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Beginnings of biospheric evolution and their biogeochemical consequences

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Abstract.—The beginnings of biospheric evolution had far-reaching biogeochemical consequences for the related evolutions of atmosphere, hydrosphere, and lithosphere. Feedback to the sedimentary record from these several simultaneously interacting aspects of crustal evolution provides the evidence from which historical biogeology is reconstructed. The interpretation of that evidence, however, is beset with pitfalls. Both biogenicity and a primary origin need to be demonstrated, or confidence limits established for each supposed morphological and biochemical fossil. Relevance to biospheric or related evolutions must be critically evaluated for every geochemical and sedimentological anomaly.

Indirect evidence suggests primitive, oxygen-generating autotrophy by $\sim 3.8 \times 10^9$ years ago (3.8 Gyr or gigayears), while free O_2 first began to accumulate only ~ 2 Gyr ago. Various reduced substances in the atmosphere and in solution functioned as oxygen sinks, keeping photolytic and biogenic O_2 at levels tolerable by primitive anaerobic and microaerophilic procaryotes.

The oldest demonstrably biogenic and certainly primary microstructures are procaryotes from $\sim$ or $>$ 2 Gyr old strata around Lake Superior. Improved biologic O_2 mediation, continued carbon segregation, and filling of O_2 sinks initiated atmospheric O_2 buildup, leading to an ozone screen $\sim$ or $<$ 2 Gyr ago. Consequences were essential termination of banded iron formation, onset of red beds, and O_2 shielding of anaerobic intracellular processes, heralding the eucaryotic cell.

Probable eucaryotes appear in $\sim$ 1.3 Gyr old rocks in California as large unicells and large-diameter, branched, septate filaments. Likely consequences of eucaryotic evolution were increased atmospheric O_2, increased carbonate and sulfate ion, and the rise of sexuality. Meiosis had definitely evolved $>$ 0.7 Gyr ago and probably $>$ 1.3 Gyr ago, perhaps simultaneously with the mitosing cell. Whatever the timing, it completed the evolution of the eucaryotic heredity mechanism and foreshadowed (given sufficient free O_2) the differentiation of tissues, organs, and advanced forms of life—with all their potential for biogeochemical feedback to sedimentary, diagenetic, and metallogenic processes. The first Metazoa appeared $\sim$ 0.7 Gyr ago. Being dependent on simple diffusion for O_2, they lacked exoskeletons. The latter appeared, perhaps 0.6 Gyr ago, when increasing O_2 levels favored the emergence of more advanced respiratory systems.

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Introduction

Some 85% of Earth history had elapsed before the appearance of the Metazoa and even more before the first vascular plants. Yet conventional historical geology deals mainly with the record of multicellular evolution and that of the physical world in which Metazoa and vascular plants prevailed. In contrast to the now rather detailed knowledge of this Phanerozoic history, what we think we know of earlier Earth history is by no means universally agreed upon among students of the problem and is widely misunderstood among those who are not involved in the study. Even some recently published papers share the illusion that the possibility of a record of life anterior to Phanerozoic times was largely rejected by our predecessors, whose works go unread. On the contrary, the existence of an extensive record of lowly forms of plant life, inferred from the primarily biogenic sedimentary structures called stromatolites, has been recognized for at least 60 years. And geologists since the

time of Darwin have hypothesized a long interval of sub-Cambrian diversification from unknown but inferred metazoan ancestors.

Indeed the search for that presumed metazoan record, although partly successful (e.g. Ediacarian fauna of Glaessner and Daily 1959; Glaessner 1966), to an important extent diverted investigation from the truly significant records of early biospheric evolution, which we now realize are microscopical and primarily microfloral. Although the weight of conventional judgment was too great for its general acceptance when first proposed (Cloud 1948), and even as late as 1965, it is now widely conceded that the relatively abrupt appearance of a metazoan record late in geologic time is a reality and not simply an artifact of poor preservation, metamorphism, nondeposition, or erosion, (e.g. Glaessner 1972; Schopf 1974, 1975; Stanley 1976). It is also now widely conceded that the time of the initial metazoan appearance was ~ 680 to 700 $\times 10^6$ years ago, and that the diversification observed in early Phanerozoic faunas, while real and relatively abrupt, was also much more gradual in reality than it is in some textbooks. By etymology, if not by definition, the appearance of Metazoa dates the beginning of Phanerozoic history, including the sub-Cambrian rocks that contain the mainly soft-bodied Ediacarian fauna, now known to occur on 4 or 5 different continents. Older rocks and older history thus are pre-Phanerozoic, and it is to the biological and biogeochemical aspects of that pre-Phanerozoic history that this paper is devoted.

Modern investigation of pre-Phanerozoic paleomicrobiology began with the discovery of the now-classic Gunflint microbiota by economic geologist Stanley Tyler in 1953 (Tyler and Barghoorn 1954). It gathered momentum and became wedded to biogeochemistry and biosynthesis following the Woodring Conference on major biologic innovations and the geologic record, convened by Cloud and Abelson in 1961, since which time some 95% of all the relevant papers have been published.

In effect a new interdisciplinary subject emerged from the Woodring Conference, as people from diverse fields of paleontology, biology, geology, and chemistry sought to communicate with one another. That is the field which I call biogeology, as an inclusive designation for the entire body of subject matter that bears on our understanding of life processes in crustal evolution—biological, paleontological, sedimentological, and chemical, including biochemical, geochemical, and cosmochemical. Thus the present inquiry is a biogeological one, and it starts with a biogeological reflection.

The present biosphere comprises less than three billionths of the total mass of the earth, while biosphere, atmosphere, hydrosphere, and lithosphere together represent less than half of one percent of the same mass (Gilbert 1964). Yet the record from which we attempt to reconstruct Earth's past history is almost restricted to this tiny fraction of our planet and to the surface of the moon. Insignificant though the mass of the biosphere may be at any given time, however, its affect on surface processes and thus on the sedimentary record of Earth history is enormous. Some, if not all, major steps in biospheric evolution are inevitably, if subtly, reflected in the development of Earth's growing sedimentary pile, and perhaps, more subtly still, in the kinds of igneous rocks that ascend from molten sources within the crust.

What can we say about events in biological and biogeochemical evolution that took place between the final aggregation of our planet ~ 4.65 Gyr[2] ago and the appearance of relatively advanced forms of life ~ 700 Myr ago? [Gyr, for gigayear, and Myr, for megayear, are the preferred international symbolism for years $\times 10^9$ and years $\times 10^6$ respectively, in keeping with current usage for corresponding physical measurements. Equivalent designations are BY, b.y., Ga, and aeon for 10^9 years and MY, m.y., and Ma for 10^6 years.] And what is a biogeochemical *consequence* of biospheric evolution?

Most students of the primitive earth would probably agree that a major biogeochemical consequence of biospheric evolution is the oxidation of solid and dissolved substances and gases at or near Earth's surface by O_2 of photosynthetic origin, even though such oxidation could not occur without the simultaneous or prior segregation of equivalent carbon. Granted this, how can we tell what part of the total oxidation of surficial and atmospheric materials over geologic time is biogeochemical and what part due to O_2 resulting from purely photolytic dissociation of H_2O with gravita-

TABLE 1. Main events enroute to higher organisms.

Event or precondition	Likely stimuli	Probable consequences	Time of event (yrs × 10^9 BP)
12. Tissues, organs	Sexuality, competition, increased O_2	Metazoa, higher plants, changed $CaCO_3$ patterns, land biota, intensified weathering, subsequent evolution	~ 0.7
11. Eucaryotic sexuality (meiosis)	Eucaryotic cell, increased free O_2	Complete eucaryotic hereditary mechanism	> 0.7 probably > 1.3 possibly > 1.5
10. Eucaryotes (mitosis)	> 1% PAL free O_2, shielding of intracellular anaerobic functions	More O_2, CO_3^{--} and SO_4^{--}, less CO_2. Higher algae	< 2 > 1.3 possibly > 1.5
9. Fully oxidative metabolism (superoxide dismutase)	1% PAL free O_2, enzymic neutralization of H_2O_2 and O_2^-	Increased O_2, ozone shield, red beds, eucaryotes	~ 2
8. Cyanophytes (or protocyanophytes)	Heme proteins, Mg porphyrin, biophotolysis of H_2O	Microaerophilism, BIF, CO_3^{--} increase, finally O_2 increase and fully oxidative metabolism	~ 3.8
7. Primitive autotrophs	Competition for components and energy	Cyanophytes, subsequent evolution	> 3.8
6. Life (anaerobic heterotrophs)	Energy transfer, genetic code	Procaryotic diversity, biogeochemistry	
5. ATP, RNA, DNA	Chemical evolution, autocatalysis	Transient negentropy, reproducibility	
4. Sugar-phosphate bonds, nucleotide bases		ATP, DNA, RNA	
3. Amino acids, polypeptides			
2. Simple organic molecules (HCN, HCHO, etc.)	UV irradiation of O_2 free atmosphere	Amino acids, polypeptides	
1. Atmosphere and hydrosphere	Outgassing of earth	Chemical evolution	

tional escape of H_2—or even to more arcane sources of O_2 such as (at low Eh) the physicochemical reaction $2S + 2H_2O \rightleftharpoons 2H_2S + O_2$. Most might agree also that biogeochemical consequences are observed in the formation of tropical laterites by silica-accumulator plants (Lovering 1959) or the leaching of other soils by plant acids, not to mention the concentration of Fe, Cu, Zn, Mn, Ni, Mo, and other metals by plants. Indeed all true soil formation, most rock weathering, and some metallic ore formation are at least in part biogeochemical manifestations of biological processes, while biospheric evolution itself is a kind of biogeochemical consequence of the hereditary mechanisms of antecedent biotas.

