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OBSERVATIONS ON THE *SCYTONEMA* MATS OF SAN SALVADOR, BAHAMAS

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ABSTRACT

Mats of the cyanobacterium *Scytonema myochrous* are described from a range of supralittoral and littoral lacustrine sites on San Salvador, Bahamas. *Scytonema* occurred as flat, polygonal mats, as low rounded colonies and as irregular, partially lithified heads and crusts. Little difference was found in the species composition or biomass per unit area but biomass was extremely low (cell volume excluding sheath) at all sites.

Just below the mat surface, low magnesian calcite accreted, probably through precipitation *in situ* as a result of evaporation and/or photosynthesis. Lithification was infrequent and the deposits were mostly poorly consolidated with high porosity (62-18%). Growth of stromatolitic algal heads in Storr's Lake was undetectable during July using carborundum marking and the growth and calcification of *Scytonema* in relation to salinity is briefly discussed.

INTRODUCTION

Cyanobacterium mats are a characteristic feature of many low-lying tropical landscapes, where higher plant growth is restricted by high salinity or sediment instability. It has been realized for several decades that these mats are of more than passing interest to geologists, for under certain conditions the mats may calcify, or trap and bind suspended particles, then become preserved as stromatolites.

Many types of cyanobacterium mats have been described and among the most important are those formed by *Scytonema*. These were first described from the Bahamas by Black (1933). Investigations in the Florida everglades by Dachnowski-Stokes & Allison (1928) resulted in further discoveries and it soon became apparent that *Scytonema* was a major primary producer and sediment stabilizer in the region. In a series of papers, Monty (1972; 1976) and Monty & Hardie (1976) have further described these mats in some detail and Gleason (1972) made further investigations in the Everglades. Although Andros Island, with its extensive inland marshes remains the *locus classicus* for *Scytonema*, the mats are well developed on other islands. On San Salvador, they are commonly encountered around the lakes and in places they become partially lithified. This paper describes some of these mats and their significance as precipitators of calcium carbonate.

METHODS

Mats were sampled during July, 1987 from 7 sites on San Salvador (Fig. 1) and also from Richmond Hill, Great Exuma. After careful removal of the mat, vertical columns measuring c. 2 x 2 mm were cut through the water-saturated material with a razor and the columns divided into a series of segments 1-4 mm deep to investigate the depth-distribution of cyanobacteria. Each block was decalcified with EDTA, briefly homogenized with a shearing piston and aliquots of suspension counted under an inverted microscope. By calculating the average cell volumes of each species present, the abundance of each species could be expressed on a unit volume basis. Details of the method are described elsewhere (Pentecost, 1982).

The associated mat sediments were carefully detached, washed to remove soluble salts, dried at 105 C and weighed. They were then soaked in air-free water under partial vacuum, weighed, decalcified and reweighed. Finally the organic matter content was calculated by weighing after ignition at 500 C. Selected samples were critical-point dried with carbon dioxide, Au-Pd coated and examined with a Philips EM 501B scanning electron microscope. Other samples were embedded with epoxy resin and sectioned for petrological examination.

