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GEOLOGICAL EVIDENCE FOR EARLY EVOLUTION

ANDREW H. KNOLL

Harvard University. The Biological Laboratories.
16 Divinity Avenue.
Cambridge, Massachusetts 02138 USA.

INTRODUCTION

In 1952, while routinely examining samples of sedimentary rock from the Gunflint Iron Formation exposed along the north shore of Lake Superior, Canada, Stanley Tyler made an unexpected discovery. Viewing thin sections (paper thin slices of rock mounted on glass slides) of his samples under the microscope, Tyler found locked within the rock matrix thousands of minute filamentous and spheroidal bodies that closely resembled modern algae and bacteria. Realizing the implications of his observations, he contacted Elso Barghoorn who confirmed the biological nature of the microstructures. The ensuing report (Tyler and Barghoorn, 1954) was brief, but it demonstrated that the fossil record of life on earth extended back many hundreds of millions of years further than had been conventionally believed.

In fact, Tyler and Barghoorn were by no means the first naturalists to seek (and in some cases *find*) evidence of ancient life in Precambrian rocks. Walcott (1914), Moore (1918), Gruner (1922), and others had reported the presence of microfossils in strata antedating the oldest invertebrates and stromatolites. Laminated sedimentary structures built by the action of microbial communities (see below), had been recognized in Precambrian rocks as early as 1870 (Bell)[1,2]. Such studies did not go

1. Debate over the recognition of biological structures in the Precambrian rock record actually dates back to 1863 when Sir William Logan described what he interpreted to be stromatolites from metamorphosed Grenville limestones in eastern Canada. Given the name *Eozoon canadense* (dawn life of Canada), these laminated structures were the focus of a heated controversy that lasted some thirty years. *Eozoon* is now considered to be abiological in origin – an interlamination of carbonate and serpentine caused by metamorphism.

2. Although Precambrian stromatolitic structures were observed by Bell in 1870 and given Linnean names by Matthew in 1890, their true microbial nature was not appreciated until 1908 (Kalkowsky; see Hofmann, 1973, and Krumbein, 1983).

unrecognized in their day, but they were received with an ambivalence that, in retrospect, seems curious. One must remember, however, that the scientists who read the papers of Walcott and Gruner did not fully appreciate the antiquity of the Precambrian geological record; neither did they understand the evolutionary importance of prokaryotic microorganisms. Most geologists engaged in field studies of Precambrian rocks at that time would have been looking more for early brachiopod shells than for algal remains. Indeed, the geological literature of the late nineteenth and twentieth centuries contains many references to invertebrate fossils preserved in Precambrian sedimentary strata. Dawson (1897), for example, discussed the presence of worms, pteropods, sea stars, ostracodes, hyolithids, brachiopods, sponges, foraminiferans and an early cephalopod-like mollusc in beds just below the oldest Cambrian strata. In older «Huronian» rocks, he reported corals (or stromatoporoids), worms, and foraminifera, in addition to algal thalli. The erroneous nature of such claims was apparent to many turn of the century geologists; how much more believable could be reports that tiny microbes consisting totally of «soft parts» had been preserved over periods of many hundreds of million years? Whatever the reasons for the attitudes prevalent among geologists and biologists during the first half of this century, it is fair to state that it was Tyler's and Barghoorn's discovery of the Gunflint microbiota, coupled with Hurley *et al.*'s (1962) geochronological analysis suggesting an age of 2000 million years (M.y.) for the fossils, that changed the way in which scientists think about the early record of life on earth.

Over the past two decades, the known Precambrian fossil record has increased dramatically. Nearly two hundred microbiotas ranging in age from 3400 to 570 M.y. (the base of the Cambrian Period) have been discovered (Schopf, 1983; Knoll, 1985a); numerous occurrences of ancient stromatolites have been documented (Walter, 1976, 1983); and in latest Precambrian clastic rocks, a widespread and diverse fauna of primitive soft-bodied metazoans has come to light (Glaessner, 1984). Concomitant with this growth of the ancient fossil record have come major advances in our understanding of Precambrian geology, as well as microbial evolution and ecology (Knoll, 1984a). Because of the great age of early fossils, Precambrian paleontology has been enveloped in an aura of romance paralleling that once accorded the study of giant dinosaurs. In many ways this is as it should be, because the study of early evolution *is* exciting, and there *is* a certain thrill to looking at the remains of organisms which lived 2000 M.y. ago that doesn't fade with familiarity. At the same time, it is well to bear in mind that the Precambrian fossil record is not a complete and unbiased chronicle of early evolution on earth. There are many environments and many types of organisms not represented by Precambrian fossils; consequently, there are many questions about early biological history that the record cannot answer. At the conclusion of this chapter, I will present a broad overview of the evolutionary patterns that can be inferred from geological and paleontological evidence; however, before proceeding to this discussion, it is important to consider what the Precambrian fossil record is like and how one can interpret it.

THE NATURE OF THE RECORD

If we wish to understand the nature of the Precambrian fossil record, we must first ask why such a record exists at all. The tiny prokaryotes and unicellular pro-

tists preserved in Precambrian sedimentary rocks lacked the phosphatic bones of vertebrates, the calcareous shells of molluscs, or even the delicate siliceous tests of diatoms and radiolarians – in short, early organisms possessed none of the skeletal features generally associated with fossilization. It is well known that upon the death of an organism, its constituent organic matter is generally decomposed rather quickly and completely by bacteria. This is equally true for elephants and amoebae. The microfossil record of the Precambrian, then, must consist of those populations in which post-mortem bacterial degradation was arrested before it could proceed to completion. Considered from this perspective, the residual nature of the record becomes apparent. Post-mortem degradation has acted as a filter, removing all but a few organisms.

Under what conditions might degradation be arrested? Bacterial decomposition proceeds most rapidly and efficiently in the presence of O_2; thus, early removal of organic remains to an anaerobic environment, accomplished through rapid burial or organically induced depletion of ambient oxygen, is prerequisite to fossilization. Some of the best preserved Precambrian microbiotas (e.g., those of the Late Proterozoic Limestone-Dolomite series, Greenland, and Draken Conglomerate Formation, Svalbard) clearly document the rapid burial of organic-rich sediments during storms. Infiltration by highly saline groundwaters can also contribute to the abortion of cellular decomposition (Golubic and Barghoorn, 1977), and this appears to have been a factor in the preservation of a number of Proterozoic microbiotas (eg., the Belcher, Gaoyuzhuang, Amelia, Balbirini, and Narssârssuk assemblages). Modern analogs to this process exist; Golubic (1973) has described cyanobacteria (blue-green algae) yielding radiocarbon ages of 8000 years morphologically preserved in stromatolites from the Persian Gulf. In essence, these incipient fossils have been pickled.

Early diagenetic sedimentary environments favoring the retardation of postmortem degradation are not uniformly distributed among marine ecosystems. Such conditions are likely to be encountered in tidal flats or in somewhat restricted lagoons and evaporite basins, but may be found less frequently in shallow water environments having normal marine circulation. Thus, the environmental factors that control the postmortem decomposition of microorganisms introduce a significant ecological bias into the Precambrian fossil record (e.g., Horodyski and Donaldson 1981, 1984; Knoll 1985b).

Short term preservation can be effected by the termination of bacterial degradation, but the preservation of delicate cell morphologies over periods upwards of 1000 M.y. in duration is often ensured by a further step. Most of the stromatolitic microbiotas known from Precambrian rocks are preserved in chert, and indeed silicification is the key to the beautiful preservation of microorganisms such as those found in the Bitter Springs (Schopf, 1968; Schopf and Blacic, 1971) or the Gunflint (Barghoorn and Tyler, 1965) formations. As in the petrification of wood, silicification of microbes does not involve the replacement of organic walls and envelopes by SiO_2. Silica, often replacing carbonate during early stages of diagenesis, permeates the buried mat, filling in voids and embedding partially decomposed cells in a mineral matrix. Because it is relatively difficult to recrystallize, compress, or shear, chert preserves delicate cell morphologies in three dimensional detail. The distribution of early diagenetic silica in Late Proterozoic carbonates appears to reflect the distribution of originally organic-rich sediments (with due allowance made for factors such as sediment permeability); thus

in a general way it may be stated that rather than introducing an additional environmental bias in preservation, silicification reinforces the patterns introduced by organic sedimentation (Knoll, 1985b).

From the above arguments, one can infer that not all ecosystems are equally likely to be represented in the fossil record of silicified microorganisms. It is further true that not all organisms within a given environment are equally likely to be preserved. The cellular remains of organisms vary tremendously in their resistance to decomposition and in their tolerance to the changing osmotic pressures that accompany burial and degradation. For example, many cyanobacteria of the intertidal zone are quite resistant to post-mortem obliteration because of their tough external envelopes or sheats of hydrated polysaccharides (Golubic and Barghoorn, 1977). Bacteria found below the surface of intertidal mats appear in many cases to be less resistant. Although anaerobic photoautotrophs and heterotrophs are prominent members of modern vertically zoned mat assemblages, their remains have not been recognized in silicified Precambrian stromatolites (Awramik *et al.*, 1978). One cannot discount the possibility that unlike their modern analogs, Precambrian stromatolitic communities exhibited no vertical zonation; however, differential preservability may well explain the apparent paucity of non-cyanobacterial monerans in ancient microbial mat assemblages. In a discussion of preservability among subtidal microbes, Golubic and Barghoorn (1977) state that planktonic and permanently submerged benthic cyanobacteria often show little resistance to degradation – «they lyse explosively at slight changes in osmotic pressure or temperature, leaving little or no detectable structural remains». Eukaryotic microbes are similarly variable in their resistance to postmortem alteration (Golubic and Barghoorn, 1977).