The subject of this discussion is thus both broad and complex. But if anything can be called *the* scientific method, it is the instinct that scientists have for dealing with broad and complex problems by breaking them down into researchable components. Eventually, if enough separate investigatations are made, the orderly cumulation of data and well-founded interpretation from different lines of evidence can be brought to bear simultaneously on the

main problem. Here, therefore, I attempt to bring together the main lines of information and testable hypotheses that have arisen from study to date of these researchable components up to the time of origin of the Metazoa and the land plants.

It turns out that much of what we can infer from the geologic past about the beginnings of biospheric evolution is based on the biogeochemical consequences rather than the reverse. From this arises a central biogeological question: What are the biogeochemical and other evolutionary preconditions for the origin of higher organisms, and what sorts of discoverable traces might they leave in the geologic record?

Twelve main preconditions or related groups of preconditions ("events" of Table 1), together with some of their likely stimuli, probable consequences, and currently estimated times of origin are listed in Table 1. Research has as yet revealed no records of the first 7 of these 12 preconditions, although indirect evidence suggests that they, and perhaps precondition 8, had all been achieved before the oldest known sedimentary rocks were deposited ~ 3.8 Gyr ago. The balance of this work deals, all too briefly, with what I perceive to be the best of the still dismayingly scanty evidence for the time of origin of these main steps and their hypothetical geochemical consequences. This is a progress report, outlining some views which are supported but not necessarily demanded by the evidence; trying to distinguish clearly between evidence, conclusions, and levels of confidence; suggesting some possibilities for future research; and warning of hazards along the way.

Some Cautionary Remarks on the Nature of the Evidence

The evidence of interest consists of demonstrable or highly probable remains of life found as primary components in rocks of known or reasonably estimated age, as well as the probable sedimentary consequences of life processes, both chemical and physical. Once life originated, interactions among biospheric, atmospheric, hydrospheric, and lithospheric evolutions would commence; and, with the appearance of photoautotrophs, the sedimentary record would be irreversibly changed. Reduced carbon, enriched in the light isotope ^{12}C, would become a conspicuous sedimentary component, and carbon and other biological products would enter into chemical reactions that leave traces in the sedimentary record.

I will go into both the direct and indirect kinds of evidence shortly. First, however, consider some pitfalls. Space does not permit a detailed consideration at this place of the hazards of radiometric numerology. Suffice it to say that basic though it is to the elucidation and time-calibration of pre-Phanerozoic history, and careful though its practitioners are in citing methods, materials, limits of laboratory error, and cautionary admonitions, the numbers tend to appear devoid of qualification in geological (including biogeological) publications. They are also sometimes derived by very indirect approximations, involving inferred correlations with and bracketing by dated rocks. In this paper also, in the interest of brevity, I will not specify method, limit, or refinements, where that has previously been done (in Cloud 1976, or references there cited), but the reader should understand that all numbers mentioned are approximate, some more than others.

In this cautionary prelude I am more concerned with the question: how can we be sure that a given microstructure, reported as a microorganism of great age, is both biogenic and contemporaneous with enclosing sediments (primary) when similar-appearing microstructures can be shown to have a nonbiogenic origin and when opportunities for contamination begin with the settling of sediments below the depositional interface and never end? Even under a clean-laboratory regime one does not eliminate, but merely reduces, the prospects of contamination. Caution and a knowledge of "in-house" contaminants is still in order.

It is, in fact, so difficult to *demonstrate* that a given assemblage of microstructures is, in reality, both biogenic and primary that few of the now numerous published reports of potentially informative microbiotas older than about 700 Myr can be considered well authenticated, and the most ancient of these cannot be much more than 2 Gyr old. A good tabulation is that of Schopf (1975). Adding the recently announced Nabberu Basin microbiota (Walter et al. 1976), the Biwabik phase of the Gunflint microbiota (Cloud and Licari 1968a),

probably some of the late pre-Phanerozoic occurences in the USSR (e.g. Timofeev 1969, 1973a–b) and some new and yet undescribed occurrences, we get a total of probably no more than 40 reliable data points. Rapidly though our data base for early biospheric evolution is growing, the array of compelling paleomicrobiotas is, as yet distressingly sparse. Visualize, for instance, that we wish to paint a grand panorama of life antecedent to the Metazoa where one km equals a million years of history. It is as if, on a strip of canvas stretching from Nairobi to the southern tip of India we had to reconstruct this panorama from perhaps 40 widely separated images along the younger half of the strip, with a few blurred outlines between and toward the older end.

As for a primary origin, that is difficult to demonstrate except from paragenetic relationships between microstructures of interest and mineral grains or demonstrably primary textures in the rocks, observable best in thin section or under the scanning electron microscope (SEM). A primary origin may, of course, be suggested by the distinctiveness of assemblages observed or by performing identical maceration procedures on control samples; but it is hazardous to rely too strongly on such criteria, as Cloud and Hagen (1965) have shown.

To *suggest* a biological origin for a given assemblage of non-living microstructures is permissible if they are demonstrably carbonaceous, reasonably abundant, show a narrow or approximately polymodal size distribution, and have a morphology that is consistent with the proposed origin (Cloud and Licari 1968b). A degree of confidence is justified only if, in addition, one observes a level of complexity not known to occur as a result of purely physical processes. And a given microstructure can be considered *demonstrably* biogenic only if some of its representatives display a level of cellular, microstructural, or biogeochemical differentiation comparable with that of living organisms and implying a similarity of function and continuity of evolution between them. Such considerations become doubly important where we seek to extend our knowledge of biospheric evolution in time or space. Here it becomes crucial, *in order not to dilute the credibility of well established evidence*, to differentiate between levels of confidence, both as to biogenicity and primary origin.

A comprehensive tabulation of the artifacts and contaminants that have been illustrated as pre-Phanerozoic microorganisms would be a disheartening exercise; yet a few examples are needed to illustrate the problem. Some common pseudomicrofossils are the strings of bubbles that appear in the formvar used for mounting microtome slices and replicating surfaces for transmission electron microscopy (TEM), as well as wrinkles and breaks in the same formvar. I have been misled by these myself (Cloud et al. 1965), as have Schidlowski (1970, Oberlies and Prashnowsky (1968), and a competent Phanerozoic paleontologist who not only pronounced my "Archean" microproblematica (and almost certainly artifactual "fossils") from the Soudan Iron Formation to be Foraminifera but, in addition, suggested (perhaps correctly!) an affinity with forms described by Pflug (1966) from the much younger Belt Supergroup of Montana.

Other deceptive non-biogenic look-alikes for real microorganisms are provided by various spherulitic or colloform structures in glassy or cherty rocks (e.g. Tyler and Barghoorn 1954, figs. 1–2). In addition, spheroidal, framboidal pyrite or antecedent marcasite of non-biologic origin may take on a very lifelike appearance, (Plate 1, figure 2), or, by growing in carbonaceous sediments, may aquire a carbonaceous exterior coating or even, and apparently commonly, may also infiltrate real microorganisms (e.g. Moorman 1974). Some of the roughly 3.4 Gyr old carbonaceous Onverwacht microstructures described by Brooks and Shaw (1973, pp. 280–291; also Plate 1, figures 1 & 3 of present paper) display a crude morphology resembling that of FeS_2 aggregates, while lacking microstructural detail or size range indicative of a biological origin. Maceration residues may clump on strewn slides, or carbonaceous matter in sediments to produce circular, spherical, or linear aggregates (cf. Pflug 1966; also present Plate 1, figures 4, 6–7). Or bubbles of mounting medium and perhaps natural fluids in porous rocks may take on the appearance of spheroidal unicells by becoming coated with and engulfing particulate matter in either thin sections or porous rock (Plate 1, figures 9–15) or strewn slides of maceration residues (Plate 1, figures 6–8?).

