

Africa and Precambrian biological evolution

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ABSTRACT

African sedimentary rocks and their contained fossils have played a fundamental role in the unravelling of Precambrian biological history. Various lines of evidence including stromatolites, filamentous and coccolidal microfossils, stable isotope ratios, organic carbon distribution, and oxide facies iron formation suggest that a complex prokaryotic ecosystem fueled by photosynthesis, and perhaps including aerobic photoautotrophs, existed as early as 3 500 m.y. ago. The primary sources of data on early Archean life are rock sequences in southern Africa and Australia. The diversity of later Archean (ca. 2 700 m.y.) communities is attested to by abundant and varied stromatolites found in Zimbabwe.

The extensive growth and consolidation of continents that heralded the Proterozoic Eon had profound effects on the earth's biota. Primary productivity must have increased substantially, resulting in the establishment of an O₂-rich atmosphere, and, subsequently, the radiation of aerobic respirers. Southern African sequences provide critical evidence bearing on this crust/atmosphere/biota interaction; however, the best known microfossils of this age come from North America.

Upper Proterozoic sedimentary rocks abound in Africa. Stromatolites from northwestern Africa have been well studied; however, microfossil occurrences remain but sketchily described. Contemporaneous sequences from Scandinavia and Australia document the initial radiation of eukaryotes in the planktonic realm, as well as a terminal Precambrian episode of extinction among plankters. Early heterotrophic protists are known from several continents. The Nama Group of South West Africa/Namibia contains important evidence of early invertebrates.

In general, Precambrian evolution can be viewed as a series of increasingly elevated biological plateaus connected by steps marking relatively short periods of evolutionary innovation and radiation. With each step, communities have increased in complexity, but prokaryote mediated element cycles established early in biological history remain at the core of functioning ecosystems.

RÉSUMÉ

L'AFRIQUE ET L'ÉVOLUTION BIOLOGIQUE PRÉ-CAMBRIENNE

Les roches sédimentaires africaines et leur teneur en fossiles ont joué un rôle fondamental dans l'étucidation de l'histoire biologique pré-cambrienne. Diverses preuves incluant des stromatolites, des micro-fossiles filamenteux et coccolidaux, des proportions stables d'isotopes, la distribution du carbone organique et la formation d'oxyde de fer suggèrent qu'un écosystème prokaryotique complexe, alimenté par photosynthèse et incluant peut-être des photoautotrophes aérobiques existaient déjà il y a 3 500 millions d'années. Les premières sources de données sur le début de la vie archéenne sont les séries de roches de l'Afrique australe et de l'Australie. La diversité des communautés durant la suite de l'Archéen (ca. 2 700 millions d'années) est attestée par les stromatolites abondants et variés trouvés au Zimbabwe.

La croissance importante et la consolidation des continents qui annoncèrent l'âge protérozoïque eurent de profondes influences sur la faune et la flore terrestres. La productivité primaire doit s'être accrue substantiellement, aboutissant à l'établissement d'une atmosphère riche en O₂ et, par la suite, l'expansion de respirateurs aérobiques. Les séries de l'Afrique du Sud fournissent la preuve de l'interaction: croûte/atmosphère/flore et faune; cependant les micro-fossiles les mieux connus de cet âge proviennent de l'Amérique du Nord.

Les roches sédimentaires du Protérozoïque supérieur abondent en Afrique. Les stromatolites de l'Afrique du Nord-Ouest ont été bien étudiés; cependant la présence de micro-fossiles reste à peine esquissée. Des séries contemporaines de Scandinavie et d'Australie nous renseignent sur l'apparition d'eukaryotes dans le domaine planctonique, aussi bien que sur un épisode d'extinction de certains constituants du plancton, à la fin du Précambrien. Les protistes hétérotrophiques primitifs sont connus dans plusieurs continents. Le groupe Nama du Sud-Ouest africain/Namibie, comporte une preuve importante des premiers invertébrés.

En général l'évolution pré-cambrienne peut être vue comme une série de plateaux biologiques de plus en plus élevés, connectés par des échelons marquant des périodes relativement courtes d'innovation et de radiation évolutionnaires. A chaque échelon, les communautés augmentèrent en complexité, mais les cycles d'éléments interposés prokaryotes établis à l'origine de l'histoire biologique demeurent au coeur des écosystèmes en opération.

INTRODUCTION

The extensive Precambrian terrains of Africa have played an important role in the study of early crustal, atmospheric, and biological history. The purpose of this paper is to review briefly the evidence for Precambrian biological evolution, making a clear distinction between facts and the interpretations, however reasonable, that have been drawn from those facts. Major emphasis will be

placed on African rocks, the evidence of early life they contain, and the potential for further paleontological investigation on this continent (Fig. 1).

