

# Recent cyanobacterial stromatolites in the lagoon of Tikehau atoll (Tuamotu Archipelago, French Polynesia): preliminary observations

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Prokaryotic microorganisms have dominated marine environments during early geologic history (Schopf & Klein, 1992), leaving laminated stromatolitic structures as the most common fossil evidence of ancient microbial activities. Stromatolites are interpreted as biosedimentary structures formed at the sediment-water interface through interactions between microorganisms and sediments, involving trapping and binding of sediment particles and/or mineral precipitation (Awramik & Margulis, cited in Walter, 1976). Deposition of minerals in stromatolitic structures (Lowenstam, 1986) promotes their preservation in the fossil record (Pentecost, 1991). The importance of microbial sediment trapping vs. mineral precipitation is still a subject of controversy. Rhythmic precipitates were found to form stromatolitic structures particularly prevalent in the Archaean and early Proterozoic marine deposits (Grotzinger & Read, 1983). The study of fossil stromatolites is generally constrained by diagenetic alterations and paucity of preserved microbial remains. The nature of the organo-sedimentary interactions and of the genesis

of stromatolitic structures rely, therefore, on studies of their putative modern counterparts.

Filamentous and coccoid cyanobacteria are the principal primary producers of microbial communities involved in stromatolite formation (van Gemen, 1993). Prior to evolution of eukaryotic algae and plants, cyanobacteria have dominated the primary productivity of the oceans. Today, their dominance remains unchallenged under certain extreme environmental conditions. For example, most modern stromatolites and microbial mats develop in intertidal and shallow marine settings characterized by fluctuating water supply and salinity. Under normal marine conditions, cyanobacteria form short-lived pioneer communities leading to stabilization of loose sediments (Yallop *et al.*, 1994; Golubic & Browne, 1996). They become replaced by eukaryote-dominated marine benthic communities and tend to recur only under conditions of environmental stress (Golubic, 1994).

Soft, dome and biscuit-shaped, internally finely laminated stromatolitic structures, which incorporate substantial quantities of fine grain (micritic) carbonate, were discovered in the lagoon of the Tikehau atoll (Tuamotu Archipelago, French Polynesia) at depths of 15-23 m (Charpy-Roubaud *et al.*, 1993) (Fig. 1). These modern stromatolites cover large areas throughout the lagoon floor, and are especially numerous around patch reefs. These stromatolitic structures are built by filamentous, sheathed, nonheterocystous cyanobacteria recognized as two new species of *Phormidium* (Fig. 2).

Both form gelatinous generally domes up to 15 cm in diameter. The laminated interior of these stromatolites principally contains empty sheaths covered by fine grains of carbonate. Live cyanobacterial trichomes are concentrated on the surface of the structures. The sheaths of both cyanobacteria are thin and firm, containing one trichome per sheath. Their stromatolitic structures often



Figure 1. Stromatolitic dome from Tikehau atoll.

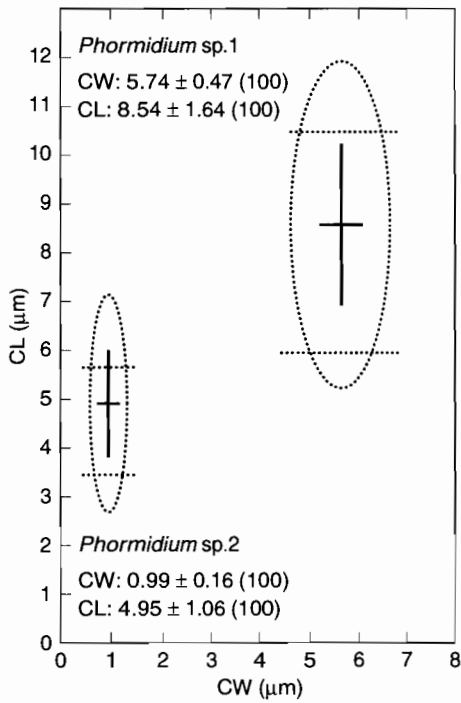


Figure 2. Graphic display of morphometrics data for *Phormidium* sp. 1 and P. sp. 2. Cell length (CL) vs. cell width (CW) measurements are plotted and summarized as means  $\pm$  standard deviation (crosses).

co-occur. They are similar in shape, consistency and size and differ macroscopically only in color. Microscopically, the size difference between the two organisms is significant and conspicuous.

