around or bound to cyanobacterial sheaths, precipitated between the filaments of Gongrosira and attached (trapped and bound) to the mucilage of various groups of organisms. This produces a mineral in which the biogenic imprint of the microorganisms is often preserved in the shape of the crystal. The calcite occurs as individual crystals and aggregates of crystals. The micrite ranges from 1/2 um (minimicrite) to micrite about 5 or 6 um in diameter, the average being 2-4 um. Larger (5-6 um) crystals may represent neomorphic alteration of smaller micrite to microspar. "The modal size of microspar is about 5 um, representing a doubling of micrite grain diameter" (Folk, 1974). Further studies are necessary to determine if there is a temporally variable bimodal distribution of micrite and microspar in the stromatolites. The average length of a typical sparry calcite crystal, taking 20 random measurements, in situ, in the mat at El Mojarral, is 34 um, with a range of 20 to 50 um. These sizes are generally representative of the calcite examined at all the sites.

The calcite crystals in the stromatolites do not grow in the classic euhedral habit of pure calcium carbonate. They are often rounded to slightly rounded-elongate in shape with curved sides and pitted faces and edges, resembling the "gothic arch" and "edge-guttered" calcite described by Folk, Chafetz, and Tiezzi (1985). The cause of this deformation could be related to the interference of either the magnesium ion (Katz, 1973, Folk, 1974) or the sulfate ion (Folk, Chafetz, and Tiezzi, ibid) on the calcite crystal lattice.

Alternatively, the rounded edges and loafish shapes of the calcite crystals could be the result of dissolution of the calcite, as shown by Berner (1980) for calcite in sea water.

One source of detrital material to the stromatolites comes from micrite which precipitates in the water on calm mornings in many of the lakes, particularly Pozos Azules. These rapidly formed micrites are not sheets or hexagonal crystals with basal pinacoids as usually form under conditions of rapid lateral growth which occur in a stream or lake with low magnesium and sodium ion concentrations (Folk, 1974). Rather they are the typical slightly elongate, rounded micrites characteristic of those found on the stromatolites. These crystals rapidly sink and stick to the mucilaginous material being added to the surface of the stromatolites by the cyanobacteria and diatoms.

Gypsum grains are occasionally found in the residue when the samples are treated to remove calcite only. Gypsum is transported by the frequent winds in the valley, from old dunes and lake beds to the active stromatolite sites but x-ray analyses show that there are no more than minor traces in the stromatolites. Quartz appears in the insoluble residue as irregular-shaped grains and doubly-terminated crystals. The possible source of the quartz is discussed in section 3.1.4.3.

To determine if there was anything unusual about the surface sediments that might influence stromatolite development, a sample of the surface soil was collected near the Rio Mesquites and subjected to Atomic Adsorption Analysis. The results (Table 3.6-1) are compared to a suite of values for average soil. There are no unusually high concentrations of elements that could suggest an influence on the success of stromatolite-building organisms over other species in the lakes and streams.

3.7. Results of Physical Measurements

The physical (as well as geographic) parameters associated with the stromatolite sites include morphometry, depth, light, water temperature, water current and substrate nature. These characteristics are included in Table 3.7-1.

3.7.1. Depth

Of the three lake sites, in surface area Pozo Azul is the largest lake, followed by El Mojarral and Garabatal. Pozo Azul is 13 m deep, 8 m deeper than the other sites. El Mojarral is 5 m deep at the cave mouth but is much more shallow over the majority of the lake. Few places in the Rio Mesquites approach 3 m in depth but the vast majority of the stream is about 2 m deep.

3.7.2. Light

Measurements of spectral light distribution were made on a profile from bottom to top of Pozo Azul (0-13 m depth) in Nov. 1986 and May 1988. Results of these measurements were the same in both instances. Fig. 3.7.2-1 is a graph of the spectral composition as log % Surface Quantum Scalar Irradiance, or Photon Flux Fluence Rate for the 1986 data. The slopes represent the integral of photon flux radience (in the 400-700 nm waveband) at a point over all directions about the point. The filters, and the wave length at which they transmit light in distilled water, are blue (460 nm), green (510 nm), yellow (560 nm) and red (720 nm). The data are normalized to depth readings of 1 m (=100%) to avoid errors in determining surface irradiance at 0 m.

In Nov 86, the red light the most attenuated, followed by blue, yellow, and green. Attenuation includes the diminution of radient energy with depth, by both scattering and absorption mechanisms (Wetzel, 1975). If there was no scattering of light the theoretical plot would show red as the most attenuated, followed by yellow, green, and blue.

The color of the water is a blue-green. The blue visible at the surface is due to Rayleigh scatter (selective scattering below the surface by molecules smaller than the wavelength of light, in this case water molecules, leading to the attenuation of the blue component in downwelling radiation (Smith, 1982)); the color experienced by the deeper flora is, in fact, more green, as shown by the graph. A study of photosynthetic action spectra and adaptation to spectral light distribution in a benthic cyanobacterial mat showed that blue light (450 nm) was attenuated ten-fold more strongly than red light (600 nm) (Jorgensen, Cohen, and Des Marais, 1987). The photosynthetic responses of the stromatolite community at Cuatro Ciénegas reflect the broad light harvesting capabilities of the diatom carotenoids and chlorophyll as well as the efficient harvesting by the phycobilins of the cyanobacteria.

100% of surface upwelling quantum irradiance on an overcast day (9 Nov 86) was 185.5 uE m^2s^{-1}, and on a sunny day (10 Nov 86) was 1526 uEm^2s^{-1}. To compare this with the photosynthetic needs of diatoms, for example, "Gross photosynthetic rates of diatoms generally become light-limited at irradiance intensities in the range of 50 to 120 uEm^2s^{-1} PAR" (Harris, 1978). Parker and Simmons (1981) report on cyanobacterial stromatolites in Antarctic lakes growing non-heterotrophically on aprox. $1.0uEm^2s^{-1}$ PAR.

3.7.3. Temperature

Water temperature is almost constant and remains warm over the entire year at El Mojarral and the Rio Mesquites. It varies considerably over the annual cycle at Garabatal and Pozo Azul, although the actual temperature at the spring vents in the bottom pf Pozo Azul probably does not show as wide an excursion as the temperature does a short distance below the surface (where it is often measured). Divers report that in winter the water emerging from the springs at Pozo Azul is noticeably warmer than the temperature of the surrounding water column.

3.7.4. Water Current

There is considerable variation in the velocity and directionality of the water current in areas where stromatolitic structures are forming. The current is swift near the spring vents at El Mojarral West, producing a localized boil at the water surface directly above. Very coarse sand to granule size sediment accumulates on the shallow shelf area where the stromatolites form. Finer clay-size, light tan, sapropelic carbonate mud is transported to slack areas between the inflow spring and the outflow siphon at the other end. In this part of the lake colonies of the water lily Nymphea thrive, but there are no stromatolites. The same is true of the larger lake, El Mojarral East. The current is sufficient in the upper part of the lake to remove the fine sediment permitting the formation of microbial crusts and oncoids on the solid carbonate bottom. In the downflow side of the lake there is a thick accumulation of organic-rich muds, aquatic to marsh vegetation, and no stromatolites.

Prevailing winds from the north and east contribute to sediment transport, during episodic storm/wind driven currents.

The Rio Mesquites has always demonstrated an obvious and brisk flow along the deep, narrow stretch of the stream, decreasing in velocity at the lower part of its reach where it broadens to a slower-moving regime. This flow is sufficient to inhibit the accumulation of fine sediments except where an obstruction blocks the flow. In these areas, aquatic vegetation can take root and stabilize the sediment. Much of the channel is scoured clean and littered with oncolids.

In contrast to the Rio Mesquites, there is no obvious current flow in Pozo Azul. At times, a current can be seen at the spring vents in the bottom of the lake, but none could be measured at the surface. Suspended sediment and other particles rain directly down on the stromatolites. There must be some circulation however, as the carbonate mud floor of the lake is flat between the stromatolites. The material that is not trapped and bound to the structures does not form a talus slope around them so it must obviously be removed.

At Garabatal the current is swift (about 0.4 m/sec) when the water table is high and declines somewhat as the water level recedes. Streams are scoured clean of fine material. The structures in the shallow streams form over older lithified microbial crusts and buried or eroded stromatolites. The major accumulations of stromatolites are concentrated in areas where the current regime decreases, as in bends in the streams, the inflow streams at the lake margin, and on the other side of the lake where the water flows out of the lake. There always appears to be some water movement in the areas where stromatolites are forming. In the center of the lake, where the water gets stagnant there is no stromatolite development.

3.8. Results of Biological Analyses

3.8.1. Productivity Investigations

In order to determine the role of planktonic organisms in the water column, on the lake system, a light-dark bottle study at Pozo Azul, done under typical, clear weather conditions. Water from a third of a meter below the surface showed that little if any photosynthesis was taking place in the upper part of the water column, no measurable productivity could be detected in any of the 6 replicate samples. This was verified by examination of duplicate 1-liter phytoplankton samples collected at the same time as the productivity study. When these samples were concentrated to a small volume and the entire contents examined, there was almost no algae in the sample and the only organisms present were the dinoflagellate *Peridinium inconspicuum* and copepods (mostly harpacticoids). These data conform to the results of regular 1-liter phytoplankton samples collected regularly over a 10 year period. No planktonic diatoms or cyanobacteria other that the occasional coccoid form have been observed in the water column.

3.8.2. Colonization Experiments and Growth Estimates

Several marking techniques were attempted to detect stromatolite growth, with very limited success. The problems were both disappearance of the experiments (frequently by human vandalism) and inability to find the labeled horizon in the recovered material. Preliminary results from a labeled stromatolite in the Rio Mesquites show an estimated growth rate of 1-3 mm per year in the rapid current, about 1/3 m below the water surface. This was determined by marking a stromatolite (covered with a healthy active growth of Gongrosira) with synthetic graphite and collecting a 10x15 cm piece with a sledge hammer a year later. Under the dissecting microscope a faint gray trace of the graphite could be detected in various places over the piece, at between 1 and 3 mm below the surface.

At Garabatal, on the other hand, it is not uncommon for a colony of Filamentous cyanobacteria 2 cm thick to grow on the hard crusty carbonate substrate in a matter of a few months. The Scytonema colonies shown in Fig. 3.4.2-3 B were not present three months before that picture was made, and rang when hit with a hammer at the time the photo was taken. The calcified sheaths were already well cemented.

Short term colonization was studied at El Mojarral using a Catherwood Diatometer fitted with standard glass microscope slides. Colonies of the adnate diatom species Achnanthes and Cocconeis had become established on the glass surface in two days. There was no evident bacterial coating on the slides, but a thin crust of calcite could be found in a few places on the slides.

Natural and man-made substrates, (cans and bottles) were examined as well, and showed the same general patterns. The diatoms on the surface were joined by coccoid cyanobacteria and other material, by the time a mucilaginous layer was deposited.

Diatoms are also the first group of species found in newly formed surface mats at Pozo Azul. With the possible exception of bacteria, which were observed in all samples in small numbers, diatoms were the first organisms to colonize a fresh surface. This was the case in every sample examined (over 50 samples) of fresh mat material collected from the mud surface in the shallow areas of Pozo Azul. In addition to diatoms, coccoid cyanobacteria such as _Merismopedia_ and _Gloeothece_ were also present in small numbers. Filamentous cyanobacteria colonize the mat when a firm substrate becomes established, and epiphytic diatoms coat the surface of the cyanobacteria providing a gelatinous, irregular projection into the water column to further trap carbonates and other particles.

At Garabatal coccoid cyanobacteria and diatoms are the first organisms evident on the dry surface of the previous season. The organisms that can go into a dormant stage while the lakes are dry, and resume growth when rewetted would have the advantage over those species which are re-inoculated on the stromatolite surface. The timing of rewetting events with respect to overall seasonality of individual organisms may play a role in determining which organisms are involved in the initial colonization process, although the evolution to a stable community (and the production of laminae) once a mat has become established follows a predictable sequence of changes in community architecture.

In order to investigate long-term stromatolite colonization, hemispherical samplers 4 cm in diameter, with a surface area of 25.13 cm^2 were made out of neat cement poured into a latex mold. These hemispheres were equipped with square plastic supports which held them rigidly into a base, in sets of 2 and 4 hemispheres per base (Fig. 3.8.2-1A). Six of the artificial substrates (three bases with 2 hemispheres and three with 4 hemispheres) were placed in selected areas in Bano Escobedo (Fig. 3.8.2-1B), a spring pool with stromatolites and oncoids of the same type as El Mojarral. This lake, located a few km south of El

Mojarral, was selected for the study because it is much more isolated that El Mojarral and not as often visited and disturbed by people, but has very similar physical and chemical parameters and produces type 1 stromatolites. The lake has a surface area of 854 m^2, depth of 4.6 m and a discharge rate of about 0.03 m^3/sec. It contains spring boils in the bottom and has an outflow canal about 1 1/2 m wide and up to 0.45 m deep. Table 3.8.2-1 is a summary of the environmental characteristics of Escobedo, The water chemistry information can be found on Table 3.5-1.

A portion of the hemispheres from each of the artificial samplers were recovered after 2, 5, and 15 months. In areas where there was a well-defined current, a distinct terraced growth pattern composed of radiating colonies of _Homoeothrix_ _balearica_ was evident by 5 months (Fig. 3.8.2-2 A,B) and well developed calcified terraces 2-4 mm thick were present by 15 months. Figure 3.8.2-3 A, is a sampler which has been in the water for 15 months, and clearly shows the terraced pattern on both the hemispherical surface and the flat base as well. Figure 3.8.2-3 B is a natural crust, photographed in situ, from the same area of Escobedo in which the artificial substrates were incubated.

Results of the artificial stromatolite study at Escobedo provide some information about the rate and pattern of colonization under conditions of unidirectional, moderate current. They show that colonization is rapid and follows a predictable pattern which leads to development of a stable community architecture whose growth habit is expressed in the form of regularly spaced microterraces. The species involved include the filamentous cyanobacteria *Dichothrix*, *Schizothrix*, and an unidentified rivulariacean. Diatoms are dominated by *Cymbella cesatii*, *C. norvegica*, *Nitzschia denticula*, *Achnanthes affinis*, and *Anomoeoneis serians*. There were no chlorophytes and very few animals (no snails). In one, whole, 5-month old hemisphere sample no chironomids, amphipods, isopods or ostracods could be found, only protozoans and nematodes. In a 15 month old sample there were a few chironomids and small animals such as amphipods and protozoans, but the animal population was depauperate in comparison to a natural, mature mat.

A mat thickness of up to 4 mm was measured on the hemispheres after 15 months. It is important to note that the rate of colonization on artificial surfaces, prior to the development of thick stromatolitic crusts, is probably retarded in comparison to the rate of colonization over a previous lamina on a natural stromatolite. This is because of the difference in porosity of the artificial substrate. The neat cement does not permit the circulation of pore water through the artificial structure that might take place in a natural substrate. Hence the rate of carbonate encrustation on cyanobacteria and internal cementation is probably slower. Another aspect of colonization on artificial substrates that may be different from natural substrates is the size and diversity of the animal community.

Some of the artificial structures in Bano Escobedo were set out in fish exclusion cages covered with plastic screen which drastically reduced the current, and light as algae grew on the screen. These hemispheres were heavily colonized by microorganisms but in a uniformly dense fashion, and with very little calcification. They exibited no evidence of the formation of microterraces. Rather they resemble the cyanobacterial mats which form just below the surface of the water along the margin of the lake. These mats also do not show evidence of calcification.

Cans and bottles found in the water at Escobedo were also examined for colonization patterns. A glass bottle with a 1-2 mm layer of growth showed the same terraced pattern as the natural substrates. The bottle had a thin coating of calcite on which was a layer of diatoms and cyanobactria (Scytonema and Schizothriz?). The diatoms were dominated almost exclusively by Epithemia, a large adnate form also common on the hard surface of the El Mojarral oncolites. The characteristic terraced pattern also develops on cans.

Artificial substrates were set out in Pozo Azul from May to November, 1988. The survivors were recovered earlier than planned (after six months) due to problems with theft. By this time a microbial mat between 1 and 3 mm thick, with an irregular surface had developed (Fig. 3.8.2-4). The material consisted of carbonate grains, mostly 3-15 um in dia., and fecal pellets. Diatoms were abundant on each grain of calcite. Brachysira serians was by far the dominant diatom, with occasional cells of B. vitrea, Nitzschis denticula, Denticula elegans, and Cymbella microcephala. Filaments of Dichothrix were occasionally present, as well as as tiny Schizothrix and an unidentified rivulariacean. Gongrosira was found growing beneath the cyanobacteria. The Dichothrix, covered with a thick coating of particles, protrude occasionally above the surface. Small protozoans, nematodes and chironomids were observed in freshly preserved material. Ten chironomid larvae occupied one typical hemisphere, mainly beneath the hemispheres on the surface of the support base, where there was a gap providing room for their cases.

Chapter 4. DISCUSSION

4.1. Lamination

4.1.1. Concepts of Lamination

The term stromatolith (Kalkowsky, 1908) was originally used to describe laminated fresh water stromatolites. Lamination may be a primary depositional feature (the instantaneous biological stratification of Monty (1976)) or a product of early diagenesis. In the geological sense, a lamina is the product of all the biological, mineralogical, diagenetic, geochemical, and tectonic processes to which the deposit has been subjected. Monty (1973) calls this "historical biomineralogical stratification". It is generally agreed that with respect to stromatolites, a lamina is the smallest unit of layering (Walter, 1976).

Monty (1976) in detailing the origin of layered cryptalgal fabrics describes a number of biological, geochemical, physical, and sedimentological factors to account for the development of lamination. These features include phototactic responses, an alternating growth pattern of the component organisms, periodic differentiation of an algal assemblage leading to an alternation of dominant algae, internal growth, periodic calcification, precipitation of crystals with different habits, periodic enrichment in various chemicals, periodic influx of detrital particles, and periodic inorganic cementation. A shift in the surface mat community architecture may be caused in turn by changes in such things as nutrient input or other chemical parameter, current velocity, degree of submergence; or by a biological response such as seasonality, a shift in grazing pressures, or different blooming conditions. Aitken (1967) proposed the term "thrombolitic" fabric for microbial structures "lacking lamination and characterized by a macroscopic clotted fabric"... which "consists of centimeter-sized patches or clots of microcrystalline limestone (grain size 8-20 microns)...". The diagnostic features of a thrombolite sensu Kennard and James (1986) are the lack of trapped and bound detrital particles and the presence of the mesoclot or mesoscopic constituent as opposed to the submillimeter-size clotted pelletal microstructures. Monty (1976) expanded the thrombolite definition of Aitken (1967), to include those non-laminated structures produced in a variety of ways including those built by botryoidal or radial colonies of filamentous cyanobacteria (often mixed with diatoms).

4.1.2. Nature of Cuatro Ciénegas Lamination

At three of the sites at Cuatro Cienegas an obviously layered fabric is produced which reflects what appears to be stable, steady-state growth with little change in community architecture until a change or discontinuity occurs. A lamina is "the thinnest recognizable unit layer of original deposition in a sediment or sedimentary rock differing from other layers in color, composition, or particle size", and is "less than 1 cm in thickness, (commonly 0.05 - 1 mm)" (Bates and Jackson, 1980). The layering in Cuatro Ciénegas structures generally conforms to these size limits, with the exception of occasionally rapid cyanobacterial growth and concomitant lithification at Garabatal, which deposits a layer 2-3 cm thick, in less than a season.

At El Mojarral the stromatolites and oncoids contain laminae that are composed of an alternation of erect and prostrate cyanobacteria producing one type of lamina and carbonate-rich deposition responsible for the other lamina (repetitive lamination of Monty (1976)). 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_ (in place of _Homoeothrix_), 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. Another good example of such a succession has been nicely 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). El Mojarral coated pebbles that develop into irregularly-rounded oncoids are also similar to those described by Weiss (1970) for oncoids forming around _Goniobasis_ snails. The recurrent theme is the vertical growth of long, thick cyanobacterial filaments through a felt of thinner ones.

Abundant evidence for the existence of calcifying bacteria and cyanobacteria in cave environments (Danielli and Edington, 1983, and Jones and Motyka, 1987) suggests that a bacterial or cyanobacterial mechanism could be involved in the deposition of the iron- and manganese-rich laminae in the El Mojarral cave. Other examples of biogenic deposition producing clusters of grains resembling the El Mojarral cave deposit are Folk and Chafetz (1983) who describe bacterial pisolites in stream oncoids, that have a calcite grain morphology similar to the cave stromatolites; and Chafetz and Folk (1984) who report on a similar fabric produced by bacterial clumps in travertine.

Fossil palustrine deposits that resemble the lamination pattern of El Mojarral stromatolites and oncoids include the Paleogene non-marine algal deposits of the Ebro Basin in Northeastern Spain (Anadón and Zamarreño, 1981). The oncoids and algal crusts on which they report contain radially growing calcified filaments periodically pervaded by concentrically disposed micrite films or disrupted by the invasion of chironomid larvae. 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 deposits of Valencia, in Eastern Spain (Monty and Mas, 1981). These fossils were built by the superposition of spongious loose laminae produced by populations of a carbonate-coated filamentous cyanobacterium, separated by micritic rinds.

At the Rio Mesquites, layering is discontinuous over the whole structure, as it is associated with each of the individual digitate projections containing living Gongrosira colonies. The layers appear to represent rhythmic variations in the quantity of Gongrosira filaments in proportion to the quantity of sediment deposited (simple repetitive lamination). Pentecost (1988) suggests that the ill-defined concentric laminations in Rio Mesquites may have resulted from periodic changes in the suspended load. The Rio Mesquites pattern or fabric of growth may be better considered as a lenticular laminoid fabric, one that does not show laminae, but the presence of well aligned structural features which tend to outline an overall layering. This fabric is due to "an irregular juxtaposition and superposition of algal cushions or mats much smaller than the width of the stromatoid" (Monty, 1976).

Stream oncoids with a calcite grain morphology similar to the Rio Mesquites, constructed by Gongrosira, Homoeothrix, and Phormidium were described by Roddy (1915) and later by Golubić and Fischer (1975) from Little Conestoga Creek in Pennsylvania. Minckley (1963) described a calcareous encrusting community from Doe Run, a stream in Kentucky, consisting of Gongrosira, Phormidium, Schizothrix, and diatoms.

At Pozo Azul a fabric with biological layering at the surface and a non-layered interior is produced. In the Pozo Azul surface mat, sometimes there are two distinct laminae about 2 mm apart. They consist of a tan porous surface lamina underlain by a slightly paler and more dense lamina characterized by a much greater proportion of carbonates and diatoms to cyanobacteria. This thin laminated pattern is sometimes repeated once or twice but these laminae are not distinguished in the cemented interior of the structures.

The upright, anastomosing to digitate columns which are the primary constructional material of the stromatolites sometimes contain subtle macroscopically visible bands, about 7 mm apart, produced by variations in the density of the carbonate within the columnar elements. These are not visible in thin section. The columnar elements consist of bundles of upright to radially oriented, cemented, hollow tubes of calcite that show no lamination. These columns become cemented by percolation of carbonate-saturated pore water through the chambers between them. The result is an unlaminated fabric built by knobby projecting colonies separating irregular debris-filled internal cavities, perhaps similar to that described by Monty (1976) from the Hoyoux River in Belgium.

The definition of Kennard and James (1986) corresponds morphologically to the stromatolites at Pozo Azul, but the infilling between the lithified columns is not necessarily a primary feature, and whereas Kennard and James interpret thrombolites as being poorly differentiated coccoid-dominated microbial communities, the Pozo Azul stromatolitic communities are dominated by filamentous rather than coccoid cyanobacteria. The definition of a thrombolite sensu Monty (1976) is tentatively appled to the Pozo Azul stromatolites.

Garabatal laminae are composed of different sets of organisms which alternate, depending on particular environmental conditions that may be acting alone or in concert to produce a shift in the predominant species Cyclothemic lamination is the succession of at least 3 different laminae which always appear in the same order (Monty, 1976). This term may apply to Garabatal stromatolites, or they may be called composite alternating lamination, the alternation of two types of layers, one or the two of which contain a second order lamination (Monty, ibid). Filaments of _Scytonema_ cf _mirabile_ are predominantly upright, falsely branched and slightly divergent, forming a coarse, vertically striated layer, whereas filaments of _Schizothrix_ cf _affinis_ are prostrate and intertwined, producing a thin horizontally striated lamina. Under certain environmental conditions thick layers of diatomaceous material are produced as well.

At the beginning of the wet season at Garabatal, what appears to be pure colonies of rapidly calcifying _Scytonema_ encrust the dry stromatolite surface. Black (1933) observed that with salinities between 1 and 10 ppt there tends to be an alternation between Scytonema and the Schizothrix-Aphanocapsa association, and where the salt content of the water is appreciably less than 1 ppt flourishing colonies of pure Scytonema were found, with the filaments assuming a radial arrangement and depositing a finely crystalline cement of calcium carbonate between the filaments.

The lamination pattern and cyanobacterial association at Garabatal is very similar to the Fresh Creek stromatolites described by Monty (1965, 1967, 1976). The habitat at Fresh Creek may be similar to Garabatal, as the organisms there represent a Scytonema-Schizothrix calcicola association, not unlike Garabatal.

Deposition of concentric layers on stromatolites and oncoids is usually ascribed to a seasonal rhythm with timing related to the degree of calcite saturation (see discussion in Jones and Wilkinson, 1978). If the degree of calcite supersaturation plays a role in determining the nature of the laminae at the Cuatro Ciénegas sites, consideration must be given to the possibility that episodic rains that produce freshening events in the lakes and streams may regulate laminar morphology by diluting the ionic strength of the water. This could result in limiting calcite accretion to biogenic precipitation by a calcifying cyanobacterium or alga, until the saturation coefficient again becomes high enough for physico-chemical precipitation.

4.2. Stromatolite Diagenesis

4.2.1. Physico-Chemical Characteristics of Diagenesis

Stromatolite formation at Cuatro Ciénegas includes two components. Anabolic metabolism (those processes that lead to the synthesis of protoplasm and hard parts from simpler molecules) (Brock et al, 1984), and diagenetic processes. Early diagenesis is "the sum total of processes that bring about changes in a sediment or sedimentary rock subsequent to deposition in water" Berner (1980). These include the physical and biological processes of compaction, burial, diffusion, bioturbation and transfer across the sediment-water interface. They also include the chemical processes of equilibrium (rapid adsorption and ion exchange), bacterial decomposition, homogeneous reactions, and dissolution and precipitation of carbonates and other minerals. Weathering is a separate process although in instances of periodic subaerial exposure, as at Garabatal, it is intimately associated with early diagenesis. Many of the processes relevant to the production of the "final" three-dimensional stromatolitic structure are clearly processes of early diagenesis. The diagenetic processes of compaction, burial, diffusion, and chemical reactions including catabolic microbial reactions are described and discussed in terms of their relationship to the Cuatro Ciénegas stromatolites.

4.2.1.1. Compaction

Compaction (loss of water due to compression of overlying sediments) during early diagenesis entails the closer packing together of solid particles. This is evident in the upper few millimeters of the mats at El Mojarral where surface particles are rapidly packed into discrete laminae. Measurements of lamina thickness with increasing distance into the structure show little compaction below the top few millimeters. At the Rio Mesquites there is little evidence of compaction. At Pozo Azul the calcified filaments retain their growth orientation but detrital material becomes densely packed between the filaments. At Garabatal the compaction is differential, determined no doubt by the integrity of the predominant organisms and the amount of mucilage accumulated in the stromatolites. The extent of synsedimentary substrate modification that takes place near the interface between the living microbial mat and the lithified interior of the structure shortly after deposition is crucial to the type of structure ultimately produced.

4.2.1.2. Burial and Diffusion

Burial refers to depositional or accretionary rate, which in our case is probably non-constant, as "growth more often occurs in spurts, when substrate becomes available, followed by an extended stationary phase after the substrate is used up (Brock *et al*., 1984). Further evidence of a non-constant accretionary rate is the alternation of thick organic-rich and thin carbonate-rich laminae. It also refers to depositional burial, a process fundamental to the preservation of stromatolites for long periods of geological time. Incorporation of stromatolites into a sedimentary bed produces a new phase of diagenetic activity. The depositional and ground water conditions at that time determine the nature of further processes.

"Diffusion", as used here (and in stromatolite literature generally) actually includes molecular diffusion, dispersion, wave and current stirring, and bioturbation. The major process of benthic boundary diffusion is bioturbation, the process by which sediments are mixed by benthic organisms (Berner, 1980). Snails crawl through the sediment, and worms burrow into it, digesting some particles. Organisms that live in their burrows may flush them by irrigating with overlying water, enhancing the exchange between pore water and overlying water. These burrows are evident in the stromatolites of all the Cuatro Ciénegas sites. Bioturbation is a factor affecting initial porosity; the construction and constant irrigation of burrows results in a higher water content of the sediments than would occur without the benthos (Berner, ibid). It probably increases the oxygen content as well.

Deposit feeding organisms and others produce fecal pellets with organic coatings that degrade and result in chemical changes immediately surrounding the pellets (Berner, ibid). Results of these chemical reactions are reflected in different styles of rim cements surrounding the fecal pellets in a thin section from an El Mojarral stromatolite (see fig. 3.1.3.3-1B,C). As Berner points out, diagenetic chemical reactions that occur close enough to the sediment-water interface set up sharp concentration gradients in the overlying water resulting in transfer by diffusion and advection of dissolved chemical species between the sediment and the overlying water.

4.2.1.3. Chemical Reactions and Processes

Chemical processes are the driving force for most diagenetic change in sediments and include equilibrium processes, catabolic microbial reactions, precipitation and dissolution (Berner, 1980). The behavior of the interstitial waters of a stromatolite can radically affect the mineralization processes and bring about formation or destruction of specific minerals. Changes in porewater chemistry to a less saline condition, such as may occur at Garabatal when the dry lakes fill up seasonally with fresher water than was present at the end of the previous season, can bring about internal dissolution of calcite, whereas when the surface-water becomes more saline than the porewater, dissolved chemicals in the surface-water may diffuse into the porewater of the structure and increase cementation. More drastic evaporation of the surface water can directly alter the porewater by evaporative pumping, as takes place in a playa lake (Torgersen et al., 1986). By the end of the growing season, the surfaces of Garabatal stromatolites are often capped by a layer composed primarily of diatoms. As this layer loses water it shrinks and cracks. By the end of a particularly harsh dry season small sections and flakes may be all that is left of the diatom mat. Syneresis cracks, sometimes attributed to spontaneous dehydration of certain clays, are generally thought to be characteristic also of gel-like material. Such cracks as these occur for example in sediments of the Gavish Sabkha in the hydroplastic layers composed of extracellular polysaccharides (Gerdes and Krumbein, 1985). Dissolution patterns associated with these interruptions allow rainwater to enter the structure enhancing internal dissolution.

Mineral precipitation includes the stages of nucleation and crystal growth. After the critical nucleus has formed, crystal growth occurs principally by rate controlling mechanisms of transport of ions (atoms, molecules) to the surface of a crystal, and various surface reactions that result in incorporation of ions into the crystal lattice (Berner, 1980). At high supersaturation rapid precipitation by rapid nucleation results in formation of very fine-grained precipitates whereas slow nucleation results in fewer and larger crystals.

The relative roles of transport and surface-reaction controlled crystal growth are important in the nature of the stromatolitic structure produced. In transport controlled growth, rapid attachment of ions to the surface of a crystal lowers the concentration of the solution immediately adjacent to the crystal to equilibrium or saturation level, thereby limiting growth to the rate at which additional ions can migrate to the surface via diffusion and advection (Berner, ibid). Berner notes that under these conditions faster growth results from increased flow velocities. He also points out that "crystal growth via transport-controlled kinetics for a given substance should always be faster than via surface-reaction control". In the Rio Mesquites, a rapid, uniform, current creates a situation where transport controlled growth may be the overriding mechanism in the formation of stromatolites. This is in contrast to a stagnant water situation such as at Pozo Azul where transport-controlled growth is slowest, because most of the transport of material to the surface of a growing crystal must occur via molecular diffusion (Berner, ibid) and animal irrigation. The thickness of the boundary layer, which should be greater in the still water of Pozo Azul, may therefore be important in the nature of the different fabrics produced by the different stromatolite types.

Experimental studies of calcite dissolution under different pH conditions (Nancollas *et al*., 1983) have suggested that both surface and mass transport are important in controlling the rate, such that at lower pH values the dissolution mechanism depends on the formation of carbon dioxide (determined by total alkalinity) and mass transport of ions from the calcite interface; whereas at higher pH values, surface control processes may be important. Water alkalinity also affects uptake rate of CO_2, across a lake's surface from the atmosphere, as it influences the degree to which chemical reactions (in addition to diffusion) may operate (Emerson, 1975).

In the case of surface-reaction controlled growth, rate is limited by the rate of surface reactions, not flow, and depends on the slowest or rate-controlling step at the surface. Berner postulates that one mechanism by which surface nucleation may take place is growth at intersections of atomic-sized displacements along the axis of a row of atoms, and calls it "growth at intersections of screw dislocations with the surface of the crystal or dislocation-controlled growth". If the presence of large amounts of the Mg^{++} or SO_4^{--} ions causes the wrong ion to substitute for Ca^{++} or CO_3^{--} in the lattice, increasing the number of dislocations, this may be an additional mechanism for increased carbonate precipitation if calcite growth is enhanced by these crystal surface deformities.

By the above mechanisms, due to differences in pore-water chemistry (especially pH), carbonates are either being dissolved or precipitated within the interior of stromatolites while the surface mat (synoptic profile) is adding fresh material. The result of these processes can be chemical phase-separations causing lithologic alterations which may either destroy or produce lamination. Beiersdorf and Knitter (1986), for example, describe five examples from the geologic record in which diagenetic processes of dissolution, re-precipitation, and compaction in organic-rich limestone-marl-clay sequences have produced lamination.

4.2.1.4. Microbial Diagenesis

Microbial (metabolic) diagenetic chemical reactions are catabolic reactions mediated by microorganisms and include those dissimilation processes which involve breakdown of already synthesized organic molecules to simpler molecules or inorganic processes, as opposed to anabolic processes. According to Berner (1980) "the overall net result of diagenesis is the destruction of organic compounds". In sediments buried deeper than 10-20cm, bacteria account for a major portion of the turnover of chemical compounds due to the large surface area exposed to the sediments per unit mass of protoplasm (Berner, ibid). In the example of stromatolites cyanobacteria and diatoms assume a more significant role in diagenetic reactions taking place at the mat surface and the bacteria, especially those that reduce sulfate to sulfide, become more important in the anoxic zone beneath.

Microelectrode studies show that these dissimilation or decomposition processes follow a definite succession, depending on the nature of the energy source. Aerobic decomposition, using dissolved oxygen as the electron donor is followed by nitrate reduction (when the oxygen concentration is less that about 5%), then by anaerobic processes using the oxygen in iron and manganese oxides, sulfates, and organic matter as an energy source (Berner, 1980). This succession of reactions is explained in terms of metabolic free energy yield, each reaction succeeding the previous one in the order of their free energy yield, as each oxidizing agent is successively exhausted (with a consistant decrease in energy yield). The ultimate result of these processes is the establishment of an architecture to the stromatolite mat, in which each class of organisms has a specific position and role.

4.3. Colonization and Succession in Relation to Substrate Modification

4.3.1. Colonization

Colonization has been discussed in terms of the initiation of mat growth at Pozo Azul and on artificial substrates. With the exception of Garabatal there is no obvious cessation of stromatolite growth from one year to the next. At Garabatal transport of innoculant to the stromatolites by various methods of dispersal could play a role in colonization at the beginning of the growing season. Aerial transport studies have shown (Maguire, 1963, Schlichting, 1969) that captured species include aquatic and soil algae, protozoans, and the occasional rotifer. Schlichting provides a list of 187 taxa of viable airborne algae and protozoa reported from different parts of the world. The list includes 76 chlorophytes, 55 cyanophytes, 7 chrysophytes, 14 diatoms and 35 protozoans. Schlichting further noted that airborne algae were most abundant and diverse in dry dusty air (8 algal cells and 3 protozoans per 0.3 m^3). Thus airborn dispersal could be a mechanism regulating colonization at Garabatal.

Beginning with Charles Darwin (1859), investigators have demonstrated that waterfowl are also important in the dispersal of aquatic microbes. Not only are organisms transported on plumage, feet, and bills, but also internally in fecal material and gullets

(Schlichting, 1960). Atkinson (1972) demonstrated that several species of benthic diatoms were viable after passing through the gut of ducks and other wildfowl. Aquatic fauna such as fish and turtles are also vectors but an obvious source of inoculant to the stromatolites is direct flow in the ground water from one lake to another, sheet-flow from the marsh during high water, and current drift within lakes and streams. In spite of the facility of inoculation by the above mechanisms immigration through casual dispersal probably does not determine the composition of a stromatolite mat as each stromatolite site is inhabited by its own unique set of organisms from one year to the next.

Immigration may be an important process in benthic diatom colonization and succession, with rapid colonizers that are not competitive in the low resource environment of high-density benthic mats replaced by shade-tolerant species that can efficiently sequester nutrients when nutrients are in low concentrations (Stevenson and Peterson, 1989). In terms of r- and K-selection (Pianka, 1970), there is thus a rapid shift during the beginning of a new layer on a stromatolite, from r (early colonizers) to K type plants (efficient competitors).

4.3.2. Succession

There is usually a constant pattern of growth within a lamina, with one or a pair of filamentous cyanobacteria persisting for almost the entire thickness of the layer. This persistence of a continuous community between laminae implies that the succession time from colonization on the surface of a lamina to growth of a stable and persistent community structure within that lamina was relatively rapid, as were the physical changes in the microhabitat which accompany biological growth and change. Although these changes are rapid in comparison to terrestrial succession, they probably represent a corresponding order of magnitude of time to the relationship between the longevity of an individual and the successional shifts in populations observed in classic terrestrial succession. "A plant community which takes over a site and reproduces there, maintaining dominance and successfully resisting invasion so long as environmental conditions remain substantially unmodified, has fulfilled the conditions for a climax community" (Blum, 1956). In a study of the Plio-Pleistocene lacustrine stromatolites in the Gregory Rift Valley of

Tanzania and Kanya, Casanova (1986) described a regular succession of ripples or ridges induced by the development of a microbial community which Casanova interpreted as being at its climax condition.

At all sites, except in the rapid current of the Rio Mesquites, this successional process coincides with the gradual firming of the unconsolidated substratum as it is progressively covered by a thicker deposit of mat material. This firming of the substrate is an early diagenetic process called synsedimentary substrate modification (Walker and Diehl, 1986). The process applies to all sediments deposited subaqueously but the effects are most pronounced in fine sediments such as muds, where the initial water content may be 60% or more. These authors include in this process (1) a reduction in the water content of the sediment changing its consistency from soft to firm, (2) a change in the roughness, surface pattern, or surface hardness brought about by organism colonization and the changing mix of substrate niches, and (3) early cementation leading to hardground formation.

This process of sediment modification, or lack thereof as discussed with reference to the modification of laminar texture, can also be applied to the initiation of primary growth of a new structure. At Pozo Azul initiation of stromatolite growth is on soft mud, at Garabatal it is on soft mud, sand and solid substrates, at El Mojarral the structures will grow on sandy sediments or solid substrates and at the Rio Mesquites on sand and solid substrates. These differences in initial substrate mean that the processes which regulate successional characteristics vary from one site to the next, at least initially before a hard substrate has been established. Such chemical aspects as the timing and nature of delivery of nutrients to the system, or the development of oxygen and pH gradients in the mat, for example are variables whose importance remains unknown.

Microhabitat studies indicate that substrate preference is significant in determining the composition of the community. At Cuatro Ciénegas the initial soft sediment community consists of species that develop on soft muds at the sediment water interface. These are mostly small individuals, including colonial coccoid cyanobacteria, small motile diatoms, and protozoans. Filamentous cyanobacteria are generally absent. The major components are characteristic epipelic forms.