THE ARCHEAN

Precambrian time, which extends from the origin of the earth some 4 600 m.y. ago to the first appearance of diverse well-skeletonized invertebrates 590 m.y. ago, is divisible into two major periods, the Archean and Proterozoic Eons. The boundary between the eons at approximately 2 500 m.y. B.P. is not arbitrarily drawn; it reflects the separation of

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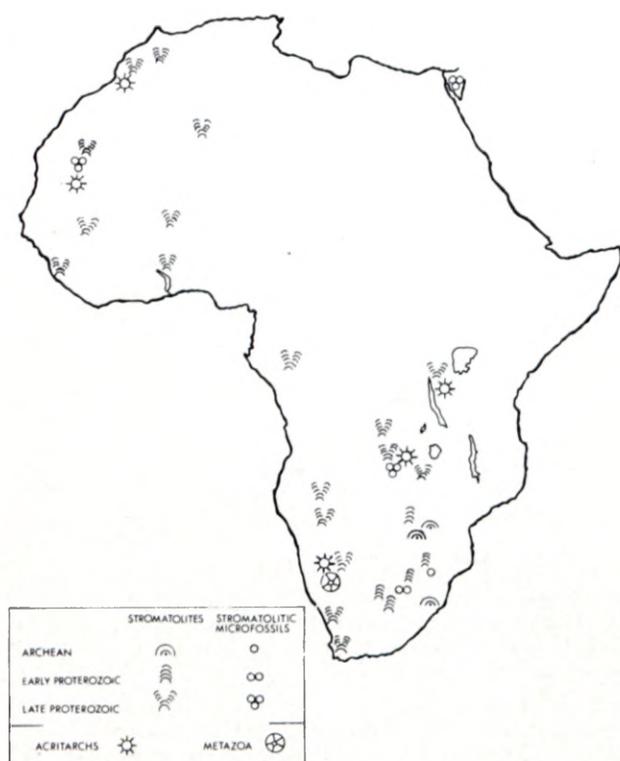


FIG. 1. — Distribution of known Precambrian fossils and stromatolites in Africa.

two periods of earth history characterized by markedly contrasting tectonic and, hence, sedimentary styles. The Proterozoic earth featured large stable continents and linear geosynclines similar in dimensions and sedimentary-tectonic evolution to those of more recent periods. In the Archean, on the other hand, cratonic areas were limited; the preponderance of ultramafic to intermediate (and sometimes felsic) lavas and poorly sorted greywacke sandstones and shales in Archean supracrustal sequences attests to the fact that different tectonic patterns shaped the early earth's surface. Perhaps the easiest way to envision the Archean earth is to imagine that the entire globe resembled the present day Indonesian archipelago. The Archean-Proterozoic boundary thus represents a period of large scale cratonization, a fundamental geological shift that I believe must have had profound consequences for the evolving biota.

If we strip our knowledge of early Archean (>3 000 m.y.) biology of all interpretation and limit ourselves to the facts, we can say the following: 3 500 m.y. ago there existed organisms, some of which were filamentous. As is well-known to African scientists, the extraordinary antiquity of life was first established on the basis of the micropaleontological study of carbonaceous cherts from the Onverwacht and Fig Tree Groups of the Barberton Mountain Land, South Africa and Swaziland (Pflug, 1966; Barghoorn & Schopf, 1966; Schopf & Barghoorn, 1967). Many authors have illustrated Onverwacht and Fig Tree microstructures interpreted as fossil micro-organisms; however, many or most of these structures are abiogenic (Schopf, 1976, 1980b). The microstructures that most likely do represent the preserved organic remains of prokary-

otic organisms are micron sized bacterial rods reported by Barghoorn & Schopf (1966) and 2–4 μm spheroids, some in various stages of division, discussed by Muir & Grant (1976) and Knoll & Barghoorn (1977). Fig. 2.6–2.9.