At a still smaller level, it can be observed that within a *single* microorganism, some materials are more resistant to degradation than others. Numerous studies of cyanobacterial degradation - both field analyses of Recent assemblages in natural habitats and laboratory experiments on monospecific cultures – suggest that extracellular sheaths and envelopes are often preferentially preserved relative to the cell itself (Awramik *et al.*, 1972; Knoll and Barghoorn, 1975; Horodyski and Vander Haar, 1975; Golubic and Hofmann, 1976; Aizenshtat *et al.* 1984). The Precambrian cyanobacterial record corroborates this picture of preferential envelope preservation (Knoll *et al.*, 1975; Hofmann, 1976; Golubic and Hofmann, 1976; Knoll and Golubic, 1979). Francis *et al.* (1977) examined the preservation potential of a large suite of prokaryotic and eukaryotic microorganisms and found that materials such as cyanobacterial sheaths, some eukaryotic cell walls, and certain intracellular inclusions (polyphosphate granules in cyanobacteria and starch bodies in green algae) are likely candidates for fossilization. Delicate organelles such as mitochondria or nuclei have little chance of being preserved, although studies of Phanerozoic plant remains suggest that occasionally the unlikely occurs (see especially Niklas *et al.*, 1978).

Thus, it can be seen that while fossils of microbes preserved in silicified stromatolites provide the foundation upon which much of our understanding of early evolution is based, these assemblages are to a greater or lesser degree biased with respect to environment, the types of organisms preserved, and the parts of organisms preserved. This is not to imply that evolutionary histories inferred from this evidence are incorrect; on the contrary, interpretations based primarily upon silicified microorganisms may reflect reasonably well the early course of terrestrial biology. One

must simply remember both the strengths and the weaknesses of the data.

Detrital sedimentary rocks (sandstones, siltstones, shales) represent a variety of Precambrian platform, continental shelf, and continental slope depositional environments, and so fossils contained in these strata serve to expand the range of habitats from which evidence of early evolution can be drawn. As might be expected, the microfossils found in detrital rocks differ significantly from those characteristic of stromatolitic carbonates. Most are unicellular (solitary or in aggregations of a few to several dozen individuals) and presumably represent the cysts of ancient algae (Downie, 1973), although both cyanobacterial and heterotrophic protists are also known from siltstones and shales. Many of these microfossils cannot be related unequivocally to any extant taxonomic group; hence, they must be classified as acritarchs[3] (Vidal, 1976; see Figures 2j and 3i).

Again, the fossil assemblages preserved in Precambrian detrital rocks do not constitute unbiased records of early planktonic communities. Clastic bottom environments favor preservation of those organisms which produce degradation resistant walls, sheaths, spores or cysts. In exceptional cases, however, fragile microbial remains can be and have been preserved in detrital facies (e.g. Jankauskas, 1982). Phosphate nodules from the late Precambrian Visingsö Formation of southern Sweden contain thecate microfossils that are not found in surrounding shales (Knoll and Vidal, 1980). Like the coal balls of Carboniferous coal deposits, these small nodules composed predominantly of the calcium phosphate mineral apatite [$Ca_5(PO_4)_3F$] appear to preserve delicate remains that would not become fossilized under normal conditions. Karl Ewetz first described microfossils from Precambrian phosphate nodules in 1932, but they remain largely untapped as a source of paleobiological information.

In addition to acritarchs, late Precambrian detrital rocks also contain the fossils of megascopic algae and early, soft bodied metazoans preserved as carbonaceous ribbons and sheets (Gnilovskaya, 1971; Hofmann and Aitken, 1979; Hofmann, 1985), or as impressions, casts and molds (Glaessner and Wade, 1966; Fedonkin, 1980; Glaessner, 1984). Preservation of animals without hard parts requires special conditions of fossilization. Schäfer (1941) has described how jellyfish living in the North Sea are occasionally stranded on muddy tidal flats where they may leave an impression in the underlying sediments. Upon exposure to air, the gelatinous body of the jellyfish begins to dehydrate, but a thin organic pellicle enclosing the medusa retains its integrity and the mud dries against this «skin». Sediments deposited by the next tidal advance seal the mold. In modern environments such incipient fossils are often destroyed by burrowing animals, but in the late Precambrian, prior to the proliferation of pervasive bioturbating communities, many impressions of soft-bodied organisms became permanent parts of the geological record.

INDIRECT EVIDENCE OF PRECAMBRIAN LIFE

Clearly, actual fossilized organisms provide the best evidence of early life, but indirect information gleaned from the sedimentary rock record is also necessary for the reconstruction of biological history.

3. In 1963, Evitt coined the term 'acritarch' as an informal designation for small, organic walled microfossils of uncertain taxonomic affinities. Downie *et al.* (1963) subsequently divided acritarch genera into a series of informal groups bases on morphology. Good introductions to this group of microfossils are those written by Downie (1973) and Tappan (1980).

The nature of this indirect data is briefly summarized in the following paragraphs.

1. Stromatolites

It is easiest to explain what a stromatolite is by describing how one forms. Stromatolitic structures (Fig. 1) are initiated by the establishment of a thin mat of microbes on a sediment surface. Mat-building populations are usually filamentous cyanobacteria, but a few coccoid 'blue-greens', as well as several other types of bacteria and eukaryotic algae, are capable of forming stromatolites.

As sediment particles accumulate on top of the mat, they are trapped and bound into a coherent layer by the microbes. Microbial precipitation of calcium carbonate can also contribute to sediment accumulation and stabilization. The mat-building microbes require light for photosynthesis and so cannot remain buried beneath accumulating sediments. By moving or growing upward through the thin sediment layer or, in the case of the coccoidal Entophysalidaceae, by flooding the surface with a host of reproductive bodies, the microorganisms establish a new mat on top of the old one. This mat, in turn, traps and binds more sediment. A stromatolite is the accretion product of this on-going interaction between the organisms of the mat community and the physical processes of sedimentation. The laminated structure characteristic of most stromatolites records former positions of the living mat (Hofmann, 1973).

It is the dual biological and sedimentological nature of stromatolites that makes them particularly useful in studies of Precambrian life. Although the mat-building organisms themselves may disappear rapidly, the unique sedimentary structures they form are as permanent as the rocks in which they are found, succumbing only to erosion or pervasive metamorphism. Thus, while microfossils of Precambrian mat-building assemblages are known from relatively few localities, we know that these communities were extremely widespread in shallow marine environments because of the ubiquity of stromatolites.

Stromatolites vary in shape from flat, domed, or conical to cylindrical (columnar) or spherical. Often the cylindrical forms are branched (Walter, 1972, 1976; Hofmann, 1973). The microstructure of stromatolite laminae is determined by the composition of the mat-building community (Monty, 1976; Bertrand-Safarti, 1976), but overall shape is controlled at least in part by such environmental factors as current speed and direction (e.g. Horodyski, 1977). In spite of this environmental influence on form, the types of stromatolites present in Precambrian rocks appear to change systematically as one progresses from older to younger strata. Soviet geologists have employed stromatolites in the biostratigraphic subdivision of middle and late Precambrian ($1650 \pm 50 - 570$ M.y.) carbonate sequences (Krylov, 1963, Raaben, 1969; citations in Walter, 1976), and this system has proven applicable to rocks from other continents, including North America and Australia (Preiss, 1976). Presumably, the temporal changes in stromatolite structure reflect either evolutionary changes in mat-building microorganisms or directional changes in the physical or biological environment of mat communities.

2. Trace Fossils

Just as stromatolites document the presence of microbial communities long after the organic remains of the constituent microorganisms have disappeared, so, too, do tracks, trails, and burrows found in latest Precambrian detrital rocks record the pre-