Epipelic species are all actively motile, and positively phototactic in order to return to the surface after burial (Round, 1981). As the substrate becomes firmer, there is a shift in the relative proportions of epipelic species, toward greater numbers of epilithic and epiphytic species that can anchor themselves to the now harder substrate. These include larger filamentous cyanobacteria and epiphytic diatoms both of which are able to overstory (overtop) the prostrate mat formers by growth out into the water column. Eventually, as the three-dimensional mosaic takes form, another component, the plocon, is added. Round (ibid) defines the plocon as those species, many nonmotile, which live as a layer, loosely associated with the sediments but not creeping on and between the particles. Round suggests that the plocon community "can develop only in waters where there is a back-and-forth bottom surge and not where the flow is unidirectional". This plocon community may have the opportunity to develop at Pozo Azul. As niche-space is increased, new taxa are added to the population and competition for space at various levels within the mat surface becomes an even more significant driving force in the regulation of community architecture.

In contrast to the lacustrine habitats, the stromatolites in the Rio Mesquites and the streams at Garabatal are not associated with soft sediment, rather they represent an encrusting community from the onset of colonization to dominance. There appears to be an acceleration (or compaction) of the successional process as there is little modification of substrate or environmental conditions involved. The process is probably regulated by the actual time required for growth and competitive dynamics.

4.4. Stromatolite Associations

The term stromatolite association refers to the group of species, both plant and animal, which characteristically reoccur under a given set of environmental conditions. While the biota associated with stromatolites is diverse, the organisms belonging to that part of the association that are actual <u>constructive</u> agents often constitute a small fraction of the total population (Monty, 1965, Golubić, 1973, 1976a). Filamentous cyanobacteria are generally given credit for providing the structural integrity essential to stromatolite formation (see Golubić, 1976b for a detailed discussion of the taxonomy of extant stromatolite-building organisms). This is certainly true at most sites in the basin. There is at least one large filamentous cyanobacterium present at El Mojarral, Pozo Azul and Garabatal that precipitates much of the carbonate. These genera include Dichothrix, Scytonema, Homoeothrix and one of the Schizothrix species. Gongrosira occupies this niche in the Rio Mesquites.

Other species inhabit the mat but do not contribute directly to the precipitation of carbonates. At Cuatro Ciénegas, Schizothrix and certain coccoid cyanobacteria, particularly Gloeothece and a select group of diatoms produce copious amounts of mucilage, bind the sediment and prepare the substrate for colonization by the larger calcifying filamentous forms. These colonies and small filamentous cyanobacteria also disrupt the mat by internal growth. At the Gavish Sabkha where these genera form the surface mats, Gerdes and Krumbein (1987) suggest that slime production is increased in order to escape phototoxic conditions, and is also stimulated by increase in salinity and temperature. Another characteristic of this extracellular material mentioned by Gerdes and Krumbein (ibid) is that the gel under the translucent mat may be an ideal medium for the channelling of light, which may benefit the other species in the mat. As a result of the increase of light through this mechanism internal mat growth such as is seen in El Mojarral may be increased.

Each of the stromatolite associations consists of an architecturally similar assemblage that is distributed spatially along an environmental gradient (oxygen-pH) perpendicular to the growing surface, with the result that niche partitioning segregates the various groups of organisms according to their particular metabolic requirements. These groups of organisms are often visible as bands of different colors. The chemical gradient has been demonstrated in uncalcified mat settings with the use of microelectrodes (Revsbech, 1983, Jorgensen, Revsbech and Cohen, 1983, Revsbech and Ward, 1984, Jorgensen and Revsbech, 1985, Carlton and Wetzel, 1986). Results of these studies show that the distribution of dissolved oxygen in periphyton communities varies on a diurnal basis from supersaturated to anoxic within a single microzone and the distribution of oxygen is markedly different among different periphyton types. A finding relevant to the Cuatro

Ciénegas mats is that "(1) through the diurnal period, periphyton of all types act alternately as sources and sinks for oxygen and that (2) the substrate for epiphytic, epilithic, and epipelic periphyton varies greatly in their function in the oxygen dynamics of their respective communities" (Carlton and Wetzel, 1986).

The organisms that characterize the living stromatolite mat are differentially preserved in the lithified stromatolites. At El Mojarral, and certainly at the other sites as well, the cyanobacteria are differentially preserved in the stromatolites depending on their species and the nature and rapidity of the lithification process. In thin section, cyanobacterial filaments are clearly evident, in growth position, to a distance of more than one cm beneath the surface of one typical El Mojarral oncoid (please refer back to Fig. 3.1.4.3-2). Neighboring filaments are separated by interlocking spar crystals. A thin layer of small individual crystals appear to indicate the former surface of the cyanobacterial filament. The interior of the sheaths has been filled with micrite and the original wall material is gone.

A different type of preservation is seen in a thin section cut from a partially submerged stromatolite growing in a shallow stream feeding El Mojarral lake. Dense masses of dark filaments 1-2 um in dia. are irregularly distributed in a matrix of micrite (Fig. 4.6.3-2 A,B). When treated with dilute acid the micrite dissolves and a mass of flexible sheath material is left behind (Fig. 4.6.3-2 C). Cells of a Synechococcus-like organism 2.4 x 4.0 um are also visible in the same figure. This collection of biogenic fabrics may represent various stages in the syndepositional and early diagenetic processes which take place during and shortly after growth of the surface mat.

At Cuatro Ciénegas, natural selection has favored the evolution of stromatolite associations dominated by species that precipitate calcite. The strategy is widespread, occurs in different habitats and involves several unrelated species. This may be a default response- those that do it are successful in compensating for the constant accumulation of carbonate particles by increasing their rigidity, hence the ability to grow upright and outward from the sediments faster than they can accumulate. On the other hand calcificaton may have evolved as a function of escape from predation, or may also serve as a competitive regulator in maintaining the stromatolite associations.

4.5. Relationship Between Biological Associations, Habitat, and Stromatolite Type

At each site a set of species occur repeatedly from one year to the next, that is different from the sets that occur at the other sites. There is sufficient variation among these habitats to permit different sets of species to become and remain dominant at their respective sites, and different types of stromatolitic structures to be produced. Certain environmental parameters do not vary from one stromatolite site to the next. The water chemistry of the various stromatolite sites is very similar, however the amplitude of change in salinity at Garabatal over an annual cycle may be important. Salinities are almost identical, at 1.5 ppt. All sites appear to be oligotrophic, limited by low phosphate concentrations, all are supplied by spring water, and all associated with extensive adjacent marsh systems.

Substrate composition puts constraints on stromatolite formation, but the response of different stromatolitic organisms to these constraints may vary in degree. Stromatolites do not form on dark sapropel mud, where it is present in some parts of El Mojarral, Rio Mesquites, and Garabatal, perhaps due to the presence of organic acids from the rotting vegetation. Stromatolites also do not form where the substrate is a sufficiently unstable and shifting carbonate mud. Excessively rapid abiogenic carbonate deposition, producing fluid micritic muds, precludes development of a stable mat, and formation of stromatolitic structures. Stromatolite formation is limited to those lakes and streams in the basin which are in the early stages of the evaporitic sequence where calcite and bicarbonate are still sufficiently concentrated to allow ready precipitation of calcite (and gypsum has not begun to precipitate). Where the substrate is composed of evaporites, if the water chemistry behaves as the model states in sect. 3.5, then there is probably no calcium carbonate available for precipitation by cyanobacteria and subsequent cementation.

The most obvious environmental parameters significant to stromatolite development that are different from one site to the next are summarized on Table 4.5-1. These include light, depth, current, and desiccation. The amount of light available for growth is essentially the same in the shallow parts of El Mojarral, Garabatal, and Pozo Azul, and somewhat less in the Rio Mesquites and in the deeper parts of Pozo Azul. The effect of depth, in the lower parts of Pozo Azul, is greatly reduced light conditions, that modify stromatolite shape and eliminate the large filamentous cyanobacteria, favoring _Schizothrix_, coccoid forms and diatoms.

Current varies between sites, being highest in the Rio Mesquites (0.6 m/sec). The _Gongrosira_-_Homoeothrix_-diatom association which characterizes the Rio Mesquites is similar to communities in similar habitats in other parts of the world. Minckley (1963) suggests current as the reason for a _Gongrosira_-dominated tufted, calcareous, encrusting community in the swift parts of Doe Run Stream, in Kentucky, where _Phormidium_ is a secondary species. He notes that in the swift areas cyanobacterial trichomes appeared unable to persist projecting from the surface of the _Gongrosira_ mass and _Gongrosira_ remained the dominant organism. _Homoeothrix_ probably occupies a similar niche in the Rio Mesquites. Minckley also found large numbers of diatoms in the crusts, that *Gongrosira* proliferated in spring and early summer, and that it was followed by cyanobacterial development in midsummer and autumn. Cuatro Ciénegas does not have the degree of seasonality that Kentucky has, perhaps this is an important reason why there is no switch in *Gongrosira* dominance in this more equatorial site.

Desiccation is the environmental variable that distinguishes Garabatal from the other sites. Water chemistry does not change appreciably but as the stromatolites become emergent the effects of osmotic stress may be a principle factor regulating the shift in composition from a submerged to a subaerial community (diatom-*Gloeothece* association).

4.6. Cuatro Ciénegas Stromatolite Morphologies, and Comparable Deposits

The environmental conditions at each of the sites are sufficiently different, one from the other, that different stromatolite morphologies have evolved to accommodate these differences. This is the case despite the probability that a common pool of species is available to each of the sites. The water bodies are close enough to permit the ready transport and inoculation presumably of all important microorganisms by groundwater, wind, floodwater, birds, fish, reptiles or people. These 4 categories of stromatolites are not meant to imply any phylogenetic relationships. Rather, they are local expressions of variation on the theme of stromatolite growth.

Type 1 structures, represented by stromatolites and oncoids at Laguna El Mojarral, are characterized by a growth pattern expressed on the surface as a regular series of small horizontal protruding ledges or terraces produced by upright intermingled, closely bound bundles of _Homoeothrix_ _balearica_, and _Schizothrix_ _lacustris_. 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 upper and outer surfaces which leads to the formation of the ridges. Each ridge forms a "canopy" that shades tha area directly around and beneath it. Commonly, but not always, the cyanobacterial layers are thicker beneath the ridges. The development of ridges appears to require some minimum amount of steady current. Large oncoids develop a rudimentary ridged pattern and some with a ridged pattern exhibit sharply juxtaposed growth orientations (the ledges always form close to horizontal) in sequential growth periods suggesting that movement of at least the larger oncoids is episodic in nature rather than continuous or regular, perhaps requiring the surge of a storm-induced increase in current. This same observation was made by Jones and Wilkinson (1978) who recognized that their large oncoids were overturned infrequently. Krylov (1982), on the other hand, concluded that lacustrine oncoids of the Pliocene Kyzylgir Formation grew in place, without movement.

This surface pattern of ridges or terraces is 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-.3 cm high) and a small irregular "basin" or depression (1.3-2.5 cm wide) behind the smooth microcrystalline carbonate rim. Similar appearing 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); and Gomes (1985) described tabular "crinkled stromatolites" from Wondergat Sinkhole in the Western Transvaal of South Africa. From Gomes' illustration and description these appear to be similar in size and shape to the El Mojarral structures. Monty (1972) discusses and illustrates lineations called ridges on pinnacle-bearing stromatolites subjected to water currents driven by persistent trade winds, in a lake on Andros Island in the Bahamas. Chafetz and Folk, 1984 also describe a microterraced pattern developed subaerially on travertine.

In the fossil non-marine stromatolite record there are several examples of the ridged or terraced morphology. Dixit (1984) refers to Pleistocene lacustrine ridged oncoids from Lake Manara in Tanzania as having "peaked ridges formed by laminae having a cuspate profile". The laminar pattern of the El Mojarral ridged structures closely resembles the layering described by Monty (1981) for his type 2 oncoids from the Lower Cretaceous algal deposits of Valencia. They also superficially resemble the Plio-Pleistocene lacustrine stromatolites of the Gregory Rift Valley of Tanzania and

Kenya illustrated by Casanova (1986).

Type 2 stromatolites, found in the swift current of the Rio Mesquites, are characterized by the dominance of the alga Gongrosira growing in small, regular cushions at the ends of digitate, many-branched columnar elements, formed of dense precipitated calcite. Cyanobacteria and diatoms form a secondary component in this system. The combination of high current and low light presumably select strongly for the Rio Mesquites Gongrosira community. No oncoids or stromatolites with healthy digitate growth patterns were found forming close to the surface in a high light regime. Stromatolites observed on the shallow margins were infilled with sediment and colonized by filamentous algae uncharacteristic of the type 2 morphology. Gongrosira incrustans (Reinsch) Schmidle forms green, lithified crusts in calcareous freshwater springs (Golubić, 1976a, Round, 1981), waterfalls (Pentecost, 1988) and streams (Golubic and Fischer, 1976). Minckley (1963) describes a Gongrosira dominated encrusting community in the high-current parts of Doe Run, a small, shaded stream in Kentucky. From reports of its occurrence, Gongrosira appears to favor a shaded habitat with some current. It is present at El

Mojarral, Garabatal and Pozo Azul, but only as an understory component, well shaded by the cyanobacteria.

McIntire (1966, 1973) found that in his experimental streams the flora varied according to the flow rate and the illumination, but that a large biomass of periphyton can accumulate under low light and nutrient conditions if grazers (snails) are excluded. The fast current communities which developed in his experiments excluded any loose oscillating cyanobacterial filaments, as does the Rio Mesquites, and were characterized primarily by diatoms and other species that formed a dense, felt-like growth on the surface.

Type 3 stromatolites, which form in the large, still pools of Los Pozos Azules, are large, internally non-laminated, globose structures with a regular, sinuous, incised, brain-like surface pattern. The surface mat consists of botryoidal colonies of the filamentous cyanobacteria *Scytonema* sp., *Dichothrix* sp., and *Cyanostylon* sp. mixed with amorphous accumulations of coccoid cyanobacteria, diatoms, detrital material, and carbonates, producing a non-laminated thrombolitic fabric (*sensu* Monty, 1976). The surface mat is not continuous but produced at the ends of irregularly fluted, interconnected vertical structures which form the principle constructive elements.

Pozo Azul is different in several respects from the other sites. There is no significant current flow, a much greater water depth and a different type of composition to the material on the surface of the mat. The stromatoites accumulate more detrital material probably much more rapidly than the other sites yet the mats are relatively slow to become cemented.

The Pozo Azul structures are more complex than anything described in the literature but in a general way they resemble the freshwater thrombolitic deposits in Green Lake, New York (Bradley, 1929, Dean and Eggleston, 1975, Eggleston and Dean, 1976), which are laminated near the surface only and not in the interior, as are the Pozo Azul structures. They are also similar to deposits forming in the Hoyoux River, Belgium (Monty, 1976) where diatoms are present in globose masses, in addition to the tufts of filamentous cyanobacteria.

The concave phylloid structures that form in the deep parts of Pozo Azul are a classic phototropic response to low, scattered light. Golubić (1973) describes and illustrates similarly shaped, but smaller, light-oriented travertine formations from similar low light moist habitats in cave entrances in Yugoslavia. In these low-light structures there is a significantly greater proportion of mucilaginous material to carbonate that there is in any other morphology. These phylloid structures at Pozo Azul resemble, in shape and size, Permian phylloid algal thalli described by Cross and Klosterman (1981) which are shaped like a conical vase and encrusted and bound by stromatolites. One difference is that the ones at Pozo Azul grow outward from the face of a vertical wall, whereas the fossil structures grow upright.

Complex patterns of dissolution and precipitation make interpretation of the tabular shapes in the low light parts of Pozo Azul difficult. One thing that distinguishes these tabular stromatolites is their community architecture. Encrustations of sponges form a major part of this community, sometimes covering an estimated 30-50% of the surface area, on the material examined, and the large, filamentous cyanobacteria are absent.

Type 4 stromatolites, characteristic of the ephemeral lakes at Garabatal, contain stromatolites with a sequence of up to three different layers each dominated by a different micro-organism or set of micro-organisms, including *Scytonema* cf *mirabile*, and *Schizothrix* *affinis*. The result is a fabric of alternating layers of horizontal and vertical fabric both built by cyanobacteria. The surface texture of young structures is similar to the pattern in Pozo Azul, with radial colonies of cyanobacteria covering a regularly rounded surface, incised with open vertical channels. Growth proceeds throughout the wet season, with an alternation between *Scytonema* forming upright colonies that produce coarse vertically striated laminae, and *Schizothrix* contributing thin, horizontally striated laminae. The cause of the alternation is unknown. The pattern is interrupted periodically by the addition of diatomaceous laminae. When the water recedes from the stromatolites, a final, sometimes very thick, layer is produced almost entirely by diatoms and their extracellular material. This alternation of dominant communities distinguishes the Type 4 stromatolites. The diatomaceous laminae are similar to structures forming in a quarry in Lagerdorf, W. Germany (Winsborough and Golubić, 1987), where water flows as a thin sheet over diatomaceous stromatolites, in a setting much like Garabatal at the end of the wet season.

4.7. The Role of Diatoms in Stromatolite Morphogenesis

Diatoms represent the taxonomically and numerically most abundant group of algae (including cyanobacteria) at Cuatro Ciénegas. Over a hundred species have been identified from the various water bodies within the basin. The advantage of looking at diatoms include the ease of identification of each cell, something not usually possible with cyanobacteria. Diatom collections were made concomitant with water chemistry sampling at 20 aquatic locations in the basin during July, 1983. The purpose was to define the habitats available for diatom colonization and to relate these chemical data to stromatolite diatom associations. A total of 99 diatom species and varieties were tabulated from the 20 sites with 34 species representing at least 5% of the population at any one site. The following discussion is based on a count of 500 individuals from each of the 20 sites.

The hypersaline sites contained a depauperate flora which included only Nitzschia cf rostellata and Amphora coffeaeformis. No sampling sites were intermediate between hypersaline and brackish salinities. The next freshest habitats are two mesohaline (brackish) sites with salinities of 6.2 and 4.8 ppt which support 12 and 18 diatom species respectively. The next twelve sites, in order of decreasing salinity are oligohaline, have salinities between 0.81 and 1.52 ppt, and diatom species totals which range from 20 to 40. Included in this group are the stromatolite sites. The sites in this bracket fall within a narrow TDS range (between 2266 and 2500 mg/l) of the total variation in dissolved solids (the sum of the major ions) measured from the water bodies in the basin. Two sites, about twice as dilute as these sites, are located on the north and south periphery of the basin. The other sites with water chemistry data are at least 3 to 4 times more concentrated (Table 4.7-1).

Species diversity was one parameter used to examine the structure of the diatom communities at each stromatolite site. Diversity is the information contained within the structure of a community and is related to the number of taxa present in a sample as well as the apportionment of individuals among the resident taxa. The diversity measures of the stromatolitic diatoms were similar at all four sites (Table 4.7-2). The percent relative abundance is the most practical way of estimating a diatom species' relative success in a population, and has the weaknkess of combining (confounding) these 2 characteristics. Factors influence the relative abundance of a taxon at any one time, including seasonal succession and variable grazing pressures. Relative abundance was used to identify the proportion of characteristic or dominant species (10% or greater) at each site. These species make up distinct associations- assemblages of species that recur under comparable ecological conditions in different places (Hutchinson, 1967).

Results of a stromatolite diatom analysis based on counts of 500 and 1500 cells extracted from the surface mat of stromatolites at each of the four sites are summarized in Table 4.7-3. In the 500 count, four distinct associations, are identified. Each site has no more than two dominant species in common with any other site, and each site has at least one of its most common species in common with two other sites (Table 4.7-4).

The 1500 count part of the table represents an expanded data base consisting of 3 combined 500-count samples from each site, with each of the 3 samples collected at different times of the year. The 1500 cell counts were used to determine more reliably the relative degree of difference in the composition of the diatom associations among the sites. The idea was to eliminate problems of patchiness, seasonality, blooms of one species, grazing effects etc. that could bias the results. In the expanded data base the diatoms from each site were compared pairwise (site 1 with site 2, 1 with 3, 1 with 4, 2 with 3, 2 with 4, and 3 with 4. The euclidian distances between these pairs were calculated according to the formula:

$$\text{Euclidean Distance} = d_{jk} = \sqrt{\sum_{i=1}^{n} (P_{ij} - P_{ik})^2}$$

These results, depicted as the relative distances between diatom associations at each pair of sites, are plotted in Fig. 4.7-1. The euclidean distances were calculated and plotted on the basis of both the 8 and 50 most abundant diatom species. In both of these orthographic projections, the point representing El Mojarral is more distant from the other three points than the others are from each other indicating that the composition of the diatom community at El Mojarral is most distinctly different from the other three.

A major characteristic of many benthic diatoms is their ability to become permanently attached to surfaces (Daniel et al 1987). In addition to permanent attachment, motile forms secrete a substance which provides temporary adhesion as they crawl over a surface. This life style is made possible by the secretion of extracellular mucilaginous substances in the form of pads, envelopes, balls, stalks, tubes, films, filaments and trails. Cytochemical staining techniques have shown that this material is an acid polysaccharide, with carboxylated or sulphated components (ibid). This polysaccharide material also increases the cohesion of calcite grains and binds them together (Fig. 4.7-2).

Quantitative and qualitative observations of sediment stabilization by benthic diatoms (Voss et al., 1988) have shown that epipsammic (attached to grains, immobile) and epipelic (motile, biraphid) diatoms play an important role in stabilizing intertidal sediments, with the magnitude of the sediment stabilizing activity dependent upon the density and mucilage secretion of the various diatom species. The two effects which these authors observed were a cohesive effect and a network effect. With regard to the cohesive effect, mucus secreted on sand grains by both epipsammic and epipelic diatoms and bacteria produced an organic coating which caused a 5-17% increase in critical erosion velocity, relative to sterile sediment. The network effect, which was more important in the studies of mud-flat sediment stability than the cohesive effect, refers to the accumulation by epipelic diatoms of mutual attachment and mucus threads which, in their experiments, increased the threshold water velocity required for sediment motion by 25 to 100%.

Voss, et al (1988) observed that epipelic and epipsammic diatoms obstruct each other's prosperity because epipelic species tend to stabilize sediments by creation of an organic network whereas epipsammic diatoms may benefit from regular reworking of the sediment. They suggest that competition for nutrients, related changes in pore water chemistry and frequency and magnitude of reworking determine the proportion of epipsammic to epipelic forms and that small ecological changes may have a great effect on the role of diatoms in sedimentation.

At Pozo Azul experiments showed that the initial mat is produced by motile diatoms which crawl rapidly through the sediment to the surface and produce an organic film. (Lens paper placed on this surface was colonized within a matter of minutes by species of _Mastogloia_ and _Stauroneis_ that crawled through the inter-fiber openings of the paper). Micritic grains of calcite are trapped and bound into this organic film after they have settled through the water column. Diatom mats can be seen as a golden brown covering on the sediment surface at Pozo Azul. In Pozo Azul lake, one of the most abundant diatom genera, _Mastogloia_ produces gel balls many times the diameter of the individual cell. _Mastogloia_ is able to inhabit the upper surface of the fine loose muds perhaps due to the added buoyancy of the gel and the reputed ability of the gel to decrease photooxidation by screening some of the light. In addition to its role in osmoregulation the gel may serve a protective function for the diatom gametes during auxospore formation. This includes not only those species that produce the gel, but species such as _Amphore_, _Denticula_, and _Rhopalodia_ which move into the gel mass between other cells when their zygotes are formed (Geitler, 1932). On the stromatolites the gel acts as a binding agent for the grains of carbonate, diatoms, dinoflagellates, ostracods, and fecal pellets which are bound into the mat. In Pozo Azul the diatom population in the thin mat is augmented by attached epipsammic species particularly *Amphora*, *Gomphonema* and *Cymbella* when the mat becomes stabilized.

There is a spatial architecture to the diatom distribution on surface mats of mature stromatolites, as there is to the cyanobacteria. The basal layer consists of small diatoms such as *Achnanthes affinis* and *Cocconeis placentula* Ehr. found living in crevices or as early colonizers of freshly exposed surfaces. Monoraphid diatoms such as *Cocconeis* and *Achnanthes* typically adhere tightly to substrates and are able to persist on substrates through disturbances and dominate flora in such rigorous habitats as epipsammon, and substrates exposed to rapid stream current (Stevenson and Peterson, 1989).

Important adaptive features for resisting grazing or current effects often include a sessile habit with a low profile, lanceolate body shape with rounded apices, and an attached raphe valve, with a slightly concave valve face, where mucilage accumulates and remains in the puncti of recessed concave striae, and surrounds the valve face-mantle edge (Rosowski et al, 1986). Both Cocconeis and Achnanthes posess these adaptive features. They produce a mucilage pad which leaves a bas-relief impression of the cell when it is scraped away. Diatom forms that produce mucilaginous balls or masses are also generally well embedded in the mat where the current is reduced through the baffling effect of the large filamentous cyanobacteria. Stalk-forming diatoms attach to calcite crystals and to larger filamentous cyanobacteria and form part of the top story of the mat. Gomphonema, for example, by the production of a long stalk can grow well out into the water column where light and possibly nutrients may be more available. The epipelic species crawl among the carbonate grains and fecal pellets, while those diatoms with an epilithic habitat preference and are associated with hard, stable substrates.

Percival (1979) attached a functional significance to the mucilaginous sulphated polysaccharides (such as produced by Amphora veneta, a dominant at Cuatro Ciénegas), observing that these extracellular mucilaginous secretions are associated with cell wall strengthening coupled with increased flexibility, protection from dessication and cation exchange. In contrast, she found that adherent forms such as *Cocconeis* produce a mucilage that is predominantly carboxylated polysaccharide which makes a very stiff strong gel in the presence of calcium ions. Calcium ions are a component of the mucilage envelope at least some diatoms including *Amphora veneta*, and *Amphora coffeaeformis* (another dominant species at Cuatro Ciénegas) and function as bridging agents between the substratum, cell and adhesive during attachment of marine benthic diatoms (Daniel *et al*, 1987).

Cation exchange has relevance to the question of the role of diatoms in stromatolite morphogenesis. In a study on the mechanism of travertine formation Emeis et al (1987) found that epiphytic diatoms coat young moss sprouts with mucous secretions and rapidly form a dense and sticky lawn on the moss surface which acts as a filter for micritic carbonate particles. These carbonate grains act as seed crystals, and availability of nucleations sites (not just supersaturation) is responsible for the onset of carbonate precipitation. A sparry calcite surface crust forms, resettled by diatoms that trap calcite seed crystals and increase the thickness of the deposit (ibid). They found filamentous cyanobacteria and bacteria settled on the mat adding to the density of the retaining surface.

Emeis _et al_. (1987) suggest that carbonate buildups in fresh water require "1. calcite supersaturation, 2. the presence of calcite seed crystals, and 3. biological activity and formation of mucus in response to environmental stress to tap the crystal seeds and initiate precipitation". They found that diatoms play a fundamental role as epiphytes at Plitvice and elsewhere, and suggest that where there are high calcium concentrations in the water, the excretion by diatoms of adhesive mucous rich in aspartic acid occurs as a reaction to physiological stress. Emeis _et al_. (ibid) report that "During blooms of diatoms in the surface water of lakes with high dissolved calcium concentrations, aspartic acid is dominant component of excretionary products", and that aspartic acid plays a key role as the template for the fixation of Ca^+ and nucleation of $CaCO_3$. Emeis et al add that it is possible that low nutrient concentrations add to the formation of mucus by epiphytes.

With regard to the disappearance of diatoms and concomitant appearance of quartz crystals in the interior of some stromatolites and oncoids there appears to be a correlation between porosity and diatom dissolution. In the interior of Garabatal stromatolites and El Mojarral oncoids and cave stromatolites (where Ca^{++} concentration was highest), few diatom frustules are preserved in the residue, but there are variable amounts of brown amorphous organic material, and large numbers of imperfectly formed, doubly terminated quartz crystals. These crystals usually range in size from 4.5 x 8.2 um to 20.0 x 62.5 um, with some crystals over 100 um long. In the more porous structures with alternating dense and sparsely calcified laminae, stromatolite and oncoid interiors contain large numbers of well-preserved diatom frustules but fewer or no quartz crystals.

One suggested mechanism for the dissolution of diatoms in the mat relates to sulfate reduction by the anaerobic sulfate-reducing bacterium Desulfovibrio, causing local chemical characteristics to be significantly altered. This would only occur deep enough into the mat that the diatoms present are likely to be dead. After death of the algal cell, the protective organic coatings and adsorbed cations which retard silica dissolution from frustules of living diatoms are degraded. Then because of the ready solubility of the unprotected diatom silica, diatom frustules may dissolve (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, H_4SiO_4 dissociates to $H_3SiO_4^-$ 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 CO_2 and sulfide ions, lowering pH and increasing carbonate alkalinity in the localized environment surrounding the cells, thereby causing precipitation of silica.

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 (Germany) 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. There are other examples of the dissolution of diatoms in cyanobacterial mats, accompanied by increased concentration of silicate in the pore water. Krumbein and Cohen (1977) report the in situ dissolution of diatoms taking place in Solar Lake, Sinai, at pH's below 7. Lyons et al. (1984) measured the reactive silicate in the pore waters of sediments from 4 hypersaline environments and concluded that a large amount of the dissolved silicate must be derived from the dissolution of opaline silica. Awramik (1984) observed that in the case of certain fossil stromatolites, "silicification must have nearly been contemporaneous with microbial mat growth, for well-preserved microbial fossils showing little alteration can be found within silicified stromatolitic laminae".

4.8. The Role of Benthos in Stromatolite Morphogenesis

A diverse assemblage of animals is associated with all stromatolite sites. This situation is in contradiction to the statement by Cohen et al (1984), that "The partial or total exclusion of animal grazing is essential for the accretion of the cyanobacterial mats." This statement refers to a group of sites which are particularly stressed by high salinity, sulfide, or elevated temperatures but should not be considered a generality and is certainly not the case at Cuatro Ciénegas. Dominant animals associated with these stromatolites are the same ones in terms of numbers and biomasss as are typically associated with the fine-grained sediments on the bottoms of most lakes, namely chironomids, oligochaetes, amphipods, and mollusks (bivalves) (McCall and Tevesz, 1982). The primary difference is that in the Cuatro Ciénegas area there are no bivalves, that niche being filled by a dense population of tiny hydrobiid snails. There are ciliates present but they are not generally abundant as they are unable to burrow in the fine sediment. This is not unexpected. Fenchel (1969) showed that ciliates have a maximum occurrence in fine sands, and in finer material their numbers decrease drastically. He found that organisms living in sediment with a grain size of less than 90-100 um must in general either be very small flagellates or bacteria or be sufficiently robust (nematodes) to burrow into the sediment.

The different classes of benthos impact the stromatolites in slightly different ways. The most common chironomid at Cuatro Ciénegas belongs to the genus Chironomous, sp. the most abundant midge genus in the Diptera family. These flies burrow into the sediment and live in tubes, emerging to feed. They are concentrated on the underside of the stromatolites at El Mojarral, and are irregularly distributed in the Pozo Azul and Garabatal stromatolites, but are within a centimeter of the surface in the adjoining mud bottom sediment. They were less common in the Rio Mesquites stromatolites and oncoids, possibly due to lack of soft substrate and inability to withstand rapid current.

Amphipods belonging to the genus Hyalella sp. are also common in the stromatolites. These are omnivorous substrate feeders (they consume bacteria, algae and particulate detritus of animal and plant remains), with rapid growth rates and short generation times, making them significant in comparison to other components of the benthic fauna (Wetzel, 1975). Nematodes and oligocheates are partially responsible for any disruption of the internal fabric of the stromatolite by their gregarious feeding habits. In microscopic examination of living mat material these disruptions appear to be on a scale that disturbes small areas of the mat rather than disrupting whole laminae. Insect larvae are seasonally abundant but their populations are small enough to inflict minimal disruption to the stromatolite fabric.

Observations on the grazing behavior of fish suggest that in a habitat with no discernable current, no particular pattern was clear on the stromatolite surface. Grazing patterns, however, are very predictable in an unimpeded current, and occur on the down-current side of both natural and artificial stromatolites. Heavy grazing by fish removes the terraces and sometimes bevels down whole portions of the structures. Pieces of mat up to a cm in diameter have been bitten off by fish.

Snails graze on stromatolite mats. The species at Cuatro Ciénegas are small, secretive, hydrobiid snails, about 1-2mm in size. They crawl over the surface and may become lodged in the interstices of the stromatolites where they continue to live and graze. Examination under low magnification has shown scraped areas on the mat surface in the immediate vicinity of a dead shell. The mat had clear radula patterns where the algae within reach of the snail had been removed.

Chapter 5. CONCLUSIONS

Microbial structures that include coated pebbles, oncoids, and stromatolites are forming in the warm, spring-fed sulfate-rich pools, streams and lakes of the arid Cuatro Ciénegas Basin. These are lithified, frequently laminated organo-sedimentary structures built by a diverse community of microorganisms, primarily through the process of carbonate precipitation. This report extends the known range of modern non-marine (continental) stromatolites to include continental waters with unusually high concentrations of calcium sulfate, with respect to carbonate.

Four distinct stromatolite morphologies are presently forming in the Cuatro Ciénegas Basin. The characteristics of these deposits are detailed on Table 5-1. Unique to Type 1 stromatolites and oncoids, represented by laminated structures at Laguna El Mojarral, is the development of a remarkably constant surface growth pattern of horizontally-oriented, small, protruding, 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*. with *Homoeothrix* responsible for calcite precipitation. These two dominant filamentous cyanobacteria exhibit species-specific differences in biogenic calcium carbonate precipitation. Diatoms are abundant on the surface of the structures but in those oncoids and stromatolites with thin, dense laminae they are dissolved in the interior, where there are local concentrations of quartz crystals.

Type 2 stromatolites and oncoids, found in the swift current of the Rio Mesquites, are characterized by the dominance of the calcifying green alga *Gongrosira calcifera*. It grows in small regular cushions at the ends of digitate, many-branched columnar elements, formed of dense calcite. Cyanobacteria are common among the *Gongrosira* colonies, but to a lesser extent than at the other sites. Diatoms are abundant, sometimes cover the surface of the mat, and are well preserved in the interior of the structures.

Type 3 stromatolites, forming in the deep still pools of Los Pozos Azules, are large, globose non-laminated structures with a regular, sinuously incised surface pattern, consisting of loosely cemented, trapped and bound particles of calcite, plants and small animals. The constructive organisms are *Dichothrix bonetiana*, forming calcified tubes, *Schizothrix lacustris*, and diatoms. Two deep-water variations with unique shapes have evolved, probably at least in part to maximize photosynthesis under particularly dark conditions. They are constructed by a depauperate assemblage in which some of the organisms common to the well-illuminated stromatolites are absent. Diatoms are common in all the kinds of stromatolites at Pozo Azul, and well-preserved material has been extracted from the interior of the structures.

Type 4 stromatolites, characteristic of streams and lakes at Garabatal, a shallow seasonal stream-lake complex, have a sequence of layers each dominated by a different microorganism or set of microorganisms, including *Scytonema* cf. *mirabile*, responsible for the bulk of the calcite precipitation, *Schizothrix* cf. *affinis*, and diatoms. The species producing the most recent layer of the stromatolite alternate depending upon immediate environmental conditions, which range from complete submersion to complete dryness. <u>Scytonema</u> produces the initial mat at the onset of the wet season. While submerged, the dominant species change with environmental changes, seasonal growth often terminating with a thick diatomaceous layer capping the surface of the drying stromatolites.

Certain ecological constraints on stromatolite formation at Cuatro Ciénegas have become evident. There must be water available for at least part of the year and the water must be adequately saturated with carbonate to allow cementation to take place. Cementation is essential for stromatolite preservation and occurs with varying rapidity at all stromatolite sites, the rate being directly proportional to current speed. Low phosphate concentrations, a characteristic of at least 3 of the 4 stromatolite sites, may be essential for stromatolite growth as it favors the benthic habitat over the planktonic one, and will not support the growth of massive floating mats. Assuming stromatolite mat metabolism to be similar to any other benthic microbial mat, the phosphates in the stromatolite mats are largely conserved and recycled to the mat adsorped to $CaCO_3$, from which the algae (and bacteria) probably have uptake mechanisms. Thus they are not being released into the water column. Many of the lakes that do not have stromatolites are partially surfaced by dense accumulations of thick, buoyant, floating microbial mats that do not calcify, but shade the organic-rich bottom and no doubt affect pH, carbonate precipitation and nutrient cycling, from the decay below. The water is clear, transparent, and the bottom is visible at all stromatolite sites (except the deepest parts of Pozo Azul).

A firm substrate seems to be another prerequisite for the development of this architecture. That substrate can evolve from the hardening and thickening of a diatom-rich microbial mat as in Pozo Azul; or it can be bedrock or a nucleus of tufa, travertine or organic debris as is seen in El Mojarral, the Rio Mesquites and Garabatal. Stromatolites do not form on dark sapropelic or organic-rich sediments or in brown water. Probably one of the most important constraints on stromatolite formation is that there must be a mechanism for removal or incorporation of clay-sized particles that would otherwise bury the structures.

Although never consistently dominant in biomass, except occasionally at Garabatal, the diatoms are by far the most diverse class of stromatophilic microorganisms, and are often well preserved in the lithified stromatolites. The production of extracellular mucilage in the form of stalks, envelopes, tubes, and threads, allows diatoms to take advantage of microhabitat complexity within the stromatolite. Diatoms live epiphytically on the cyanobacteria and chlorophytes, epilithically, attached to the surface of carbonates and epipelically, by crawling unattached among the loose mineral grains and organic matter. Diatoms may be critical to the development of stromatolites at Pozo Azul because the development of a firm stable diatom mat is an early, and possibly essential stage in stromatolite formation on the soft mud covering the Pozo Azul bottom. In mature stromatoltes at all of the sites there is a more diverse diatom flora than found in any other single microhabitat, demonstrating that epiphytic, epilithic, epipsammic forms all have a place in the architecture of the stromatolite community. At Garabatal diatoms continue to grow luxuriently over the surface of stromatolites wetted only by occasional splashing, after the water level has receded beyond that tolerated by the filamentous cyanobacteria; however, before water levels go down the stromatolite mats are usually dominated by cyanobacterial growth.

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 even develop in the presence of grazing and burrowing animals (Garrett, 1970a,b, Gebelein, 1976, Awramik, 1984, Gerdes and Krumbein, 1984). This hypothesis however has been criticized by Monty (1972) and Golubić and Riding (1990). The presence of a diverse animal community associated with living, actively growing stromatolites and oncoids 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. Rather than a constraint on stromatolite growth, grazers may affect possible interspecific competition between pairs of cyanobacteria in such a way that they permit the sustained growth of both species. They may also provide the mechanical agitation necessary to remove excessive fine sediment in the absence of other currents. Our observations suggest that both fish and benthic animals may play very important parts in the determination of the growth and population dynamics of the algal/cyanobacterial portion of the stromatolite community by affecting the rates of timing of stromatolite accretion. Undoubtedly, there are direct as well as indirect effects of the interactions between the grazers and the stromatolites. The predators in this community may influence stromatolites indirectly, perhaps beneficially (see Sterner, 1986) by controlling the grazers.

Members of the animal microbenthos move through the stromatolite mat with relative ease and do not appear to disrupt the mat fabric substantially. Macrobenthos (adults longer than one mm) "are probably the most potent modifiers of sediment properties because of their larger size relative to the sediment grains, their population density, their ability to move through a relatively large volume of sediment, and their feeding and respiratory habits" (McCall and Tevez, 1982). The principle macrobenthic animals associated with the stromatolites include chironomids, amphipods, worms, mites, insect larvae and snails. These may play a role in the maintenance of macroscopic open channels in stromatolites and oncoids, particularly at El Mojarral. Gaps in the mat fabric between laminae or between cortex and nucleus serve as a refuge for insect eggs and larvae. Such channels would probably become infilled with fine sediment in the absence of these animals.