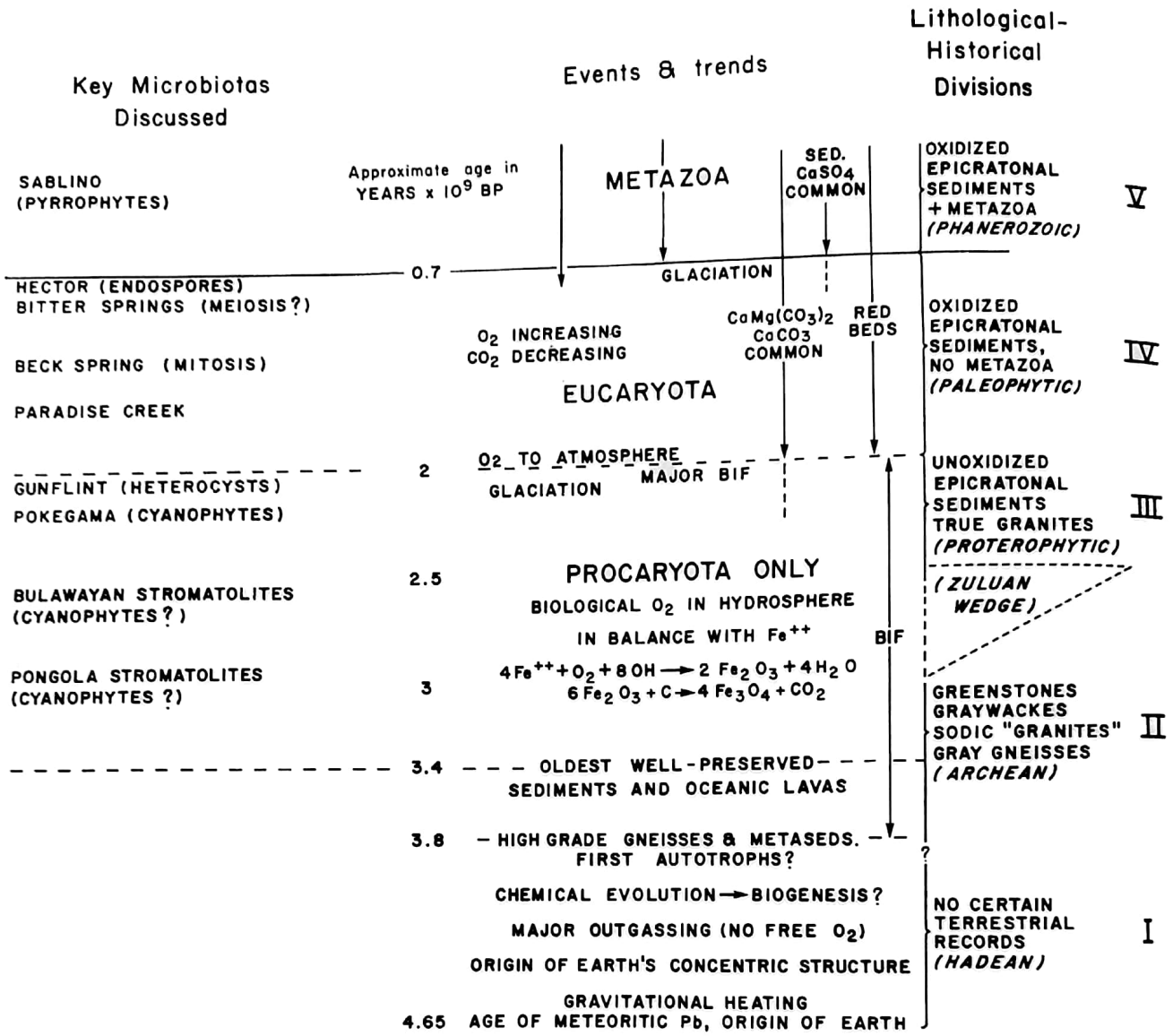


FIGURE 1. Major divisions of earth history and related aspects of biological and geochemical evolution (modified after Cloud 1965, 1972, 1974a, and amplified in Cloud 1976).

Many kinds of microlites in volcanic and other glasses (Plate 1, figure 19; Ross 1962) also resemble microorganisms, as do curving septate threads 4 μm in diameter and emerald crystals, symplectites, and some sorts of fractures and inclusions in glasses, first brought to my attention by my mineralogical colleague Edwin Roedder.

A variety of probable microcrystallites have been mistaken for fossils—for instance those described from a reportedly 2.7 Gyr old quartzite from Western Australia (Marshall et al. 1964) and interpreted both as likely microorganisms and as contemporaneous with sedimentation, even though they are restricted to a supposedly opaline matrix such as does not elsewhere on Earth have an age greater than ~60 Myr. Knoll and Barghoorn (1974) have described tracks of ambient pyrite grains in pre-Phanerozoic cherts that are so like nonseptate filamentous procaryotes that even careful workers might be fooled by them if the pyrite itself were not preserved at the ends of tracks the exact breadth of the pyrite crystal.

Then there are Fox's microspheres (e.g. Fox and Yuyama 1963). On Plate 1, figure 16 illustrates a breakage pattern of microspheres under stress that at some places resembles the trilete scars formed in spore tetrads and at others simple cell division, while figure 18 shows branching chains of microspheres that mimic filamentous algae. Where similar forms or simple isolated spheroids are found in very ancient rocks they *could* represent a

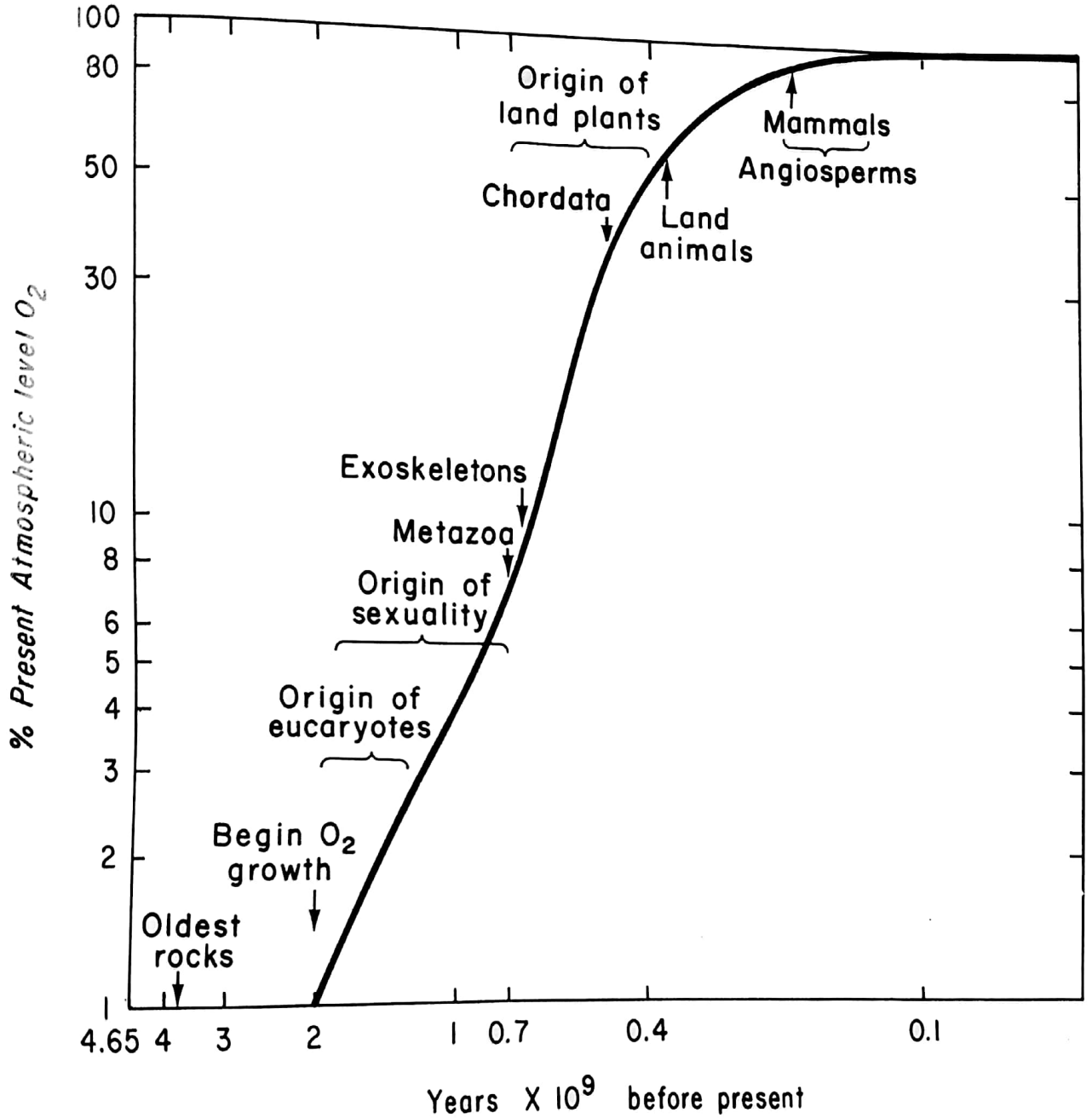
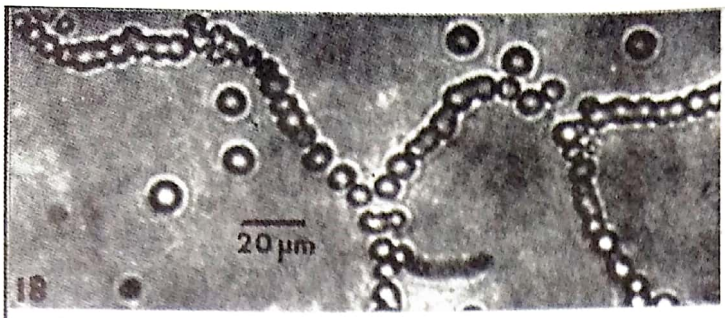