The best direct evidence of early life comes from the improbably named North Pole Barite of Western Australia in which a variety of silicified microstructures, including unmistakable filamentous microfossils, have been discovered (Awramik *et al.*, 1983). Unfortunately, prokaryotes have simple morphologies and diverse physiologies; therefore, it is impossible to draw metabolic conclusions from any of these remains. Also occurring in the North Pole rocks are stromatolites (Walter *et al.*, 1980; Lowe, 1980) — laminated organo-sedimentary structures built by the trapping and binding and precipitating activity of micro-organism populations. Today, stromatolites accreting in coastal environments that resemble the North Pole depositional setting are built by cyanobacteria. In hot springs, such as those found in Yellowstone Park, the photosynthetic bacterium *Chloroflexus* also build mats, in association with the coccoid blue-green *Synechococcus* (Brock, 1978). It is tempting to conclude that the North Pole stromatolites were built by aerobic photoautotrophs, but this is by no means certain (Walter *et al.*, 1980). The sequence containing the Australian fossils has been dated by zircons at $3\,452 \pm 12$ m.y. (Pidgeon, 1978) and at $3\,520 \pm 60$ m.y. using Sm-Nd (Walter *et al.*, 1980).

Those meagre data constitute the unadorned, but unimpeachable facts about life's earliest known record; however, by even conservative interpretations of several collateral lines of evidence, a fuller picture of early ecosystems emerges. Stable carbon isotope ratios in Archean organic matter and co-occurring carbonates suggest that 3 500 m.y. ago, as now, photosynthesis lay at the heart of the terrestrial carbon cycle (Eichmann & Schidlowski, 1975; Schidlowski, 1978). Whether this photosynthesis was aerobic or anaerobic cannot be unequivocally determined.

Dissimilatory sulfate reduction also leaves an isotopic record in sedimentary rocks, and intriguingly, pyrites from the Fig Tree Group and other sequences older than 2 800–3 100 m.y. do not bear the earmarks of biological activity (Schidlowski, 1979; Monster *et al.*, 1979). The suggestion that follows from this is that sulfate-reducing bacteria may have arisen relatively late in the Archean. Another indirect line of evidence is the sizeable deposits of oxidized sedimentary iron formation found in the Barberton Mountain Land, as well as in other Archean sequences as old as 3 800 m.y. (the Isua supracrustals; see Appel, 1980). Such deposits cannot form in the absence of a source of free oxygen, and whereas some workers have suggested that photolytic breakdown of water vapor in the upper atmosphere could have supplied the necessary oxygen, others maintain that only aerobic photosynthesis could produce O_2 at the rates necessary to oxidize the iron preserved in Archean sedimentary rocks (Walker, 1978).

