

Prokaryotic Algae Associated with Australian Proterozoic Stromatolites*

(blue-green algae/carbonate rocks/nannofossils/orientation of laminae)

G. R. LICARI† AND PRESTON CLOUD‡

† Department of Earth Sciences, East Los Angeles College, Los Angeles, California 90022; and

‡ Department of Geological Sciences, University of California, Santa Barbara, Calif. 93106

Contributed by Preston Cloud, June 29, 1972

ABSTRACT Five instances of association between distinctive stromatolites and blue-green algal nannofossils are recorded from a 100-m sequence of carbonate rocks about 1.6×10^9 years old, along the south side of Paradise Creek, northwestern Queensland, Australia. No eukaryotes were identified in any of these systematically limited assemblages, although they are known from rocks as old as 1.3×10^9 years in eastern California. Thus, eukaryotes may not have appeared until after 1.6×10^9 years ago (but before 1.3×10^9 years ago). The associations observed would also be consistent with (but do not prove) a biotic influence on stromatolite morphology. As is usual among pre-Paleozoic forms described, the morphology of the nannofossils is very similar to living forms, displaying marked evolutionary conservatism. Primary orientation of stromatolitic laminae and columns is not invariably convex upward, as conventionally believed, but convex away from and parallel to the initial point or surface of attachment, which may be horizontal or even downward beneath overhangs.

A vexing problem in biogeology has been the establishment of clear associations between the domal and columnar biogenic sedimentary structures known as stromatolites and the mainly prokaryotic communities whose record through time they almost surely represent. Analogous structures in existing shallow tropical and subtropical seas and peripheral supratidal habitats are formed primarily by the sediment-binding and calcium carbonate-precipitating activities of successive mats of blue-green algae and, to a lesser extent, bacteria. A similar mode of origin is inferred for the past. Still, identifiable algae or bacteria associated with stromatolites in a manner supportive of causal relation are rare among ancient sedimentary rocks.

Bacterial or oxidative decay appears to be the usual fate of the delicate organisms involved in the buildup of stromatolites of a carbonate mineralogy. Prospects of preservation are more favorable where the early matrix was silica. The most favorable places in which to study the associations between stromatolites and the algae responsible for them are, therefore, likely to be where a variety of stromatolites of possibly early diagenetic or primary silica occupy a substantial thickness of little metamorphosed ancient sediments. One such place is in northwestern Queensland, Australia, about 113 km airline north of Mt. Isa, along Paradise Creek, downstream from Lady Annie Mines. Here cherty stromatolites of some variety bulk large in a 100-m sequence midway in the 3000-4500-m Paradise Creek Formation (1), well exposed along the south bank of the intermittent stream. The stromatolite succession was described by Robertson in 1960 (2) from col-

lected specimens and field photographs, and the presence of a *Eucapsis*-like chroococcacean alga was later noted by Licari, Cloud, and Smith (3) in one distinctive stromatolitic form-genus subsequently named *Eucapsiphora* (4). Licari *et al.* also found that these rocks are bracketed between two radiometrically dated granitic events, implying an age of roughly 1.6×10^9 years (1.6 aeons).

Robertson recognized three "suites" of distinctive stromatolites in the Paradise Creek sequence—Alpha, Beta, and Gamma, in descending order. Associations of microorganisms in those suites with four other types of stromatolites besides *Eucapsiphora* are described below. The indigenous nature of these nannofossils is assured by their relations to rock fabric and stromatolitic structure as observed in thin section. As we were not successful in isolating any of these microorganisms by maceration procedures, and as they are too scarce to be found handily in random sections under a scanning electron microscope, our studies are limited to light microscopy. Despite exhaustive search of 88 thin sections, moreover, the material is too poor and scanty to warrant new taxonomic names. The interest of this material, then, is less intrinsic than in the associations observed and its possible implications for the time of origin of eukaryotic cells.

Stromatolites and associated algae from Alpha Suite (Fig. 1)

Distinctive domal bioherms of cherty cylindrical stromatolites with conical to subconical accretion laminae were sampled in the upper part of Robertson's Alpha Suite at Cloud's localities 1 and 2 of 20 July 1965, from the same stratigraphic interval. These bioherms (Fig. 1a), 2-3 m high and 3-10 m in diameter, consist of aggregates of long, discrete cylinders 3-6 cm in diameter. The laminations within the cylinders suggest the form-genus *Conophyton*—except that the individual cylinders are smaller than is typical for *Conophyton*, their laminae have less acute apical angles, the laminae do not cross the intercolumnar spaces as is commonly true of *Conophyton*, and the axial zone is not ordinarily well defined (Fig. 1b illustrates the best we could find). The designation *aff. Conophyton* reflects the uncertainties.