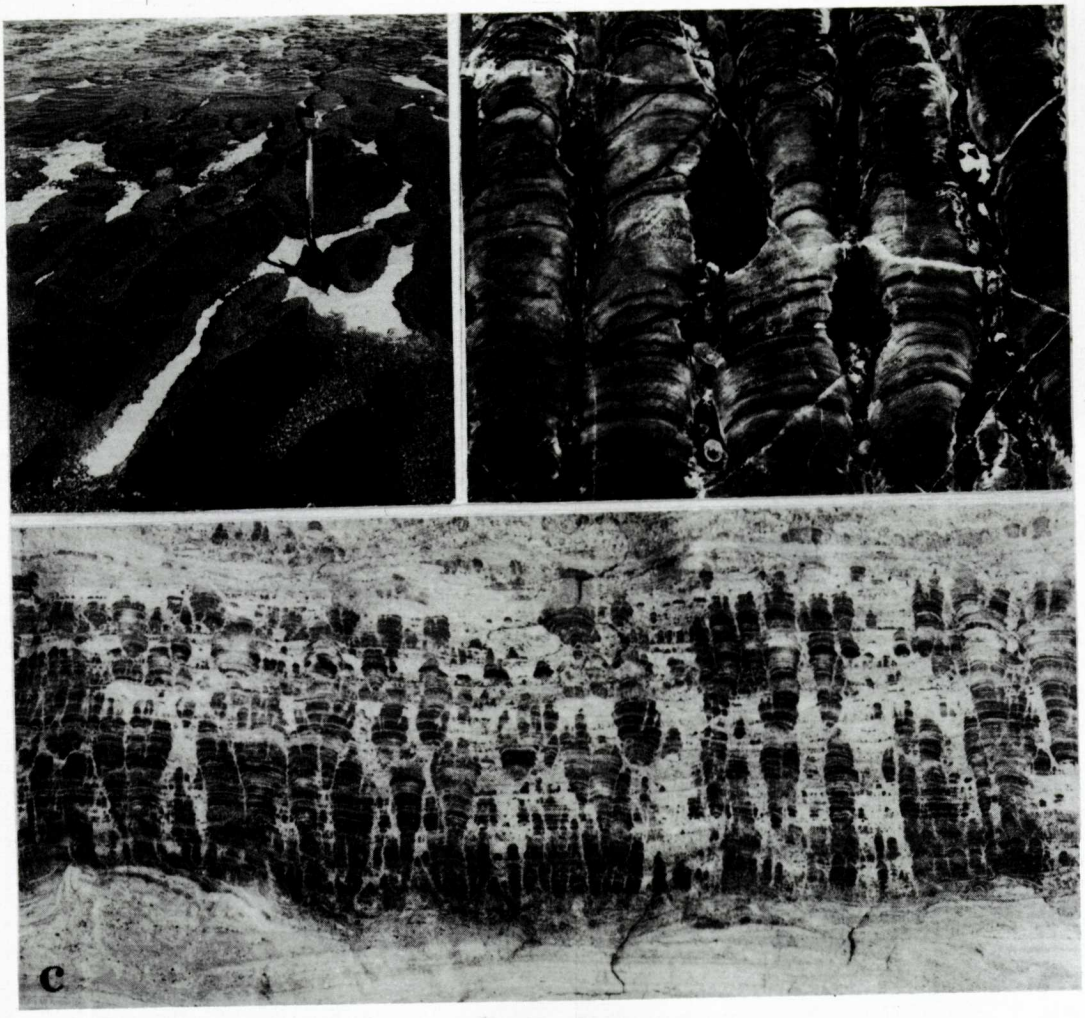

Fig. 1. Ancient and modern stromatolites.
(a) Modern stromatolites accreting in the intertidal zone of Shark Bay, Western Australia. Shovel provides scale. (b) Polished slab of 2000 M.y. old stromatolites from the Gunflint Iron Formation, Canada. Note characteristic laminations. Approximately natural size. (c) 2000 M.y. old columnar stromatolites in dolomites of the Belcher Supergroup, Belcher Islands, Canada. Width of photograph is 30 cm. (a, courtesy of S. Golubic, with permission of the Paleontological Society; b, courtesy of S.M. Awramik; and c, courtesy of H. Hofmann.)

sence of early invertebrate animals. Impressions and molds of primitive soft-bodied metazoans are rare; most early animals left no direct record. However, trace fossils (evidence of the *activity* or *behavior* of organisms) attest to their former abundance in geographically widespread areas of the Precambrian world. Metazoan trails and burrows appear to be restricted to rocks younger than 700 million years (Stanley, 1975; Sepkoski and Knoll, 1983; Glaessner, 1984), although reports of older trace fossils can be found in the literature (e.g., Kaufman; reviewed in Glaessner, 1984). In latest Precambrian sequences, trace fossil diversity begins low and then increases greatly, reflecting the evolutionary radiation of marine invertebrates. Sei-

lacher (1977) has pointed out that trace fossil preservation is facies-dependent, being optimal in interbedded sands, silts, and clays. He also cautions that deposit-feeding animals are overemphasized in the trace fossil record. These caveats aside, however, the trails and burrows of Precambrian organisms contribute significantly to our understanding of early metazoan evolution.

3. Stable Carbon Isotopes

The two stable isotopes of carbon, ^{12}C and ^{13}C, occur on earth in an average abundance ratio of $^{12}C/^{13}C = 89/1$ (Kaplan, 1975). When photoautotrophs fix CO_2 (in aquatic or marine ecosystems this will be in the form of bicarbonate ion, HCO_3^-) for photosynthesis, they preferentially incorporate the lighter isotope, ^{12}C, into synthesized organic matter. Thus, the ratio of the two isotopes in photosynthetically produced organic materials differs from that of atmospheric CO_2, and it does so by a fairly distinct and relatively constant amount. Because both isotopes are stable, their relative abundance in a given substance does not change with time (barring extensive diagenetic or metamorphic alteration; Schidloski *et al.* 1983; Hayes *et al.* 1983). This means that, in theory, one should be able to analyze the carbon isotope ratios in organic matter contained in Precambrian sedimentary rocks and determine whether or not it was produced photosynthetically. This analysis has been done, and the results have prompted the suggestion that the process of photosynthesis originated more than 3000 million years ago, early in the history of life on earth (Oehler *et al.*, 1972; Eichmann and Schidlowski, 1975; Schidlowski, 1978).

4. Sulfur Isotopes

Stable isotopes of sulfur are also fractionated by microorganisms, most notably anaerobic, sulfate reducing bacteria. Hydrogen sulfide produced by the bacterial reduction of sulfate is depleted in ^{34}S by 0 to 50 % relative to the parent material, the degree of fractionation being dependent in part on metabolic rate, itself a function of temperature and nutrient concentration (Goodwin *et al.*, 1976). As in the case of carbon, $^{34}S/^{32}S$ values for sedimentary sulfides might be expected to yield information about the presence or absence of sulfate reducing bacteria at the time of sediment deposition. Sedimentary rocks as old as 2750 million years exhibit the wide variation of sulfur isotope ratios characteristic of biogenic sulfide formation (Goodwin *et al.*, 1976), but this pattern has not been observed in analyses of older rocks (Schidlowski *et al.*, 1983). Noting this, Thode (1978) and Schidlowski (1978) have raised the fascinating possibility that biological sulfate reduction may be less ancient than photosynthesis (Monster *et al.*, 1979). Cameron (1982, 1983) has noted that sulfur isotopic ratios exhibit a further significant increase in variation about 2300 M.y. ago, about the time when other geochemical features suggest an increase in atmospheric O_2 levels (e.g., Knoll, 1984b). Perhaps the process of dissimilatory sulfate reduction is indeed very old, but oceanic sulfate availability was limited until increases in primary production infused substantial oxygen into the oceans and atmosphere.

5. Organic Chemical «Fossils»

In spite of two decades of research, Precambrian organic geochemistry remains a difficult sea in which to chart a reliable course. Many biologically important compounds (including amino acids, porphyrins, and isoprenoid alkanes) have been identified in analyses of ancient sedimentary rocks; however, these substances are present in extremely small quantities –

more than 95 % of the organic matter in Precambrian rocks is in the form of insoluble kerogen – and hence, may contain contaminants introduced after the formation of the rock. One can tell whether or not the amino acids recovered from a sample of 3000 M.y. old chert are recent contaminants, but at present there exists no procedure for determining whether those amino acids are 3000 M.y. old, 1000 M.y. old, or six million years old. McKirdy (1974) has reviewed the extensive literature of this discipline. I am strongly disposed to agree with him that at least some of the chemical «fossils» isolated from ancient rocks are indeed the products of Precambrian biological activity, but the problems of post-depositional contamination remain, making any systematic assessment of this evidence difficult.

More recently, Hayes *et al.* (1983) have demonstrated that reports of hydrogen and oxygen rich biomolecules in Archean rocks are inconsistent with the metomorphic states of the rocks themselves. Continued research in the molecular organic geochemistry of Precambrian rocks should be concentrated on the best preserved organic materials found in Late Proterozoic cherts and shales.

6. Partially Degraded Microorganisms

Fossils of decomposing bacteria have not been identified in Precambrian microbiotas, but their presence in ancient microbial mat communities can be inferred from the preserved record of partially degraded cyanobacteria.

7. Iron Bearing Sedimentary Rocks

Cherty iron formation is a distinctive sedimentary rock consisting of silica with greater or lesser amounts of iron minerals, including oxides, carbonates, silicates, and sulfides (James, 1966). Chemical evolutionists agree that when life originated, the atmosphere contained negligibly little oxygen, but iron oxides found in the oldest known sedimentary sequence on earth demonstrate that a source of O_2 must have existed very early in earth history. Some authors (Schopf, 1975, 1978; Towe, 1978) believe that the photodissociation of water molecules in the upper atmosphere could have produced oxygen now bound in the iron oxides, but others (Cloud, 1976; Walker, 1978) aver that only photosynthesis could supply O_2 at the rates necessary to produce the volumes of iron formation present in ancient sequence. Notwithstanding these disagreements most scientists concurr that the first appearance of hematite bearing sandstones (red beds) approximately 2300 M.y. ago fixes a minimum date for the evolution of the cyanobacteria. Because the evolutionary importance of iron bearing sedimentary rocks is best appreciated and discussed in a chronological framework, further consideration is reserved for the final section of this chapter.

8. Comparative Biology of Living Microorganisms

Living microorganisms contain information on their evolutionary origins in the form of informational macromolecules and biochemical pathways. Amino acid sequences in proteins (especially cytochromes and ferridoxins) and nucleotide sequences in nucleic acids (especially 16S rRNA) have been used to determine phylogenetic relationships among bacteria of diverse morphologies and physiologies (Fox *et al.*, 1980; Dayhoff, 1983). From such data, one can infer patterns of microbial diversification, and to a first approximation, the patterns are consistent with

the fossil record (e.g., Knoll, 1985c). Some metabolic pathways also invite interpretation in terms of evolutionary history. Among these are chlorophyll biosynthesis (Mauzerall, 1977), sterol synthesis (Chapman and Schopf, 1983), and energy metabolism (Gest, 1980). Studies of modern microbial communities (e.g., Cohen et al., 1984) also illuminate the historical record of early evolution seen in sedimentary rocks.

INTERPRETING THE RECORD

In 1733, Alexander Pope wrote that

> *... in order to examine the perfection or imperfection of any creature whatsoever, it is necessary first to know what* ***condition*** *and* ***relation*** *it is placed in.* ***(my emphasis)***

It is, averred Pope, the condition and relations of an organism that allow it to be placed properly in the universal order of life. Biology has changed greatly since the eighteenth century, and evolutionary theory has replaced the «great chain of being» as the basis of organic classification, but *condition* and *relations* remain of paramount importance in paleontology, especially in the interpretation of the early fossil record.