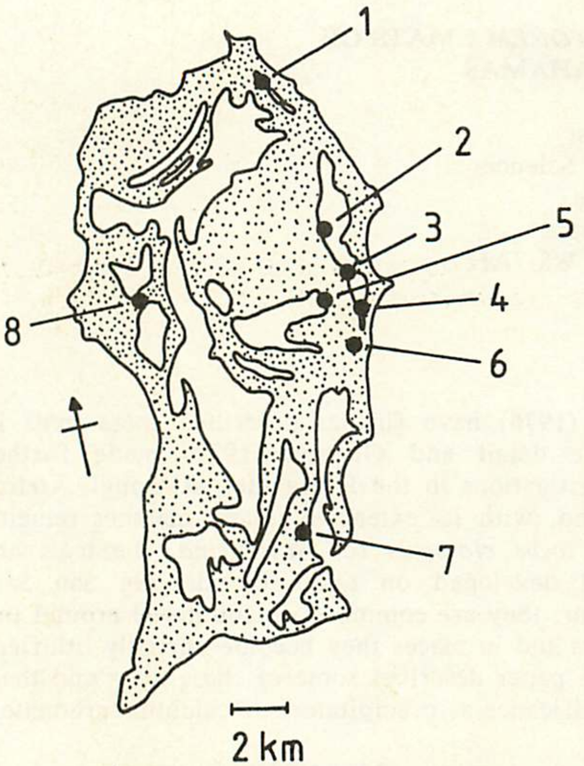

Fig. 1. Sampling sites for Scytonema *on San Salvador. 1. Upper Fresh Lake; 2. small inlet on Storr's Lake west shore; 3. Storr's Lake narrows, west shore; 4. Storr's Lake causeway; 5. Granny Lake ponds; 6. Fortune Hill Settlement pond; 7. pond at Trail Farm Settlement; 8. algal marsh complex north of Little Lake.*

RESULTS

General Structure

Scytonema myochrous (Dillw.) Ag. is widely distributed around the San Salvador lakes, occurring in areas of low-lying water-saturated ground. The colonies were rarely submerged and normally confined to the littoral fringe. Several mat morphologies were apparent. Thin black to olive-brown turfs, often with abundant desiccation cracks (Fig. 2) were common. The small polygons bore spiky tufts of vertically-arranged filaments resting upon soft, laminated carbonate sediment. These mats were well developed in many of the small ponds to the east of Granny Lake, the marshes north of Little Lake and in small patches along the shore of Storr's Lake. Many of the circular ponds forming in the limestone depressions east of Granny Lake showed well marked concentric zonation of cyanobacteria probably related to the degree of exposure to air. The centres of the circular depressions contained shallow hypersaline water with flocculent organic debris often fringed with *Batophora* (Fig. 3). This was surrounded by a narrow (30-100 cm) slightly raised *Scytonema* mat saturated but not submerged in water which merged into a darker zone, slightly lower in elevation composed of blistered *Scytonema - Gloeocapsa* mat associated with a flaky carbonate crust. Finally, there was an outer smooth black zone colonized by *Schizothrix calcicola* s. lato, *Gloeocapsa* and occasional tufts of *Lyngbya aestuarii*.

Algal heads composed predominantly of *Scytonema* were also seen in some of the ponds. The heads were varied in shape and consisted of laminate concretionary structures 5-20 cm in diameter and 2-30 cm tall (Fig. 4), with their upper surfaces usually emergent but saturated through capillary action. The heads were poorly lithified and generally easy to cut with a knife. Similar heads were found just offshore at Storr's lake narrows.

At the margin of Trail Farm Settlement, pond mats were less well-developed and consisted of discrete dull black, slight raised mounds 5-10 cm across and up to 1 cm deep on soft, unlaminated sediment overlying limestone. Smooth, thin black mats of *Scytonema* mixed with *Gloeocapsa* occurred on soft mud at the edge of Fortune Hill Settlements pond and also below the causeway at Storr's Lake. Halite was present at both sites. The mats of upper Fresh Lake resembled the polygonal mat described above but were attached to emergent lignum forming a causeway halfway along the lake. These mats had undergone lithification just below the *Scytonema* layer.

Species Distribution

The abundance of cyanobacteria within selected mat profiles is shown in Fig. 5. *Scytonema* was the dominant cyanobacterium in all profiles with greatest biomass in the upper 4 mm of mat. The biomass (cell volume excluding the sheath) ranged from 3ppt at Storr's Lake narrows to a maximum of 24 ppt at Fresh Lake. Apparently health cells were encountered at a depth of 13 mm at Storr's Lake narrows (Fig. 5A0 where light intensity must have been negligible. Empty sheaths of *Scytonema* were abundant throughout all sections and far outnumbered sheaths with trichomes.