The larger cyanobacterium, *Phormidium* sp.1, forms brown stromatolitic structures. Cells are on the average longer than wide 5.0 - 6.9  $\mu\text{m}$  (Mean  $\pm$  standard deviation =  $5.74 \pm 0.47 \mu\text{m}$ , N = 100) wide, and 5.2 - 11.8  $\mu\text{m}$  ( $8.54 \pm 1.64 \mu\text{m}$ , N = 100) long. The much smaller *Phormidium* sp.2 forms mauve gelatinous domes. Cells are narrow, mostly around one micrometer ( $0.99 \pm 0.16 \mu\text{m}$ , N = 100) wide and much longer than wide, 2.8 - 7.2  $\mu\text{m}$  ( $4.95 \pm 1.06 \mu\text{m}$ , N = 100) long.

Most specimens were soft when collected, a few older ones showed hardening by calcification. Percentage of  $\text{CaCO}_3$  in soft specimens varied between 71% and 84% of dry weight. The amount of carbonate particles entrapped in the course of the growth of the structure could not be established. However, the carbonate precipitation continues inside the structures in absence of metabolically active cyanobacterial cells, leading to lithification of stromatolites, which promotes their preservation following burial in the sediment. The relationship between total carbon (including carbonate) to organic

carbon in soft stromatolites varied from 12:3 to 12:1, and was comparable with the values obtained for the surrounding sediments. In contrast, the concentration of nitrogen and phosphorus in the structures were higher than in the surrounding sediments by a factor of 10 and 2 respectively.

Built and dominated by cyanobacteria, these stromatolitic structures create a special benthic microenvironment which harbors and maintains diverse microorganisms. Accordingly, measurements of activities in the structures and organic products are not necessarily attributable to cyanobacteria alone. Dinitrogen fixation was measured by acetylene reduction for entire stromatolitic structures. It occurs both at night and during the day, with daylight rates showing significantly higher values, up to 406 Mol N<sub>2</sub> d<sup>-1</sup> (Charpy-Roubaud, unpublished). The sites of nitrogen fixation could not be localized, but the timing correlates with photosynthetic activity. Pigments were extracted from the stromatolitic structures and analyzed using HPLC. The principal components are chlorophyll *a*, (with lesser quantities of chlorophylls *b* and *c*) and β-carotene. The ratio of chlorophylls to total carotenoids varies between 1.3 and 8.4. The samples contain significant concentration of xanthophylls specific to cyanobacteria: oscillaxanthin and myxoxanthophyll. Chlorophylls *b* and *c*, together with xanthophylls peridinin, fucoxanthin and diadinoxanthin are derived from algal cells that settled on, or were trapped within the structure.

## DISCUSSION

Massive occurrences of cyanobacteria in marine environments usually are associated with eutrophication. This general observation has been supported by observation of increased growth of cyanobacteria in Pacific coral reefs under human influence: discovery of stromatolite-forming cyanobacteria in the lagoon of the Tikehau atoll which is in pristine condition reflects the relatively higher nutrient availability in the lagoon as compared with that in the reef environment surrounding the island (Charpy *et al.*, 1990). Our study provides baseline information for evaluation of other, environmentally more threatened islands and atolls in the region. The correlation of dinitrogen fixation with photosynthetic activity in stromatolitic structures indicates that these non-heterocystous cyanobacteria contribute to the nutrient budget (cf. Gallon & Stal, 1992). An increased nutrient flux may result in an increase in growth and density of stromatolite forming cyanobacteria, or in an expansion and invasion of these life forms into the reef environments.

In a core drilled through a coral reef in Tahiti, French Polynesia, Camoin and Montagioni (1994) identified an early Holocene horizon containing frequent micritic stromatolitic structures attributable to cyanobacteria, and characterized by weakly laminated micritic carbonate textures. They have concluded that the increased stromatolite presence was concurrent with a higher sedimentary and nutrient flux during a period of increased island erosion. Although no organismal remains were found preserved in these fossils, the size, internal laminated fabric and mineral components are closely comparable with those of the *Phormidium* stromatolites described here.

In conclusion, these independent discoveries indicate that marine benthic cyanobacteria may play a more prominent role in coral reef genesis than previously assumed, and that temporal changes in the degree of participation of stromatolite-building cyanobacteria in reef construction may have environmental implications. This work was carried out in the frame work of the PNRCO.

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