In the present context, «condition» can be understood to mean the preservational state of a Precambrian microorganism. As discussed in the previous section, no Precambrian microfossil has been preserved in a pristine state; all were subject to varying degrees of post-mortem shrinkage and/or decomposition, and the morphologies that one sees under the microscope reflect this degradational history. In ascertaining the «relation it is placed in», a Precambrian paleontologist must place a microfossil in its proper ecological context. The relationships (1) among various taxa in a single assemblage and (2) between the entire biological assemblage and its physical environment, as deduced from the sedimentary rocks in which the fossils occur, are important in interpretation. By determining the post-mortem degradational history and ecological setting of a fossil population, one can arrive at the fullest possible understanding of the Precambrian biological record.

1. Taphonomy

Taphonomy can be defined as the study of what happens to an organism from the moment of its death until its subsequent discovery as a fossil (Efremov, 1940). Lawrence (1968) has referred to taphonomic changes as «post-mortem information loss» and accurately so, for the alterations resulting from decomposition, diagenesis, and metamorphism inevitably obscure or obliterate features that were clearly observable in the living community. The object of taphonomic analysis, then, is to gauge the nature and extent of post-mortem changes and then mentally «run the machine in reverse» to reconstruct, insofar as is possible, the structure of the original organism or assemblage.

In an excellent paper setting forth the principles of Precambrian microfossil interpretation, Golubic and Barghoorn (1977) have summarized the approaches used in the taphonomic analysis of microbial fossils. Rather than risk the literary information loss associated with paraphrasing, I have taken the liberty of quoting their summary prescriptions in their entirety:

> *... in order to refine the means of identification and interpretation of microbial fossils: 1. A comparison with extant counterparts is sought in comparable environments. 2. Post-mortem changes and early diagenesis are studied in modern natural populations, and experimentally induced in cultured unispecific populations of se-*

lected taxa. 3. Long-term changes are followed by studying the preservation of microorganisms in Holocene sediments. 4. Whenever possible, entire populations are studied and their morphological variability, including cell division patterns and colony formation, is evaluated. 5. Maximal attention is paid to the few well-preserved fossil taxa that offer the most complete record, in order to establish and verify the criteria for interpretation of less complete or partially obliterated specimens.

Two themes are woven throughout the above principles. The first concerns the importance of studying degradation and diagenesis in Recent populations; what German scientists have long referred to as *Aktuopälaontologie*, the paleontology of the present. From a perusal of the paleontological literature, it is evident that many if not most of the microorganisms preserved in silicified Precambrian stromatolites closely resemble modern bacteria and cyanobacteria in morphology. Therefore, by establishing patterns of shrinkage and degradation characteristic of Recent mat-building organisms, it is possible to recognize the same patterns in fossil counterparts. The second major theme involves what Ernst Mayr has called «population thinking». Within a single stromatolite, one can often discern several distinct microenvironments of preservation (Knoll and Golubic, 1979), and because of this, individuals belonging to a single microbial population may exhibit quite different degrees of post-mortem degradation. Some specimens may be almost completely reduced to amorphous organic matter, while other nearby fossils belonging to the same taxon are relatively well preserved. By considering the entire range of degradation present in a population, one can sometimes reconstruct degradational patterns from the fossils alone (Golubic and Hofmann, 1976; Knoll and Golubic, 1979).

In observations of natural populations in Recent microbial mats, Golubic and his colleagues (Awramik *et al.*, 1972; Golubic and Hofmann, 1976; Golubic and Barghoorn, 1977) have noted a common sequence of coccoid cyanobacterial degradation. Blue-green cells lose their turgidity and, like a grape turning into a raisin, shrink to form wrinkled polyhedral bodies. As degradation proceeds the cell is reduced to a small granule and may disappear entirely. As mentioned previously, the polysaccharide envelopes surrounding cyanobacterial cells preferentially retain their rounded outlines and may persist in a recognizable state well after the cell has disappeared. *Paleopleurocapsa wopfnerii* (Knoll *et al.*, 1975), a fossil pleurocapsalean cyanobacterium from the approximately 850 million year old Skillogalee Formation of southern Australia, consists of a complex crustose thallus, preserved almost entirely as empty envelopes. Highly degraded cellular remains occur in rare instances, but the patterns of cell division, packing, and endosporal reproduction recognizable in the fossil are all preserved, and faithfully so, in envelope morphologies (Fig. 3a).

Gunflintia minuta (Fig. 2d-h) is a thin (1-4 μm cross-sectional diameter) filamentous microfossil that is exceedingly abundant in silicified stromatolites from the Gunflint Iron Formation. This taxon was originally described by Barghoorn (Barghoorn and Tyler, 1965) as having distinct septa, although he noted that the presence or absence of septations was often difficult to establish because of post-depositional alterations. Licari and Cloud (1968; also Cloud, 1976) carried the interpretation of this taxon further by postulating that rare inflated structures on *Gunflintia* filaments were possible heterocysts and akinetes, specialized cells found only in certain groups of cyanobacteria (Fig. 2h). Taphonomic analysis requires that one ask whether such structures could be produced by post-mortem processes. Francis *et al.* (1978) showed inflated areas on partially

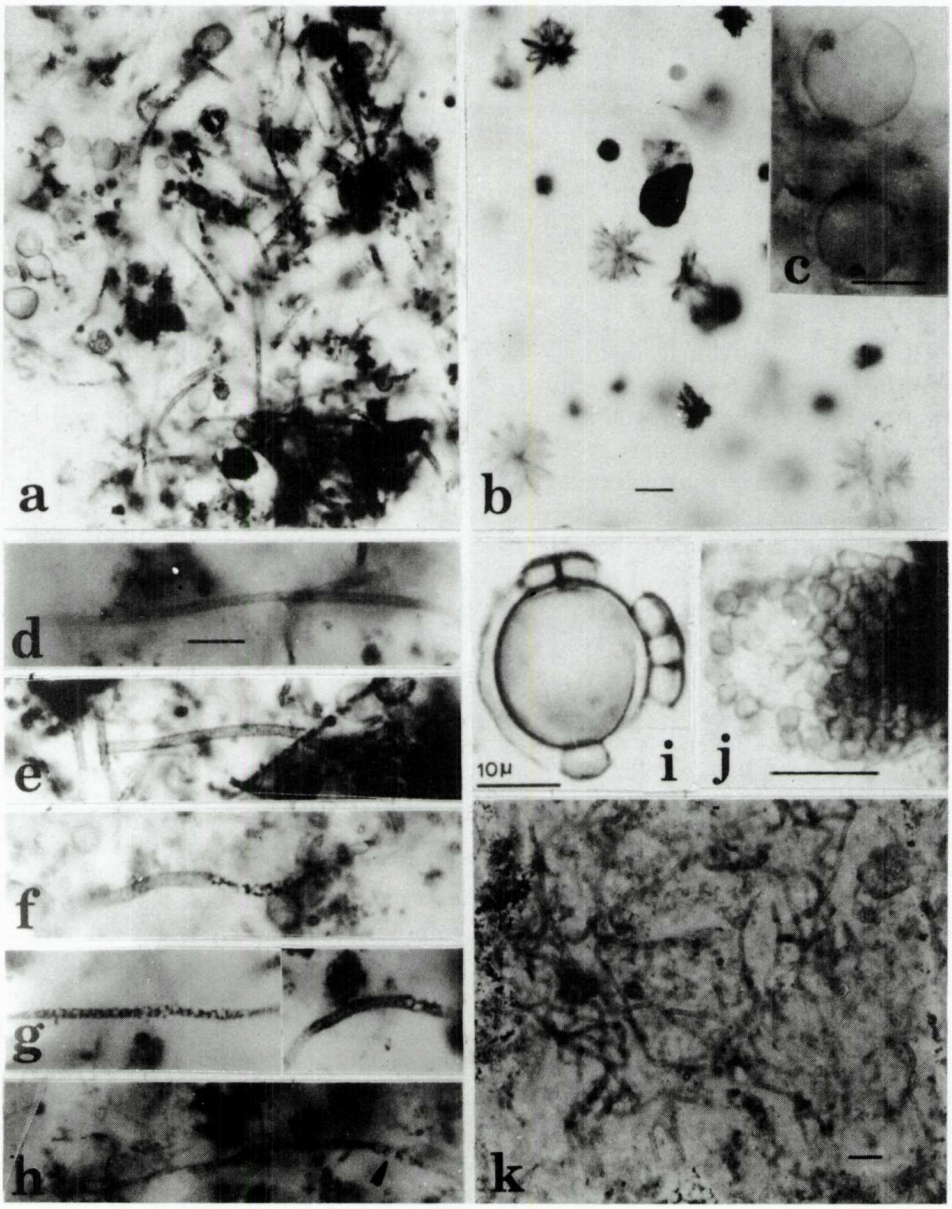

Fig. 2. a-i. Microfossils from the 2000 M.y. old Gunflint Iron Formation.
(a) Stromatolitic community dominated by the unicellular *Huroniospora* and the filament *Gunflintia*; (b) Stagnant off-shore mud community dominated by the Fe/Mn oxidizing bacterium *Eoastrion*; (c) Planktonic unicells belonging to the species *Leptoteichos golubicii* Knoll, Barghoorn, and Awramik; (d-h) *Gunflintia* filaments showing various stages of degradation – d and e are well preserved and show nonseptate tubular morphology; f. illustrates transition from area of excellent preservation (left) to region of poorer preservation; g. Apparent septations manifest in poorly preserved filaments; and h. Heterocyst-like bulges on a *Gunflintia* filament; (i) *Eosphaera tyleri* Barghoorn; (j) *Bavlinella faveolata* (Shepeleva) em. Vidal, an acritarch from the late Precambrian Mineral Fork Formation, Utah; and (k) Population of *Eomycetopsis robustus* Schopf from the Bitter Springs Formation showing vertical orientation of tangled filaments characteristic of some modern stromatolite building cyanobacteria. Bar = 10 μm in b and k (b applies also to a.); bar = 10 μm in c, d, i, and j (bar in d applies also to e-h). (i courtesy of E.S. Barghoorn).