The remaining cyanobacteria contributed little to total biomass. Most frequent were aggregates of coccoid *Gloeocapsa* cells with hyaline,

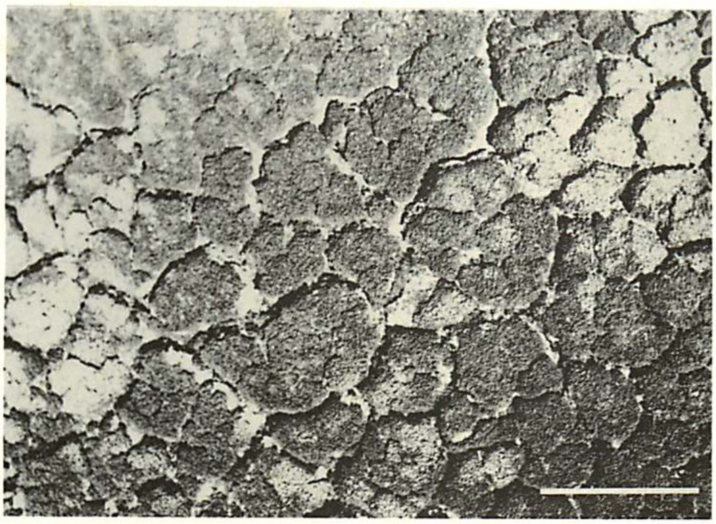

Fig. 2. Scytonema *mat, Granny Lake ponds showing desiccation polygons. Bar 5 cm.*

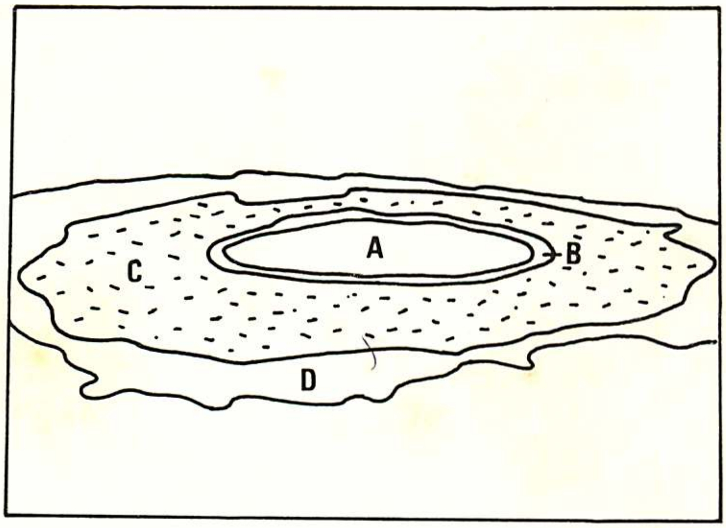

Fig. 3. Zonation of cyanobacteria in a Granny Lake pond. A. shallow open water; B. Scytonema *fringe; C. mixed* Scytonema - Gloeocapsa *carbonate crust; D. smooth* Schizothrix - Gloeocapsa *mat. Central pool 2.5 m diameter.*

Fig. 4. Section through an algal head from Granny Lake ponds. Dark upper surface shows vertically-oriented filaments of Scytonema. *Note compressed laminae of* Scytonema - Gloeocapsa *alternating with carbonate-rich layers below. Bar 5 mm.*