FIGURE 2. Apparent timing of events in biospheric evolution compared with hypothetical levels of atmospheric oxygen. (Both scales logarithmic; curve highly generalized, excursions from the mean likely.)

record of pre-biologic evolution rather than one of early life.

In other instances, structures of genuinely biological origin are not truly ancient but belong to younger fossil or living forms, while still others are laboratory artifacts. The spiny pear-shaped microspheroids illustrated by Oberlies and Prashnowsky (1968) as being from carbonate rocks of the Bulawayan Group, and earlier accepted by Schopf (1970) as authentic Archean fossils, strongly resemble the spores of certain modern hyphomycetean fungi (e.g. Kendrick and Carmichael *in* Ainsworth et al. 1973, Pls. 22–24). Other forms illustrated by Oberlies and Prashnowsky (1968) and by Prashnowsky and Oberlies (1972) from South Africa, Brazil, and Finland also resemble observed contaminants or artifacts of preparation. Filamentous structures similar in morphology and composition to those illustrated by Hallbauer and van Warmelo (1974) and by Hallbauer (1975) as microorganisms from carbonaceous Witwatersrand sediments have been replicated experimentally by David Pierce in my laboratory by heating mixtures of carbon with lead and zinc powder and filings, follow-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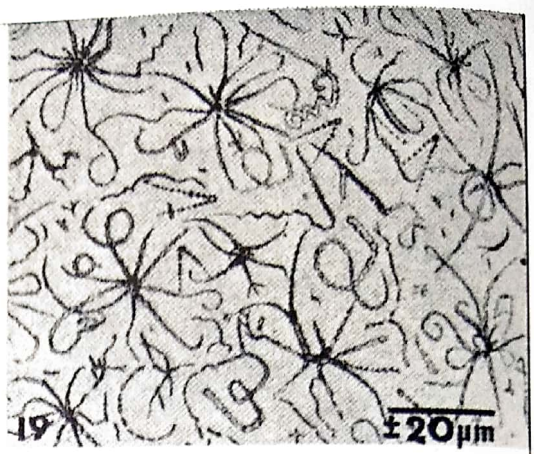
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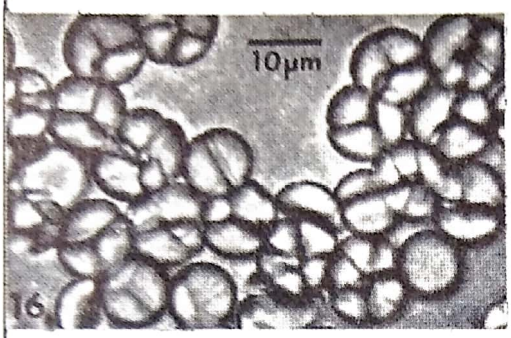
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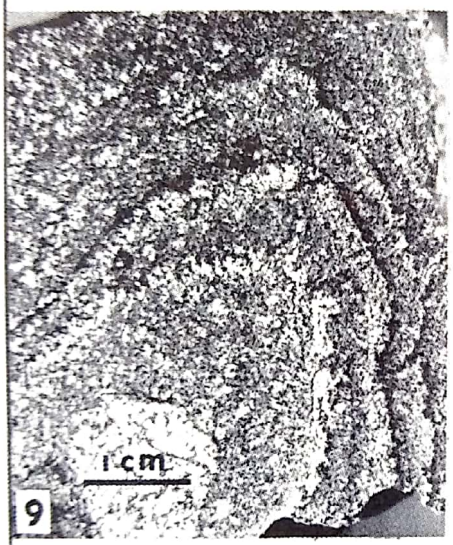
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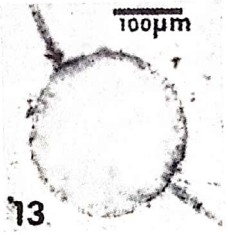
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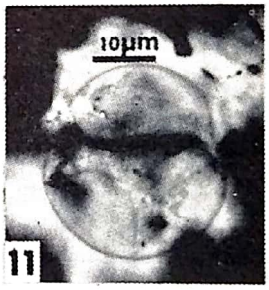
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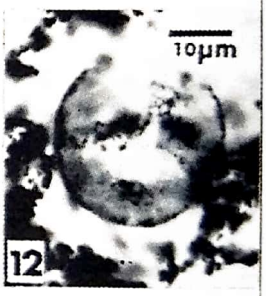
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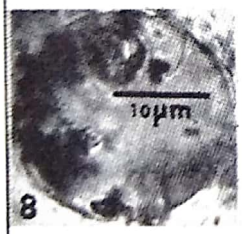
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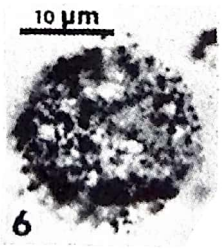
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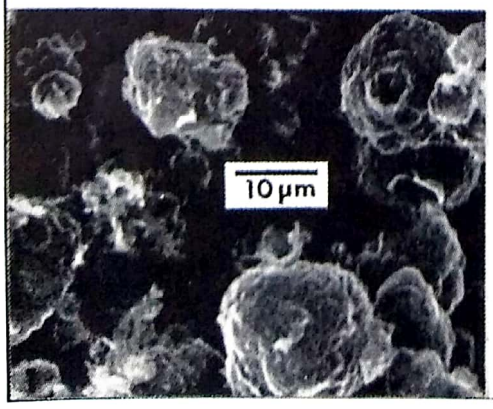
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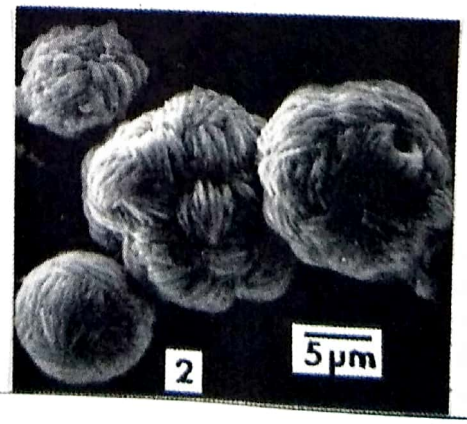
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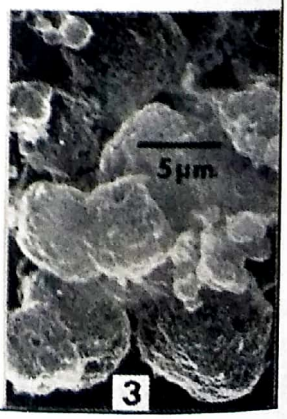
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ing the procedures employed by Hallbauer and van Warmelo. Studies by Karen Morrison in my laboratory have revealed a diverse, contaminant algal and fungal microbiota in minute cracks in fresh looking limestone from the late pre-Phanerozoic Bambui strata of Brazil—a fact that advises a cautious approach to other modern-looking microorganisms from limestone. As Keller (1959, pp. 33–34) and Krylov (1968, p. 47) have related, many of the supposedly pre-Phanerozoic spores described from the USSR up to the middle 1960's have been shown to be Paleozoic or younger contaminants that washed down along cracks in the older rocks from overlying microfossiliferous strata.