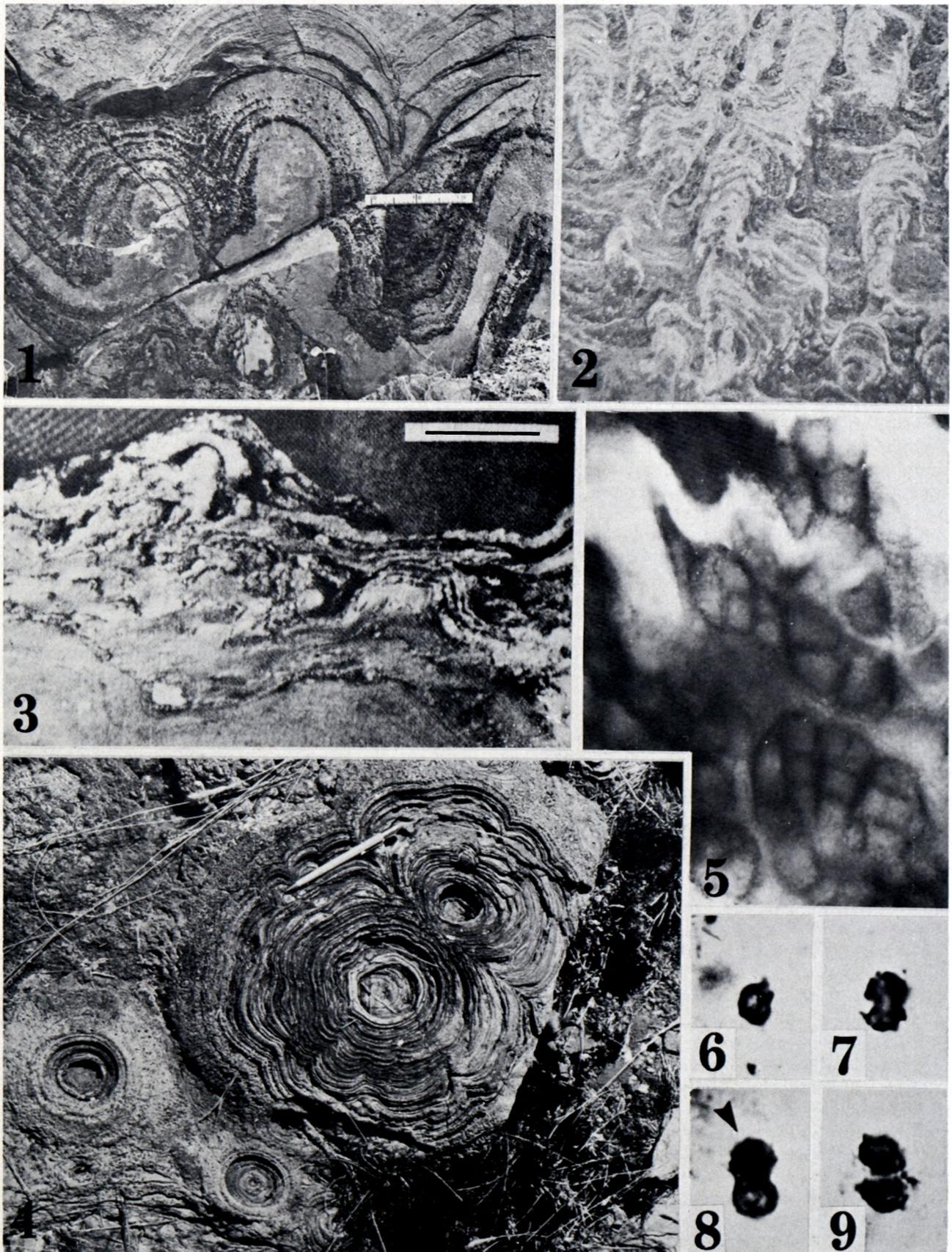


FIG. 2. — Precambrian stromatolites and microfossils. Bar in Fig. 2.3 = 2.5 cm in 1 (note 2 cm bar scale), 30 mm in 2, 7.5 mm in 3, 40 μ m in 5, and = 10 μ m in 6–9.

1 & 2, stromatolites from the Archean (2700 m.y. B.P.) Belingwe Greenstone Belt, Zimbabwe; 3, cross-section through a microbially laminated (stromatolitic) carbonate from the Archean (3000 m.y. B.P.) Pongola Supergroup, South Africa; 4, surface outcrop view of domal stromatolites from the Early Proterozoic Transvaal Supergroup, South Africa; 5, *Paleopleurocapsa wopfnerii* Knoll, Barghoorn & Golubic, a pleurocapsalean cyanobacterium from the Late Precambrian Skilloogalee Formation, Australia; 6–9, Archean (3400 m.y. B.P.) coccoidal microfossils showing various stages in cell division, from the Fig Tree Group, South Africa. 1 & 2, from Martin *et al.*, 1980, courtesy of the authors and reproduced by permission of Elsevier Publishing Company; 3, courtesy of T. R. Mason and reproduced by permission of Macmillan Journals, Ltd.; 4, courtesy of K. A. Eriksson and reproduced by permission of Elsevier.

One can hypothesize abiological ways of fractionating carbon isotopes, producing low atmospheric concentrations of oxygen, or even forming the prodigious amounts of organic matter preserved in early Archean sedimentary rocks (Reimer *et al.*, 1979); however, the most parsimonious solution to the problem of interpreting this array of data is to suggest that in the oldest unmetamorphosed supracrustal sequences on earth, we can see the record of a metabolically diverse prokaryotic ecosystem that almost certainly included photoautotrophs and which may have included cyanobacterial photosynthesizers.

In younger Archean sequences, one finds evidence of greater microbial diversity and, perhaps, sophistication. Micro-organisms preserved in cherts of the 2 800 m.y. old Fortescue Group, Australia (Schopf, 1980), include filaments that are morphologically indistinguishable from modern oscillatorian cyanobacteria. Of even greater interest are the morphologically diverse stromatolites found in limestones of the 2 700 m.y. old Belingwe Greenstone Belt in Zimbabwe (Martin *et al.*, 1980, Fig. 2.1 & 2.2) and the somewhat older microbially laminated carbonates from the Pongola Supergroup, South Africa (Mason & von Brunn, 1977, Fig. 2.3). Our available sample of Archean life is so small that it would be perilous to interpret the microfossil and stromatolite evidence as indicating a true evolutionary diversification of microbes between 3 500 and 2 700 m.y. B.P. (although that is certainly one plausible explanation for the record as read literally); an alternative that I will present, but not defend, is that in the early Archean, prokaryotes diversified rapidly and within a few hundred million years developed most of the physiological pathways possible in an oxygen poor environment. Such a hypothesis is consistent with the prokaryote phylogenetic patterns generated by Fox *et al.* (1980) on the basis of 16S ribosomal RNA characterization, as is the logical corollary that aerobic microbial physiologies radiated quickly following the subsequent accumulation of significant atmospheric O₂ concentrations.