In the stromatolite habitat at Cuatro Ciénegas, the benthic animals have evolved as a specialized association, which because of its motility can overcome the stress of rapid carbonate precipitation; however, early induration of stromatolitic structures by in situ precipitation of calcium carbonate may be responsible for stromatolite preservation in spite of the presence of diverse populations of grazers. To the extent that this compensation for burial demands deliberate directional movement in space and time, the organisms may be exhibiting active movement or transport. Otto (1983) suggests that as this type of active movement, which he calls "active transport" (not to be confused with membrane transport) "demands energy and since transportation movements usually are not consistent with other activities such as feeding and mating, it should serve an adaptive function when it occurs" (Otto, 1983).

The primary mineral constructing the stromatolites is low-magnesium calcite. Only traces of gypsum have been found in the structures. The crystallographic expression of calcite is modified by the organic product (sheaths or stalks) of microorganisms that leave biogenic imprints on minerals. The nature of cyanobacterial preservation is also variable. In some instances, the original cyanobacterial material is preserved in the lithified structures, in others organic remains have been replaced by spar. Calcite crystal shape is further modified inorganically from the euhedral habit possibly due to lattice poisoning by magnesium or sulfate during growth. These modifications are systematic in the sense that at all the sites the crystals are loaf-shaped or arched sparry calcite, with a variety of surface deformations.

Under certain microbial-mat conditions that seem to be related to the production of thin, dense stromatolite laminae, rather than thick, porous laminae, diatom frustules are not well-preserved in the interior of the stromatolites, after death of the diatom cell, but are dissolved during early diagenesis. In these cases of poor diatom preservation, quartz crystals accumulate in the stromatolite matrix. Some of these have cyanobacterial (or fungal) inclusions. It is not clear why this dissolution-precipitation phenomenon occurs, and a variety of suggestions have been made but the explanation is not yet evident. A number of suggestions have been made concerning the genesis of the quartz crystals but noone has provided an evidence-supported suggestion.

There are certain characteristics that all the sites have in common and some that are different among the various sites (please refer back to Table 3.7-1). It is these differences, particularly light intensity (directly related to morphometry), and current rate and continuity, that hint at the basic mechanisms inducing and regulating the growth of the 4 stromatolite morphologies. Certain cause and effect relationships between these parameters can be identified. For example, light intensity determines which species is capable of growth at the stromatolite surface, and contributes to regulation of the vertical distribution of organisms within the living mat. At the stromatolite surface light penetration slows down but does not stop. "light penetration through wet sand is such that attenuation to between 1 and 2 % of surface intensity occurs at around 5 mm depending on the color etc..." (Round, 1981). It is, perhaps, because of the relatively low light conditions in the Rio Mesquites Gongrosira is able to dominate the mat. Gongrosira grows only if light is slightly attenuated by shade due to lake or stream morphometry or an overstory of cyanobacteria, and achieved dominance only in a shady habitat with a swift current. Particularly high light conditions at Garabatal (it is on the western side of Sierra San Marcos, therefore not shaded in the late afternoon), coupled with an increase in photooxidation and osmotic stress as the water recedes, may suppress cyanobacterial growth in favor of diatomaceous laminae.

Current is the most obvious parameter determining the ridged growth of El Mojarral. It is swift enough to prevent an inordinant amount of debris from accumulating on and between the ridges, and consistent enough to support a regular, steady growth pattern. As stated above, a rapid current in the Rio Mesquites favors Gongrosira over cyanobacteria. Intensive aeration of the Rio Mesquites water by the current may inhibit sulfate reduction and explain why the diatoms are so well preserved. Current provides carbonate-rich water to Garabatal stromatolites, but varies in rate, with fluctuations in the water table. As current and other conditions change, shifts in composition and relative abundance of different organisms track the changing environment. Lack of current may be the reason that there is a significantly larger amount of detrital material that adhers to the Pozo Azul stromatolites and becomes incorporated. It is also the reason that they are able to grow despite a slow rate of cementation. The stromatolite pore water at Pozo Azul is probably not replenished with fresh ions and nutrients as rapidly as the Rio Mesquites or El Mojarral. This means a slower cementation rate but perhaps also less food for, therefore less activity by sulfate reducing bacteria. This situation leads to good diatom preservation.

All stromatolite sites at Cuatro Ciénegas are similar with respect to cation and anion composition, therefore gross water chemistry does not appear to be a major influence on stromatolite morphology. Subtle changes in the water chemistry may be important, however. What these structures have in common is that they all have characteristic growth patterns that develop primarily by the activity of a distinct and vertically differentiated microbial community, at least one of which is a filament that precipitates calcite. "Filaments possess greater motility and faster growth rates than coccoid blue-green algae and these abilities enable the organisms to successfully compensate for sediment deposition" (Awramik et al, 1976). All of the microbial growth patterns basically reflect a variation on the theme of upright-radial growth of colonies.

The stromatolitic structures at Cuatro Cienegas also possess certain qualities in common with stromatolites from other parts of the world. Some of these qualities include the ability to precipitate carbonate; and growth based on a microbial community acting in concert to produce a three-dimensional architecture that eventually becomes cemented and preserved in the geological record. This reflects a commonality in evolutionary processes related to the interaction between stromatolite-building organisms and their sedimentary environment. The direct methods used here to observe the ecology of the stromatolite communities have lead to the same conclusions as Monty, (1965), Golubić (1973, 1976), and

Winsborough and Golubić (1986) namely that a diverse community of plants and animals is associated with stromatolites, only a portion of which are organisms that build stromatolites.

Chapter 6. BIBLIOGRAPHY

Aitkin, J.D., 1967. Classification and Environmental Significance of Cryptalgal Limestones and Dolomites, with Illustrations from the Cambrian and Ordovician of Southwestern Alberta. J. Sed. Pet., 37, 1163-1178.

Almada-Villela, P.C. y Contreras-Balderas, S. 1984. El Bolson de Cuatro Cienégas, Coah.,Mexico. Secretaria de Desarrollo Urbano y Ecologia (SEDUE). Reunion Regional de Ecologia. Norte. 25-27 de Abril 1984. Monterrey, N.L., 125-129.

Anadón, P. and I. Zamarreño, 1981. Paleogene Nonmarine Algal Deposits of the Ebro Basin, Northeastern Spain. in: Monty, C. (ed.) Phanerozoic Stromatolites, Case Histories. Springer Verlag, 140-154.

Atkison, K., 1972. Birds As Transporters of Algae. Br. Phycol. J., 7, 319-321.

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: Nitecki, M.H. (ed.) Biotic Crises in Ecological and Evolutionary Time. Academic Press, New York, 83-102.

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

Awramik, S.M., L. Margulis and E.S. Barghorn, 1976. Evolutionary Processes in the Formation of Stromatolites. in: Walter, M.R. (ed.) Stromatolites. Elsevier, 149-162.

Barcelo-Duarte, J., 1983. Lower Cretaceous Stratigraphy and Depositional Systems in Northwestern Coahuila, Mexico. Dissertation, Univ. of Texas at Austin, 252 pp.

Bates, R.L., and J.A. Jackson (eds.) 1980. Glossary of Geology, Second Edition. American Geological Institute, p. 348.

Beiersdorf, H. and H. Knitter, 1986. Diagenetic Layering and Lamination. Mitt. Geol.-Palaont. Inst., Univ. Hamburg, SCOPE/UNEP, Sonderband, 60, 267-273.

Berner, R.A., 1980. Early Diagenesis, A Theoretical

Approach. Princeton Univ. Press, Princeton, N.J., 241 pp.

Birnbaum, J. and J.W. Wireman, 1984. Bacterial Sulfate Reduction and pH: Implications for Early Diagenesis. Chemical Geology, 43, 143-149.

Black, M., 1933. The Algal Sediments of Andros Island, Bahamas. Philos. Trans. R. Soc. London, Ser. B, 222, 165-192.

Blum, J.L., 1956. The Application of the Climax Concept to algal Communities of Streams. Ecology, 37, (3), 603-604.

Bradley, W.H., 1929. Algal Reefs and Oolites of the Green River Formation. U.S. Geol. Surv., Prof. Paper 154-G, 203-223.

Braithwaite, C.J., 1979. Crystal Textures of Recent Fluvial Pisolites and Laminated crystalline Crusts In Dyfed, South Wales. Jour. Sed. Pet. 49, (1), 181-194.

Brock, T.D., D.W. Smith and M.T. Madigan, 1984. Biology of Microorganisms. Prentice-Hall Inc., N.J., 847 pp.

Burne, R.V. and L.S. Moore, 1987. Microbialites:

Organosedimentary Deposits of Benthic Microbial Communities. Palaios, 2, 241-254.

Carlton R.G. and R.G. Wetzel, 1986. Distributions and Fates of Oxygen in Peryphyton Communities. Can. J. Bot., 65,1031-1037.

Casanova, Joel, 1986. Les Stromatolites Continentaux: Paleoecologie, Paleohydrologie, Paleoclimatologie. Application Au Rift Gregory. Thesis, L'Universite d'Aix-Marseille II, 2 volumes.

Chafetz, H.S., 1986. Marine Peloids: A Product of Bacterially Induced Precipitation of Calcite. Jour. Sed. Pet., 56,(6), 812-817.

Chafetz, H.S., and R.L. Folk, 1984. Travertines: Depositional Morphology and the Bacterially Constructed Constituents. Jour. Sed. Pet., 54, 289-316.

Charleston, S. 1973. Stratigraphy, Tectonics and Hydrocarbon Potential of the Lower Cretaceous, Coahuila Series, Coahuila, Mexico. Ph.D. Dissertation. University of Michigan, 268 pp.

Cohen, Y. and E. Rosenberg (eds.), 1989. Microbial Mats:

Physiological Ecology of Benthic Microbial Communities. Amer. Soc. for Microbiology, Washington D.C.

Cohen, Y., R.W. Castenholz, and Harlyn O. Halvorson, 1984. The Interdisciplinary Approach to the Study of Microbial Mats: Perspectives for Future Research-Discussion. in: Cohen, Y., R.W. Castenholz and H.O. Halvorson (eds.) Microbial Mats: Stromatolites. Alan R. Liss Inc., N.Y., 471-477.

Coney, P.J., 1976. Plate Tectonics and the Laramide Orogeny. in: Tectonics and Mineral Resources of Southwestern North America. L.A. Woodward and S. A. Northrup (eds.) New Mexico Geological Society Special Pub. 6, 5-10.

Contreras-Balderas, A.J. 1984. Birds from Cuatro Ciénegas, Coahuila, Mexico. Journal of the Arizona-Nevada Academy of Science v.19 (1), 77-79.

Cross, T.A. and M.J. Klosterman, 1981. Autecology and Development of a Stromatolite-Bound Phylloid Algal Bioherm, Laborcita Formation (Lower Permian), Sacramento Mountains, New Mexico, U.S.A. in: Monty, C.L. (ed.) Phanereozoic Stromatolites, Case Histories. Springer-Verlag., 45-59.

Daniel, G.F., A.H. Chamberlain, E.B. Jones, 1987. Cytochemical and Electron Microscopical Observations on the Adhesive Materials of Marine Fouling Diatoms. Br. Phycol. J., 22, 101-118.

Danielli, H.M. and M.A. Edington, 1983. Bacterial Calcification in Limestone Caves. Geomicrobiology Jour., 3 (1). 1-15.

Darwin, C., 1859. The Origin of Species. Random House Inc., New York, 386pp.

Dean, W.E. and J.R. Eggleston, 1975. Comparative Anatomy of Marine and Freshwater Algal Reefs, Bermuda and Central New York. Bull. Geol. Soc. Am., 86, 665-676.

Dixit, P.C. 1984. Pleistocene Lacustrine Ridged Oncolites From the Lake Manyara Area, Tanzania, East Africa. Sedimentary Geology 39, 53-62.

Eggleston, J.R., and W.E. Dean, 1976. Freshwater Stromatolitic Bioherms in Green Lake, New York, 1976. in: Walter, M.R. (ed.) Stromatolites. Elsevier, 479-488.

Emeis, K.-C., H.-H. Richnow and S. Kempe, 1987. Travertine Formation in Plitvice National Park, Yugoslavia: Chemical Versus Biological Control. Sedimentology, 34, 595-609.

Emerson, S., 1975. Chemically Enhanced CO_2 Gas Exchange in a Eutrophic Lake: A General Model. Limnol. and Oceanol., 20, 743-761.

Eugster H.P. and B.F. Jones, 1979. Behavior of major solutes During Closed-Basin Brine Evolution. Amer. J. Sci., 279, 609-631.

Fenchel, T., 1969. The Ecology of Marine Benthos IV. Structure and Function of the Benthic Ecosystem, It's Chemical and Physical Factors, and the Microfauna Communities with Special Reference to the Ciliated Protozoa. Ophelia, 6, 1-182.

Flores Espinosa, E., 1989. Stratigraphy and Sedimentology of the Upper Cretaceous Terrigenous Rocks and Coal of the Sabinas-Monclova Area, Northern Mexico. Dissertation, The University of Texas at Austin, 315pp.

Folk, R.L., 1974. The Natural History of Crystalline Calcium Carbonate: Effect of Magnesium Content and Salinity. Jour. Sed. Pet., 44 (1), 40-53.

Folk, R.L., and H.S. Chafetz, 1983. Pisoliths (Pisoids) in Quaternary Travertines of Tivoli, Italy. in: Peryt, T.M. (ed.) Coated Grains. Springer-Verlag, 474-487.

Folk, R.L., H.S. Chafetz, and P.A. Tiezzi, 1985. Bizarre Forms of Depositional and Diagenetic Calcite in Hot-Spring Travertines, Central Italy. in: Schneidermann, N. and Harris, P.M. (eds.) Carbonate Sediments. SEPM Spec. Pub. 36, 349-369.

Folk, R.L., and L.S. Land, 1975. Mg/Ca Ratio and Salinity: Two Controls over Crystallization of Dolomite. Amer. Asso. Pet. Geol. Bull., 59 (1), 60-68.

Froelich, P.N., Hambrick, G.A., Andrea, M.O. Mortlock, R.A. and J.M. Edmond, 1985. The Geochemistry of Inorganic Germanium in Natural Waters. J. Geophys. Res., 90, 1133-1141.

Garcia, E., R. Vidal, L.M. Tamayo, T. Reyna, R. Sanchez, M. Soto, E. Soto, 1975. Precipitation y Probabilidad de la Lluvia en la Republica Mexicana y su Evaluation. Comision de Estudios del Territorio Nacional, Instituto de Geografia, UNAM, 111 pp.

Gardner, W.S., D.S. Wynne and W.M. Dunstan. 1976.

Simplified Procedure for the Manual Analysis of Nitrate in Seawater. Mar. Chem. 4, 393-396.

Garrett, P., 1970a. Deposit Feeders Limit Development of Stromatolites. Bull. Amer. Asso. Pet. Geol. 54 (5), 848.

Garrett, P., 1970b. Phanerozoic Stromatolites: Noncompetitive Ecologic Restriction by Grazing and Burrowing Animals. Science, 169, 171-173.

Gebelein, 1976. Open Marine Subtidal and Intertidal Stromatolites (Florida, the Bahamas and Bermuda). in: Walter, M.R. (ed.) Stromatolites. Elsevier, New York, 381-388.

Geitler, L., 1932. Der Formwecehsel du pennaten Diatomeen. Arch. fur Protistenkunde, Jena, 78 (1), 1-226.

Gerdes, G. and W.E. Krumbein, 1984. Animal Communities in Recent Potential Stromatolites of Hypersaline Origin. in: Cohen, Y., R.W. Castenholz, and H.O. Halvorson (eds.) Microbial Mats: Stromatolites. Alan R. Liss, Inc., New York, 59-83.

Gerdes, G. and W.E. Krumbein, 1987. Biolaminated

Deposits. Springer-Verlag, N.Y., 183pp.

Golubić, S., 1973. The Relationship Between Blue-green Algae and Carbonate Deposits. In: Carr, N.G. and Whitton, B.A. (eds.) The Biology of the Blue-Green Algae. Blackwell Scientific Publications, 434-472.

Golubić, S., 1976a. Organisms That Build Stromatolites. in: Walter, M.R., (ed.) Stromatolites. Elsevier, 113-126.

Golubić, S., 1976b. Taxonomy of Extant Stromatolite-Building Cyanophytes. in: M.R. Walter (ed.) Stromatolites. Elsevier, 127-140.

Golubić, S, and A.G. Fischer, 1975. Ecology of Calcareous Nodules Forming in Little Conestoga Creek near Lancaster, Pennsylvania. Verh. Internat. Verein. Limnol. 19, 2315-2323.

Golubić, S. and R. Riding, 1990. Modern Stromatolites- A Progress Report. in: R. Riding (ed.) Calcareous Algae and Stromatolites. Springer-Verlag, New York, in press.

Gomes, N.A.de N.C. 1985. Modern Stromatolites in a Karst Structure From the Malmani Subgroup, Transvaal Sequence, South Africa. Trans. Geol. Soc. S. Afr., 88, 1-9.

Harris, G.P., 1978. Photosynthesis, Productivity and Growth: The Physiological Ecology of Phytoplankton. Ergeb. Limnol., 10, 1-169.

Humphrey, W.E., 1956. Tectonic Framework of Northeast Mexico. in: Rogers, J.K. (ed.) Transactions of the Gulf Coast Association of Geological Societies, San Antonio, 6, 25-35.

Hutchinson, G.E., 1967. A Treatise on Limnology. II. Introduction to Lake Biology and the Limnoplankton. John Wiley and Sons, New York, 1115pp.

Jones, B. and A. Motyka, 1987. Biogenic Structures and Micrite in Stalactites from Grand Cayman Island, British West Indies. Can. J. Earth Sci., 24, 1402-1411.

Jones, F.G. and B.H. Wilkenson, 1978. Structure and Growth of Lacustrine Pisoliths from Recent Michigan Marl Lakes. J. Sed. Petrol., 48, 1103-1110.

Jones, N.W., J.W. McKee, B. Marquez, D.J. Tovar, L.E. Long, and T.S. Laudon, 1984. The Mesozoic La Mula Island, Coahuila, Mexico. Geological Society of America Bull. 95, 1226-1241.

Jorgensen, B.B., Y. Cohen, and D.J. Des Marais, 1987. Photosynthetic Action Spectra and Adaption to Spectral Light Distribution in a Benthic Cyanobacterial Mat. Applied and Env. Microbiol., 53 (4), 879-886.

Jorgensen, B.B., N.P. Revsbeck and Y. Cohen, 1983. Photosynthesis and Structure of Benthic Microbial Mats: Microelectrode and SEM Studies of Four Cyanobacterial Communities. Limnol. Oceanogr., 28, 1075-1093.

Jorgensen, B.B., and N.P. Revsbeck, 1985. Diffusive Boundary Layers and the Oxygen Uptake of Sediments and Detritus. Limnology and Oceanography, 30, 111-122.

Kalkowsky, E., 1908. Oolith und Stromatolith im norddentschen Buntsandstein. Dtsch. Geol. Ges., 60, 68-125.

Kann, E., 1941. Krustensteine in Seen. Arch. Hydrobiol. 37 (4), 495-503.

Kann, E. and F. Sauer, 1982. Die "Rotbunte Tiefenbiocoenose" (Neue Beobachtungen in osterreichischen Seen und eine zusammenfassende Darstellung). Arch. Hydrobiol., 95 (1), 181-195.

Katz, A., 1973. The Interaction of Magnesium with Calcite During crystal Growth at 25-90 C and One Atmosphere. Geochimica et Cosmochimica Acta, 37, 1563-1586.

Kellum, L.B., R.W. Imlay and W.G. Kane. 1936. Evolution of the Coahuila Peninsula, Mexico, Part I. Relation of Structure, Stratigraphy and Igneous Activity to an Eary Continental Margin. Bull. Geol. Soc. Amer., 47 (7), 992-1006.

Kennard, J.M., and N.P. James, 1986. Thrombolites and Stromatolites: Two Distinct Types of Microbial Structures. Palaios, 1, 492-503.

Kingston, H.M., I.L. Barnes, T.J. Brady, T.C. Rains and M.A. Champ, 1978. Separation of Eight Transition Elements from Alkali and Alkaline Earth Elements in Estuarine and Seawater with Chelating resin and Their Determination by Graphic Furnace Atomic Absorption Spectrometry. Analytical Chemistry, 50, 2064-2070.

Kovach, W.L., 1986. M.V.S.P. A Multivariate Statistical package for the IBM PC and Compatibles Version 1-3. Department of Biology, Indiana University, 19pp.

Krumbein, W.E. and Y. Cohen, 1977. Primary Production, Mat Formation, and Lithification: Contribution of Oxygenic and Facultative Anoxigenic Cyanobacteria. in: Flugel, E. (ed.) Fossil Algae, Recent Results and Developments. Springer-Verlag, Berlin, 37-56.

Krumbein, W., and D. Werner, 1983. The Microbial Silica Cycle. in: Krumbein, W.E. (ed.) Microbial Geochemistry. Blackwell Scientific Pubs., 125-157.

Krylov, I.N., 1982. Lacustrine Stromatolites from the Kyzylgir Formation (Pliocene), Altai Mountains, USSR. Sed. Geol., 32, 27-38.

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

Lewin, J., 1966. Silicon Metabolism in Diatoms. V. Germanium Dioxide, a Specific Inhibitor of Diatom Growth. Phycologica 6 (1), 1-12.

Longoria, J.F., 1985. Tectonic Transpression in the Sierra Madre Oriental,Northern Mexico: an Alternative Model. Geology, 13, 453-456.

Lyons, W.B., D.T. Long, H.E. Gaudette and P.B. Armstrong,

1984. Calcification of Cyanobacterial Mats in Solar Lake, Sinai. Geology, 12, 623-626.

Maguire, B., Jr 1963. The Passive Dispersal of Small Aquatic Organisms and Their Colonization of Isolated Bodies of Water. Ecol. Monogr., 33, 161-185.

Marsh, P.C. 1984. Biota of Cuatro Ciénegas, Coahuila, Mexico. Preface: Proceedings of a Special Symposium Held During the Fourteenth Annual Meeting of the Desert Fishes Council, Arizona State University, Tempe, Arizona, U.S.A. 18-20 November 1983. Journal of the Arizona-Nevada Academy of Science v. 19 (1), 2-3.

McCall, P.L.and M.J. Tevesz, 1982. The effects of benthos on physical properties of freshwater sediments. in: P.L. McCall and M.J. Tevesz (eds.) Animal-sediment Relations, The biogenic alteration of sediments. Plenum Press, N.Y., 105-176.

McCoy, C.J. 1984. Ecological and Zoogeographic Relationships of Amphibians and Reptiles of the Cuatro Ciénegas Basin. Journal of the Arizona-Nevada Academy of Science, 19 (1), 49-60.

McIntire, C.D., 1966. Some Effects of Current Velocity on Periphyton Communities in Laboratory Streams. Hydrobiologia, 27, 559-570.

McIntire, C.D., 1973. Periphyton Dynamics in Laboratory Streams: A Simulation Model and its Implications. Ecol. Monogr., 43, 399-420.

McKee, J.W., N.M. Jones, and L.E. Long, 1984. History of a Recurrent Fault in Northeastern Mexico. Geology, 12, 103-107.

Meyer, E.R. 1973. Late -Quaternary Paleoecology of the Cuatro Ciénegas Basin, Coahuila, Mexico. Ecology, 54 (5), 982-995.

Minckley, W.L., 1963. The Ecology of a Spring Stream, Doe Run, Meade County, Kentucky. Wildlife Monographs, (11), 5-124.

Minckley, W.L. 1969. Environments of the Bolson of Cuatro Ciénegas, Coahuila, Mexico. Texas Western Press, The University of Texas at El Paso, 65pp.

Minckley, W.L. and Cole, G.A. 1968. Preliminary Limnologic Information on Waters of the Cuatro Ciénegas Basin, Coahuila, Mexico. Southwestern Naturalist, 13, 421-431.

Monty, C.L. 1965. Recent Algal Stromatolites in the Windward Lagoon, Andros Island, Bahamas. Ann. Soc. Geol. Belgique, 88 (6), 269-276.

Monty, C.L. 1967. Distribution and Structure of Recent Stromatolitic Algal Mats, Eastern Andros Island, Bahamas. Ann. Soc. Geol. Belgique, 90 (1-3), 55-100.

Monty, C.L. 1972. Recent Algal Stromatolitic Deposits, Andros Island, Bahamas. Preliminary Report. Geol. Rundschau, 61, 742-783.

Monty, C.L., 1973. Remarques Sur la Nature, la Morphologie et la Distribution Spatiale des Stromatolithes. Sciences de la Terre, 8, no. 3, Nancy, (France), 189-212.

Monty, C.L. 1976. The Origin and Development of Cryptalgal Fabrics. in: Walter, M.R. (ed.) Stromatolites. Elsevier, 193-249.

Monty, C.L. (ed.), 1981. Phanerozoic Stromatolites, Case Histories. Springer-Verlag, N.Y., 249 pp.

Monty, C.L., and L.A. Hardie, 1976. The Geological Significance of the Freshwater Blue-green Algal

Calcareous Marsh. in: Walter, M.R. (ed.) Stromatolites. Elsevier, 447-477.

Monty, C.L., and J.R. Mas, 1981. Lower Cretaceous (Wealdian) Blue-Green Algal Deposits of the Province of Valencia, Eastern Spain. in: Monty, C.L. (ed.) Phanerozoic Stromatolites Case Histories, Springer Verlag, 85-120.

Morafka, D.J., 1977. A Biogeographical Analysis of the Chihuahuan Desert Through Its Herpetofauna. W. Junk, the Hague, 313 pp.

Mortlock R.A. and P.N. Froelich, 1987. Continental Weathering of Germanium: Ge/Si in the Global River Discharge. Geochem. Cosmochem. Acta, 51, 2075-2082.

Murnane, R,M, and B.W. Winsborough (in prep) Water Chemistry Characteristics of the Cuatro Ciénegas Basin and Their Relationship to Diatom Growth.

Nancollas, G.H., K. Sawada and E. Schuttringer, 1983. Mineralization Reactions Involving Calcium Carbonates and Phosphates. in: Westbroek, P. and E.W. de Jong (eds.) Biomineralization and Biological Metal Accumulation, 155-169.

Nealson, K.H., 1983. Microbial Oxidation of Manganese and Iron. in: Westbroek, P. and E.W. de Jong (eds.), Biomineralization and Biological Metal Accumulation, D. Reidel Pub., 459-479.

Otto, C., 1983. Adaptations to Benthic Freshwater Herbivory. in: Wetzel, R.G. (ed.) Periphyton of Freshwater Ecosystems. W. Junk, The Hague, 199-205.

Padilla y Sanchez, R.J., 1982. Geologic Evolution of the Sierra Madre Oriental Between Linares, Conception Del Oro, Saltillo, and Monterrey, Mexico. Dissertation, The University of Texas at Austin, 217pp.

Parker, B. C. and G.M. Simmons Jr., 1981. Blue-green Algal Mats- Living Stromatolites- From Frigid, Light-limited Antarctic Lakes. Trends in Biochemical Sciences I-II, Elsevir.

Pentecost, A., 1988. Observations on the Growth Rates and Calcium Carbonate Deposition in the Green Alga Gongrosira. New Phytol., 110, 249- 253.

Percival, E., 1979 The Polysaccharides of Green, Red and Brown Seaweeds: Their Basic Structure, Biosynthesis and

Function. Br. Phycol. J., 14, 103-117.

Pianka, E., 1970. On r- and K-Selection. Amer. Natur., 104, 592-597.

Pinkava, D.J. 1984. Vegetation and Flora of the Bolson of Cuatro Ciénegas Region, Coahuila, Mexico: IV. Summary, Endemism and Corrected Catlogue. Journal of the Arizona-Nevada Academy of Science, 19 (1), 23-48.

Piper, A.M., 1944. A Graphic Procedure in the Geochemical Interpretation of Water-Analyses. Trans. Amer. Geophys. Union, part 6, 914-928.

Pursell, V.J., 1985. The Petrology and Diagenesis of Pleistocene and Recent Travertines from Gardiner, Montana, and Yellowstone National Park, Wyoming. Unpublished Masters Thesis, Department of Geological Sciences, The University of Texas at Austin, 153pp.

Revsbeck, N.P., 1983. In Situ Measurement of Oxygen Profiles of Sediments by Use of Oxygen Microelectrodes. In: Polarographic Oxygen Sensors. Ed. by E. Gnaiger and H. Forsner. Springer Verlag, New York, 265-273.

Revsbeck N.P. and D.M. Ward, 1984. Microelectrode

Studies of Interstitial Water Chemistry and Photosynthesis Activity in a Hot Spring Microbial Mat. Appl. Environ. Microbiol., 48, 270-275.

Rippka, R., J. Deruelles, J.B. Waterbury, M. Herdman and R.Y. Stanier, 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.

Rosowski, J.R., Roemer, S.C., Palmer, J., Hoagland, K.D., 1986. Extracellular Association and Adaptive Significance of the Bas-Relief Mucilage Pad of Achnanthes lanceolata (Bacillariophyceae). Diatom Research, 1, (1), 113-129.

Round, F. 1981. The Ecology of Algae. Cambridge University Press, N.Y., 653 pp.

Schafer, A. and K.R.Stapf, 1978. Permian Saar-Nahe Basin and Recent Lake Constance (Germany): Two Environments of Lacustrine Algal Carbonates. Spec. Pub. Int. Assoc. Sedimentol., 2, 83-107.

Schlichting, H.E., 1960. The Role of Waterfowl in the Dispersal of Algae. Trans. Amer. Microscopical Soc., 79 (2), 160-166.

Schlichting, H.E., 1969. The Importance of Airborne Algae and Protozoa. Jour. of Air Pollution Control Asso., 19 (12), 946-951.

Smith, H., 1982. Light Quality, Photoperception, and Plant Strategy. Ann. Rev. Plant Physiol., 33, 481-518.

Sterner, R.W., 1986. Herbivores' Direct and Indirect Effects on Algal Populations. Science, 231, 605-607.

Stevenson, R.J., and C.G. Peterson, 1989. Variation in Benthic Diatom (Bacillariophyceae) Immigration With Habitat Characteristics and Cell Morphology. Jour. Phycol., 25 (1), 120-129.

Strickland, J.D. and T.R. Parsons, 1968. A Practical Handbook of Seawater Analysis. Fisheries Res. Board of Canada, Bull., 167, 311pp.

Torgersen, T., P. De Deckker, A.R. Chivas and J.M. Bowler, 1986. Salt Lakes: A discussion of Processes Influencing Palaeoenvironmental Interpretation and

Recommendations for Future Study. Paleogeography, Paleoclimatology, Paleoecology, 54, 7-19.

Voss, P.C., P.L. de Boer, and R. Misdorp, 1988. Sediment Stabilization by Benthic Diatoms in Intertidal Sandy Shoals; Qualitative and Quantitative Observations. in: P.L. de Boer et al. eds., Tide-Influenced Sedimentary Environments and Facies. D. Reidel Pub. Co., pp. 511-526.

Walter, M.R. (ed.), 1976. Stromatolites. Developments in Sedimentology 20. Elsevier Scientific., 790 pp.

Walker, K.R. and W.W. Diehl, 1986. The Effect of Synsedimentary Substrate Modification of the Composition of Paleocommunities: Paleoecologic Succession Revisited. Palaios, 1, 65-74.

Weidie, A.E., and G.E. Murray, 1961. Tectonics of the Parras Basin, States of Coahuila and Nuevo Leon, Mexico. Trans. Gulf Coast Asso. Geol. Soc. 11, 47-56.

Weidie, A.E., J.A. Wolleben and E.F. McBride, 1978. Regional Geologic Framework of Northeastern Mexico. in: Corpus Christi Geol. Society 1978 Spring Field Conference, Minas de Golondrinas and Minas Rancherias, Northeastern Mexico, 48 pp.

Weiss, M.R., 1970. Oncolites Forming on Snails (_Goniobasis_. J. Paleontol., 44, 765-769.

Wetzel, R.G., 1975. Limnology. W.B. Saaunders Co., Phila.,743 pp.

Winsborough, B.M. and J-S. Seeler, 1986. The Relationship of Diatom Epiflora to the Growth of Limnic Stromatolites and Micronbial Mats. in: M. Ricard (ed) Proceedings of the 7th International Symposium on Living and Fossil Diatoms, Paris, 1984, 395-407.

Winsborough, B.M. and S. Golubić, 1987. The Role of Diatoms in Stromatolite Growth: Two Examples from Modern Freshwater Settings. Jour. Phycology, 23 (1), 194-201.

Winsborough, B.M., J-S. Seeler, S. Golubić, R.L. Folk, B. Maguire, Jr., 1990 (in press). Fresh-water Stromatolites, Oncoids, and Coated Pebbles from a Spring-fed Lake in Northeastern Mexico. Elsevier.

Young, K., 1983. Mesozoic History of Mexico. in: Moullade, M. and A.E. Narm (eds.) the Phanerozoic Geology of the World, vol. 2, part B. Elsevier Sci. Pub. 61-88.

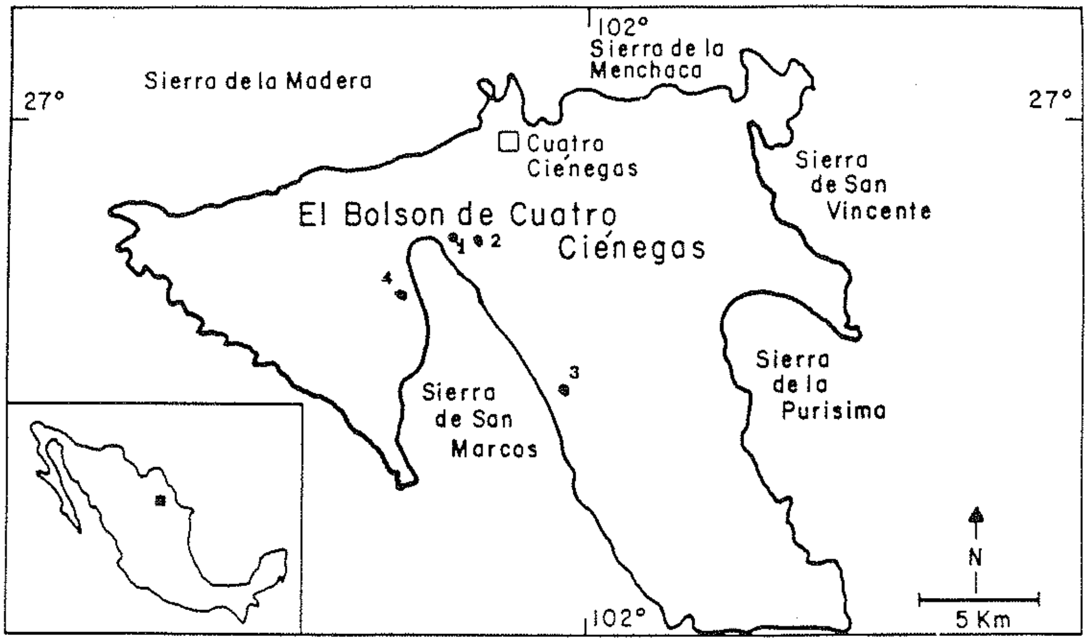


Fig. 1.4.1-1. Location map of the Cuatro Ciénegas Basin showing the town of Cuatro Ciénegas and the general outline of the basin floor. Numbers refer to stromatolite sites described in the text: 1. Laguna El Mojarral, 2. Rio Mesquites, 3. Pozo Azul, 4. Laguna Garabatal.

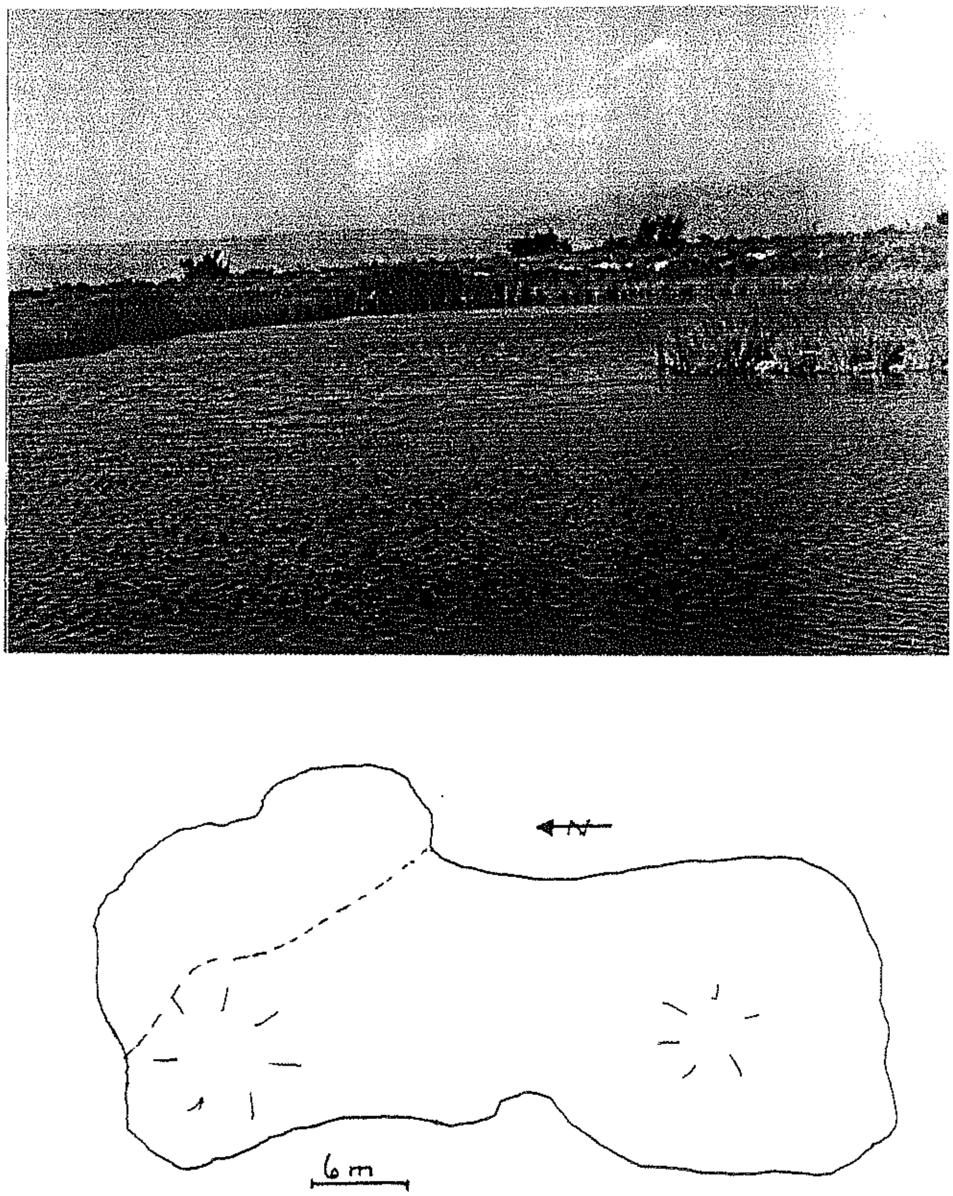


Fig. 3.1.1-1. A. Photo of Laguna El Mojarral West looking N.W. B. Plane table and alidade survey of Laguna El Mojarral West.

Fig. 3.1.2.1-1A,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, in the absence of grazing by fish. This structure will eventually topple over as the stem rots away; then it will become a potential nucleus for future stromatolite development. Scale bar is in cm.