The internal laminae of these stromatolites displayed uncommon filaments (Figs. 1c-f), most commonly preserved as hematite outlines that display the gross morphology of cells. They are aligned parallel to the growth laminae but are only locally abundant. Rarely are cells outlined by a dark organic residue. Hematite pseudomorphs after pyrite replace at least one filament (Fig. 1g), a second-order replacement with width greater than the simple hematitic filaments.

* Contribution no. 35 from Biogeology Clean Laboratory, U.C. S.B. Address requests for reprints to Dr. Cloud.

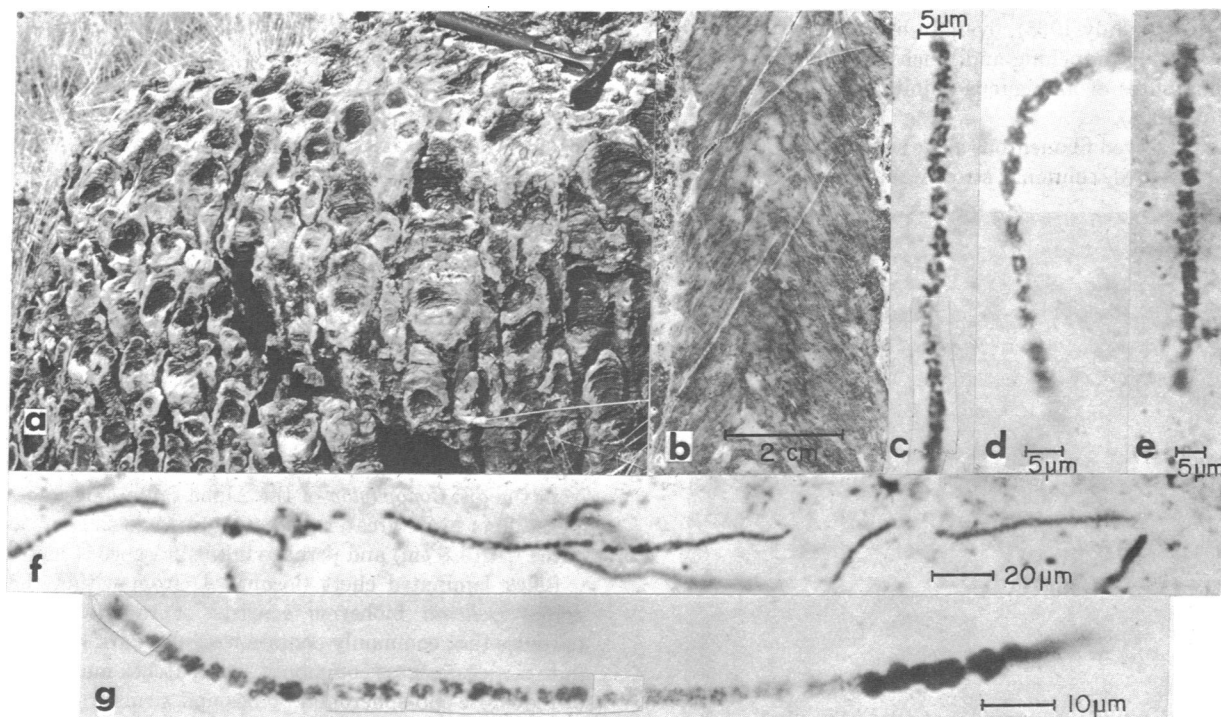


FIG. 1§. Alpha Suite; *aff. Conophyton* with associated filamentous algae, Cloud's locality 2 of 20 July 1965. (a) Columns of *aff. Conophyton* in outcropping small domal bioherm; hammer is 30 cm long. (b) Vertical cut through single column of above. (c-f) Filaments within laminae of column. C93-5: X22.4, Y12.1; X23.3, Y12.6; X25.3, Y10.4; X22.2, Y11.6. (g) Hematite after pyrite replacing cells among a filament. C93-5: X14.2, Y10.5.