Increased understanding of Archean evolution will require extensive paleontological investigation of sedimentologically well characterized ancient sequences. Relatively unmetamorphosed rock packages in Botswana, Zimbabwe, South Africa, and Swaziland (including further exploration of the Barberton Mountain Land) are likely to yield much useful information. This paleontological research must be coupled to innovative geochemical work, increasingly sophisticated nucleic acid sequencing of extant prokaryotes, and improved models of the Archean crust, ocean, and atmosphere that provided the context for early evolution.

THE EARLY PROTEROZOIC

Latest Archean alluvial and lacustrine sedimentary rocks from the Witwatersrand Basin, South Africa, contain critical evidence bearing on atmospheric and, hence, biological evolution. Along with the gold for which these beds are justly famous,

Witwatersrand conglomerates contain placers of detrital uraninite (UO₂). Uraninite is quickly oxidized in the presence of oxygen, so the fact that these Witwatersrand grains were weathered and eroded from an igneous source rock, transported by streams for some unknown distance, and then deposited in river bars and lacustrine delta distributary fans without ever being oxidized suggests that atmospheric oxygen levels were not in excess of 1% Present Day Atmosphere Level (PAL) (Grandstaff, 1980). It is possible to form isolated accumulations of uraninite beneath a oxygen-rich atmosphere by somehow coating grains to shield them from oxidation; uraninite can be found in modern stream gravels of the Indus River (Simpson & Bowes, 1978); however, the Witwatersrand conglomerate is not a unique deposit.

Earliest Proterozoic alluvial sediments from North America, Europe, Australia, and South America also contain detrital uraninite (Robertson *et al.*, 1978), and in each case, the immediately superjacent beds include red beds — sand-stones and shales tinted by tiny grains of iron oxide — but no uraninites. In fact, there are no significant accumulations of detrital uraninite in any sequences younger than 2 300–2 200 m.y. Conversely, red beds, which are unknown in older deposits, are common after this time. The conclusion drawn from this is that the atmosphere first became oxygen rich in the Early Proterozoic Era (Cloud, 1968, 1972, 1974; Frarey & Roscoe, 1973; but see Dimroth & Kimberley, 1976, for a dissenting view).

Why should the crustal transition from Archean to Proterozoic be accompanied by an equally epochal atmospheric change? Again, African rocks, specifically the Transvaal Supergroup of South Africa and the in part correlative Lomagundi Group, Zimbabwe, provide important clues for interpretation. Transvaal and Lomagundi dolomites constitute the earliest evidence of laterally extensive shallow marine carbonate platform deposits. A wide variety of stromatolites have been described from Transvaal dolomites (Truswell & Eriksson, 1975; Bertrand-Sarfati & Eriksson, 1977, Fig. 2.4).

The paleontological fact of high stromatolite diversity can be extrapolated reasonably to the interpretation of high microbial community diversity, with cyanobacteria almost assuredly being the dominant mat builders and primary producers. The extensive area covered by Transvaal and Lomagundi carbonates indicates that for the first time in earth history, broad, stable, shallow marine platforms were available for colonization by photoautotrophs. That is to say, the geological evolution of large cratons at the end of the Archean must have had biological consequences in terms of microbial ecology and productivity (Knoll, 1979). I am not arguing that the earth went from no cratons to full scale continents in a geological instant marking the Archean/Proterozoic boundary, but rather that continental growth very likely followed a logistic curve with the greatest rate of growth occurring at the end of the Archean. The biological consequences of this would be a greatly increased area available for cyanobacterial colonization, a signifi-

cant increase in benthic productivity per unit area due to the more hospitable nature of most photic zone environments, and an increased level of whole ocean primary productivity associated with nutrient run-off from eroding continents and increased upwelling along ocean basin margins.

Increased rates of aerobic photosynthesis mean increased rates of O_2 production and, for the first time, rates of O_2 production may have exceeded those of O_2 consumption, resulting in the accumulation of free O_2 (>1% PAL) in the atmosphere. The final consequence of this biota/crust/atmosphere interaction would be the evolution of aerobic respirers. Note that this interpretation does not require that physiologically modern cyanobacteria evolve just prior to the build-up of atmospheric oxygen, although two versions of that scenario have been advanced by Cloud (1976) and Schopf (1978). A fuller treatment of the Archean/Proterozoic transition and its probable ecological consequences can be found in Knoll (1979).