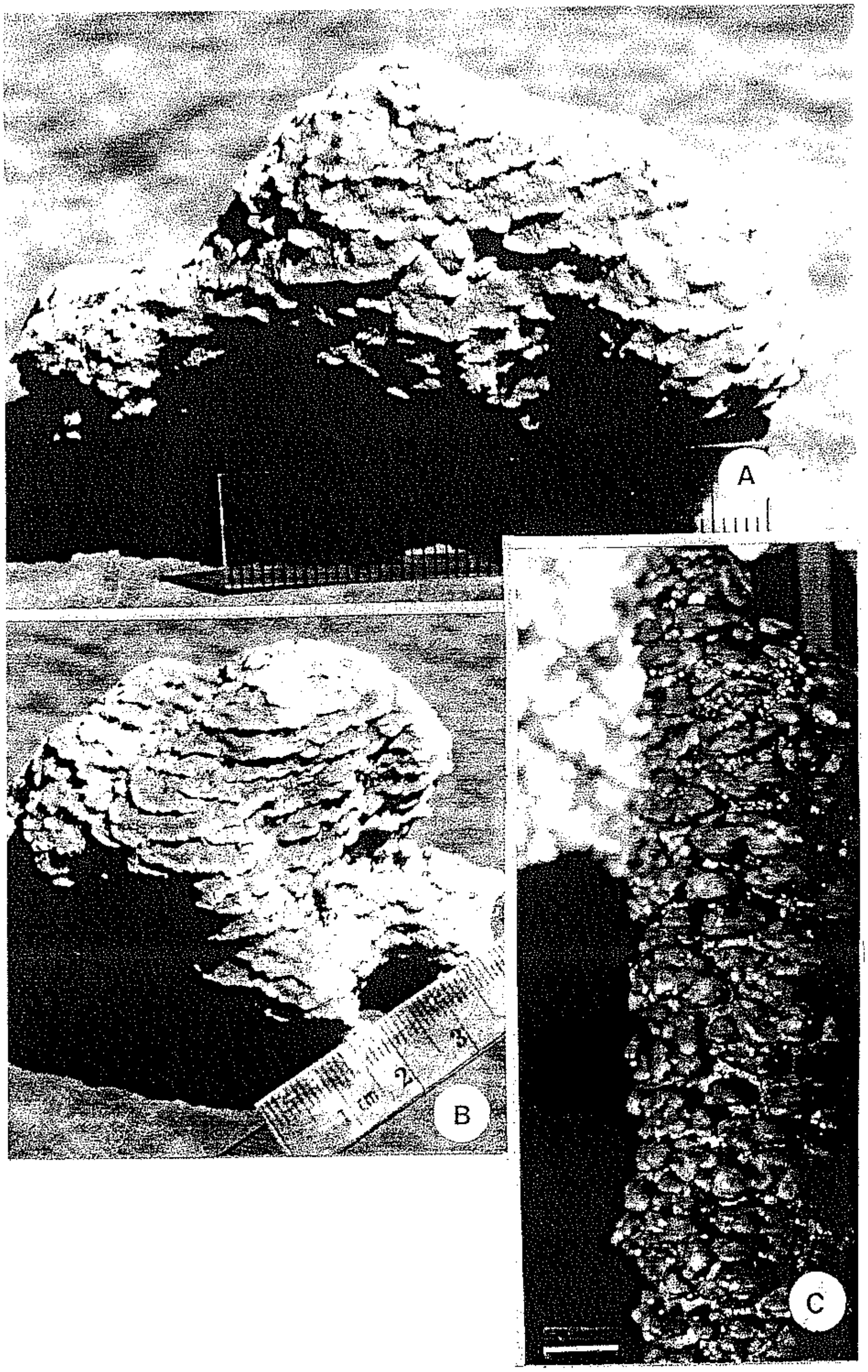
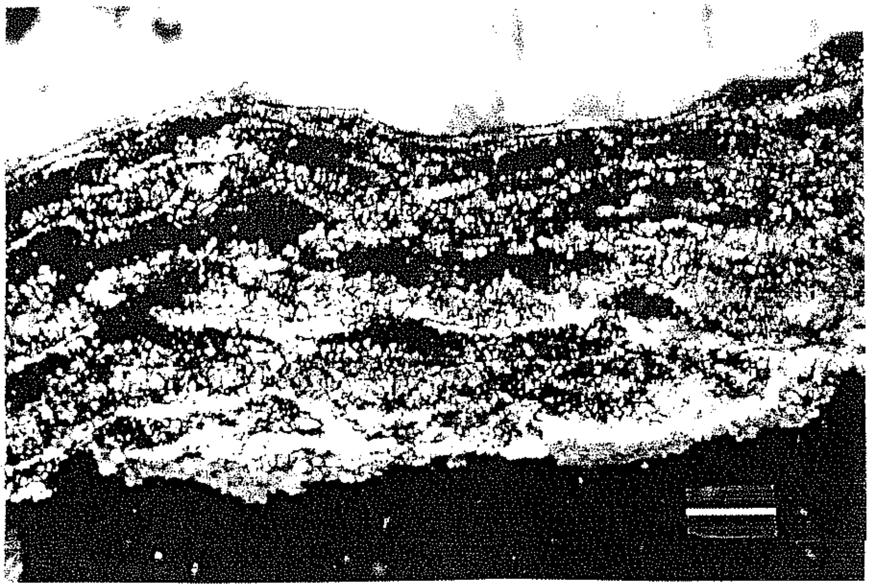

A
B
1 cm
2
3
C

Fig. 3.1.2.1-2A,B. Sections cut parallel to growth direction, through an actively growing stromatolite mat. Note the alternation of carbonate-and organic-rich laminae comprising a vertical sequence from bedrock to present growth surface. White layers represent carbonate-encrusted filaments of *Homoeothrix balearica*; the green unencrusted layers are dominated by *Schizothrix lacustris*. Scale bar = 2 mm.



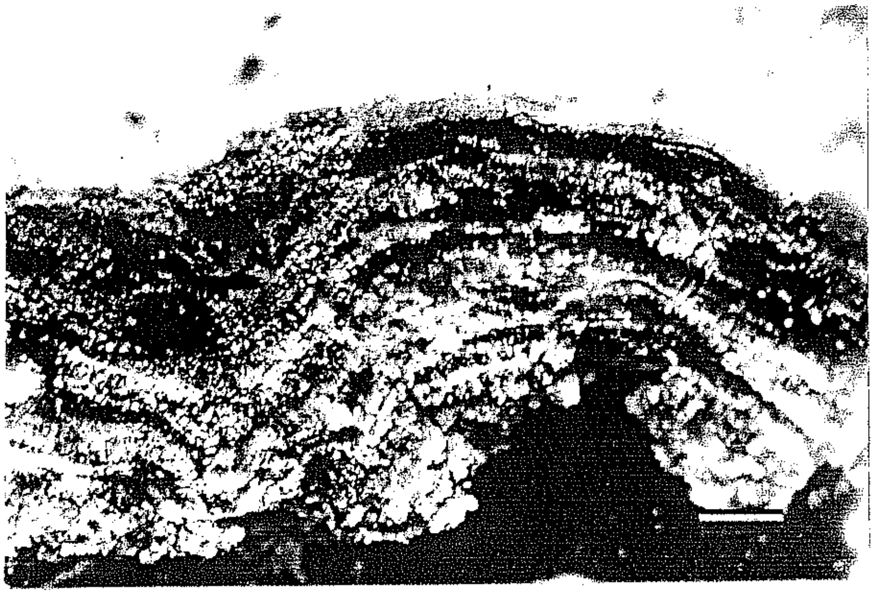


Fig. 3.1.2.2-1A,B,C,D. Community architecture of El Mojarral stromatolites. A. Micrograph of the top layer of El Mojarral stromatolite mat showing dark calcitic encrustations surrounding tapering filaments of *Homoeothrix balearica* among *Schizothrix lacustris*. Scale bar = 50 um. B. Detail showing encrusted *H. balearica* filament on lower right, dark triangular area near center of photo represents filament emerging from encrustation. Note thin monocrystalline calcite tubes precipitated around *Schizothrix* sp. filaments (arrows). Scale bar = 20 um. C. *S. lacustris* exhibiting typical branching of filament. Note also filamentous purple bacteria among *Schizothrix* sheaths (arrow). Scale bar = 10 um. D. Resin-embedded and decalcified thin section through cyanobacterial and diatomaceous community from mouth of the inflow cave. Note *Eunotia* cf. *maior* (e) and *H. balearica* (short filament, h) on the surface and an endolithic undescribed stigonematalean cyanobacterium (s) and *Plectonema terebrans* (p) below. Scale bar = 10 um. (A = plane transmitted light; B,C, = Nomarski differential interference contrast.

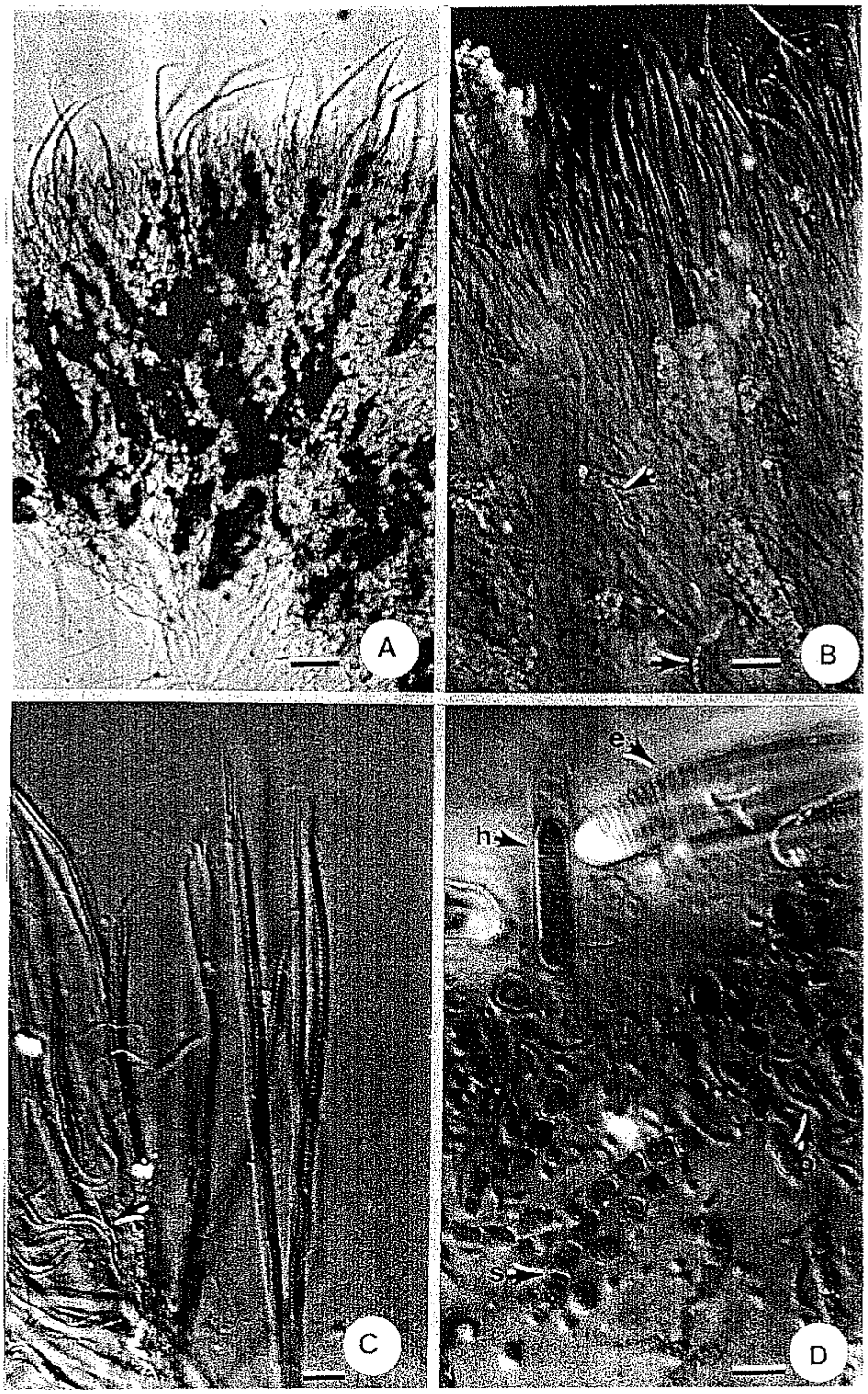
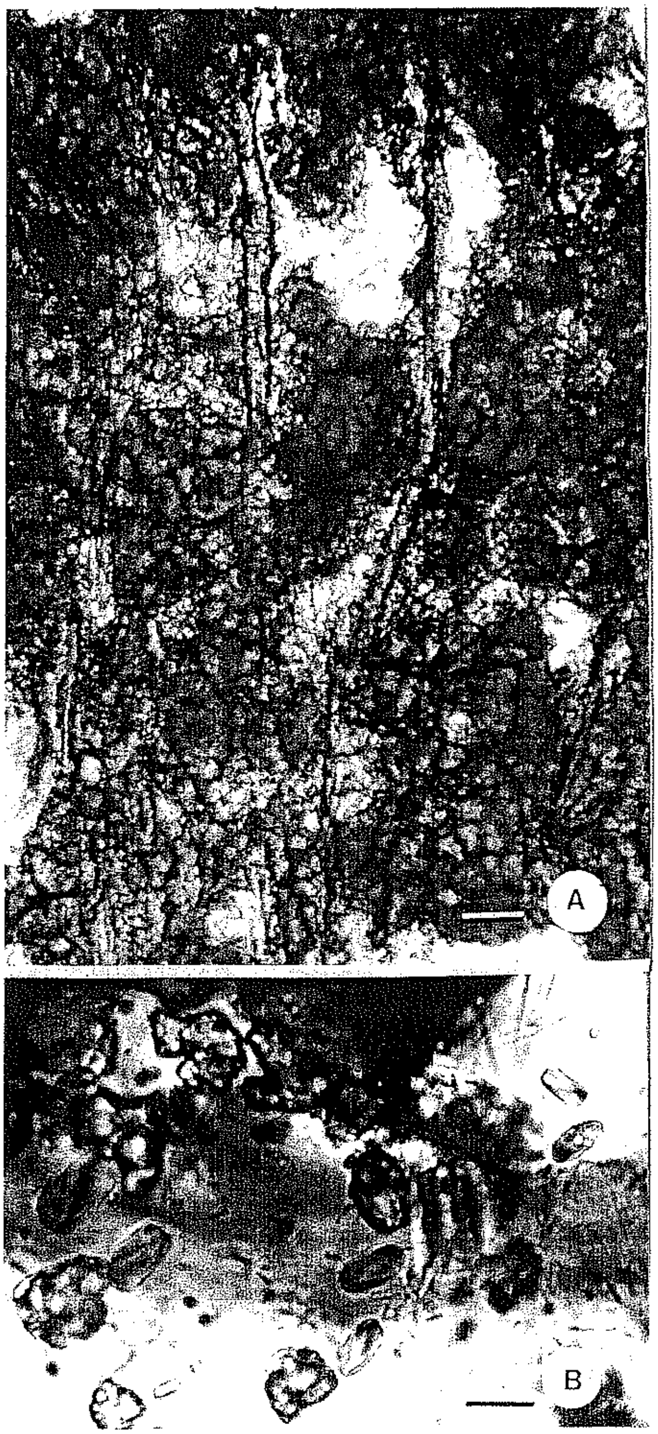

A
B
C
e
h
s
D

Fig. 3.1.2.3-1. 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 um.


A
B

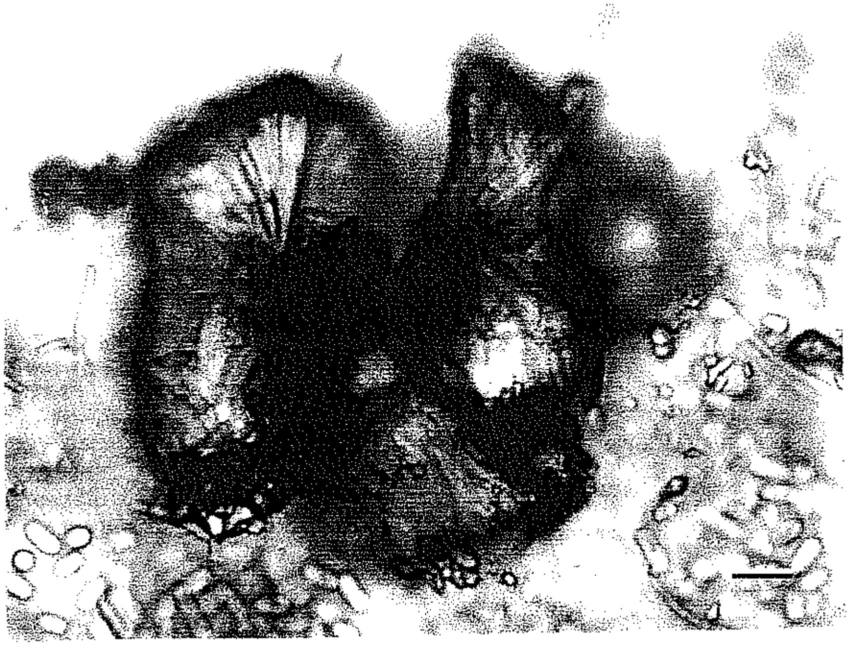


Fig. 3.1.2.3-2. Cluster of radial calcite crystals embedded in a gelatinous mass of Schizothrix and Synechococcus. Scale bar = 5 um.

Fig. 3.1.2.3-3. SEM view of cavity-lining micritic and microsparitic cement in cortex of El Mojarral 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 um.

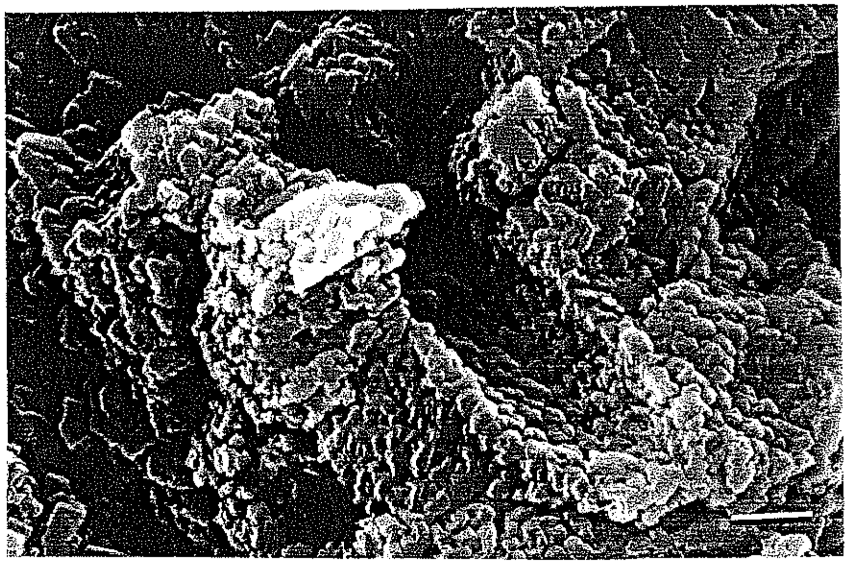


Fig. 3.1.2.3-4. SEM view of coat of calcite crystals left behind after unidentified central filament was digested with chlorox. Scale bar = 1 um.

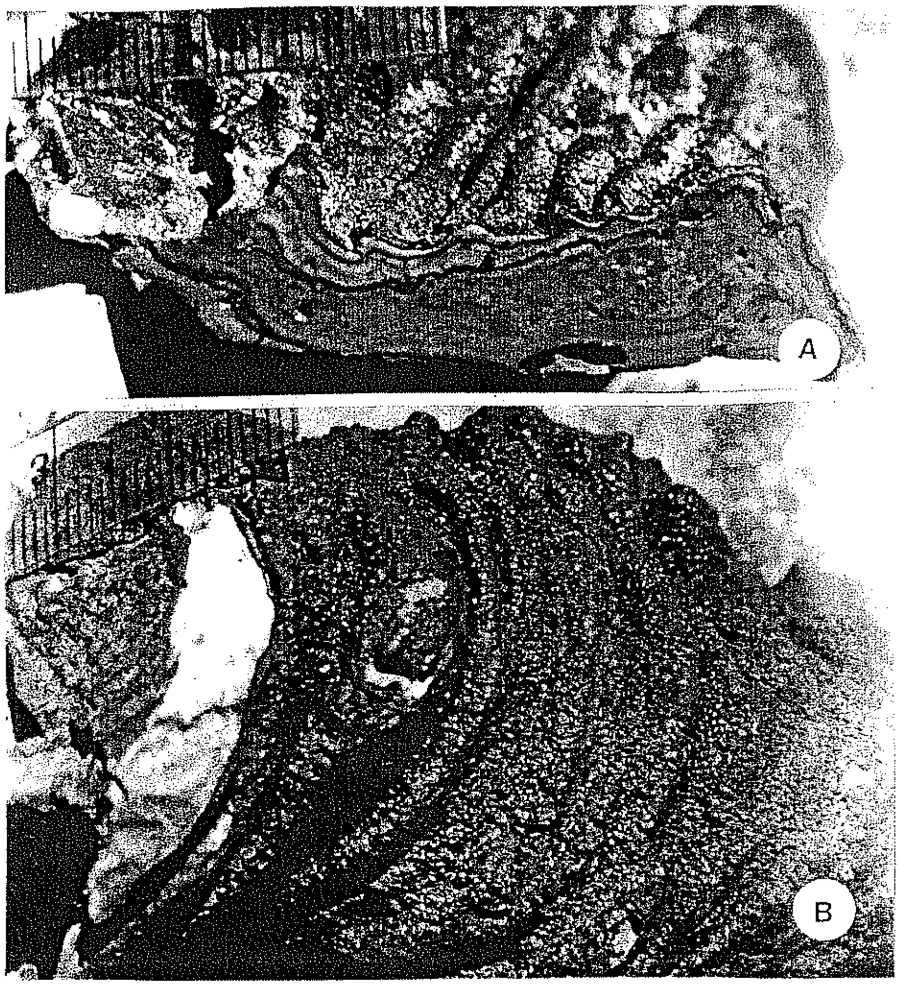


Fig. 3.1.3.1-1A,B. A. Cross-section of El Mojarral cave stromatolite showing light colored calcareous laminae which locally thickens to form sets of parallel ridges on the growing surface, and black laminae rich in metallic oxides (Fe, Mn). Scale in mm. B. Wrinkled surface covered with botryoidal accretions of metallic oxides. Scale bar in cm and mm.

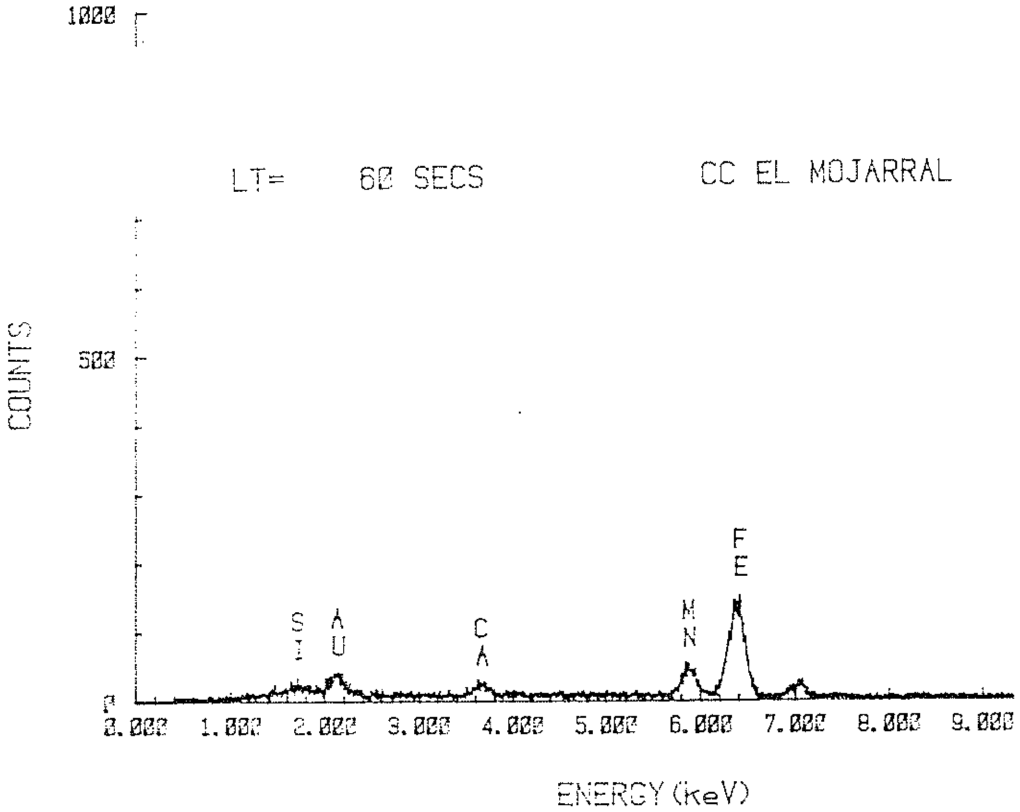


Fig. 3.1.3.3-1. EDX trace of iron- and manganese-rich surface of El Mojarral cave stromatolite.

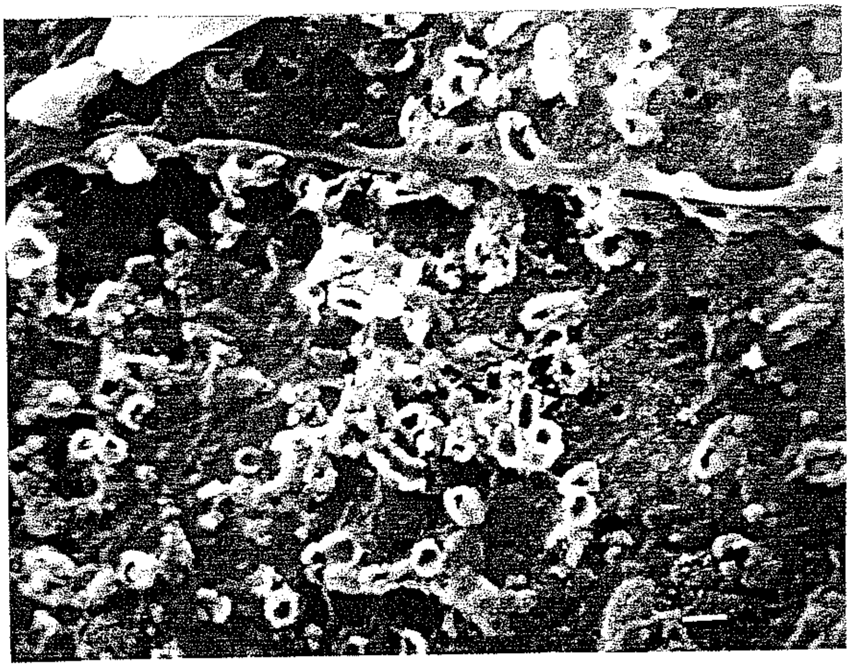


Fig. 3.1.3.3-2 Surface of metal-rich lamina showing oxides coating cyanobacterial sheaths. Scale bar = 10 um

Fig. 3.1.3.3-3A,B,C. Thin section of cave stromatolite. A. Calcareous laminae capped by metal-righ surface. Arrows point to short strands of opaque micrite. B. Cloudy peloids filling interstices. C. Peloids with multiple generations of cements, shown by arrows. Scale bars = 200um.

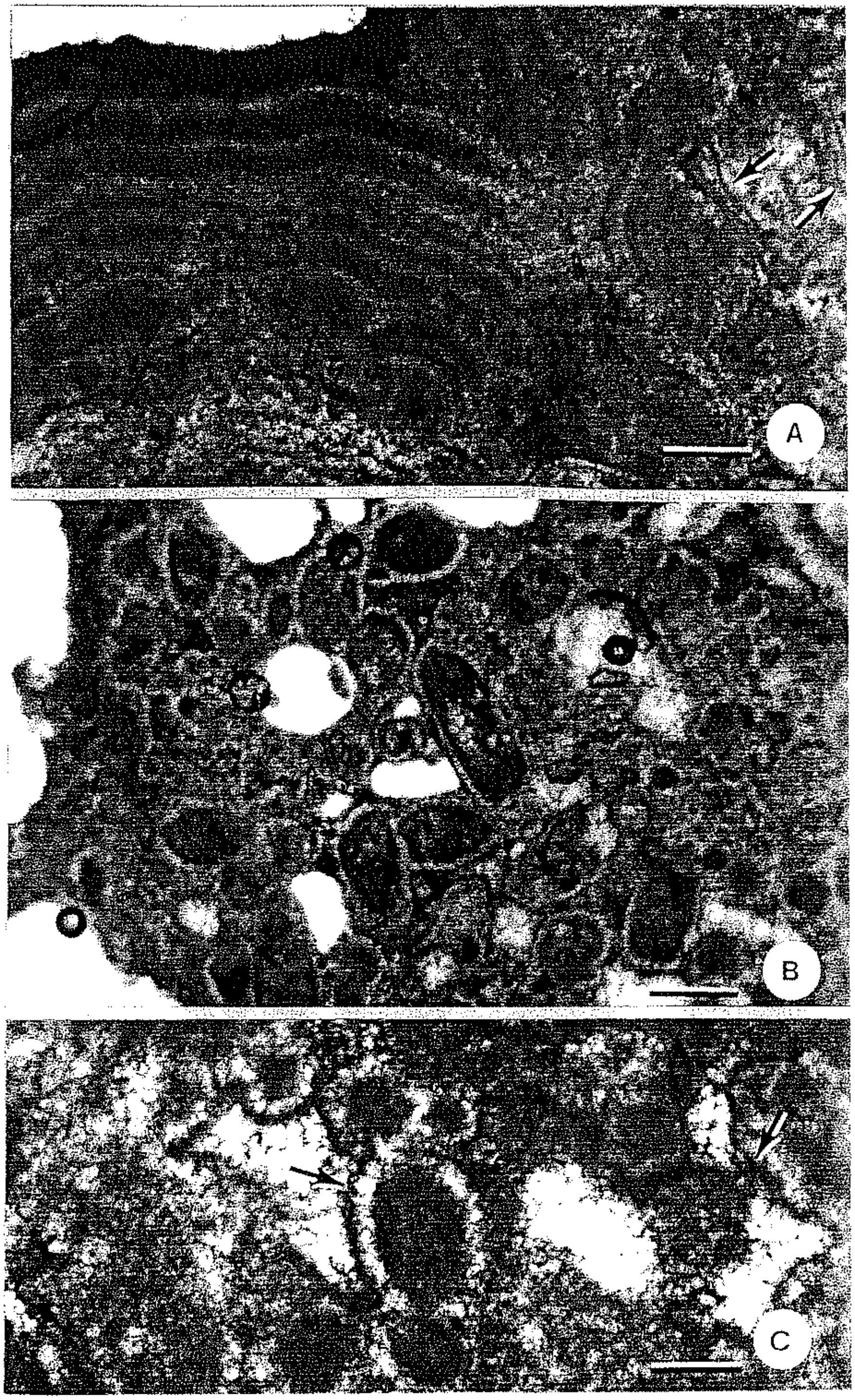

A
B
C

Fig. 3.1.4.1-1A,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 bar in cm.


A
B

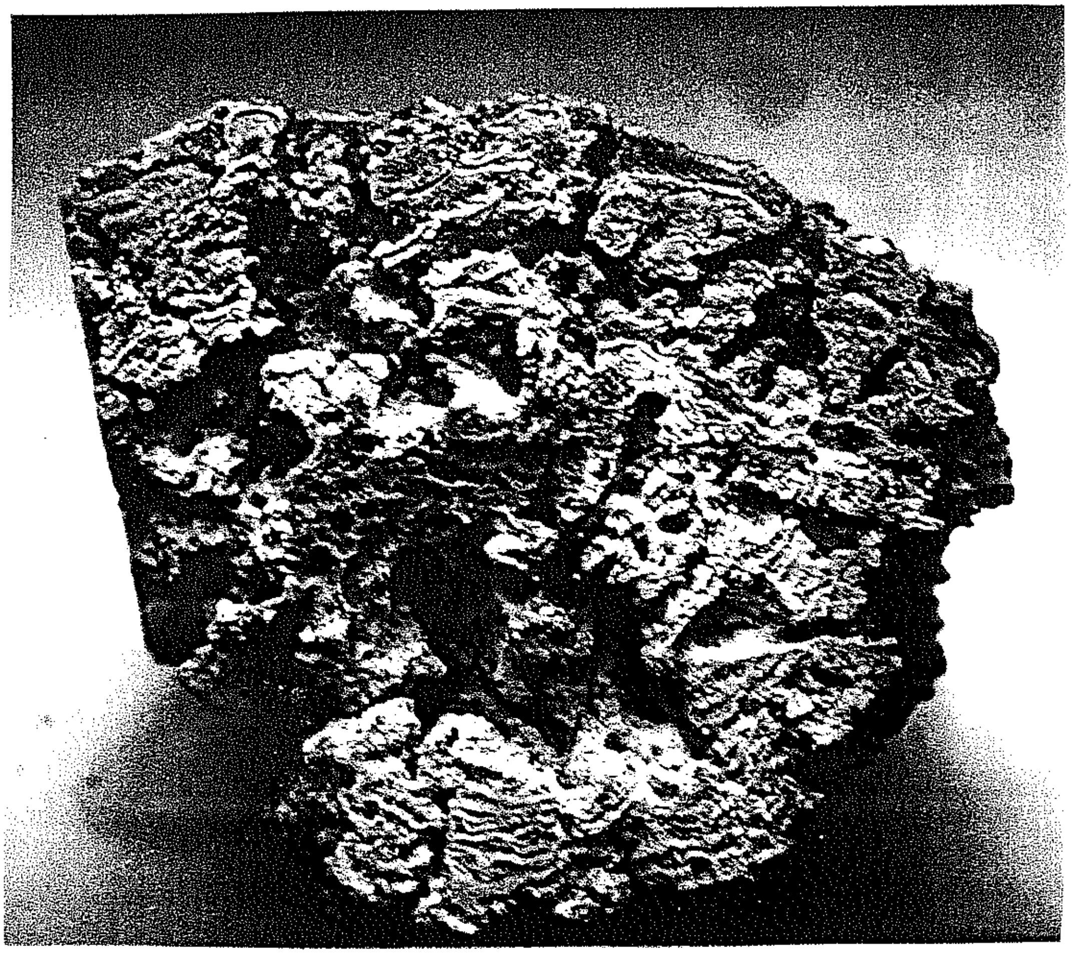


Fig. 3.1.4.3-1. Sawn section through typical oncoid. Dark center is nucleus of porous tufa. Scale bar = 5 mm.

Fig. 3.1.4.3-2A,B. A. Thin section about 1 cm into interior of oncoid showing Homoeothrix filaments in growth position. B. Higher magnification showing micritic calcite at position of former filament surface. Note interlocking sparry calcite crystals between filaments. Scale bars = 10 um.

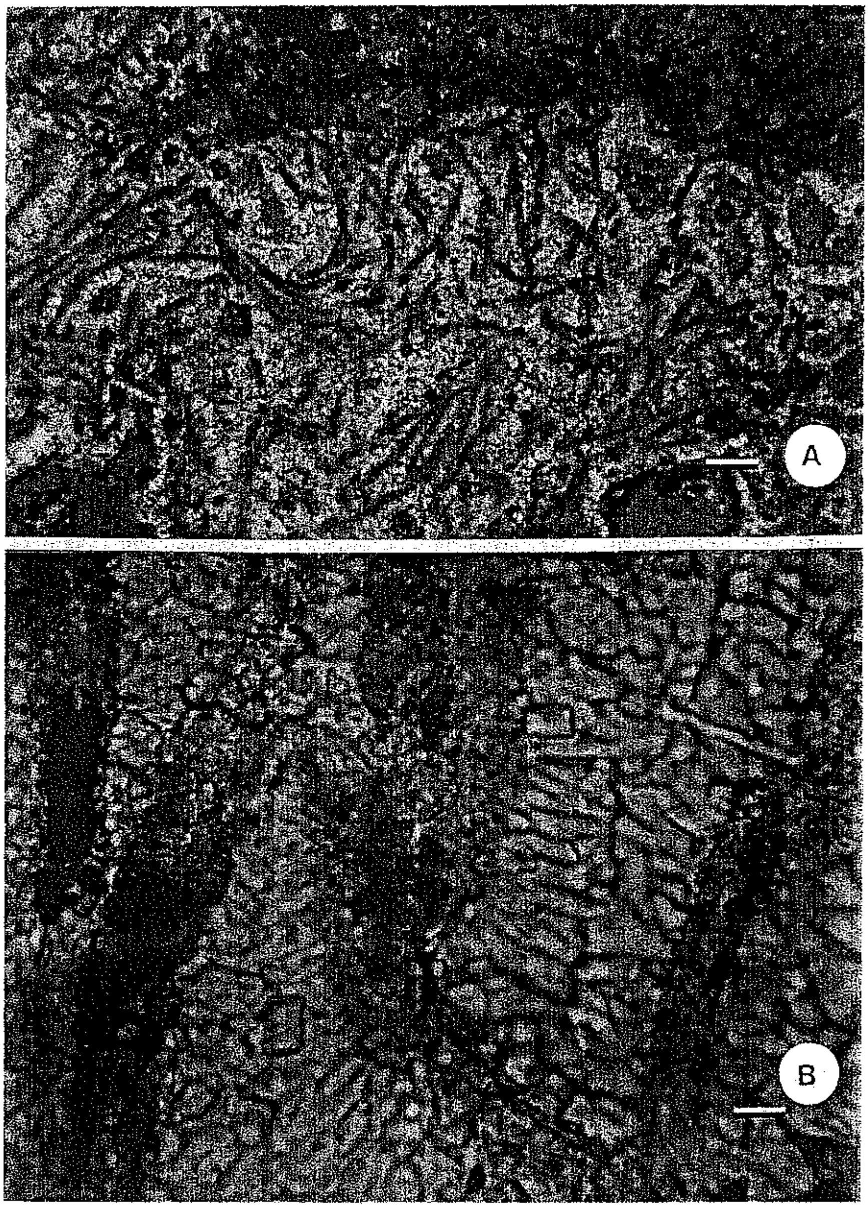

A
B

Fig. 3.1.4.3-3A,B. Sem view of calcite crystals lining cavity in cortex of oncoids. Rows of micrite-sized crystal growths ornament the face of a spar crystal. A. Scale bar = 5 um. B. Scale bar = 1 um.

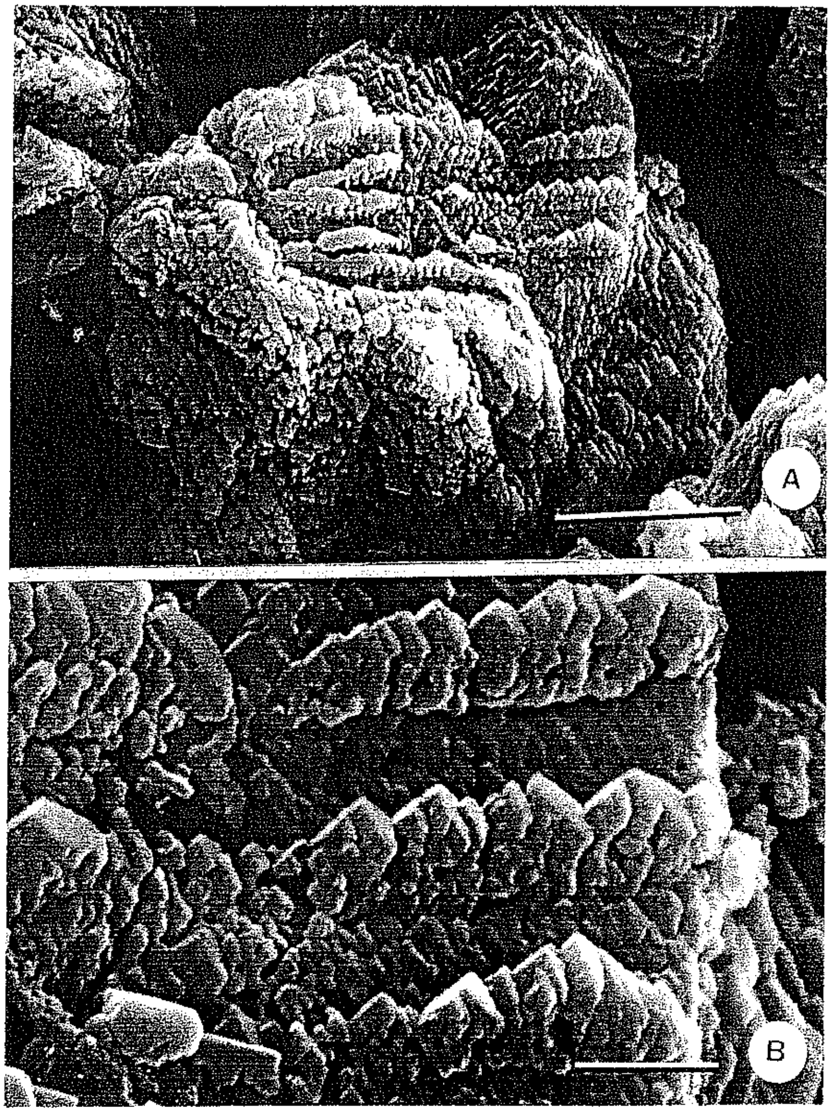

A
B

Fig. 3.1.4.3-4. Quartz crystals liberated by acid treatment of stromatolite mat. Note possible cyanobacterial or fungal filaments in crystal on lower left (see arrows). Scale bar = 10 um.