Filaments (trichomes) are nonattenuated, uniseriate, and nonbranching; they form open mats. They are straight or curved, rarely looped, and fragments observed reach 160 μm in length. Individual cells are commonly separated. Among 25 individual trichomes measured, diameters range from 1.2–2.6 μm , average 1.8 μm , and rarely exceed 2 μm . The shape of an individual cell is most often cylindrical, rarely keg-like, and quadrate in outline. Length averaged 1.9 μm , and diameter 1.8 μm , for 34 cells measured.

No specialized intercalary or terminal cells were observed, but the size and general morphology of these filaments strongly suggests affinities to modern blue-green algae (Cyanophyta) of the Order Nostocales. The generally poor preservation and lack of differentiated cells prevents assignment to a definite family, but similar nonbranching filaments and quadrate cells are well known among the Oscillatoriaceae (5).

The oldest oscillatoriacean algae so far unequivocally recognized are from the roughly 0.8–0.9 aeon-old Bitter Springs microflora of central Australia (6), although probable oscillatoriaceans are present in the $1.9 \pm$ aeon-old Gunflint Iron Formation of southern Ontario (7, 8). Well-preserved filamentous cyanophytes of intermediate age from the $1.3 \pm$ aeon-old Beck Spring Dolomite of California (9), and the common filament type of the Gunflint Iron Formation belong to the Family Nostocaceae—possessing probable heterocysts

§ Location of individual fossils is given by reference to the C-number of individual thin sections, followed by distance in mm along the X and Y coordinates from the nearest left-hand corner of the cover slip or a reference X near that position, when the label is at the right and the microscope faces toward the observer.

and akinetes, as well as showing no false-branching or tapering (9, 10).

The orientation of the filaments parallel to the growth-laminations within the stromatolites, and the striking analogy with modern cyanophycean algae which trap, bind, and precipitate calcium carbonate, supports a formative role in the building of the associated stromatolites.

Stromatolites and associated algae from base of Alpha Suite or top of Beta Suite (Fig. 2)

7–10 m beneath the level of *aff. Conophyton*, irregular columnar bioherms about 0.5–2.5 m high and up to 8 m in diameter cap and encrust pinnacles of pre-existing carbonate rocks (Fig. 2a). These erect digitate-branching, in part laterally linked, silicified columnar stromatolites (Cloud's locality 3 of 20 July 1965) were found by Licari, Cloud, and Smith (3) to contain rare and mostly poorly preserved cubic packets of unicells, morphologically identical to modern chroococcacean cyanophytes, in siliceous blebs around the exterior of the columns (Figs. 2b–c). This coccoid alga is strikingly similar in arrangement and size of *Anacystis*-like cells (2.2- μm mean diameter for $n = 128$) to the living *Eucapsis minuta* Fritsch. As no morphologic difference could be detected between it and its living analog, the designation *Eucapsis* (?) is used—although Drouet and Daily (11) disavowed this colonial genus in favor of a broadly constituted *Anacystis*. Cloud and Semikhatov (4) subsequently recognized the parent stromatolite as a new form genus called *Eucapsiphora*. No filamentous algae were found.

Stromatolites and associated algae from Beta Suite (Figs. 3–4)

About 10–17 m beneath the stromatolite-algal association described above, in the Beta Suite, are large domes of *Collenia*

(locality 4 of 20 July 1965), overlain by a zone of other large domes of weakly-branching and much interconnected columnar stromatolites of ambiguous affinity (Figs. 3a-b; locality 5 of 20 July 1965).

Poorly preserved filamentous algae are found in parts of the generally silicified, columnar stromatolites of locality 5 (Figs.

