

Role of algal eukaryotes in subtidal columnar stromatolite formation

(cyanobacteria/Proterozoic/Shark Bay)

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ABSTRACT Columnar stromatolites were abundant and widespread in the Proterozoic but are exceedingly rare in modern seas. Consequently, the stromatolites at Hamelin Pool in Shark Bay, Western Australia, have been widely interpreted as unique modern analogs of ancient stromatolites constructed by complex communities of cyanobacteria. However, the Shark Bay columnar stromatolites contain sediment that is unusually coarse for stromatolites both ancient and modern, and the subtidal columnar stromatolites have a significant component of algal eukaryotes dominated by motile diatoms with mucilaginous tubes. This suggests that Shark Bay columnar stromatolites are not strict analogs for most ancient cyanobacterial stromatolites, least of all for those from subtidal environments. We argue that algal eukaryotes may play a substantial role in the formation and maintenance of subtidal columnar stromatolites at Shark Bay and are capable of trapping coarse sediment. In contrast, cyanobacteria have difficulty in trapping coarse sediment and produce essentially fine-grained stromatolites. We propose that there are two major types or end members of Recent marine stromatolites: (i) eualgal–cyanobacterial stromatolites that are generally coarse-grained, and (ii) cyanobacterial stromatolites that are generally fine-grained.

Algae, in contrast to cyanobacteria, have usually only been regarded as minor components of stromatolite communities (1) and it has even been suggested that algal (*sensu stricto*) stromatolites are improbable (2). On the basis of enclosed silicified microfossils and comparisons with Recent examples, it has been generally assumed that Proterozoic stromatolites were the products of microbial communities dominated by cyanobacteria (3). Unequivocal benthic algal eukaryotes are rare in Proterozoic stromatolites, and their role in construction appears to be negligible. Concomitant with the biological crisis for stromatolites caused by the appearance of burrowing and grazing metazoans near the Precambrian–Cambrian boundary (4, 5), there was a sedimentological crisis for cyanobacterial stromatolites due to the advent of abundant coarse-grained skeletal sediment produced by biomineralization processes in shallow marine carbonate environments from the early Paleozoic onward (6). We propose that eualgal–cyanobacterial stromatolites represent a Phanerozoic response to these pressures. “Eualga” is used to denote and stress the eukaryotic algal component within the microbial community. The ability of eukaryotic algae to trap coarse sand in areas of mobile sediment in concert with cyanobacteria allows this complex community of eukaryotes and prokaryotes both to deal with coarse bioclastic material and to occupy environments in which metazoan grazers will be limited by sediment instability.

Both cyanobacterial and eualgal–cyanobacterial columnar stromatolites are present at Hamelin Pool, Shark Bay,

Western Australia. These are superficially similar yet fundamentally different. The intertidal columns (Fig. 1a) are primarily built by two communities of cyanobacteria, one dominated by *Entophysalis* and the other by *Schizothrix*, with numerous other cyanobacteria (7) (Fig. 1e). Algal eukaryotes are inconspicuous. Our study agrees with studies of others (8) that the sediment composing these intertidal columns (Fig. 1c) is largely fine-sand size (0.125–0.250 mm) peloids and ooids, with some coarser bioclasts, lithified by aragonite cements (9). All intertidal stromatolite samples examined petrographically (11 thin sections from four stromatolites) showed distinctly finer sediment than that forming the subtidal columns.

The subtidal columns (Fig. 1b) have a complex community that includes diatoms (7, 10, 11), an unidentified colonial coccoid eukaryote (10), an as yet unidentified coccoid entophysalidacean cyanobacterium (7), plus diverse cyanobacteria. Abundant amounts of gel are produced by this microbial community. The dasycladacean *Acetabularia* commonly grows on the sides of the columns (8, 12). Diatoms (e.g., *Mastogloia* sp., *Nitzschia* sp., *Amphora* sp., *Diploneis* sp.) (11) are conspicuous in our samples collected in March 1985, although we do not rule out the possibility that there is seasonal variation in dominance among the diatoms, other algal eukaryotes, and cyanobacteria. The diatoms building these stromatolites function in a manner analogous to that of cyanobacteria in that they produce extracellular gel, are motile, phototropic, can trap and bind sediment, and produce surface irregularities of the mat. The diatoms, however, in particular *Mastogloia* (Fig. 1f), produce copious amounts of gel. In our study we estimate the gel to individual cell ratio to exceed 10:1 for some of these eukaryotes. Broad, branching mucilaginous tubes, averaging 65 μm in diameter, produced by the diatoms (Fig. 1f) are common in the upper 1–3 mm of the mat. Diatom mats are important sediment stabilizers in nonmarine environments (13, 14) and in subtidal marine settings they appear to be capable of trapping and binding coarser sediment than do those dominated purely by cyanobacteria (15).