Finally, a variety of diagenetic and metamorphic structures have been interpreted as "microphytolites" of biogenic origin by Kolosov (1975, Pls. 14, 15, 25, 30), Vologdin and Drozdova (1964), and some other Soviet workers; not to mention a variety of other probable artifacts and contaminants noted by Schopf (1975, pp. 235–240), who has now joined Cloud (1974b) in his "reservations about either the demonstrable biogenicity or the provenience" of all Archean microbiotas so far reported.

Thus the problem is real, but it is far from hopeless. Although intrusion of contaminants from burial to laboratory may plague us, although pseudofossils and dubiofossils may lie in ambush, and although radiometric ages we

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PLATE 1. Non-biogenic and doubtfully biogenic structures resembling microorganisms (all are optical photomicrographs, except for figures 9 and 19).

FIGURES 1 & 3. Carbonaceous residues after HNO_3 dissolution of pyrite (FeS_2) framboids from HF maceration residues of Swartkoppie Fm., uppermost part of Onverwacht sequence, S. Africa (loc. 2 of 16/9/65; x-ray diffraction of framboids by W. W. Wise shows 90% pyrite, 10% quartz).

FIGURE 2. Framboids of marcasite (FeS_2) made in laboratory by passing H_2S through a solution of ferrous chloride and aging precipitate in sealed solution with excess S. Compare aperture-like indentation in specimen on right (from crystallization around end of a sulfur crystal) with similar features in figures 1 & 3.

FIGURE 4. "Filamentous type D microfossil" of Pflug (1966, Pl. 3, fig. 14) from maceration residue of shale in Fig Tree sequence, eastern S. Africa.

FIGURE 5. "Type E Pseudofossil" of Pflug (1966, Pl. 3, fig. 19), recognized by him as a fracture filling in thin section of chert from Fig Tree.

FIGURES 6–7. "Globular type A microfossils" of Pflug, 1966, Pl. 1, figs. 8 & 14) from maceration residues of shale in Fig Tree. Compare with figures 10–15.

FIGURE 8. A "Sphaeromorph with two prominent plastid bodies" (Gowda and Sreenivasa 1969, Pl. 9, fig. 5) from maceration residue of weathered and caliche infiltrated sediments in $>$ 2.34 and probably $>$ 2.6 Gyr old Dharwar System, Chitradurga (formerly Chitaldrug) Schist Belt, S. India. See figure 9 on this plate and description of loc. 1 of 8/12/71.

FIGURE 9. Polished surface of rock from which object illustrated in figure 8 is reported to have come (loc. 1 of 8/12/71). The light colored bands and spots throughout this deeply leached clastic rock consist of modern, caliche-like infiltrations. Figures 10–12 are of bubbles from this specimen.

FIGURES 10–12. Bubbles with adherent and engulfed particulate matter trapped in microcavities in thin section of caliche-infiltrated weathered sediments from rock illustrated in figure 9; same locality as figure 8 (loc. 1 of 8/12/71). Note in figure 11 pinching between projections, and in figure 12 rupturing at top center.

FIGURES 13–15. Bubbles of mounting medium similar to figures 10–13 in recent obsidian from East Paulina Lake, Oregon. Note thickening of peripheral debris in figure 13 as bubble breaks upward and to the right across a band of particulate matter. Figure 14 shows parts of three vesicles with debris coated bubbles inside.

FIGURE 16. "Trilete scars" and appearance of "cell" division produced by slight pressure on coverglass above abiotically generated microspheres (from Fox and Yuyama 1963, Fig. 5). Compare with figure 17.

FIGURE 17. Structures similar to those of figure 16 in the living cyanophyte *Xenococcus* sp. (cf. *Entophysalis* sp.)

FIGURE 18. Chains of abiotically generated microspheres grown between coverglass and slide (from Fox and Yuyama 1963, Fig. 6).

FIGURE 19. Trichites (microlites) in volcanic glass from Nevada. Note resemblance to budding bacterium *Metallogenium* (see Plate 4), spirochaetes, and filamentous and coccoid procaryotes. (From Ross 1962, Fig. 1–6, after a drawing by Zirkel; *magnification estimated* from similar measured trichites illustrated by Ross op. cit.)

thought were real may give way with little or no notice to new numbers, we can, with patience, a guarded outlook, and a synergistic blending of all lines of relevant evidence, extract some crumbs of biological reality from the obstinate rocks.

Indirect Evidences of Early Biogenic Evolution

The commonest and most readily visible, although indirect, evidences of pre-Phanerozoic life are the domal or bun-shaped to columnar and commonly branching biogenic sedimentary structures called stromatolites (Cloud and Semikhatov 1969; Hofmann 1969, 1973), of which samples are illustrated on Plate 2, figures 3–6. Stromatolites are ordinarily found in carbonate rocks, commonly associated with wavy crinkled lamination suggesting algal mat construction. Oölites and flat-pebble conglomerates are common associates. Stromatolite distribution among pre-Phanerozoic rocks, is in fact, closely related to the presence or absence of dolomites and limestones. However, they may also be associated with bedded cherts, and even in carbonate sequences they often consist of diagenetic or secondary silica in the form of chert. Some of these ancient columnar and domal structures, particularly the ones comprised of dark chalcedonic chert, actually display concentrations of filamentous and coccoidal microorganisms along the upwardly convex accretionary laminae of which they are constructed. But most of them reveal only their gross morphology and details of branching, surface structure, lamination, and grain arrangement.

Study of modern analogs, reinforced by the preservation of demonstrable cyanophytes (or, as some prefer, cyanobacteria) in a few stromatolites having ages up to 2 Gyr, points to the conclusion that *most* are, in fact, the synoptic growth products of successive mats of $CaCO_3$ precipitating and sediment-binding cyanophyte or cyanophyte-like microorganisms. In modern sediments they are commonly associated with bacteria and occasionally chlorophytes. Similar structures also are seen in deep-sea manganese crusts, boiler crusts, and non-biogenically bonded precipitates of hot springs silica, while the morphology of other siliceous aggregations in certain Yellowstone hot springs (Walter et al. 1972) appears to be controlled primarily or in part by associated filamentous bacteria. Granting such exceptions, well defined stromatolites, especially of distinctive columnar morphologies of wide areal extent, may be taken as presumptive evidence of life, most probably dominated by photoautotrophic cyanophytes, or at some remote time perhaps by protocyanophytes for which we know no close living analogs.

Now stromatolites first became locally common ~ 2.25 Gyr ago, when the oldest areally extensive, although not yet generally prevalent) carbonate rocks are seen in the middle Transvaal beds of South Africa. They do, however, appear sporadically in older strata where carbonate rocks are present (commonly dolomites or ferrodolomites). In fact, the oldest stromatolites yet known are tiny forms that occur in wavy laminated ("cryptalgal") dolomites near the base of the Pongola System of northern Natal Province, South Africa (Plate 2, fig-

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PLATE 2. Indirect evidences of early biospheric evolution—vertical profiles through stromatolites and banded iron formation (BIF).

FIGURE 1. Deformed ~ 3.8 Gyr old BIF from main ore body at Isua, SW Greenland (white mesobands are iron-poor silica, black mesobands are iron-rich; loc. 9 of 27/8/74).

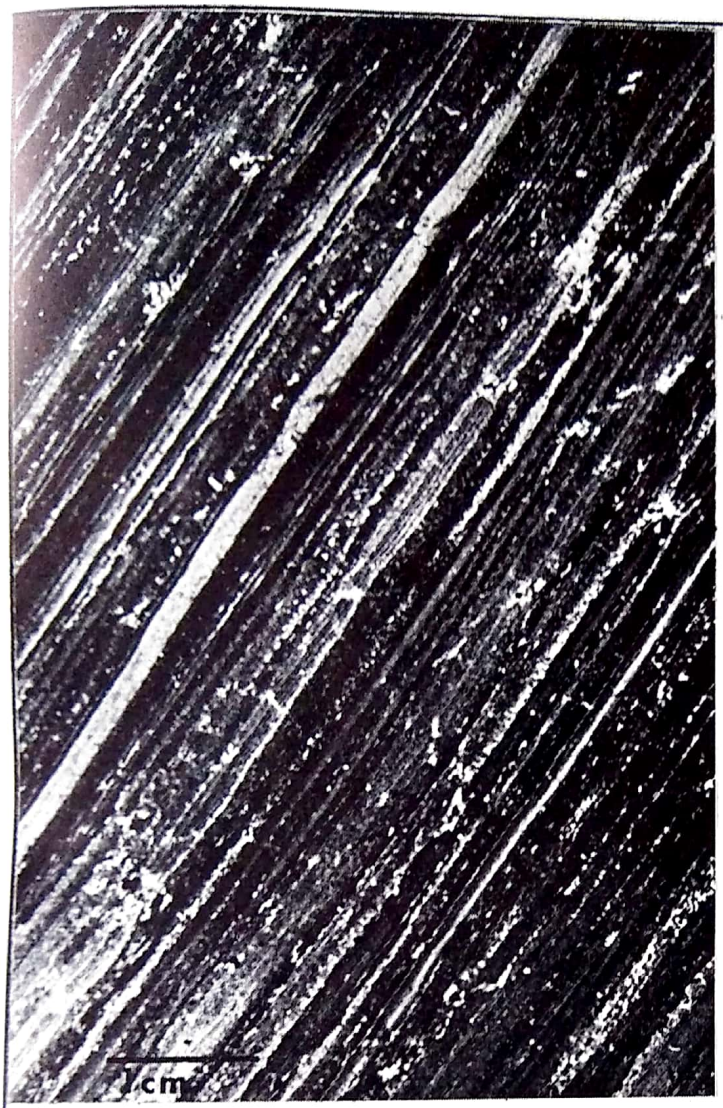
FIGURE 2. Microlaminated ~ 2 Gyr old BIF from Krivoi Rog, Ukraine.