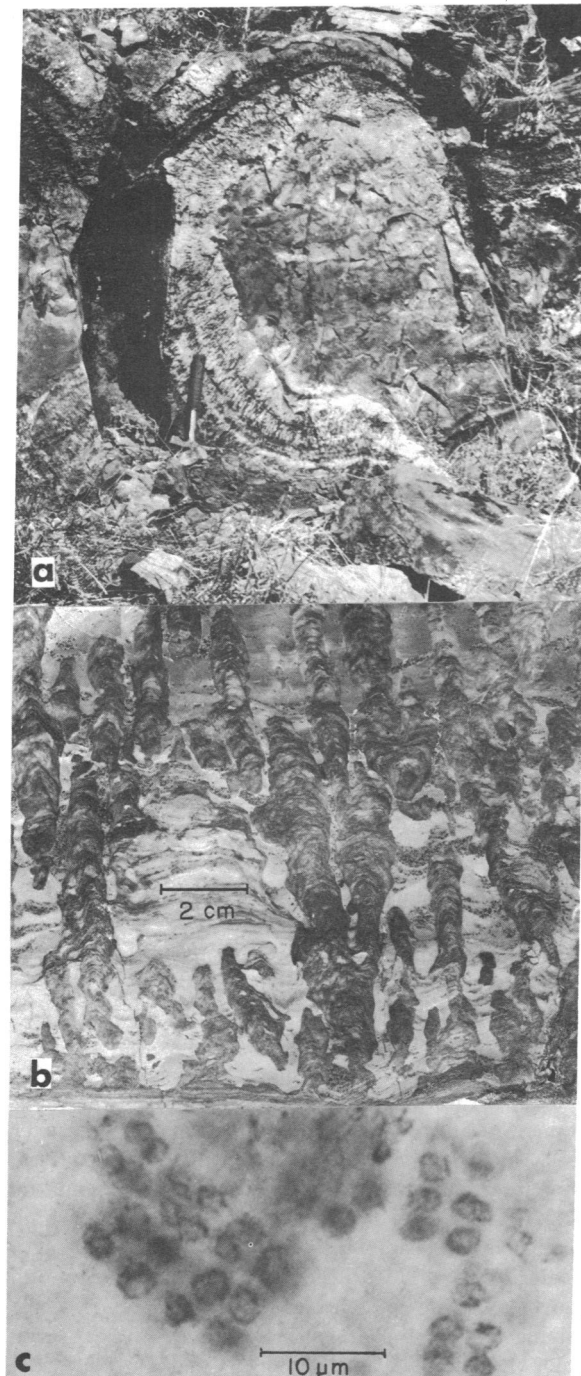


FIG. 28. Base of Alpha or top of Beta Suite; *Eucapsiphora* with associated cell-aggregates. Locality 3 of 20 July 1965. (a) Vertical profile of colonial stromatolite whose component columns encrust pre-existing dolomite pinnacles. Hammer is 30 cm long. (b) Vertical cut through a group of weakly-branching stromatolitic columns that grow upward from a common basal stratum. (c) *Eucapsis*(?) showing quadrate cell aggregates, from siliceous bleb at periphery of stromatolite column. C75-26: X18.4, Y17.1 (from reference X).

3c-d)—the upper of the two localities. Trichomes are preserved as hematite replacements or as organic residues that outline cells. They are uniseriate, nonbranching, nontapering, straight to sinuous, and rarely looped. Aggregates of filaments occur within curved stromatolitic laminations. Individual trichome fragments are up to 280 μm long (9 measured). Cell length is from 1.7–3.4 μm (average 2.5 μm for 25 cells measured). Diameter ranges from 1.7–2.8 μm (average 2.2 μm for 25 cells measured). Individual cells are cylindrical or kegg-shaped, with slight constrictions at septa. One relatively enlarged cell (3.8 μm diameter), perhaps a heterocyst, was observed near the middle of the filament illustrated in Fig. 3c. If this structure is a heterocyst, this small-diameter, nonbranching, nonattenuated, obviously nostocalean blue-green alga likely belongs to the Family Nostocaceae. Although generally similar to the filamentous cyanophytes described from the aff. *Comophyton* of the Alpha Suite (Figs. 1c-g), this alga differs in its greater diameter (average 2.2 μm as compared with 1.8 μm) and perhaps in the presence of heterocysts.

Black laminated chert (locality 4) from within the lower domal *Collenia* bioherms consists of rounded, sand-sized particles that commonly contain irregular dark areas of indefinite structure. Less commonly such patches merge into areas of indefinite sub-spheroidal bodies and structurally preserved unicells with well-defined boundaries (Figs. 4a-c). Such aggregates of poorly preserved unicells within the silica clasts internal to the bioherms are separated by patches of dark residue suggesting remnants of decomposed cells. Objects recognized as unicells are usually discrete, but occasionally they are appressed to other cells, at places forming irregular aggregates of hundreds. Mean diameter ranges from 2.9 to 7.7 μm , with an average for 87 unicells of 4.4 μm . The general size and organization of this alga (except for the apparent absence of associated fungi) resembles the living *Anacystis montana* (Lightfoot) Drouet and Daily, a blue-green alga of the Family Chroococcaceae (11). Marine species of the genus *Anacystis* may form mucilaginous mats that trap and bind CaCO_3 (12) or form coatings on grains and particles (11, 13) that may bind them together.