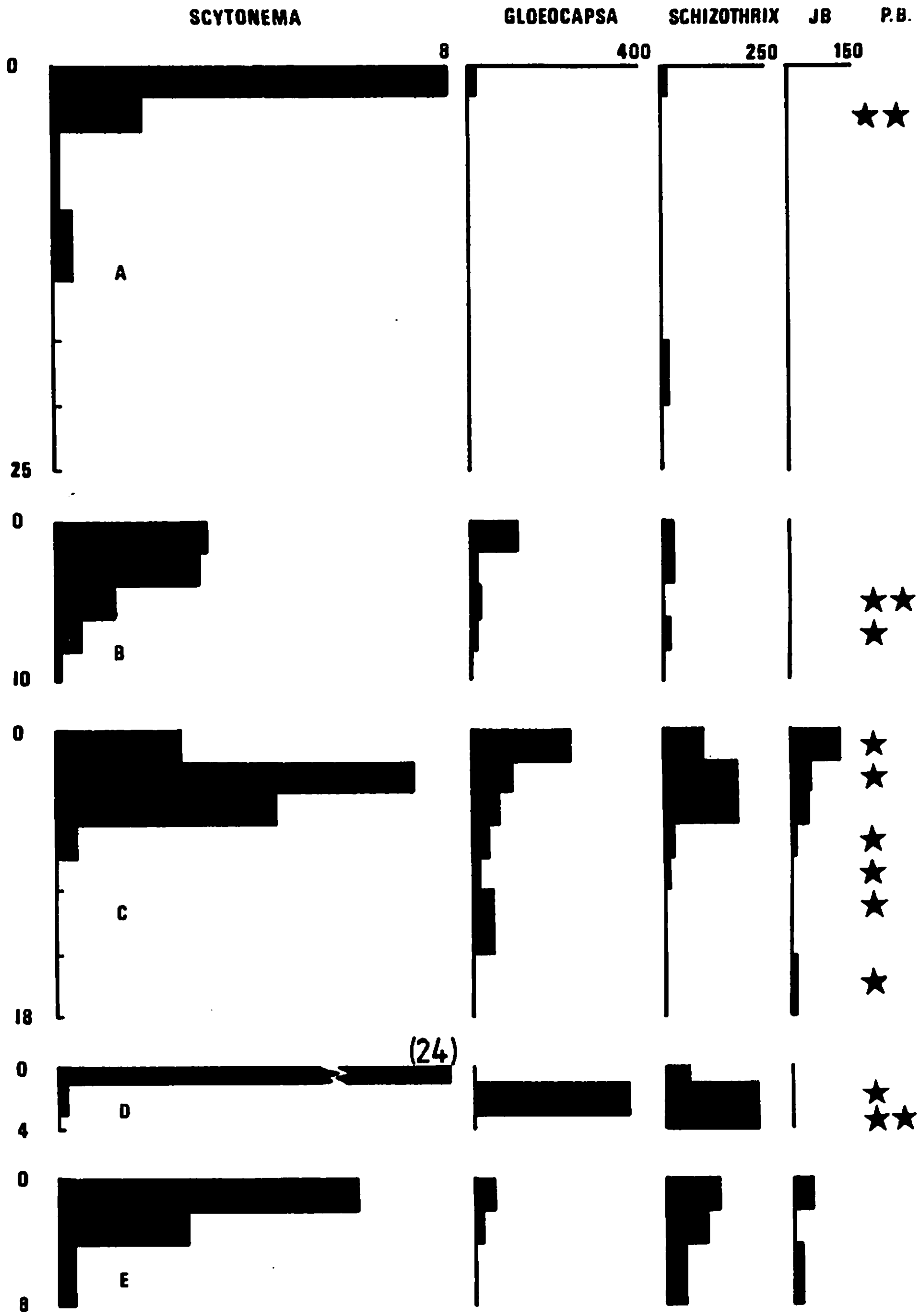

Fig. 5. Species composition of Scytonema *mats expressed as the volume occupied by cells. Abscissa:* Scytonema *volumes in parts per thousand, remaining volumes in parts per million. Ordinate: depth from mat surface (mm).*

*A. partially lithified algal head, Storr's Lake narrows; **B.** unlithified mat, narrows; **C.** soft algal head, Granny Lake ponds; **D.** lithified crust on submerged wood, upper Fresh Lake; **E.** unlithified mat from the supralittoral algal marsh, Richmond Hill, Great Exuma. **JB** =* Johannesbaptista *sp. **PB** = photosynthetic bacteria (presence indicated by stars).*

brown and occasionally violet-pigmented sheaths. The cells ranged from 1-8 μm in diameter. A distinctive form with exceptionally large cells, resembling *G. gigas* was found in small numbers at Storr's and Granny Lakes and small numbers of *Aphanocapsa* were also detected. *Gloeocapsa* is difficult, if not impossible to separate from poorly developed *Entophysalis*. Well-developed mats of *Entophysalis* were often associated locally with the *Scytonema* mats and much of the coccoid material sampled may in fact belong to this taxon.

Fine filaments of *Schizothrix calcicola* s. lato were encountered in all mats but the species rarely formed discrete layers. It was frequently seen in the algal heads of Granny Lake and at Fresh Lake, the filaments were associated with the lithified underlayer (Fig. 5D). A species of *Johannesbaptista* with filaments 3-6 μm wide was found in small numbers, particularly at Fresh Lake. Although none of these cyanobacteria matched the biomass level of *Scytonema*, their distribution with depth followed a similar pattern. A few other cyanobacteria were occasionally seen and included a *Calothrix* at Fresh Lake and a

Phormidium with trichomes 7 μm wide at Granny Lake. Diatoms were seen at all sites, but were generally rare. Only at Storr's Lake was a thin slime containing *Nitzschia* cells occasionally observed. Purple photosynthetic bacteria were commonly encountered 2-10 mm below the mat surfaces (Fig. 5), but no attempt was made to identify or enumerate them.