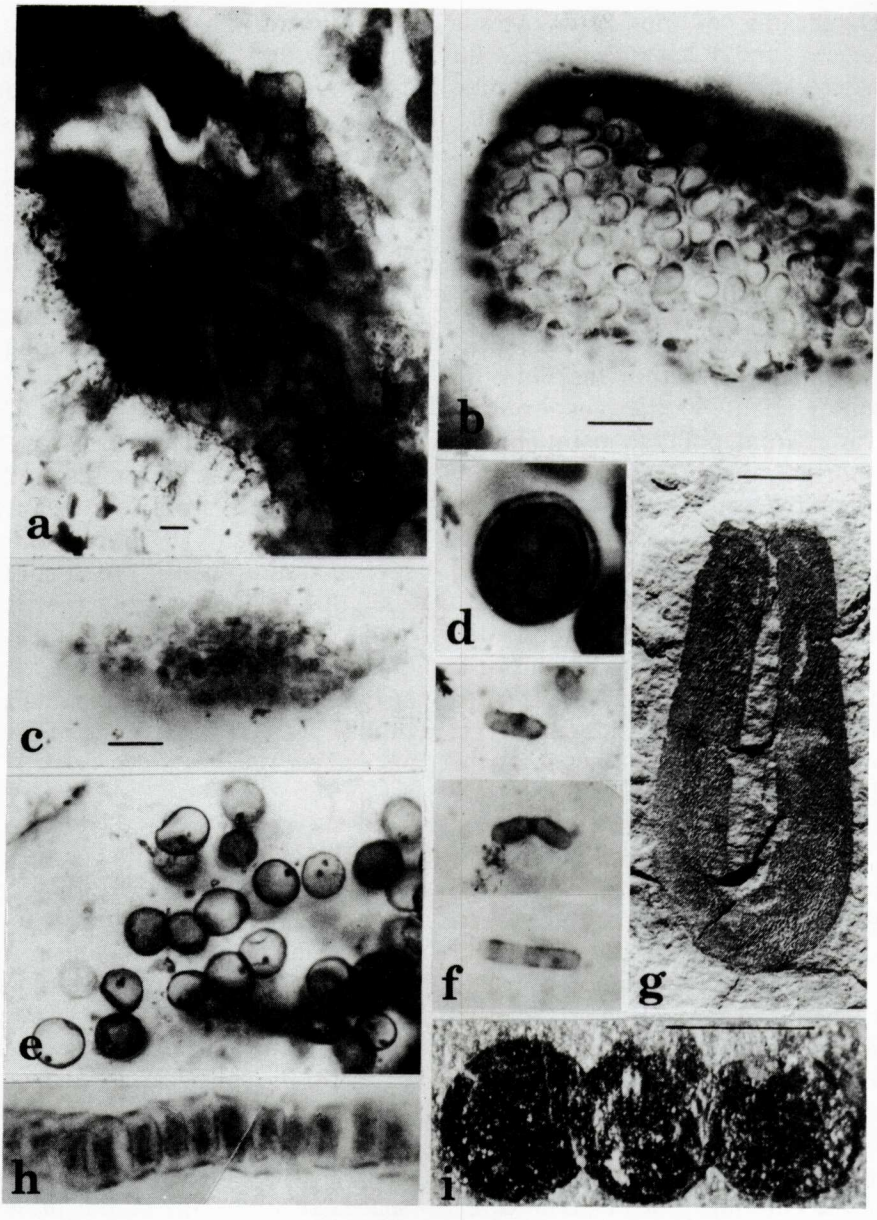

Fig. 3. (a) *Paleopleurocapsa wopfnerii* Knoll, Barghoorn, and Golubic from the approximately 850 M.y. old Skillogalee Formation, Australia; (b) *Eoentophysalis belcherensis* Hofmann from the 2000 M.y. old Belcher Supergroup, Canada; (c) Cluster of unnamed unicellular cyanobacteria from the late Precambrian Narssârssuk Formation, Greenland; (d) Chroococcoid cyanobacterium from the approximately 850 M.y. old Bitter Springs Formation, Australia; (e) *Glenobotrydion aenigmatis* Schopf from the Bitter Springs Formation; (f) *Eosynechococcus* sp. from the Narssârssuk Formation; (g) *Tawuia dalensis* Hofmann and Aitken from the late Precambrian Little Dal Group, Canada; (h) Partially degraded oscillatorialean filament from the Narssârssuk Formation; and (i) *Chuaria circularis* Walcott from the approximately 950 M.y. old Uinta Mountain Group, Utah. Bar scale = 10 μm for a, b, and c (scale in c also applies to d-f, h); bar = 5 mm in g; bar = 1 mm in i. (b, g, and i courtesy of H. Hofmann).

degraded sheaths of non-heterocystous cyanobacteria, and I have seen beautiful pseudoheterocysts on the long arm-like projections of Devonian acritarchs. Thus, as Schopf suggested in 1975, the inflated areas of the Gunflint filaments may be degradationally produced. Examination of *Gunflintia minuta* populations further suggests that many of the apparent septations in the fossil filaments may also be degradational in origin. Because of small scale variations in diagenesis within the Gunflint stromatolites, quality of microfossil preservation varies from point to point. In the best preserved areas, *Gunflintia minuta* specimens often can be seen to be non-septate sheaths of uniform thickness (Fig. 2d, e). In more poorly preserved areas, coalified filaments appear to have cross-walls (Fig. 2g). Presumably, the former state of preservation is closer to the morphology of the original undegraded materials; thus, a population-based taphonomic analysis would suggest that the original *Gunflint minuta* organisms were filamentous prokaryotes that formed well defined extracellular sheaths. Support for this interpretation comes from individual filaments that traverse the boundary between adjacent zones of excellent and poor preservation. In such specimens (Fig. 2f), the portion in the area of good preservation is a hyaline tube, while the other part has variably distinct markings along the length of the filament. (This is not meant to imply that no thin cellular trichomes or chains of cells within small sheaths can be found in the Gunflint. They can; however, most of the best preserved filaments appear to be sheaths.) The terms of this interpretation permit comparison of *Gunflintia* filaments to cyanobacterial remains, but they also suggest that these Gunflint fossils are morphologically indistinguishable from the iron-coated sheaths of modern filamentous iron-bacteria, organisms that might be expected to thrive in an iron-rich environment. The *Gunflintia* example illustrates that post-mortem changes can alter microbial morphology in important ways; taphonomic analysis of fossil populations is imperative for the interpretation of ancient organisms.

Applications of taphonomy to the Precambrian fossil record are numerous and increasing. Knoll and Golubic (1979) demonstrated how, by superimposing a common pattern of degradation upon the different stages of a simple divisional cycle, one could generate all of the individual morphologies present in a large, morphologically variable assemblage of Bitter Springs unicells from one locality. Golubic and Hofmann (1976) also showed that several microfossil types present in 2000 M.y. old rocks from the Belcher Islands, Canada, were degradational variants of a single biological species. Clearly, such analyses affect not only taxonomic classification, but also discussions of diversity in ancient ecosystems.

2. Paleoecology

Whereas taphonomy deals with the post-mortem history of an organism, paleoecology is concerned with its biological relationships while alive – relations with other organisms in the same assemblage as well as with the physical environment. The study of silicified stromatolites in petrographic thin section is particularly well suited for paleoecological analyses because the spatial relationships of the preserved microorganisms are retained.

The orientation and distribution of microfossils within the encompassing rock can provide information critical to the interpretation of a fossil organism. For example, *Eomycetopsis robusta*, a long, thin, tubular microfossil (2-5 μm in cross-sectional diameter) found in the Bitter Springs Formation, was originally described as a

probable fungus belonging to the order Phycomycetae (Schopf, 1968). The resemblance of *Eomycetopsis* to fungal hyphae preserved in petrified plant axes from the Devonian Rhynie Chert of Scotland made this interpretation plausible, as did occasional kinks in the tubes that resemble septa. Hofmann (1976), however, reexamined the type populations of *Eomycetopsis* and, based on observations of degradational patterns in moribund cultures of modern filamentous cyanobacteria, concluded that the fossils are the sheaths of partially degraded cyanobacteria or iron bacteria. More recently, Knoll and Golubic (1979) have been able to establish unequivocally not only the cyanobacterial nature of the Bitter Springs *Eomycetopsis*, but also its ecological role as a major mat-building organism in some Bitter Springs environments. In part, this interpretation is derived from the discovery of rare highly degraded cellular trichomes inside the sheaths, but the critical evidence comes from thin sections in which populations of *Eomycetopsis* filaments are interwoven in the alternately vertical and horizontal pattern characteristic of some extant, mat-building blue-greens (Fig. 2); (see also Knoll, 1981, 1985a).

The unicellular microfossil *Glenobotrydion aenigmatis* (Fig. 3e), also from the Bitter Springs Formation, further illustrates the value of spatial data in paleoecological interpretation. It is the patchy distribution of scattered individuals and loosely organized clusters of *Glenobotrydion aenigmatis* in one facies of the formation that allowed Schopf (1968) to conclude that it was a planktonic alga, a determination of obvious ecological importance. Similar distributional arguments have been used to infer the planktonic nature of *Leptoteichos golubicii*, a spheroidal microorganism found in distal facies of the Gunflint Iron Formation (Knoll *et al.*, 1978).