The best microfossil evidence of Early Proterozoic life comes not from Africa, but rather from North America where two distinctive types of microbiotas are known. Most famous is the biota of the 2 000 m.y. old Gunflint Iron Formation described by Barghoorn & Tyler (1965). Stromatolitic Gunflint assemblages are overwhelmingly dominated by simple spheroids and thin filamentous sheaths, with a dozen or more problematic bacteria of diverse morphologies scattered throughout the cherts. More distal facies contain a non-stromatolitic benthos dominated by the *Metallogenium*-like trichospheric bacterium *Eoastrion* Barghoorn, as well as populations of large spheroidal unicells interpreted as plankton (Knoll *et al.*, 1978). The silicified coastal carbonates of the Belcher Supergroup, eastern Hudson Bay, contain few, if any, taxa in common with the Gunflint. Instead, a Bitter Springs-like biota of diverse, morphologically modern blue-greens is found (Hofmann, 1976). The recent discovery of a new Gunflint-like microbiota in the Sokoman Iron Formation of northeastern Quebec confirms the hypothesis that the Gunflint and Belcher types of biotas lived contemporaneously in different environments (Knoll & Simonson, 1981). Gunflint biotas seem to have thrived in habitats where sedimentary iron deposition was possible (this does not carry the implication that the organisms were directly responsible for iron precipitation), whereas Belcher communities inhabited sabkha-like environments, much as their morphologic counterparts do today (Golubic & Hofmann, 1976). Early Proterozoic microfossils have been described from Transvaal carbonates (Nagy, 1974, 1978; Macgregor *et al.*, 1974); however, recent investigations have opened the possibility that at least some of these remains may be endolithic microbes that are much younger than the rocks in which they are found (Hofmann, in press). Thin (cm scale) but remarkably persistent horizons of organic matter found in Witwatersrand sequences also contain microstructures of probable biological origin (Hallbauer & Van Warmelo, 1974; Hallbauer, 1975).

THE LATE PROTEROZOIC

The major biological events of the Late Proterozoic Era were the evolution of the eukaryotic cell and the origin of multicellular plants and animals. Surprisingly, relatively little of the critical evidence bearing on the timing and consequences of these events comes from African rocks. I say 'surprisingly', because the *potential* for major African contributions to our understanding of both events is great.

Stromatolites abound in late Precambrian carbonates of Africa, and many of these have been well described, especially those in the northwestern part of the continent (*e.g.*, Bertrand-Sarfati, 1972a, b; Fig. 3.3). These structures indicate that through the end of the Proterozoic (and in many places well into the Paleozoic), cyanobacterial mats continued to form wherever bottom conditions permitted, even in the face of radiating eukaryotes and, later, metazoans. A few somewhat sketchy reports of stromatolitic microbiotas have been published (*e.g.*, Boureau, 1975, 1976; Edhorn, 1978), but these fossils tell us little in comparison to the beautifully preserved microfloras of Australia (Schopf, 1968; Schopf & Blacic, 1971; Oehler, 1978) and Svalbard (Knoll, 1982, Fig. 2.5 & 3.4–3.6). Descriptions of organic walled acritarchs (presumed planktonic cells of uncertain systematic position) from detrital facies are likewise few in number and limited in content (Binda, 1972; Lopukhin *et al.*, 1974; Choubert *et al.*, 1979; and others).

From sequences in other parts of the world, principally Scandinavia, the Soviet Union and, increasingly, North America, a picture of eukaryotic cell evolution has begun to emerge. Large, robust walled acritarchs (Fig. 3.1 & 3.2) are common in open marine siltstones and shales younger than about 1 400 m.y., but are extremely rare or absent in similar older rocks (Schopf & Oehler, 1976). The implication is that this striking change in the Precambrian fossil record may record the appearance of fossilizable nucleated cells in marine ecosystems. Relatively little is known about early acritarch assemblages, but sequences spanning the interval from 1 000 m.y. to the base of the Cambrian have been well studied (*e.g.*, Vidal, 1976), and these yield a consistent picture of increasing structural diversity among acritarchs, interpreted as a late Precambrian radiation of eukaryotic phytoplankton (Vidal & Knoll, 1983). Curiously, nucleated cells seem to have come to dominate the planktonic realm long before they displaced cyanobacterial communities from shallow benthonic niches. More curious, it is clear that the plankton biota suffered major extinctions at the end of the Precambrian, roughly coincident in time with the widespread deposition of glaciogenic sediments (Vidal & Knoll, 1983). Latest Precambrian acritarch assemblages are remarkably depauperate relative to biotas 100 m.y. older; plankton diversity didn't recover until the radiation of morphologically microplankters in early Cambrian times.