The algal distribution patterns in all mats was essentially the same, despite considerable differences in mat morphology. The polygonal mats sampled at Storr's Lake (Fig. 5B) closely resemble the mats of the supralittoral marine marsh at Richmond Hill, Great Exuma (Fig. 5C). The algal heads (Figs 5A and C) were sampled to a greater depth, but floristically closely resembled the polygonal mats.

All mats were associated with fine sediment which was generally unconsolidated. Polygonal mats at the edge of Storr's Lake were associated with uncemented micrite, but the top 2 mm of mat was virtually free of sediment (Fig. 6). Petrological sections revealed irregular or tubular clumps of micrite attached to the *Scytonema* sheaths. Deeper within the mat the tubes coalesced, but there was no evidence of recrystallization immediately below the mat. The partially lithified heads from the same lake were similar consisting of fine, mostly anhedral calcite crystals 1-6 μm in diameter. In all of these mats, the porosity was high and consequently the calcium carbonate content correspondingly low (Table 1). Low magnesian calcite was identified in all samples using X-ray diffraction and atomic absorption spectrophotometry. Traces of dolomite were found in the Granny Lake samples. All sites were brackish to hypersaline (Table 1) and in many isolated pools, salt crystallized out on the mat surface. Carborundum marking of algal heads at Storr's Lake narrows and the inlet over a period of 7 days, failed to reveal any algal growth.

DISCUSSION

Before sediment accumulation rates can be estimated beneath these mats, more data on the growth of *Scytonema* are urgently required. Black (1933) made no measurements, but notes that *Scytonema* growth was extremely slow on Andros Island. Monty (1976) noted a 2-3 cm increment in mat thickness in 8 weeks, equivalent to 350-500 μm per day which is certainly much faster than the growth of the algal heads in Storr's Lake measured in July. In cool-temperate climates, Thunmark (1926) and Pentecost (unpublished) observed rates of 1-3 mm per annum but these are unlikely to reflect the growth potential in lower latitudes. Salinity may be responsible for these differences. On Andros Island, *Scytonema* mats are best developed on the freshwater marshes and when the water becomes brackish, the growth of *Scytonema* is replaced by *Schizothrix* (Monty, 1976) suggesting that high salinity might be detrimental to growth. *Scytonema* is typically a freshwater genus, occurring abundantly in the Everglades and calcareous marshes worldwide, but it also occurs adjacent to many saline lakes where it may be subject to seepages of fresh groundwater. Thus, bursts of growth may occur when salinity falls, possibly explaining the wide range of growth rate encountered. Many of the San Salvador mats appear to fall into this category and on the west shore of Storr's Lake, some evidence for fresh water seepage was obtained from the salinity measurements (Table 1). A similar phenomenon could be responsible for the lithified *Scytonema* heads of Lake Clifton, Western Australia (L. S. Moore, pers. com.). A few species of *Scytonema* are truly marine and must, therefore, grow at high salinity. One form is

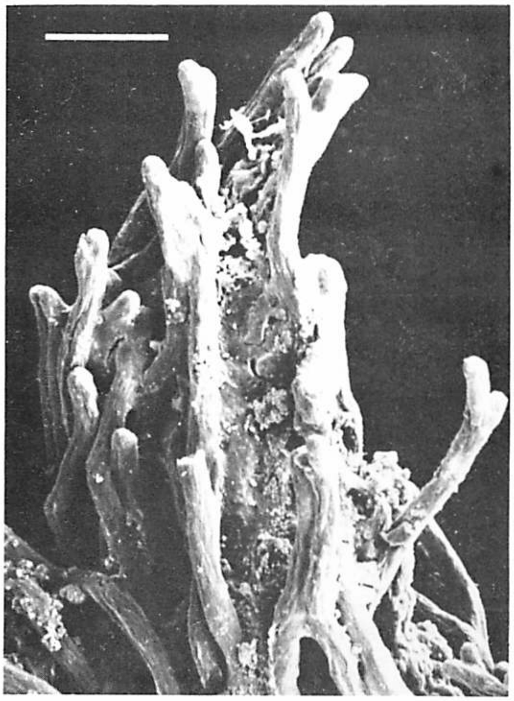

Fig. 6. Tuft of Scytonema *filaments from the surface of a polygonal mat at Storr's Lake narrows. Note filament aggregation, false-branching of filaments and sparse patches of adherent micrite. SEM micrograph. Bar 100 μm.*