FIGURE 3. Oldest known "cryptalgal" dolomite with microstromatolites at lower center; lower part of 3 to 3.1 Gyr old Insuzi Group, Pongola System, section on White Mfolozi River, Northern Zululand, S. Africa.

FIGURE 4. Compound domal stromatolite from ~ 2.6–2.7 Gyr old limestone on west flank Mumpurumu Syncline, ~ 15 km airline SSW from Shabani, S. central Rhodesia, zone 24 of 33 correlatable zones recognized in unpublished work of Antony Martin. Age is essentially that of well-known stromatolitic limestones of Bulawayo Group (Hawkesworth et al. 1975; Bickle et al. 1975)

FIGURE 5. Large columnar stromatolite from dolomite in the > 2.25 Gyr old Transvaal sequence of S. Africa (loc. 1 of 9/9/65).

FIGURE 6. Columnar stromatolite *Inzeria tjomusi* Krylov from ~ 0.7 Gyr old Hinde Dolomite of Northern Territory, Australia (loc. 2 of 2/8/65).



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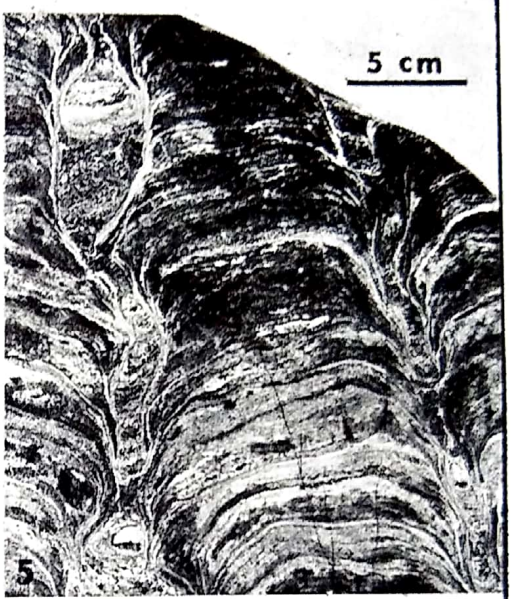

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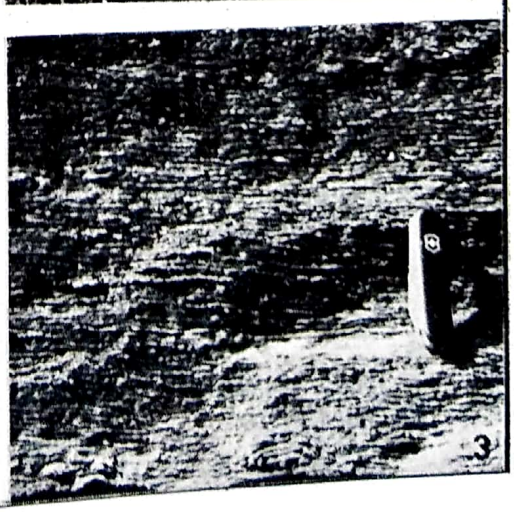

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ure 3; see also Mason and von Brunn, in press), having a zircon age of 3.1 Gyr (Burger and Coertze 1973). Somewhat younger (~ 2.6–2.7 Gyr per Hawkesworth et al. 1975) are the often-cited Bulawayan stromatolites, originally noted by MacGregor (1941) and most recently reviewed by Schopf et al. in 1971. More abundant and varied stromatolites of similar age to the Bulawayan (e.g. Plate 2, figure 4) have recently been described from the Shabani district of south central Rhodesia (Bickle et al. 1975).

Valid caveats aside, the wavy laminated to microstromatolitic dolomite of the lower Pongola System strongly suggests the existence of a $CaCO_3$ precipitating and sediment binding cyanophytic microbiota ~ or > 3 Gyr ago, and thus a cyanophytic biochemistry (although not necessarily identical in detail to that of living cyanophytes). And stromatolites occur intermittently through the stratigraphic record from then until now.

Other unusual sedimentary structures that may have important biogeological significance are the alternately iron-rich and iron-poor laminated rocks, most commonly cherty, that comprise the so-called banded iron formation or BIF (see James and Sims 1973 and UNESCO 1973). This interesting rock is also known in its cherty aspect as taconite or jaspilite, and, where the chert is recrystallized, as itabirite or ferruginous quartzite. The kinds of BIF need not delay us beyond noting that the two main types (Plate 2, figures 1–2) do not generally occur in rocks younger than ~ 2 Gyr (although conspicuous exceptions to that rule are noted by Young 1976, and Cloud 1973a). What is important is the remarkable continuity and cyclicity that the BIF often shows in well preserved deposits.

A major geochemical dilemma is posed when we consider how the iron in an individual iron-rich lamina of BIF could have remained in suspension over areas of sea bottom up to 300 km or more across (e.g. Trendall 1973) except as dissolved or colloidal ferrous hydroxides, and how it could have been abruptly and episodically precipitated except as a result of episodic, temporary exposure to dissolved O_2.

Two possible explanations come to mind. One calls on periodic transfer of ferrous iron from the depths of anaerobic basins into oxygenous surface waters. This results in the precipitation of ferric hydroxides, which go to Fe_2O_3 upon loss of H_2O and then to Fe_3O_4 on reaction with C (Perry and Tan 1973; Perry et al. 1973). Meanwhile silica continues to precipitate from ocean waters locally saturated in volcanic SiO_2 or generally so saturated before the evolution of eucaryotic silica precipitators. The second explanation invokes a biological source of oxygen that is in some way dependent on the oxidation of ferrous iron to keep free O_2 at sublethal levels, and which itself has an episodic aspect.

I have called on the first mechanism to explain certain unusual and limited Paleozoic and later pre-Phanerozoic BIF's such as those associated with the marginal facies of eugeosynclinal basins in southern Transuralian USSR (Kalugin in UNESCO 1973) where a submarine volcanic source of iron and silica can be visualized. This might work also for late pre-Phanerozoic BIF's associated with diamictites and steep topography (Young 1976). The common association of these and older BIF's with evidences of glaciation, as noted by Young (1976) would also be consistent with glacial control of episodic upwelling of waters rich in basinally stored Fe^{++}, as suggested by Cloud (1973a).

A mechanism dependent on oxygen-rich surface waters, however, while it might work for lenticular deposits in basins of limited extent, can hardly explain the very extensive, thinly and continuously laminated, mainly shallow shelf to shelf-basin deposits of cherty BIF, so characteristic of post-Archean deposits in the age range of ~ 2.2 to 2 Gyr ago. Here it is necessary to keep the iron in solution over vast areas before it is converted to the ferric state; this is hard to visualize *if* the contemporaneous atmosphere were generally oxidizing. It also runs into serious difficulties of scale even for the less extensive and commonly lenticular Archean deposits. If the surface waters of basins in which Archean BIF was precipitating were *generally* oxidative, that would imply that the Archean atmosphere was also oxidative. And, if the atmosphere had been oxidative, we might expect to see oxidized sediments other than BIF in arkosic fluviatile and basin margin deposits such as are associated with the > 3 Gyr old Moodies and ~ 3 to 3.1 Gyr old Pongola sequences of eastern South Africa.

We might also expect to see more Archean carbonate rocks, and those we do see should not include ferrodolomites as they commonly do. Finally, we should not see extensive easily oxidized detrital uraninite and pyrite as we do in the stream and delta deposits of rocks older than ~ 2.3 to 2.2 Gyr in South Africa, Australia, Brazil, and Canada (e.g. Ramdohr 1958; Robertson 1974; Roscoe 1969; Salop 1972; Reimer 1975).