This *Anacystis*-like alga differs from the *Eucapsis*(?) of sample 3 of 20 July 1965 in its greater size (average diameter of 4.4 μm compared to 2.2 μm) and in its lack of the cubic arrays of cells that characterize *Eucapsis*. It resembles a genus of coccoid blue-green algae from the $1.3 \pm$ aeon-old Beck Spring Dolomite of eastern California (Licari, Ph.D. thesis). The California form clusters about silicified ooids as many separate cells, having a mean diameter of 5.6 μm . *Palaeoanacystis* Schopf (6) consists of appressed noncubic colonial masses of cells having a mean diameter of 5.5 μm .

Stromatolites and associated algae from Gamma Suite (Fig. 5)

The lowest stratigraphic level sampled is within medium-sized silicified hemispheroidal collenias (Fig. 5a) of Cloud's locality 7 of 20 July 1965, representing the Gamma Suite of Robertson. Although the crenulated, black siliceous laminations within these stromatolites appeared of favorable lithology for preservation of nanofossils, study under oil-immersion of 30 thin sections produced only a few short filament fragments, or chains of coccoid cells, generally lacking in detail. The best preserved fragment (Fig. 5b) consists of short subcylindrical to ovoidal cells with thick constricted

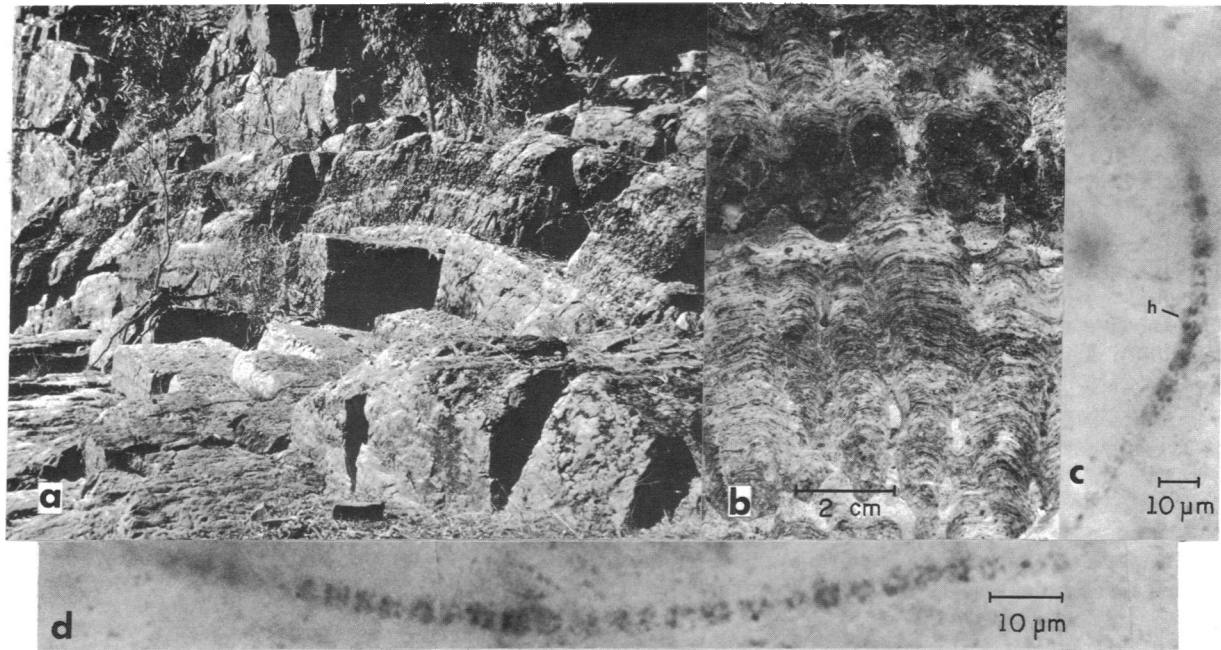


FIG. 3§. Beta Suite: laterally linked columnar stromatolites and associated filamentous algae. Locality 5 of 20 July 1965. (a) Vertical profile of domal parent bioherm as it appears in the field; amplitude of dome about 3 m. (b) Vertical cut through component columns. (c) Filament with possible heterocyst (*h*). C118-1: X5.0, Y5.1. (d) Long filament with faintly outlined cells. C118-8: X11.9, Y14.9.

septa between the cells. Cells along this chain ranged from 1.6–2.2 μm in diameter (mean 1.9 μm). These cells contrast with the quadrate-outlined cylindrical cells in filaments from the Alpha and Beta Suites. Although the scarcity and incompleteness of these trichomes does not allow confident

comparison, their general morphology and size is most consistent with the filamentous blue-green algae.