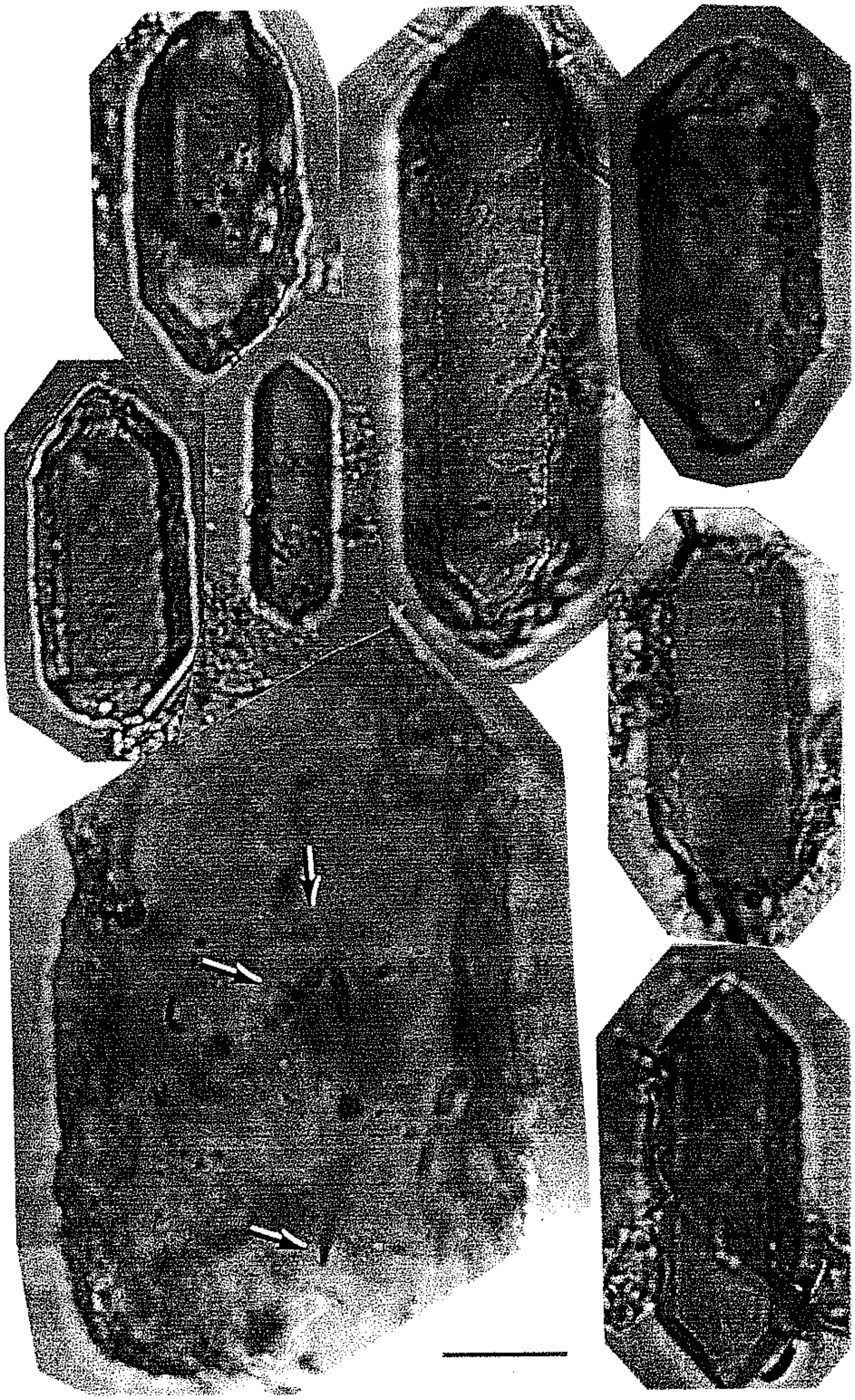
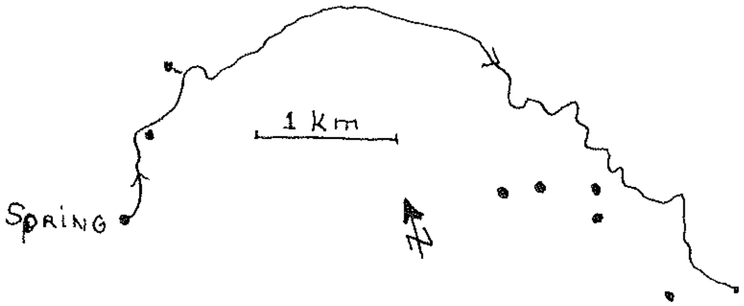


Fig. 3.2.1-1A,B,C. A. Map of Rio Mesquites traced from CETENAL 1:50,000 map of Cuatro Ciénegas Basin. Circles are springs that contribute to the flow of the stream. B. View of the Rio Mesquites about 4 km from the headwaters. Note characteristic marsh vegetation and absence of trees. Side stream at center of photo carries water from a nearby spring. Stream width is about 8-10 m. C. Lower part of Rio Mesquites where it broadens to form a lake. Width is about 50-60 m (note swimmer for scale).


1 Km
SPRING
N

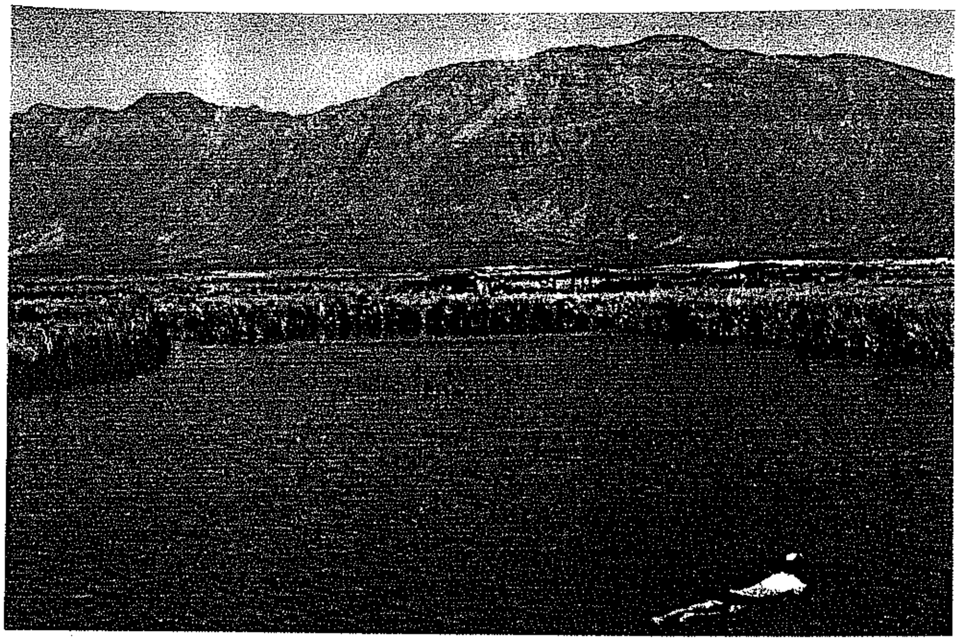
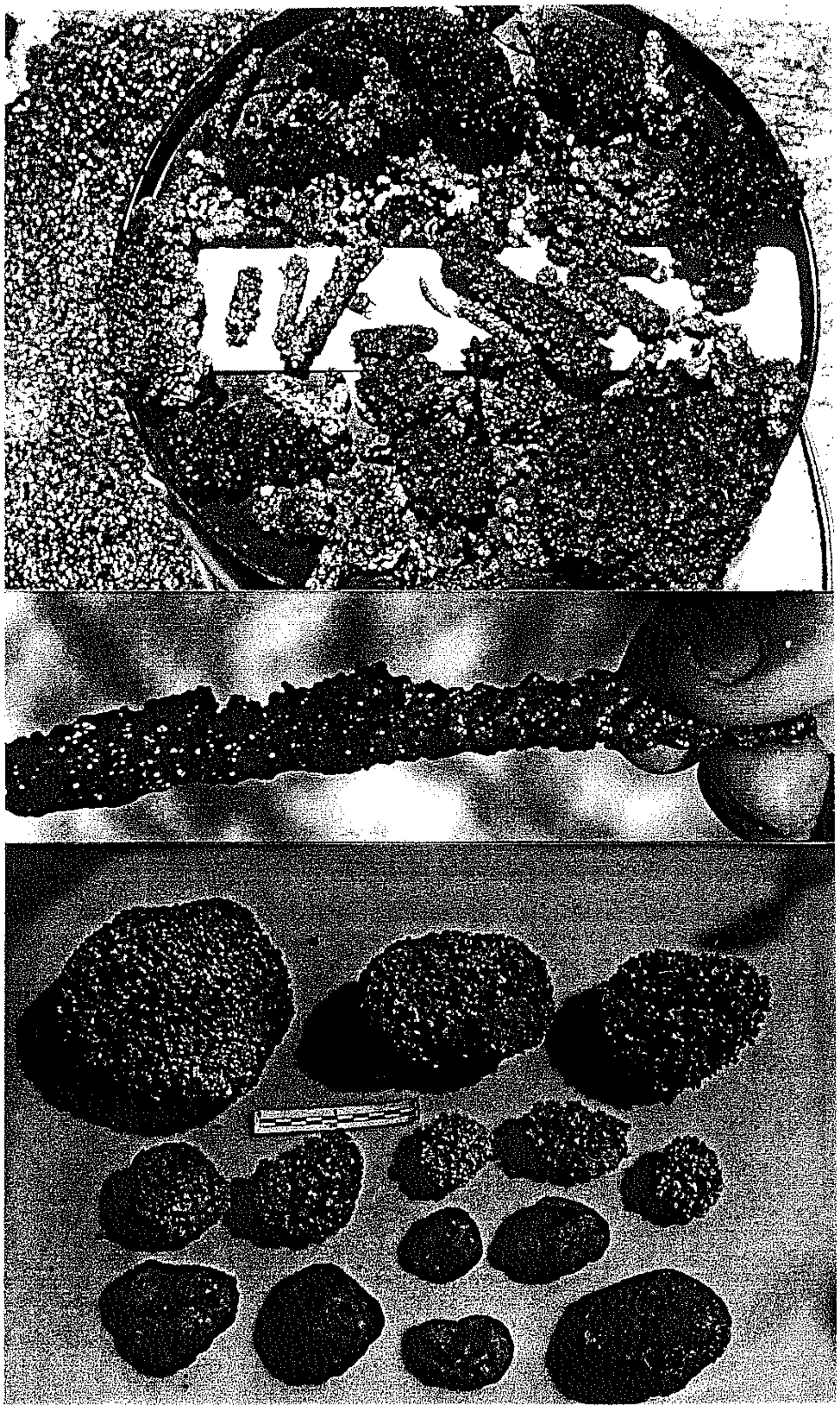


Fig. 3.2.2-1. Elongate stromatolite at the margin of the Rio Mesquites. Length is about 1 m.

Fig. 3.2.2-2A,B,C. A. Small oncoids collected at random from the middle reaches of the Rio Mesquites. Scale bar in mm. B. Cylindrical oncoid that has beed dipped halfway in a marker solution of synthetic graphyte (left half) and replaced in the stream. C. Oncoids from the upper and lower reaches of the Rio Mesquites illustrating the range of morphological variation. Scale bar in cm.



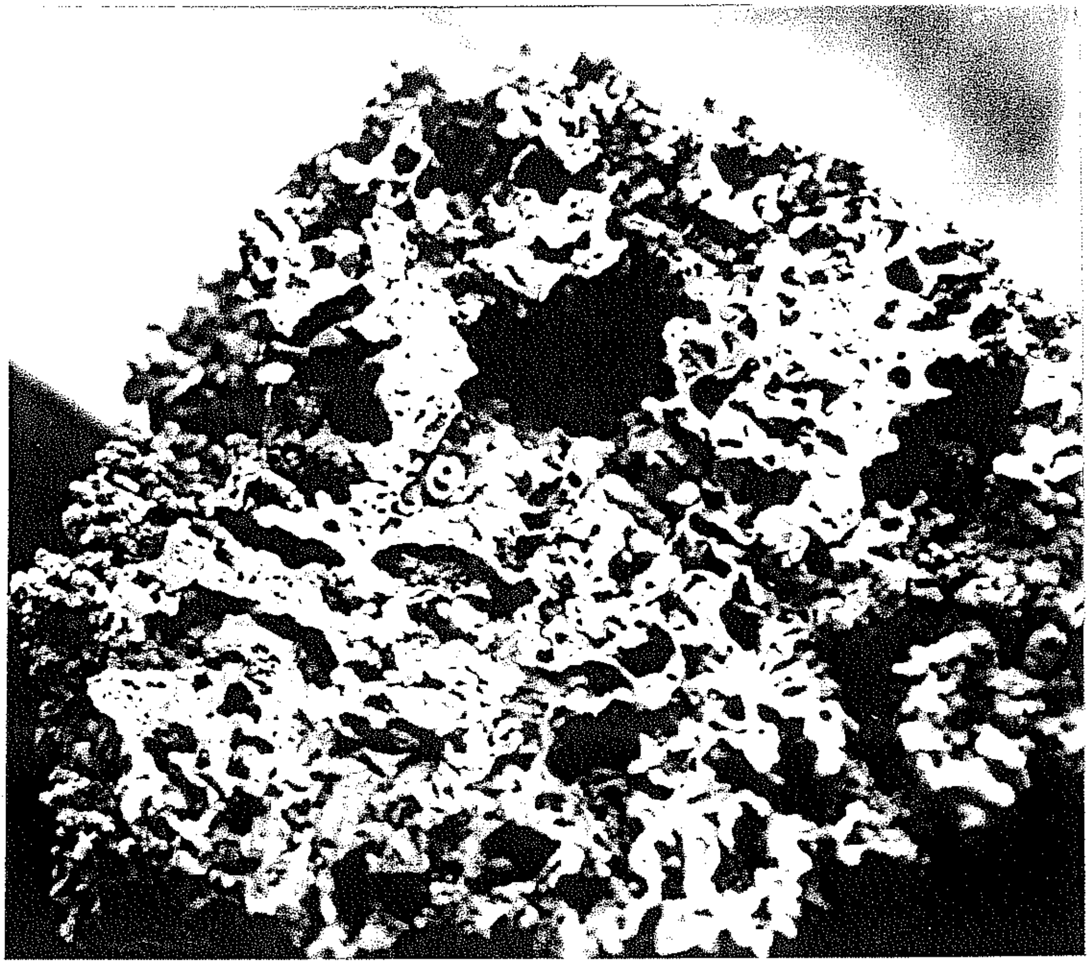


Fig. 3.2.2-3. Sawn face of Rio Mesquites oncoid. True scale.

Fig. 3.2.3-1. Photomicrographs of Gongrosira calcifera colony on surface of Rio Mesquites oncoid. Gongrosira filaments parallel to growth. Note laminated carbonate tubes surrounding the individual filaments. Scale bar = 20 um.

Fig. 3.2.4-1A,B. SEM views of interior of Rio Mesquites oncoids. A. Spar crystals lining cavity. Scale bar = 10 um. B. Composition of oncoid interior. Note spar crystal in lower center with irregular rounded faces, and chain of diatoms (*Fragilaria*) across upper part of photo. Scale bar = 50 um.

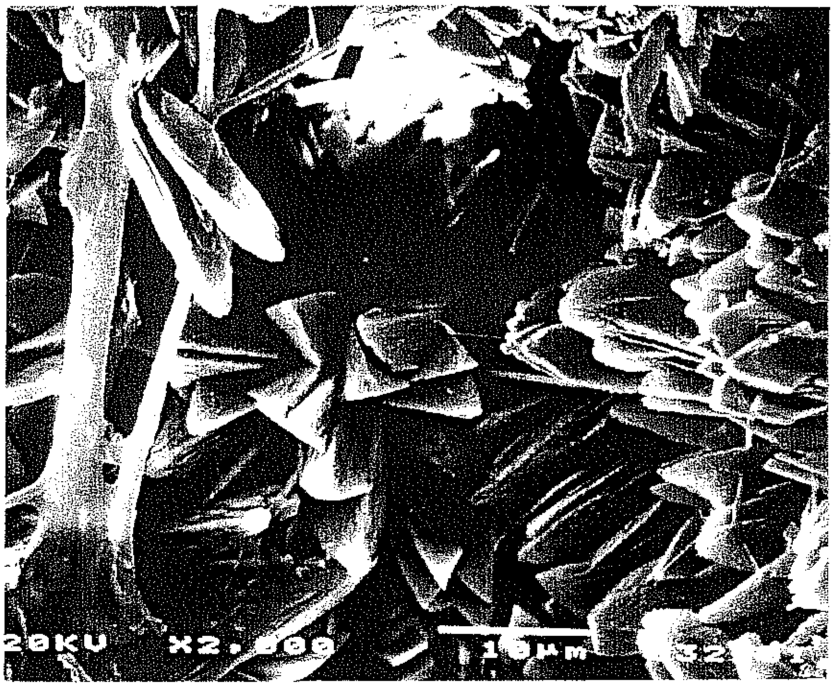
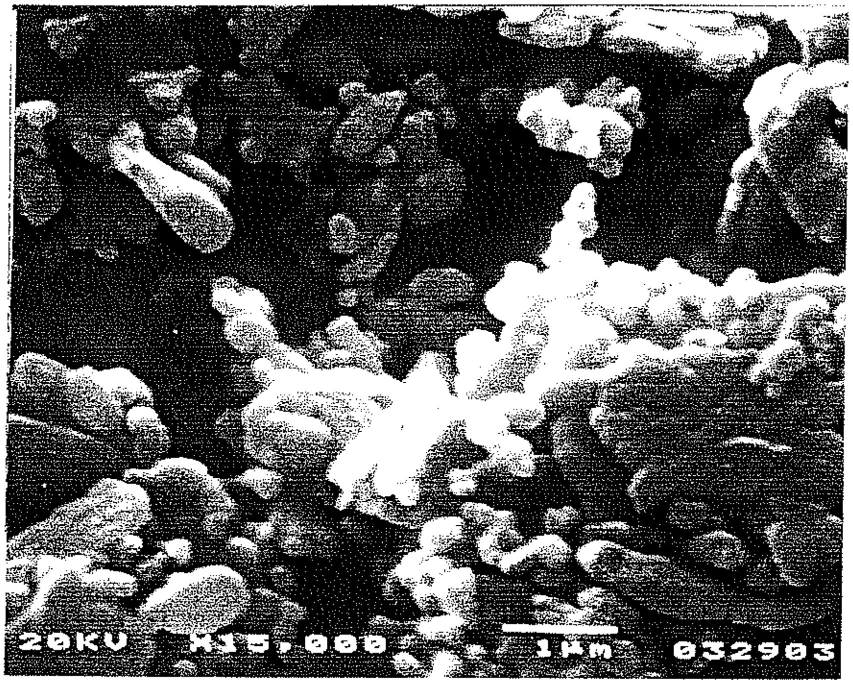

20KU
X2,000
10µm
32

Fig. 3.2.4-2A,B. SEM views of untreated Rio Mesquites material showing calcified bacteria from interior of a hard nubbin-like projection broken from an oncoid surface. Note that calcification occurs preferentially in layers or sheets about the thickness of 1 bacterial cell. Scale bars = 1 um.


20KV
X15,000
1µm
032903

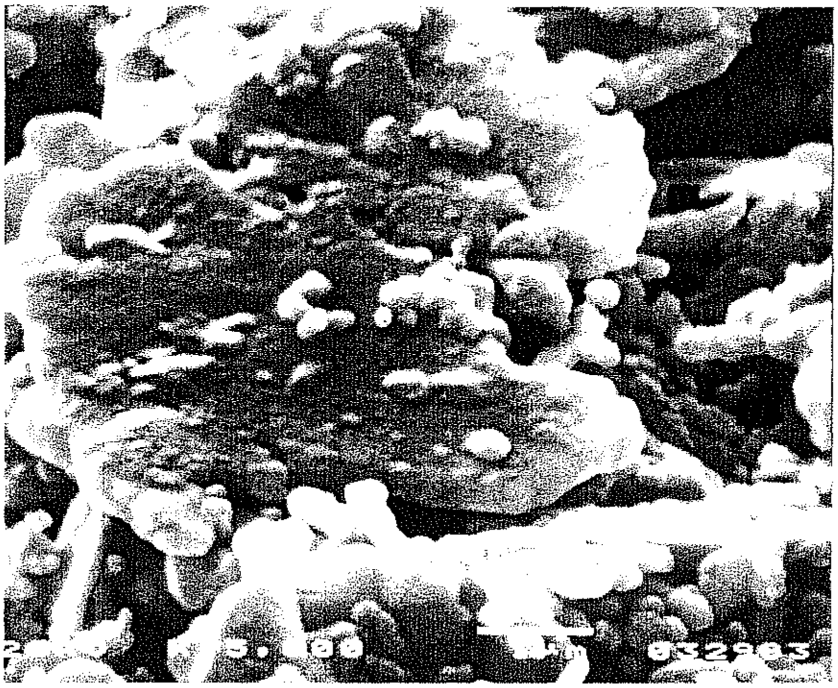
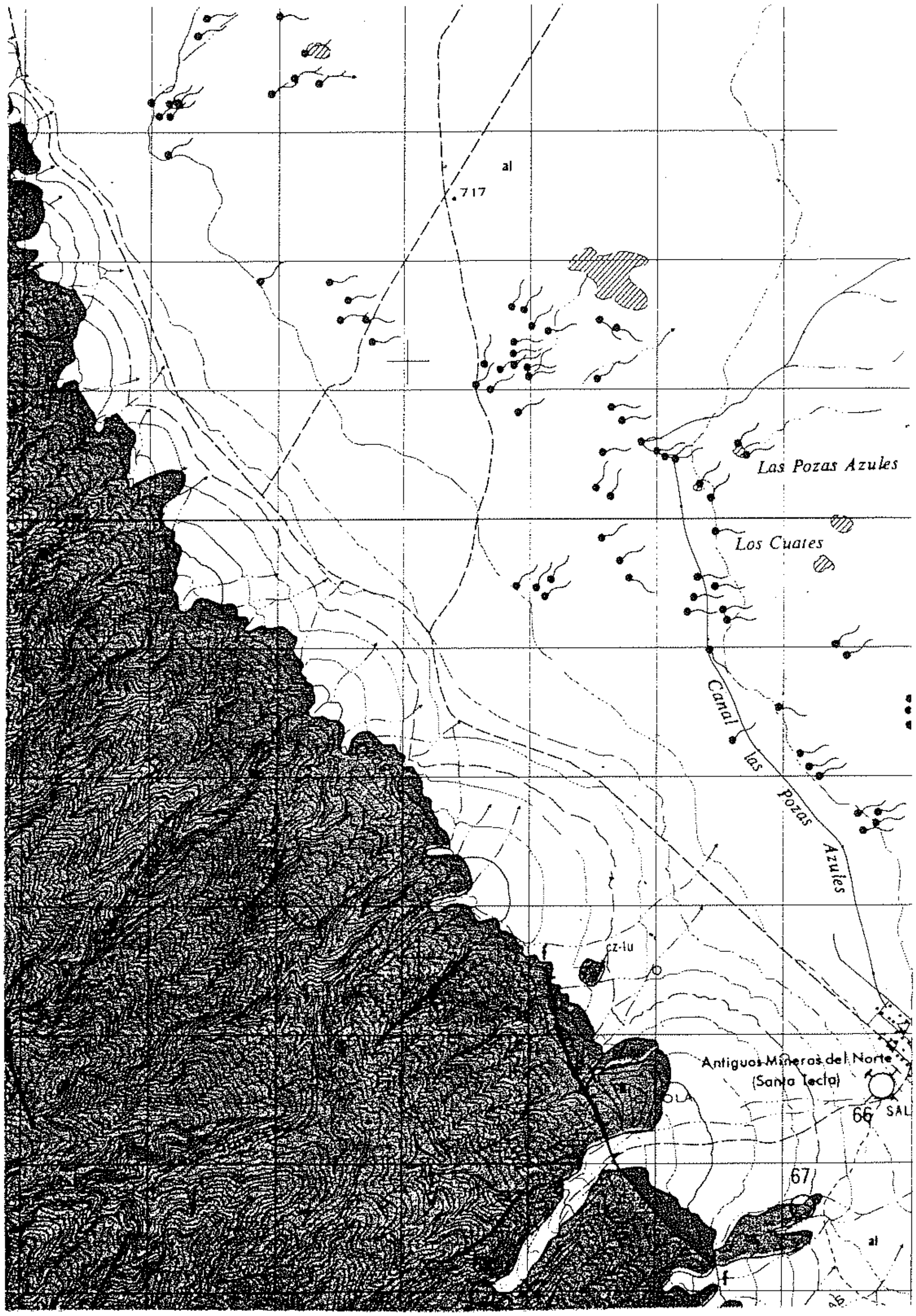

5,000
032903

Fig. 3.3.1-1. Portion of CETENAL topographic map (1:50,000) showing the density of springs in the vicinity of Pozos Azules. Grid is 1 km on a side. Alluvial fans of Sierra San Marcos cross photo from upper left to lower right.


al
717
Las Pozas Azules
Los Cuates
Canal las Pozas Azules
cz-lu
Antiguos Mineros del Norte
(Santa Tecla)
66
SAL
67
al
f

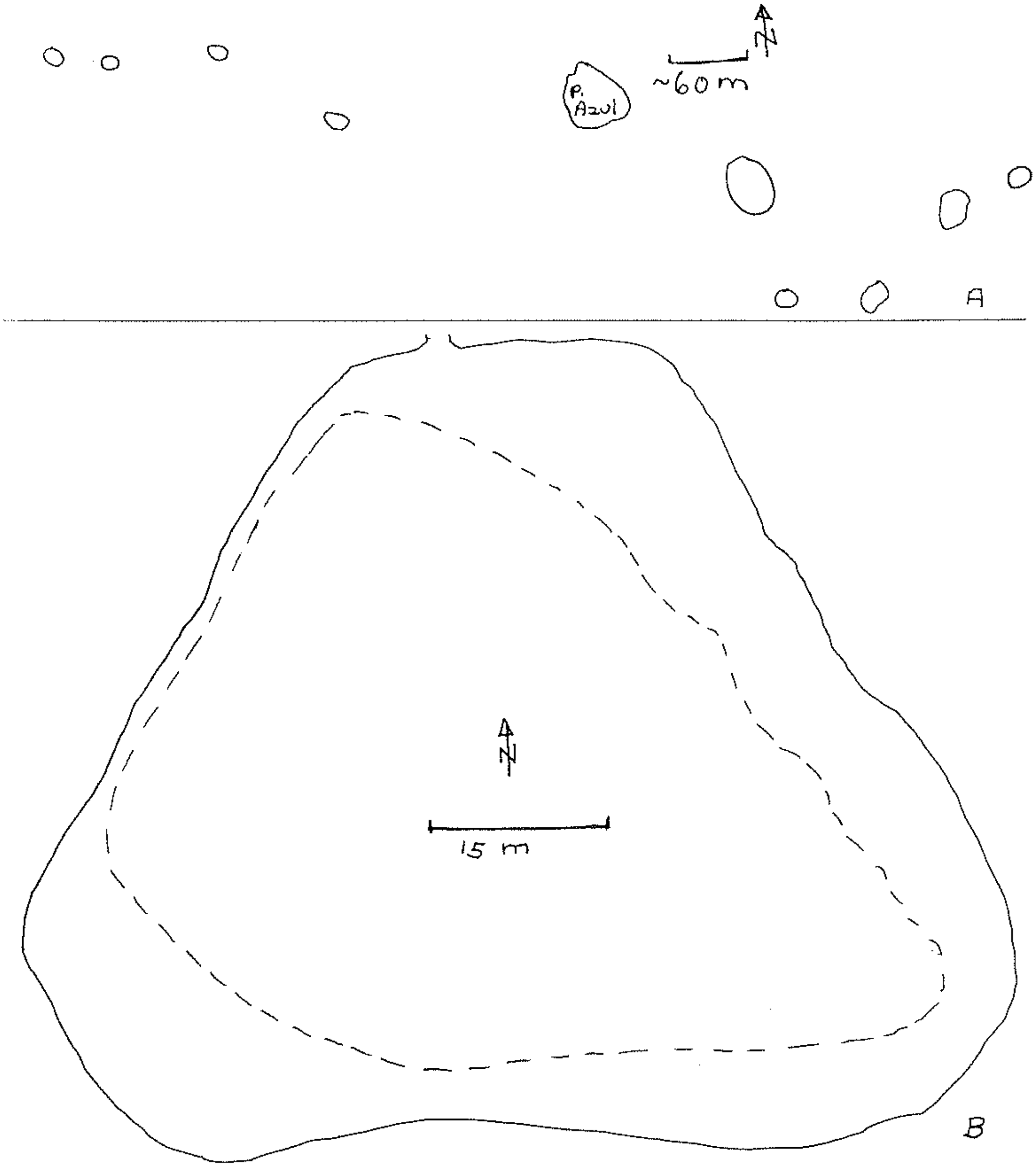


Fig. 3.3.1-2A,B. A. Plane table and alidade survey of lakes in the vicinitry of Pozo Azul. B. Sketch map of Pozo Azul.

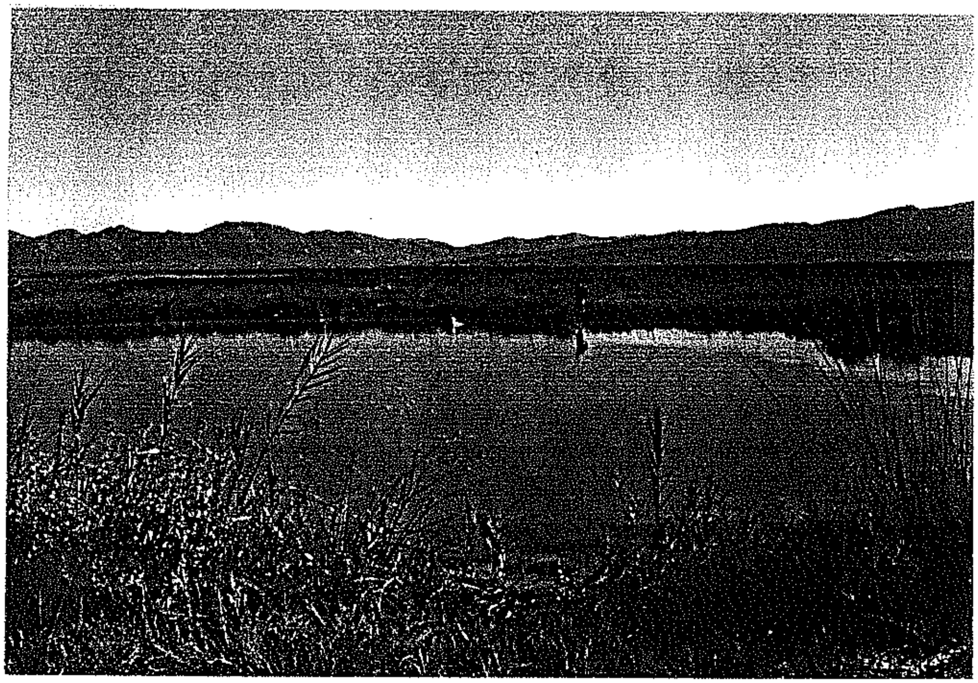


Fig. 3.3.1-3. View across Pozo Azul looking toward the N.E. Note person in background for scale.

Fig. 3.3.2-1A,B,C,D. A,B,C are underwater photographs of Pozo Azul stromatolites. A,B. Mushroom-shaped stromatolites about 1 m wide, photographed about 5 meters below the water surface. C. Stacks of linked stromatolites along the steep vertical wall. D. Shallow stromatolites about 0.4 m wide from near the margin of Pozo Azul. Note that no sediment accumulates around the base of the structures.

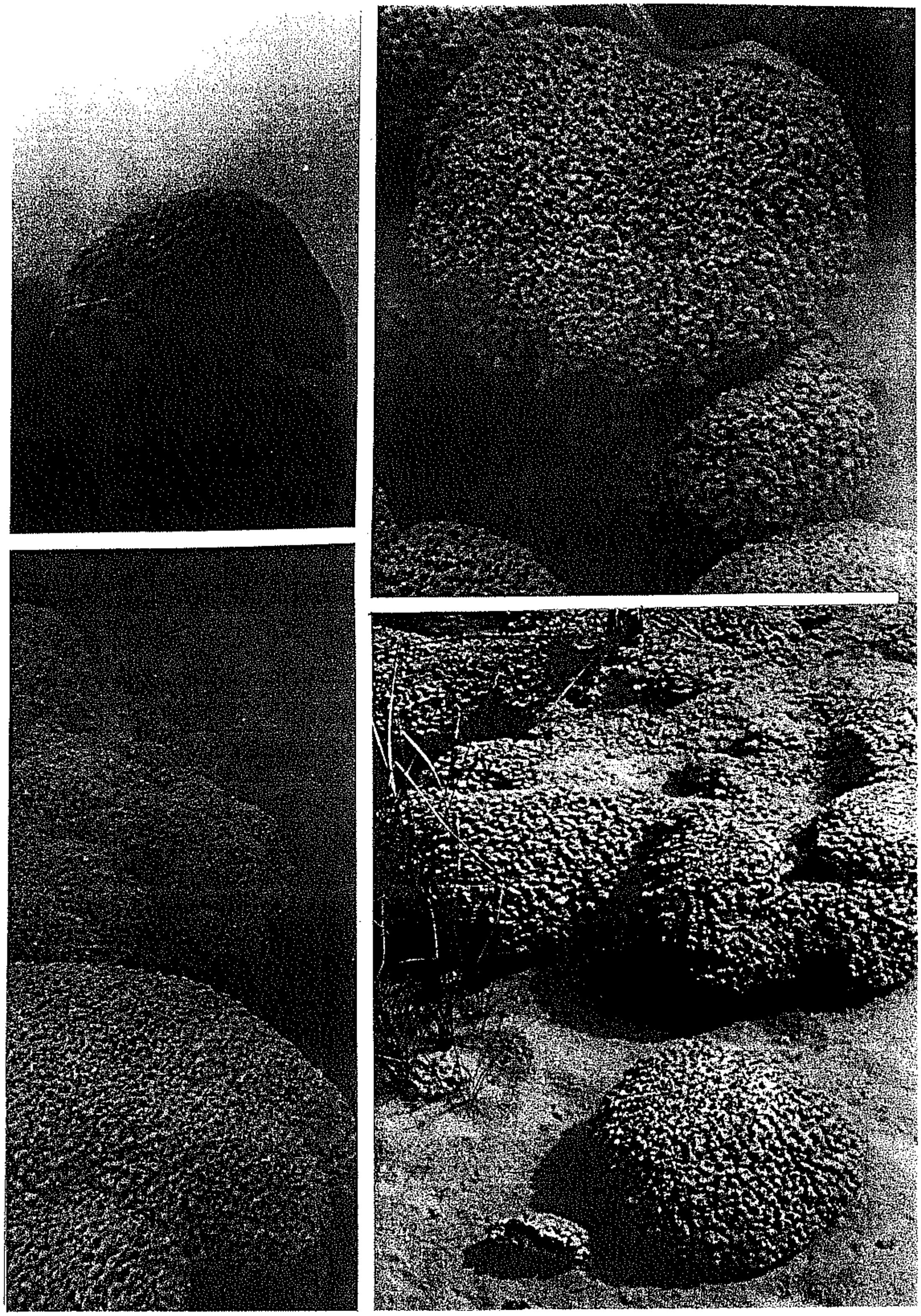
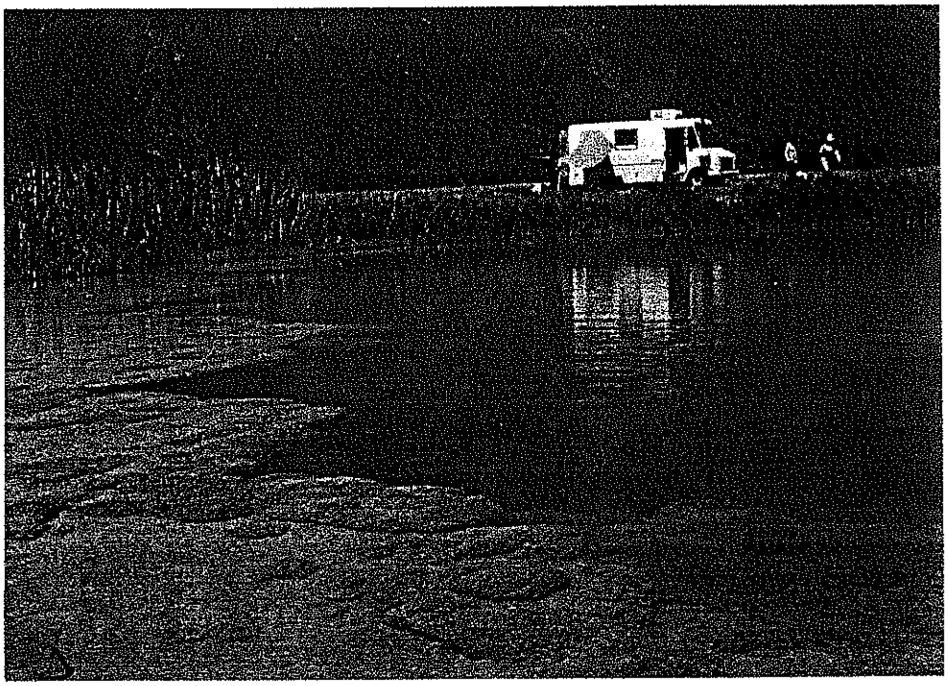


Fig. 3.3.2-2A,B. A. View of Pozo Azul looking toward the west. Shallow shelf on left side drops off abruptly to 13 m. B. Stacked stromatolites shown in foreground of A. Largest stromatolites are about 2 m wide and 0.6 m thick. Pen is floating on water surface about 20 cm above the tops of the stromatolites.