The alternative possibility (Cloud 1965) is that BIF older than the oldest clearly oxidized terrestrial or marginal marine sediments is in some way related to a biological source of oxygen. I have discussed this in detail at other places (e.g. Cloud 1973a, 1974a). Briefly, I visualize cyanophytic (or proto-cyanophytic) O_2 producing photosythesis as the source of the O_2 that converted ferrous to ferric hydroxides and then oxides in the BIF, the ferrous ion serving as an O_2 depressant and possibly electron donor that permitted the early oxygen-sensitive cyanophytes to survive. Some blue-green algae even today prefer anaerobic or nearly anaerobic conditions, depending on reduced substances such as sulfides to keep the O_2 down to tolerable levels (e.g. Stewart and Pearson 1970). They include the active stromatolite builder at Yellowstone Park, the genus *Phormidium*, and perhaps other mat-forming and benthic blue-greens generally (Weller et al., in press). Thus it is consistent with what is known both about living cyanophytes and BIF to hypothesize that BIF 2 Gyr old or older is primarily a biogeochemical consequence of cyanophytic evolution and hence evidence for it. The episodicity that gave rise to the alternating iron-rich and iron-poor microbands in at least one major BIF basin is probably annual (Trendall 1973)—presumably reflecting seasonal upwelling of either nutrients for algal blooms, or ferrous iron in solution, or both.

This line of reasoning has some interesting implications for plant evolution. It suggests that not only life itself but probably a low level of O_2 producing photosynthesis was already in existence > 3.76 Gyr ago when the oldest known BIF was being deposited in southwest Greenland (Plate 2, figure 1; Moorbath et al. 1973)—some 700 to 800 Myr *before* even the oldest known stromatolites!

If correct, that means that events or preconditions 1 through 8 at the left of Table 1 had already occurred > 3.76 Gyr ago, along with their likely stimuli and most of their probable consequences. Event 1, on the other hand, the outgassing of Earth to form the initial atmosphere and hydrosphere, presumably began as soon as the accretion temperature of the earth reached the melting point of rock, with water condensing out as soon as the surface of the accreted earth cooled below its boiling point. Major outgassing may have lasted a good part of the time from shortly after planetary origin ~ 4.65 Gyr ago to the deposition of the very ancient BIF in southwest Greenland. Of course, events or event-sets 2 through 5, representing the reactions of prebiotic chemistry (e.g. Calvin 1975), were probably going on almost simultaneously with the initial development of hydrosphere and atmosphere accompanying and following the primordial outgassing. Thus life probably came into existence almost concurrently with the primary hydrosphere, perhaps while it was still limited and disconnected enough to present relatively small warm pools, rich in the molecular precursors of life, somewhat as Darwin visualized in his often cited letter to Hooker (1 Feb., 1871, per Calvin 1975), or on crystal templates as suggested by Bernal (1967) and Cairns-Smith (1972).

Although we do not and never can know with certainty, what the first organism looked like, the likeliest chemistries of its origin say that it was anaerobic, most probably heterotrophic, and certainly procaryotic. Most likely it consisted of minute, subspherical unicells that we would be unable to identify with confidence as once-living objects even if we were to find them. The above reasoning nevertheless envisages the ancient BIF of southwest Greenland as indirect evidence that all steps up to the origin of procaryotic organisms with the biochemical equipment for oxygen-generating photosynthesis were taken before ~ 3.8 Gyr ago; presumably over a geological interval of no more than ~ 400 Myr, following the condensation of the initial hydrosphere.

Now one may well ask, if all that happened so early in Earth history, why did it take another 1.8 Gyr to evolve the oxygen defenses that made possible fully oxidative metabolism? To that I can respond only that I see biologic evolution as basically a shaping of existing biosystems to changes in environments, geog-

raphy, and antecedent biosystems that create new evolutionary opportunities, new niches, and new isolating mechanisms. The geologic record of life, as I read it, implies that evolution is strongly opportunistic, that successful biologic innovations happen or expand in a geological sense when appropriate ancestral types and suitable opportunities exist (Cloud 1973b). In the case of oxidative metabolism, the stimuli were probably the filling of all surficial O_2 sinks, with buildup of O_2 above the Pasteur Level (10^{-2} present atmospheric level or PAL) and evolution of advanced oxygen-mediating enzymes. Indeed, as we know from the works of Gerschman (1962), Gilbert (1964, 1972), and Haugaard and others in Dickens and Neil (1964) and Hayaishi (1974), and as we have understood dimly since Lavoisier and clearly for nearly a century, oxygen was probably as much an obstacle as an opportunity to evolution. As Gilbert (1972) points out, photosynthesis itself is inhibited by O_2 toxicity which thereby acts as a brake on O_2 increases. Thus, as Singer and Edmondson (1974) have suggested, the main evolutionary advantage of the invention of a respiratory apparatus able to reduce O_2 to H_2O may have lain in the elimination of the toxic products of the univalent and divalent reduction of O_2 rather than in the greater efficiency of aerobic respiration as compared with anaerobic fermentation.

To cope with oxygen toxicity so that free O_2 could increase, it was necessary for primitive anaerobic or microaerophilic photosynthesizers to evolve a variety of antioxidant enzymes—among them cytochromes, carotenoids, perhaps catalases, and eventually superoxide dismutase. Most important, it turns out, is superoxide dismutase, ubiquitous in aerobic cells and the only suppressant of the superoxide O_2^-, an intermediate product in the reduction of O_2 to H_2O_2 and water (McCord et al. 1971; Singer and Edmondson 1974). Thus we must add to the filling of all of the primitive O_2 sinks and the evolution of a proper complement of cytochromes and catalases, the ability to manufacture a continuing supply of superoxide dismutase, before a fully oxidative metabolism (and an eucaryotic level of development) is possible. In view of the fact that there were no obvious selective pressures toward the latter *until* all major O_2 sinks were filled or nearly filled, it does not seem surprising that oxidative metabolism and the eucaryotes were late in making their appearance.

A few words, finally, about organic geochemistry, which can, in theory, provide indirect evidence about early plant evolution but which is beset with problems. Extractable organic geochemicals all contain the uncertainty that the same volatility which makes them extractable would also have made it possible for them to move through even minutely permeable rocks and thus to be introduced secondarily at various post-depositional times. Solid carbonaceous residues (kerogen) on the other hand, while presumably (but not necessarily) both indigenous and coeval with sedimentation or diagenesis, are generally so altered in pre-Phanerozoic sediments that they provide little information about organic molecules at a level of complexity of interest for biogeochemical evolution (Leventhat et al. 1975).

Of more than ordinary interest are the carbon isotope ($^{13}C/^{12}C$) ratios ($\delta^{13}C$) of carbonaceous residues, where enrichment in light carbon has been taken as indicative of photosynthetic fractionation. But even granites and volcanic rocks (at least young ones) give $\delta^{13}C$ values for noncarbonate carbon as low as –20 to –12 parts *per mil* (Feux and Baker 1973), while the minimal $\delta^{13}C$ value observed by Calder and Parker (1973) for cyanophytic algal mats in Holocene sediments was –18‰. Indeed the latter authors conclude that observed $\delta^{13}C$ values, taken literally, "are not consistent with the idea that blue-green algae were the primary source for organic matter" during pre-Phanerozoic time—which suggests the possibility either of evolution of CO_2 fixation pathways in early protocyanophytic populations or of metamorphic alteration of carbon ratios in ancient sediments. The conclusion I regrettably draw from these and other suggested implications of C isotope ratios (e.g. Broecker 1970; Becker and Clayton 1972; Oehler et al. 1972; Schidlowski et al. 1975) is that we do not yet understand enough about them or other organic geochemical data from pre-Phanerozoic rocks to go very far beyond the inference that abundant reduced carbon in sediments suggests (but does not of itself prove) the contemporaneous or prior existence of life.