In addition to the “filaments,” isolated unicells (Fig. 5c) 10–12 μm in diameter, as well as smaller reticulate-surfaced unicells, are occasionally seen. These few specimens cannot be classified with any confidence at this time, although they most probably are blue-green algae.

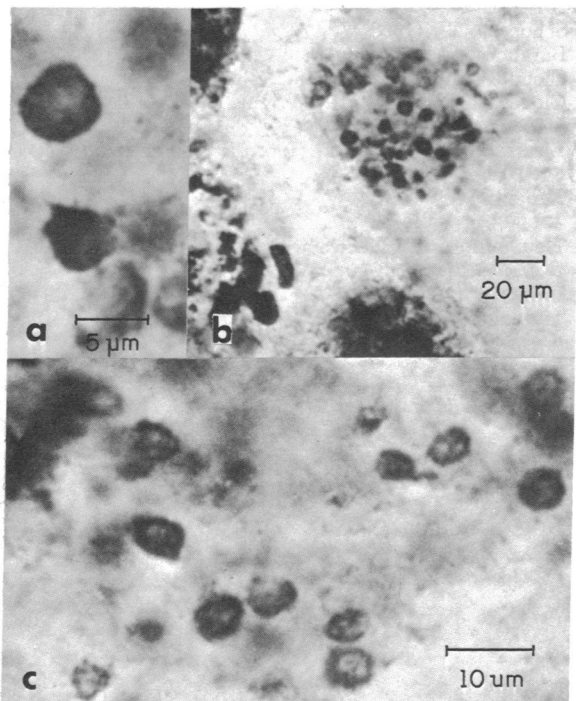


FIG. 4§. Beta Suite; coccoidal nanofossils associated with large domal *Collenia*. Locality 4 of 20 July 1965. (a) Individual *Anacystis*-like unicells. C79-10: X5.3, Y10.5. (b) Cluster of unicells near edge of silica particle. C79.2: X14.9, Y15.0. (c) Array of unicells. C79-2: X14.9, Y15.0.

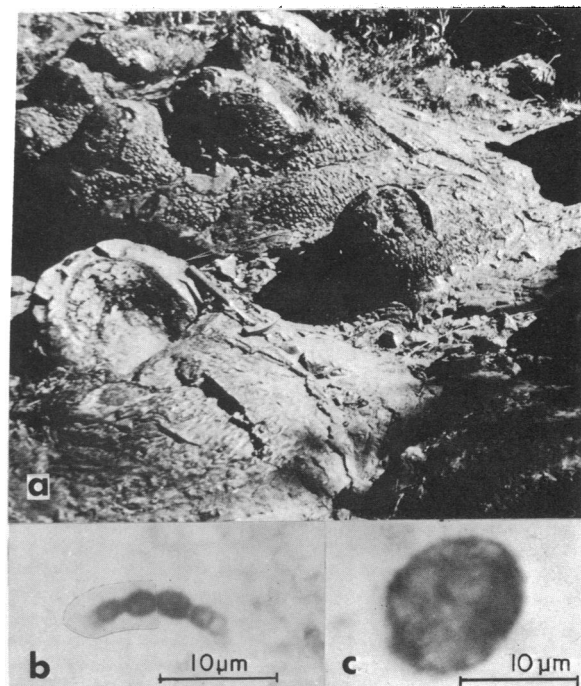


FIG. 5§. Gamma Suite: small domal *Collenia* and associated nanofossils. Locality 7 of 20 July 1965. (a) Outcropping domes. *Hammer* is 30 cm long. (b) Filament fragment. C275-6: X27.9, Y13.4. (c) Unicell. C275-6: S22.4, Y13.2.