Most of the late Precambrian microfossil record consists of algae and cyanobacteria, but in rocks 750

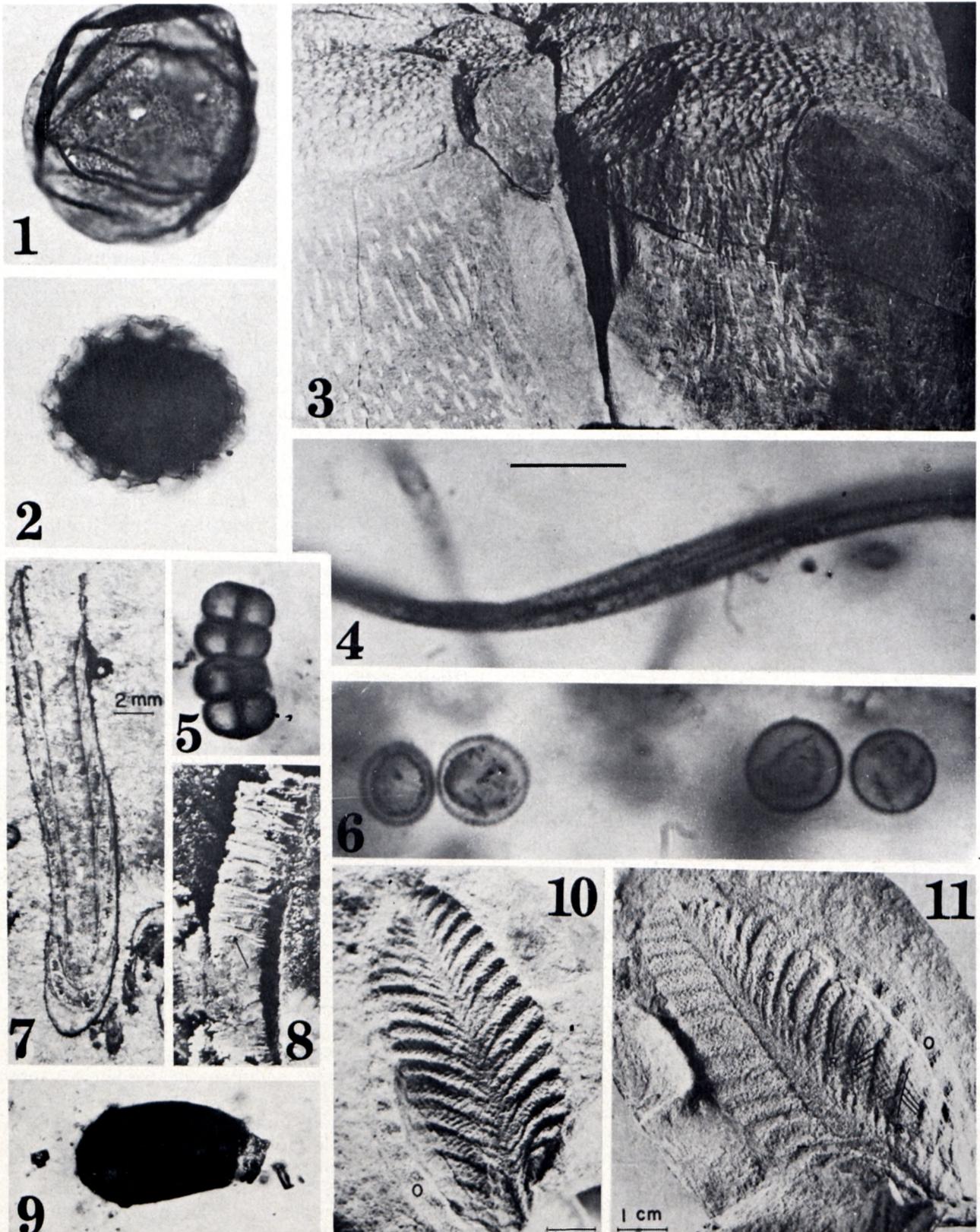


FIG. 3. — Late Precambrian stromatolites, microfossils, and macrofossils. Bar in Fig. 3.4 = 20 μ m for 1 and 2, 20 cm for 3, 13 μ m for 4–6, 6 mm for 7 and 8, 50 μ m for 9, and 18 mm for 10 and 11.