Table 1

Chemical and physical data of Scytonema mats 15-20.7.1987

Location	t °C	o/oo salinity	% vol $CaCO_3$*	% weight $CaCO_3$	% organic	% residue	Mg mol %
Storr's Lake narrows							
polygonal mat	36	24	28 (0-4)	93.3	6.2	0.5	2.1
algal heads	32	83	22 (5-10)	92.6	7.2	0.3	2.0
Granny Lake pond							
Gloeocapsa/Scytonema crust	32	47	19 (0-4)	74.8	18.9	6.4	0.7
algal heads	32	148	-	-	-	-	-
Fresh Lake							
crust on lignum	31	-	38 (1-2)	87.3	11.5	1.2	2.1

* depth sampled below surface (mm) in parentheses.

associated with the stromatolites of Hamelin Pool, Western Australia (Logan et al., 1974) where the salinity ranges from 55-70 o/oo.

Scytonema remains moist by capillarity and is rarely seen submerged by water. The large surface area exposed by the upward-growing filament bundles, combined with the dark coloration caused by a sheath pigment must ensure rapid evaporation of water and the concentration of salts. Such conditions probably promote the precipitation of calcium carbonate and this must be considered a likely origin for the associated sediment. Photosynthesis removes carbon dioxide from the water and can also precipitate carbonate and there is some evidence that this occurs in the freshwater marshes of Andros Island and the Everglades (Gleason, 1972; Monty, 1976; Monty & Hardie, 1976). It may also occur in the San Salvador mats, where despite the low cell biomass, a rapid turnover could give high rates of photosynthesis. Since chemolithotrophic (photosynthetic) bacteria were also abundant just below the mat surface, subsurface, photosynthetic precipitation of calcite is also a possibility.

The scarcity of obvious detrital material and the occurrence of micrite tubes surrounding the sheaths of *Scytonema* strongly suggest *in situ* precipitation. Calcification of *Scytonema* in freshwater environments has been observed widely (Gleason, 1972; Gebelein, 1976; Lowenstam, 1986; Pentecost & Riding, 1986) and calcite is often nucleated directly upon the sheath surface. However, although the carbonate is closely associated with the San Salvador *Scytonema*, no evidence of direct nucleation on the sheath was found, suggesting a more passive role for the organism in these sites. Lithification of *Scytonema* heads has been previously described from Andros Island (Gebelein, 1976; Monty, 1976) but appears to be the exception rather than the rule. Shinn et al (1969) reported *Scytonema* cementation from Andros Island with small amounts of associated fine-grained dolomite. Field evidence also suggests that calcification is inhibited at high salinities (Monty, 1972; 1976) though it is apparent that on San Salvador at least, this may not be the case. Stromatolite domes composed of *Scytonema* were reported by Monty (1972) from flats bordering lakes on Andros Island with calcite laminae, and are figured in Monty & Hardie (1976).

Modern stromatolites have been described from San Salvador from two areas. Dakoski & Bain (1984) found a range of mats and stromatolites in Granny Lake and the adjacent ponds. Lithified columnar stromatolites occurred in the latter, but the associated microorganisms were not described. Similar forms were observed in 1987 by this author and colonized by *Gloeocapsa*. Laminae of high magnesian calcite were reported associated with many of these mats. In Storr's Lake embayment, Mann & Hoffman (1984) found unlaminated algal heads in shallow water associated with two *Phormidium* species. In shape and size they resemble the *Scytonema* heads described here, but none of the former was collected in 1987.

The *Scytonema* heads of San Salvador, in contrast to the polygonal mats, had a laminate structure, particularly those at Granny Lake. The laminae appear compressed below, probably as a result of the high initial porosity and organic matter content (Table 1).

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