Significance of the observed associations

The associations and entities described above lead to the following conclusions:

- (i) Although assemblages observed are of little variety and poorly preserved, they are locally numerous and all are attributable to the prokaryotic blue-green algae. Inasmuch as eukaryotes are no less likely to be preserved, are ordinarily larger and more conspicuous, and are common in modern algal mats, it is possible that the original microbiota was wholly prokaryotic. The oldest eukaryotes so far known with confidence are green and perhaps yellow-brown algae about 1.3 aeons old, from the Beck Spring Dolomite of eastern California. Thus, although the evidence is sparse and shaky, present data suggest eukaryotic cells *may* have evolved between 1.6 and 1.3 aeons ago.
- (ii) Nannofossils representing what appear as different monospecific algal associations, as well as assemblages of limited diversity, are known from five varieties of stromatolites representing the three stromatolite suites of Robertson (2). These observations would be consistent with (but not proof of) the interpretation that biotic variables have influenced the morphology of stromatolites at Paradise Creek. Filamentous species and organized cell aggregates seem to be concentrated mainly in columnar forms, while simple coccoidal assemblages and chains are found in simple domal stromatolites. The degree to which environmental, as distinct from biotic, controls have influenced stromatolite variation is, of course, difficult to appraise. Evidence for shallow, turbulent water—probably intertidal or shallow subtidal—is present throughout the sequence in the form of interstitial breccias, truncated structures, and stromatolite-encrusted pinnacles. Rates of deposition, action of waves and currents, turbidity, subaerial exposure, and other variables may not only have shaped the algal mats but may also have influenced the composition of the algal communities within the mats. More information will be needed about algae within stromatolites and the paleoecologic and sedimentologic variables at many places before disagreements about the causes of stromatolite morphology can be finally resolved.
- (iii) The morphologies of nannofossils here recorded reinforce the concept, clearly enunciated by Hutchinson (14), of

morphologic evolutionary conservatism among the blue-green algae. It is difficult, if not impossible, to differentiate Proterozoic from living cyanophytes on morphological grounds alone.

- (iv) Encrustation of pinnacles of pre-existing rock (ancient sea stacks) by stromatolitic growth reveals some interesting features of that growth, formerly interpreted as consisting of persistently convex-upward internal lamination. The direction of growth of the stromatolitic columns, and the convexity of the laminae in them, however, is simply away from the surface of initial attachment—upward where it is horizontal, outward where it is vertical, and downward under overhangs. Although in most instances the orientation will be convex upwards, discretion must be applied in using stromatolitic growth forms and laminations as indications of the vertical in deformed rocks.

This research was supported mainly by National Science Foundation Grant GB-23809, and also by National Aeronautics and Space Administration Grant NGR-05-010-035. Fieldwork by P. C. in 1965 was supported by NSF Grant GB-1807, and by the Australian Bureau of Mineral Resources, Geology, and Geophysics, and many of its staff, who provided field guidance and transportation throughout Australia. Mount Isa Mines, Ltd., and members of its staff, provided transportation and guidance to the local field area.

1. Carter, E. K., Brooks, J. H. & Walker, K. R. (1961) *Aust. Bur. Miner. Resour. Geol. Geophys., Bull.* **51**, 334 p.
2. Robertson, W. A. (1960) *Austr. Bur. Miner. Resour. Geol., Geophys. Rep.* **47**, 12 p.
3. Licari, G. R., Cloud, P. & Smith, W. D., (1969) *Proc. Nat. Acad. Sci. USA*, **62**, 56-62.
4. Cloud, P. & Semikhatov, M. A. (1969) *Amer. J. Sci.* **267**, 1017-1061.
5. Drouet, F. (1963) *Proc. Acad. Natur. Sci., Philadelphia*, **115**, 261-281.
6. Schopf, J. W. (1968) *J. Paleontol.* **42**, 651-688.
7. Barghorn, E. S. & Tyler, S. A. (1965) *Science* **147**, 563-577.
8. Cloud, P. (1965) *Science* **148**, 27-35.
9. Cloud, P., Licari, G. R., Wright, L. A. & Troxwel, B. W. (1969) *Proc. Nat. Acad. Sci. USA* **61**, 623-630.
10. Licari, G. R. & Cloud, P. (1968) *Proc. Nat. Acad. Sci. USA* **59**, 1053-1060.
11. Drouet, F. & Daily, W. A. (1956) *Butler Univ. Bot. Stud.* **12**, 69, 76.
12. Neumann, A. C., Gebelein, C. D. & Scoffin, T. P. (1970) *J. Sediment. Petrology* **40**, 274-297.
13. Gebelein, C. D. (1969) *J. Sediment. Petrology* **39**, 49-69.
14. Hutchinson, G. E. (1960) *Amer. J. Sci.* **258-A**, 98-103.