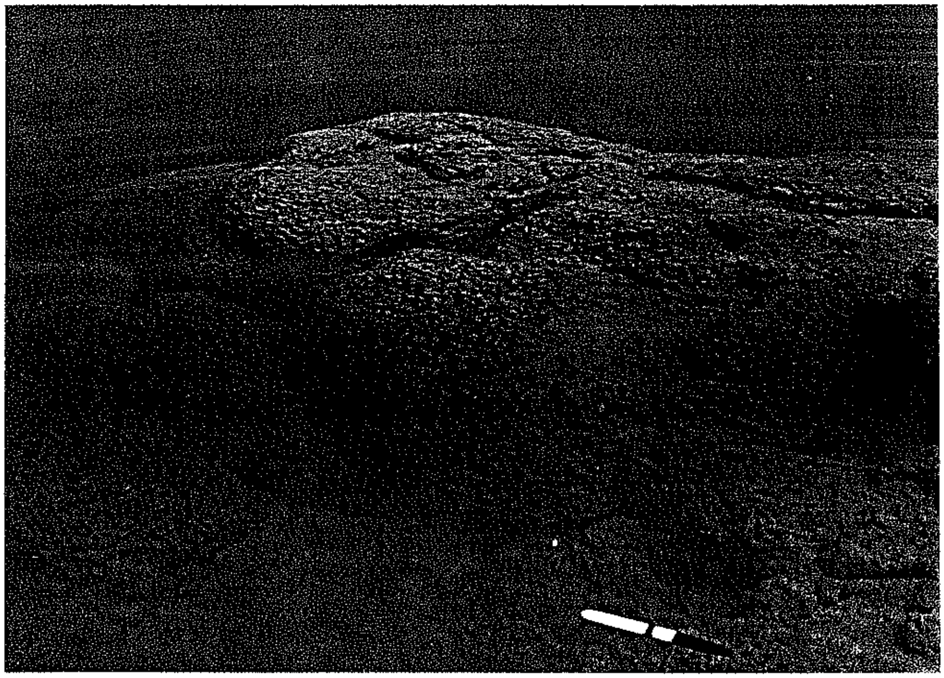
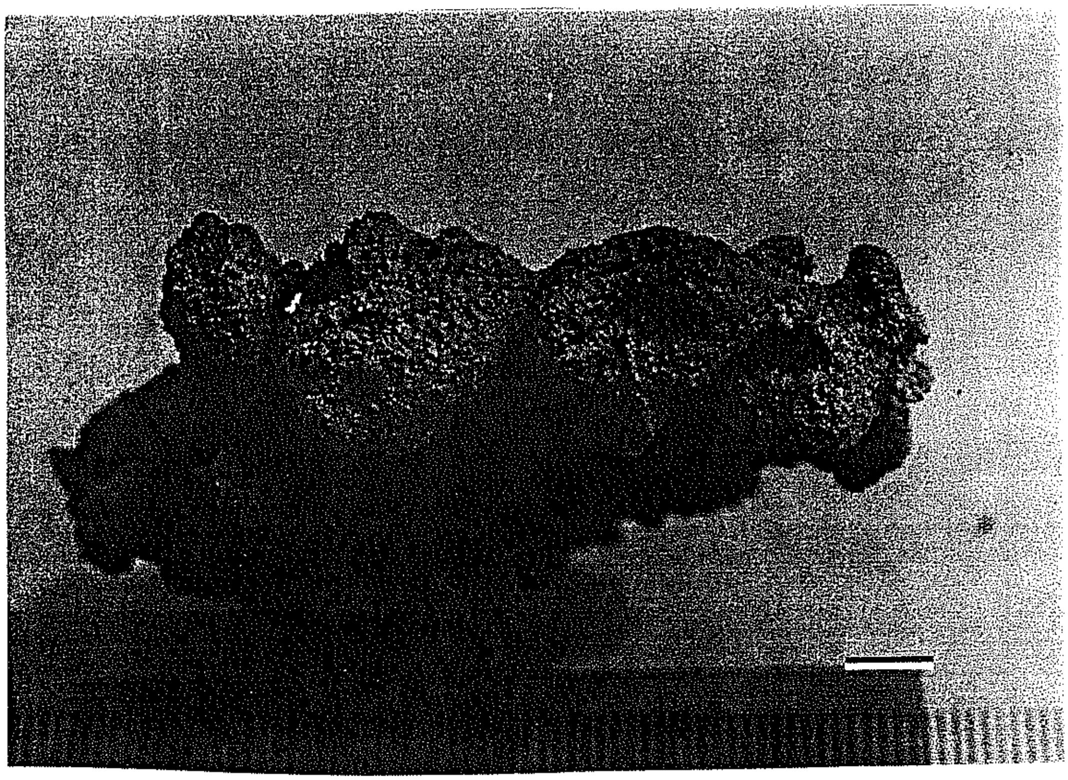
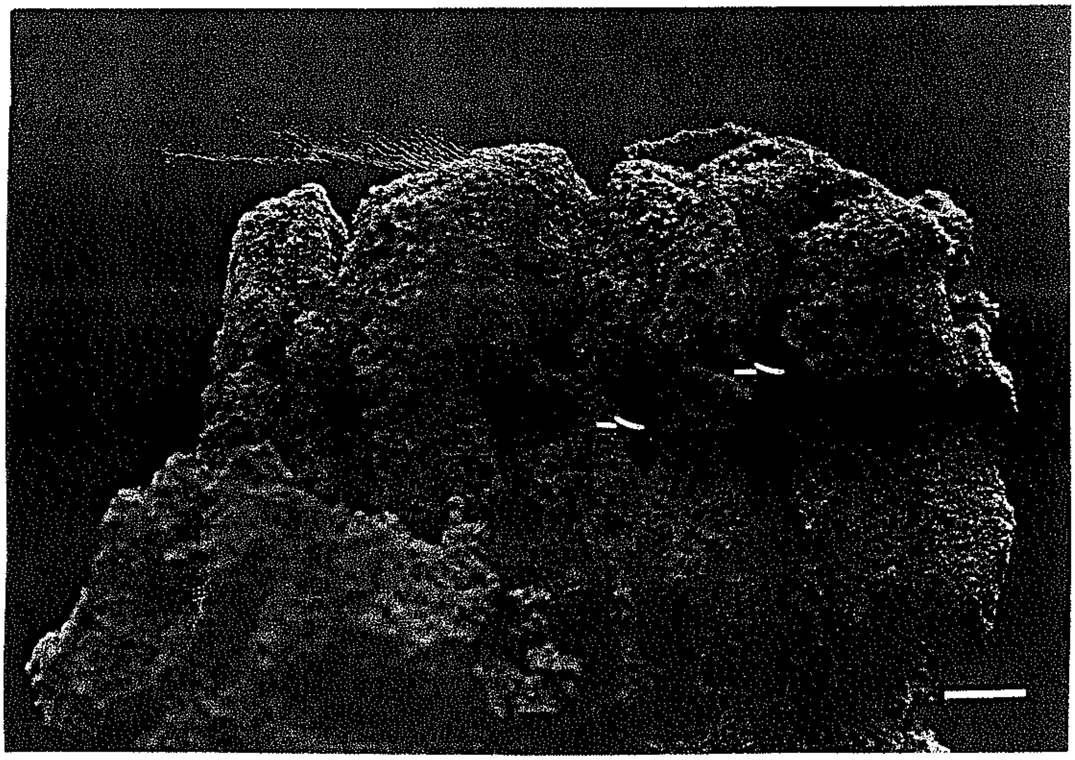


Fig. 3.3.2-3A,B. A. View across Pozo Azul toward N.W. Note individual stromatolites growing on the shallow shelf area. Water depth is about 1 m. Structures range from 0.3 m to 1.0 m in dia. Dark patches on mud surface between stromatolites are diatom mats. B. Small stromatolites along margin of lake on shelf. Dark color of fine sediment between stromatolites is produced by continuous mat of diatoms. Stromatolites are about 0.3-0.4 m in dia. Note the great clarity of the water.

Fig. 3.3.2-4A,B. Typical stromatolite morphologies in well-illuminated areas of Pozo Azul. A. Top view along natural break showing the porous rounded bulbous features capping the vertical columns. Scale bar = 10 mm. B. Side view of vertical columns shown in A. Note shallow cuspate projections shown by arrows. Scale bar = 10 mm.





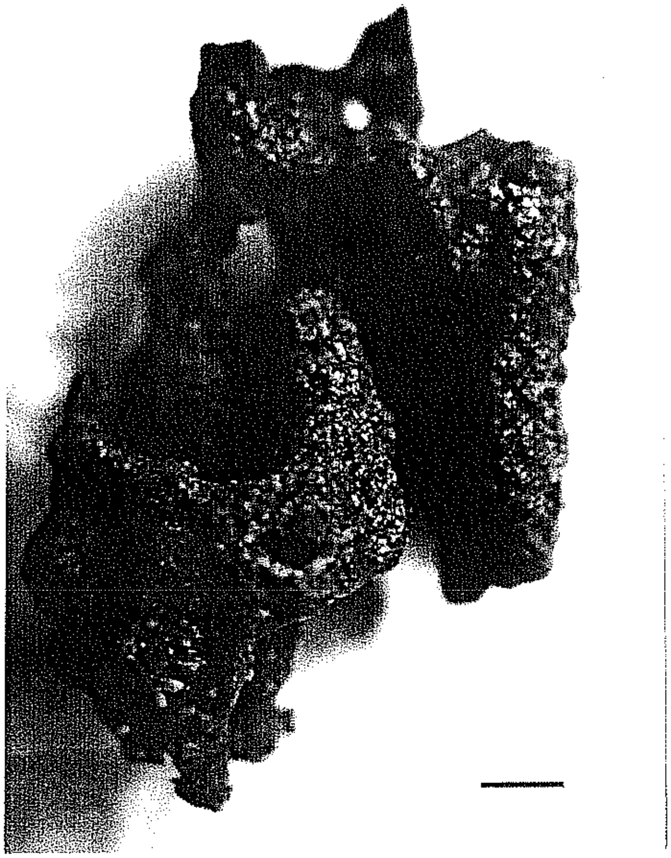


Fig. 3.3.2-5. Fragment of tabular stromatolite in growth orientation from near the bottom of Pozo Azul. Note that holes penetrate entire thickness of stromatolite. Scale bar = 1 cm.

Fig. 3.3.2-6A,B. Auriculate stromatolites collected from vertical walls in the deeper parts of Pozo Azul. A. Surface pattern resulting in part from incisions made by grazers. Scale in cm amd mm. B. Surface profile of auriculate stromatolites. Note cone-shaped bases of lower stromatolite. Scale bar = 10 mm.

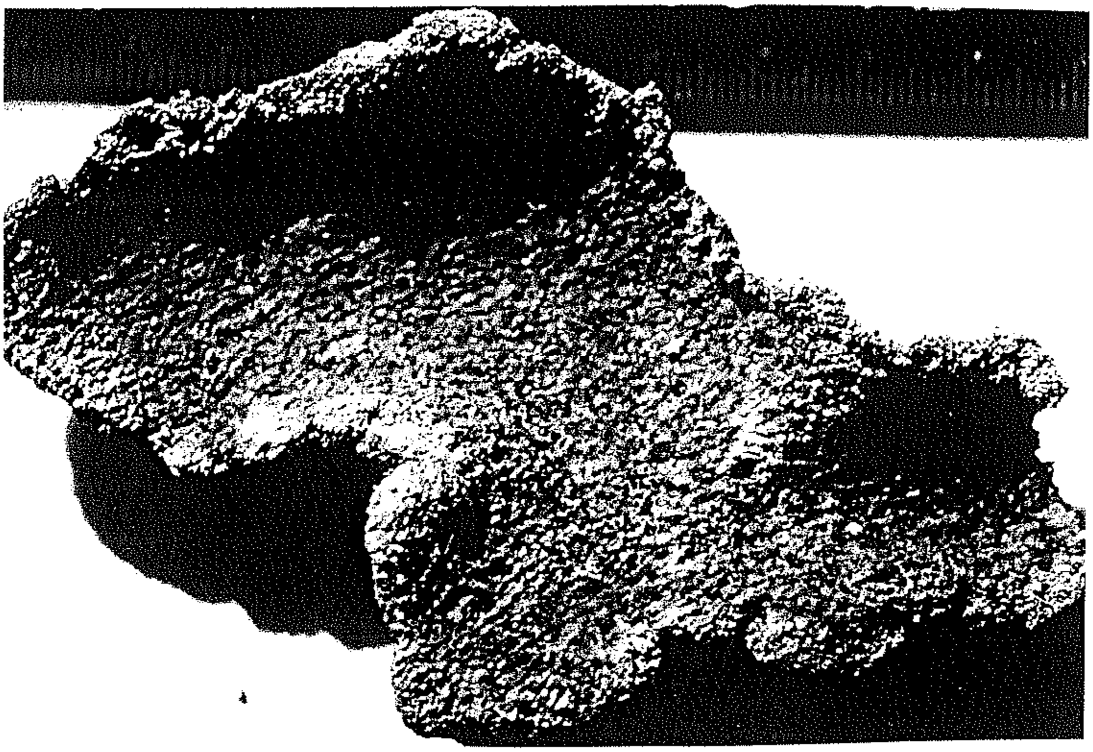


Fig. 3.3.3-1. Colony of *Dichothrix bonetiana* from the surface of a Pozo Azul stromatolite. Note the thick coating of epiphytic diatoms, particularly *Achnanthes* spp. of the *Dichothrix* sheaths. *Schizothrix lacustris* can be seen at the base of the *Dichothrix*. Scale bar = 20 um.

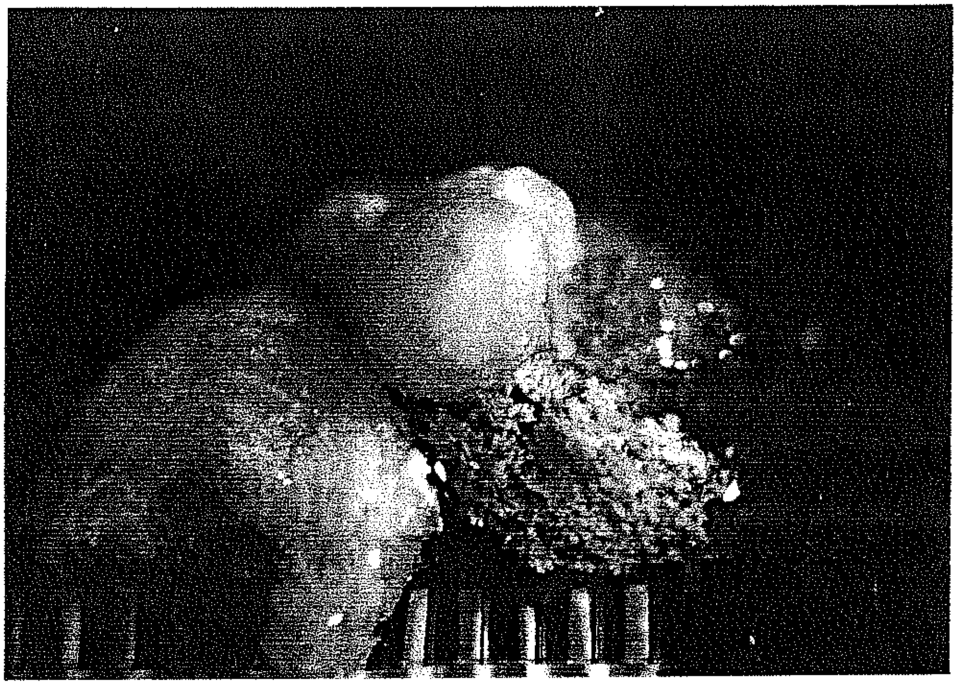


Fig. 3.3.3-2. Colonies of Ophrydium versatile from the surface of a Pozo Azul stromatolite. Sample on lower left side of photo has been cut in half to show carbonate rich laminae in interior. Scale bar in mm.

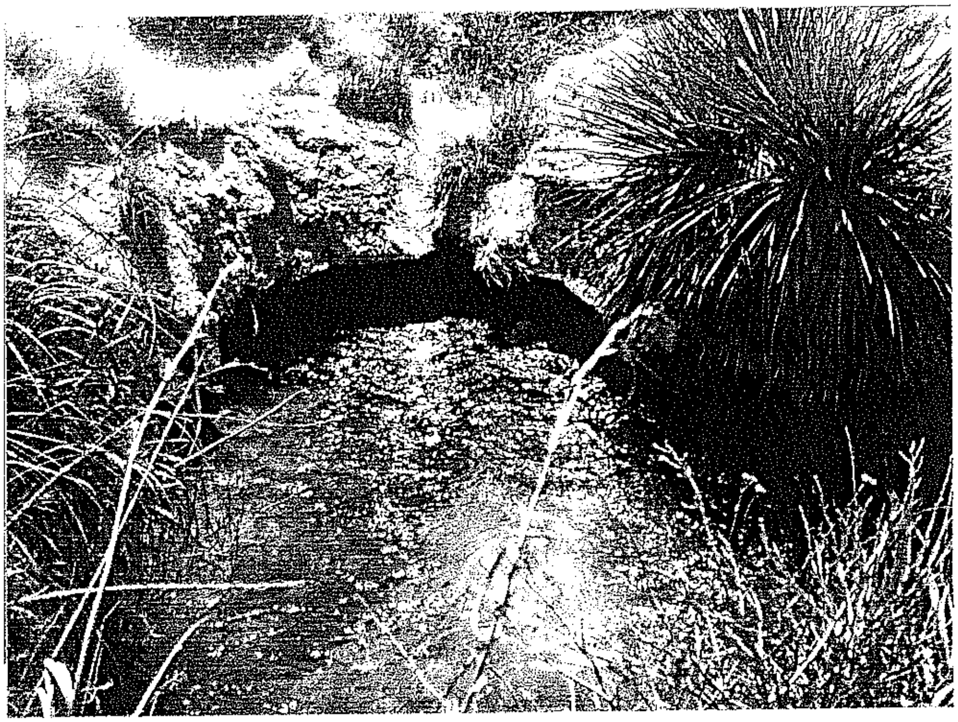


Fig. 3.4.1-1. Rheocrene spring at Garabatal.
Mouth of spring is about 3 m wide and 1.5 m deep.

Fig. 3.4.1-2A,B. Stromatolites lining spring-fed seasonal stream from marsh, leading to Laguna Garabatal. Stromatolites are about 0.3-0.4 m tall. A. Photo taken April, 1979 during dry (dormant) season. B. Photo taken Jan. 1989.

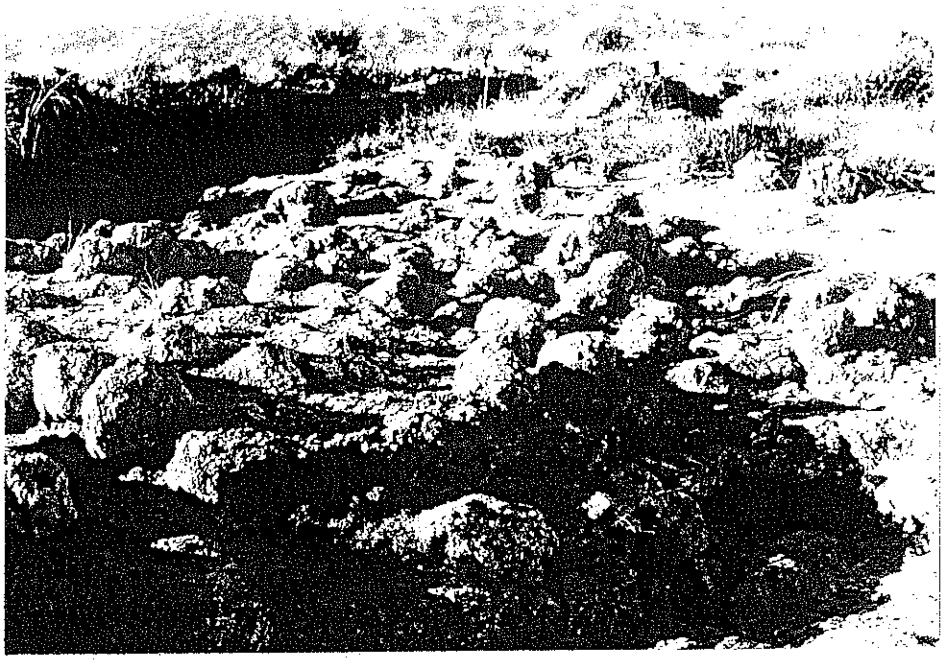


Fig. 3.4.1-3A,B. Laguna Garabatal during high water. A. View toward the west. Note rim of linked stromatolites in background along lake margin. B. Stromatolites shown in A. Older generations of stromatolites at higher elevations can be seen behind person in center of photo.

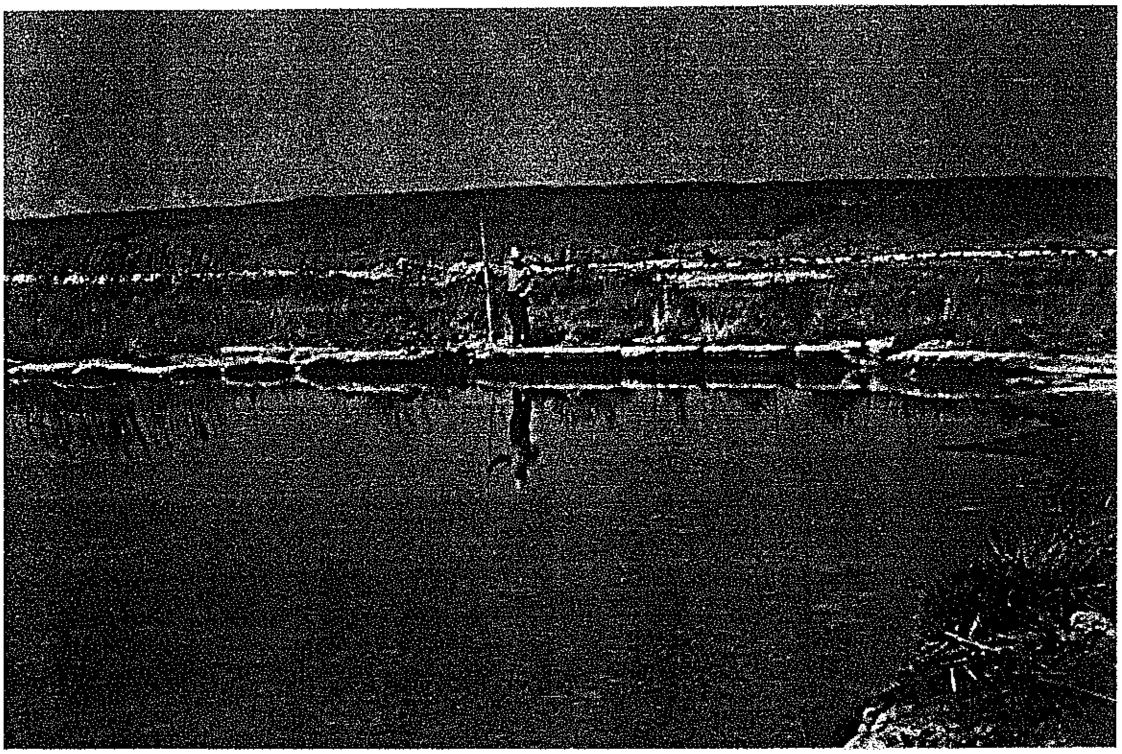
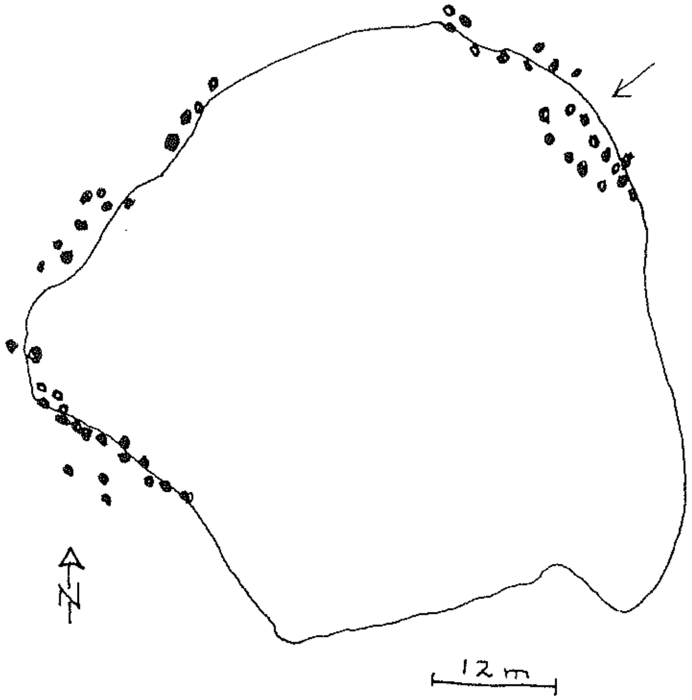
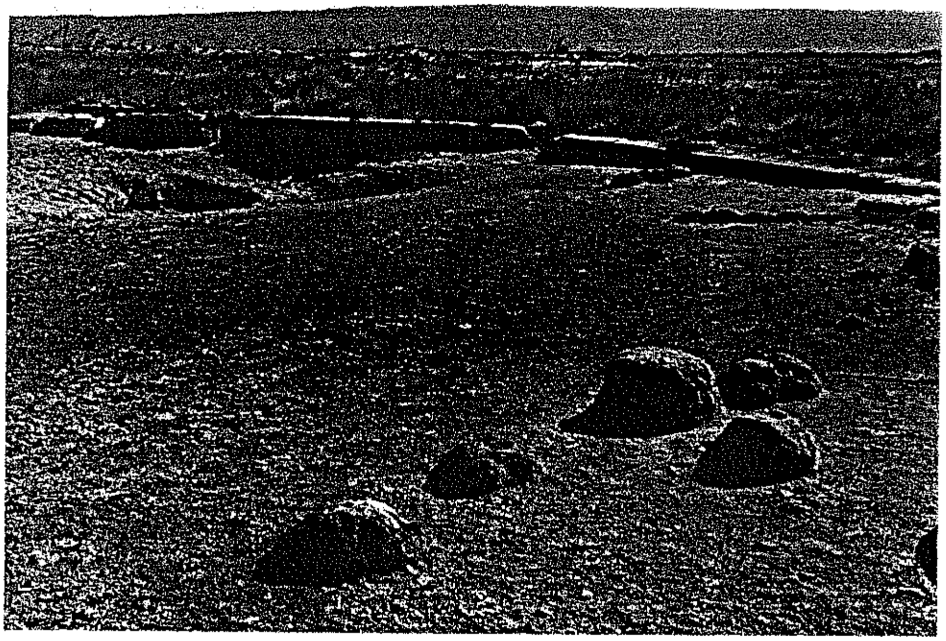


Fig. 3.4.1-4A,B. A. Plane table and alidade survey of Laguna Garabatal. Circles represent individual stromatolites. B. Laguna Garabatal during the dry season. view is of the same area as shown in Fig. 3.4.1-3B. Microbial crust covers sandy bottom.


N
12 m



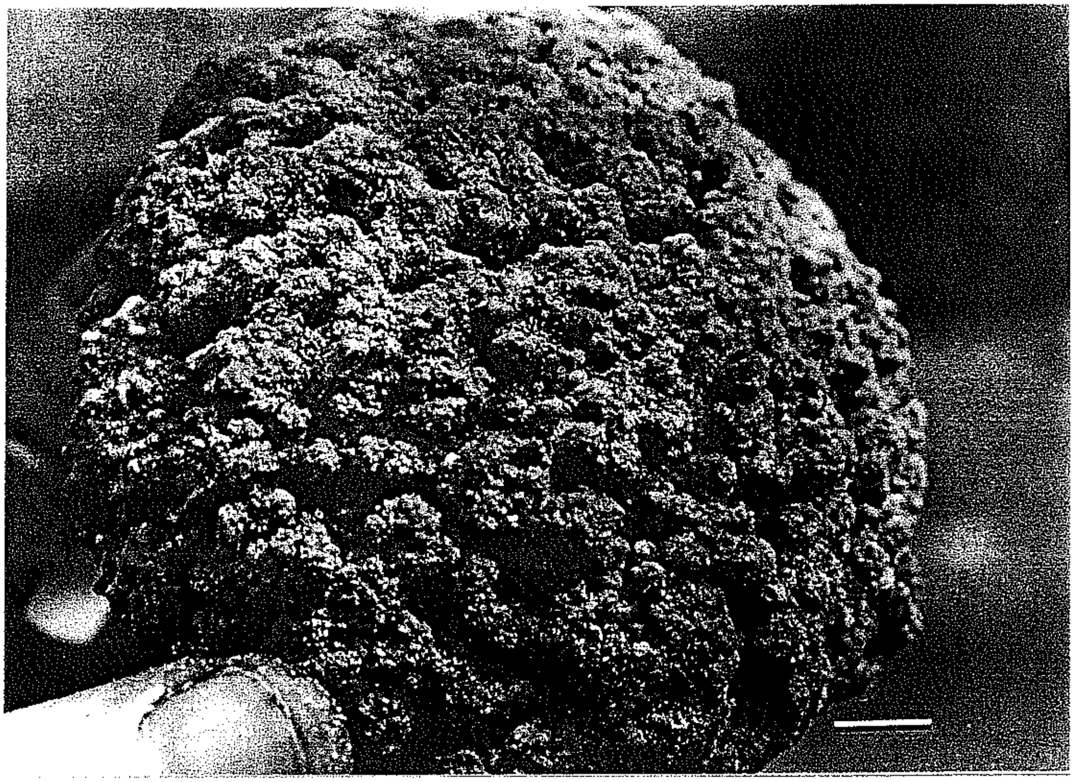
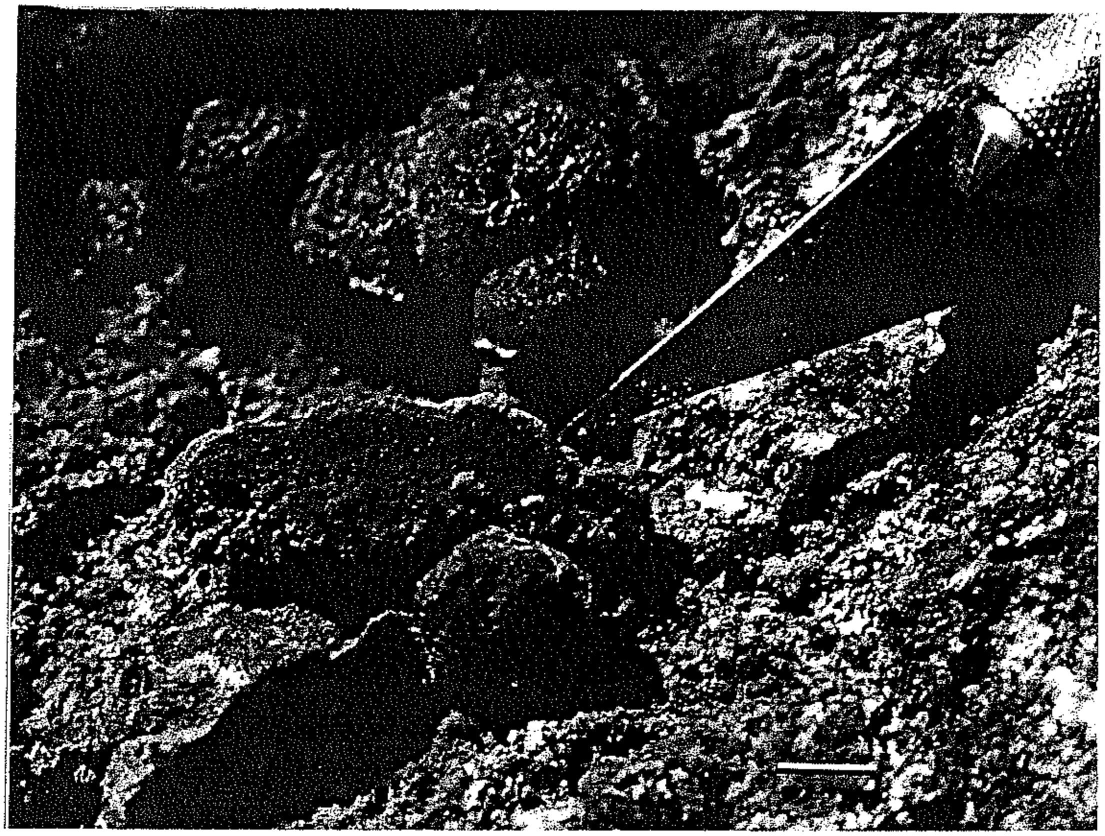


Fig. 3.4.2-1. Young stromatolite collected while still submerged and actively growing. Scale bar = 1 cm.

Fig. 3.4.3-1. SEM micrograph of lamina produced by <u>Scytonema</u> <u>mirabile</u>. Note hollow spar tubes representing the biogenic imprints left by the cyanobacterium. Scale bar = 100 um.

Fig. 3.4.3-2A,B. A. Small cauliflower-shaped laminated _Scytonema_ colonies from the submerged side of large flat-topped stromatolites in Laguna Garabatal. Scale bar = 5 mm. B. Surface view of lithified _Scytonema_ crust after emergence at end of brief growing season. Colonies formed and lithified in about 2 months. Note hammer for scale.



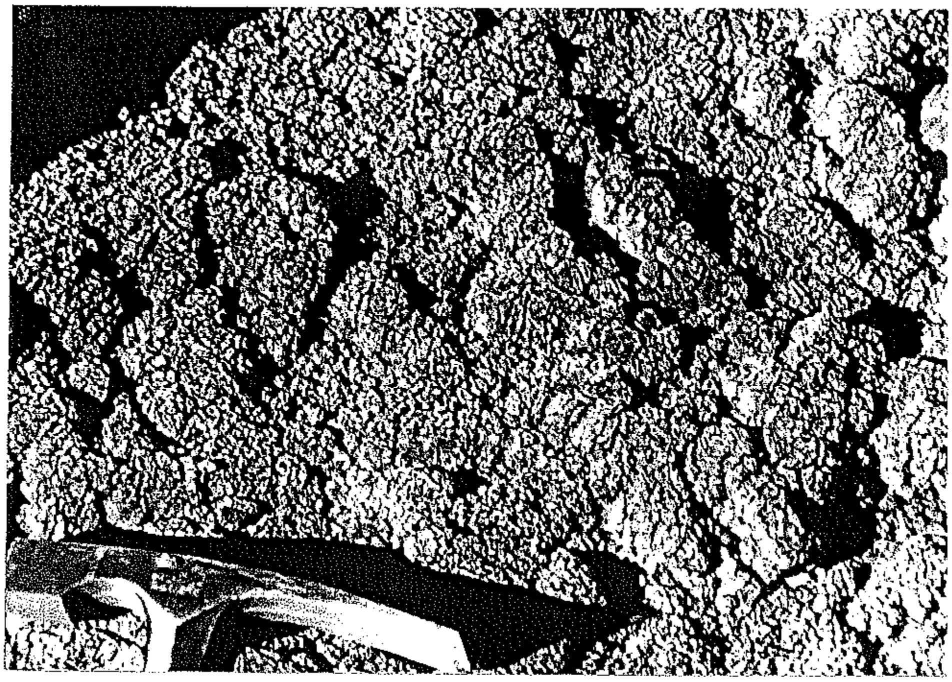
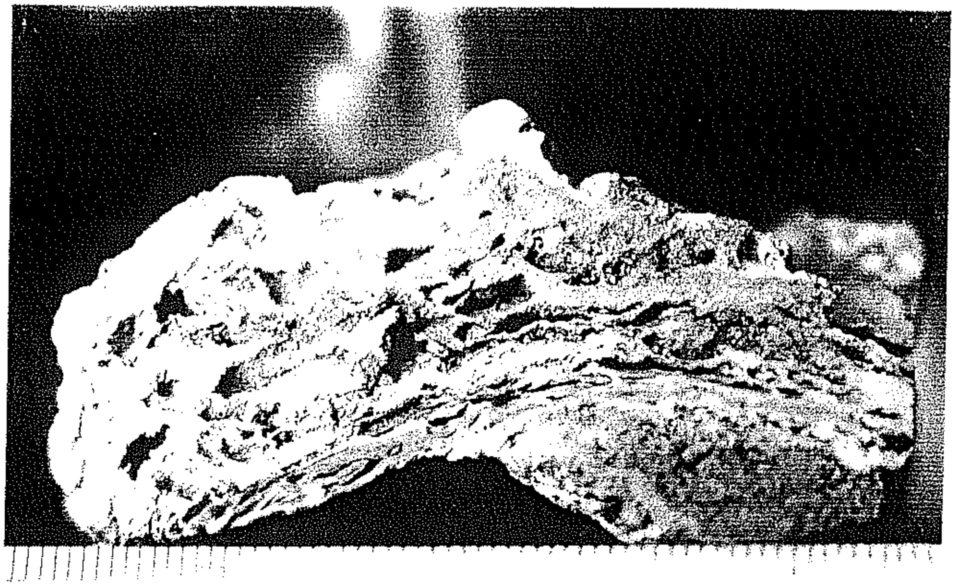


Fig. 3.4.3-3. A. Thick dry diatomaceous lamina from surface of stromatolites in inflow stream to Laguna Garabatal. Porosity caused by gaps in fabric were probably produced by trapped gases. Scale bar in mm. B. Surface view of thin pale grey diatomaceous "tissue" lamina covering a stromatolite in Garabatal. Note shrinkage tears caused by dehydration of diatom mucilage. Scale bar = 5 mm.



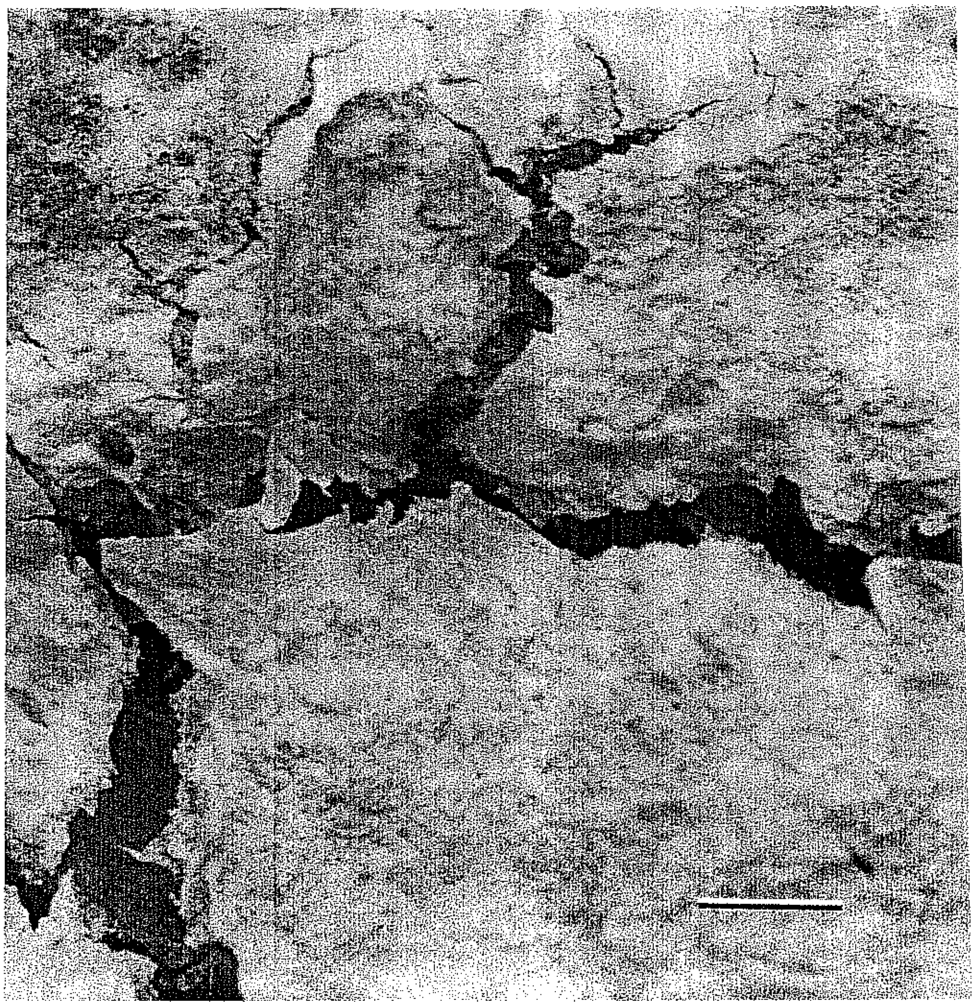


Fig. 3.4.3-4. SEM micrograph of diatomaceous lamina shown in previous figure. Calcite grains adhere to diatom surfaces. Diatom frustules are oriented with current direction. Scale bar = 10 um.