Our sedimentological and microstructural study of the Hamelin Pool subtidal stromatolites (slabs and thin sections) revealed that the sediment (Fig. 1d) is mainly coarse to very coarse (0.5–2.0 mm) sand-sized bioclasts and ooids with some granule-sized mollusk fragments. Differences between the subtidal and intertidal columns also extend to gross morphology and microstructure. The subtidal columns are poorly laminated with coarse laminoid fenestrae. They exhibit a variety of cylindrical, domical, and club-shaped morphologies, and they occasionally branch. The intertidal columns have fine to medium laminoid and irregular fenestrae, and they are either finely laminated or lack lamination (8). The intertidal columns are commonly club-shaped, broadening upward.

Subtidal stromatolites up to 1 m tall, with a significant component of algal eukaryotes, have been reported from oolite shoal environments at Eleuthera in the Bahamas (16).

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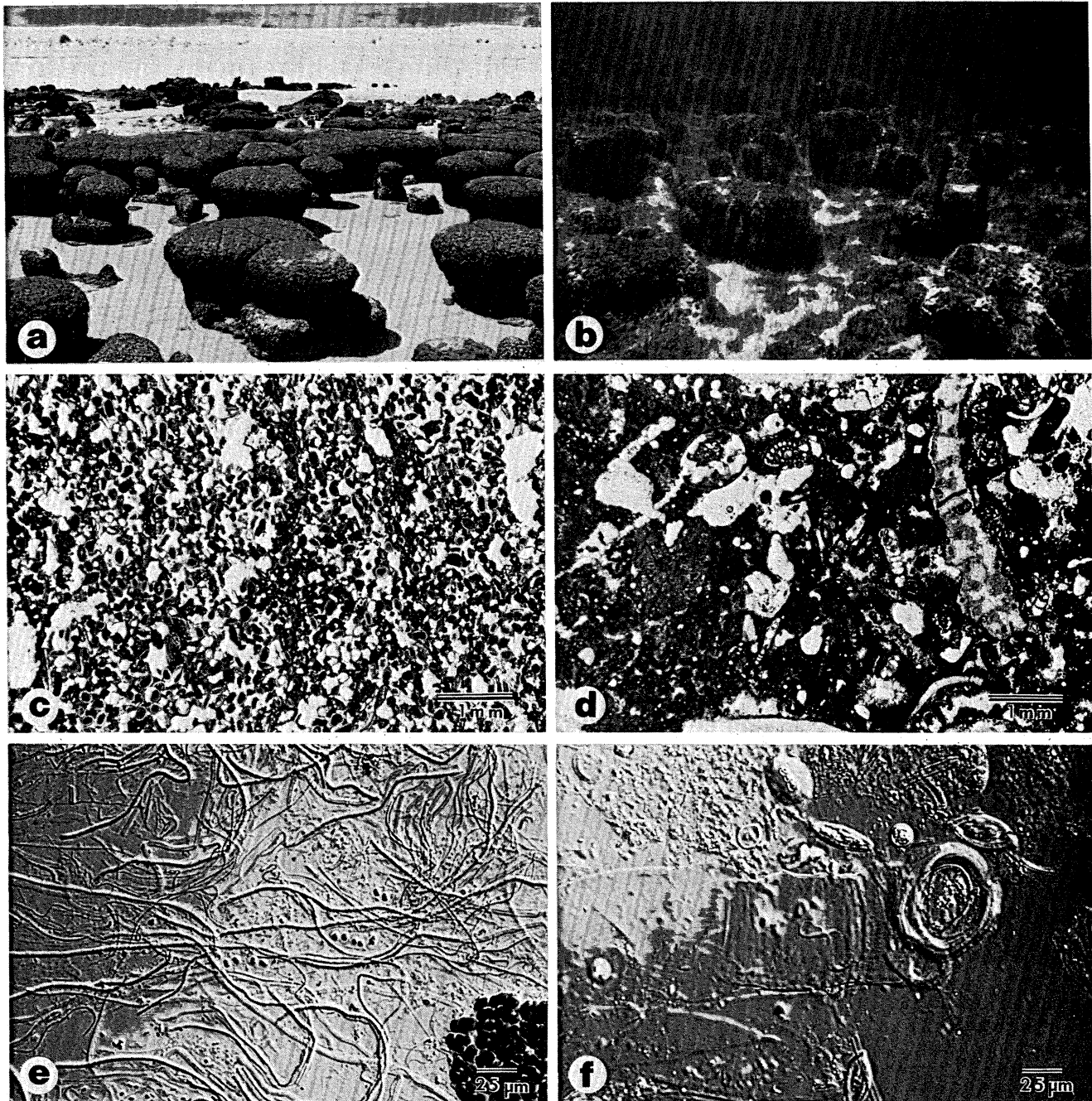