Within fossil microbiotas, taxa can be grouped in recurring associations that constitute microbial paleocommunities. By relating these, in turn, to the sedimentary rocks in which they are found, one can develop some idea of the factors that controlled the distribution of microbes in Precambrian basins. For example, shallow water, a relatively high energy environment in the Gunflint sea, supported a distinctive assemblage (Fig. 2a) of coccoid and filamentous stromatolite building microbes (Barghoorn and Tyler, 1965), while in siliceous muds accumulating farther from shore, a very different community (Fig. 2b) dominated by apparent iron and manganese oxidizing bacteria thrived (Barghoorn *et al.*, 1977; Awramik and Barghoorn, 1977). Unpublished observations suggest the presence of intermediate assemblages that contain elements of the two end member benthonic communities as well as several taxa peculiar to these intermediate areas. The association of iron oxides with the stromatolitic microbes and iron carbonates with the off-shore assemblage suggests that Eh (i.e. redox potential) was a major factor in community distribution. A planktonic assemblage (Fig. 2c) that presumably proliferated in oxygenated waters above the O_2-poor off-shore muds adds to this emerging picture of a complex distribution of microbes in the Gunflint basin. Similar distributions of microfossil assemblages can be found in the approximately coeval Sokoman (Knoll and Simonson, 1981) and Duck Creek formations (Knoll *et al.*, 1986).

On a much smaller scale, Knoll and Golubic (1979) recognized three distinct community associations within a single four centimeter thick specimen of silicified flat laminated stromatolite from the Bitter Springs Formation. Throughout most of the time represented by this thickness of mat, cyanobacteria indistinguishable from members of the modern genus *Ento-*

physalis were the dominant mat-builders. Within the entophysalidacean framework, small blue-greens similar to modern *Gloeothece* thrived. A second assemblage consisting of *Chroococcus*-like cyanobacteria lived (or was stranded) in evanescent pools left on the mats when the tide retreated. Twice within the time span during which this stromatolite accreted, minor shifts in ambient environmental conditions allowed filamentous *Eomycetopsis* mats to become established. Such shifts were short-lived, however, as the entophysalidacean community soon recolonized the area.

Comparison of these Bitter Springs assemblages with modern mat-building communities suggests that this drama was played out in an intertidal environment marginal to a warm, shallow, perhaps somewhat hypersaline lagoon. Similar entophysalidacean-dominated microfossil assemblages have been found in Precambrian sediments of Canada (Hofmann, 1976; Golubic and Hofmann, 1976), Australia, Greenland (Strother *et al.*, 1983), and China (Zhang, 1981) where they are found in association with mudcracks, halite and gypsum casts, and flat-pebble breccias, all sedimentary structures that indicate an intertidal environment in a warm, arid area.

Acritarchs preserved in siltstones and shales from the late Precambrian Mineral Fork Formation of Utah (U.S.A.) provide a final illustration of the role of paleoecology in the interpretation of ancient fossils. Microfossils are extremely abundant in Mineral Fork sedimentary rocks, but they have a very low taxonomic diversity relative to acritarch microbiotas from other late Precambrian detrital deposits. In fact, a very small number of taxa completely dominate the assemblage. The combination of numerical abundance and low diversity suggests that the assemblage lived under stressed ecological conditions, and indeed geological evidence indicates that the fossiliferous Mineral Fork sediments accumulated in shallow embayments marginal to a melting glacier. Geological and ecological determinations thus fit together in a very satisfying way. Under the conditions of variable salinity, cold temperatures, and high rates of nutrient influx associated with early stages of glacial retreat, a few opportunistic species were able to expand rapidly to dominate this distinctive late Precambrian environment (Knoll *et al.*, 1981).

These few examples do not exhaust the paleobiological possibilities of taphonomic and paleoecological reasoning, but they do demonstrate some of the uses of these disciplines in the interpretation of the Precambrian fossil record.

A CHRONOLOGICAL SYNOPSIS OF THE EARLY FOSSIL RECORD

The time-line shown in Figure 4 reduces earth history to a bar several centimeters in length. On this scale such seemingly ancient events as the rise of the Maya or the flourishing of culture at Teotihuacan plot virtually at the right hand edge of the line. Indeed, the entire span of human history and prehistory from *Australopithecus afarensis* to the present computer era occupies a space of less than 100 μm (about the thickness of this page) on the graph.

Landscapes exhibited trees and land dwelling animals long before the evolution of hominids, but in terms of the total expanse of geological history, the colonization of the continents by vascular plants and tetrapod vertebrates is also a comparatively recent development. The first simple vascular plants escaped from the aqueous environment of their algal ancestors some 400 M.y. ago, and amphibians emerged from streams and lakes soon afterward [approximately 350 M.y. before present

(B.p.)]. Even the remains of well skeletonized marine invertebrates extend the record of life backward only to 570 M.y. B.p. The initial evolution of mineralized skeletal elements in such diverse phyla as the Archaeocyathida, Mollusca, Brachiopoda, and Arthropoda (trilobites) marks the beginning of the Cambrian Period; thus, the vast ocean of time stretching before this event, comprising approximately 87 % of our planet's history is referred to as the *pre*-Cambrian, or more properly Precambrian, Era.

Based on profound differences in geological style, the Precambrian can be divided into two eons, the Archean and the Proterozoic. Rocks of the Archean Eon constitute the earliest direct record of geological activity on earth. They suggest that the earth's interior was hotter than it is today and that, consequently, tectonic processes affecting the crust operated at faster rates than at present. Areas of continental crust existed as early as 3700 M.y. B.p., but there is little evidence to suggest the presence of large continents. The period between 2900 and 2500 M.y. B.p. was one of rapid continental accretion, with as much as 50 % of the present volume of continental crust being formed during this interval (O'Nions and Pankhurst, 1978). The stabilization of this crust to form extensive cratons and the concomitant modification of predominant sedimentary and tectonic patterns marks the transition from the Archean to the Proterozoic Eon (Windley, 1984; Knoll, 1984b). Lower Proterozoic strata record the first widespread occurrence of deposition on stable platforms inundated by shallow epicontinental seas and the initial evolution of long mio- and eugeosynclinal belts marginal to the continents.

Not surprisingly, the biological evidence contained in Precambrian rocks differs in both quantity and quality from the Archean to the Proterozoic. The latter record is relatively clear and easy to interpret, but the former is often enigmatic and presents, to borrow Darwin's classic description of angiosperm origins, an «abominable mystery». The geological transition constituting the Archean-Proterozoic boundary may have influenced the subsequent course of microbial evolution; it *certainly* influences *our perception* of the fossil record.

1. The Archean (3800 M.y.-2500 M.y.)

The earliest history of the earth must have been tumultuous, marked by internal melting, volcanic degassing, and meteoritic bombardment. Unfortunately, no vestiges of this epoch are preserved on the earth's surface; the oldest terrestrial rocks known at present comprise a sequence of metamorphosed sedimentary and volcanic strata from the Isua region of southwestern Greenland. Although somewhat altered by the metamorphic effects of heat and pressure, the original nature of the Isua supracrustals can still be determined: basaltic lavas and tuffs were interbedded with argillaceous sedimentary rocks. Conglomerates, carbonates, and sedimentary iron formation were also deposited (Allaart, 1976). Radiometric dates indicate that this sequence accumulated approximately 3800 M.y. B.p. (Moorbath, 1977; Michard-Vitrac *et al.*, 1977).

Reduced carbon contained in the Isua metasediments is largely graphitic, and no fossils have been discovered to date, but because metamorphism changes organic matter to graphite and destroys delicate microfossils, this absence of biological remains does not necessarily mean that the Isua rocks are remnants of a prebiological earth. Ratios of stable carbon isotopes can be used to indicate the operation of a photosynthetically modulated carbon cycle, but the ^{13}C-^{12}C ratio is also affected by

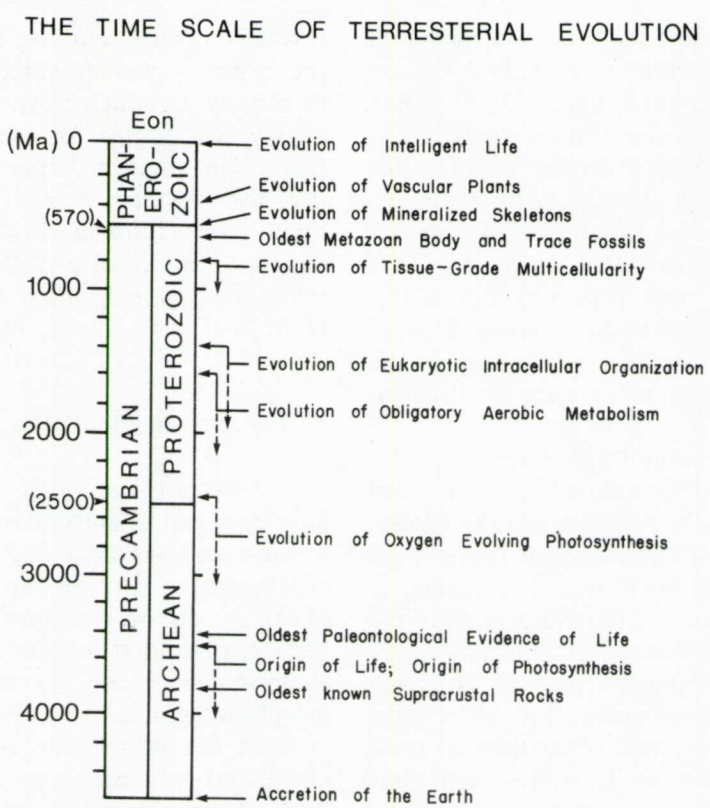

Fig. 4. Chart showing the chronology of biological evolution on Earth. For events whose timing is not known with certainty, the horizontal arrow points to the earliest time of origin consistent with the geological record while the vertical arrow indicates that an earlier origin is probable. (Redrawn from Knoll, 1986).

high-grade metamorphism, making unequivocal interpretation of Isua isotopes impossible. Manfred Schidlowski (1978; Schidlowski *et al.*, 1979) has suggested that carbon isotope ratios from the Isua metasediments are consistent with the hypothesis that photoautotrophs were in existence 3800 M.y. ago. If true, this means that the evolutionary steps leading to photosynthetic life – the synthesis of biologically important molecules from simple inorganic precursors, the assembly of these compounds into functioning cells, the differentiation of distinct archaebacterial and eubacterial lines of descent, and the evolution of photosynthesis – all must have occurred extremely early in our planet's history.