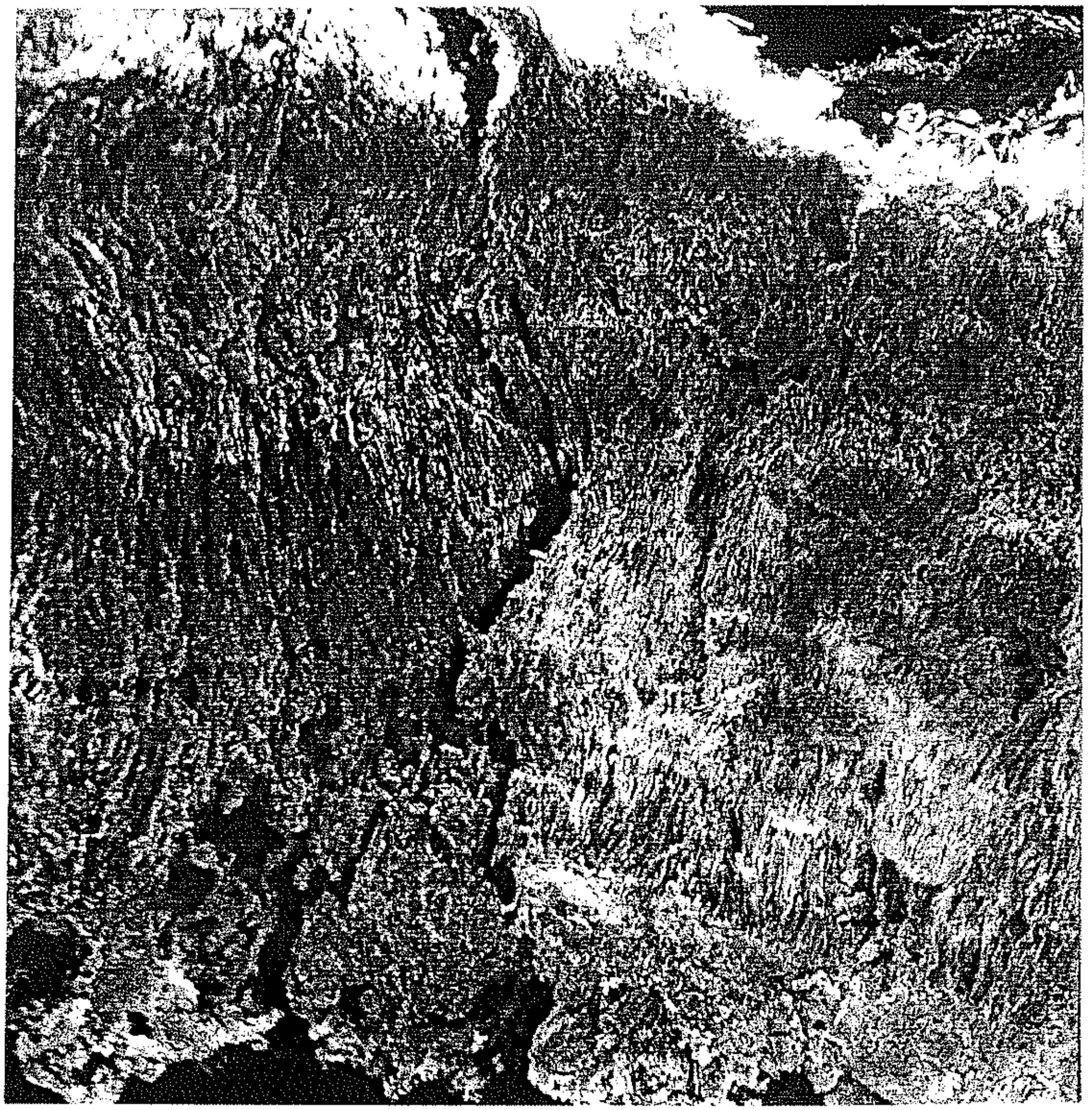


Fig. 3.4.4-1. SEM micrograph of vertical section through Laguna Garabatal stromatolite surface mat showing various types of laminae, predominantly those dominated by *Scytonema*. Mat thickness shown is about 2 mm.

Fig. 3.4.4-2A,B. Sparry calcite cement lining a cavity in a Garabatal stromatolite. Note bezeled edges of crystal faces and shaggy texture of crystal faces. Scale bar = 5 um.

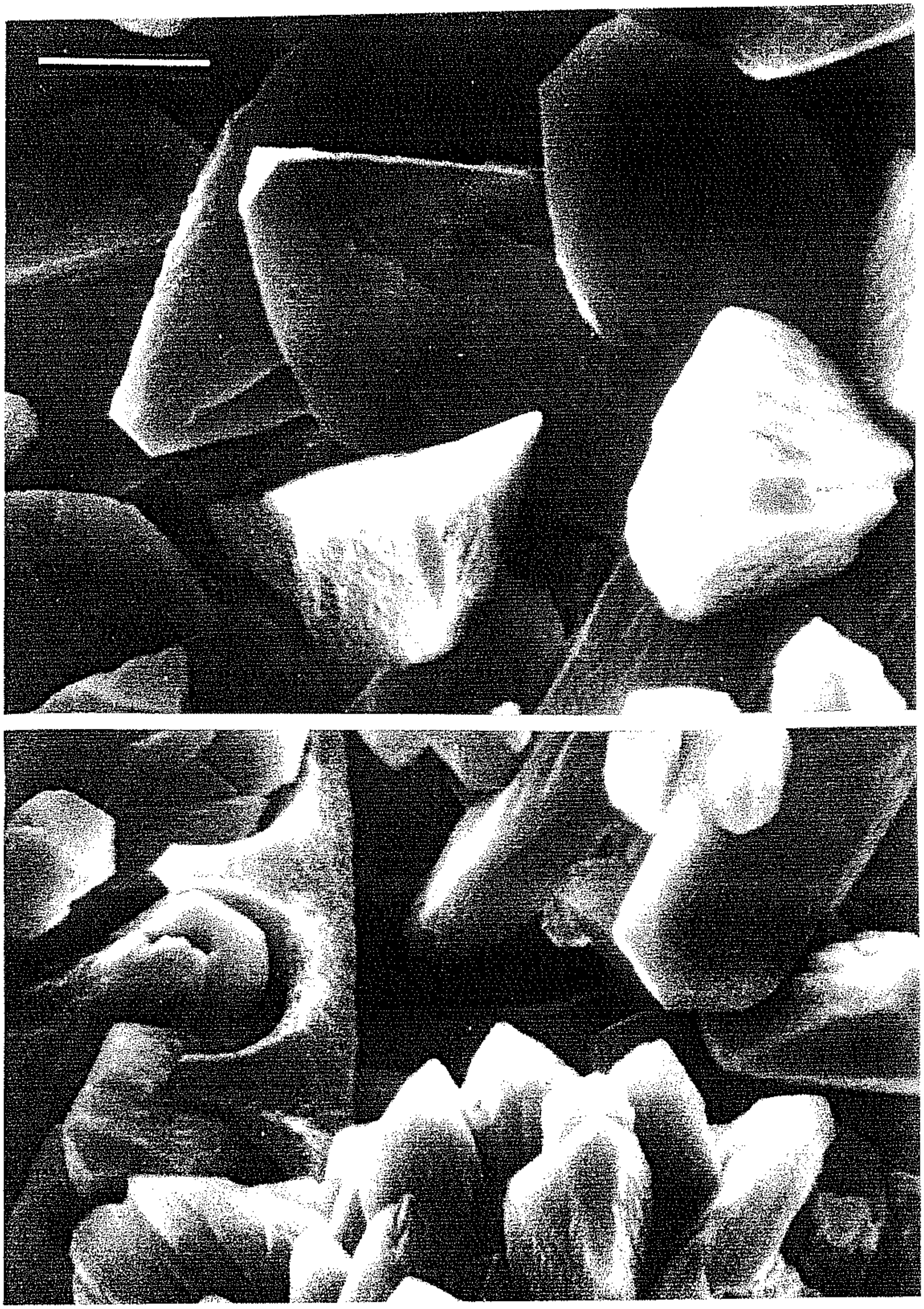
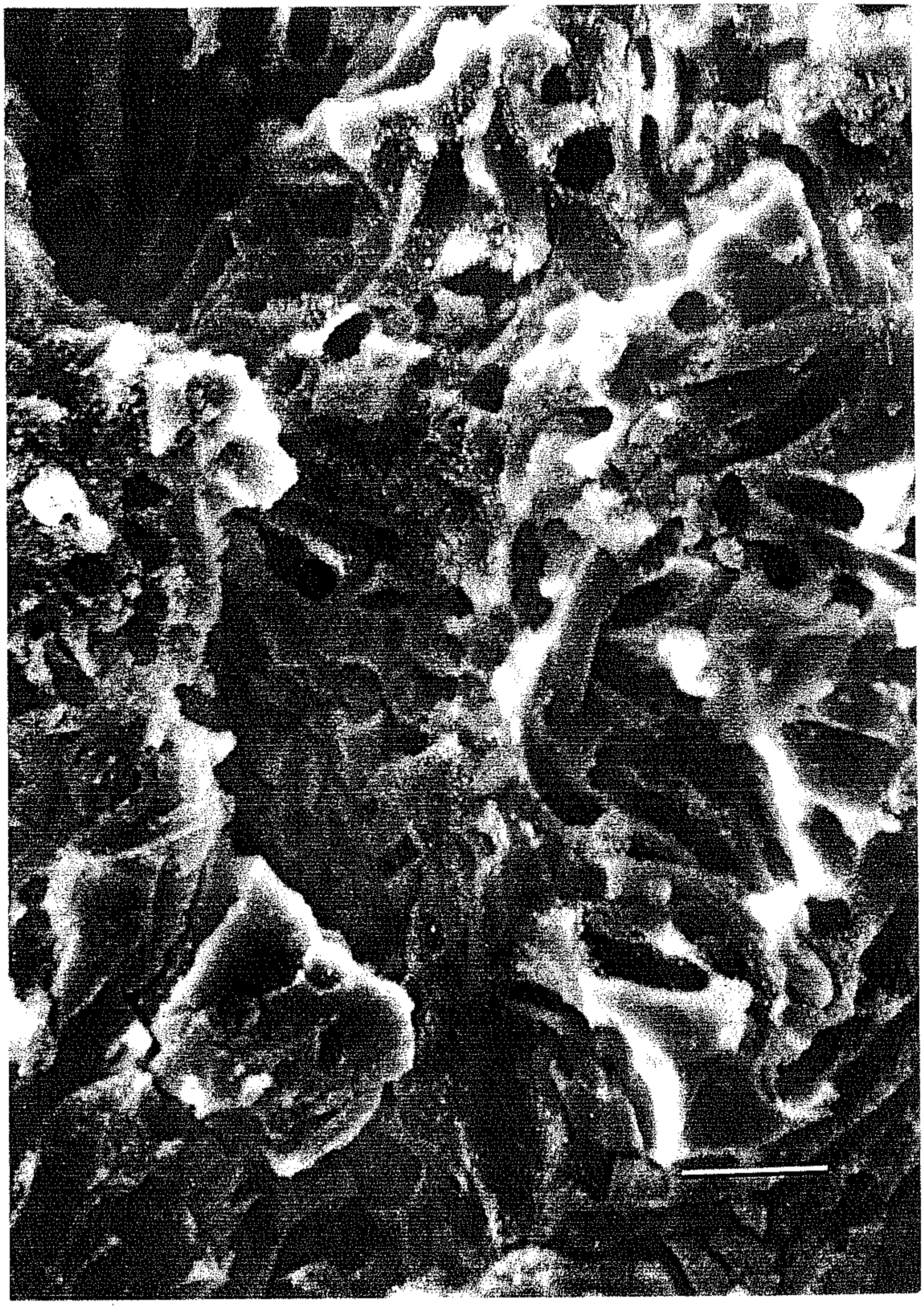


Fig. 3.4.4-3. Interior of Garabatal stromatolite. SEM micrograph cut perpendicular to plane of mat growth. Spar crystals surround holes representing sites of *Scytonema* filaments (moldic porosity). Scale bar = 50 um.



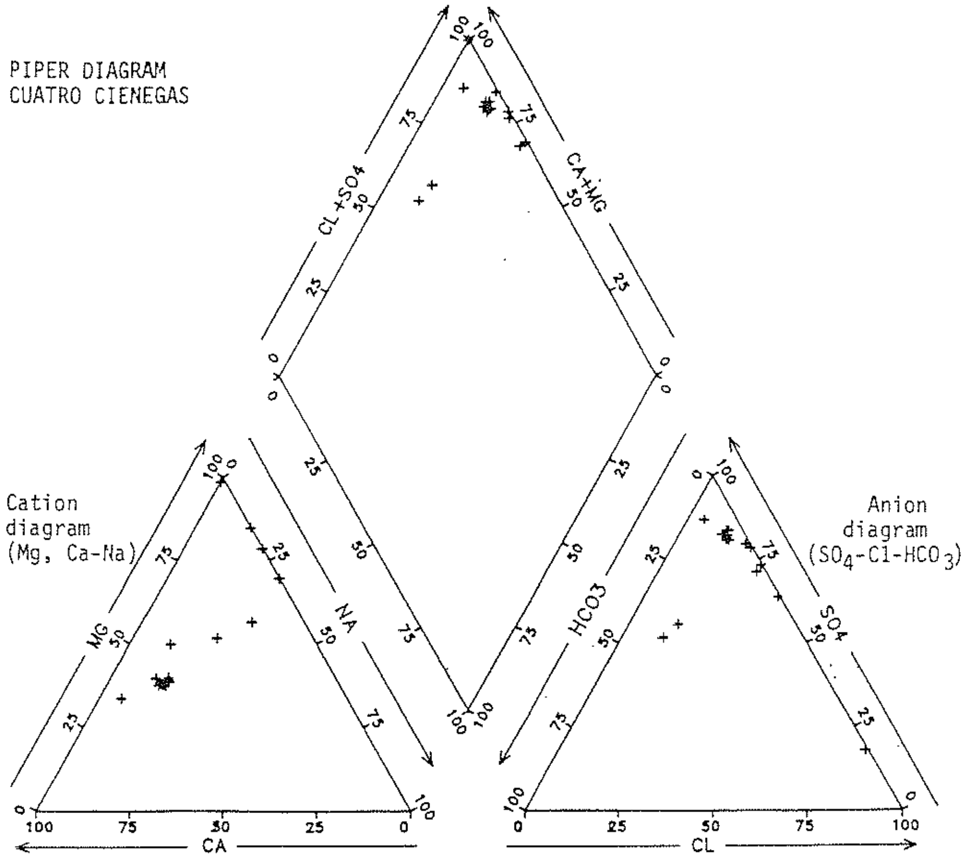


Fig. 3.5-1. Piper Diagram of water chemistry measurements in the Cuatro Ciénegas Basin. The large tight cluster represents the stromatolite sites. Outlying points are non-sulfate-bearing springs and hypersaline brines.

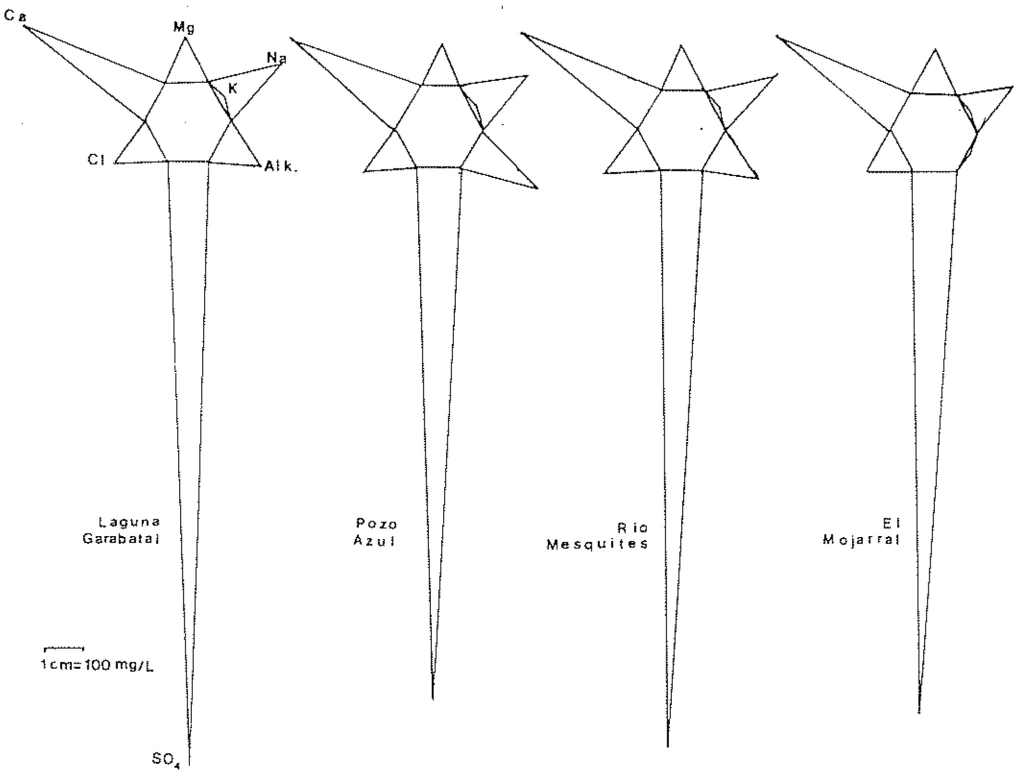


Fig. 3.5-2. Water chemistry of stromatolite sites plotted in rose diagrams, to show constituents in absolute concentrations (mg/l).

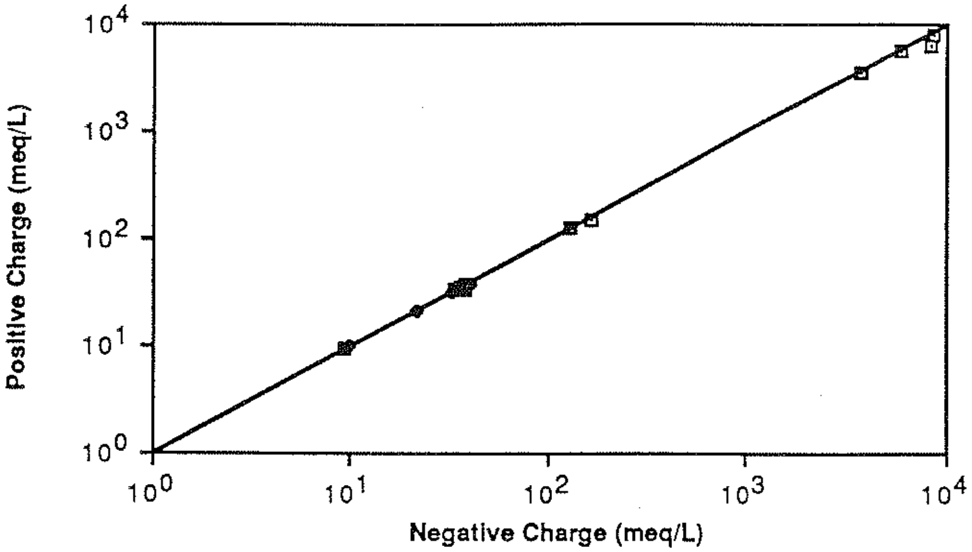


Fig. 3.5-3. Plot of total equivalents of positive vs. negative charge for Cuatro Ciénegas waters. Solid line represents a 1 to 1 correspondence. Open squares (right end) are relatively concentrated samples, filled squares come from streams or ponds at a distance from the source springs and diamonds (clustered to left of center on line) are samples from or close to springs.

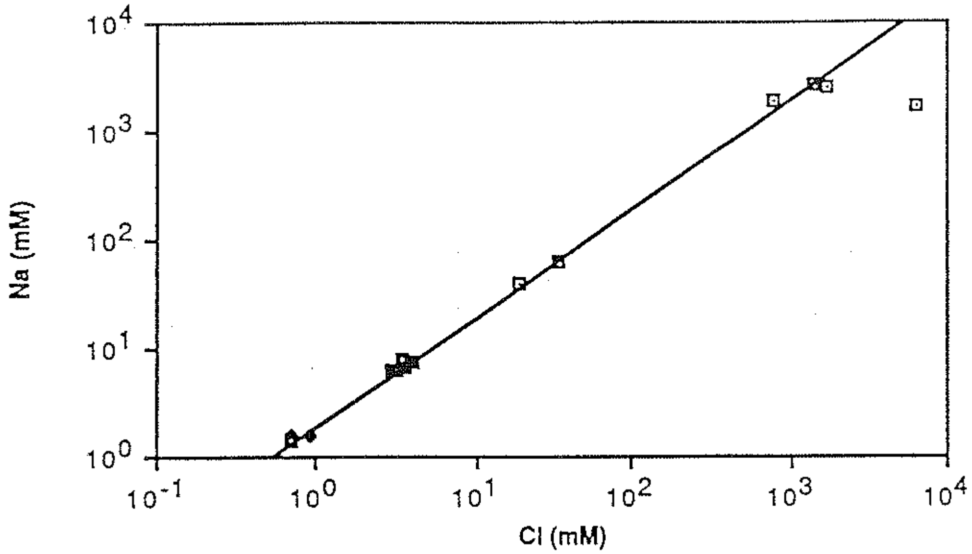


Fig. 3.5-4. Plot of sodium and magnesium versus chloride for water analyses. Figure symbols are as in Fig. 3.5.3. Sodium displays conservative behavior through a wide range of evaporative concentration. Magnesium appears to have close to conservative behavior.

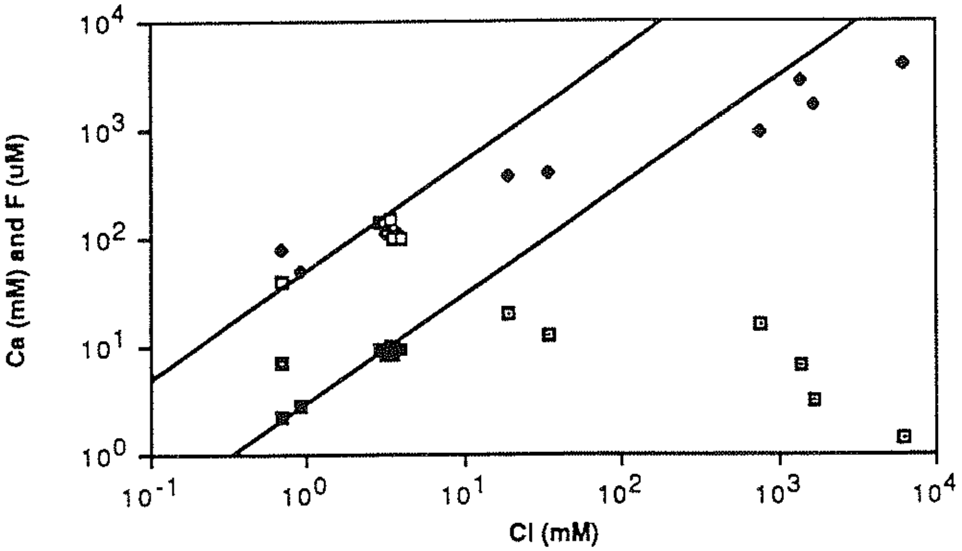


Fig. 3.5-5. Plot of calcium and flouride versus chloride concentrations in Cuatro Ciénegas water. Figure symbols as in Fig. 3.5-3. The set of symbols clustered about the upper diagonal line are flouride analyses, the lower set are calcium. Calcium is removed once chloride is concentrated about 15 times. Flouride is also lost though not at the same rate.

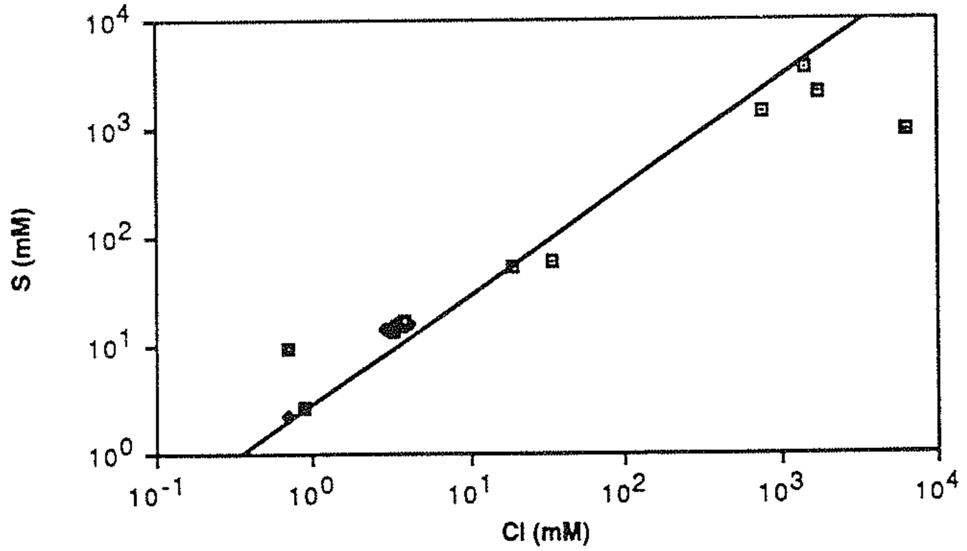


Fig. 3.5-6. Plot of sulfur versus chloride concentrations in Cuatro Ciénegas water. Sulfur behaves rather conservatively except where chloride concentrations are highest. Symbols are the same as in Fig. 3.5-3.

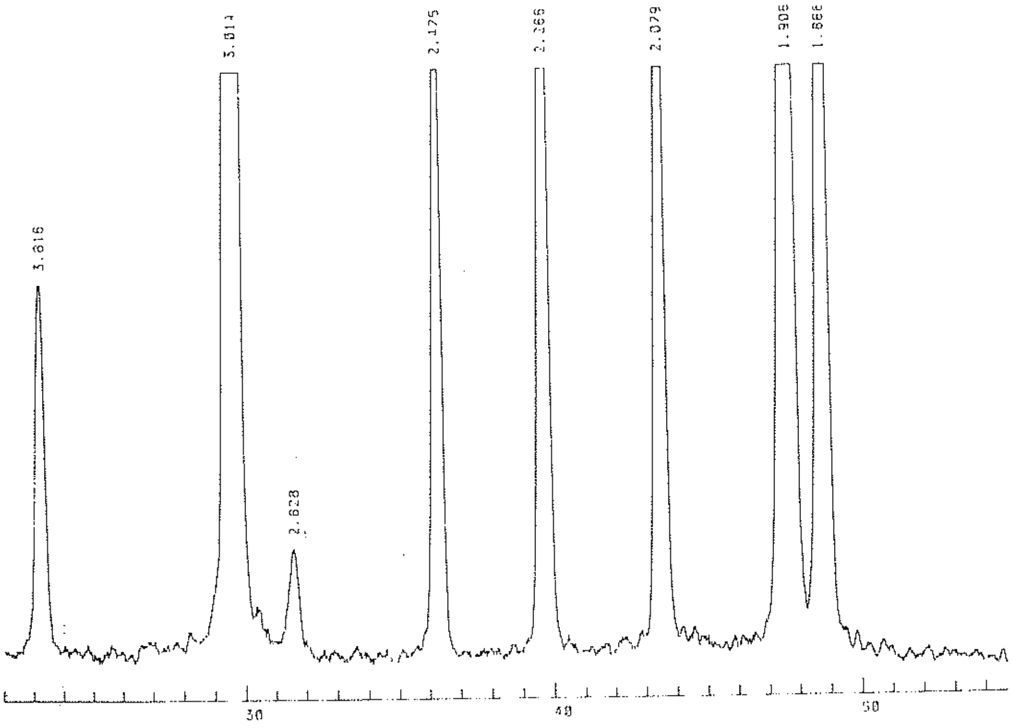


Fig. 3.6-1. X-ray plot of Pozo Azul stromatolite material. Peaks represent low magnesium calcite.

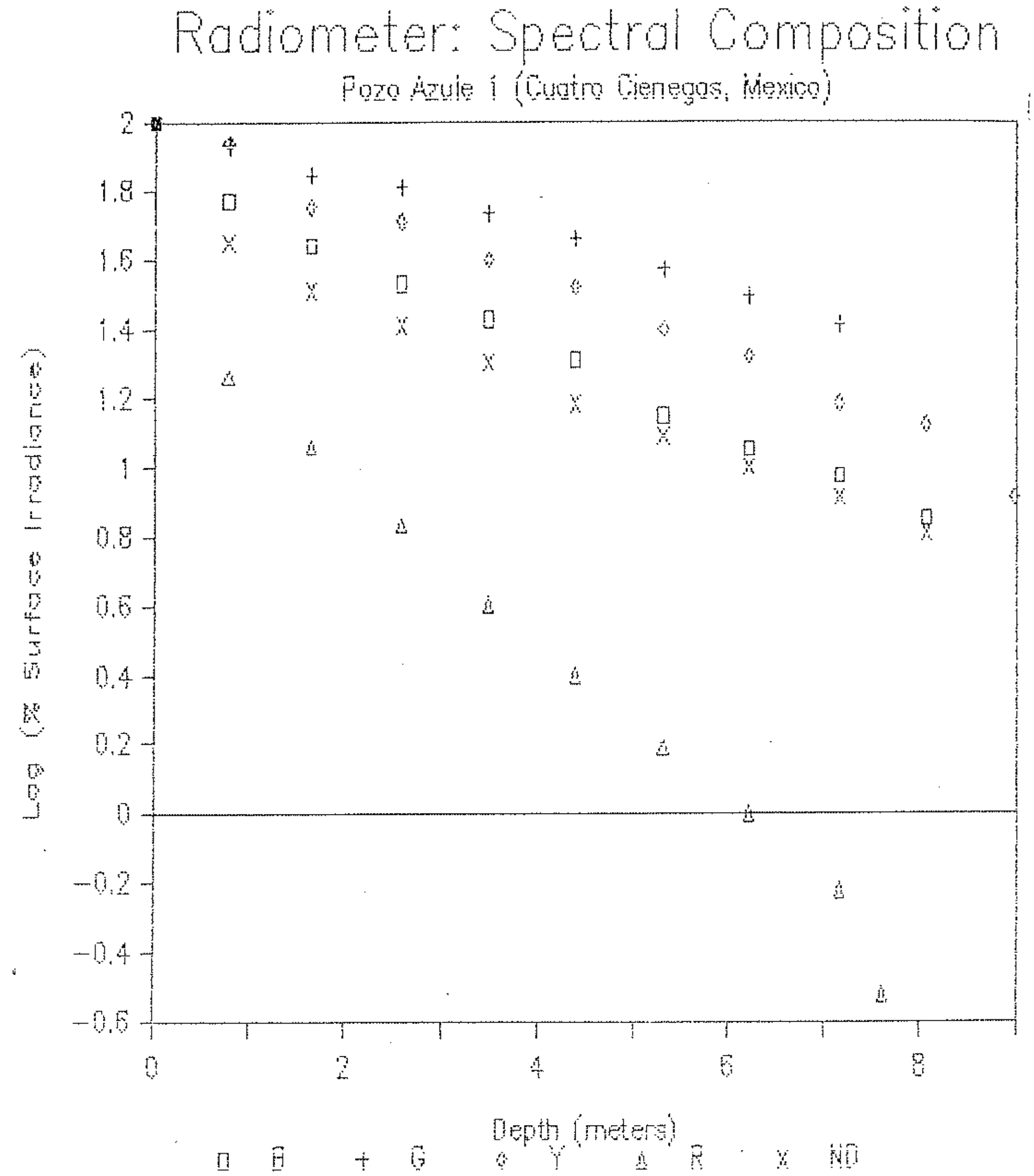


Fig. 3.7.2-1. Graph of spectral composition of Pozo Azul water expressed as log % od surface irradiance. Measurements made in Nov. 1986. B = blue, G = green, Y = yellow, R = red, and ND = neutral density.

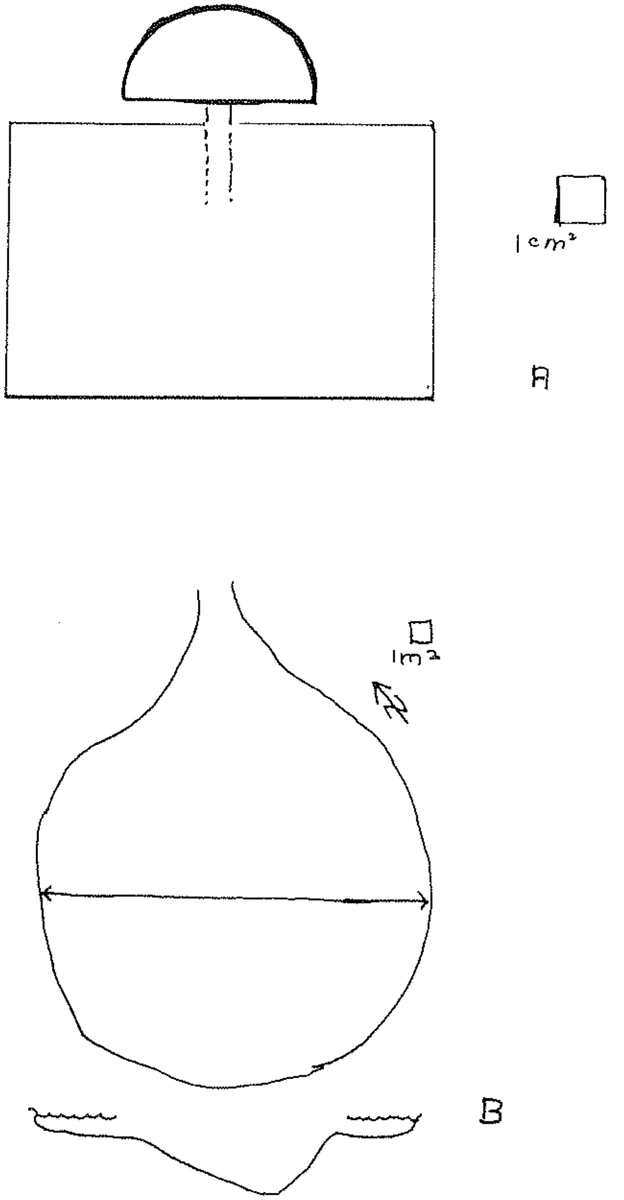


Fig. 3.8.2-1A,B. A. Configuration of the artificial stromatolite sampler, complete with substrate and holder. B. Sketch map of Bano Escobedo with depth profile.

Fig. 3.8.2-2A,B. Surface of artificial stromatolites incubated in Escobedo for 5 months at 1 m depth. *Homoeothrix balearica* colonies indicate beginning of well-developed ridges. Scale bar = 2 mm.

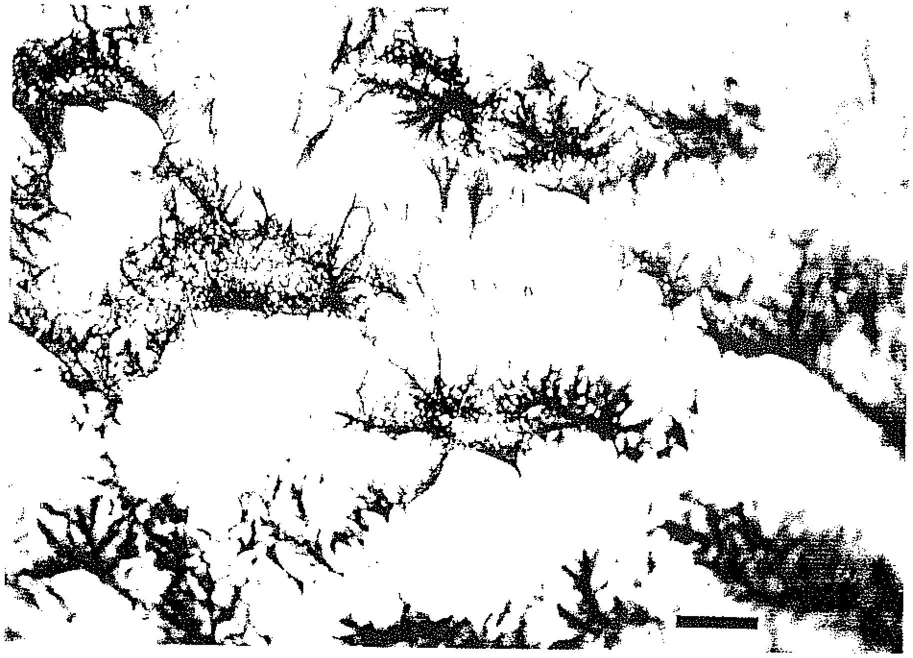
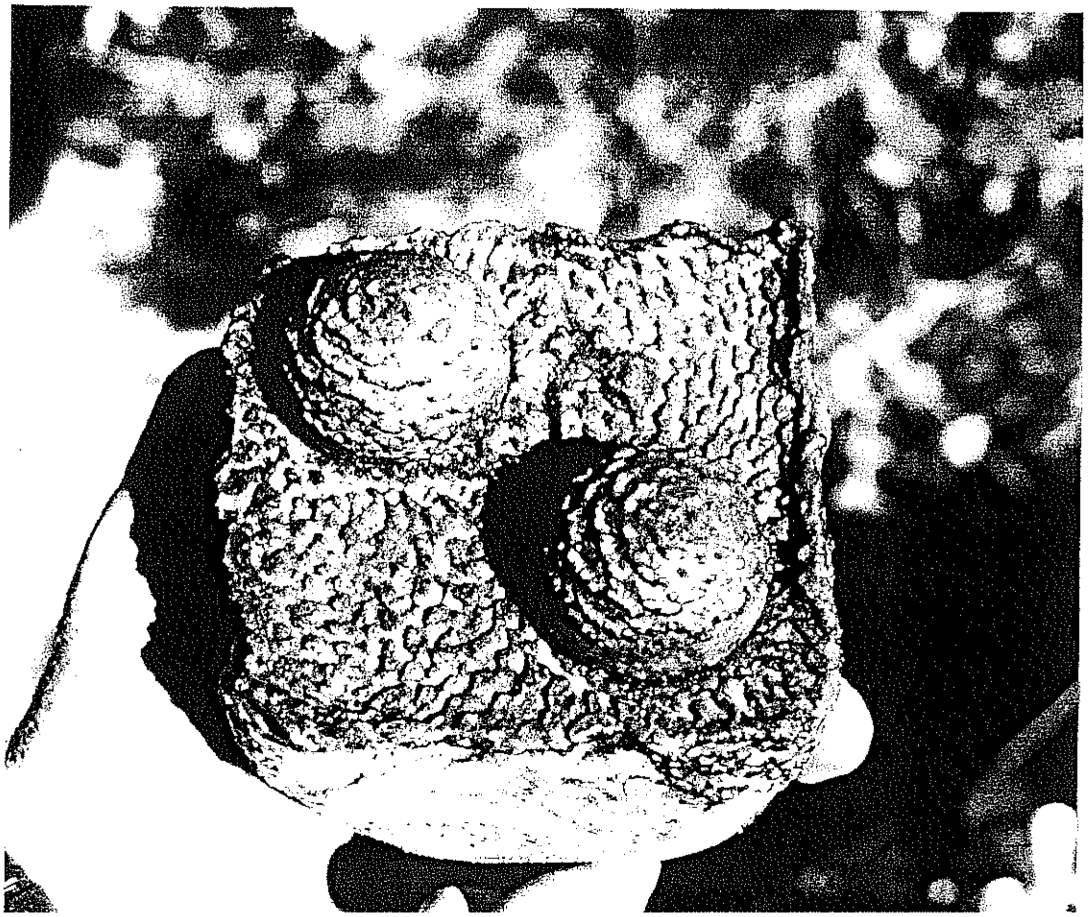
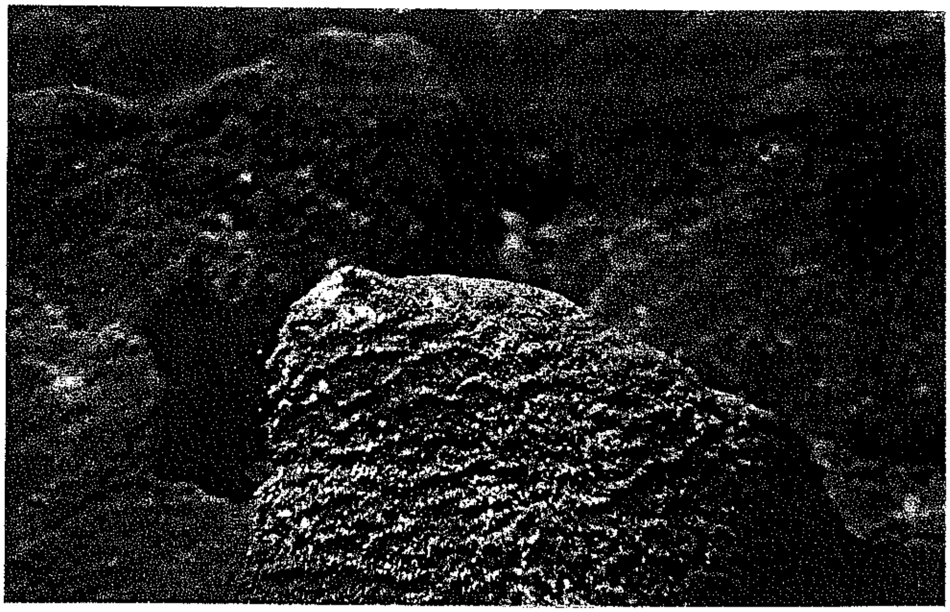


Fig. 3.8.2-3A,B. A. Artificial stromatolites after 15 months in Escobedo, incubated at 1.5 m depth. Current direction is toward the top of the photo. Note that grazing is heavier on the down-current side of the hemispheres. Diameter of hemispheres is 4 cm. B. Natural stromatolite photographed underwater _in situ_ from the same area of Escobedo in which the artifiacial stromatolites were incubated. Scale aproximately the same as in A.