FIG. 1. Intertidal (a) and subtidal (b) columnar stromatolites at Shark Bay, Western Australia. (c) Fine-sand size peloids and ooids composing intertidal columns. (d) Coarse to very coarse sand size bioclasts with a granule-sized mollusk fragment composing subtidal columns. (e) *Schizothrix* with some *Entophysalis* from intertidal mat surface. (f) Diatom *Mastogloia* sp. in its mucilaginous tube from the surface of subtidal column.

In this case, the dasyclad *Batophora*, together with cyanobacteria, was reported to trap medium sand, which is then bound and cemented by acicular aragonite and chasmolithic green algae (16). This suggests that there is an algal-dominated community capable of constructing coarse-grained columnar stromatolites in both hypersaline and open marine subtidal environments, which includes diatoms and/or chlorophytes. Similar, even larger (up to 2 m tall) columnar to domical subtidal stromatolites have been found off Lee Stocking Island, Exuma, the Bahamas (17), where ooid sands (diameter, $\approx 200 \mu\text{m}$) are trapped and bound by a eualgal-cyanobacterial community composed of green algae, coccoid and colonial chrysophytes, diatoms, and other algae together with coccoid and filamentous cyanobacteria (J. A. West, personal communication).

Recent cyanobacterial mats in both subtidal and intertidal environments normally incorporate fine-grained material even when coarse sediment is readily available (18, 19). The relative coarseness of the intertidal columns at Shark Bay can be attributed to biogenic trapping by cyanobacteria and by beachrock-type cementation, whereas the even greater coarseness of the subtidal Shark Bay and the Bahamian columns can be attributed to the trapping and binding abilities of algae in addition to cyanobacteria. Subtidal environments were the principal sites for columnar stromatolites in the Proterozoic (20), and both subtidal and intertidal stromatolites occurred throughout the geological record (21). In the late Proterozoic some stromatolites, such as *Tungusia inna*, incorporated carbonate sand, including ooids (22), but the great majority are fine-grained. In a preliminary

study on grain size in fossil stromatolites, we found that in 46 stromatolite taxa (22–27) from the Proterozoic and Cambrian, for which there are data on grain size in laminae, only five have dark laminae composed of grains $\geq 100 \mu\text{m}$ (maximum, 2 mm) in diameter, and three of the five (including the taxon with 2-mm sized grains) were from the Cambrian. Eighty-nine percent of the Proterozoic taxa have dark laminae composed of lime mud ($< 62 \mu\text{m}$).

We postulate that both metazoan competition and coarse bioclastic sediment have progressively restricted the extensive formation of marine cyanobacterial stromatolites to intertidal areas where both metazoan activity and coarse sediment are generally reduced. Neither eualgal–cyanobacterial stromatolites (such as those from Shark Bay and the Bahamas), nor the cyanobacterial intertidal columns at Shark Bay, are general analogs for ancient stromatolites, presumed to be cyanobacterial, which normally did not incorporate coarse sediment, and least of all for those in the Proterozoic, which exhibit delicate regular laminae composed of micrite.

Two sources of lime mud or micrite are possible in the Proterozoic (excluding the micritization of grains by endoliths): (i) the spontaneous precipitation of micrite from oceanic waters (the so-called whittings); and (ii) the precipitation of micrite within, on, and immediately in the vicinity of the stromatolite-building cyanobacteria (28). Before the evolution of calcium carbonate biomineralization by animals and algae near the base of the Cambrian, the oceans were probably saturated with respect to dissolved calcium carbonate and chemically it was a relatively simple matter to precipitate calcium carbonate.

At present there are no known modern marine analogs for the great majority of Proterozoic columnar stromatolites. Coarse-grained eualgal–cyanobacterial stromatolites represent a post-Proterozoic development in stromatolite formation reflecting the appearance of a new complex community capable of coping with coarse-grained sediment. Reduced metazoan competition caused by sediment mobility (16) and/or hypersalinity (5) would also benefit this association. Variants of this association have probably been performing this function since at least the late Mesozoic (benthic diatoms), and possibly since the Early Paleozoic or earlier (chlorophytes and other algae). Eualgal–cyanobacterial stromatolites may be much more widespread than previously suspected, especially in Recent and Cenozoic subtidal environments.

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