Slightly younger Archean rocks contain a somewhat better record of early biological activity, although it is still far from satisfactory. Simple organically preserved unicells, some fossilized in various stages of division, and simple filaments are known from 3400-3500 M.y. old cherts from both the Swaziland Supergroup in South Africa (Muir and Grant, 1976; Knoll and Barghoorn, 1977; Walsh and Lowe, 1985; Figure 5) and the Pilbara Supergroup of northwestern Australia (Awramik et al., 1983). Unfortunately, there is no way of determining the physiological capabilities of these microfossils. In both environmental setting and morphology, they resemble younger Precambrian cyanobacterial fossils such (in the case of the

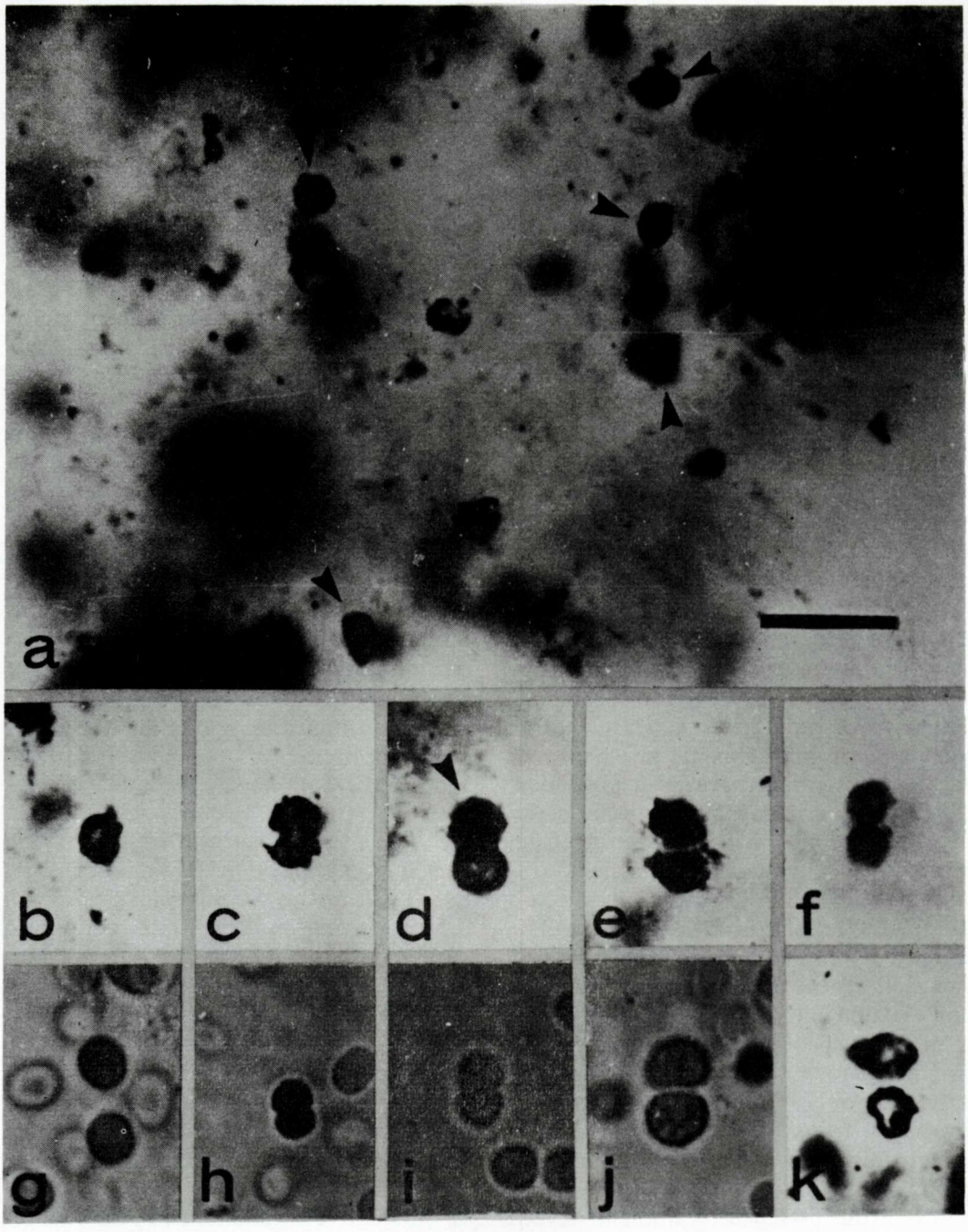

Fig. 5. Simple microfossils from 3400 M.y. old sedimentary rocks of the Barberton Mountain Land, South Africa. (a) Distribution of microfossils in laminated cherts; (b-e) Stages in binary cell division preserved in the fossil population; (f and k) Fossil dyads; (g-j) *Aphanocapsa* sp., illustrating binary cell division in modern prokaryotes. Bar = 10 μm for all photos. (With permission of the American Association for the Advancement of Science.)

unicells) as *Sphaerophycus parvum* Schopf (1968) and modern coccoid cyanobacteria such as *Aphanocapsa*; however, their simple morphology is equally comparable to those of diverse other bacteria, both photosynthetic and heterotrophic. Carbon isotope ratios from reduced carbon and carbonates in the same formations strongly suggest a photosynthetic origin for the abundant organic matter preserved in these sedimentary sequences (Eichmann and Schidlowski, 1975), although again the relative contribution of cyanobacterial and bacterial photosynthesis is not clear.

Stromatolites are also known from both sequences (Walter et al., 1980; Lowe, 1980; Byerly et al., 1986), but such structures are not common in Archean strata. It is sometimes assumed that this dearth of microbial mats is indicative of basic biological differences between Archean and Early Proterozoic microbiotas; however, more likely, it results from the fact that most well preserved Archean shallow marine sequences are dominated by sediments indicative of rapid rates of clastic influx and, thus, of environments in which mat development would have been precluded. Quiet water carbonate and mud flat deposits are sometimes encountered in Archean columns, and in these units ancient stromatolites are found (e.g.; Mason and von Brunn, 1977; Martin et al., 1980). The scarcity of stromatolites in Archean rocks, then, reflects the relative paucity of appropriate sedimentary rocks.

Indirect geochemical evidence from sedimentary rocks also contributes to the puzzle of Archean biology. Nonmarine sedimentary rocks of Archean and earliest Proterozoic age sometimes contain detrital grains of uraninite, UO_2. Uraninite is unstable in the presence of ambient oxygen concentrations as low as 1 % of present atmospheric levels (Grandstaff, 1973); in the presence of oxygen it is quickly oxidized to other uranium minerals. The presence of detrital uraninite grains in ancient alluvial sediments suggests that the mineral particles were exposed at the earth's surface, eroded from their igneous source rock, and transported some unknown distance to a site of deposition without ever coming into contact with appreciable amounts of oxygen. In contrast, continental sedimentary rocks approximately 2300 M.y. old and younger do not contain detrital uraninite, but instead are characterized by red beds – sandstones and siltstones in which flecks of oxidized iron, especially hematite, occur among the clastic grains. Pre-Proterozoic red beds are rare.

From the time relationships of uraninite-bearing alluvium and red beds, one can infer that the Early Proterozoic sedimentary record documents the initial rise of oxygen concentrations in the earth's atmosphere (Cloud, 1968, 1972, 1976; Frarey and Roscoe, 1973). Since the source of the atmospheric oxygen was cyanobacterial photosynthesis, some workers have suggested that the Early Proterozoic atmospheric transition marks the evolutionary appearance of cyanobacteria (e.g., Schopf, 1978a); however, others believe that this important group was present in the Archean, and that high rates of oxygen consumption related to the oxidation of reduced volcanic gases, mineral species, and organic matter matched rates of photosynthetic oxygen production, thus precluding the accumulation of excess O_2 in the atmosphere (Margulis *et al.*, 1976; Walker, 1978; Schidlowski, 1978; Knoll, 1979). The change in the tectonic framework of the crust recognized in the Archean-Proterozoic boundary in all likelihood resulted in (1) vastly increased areas of shallow water marine environments in which highly productive stromatolitic communities could proliferate, (2) decreased rates of volcanism (hence, O_2 consumption by reduced volcanic gases), and (3) increases in the supply of PO_4^{-3} produced by the

weathering of continental crust. In effect, the shift to an earth in which oxygen production exceeded consumption may have been tectonically controlled (Knoll, 1979, 1984b). Certainly, the coincidence in time of the first appearance of widespread Proterozoic-type marine sediments, the first widespread appearance of stromatolites, and the first evidence for the transition to an oxygen-rich environment supports this viewpoint.

In summary, evidence bearing on the Archean evolution of life is scarce and difficult to interpret. The clues we do have permit several contrasting hypotheses about the nature of early ecosystems. I personally believe that the Archean earth supported a metabolically diverse biota of prokaryotes, including (during its latter part, at least; see Hayes, 1983) physiologically modern cyanobacteria; however, as is true of most general statements concerning Precambrian life, this view is in part speculative and could be subject to revision as more and better evidence, as yet undiscovered, comes to light.