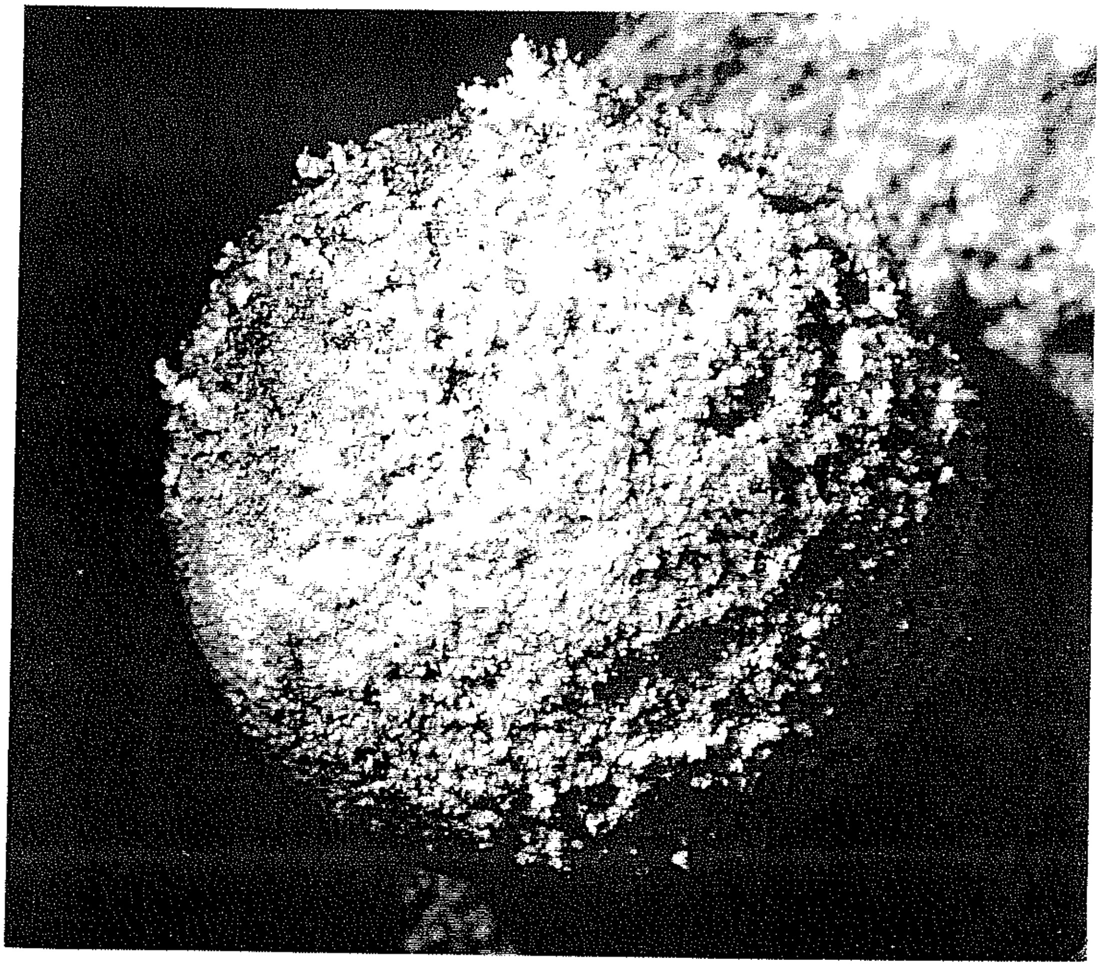
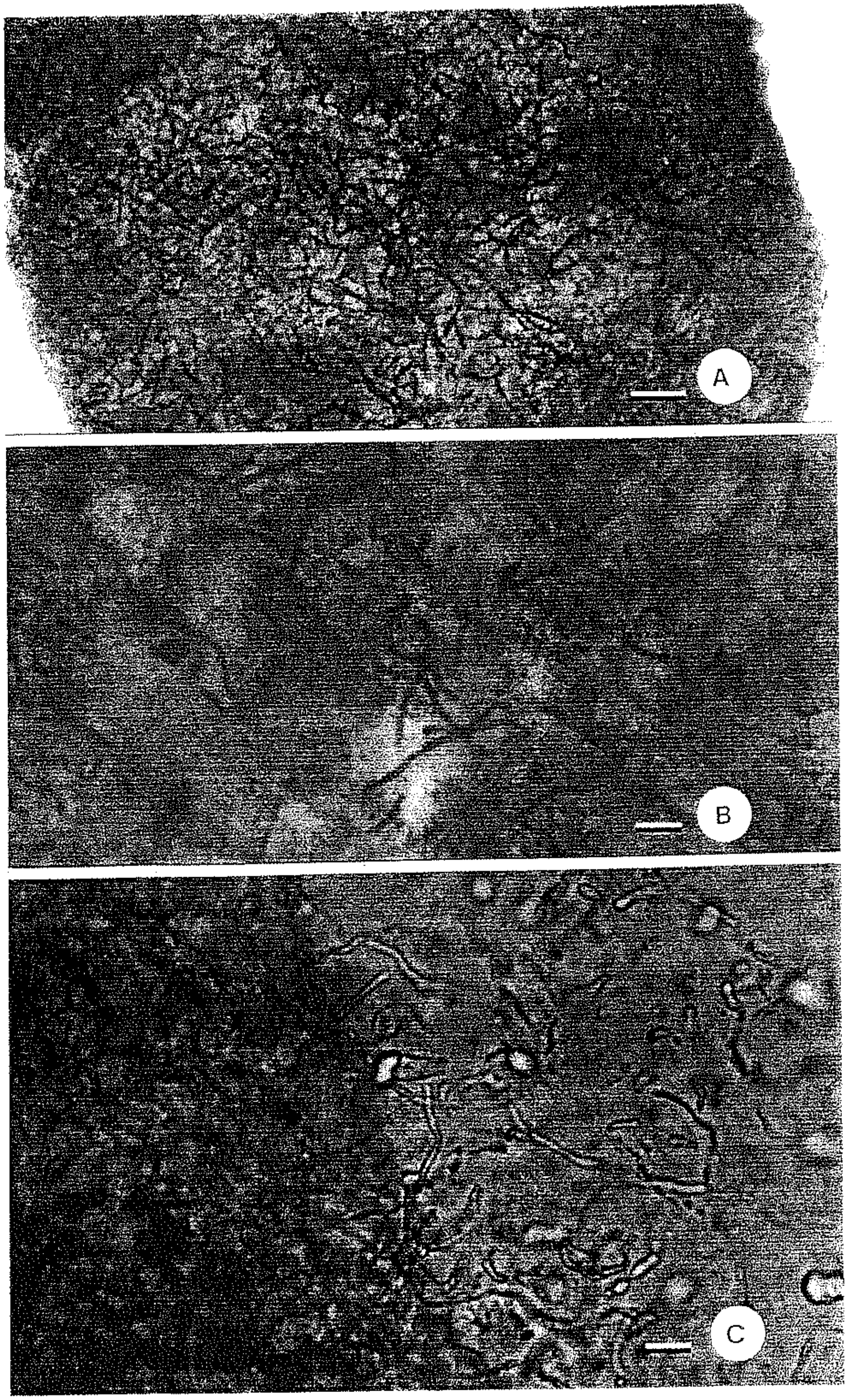


Fig. 3.8.2-4. Artificial substrate incubated in Pozo Azul in water 42 cm deep, for 6 months. Diameter of hemisphere is 4 cm.

Fig. 4.6.3-1A,B,C. Unoriented views of El Mojarral stromatolite thin section. A. General view showing density of Schizothrix sp. filaments. Scale bar = 50 um. B. Untreated close-up of material shown in A. Scale bar = 5 um. C. Same areas shown in B, after treatment with dilute hydrochloric acid to remove calcite. Filaments are flexible. Scale bar = 5 um.


A
B
C

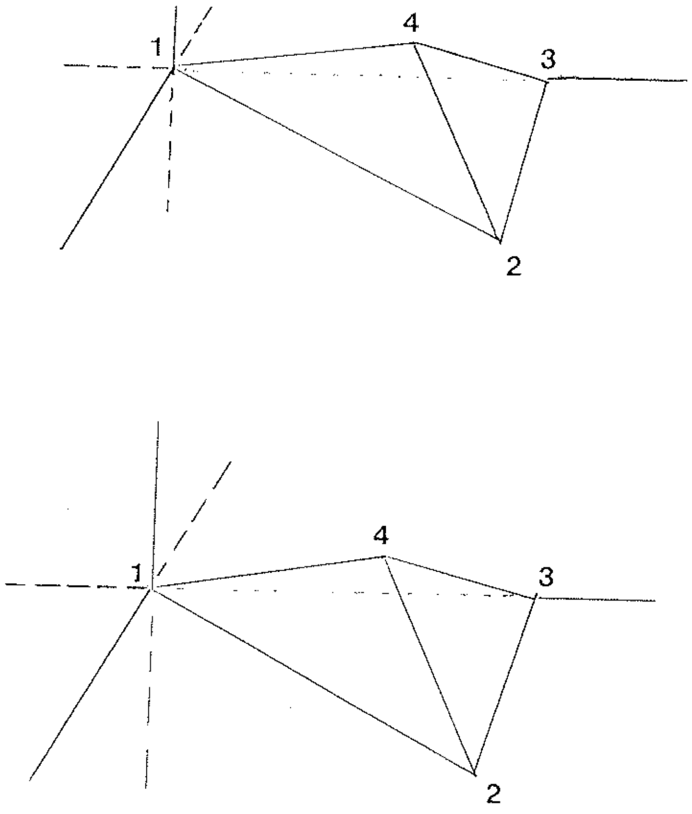


Fig. 4.7-1. 3-dimensional plots of euclidian distances between the stromatolite sites based on the composition of the diatom assemblages. 1 = El Mojarral, 2 = Rio Mesquites, 3 = Pozo Azul, 4 = Laguna Garabatal. A. Plot of euclidean distances calculated on the basis of the 8 most abundant species. B. Plot of euclidean distances calculated on the basis of the 50 most common diatom species. Note that plots are almost the same shape.

Fig. 4.7-2. SEM micrograph of polysaccharide material on the surface of a Garabatal stromatolite. Note the extent to which it increased the cohesion of the calcite grains by binding them into the mat. Scale bar = 10 um.

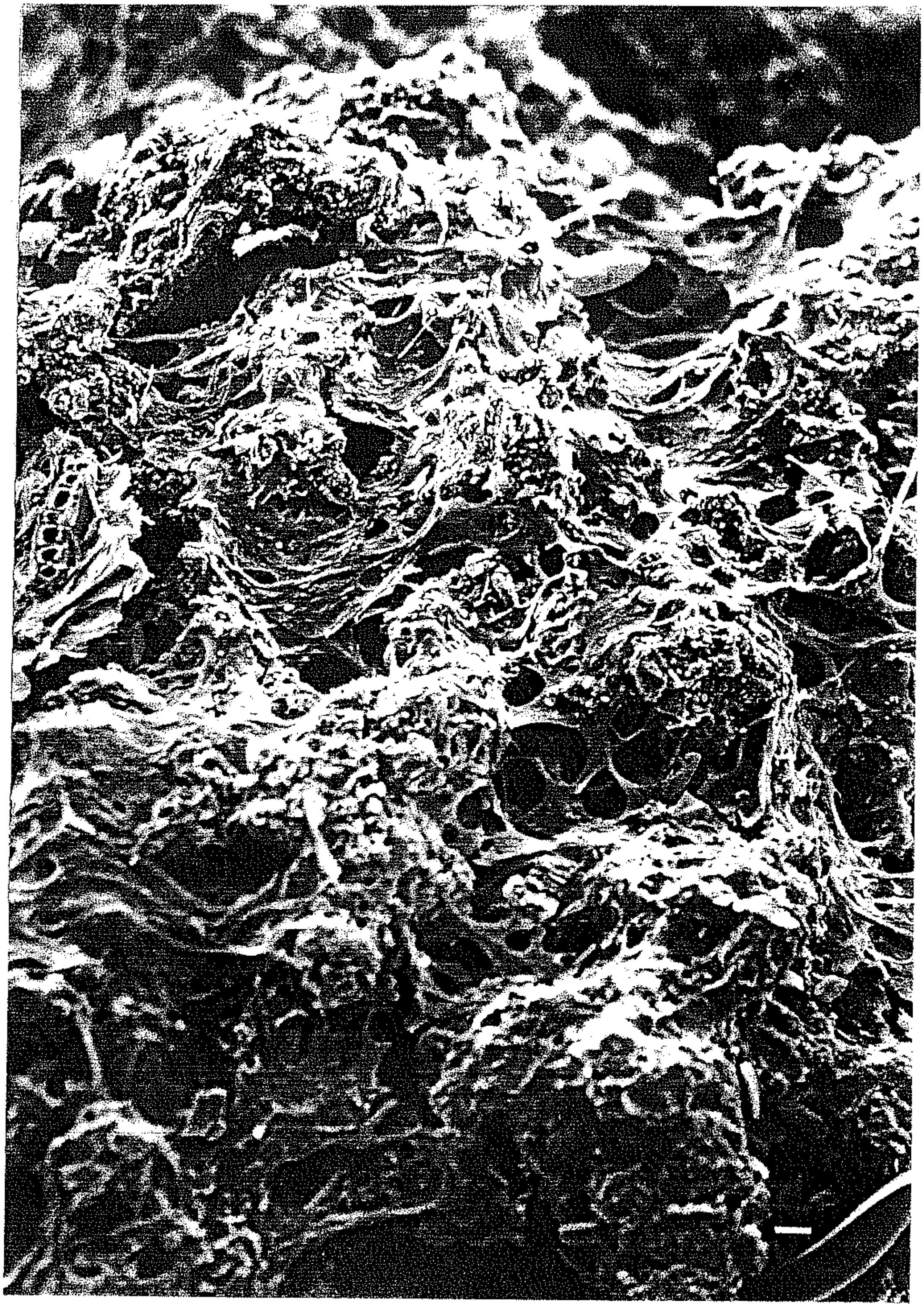


TABLE 3.1.1-1

PHYSICO-CHEMICAL MEASUREMENTS OF EL MOJARRAL (WEST) INCLUDING TEMPERATURE, PH, CONDUCTIVITY, DISSOLVED OXYGEN, TOTAL DISSOLVED SOLIDS, SALINITY, ALKALINITY, AND CARBON DIOXIDE

Date	Temp. (°C)	pH	Cond. (umhos)	Other
27 Jan 79	29.8	7.5	2910	sal: 1.7 ppt
14 Apr 79	31.0	6.9	2810	sal: 1.3 ppt
11 Aug 79	28.5	7.7	2400	sal: 1.5 ppt
26 Jul 83	32.7	7.3	2800	DO: 5.3 mg/l sal: 1.2 ppt
09 Jun 84	34.0	7.1	2800	sal: 1.3 ppt
15 Mar 87	32.5	7.2	(meas. at surface)	
15 Mar 87	32.5	6.9	(meas. at spring vent)	
25 Aug 87	32.0		2800	(meas. at surface)
25 Aug 87	30.4		2800	(meas. at spring vent)
16 Oct 87	34.2	7.1	3200	sal: 0.4 ppt, CO_2: 93.5 ppm, Alk: 199 ppm
22 May 88	33.2	6.9	2800	TDS: 1500 mg/l

TABLE 3.2.1-1

PHYSICO-CHEMICAL MEASUREMENTS OF RIO MESQUITES INCLUDING TEMPERATURE, PH, CONDUCTIVITY, TOTAL DISSOLVED SOLIDS, SALINITY AND CURRENT

Date	Temp. (°C)	pH	Cond. (umhos)	Other
12 Apr 79	27.0	7.2	2450	sal: 1.1 ppt
14 Apr 79	27.0	6.3	2820	sal: 1.5 ppt
13 Aug 79	27.0	7.2	2450	sal: 1.1 ppt
30 Jul 83	30.4	6.7		sal: 2.3 ppt
09 Jun 84	27.5	6.0	3025	sal: 1.3 ppt
10 Jun 84	29.5	6.8	3000	current 0.2 m/sec
02 Sep 85	26.0			current 0.15 m/sec
15 Mar 87	26.1	7.8		
23 Aug 87	30.0		3100	
09 Jan 88	21.7	(meas.in stream)		
09 Jan 88	25.4	(meas. at rheocrene)		
23 Nov 88	21.0	7.8	3500	TDS: 1800 mg/l
14 Mar 89	25.0	7.6	2900	TDS: 1500 mg/l

TABLE 3.3.1-1

PHYSICO-CHEMICAL MEASUREMENTS OF POZO AZUL INCLUDING TEMPERATURE, PH, CONDUCTIVITY, DISSOLVED OXYGEN, TOTAL DISSOLVED SOLIDS, SALINITY, AND ALKALINITY

Date	Temp. (^{0}C)	pH	Cond. (umhos)	DO (mg/l)	Other
09 Jun 84	30.0	6.5	2800		sal: 1.5 ppt
31 Aug 85	31.0		2970		
01 Sep 85	30.0	7.3	2920		
23 Mar 86	21.7	7.5			
21 Apr 86	27.5		2850		sal: 1.5 ppt
05 Jul 86					
(0800)	29.2	6.9	2840	5.05	
(0900)	29.5	6.9	2840	5.1	
(1000)	30.0	7.4	2900	5.7	alk: 170 mg/l
(1010)	30.0	7.2	2900	5.6	
(1020)	29.7	7.2	2900	5.6	
(1030)	29.7	7.4	2940	5.2	
(1040)	30.0	7.1	2940	5.0	
(1050)	30.1	7.5	2940	5.0	
(1110)	30.1	7.5	2910	4.8	alk: 170 mg/l

(1120)	30.1	7.4	2900	4.6	
(1130)	30.1	7.5	2920	4.8	
(1140)	30.2	7.4	2930	5.0	
(1150)	30.6	7.4	2930	5.2	alk: 167 mg/l
(1230)	31.0	7.5	2950	5.2	
(1300)	31.1	7.4	3000	5.2	alk: 170 mg/l
(1330)	31.8	7.7	3000	5.8	
(1400)	32.0	7.6	3000	5.8	alk: 170 mg/l
05 Sep 86	29.0	7.8	2920	(meas. at surface)	
05 Sep 86	30.0	(meas. at spring vent)			
24 Jan 87	21.0	7.6			
25 Jan 87	19.9	7.6			
15 Mar 87	25.0	7.5	2850		sal: 1.5 ppt
23 Mar 87	23.8		2830	6.2	sal: 1.5 ppt
23 May 87	21.1	7.6			
21 Nov 88	22.5	7.4	2800		TDS: 1500 mg/l
22 Nov 88	23.2	7.4	2800		TDS: 1500 mg/l
10 Jan 88	20.5				
27 May 88	28.5	7.5	2800		TDS: 1500 mg/l
18 Nov 88	23.0	7.4	3050		TDS: 1500 mg/l
21 Nov 88	24.0	7.4	2800		TDS: 1500 mg/l
22 Nov 88	23.3	7.4	2800		TDS: 1500 mg/l
06 Jan 89	23.7	7.5	3100		TDS: 1500 mg/l
25 May 89	30.3	7.6	2500		TDS: 1350 mg/l

TABLE 3.4.1-1

PHYSICO-CHEMICAL MEASUREMENTS OF LAGUNA GARABATAL INCLUDING TEMPERATURE, PH, CONDUCTIVITY, DISSOLVED OXYGEN, AND SALINITY

Date	Temp. (^{o}C)	pH	Cond. (umhos)	DO (mg/l)	Salinity (ppt)
14 Apr 79	25.0	7.2	2720		sal: 1.5
12 Aug 79	28.0	7.1	2980		sal: 1.8
01 Aug 83	31.9	7.6	2890	6.2	sal: 1.3
05 Jun 84	30.0	6.5	2900		sal: 1.3
09 Jun 84	30.0	7.6	2900		sal: 1.3
08 Jan 88	21.7				

TABLE 3.5-1

1983 WATER CHEMISTRY MEASUREMENTS FOR AQUATIC HABITATS IN THE CUATRO CIENEGAS BASIN, * = STROMATOLITE SITES

CC-01*	Laguna El Mojarral (West)
CC-02	Pozo Churince
CC-03	Rio Churince
CC-04	Laguna Grande
CC-05*	Laguna Garabatal
CC-06	Pozo Arbol
CC-07	Laguna Juan Santos
CC-08	Tierra Falsa (dug hole in dry lake bed)
CC-10	Laguna Santa Tecla
CC-11	Laguna Tio Candido
CC-12B	Inflow stream to Bano Escobedo
CC-12V*	Bano Escobedo
CC-12I	Outflow stream from Bano Escobedo
CC-13A	Salt works #1
CC-13B	Salt Works #2
CC-14	Rio Canon
CC-15	Rio Salado
CC-16*	Rio Mesquites
CC-17	Hundido Descanso sink hole
CC-18	Pozo Anteojo

(TABLE 3.5 CONTINUED)

Sample	Locale	Temp.°C	pH	Salinity ppt	Density
CC-01	spring	33.3	7.12	1.45	1.000
CC-02	spring	30.4	7.05	1.20	1.000
CC-03	stream	27.8	8.01	1.38	1.000
CC-04	playa	25.7	8.35	4.85	1.006
CC-05	spring	31.5	7.99	1.52	1.000
CC-06	spring	31.4	7.04	1.10	1.000
CC-07	stream	26.9	7.21	1.40	1.000
CC-08	playa	34.0	7.51	≈184	1.190
CC-10	stream	30.3	7.07	0.45	0.999
CC-11	stream	29.7	6.75	1.25	1.000
CC-12B	stream	34.5	6.18	1.37	1.000
CC-12V	spring	35.0	--	--	1.000
CC-12I	stream	29.9	--	--	1.000
CC-13A	playa	33.8	--	--	1.289
CC-13B	playa	47.4	--	--	1.295
CC-14	spring	22.6	7.05	0.48	0.998
CC-15	playa	37.0	--	--	1.434
CC-16	spring	30.4	6.70	1.41	1.000
CC-17	playa	21.3	7.64	6.20	1.006
CC-18	stream	29.7	6.40	0.81	0.999

(TABLE 3.5 CONTINUED)

Sample	Mg(mM)	Ca(mM)	Na(mM)	K(μM)	Sr(μM)	Si(μM)
CC-01	4.5	9.3	6.2	205	145	305
CC-02	4.2	8.7	6.3	179	169	304
CC-03	4.6	9.4	6.8	205	179	327
CC-04	23.9	19.5	39.2	1355	468	743
CC-05	5.1	9.8	8.1	281	177	331
CC-06	4.6	9.5	6.7	205	171	308
CC-07	4.7	10.0	6.5	230	173	328
CC-08	732	15.5	1900	70329	128	75
CC-10	1.4	2.8	1.6	51	34	239
CC-11	4.2	8.5	6.3	205	145	309
CC-12B	4.4	9.1	7.0	205	167	310
CC-12V	4.6	8.5	6.6	230	163	417
CC-12I	5.0	9.5	7.7	256	167	326
CC-13A	1511	3.1	2479	11419	378	127
CC-13B	2234	1.4	1674	43160	14	1620
CC-14	1.7	2.2	1.4	230	25	413
CC-15	2580	6.7	2637	120000	192	4004
CC-16	5.0	9.6	7.4	281	165	343
CC-17	31.3	12.7	61.4	1560	145	834
CC-18	2.4	7.1	1.6	51	75	313

(TABLE 3.5 CONTINUED)

Sample	S(mM)	Cl(mM)	Alk(meq/l)	F(μM)	NO_3(μM)	PO_4(μM)
CC-01	14.3	2.9	2.675	140	109	0.03
CC-02	13.7	3.1	2.351	140	104	--
CC-03	15.1	3.3	1.656	150	57	0.06
CC-04	53.2	18.8	1.895	370	2	0.18
CC-05	16.1	3.4	2.111	150	91	0.14
CC-06	14.9	3.4	2.481	150	103	0.10
CC-07	15.5	3.6	2.326	104	70	0.10
CC-08	1450	767	9.482	950	118	9.84
CC-10	2.6	0.9	3.716	50	139	0.15
CC-11	13.3	3.2	2.341	110	91	0.10
CC-12B	15.0	3.6	2.805	109	102	0.18
CC-12V	15.4	3.5	2.739	100	--	--
CC-12I	16.5	3.8	2.632	110	--	--
CC-13A	2065	1697	35.7	1669	--	--
CC-13B	938	6244	75.6	3915	--	--
CC-14	2.2	0.7	3.955	40	119	0.28
CC-15	3553	1409	39.3	2745	--	--
CC-16	15.5	4.0	2.466	100	90	0.06
CC-17	61.3	33.3	5.227	400	5	0.72
CC-18	9.2	0.7	2.247	80	45	0.05

(TABLE 3.5 CONTINUED)

Sample	Fe	Mn	Cu	Ge
CC-1	4.0	0.05	3.3	
CC-2	4.4±0.4	0.25±0.04	1.3±0.3	3.1±0.3
CC-3	4.4±1.5	0.45±0.08	0.5±0.3	3.8±0.3
CC-4	11.5±0.1	3.50±0.12	1.3±0.3	2.2±0.1
CC-5	2.9±0.1	0.52±0.04	0.4±0.2	4.6±0.0
CC-6	2.0±0.1	0.24±0.01	2.1±0.1	3.5±0.4
CC-7	4.3±0.5	0.13±0.02	1.8±0.2	4.2±0.3
CC-10	2.8±0.3	0.52±0.04	1.4±0.1	
CC-11	3.2±0.1	0.25±0.02	0.8±0.4	3.3±0.0
CC-12B	2.6±0.3	--	1.2±0.2	3.7±0.3
CC-14				0.7±0.1
CC-16	2.3±0.2	--	2.0±0.1	4.0±0.3
CC-17	4.3	0.30	1.8	
CC-18		0.44±0.04	3.9±0.7	1.3±0.0

(TABLE 3.5 CONCLUDED, METALS, ALL IN PPB)

Sample	Zn	Cd	Pb	Ni	Co
CC-1	4.7	0.4	--	2.6	0.1
CC-2	--	--	--	3.1±0.9	--
CC-3	2.1±0.1	--	8.0±3.2	2.7±1.1	--
CC-4	2.4±0.2	--	2.8±0.4	1.6	0.5 --
CC-5	0.02±0.02	5.6±1.0	2.3±0.9	0.03±0.03	
CC-6	9.1±0.6	--	7.8±0.3	2.1±0.4	--
CC-7	3.7±0.2	0.17±0.07	6.8±2.0	2.1±0.4	0.33±0.06
CC-10	3.6±0.2	0.16±0.05	2.4±0.8	0.8±0.2	0.24±0.24
CC-11	4.3±0.6	0.09±0.01	4.2±1.0	2.3±0.5	0.10±0.10
CC-12B	5.5±0.6	0.20±0.02	8.0±4.0	2.4±0.6	--
CC-16	4.1±0.3	0.15±0.05	--	2.4±0.2	0.03±0.03
CC-17	1.3	0.27	58.8	1.2	--
CC-18	6.4±0.4	0.20±0.04	4.8±2.0	1.6±0.5	--

TABLE 3.5-2

WATER CHEMISTRY DATA FOR STROMATOLITIC SITES IN THE CUATRO CIENEGAS BASIN

		Pozo el Mojarral	Pozo Azul	Rio Mesquites	Laguna Garabatal
Mg^{+2}(mmol/l)	"83	4.5	-	5.0	5.1
(mmol/l)	"84	4.7	4.8	5.6	5.5
(mg/l)	"83	109.4	-	121.6	124.0
(mg/l)	"84	114.3	116.7	136.1	133.7
Ca^{+2}(mmol/l)	"83	9.3	-	9.6	9.8
(mmol/l)	"83	9.7	8.9	10.9	9.6
(mg/l)	"83	372.7	-	384.8	392.8
(mg/l)	"84	388.9	356.7	436.9	384.8
Na^{+1}(mmol/l)	"83	6.2	-	7.4	8.1
(mmol/l)	"84	8.3	7.4	9.0	9.1
(mg/l)	"83	142.5	-	170.1	186.2

(mg/l) "84	190.8	170.1	206.9	209.2
S^{-2}(mmol/l) "83	14.3	-	15.4	16.1
(mmol/l) "84	14.2	14.3	14.6	16.1
SO_4^{-2}(mg/l)	1373.7	-	1479.3	1546.6
(mg/l)	1364.1	1373.7	1402.5	1546.6
Cl^{-1}(mmol/l) "83	2.9	-	4.0	3.4
(mmol/l) "84	3.6	3.5	4.0	3.9
(mg/l) "83	102.8	-	141.8	120.5
(mg/l) "84	127.6	124.1	141.8	131.2
HCO_3^{-1} (meq/l)	2.7	3.4	2.5	2.1
	-	-	-	-
(mg/l) "83	164.8	207.5	152.6	128.1
	-	-	-	-
K^{+1}(mmol/l) "83	0.205	-	0.281	0.281
(mmol/l) "83	0.345	0.261	0.278	0.267
(mg/l) "83	8.0	-	11.0	11.0
(mg/l) "84	13.5	10.2	10.9	10.4

Sr^{+2}(mmol/l) "83	0.145	-	0.165	0.177
	-	-	-	-
(mg/l) "83	12.7	-	14.5	15.5
	-	-	-	-
Si(mmol/l) "83	0.305	-	0.343	0.331
(mmol/l) "84	0.242	0.265	0.266	0.254
(mg/l) "83	18.3	-	20.6	19.9
(mg/l) "84	14.5	15.9	16.0	15.9
F^{-1}(mmol/l) "83	0.140	-	0.100	0.150
(mmol/l) "84	0.174	0.160	0.190	0.168
	2.7	-	1.9	2.8
	3.3	3.0	3.6	3.2
NO_3^{-1} (umol/l)	109	-	90	91
(mg/l)	6.8	-	5.6	5.6
PO_4^{-3} (umol/l)	0.03	-	0.06	0.14
(mg/l)	0.002	-	0.006	0.013
Zn (PPB)	4.7	-	6.4	-

Cd (PPB)	0.4	–	0.20	0.02
Pb (PPB)	ND	–	4.8	5.6
Ni (PPB)	2.3	–	1.6	2.3
Co (PPB)	0.1	–	ND	0.03
Fe (PPB)	4.0	–	–	2.9
Mn (PPB)	0.05	–	0.44	0.52
Cu (PPB)	3.3	–	3.9	0.4
TDS** (1983) (mg/l)	2265.9	2348.8	2450.2	2498.2
Temp. (1983)	33.3	–	30.4	31.5
(1984)	27.0	31.0	29.5	30.0
pH (1983)	7.1	–	6.7	8.0
(1984)	7.3	6.3	6.8	7.6

* All measurements except Pozo Azul made July 1983; Pozo Azul measurements for all parameters except alkalinity made June 1984, alkalinity measured July 1986. Nutrient and metals data collected in 1983 only. ND means not detected.

** TDS calculated for 1983 data (except Pozo Azul) and represents the sum of the major ions only.

TABLE 3.6-1

ATOMIC ADSORPTION ANALYSIS OF CUATRO CIENEGAS SOIL AND AVERAGE SOIL COMPOSITIONS. ALL VALUES IN ppm EXCEPT Al, Fe, Ca, Mg, Na, K, AND Ti, IN %

Ele.	C.C. Soil	Av Soil	Ele.	C.C. Soil	Av Soil
Al	4.4	7.10	Mn	450.00	1,000.00
Ag	0.12	0.05	Nd	16.00	35.00
As	16.70	6.00	Ni	16.40	50.00
Ba	270.00	500.00	Pb	13.50	35.00
Ca	<0.50	1.50	Sb	1.20	1.00
Cd	2.30	0.35	Se	0.350	0.70
Ce	33.00	50.00	Sn	0.770	1.40
Co	6.10	8.00	Th	5.60	9.00
Cr	31.50	70.00	Zn	87.00	90.00
Cs	8.40	4.0	Rb	77.00	150.00
Cu	16.3	30.00	V	69.00	90.00
Eu	0.65	1.00	Na	0.27	0.50
Fe	1.85	4.00	K	<0.80	1.40
Hf	2.50	4.00	Ti	0.22	0.50
Hg	0.02	0.07	Sc	6.90	7.0
Mg	4.65	0.50			

TABLE 3.8.2-1

PHYSICO-CHEMICAL MEASUREMENTS OF BANO ESCOBEDO INCLUDING TEMPERATURE, PH, CONDUCTIVITY, TOTAL DISSOLVED SOLIDS, SALINITY, ALKALINITY, CARBON DIOXIDE, AND CURRENT

Date	Temp. (^{0}C)	pH	Cond. (umols)	Other
12 Aug 79	33.0	6.7	2200	
01 Aug 79	34.5	7.3	2800	sal: 1.3 ppt
25 Jul 83	34.5	6.2		sal: 1.4 ppt
09 Jun 84	34.0	7.3	2800	sal: 1.3 ppt
23 Jan 87	33.0	7.1		
15 Mar 87	33.2			
20 Aug 87	33.0			
17 Oct 87	34.0	7.2	2700	CO_2: 95.4 ppm, Alk: 10.25 205 ppm Outflow Current: 6.3 cm/sec
09 Jan 88	32.5			
23 Nov 88	30.5	7.1	3000	TDS: 1500 mg/l

Table 4.5-1

GEOGRAPHIC AND ENVIRONMENTAL CHARACTERISTICS OF EACH STROMATOLITE SITE DISCUSSED IN THE TEXT

Site:	El Mo.	Esco.	R. Mes.	P. Azul	Gara.
Habitat	lake	lake	stream	lake	lake/st
Ele. (m)	720	725	730	710	740
Distance (m)	1400	1550	1500	3500	1800
Diameter (m)	14-48	16	2-3	40	35
Depth (m)	5	5	2.5	13	1
Light*	lo-hi	hi	lo	lo-hi	hi
Temp. ^{0}C	28-34	33-35	21-30	22-31	22-32
Current*	m	m	hi	lo	m-hi
Exch. rate*	m	m	hi	lo-m	hi-lo
Wind fetch*	m	m	lo	lo-m	m-lo
Dessication	no	no	no	no	yes
Substrate	sand, rocks	silt	sand, rocks	mud	sand, mud, rock

Key:

*Low (lo), moderate (m), high (hi) values are relative estimates based on observations over a ten year period. Distance refers to distance from base of nearest alluvial fan of Sierra San Marcos.

Table 4.7-1

DIATOM DIVERSITY MEASURES

Site	Index	Evenness	No. of species
Simpson Diversity Index, log base 10			
El Mojarral	0.8772	0.6129	27
Rio Mesquites	0.8125	0.5501	30
Pozo Azul	0.8352	0.5903	26
Garabatal	0.9135	0.6312	28
Shannon Diversity Index, log base 10			
El Mojarral	1.0330	0.7217	27
Rio Mesquites	0.9051	0.6127	30
Pozo Azul	0.9394	0.6639	26
Garabatal	1.1258	0.7779	28
Brillouin Diversity Index, log base 10			
El Mojarral	0.9090	0.6350	27
Rio Mesquites	0.7846	0.5312	30
Pozo Azul	0.8255	0.5834	26
Garabatal	0.9912	0.6849	28

TABLE 4.7-2

% RELATIVE ABUNDANCE OF STROMATOLITE DIATOMS REPRESENTING 5% OR MORE OF A POPULATION. DIAGONAL LINE SEPARTATES COUNTS OF 500 AND 1500 CELLS RESPECTIVELY. 1500 CELL COUNT IS COMPOSITE OF THREE 500-CELL COUNTS ON SAMPLES COLLECTED AT DIFFERENT TIMES OF THE YEAR

	Laguna El Mojarral	Rio Mesquites	Laguna Garabatal	Pozo Azul
Achnanthes exigua	-/23.1			
Achnanthes gibberula	-/19.8			
Achnanthes affinis	-/12.3	-/21.0		
Nitzschia denticula	52.1/8.2		17.0/12.5	-/5.0
Denticula elegans	18.0/-	11.2/17.9	-/9.7	-/46.1
Cymbella norvegica	18.8/9.7	-/6.5	-/10.7	16.6/12.3
Brachysira serians	-/5.4			11.4/ -
Amphora katii		78.0/33.4	55.2/18.7	-/33.7
Mastogloia smithii			6.0/6.2	15.6/8.5
Synedra ulna			- /18.5	
Cymbella microcephala			-/6.3	13.2/ -
Mastogloia elliptica				-/8.2

Table 4.7-3

DIATOM ASSOCIATIONS CHARACTERISTIC OF STROMATOLITIC SITES IN THE CUATRO CIENEGAS BASIN, BASED ON THE 5 MOST COMMON DIATOMS AT EACH SITE IN A COUNT OF 500 CELLS

	El Moj.	Rio Mes.	Gara.	Pozo Azul
Achn. affinis	*			
Gomp. intricatum	*			
Nitz. denticula	*	*	*	
Dent. elegans	*	*		*
Cymb. norvegica	*			*
Amph. ovalis		*		
Dipl. oblongella		*		
Mast. smithii		*		
Amph. cf katii			*	
Cymb. cistula			*	
Brac. serians			*	*
Mast. elliptica			*	*
Cymb. microcephala				*

TABLE 5-1

CUATRO CIENEGAS STROMATOLITE CHARACTERISTICS

Type 1: Laguna El Mojarral

Shape: oncoids and stromatolites
Mat thickness: 2-4 mm
Lamination: repetitive
Growth rate: 2 mm/yr
Main photosynthetic organisms: Homoeothrix balearica, Schizothrix lacustris, diatoms

Type 2: Rio Mesquites

Shape: oncoids and stromatolites
Mat thickness: 2 mm
Lamination: lenticular laminoid
Growth rate: 2 mm/yr
Main photosynthetic organisms: Gongrosira calcifera, Homoeothrix balearica, diatoms

Type 3: Pozo Azul

Shape: stromatolites
Mat thickness: 1 cm
Lamination: thrombolitic
Growth rate: 1 cm/yr
Main photosynthetic organisms: Dichothrix bonetiana, Schizothrix sp., Cyanostylon microcystoides, diatoms

Type 4: Laguna Garabatal

Shape: stromatolites
Mat thickness: 1-3 cm
Lamination: cyclothemic
Growth rate: 1-3 cm/yr
Main photosynthetic organisms: Scytonema cf. mirabile, Schizothrix affinis, diatoms