1, *Kildinella* sp. A Vidal from the Andersby Formation, East Finnmark, northern Norway; 2, *Vandalosphaeridium reticulatum* (Vidal) Vidal from the Visingsö Beds, Sweden; 3, bioherm of columnar stromatolites from the Atar Group, Mauritania; 4, *Eomycetopsis robusta* Schopf em. Knoll and Golubic, the preserved sheath of a mat building oscillarian cyanobacterium, from the Late Precambrian Draken Formation, Svalbard; 5, *Sphaerophycus wilsonii* Knoll, a mat dwelling cyanobacterium from the Draken Formation; 6, *Gloeodiniopsis gregaria* Knoll and Golubic from the Draken Formation; 7 & 8, thin section and surface views of *Cloudina hartmannae* Germs, a calcareous Metazoan tube from the Kuibis Formation, Nama Group, South West Africa (Namibia); 9, vase-shaped test of a heterotrophic protist from the Backlundtoppen Formation, Svalbard; 10 & 11, natural mold and latex cast of *Rangea schneiderhoehni* Gürich, an early coelenterate from the Kuibis Formation, Nama Group, South West Africa/Namibia. Figs 1 & 2 courtesy of G. Vidal; 3, courtesy of J. Sarfati and by permission of Elsevier Publishing Company, 7, 8, 10, & 11, courtesy of G. J. B. Germs.

to 650 m.y. in age, vase-shaped, organic tests of heterotrophic protists are being found with increasing frequency. First discovered in shales from the Grand Canyon, U.S.A. (Bloeser *et al.*, 1977), these distinctive fossils have now been found in Sweden, East Greenland, Svalbard, Brazil, and Saudi Arabia (Fig. 3.9). Biostratigraphically, they appear to be excellent index fossils, and ecologically, they provide evidence for the increasing complexity of marine ecosystems (Knoll & Vidal, 1980).

In latest Precambrian (approximately 650–590 m.y.) sedimentary sequences of Australia, Eurasia, and North America, casts and molds of simple, soft-bodied invertebrates document the initial evolution of metazoans, some of them coelomate. Among the foremost of these 'Ediacaran' invertebrate faunas is a beautifully preserved biota from the Nama Group, South West Africa/Namibia. Here abundant casts of pennatulid coelenterates (Fig. 3.10 & 3.11) are found, in addition to medusoids, a possible annelid worm, and calcareous worm tubes (Fig. 3.7 & 3.8) that constitute some of the earliest evidence for Metazoan biomineralization (Gürich, 1930; Germs, 1972a, 1973; Glaessner, 1979; Pflug, 1970). Associated trace fossils preserve the behavioral patterns of early deposit feeders (Germs, 1972b).

Early metaphytes are unknown from the African continent, but abundant ribbon-like algae up to 1 cm wide do occur in latest Precambrian shales of Eurasia (Gnilovskaya, 1971). The oldest morphologically regular carbonaceous macrofossils yet unearthed are cm-scale ellipsoidal to elongated bodies assigned to the species *Tawuia dalensis* Hofmann and Aitken, 1979. First found in shales thought to be approximately 850 m.y. old in northwestern Canada, these distinctive problematica have recently been discovered in contemporaneous strata in China and Svalbard. Intriguingly, populations of *T. dalensis* exhibit allometric growth patterns, suggesting a well integrated body plan. Whether they represent extremely regular algae or ancestral flatworm like metazoa is unknown; however, this may be resolvable by careful organic geochemical analysis. If animal, these fossils would extend in time an evolutionary transition to integrated multicellularity that at present must be viewed as extremely rapid.

Unmetamorphosed late Precambrian sedimentary sequences are widespread in Africa. Detrital accumulations of the Awat series in Egypt; clastics and carbonates from the Hoggar, Anti-Atlas, Adrar and many other areas of north-western Africa; glaciogenic and other clastic formations from Sierra Leone and Ghana; lithologically heterogeneous rocks extending in an arcuate pattern from the north-western Cape Province through Angola and into Zaire and Zambia — all of these sequences and several others are likely to contain critical evidence allowing paleontologists to test, refine and augment the ideas and evidence outlined in the above paragraphs.

In summary, Precambrian organic evolution can be viewed as a series of steps connecting successive biologic plateaus. Radiations triggered by evolutionary innovations and/or major shifts in the

physical environment were probably rapid, whereas ensuing periods prior to subsequent radiations were likely characterized by the biological fine-tuning of communities. In general, radiations resulted in increased ecosystem complexity through the addition of new taxa, rather than in the extinction and replacement of antecedent organisms (Knoll & Awramik, 1983). African rocks and fossils, and of course African geologists, have been fundamental in shaping ideas on early evolution, and it is likely that the late Precambrian sedimentary sequences of the continent will turn out to be as important to our growing knowledge of early eukaryote, metazoan, and metaphyte biology as the early Precambrian strata of southern Africa have been for Archean evolution.

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