2. The Proterozoic (2500-570 M.y. B.p.)

The Proterozoic biological record presents some fascinating problems, but relative to that of the Archean, it is quite amenable to interpretation. Perhaps the nature of Early Proterozoic life can best be understood by comparing two well known microbiotas, each approximately 2000 M.y. in age. Silicified stromatolites in intertidal to shallow subtidal carbonates from the Belcher Islands, Hudson Bay, Canada, contain a diverse assemblage of cyanobacteria comparable to the modern families Oscillatoriaceae, Chroococcaceae, and Entophysalidaceae (Hofmann, 1976). Indeed, many of the microfossils are morphologically indistinguishable from members of extant genera and species (Hofmann, 1976; Golubic and Hofmann, 1976). Of particular interest is the *Eoentophysalis* dominated community that built mamillate mats in the intertidal zone (Fig. 3b). Similar occurrences of mat-building entophysalidacean cyanobacteria in intertidal environments are known from the 1600 M.y. old Balbirini Dolomite, Australia (D. Oehler, 1978); the 1400 M.y. old Gaoyuzhuang Formation of China (Zhang, 1978); the 850 M.y. old Bitter Springs Formation of central Australia (Knoll and Golubic, 1979) and the latest Proterozoic Narssärssuk Formation, northwestern Greenland (Strother et al., 1983); as well as on the present day earth in Baja California (Horodyski and Vander Haar, 1975), Shark Bay, Australia (Golubic, 1976), and the Persian Gulf (Golubic, 1976). What the data suggest is that the same types of organisms have been dominant in arid intertidal zones marginal to warm, hypersaline lagoons for 2000 M.y. Early Proterozoic cyanobacteria were essentially modern in this aspect; and the great diversity of stromatolites of this age indicates that these microbes were also both abundant and morphologically diverse (Donaldson, 1976; Semikhatov, 1978).

The microbiota of the Gunflint Iron Formation (Barghoorn and Tyler, 1965) is approximately the same age as the Belcher assemblage, but biologically it is quite dissimilar. This is not surprising, because unlike the carbonate intertidal zone cyanobacteria of the Belcher Islands, the Gunflint microorganisms inhabited a subtidal environment rich in iron. As discussed earlier in this chapter, several distinct communities can be recognized in the Gunflint: (1) a shallow water, marginal stromatolitic community (Fig. 2a) dominated by the small coccoid microbe *Huroniospora* and the thin filament *Gunflintia* (Barghoorn and Tyler, 1965; Awramik, 1977); (2) a non-stromatolite association (Fig. 2b)

consisting mainly of trichospheric bacteria morphologically and perhaps physiologically identical to some extant manganese and iron oxidizing bacteria (Cloud, 1965; Hirsch, 1974), that inhabited muds in more distal environments; and (3) a planktonic assemblage (Fig. 2c) of large unicells, presumably cyanobacterial, that represents a community present within the water column of the Gunflint sea (Knoll *et al.*, 1978). Intermediate assemblages that contain elements of both benthic associations exist and may indicate a transitional boundary between the two distinct communities.

The taxonomic affinities of the Gunflint microbiota are of interest. Several taxa are best interpreted as Fe and/or Mn oxidizing bacteria, a reasonable conclusion in light of the environmental setting of the fossils. Other morphotypes appear to be cyanobacterial, and still others, for example *Eosphaera tyleri* (Figure 2; Barghoorn and Tyler, 1965) are entirely problematic – their systematic relationships are simply not understood in even a general sense. The stromatolite building taxon, *Gunflintia minuta* Barghoorn, discussed in a previous section of this chapter, illustrates well the problems involved in the systematic interpretation of Gunflint microorganisms.

Whatever the taxonomic relationships of the Gunflint microfossils, they demonstrate two important facts: (1) Early Proterozoic iron formation environments supported a microbial biota different from microfloras inhabiting less Fe rich habitats; and (2) this iron formation biota was diverse and divided ecologically into a complex series of microbial communities. Taken together, the Belcher Islands and Gunflint microbiotas paint a picture of an Early Proterozoic earth inhabited by a morphologically and physiologically diverse biota dominated by, but perhaps not restricted to, essentially modern types of prokaryotic organisms.

The premier biological event of the mid-Proterozoic era (approximately 1800-1000 M.y. B.p.) was the evolution of the eukaryotic level of cellular organization (Schopf, 1974; Knoll, 1983). The geologic record tells us little about how nucleated organisms evolved. The ultrastructural details necessary to document this evolution are not preserved in the fossil record, so information on eukaryote origins must come from observations of modern microorganisms, a topic extensively treated by Margulis (1981). On the other hand, *only* the geological record can indicate when eukaryotes first appeared. Primitive eukaryotes were morphologically very simple, and one might expect that following partial degradation by decomposing bacteria their spheroidal remains would be difficult to distinguish from those of externally similar cyanobacteria. Further, one might well imagine that the many steps involved in the origin of nucleated cells took place over a long period of time, and that, consequently, some problematic Precambrian fossils might represent transitional stages in the evolution of fully eukaryotic organization. In light of these difficulties it is not surprising that some of the evidence bearing on the initial appearance of eukaryotes can be interpreted in several ways. Nonetheless, the suggestion of J.W. Schopf (1974, 1978) that nucleated cells evolved approximately 1400 M.y. ago provides a reasonably broad estimate of the timing of this evolutionary transition. Perhaps the best evidence in support of this date comes from planktonic microfossils preserved in Precambrian clastic rocks. Pre-1400 M.y. siltstones and shales rarely contain these microfossils, but in sequences deposited after this date, planktonic microfossils are common (see, for example, Peat *et al.*, 1978). The simplest explanation for this apparent discontinuity in the fossil record is that approximately 1400 M.y. ago, a new type of cell capable of producing a de-

gradationally resistant wall emerged. From their large sizes (> 100 μm diameter), surface sculptural patterns and occasional encystment structures, it is reasonable to hypothesize that at least some of these microfossils are the remains of ancient eukaryotic algae (Fig. 3i). Megascopic ribbons of organic matter are also found in some 1400-1000 M.y. old clastic deposits (Walter *et al.*, 1976; Hofmann and Aitken, 1979). Of particular interest are ribbons 2-6 mm wide and up to 77 mm long, shaped like limp popsicle sticks found by Hans Hofmann and J.D. Aitken in rhythmitic limestone-siltstone beds from the 1100-800 M.y. old Little Dal Group of northwestern Canada (Figure 3g). These fossils are almost certainly the remains of eukaryotic organisms, possibly a seaweed with relatively undifferentiated cells such as modern *Enteromorpha* or *Ulva* («sea lettuce»).

Thus, the proliferation of eukaryotic microorganisms occurred more than 1000 M.y. ago. Late Precambrian clastic sequences document an increasing diversity of acritarch (presumably algal) forms (Vidal, 1981; Jankauskas, 1982; Vidal and Knoll, 1983), as well as the appearance of apparently non-algal protists (Bloeser *et al.*, 1976; Knoll and Vidal, 1980); however, in spite of the growing importance of eukaryotic organisms in mid and late Proterozoic ecosystems, cyanobacterial stromatolitic communities continued to dominate shallow marine carbonate environments until early Paleozoic times. Beautifully preserved microorganisms (Figs. 2k and 3a, c-f, h) are preserved in late Precambrian silicified stromatolites from numerous localities such as the Bitter Springs Formation of Australia (Schopf, 1968; Schopf and Blacic, 1971) and the Artic Conglomerate Formation, Spitsbergen (Knoll, 1982).

Throughout the Proterozoic, diverse types of stromatolites accreted in shallow marine environments; however, at the end of the eon, stromatolite diversity decreased dramatically (Awramik, 1971) as a consequence of the final great biological innovation of the Precambrian era, the evolution of multicellular animals or Metazoa. In environments where mat-building cyanobacteria had proliferated for untold millennia, the newly evolved metazoans precluded continued stromatolite formation by grazing on mat-building microbes, burrowing into matted substrates, and laminated surfaces where mats once flourished (Garrett, 1970; Awramik, 1971). Again the geological record can answer questions of *when* multicellular animals arose, but not *how*. The oldest known metazoans are soft bodied jellyfish, sea pens, worms, and arthropods preserved as impressions in tidal flat siltstones and sandstones deposited approximately 700-600 M.y. ago (Stanley, 1975). The trace fossil record of burrows and trails dates from about the same period, although putative burrows have been recorded from somewhat older rocks. Often referred to as the Ediacara fauna, after the Ediacara Hills of southern Australia where their remains were first discovered (Glaessner & Wade, 1966), these simple fossils document the earliest radiation of multicellular animals, prior to the evolution of mineralized skeletal elements. The impressive diversity of metazoan phyla present at the base of the Cambrian Period (defined by the first appearance of abundant skeletonized remains in the geological record) suggests that considerable diversification of invertebrate structural patterns took place in latest Precambrian times. It has variously been suggested that the evolution of sexual reproduction (Schopf *et al.*, 1971), the acquisition of the biochemical machinery necessary for the differentiation of function among genetically identical daughter cells (Schopf, 1974; Knoll, 1978), or the ecological effects of cropping (Stanley, 1973, 1977) made this radiation

possible. In all likelihood, all three factors, plus others not yet articulated, contributed to the late Precambrian rise of the Metazoa.

In a strikingly beautiful passage from *The Origin of Species*, Darwin (1859) used a botanical simile to describe the evolution of life and its geological record:

> *As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation. I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever-branching and beautiful ramifications.*

The geological record of early evolution is not unbiased. It can sometimes be interpreted in very different ways by different workers. Yet, it is a rich record, and it provides us with a glimpse of the patterns of growth and diversification that characterized the earliest shoots of Darwin's Tree.

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This paper was originally prepared for the Third Mexican Conference on the Origins of Life in January, 1979. In the six years that the manuscript has lain in a drawer since then, much has happened in the field of Precambrian paleontology, yet many of the arguments made then seem (to me) to retain their currency. Therefore, in revising the manuscript I have tried to bring the facts and reference list up to date without destroying the potential «archaeological» interest in how I and others thought about the Precambrian before I began to work on the exquisite Late Precambrian sections of the Arctic, before G. Vidal and T. Jankauskas had published many of their monographs on Proterozoic plankton, before the Precambrian Paleontological Research Group had been organized, before materials from China had become widely known, and before many other projects by many individuals had borne fruit. I am delighted that this paper is being published in a volume honoring Professor Juan Oró. Like many other scientists I have benefitted greatly from his friendship and collegiality.

Lastly, the acknowledgements made in my original manuscript remain appropriate:

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