Oldest Demonstrable Fossils and the Biogeochemical Implications of Procaryote Evolution

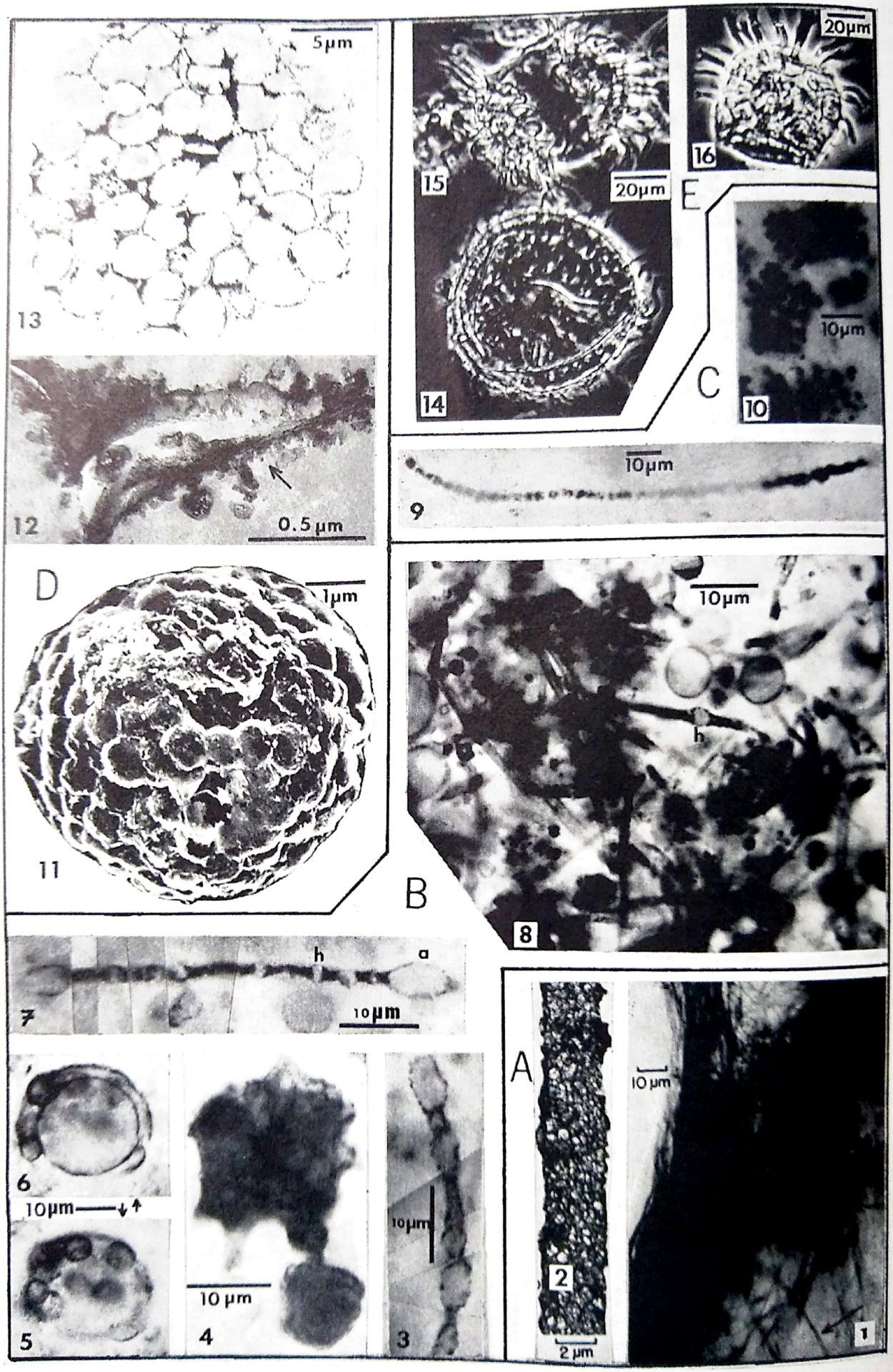
If morphology can be deceiving it can also be illuminating. Discriminating micromorphological analysis of objects and structures known to be primary may suggest a great deal about probable function, biochemistry, and affinities. It may, in fact, tell us more about biochemical evolution than the most refined organic geochemistry of mobile substances that may be contaminants or graphitic residues whose induced lysis reveals only simple precursor molecules. But if we are to get at biochemical evolution through refined morphology, it is all the more important to establish a high level of confidence that entities studied are truly fossil organisms of the same age as the enclosing sedimentary rocks and not themselves contaminants, artifacts, or abiotic precursors of living systems.

On Plates 3–5 are illustrated representatives of seven selected microstructural assemblages that I consider to be demonstrable fossil microbiotas on grounds of distinctive cellular differentiation or ultrastructural similarity to living organisms, combined with a carbonaceous composition and with paragenetic relations to associated mineral grains indicative of primary origin. Six of these illustrate the variety of morphology extant between ~0.7 and 2 Gyr ago. The seventh (Plate 3E) illustrates the level of complexity that had been reached by ~500 Myr ago, emphasizing the burr-like, hairy, or spiny, commonly bipolar, acid resistant organic structures such as first appear as primary components in Phanerozoic rocks. The relative positions of these microbiotas with reference to major lithological-historical divisions recognized is shown in Figure 1, modified from and amplified in Cloud, 1976.

The beautifully preserved, diverse, and abundant ~2 Gyr old Gunflint microbiota of southern Ontario, first announced by Tyler and Barghoorn (1954) and partially described by Barghoorn (in Barghoorn and Tyler 1965), is a good one to start with. Here the filamentous *Gunflintia minuta* Barghoorn, from black stromatolitic chert of the Gunflint Iron Formation, illustrates well the power of discriminating morphology. Licari and Cloud (1968) noted that some of these filaments show enlarged cells interspersed in and at places seemingly terminal to linear arrangements of short bead-like cells (Plate 3, figures 3,7,8). The enlarged cells are of two types, one subspherical and about twice the diameter of the intervening normal cells, the other longer and larger. Licari and Cloud (1968) noted that the subspherical enlarged cells resembled the heterocysts and the large oblong cells the akinetes, which, together with absence of false branching and tapering, differentiate living nostocacean cyanophytes from all other filamentous forms. As in living blue-green algae, the formation of akinete-like cells adjacent to heterocyst-like cells is consistent with the idea of Tyagi that the heterocyst plays a role in akinete formation. Although these enlarged cells are generally rare in *Gunflintia minuta*, they are locally common, as if their development might have responded to seasonal or microhabitat variations. In similar living forms the heterocysts, which seem to serve among other things as sites for biological nitrogen fixation (e.g. Tyagi 1965; Fay and Stewart in Carr and Whitton 1973), are commonly clear, in contrast to adjacent vegetative cells. The akinetes, however, which apparently perform as resting cysts from which new filaments germinate after intervals of desiccation or chilling, are pigmented. In the fossil material the significance, if any, of the fact that both types of enlarged cells tend to be clearer than adjacent normal cells is not obvious. Perhaps it reflects a difference in primary pigmentation due to presence or absence of heme proteins or porphyrins, but in that case the larger oblong cells, if akinetes, should also be pigmented (e.g. Licari and Cloud 1968, figs. 2, 4). Perhaps they are just large heterocysts, which might be suggested by figure 3 of Plate 3.

The cellular differentiation noted, as well as other cytological similarities to the Nostocaceae, warrants a high level of confidence in the conclusion that *Gunflintia* is not only a genuine fossil, equipped with heterocysts and probably akinetes, but is, in all probability, an ancestral nostocacean cyanophyte.

The same is true of *Gunflintia*-like filaments in non-stromatolitic cherts at the base of the Pokegama Quartzite, which underlies rocks correlated with the Gunflint Formation in northeastern Minnesota (Plate 3A). Here, however, although sheath-like ultrastructure is preserved (Plate 3, figure 2), heterocyst-like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cells are extremely rare, akinete-like structures have not been observed, and very thin (<1μm), aseptate, associated filaments may be filamentous bacteria.

Intercalary heterocyst-like cells are also found occasionally along the trichomes of filamentous forms in the ~1.3 Gyr old Beck Spring microbiota (Plate 5A), although none are here illustrated. I am unsure how to interpret the records of Lois Nagy (1974) and MacGregor et al. (1974) from thin sections of dolomite > 2.25 Gyr old near the middle of the Transvaal sequence, S. Africa. The ease with which microorganisms seem to be able to penetrate carbonate rocks causes me to pause short of an unequivocal acceptance of these records. Yet the material looks plausible, and Dr. Nagy (letter of 15 June, 1976), in kind response to earlier inquiry, assures me that tests for porosity and microcracks imply vanishingly small prospects of post-solid introduction of microorganisms. In addition, my long held reservations concerning either the biogenicity or the primary nature, or both of all Archean microbiotas reported until now have recently been seconded by Schopf (1975). Although some objects that are surely indigenous may well be microorganisms (e.g. *Eobacterium isolatum*, Barghoorn and Schopf 1966), and it is permissible so to interpret them; we agree that evidence for a biogenic origin is permissive only and not compelling. Thus the filaments of the Pokegama microbiota are the oldest surely biogenic *and* primary microstructures known, and the record of cellular and microstructural differentiation from then onward is strong evidence for a continuing record of biospheric evolution from somewhat more than 2 Gyr ago until the present.

To return to the slightly post-Pokegama Gunflint microbiota, however, its biogenicity is further reinforced by the presence in it of two genera that are here interpreted as budding bacteria (cf. Hirsch 1974). These are the forms that Barghoorn (in Barghoorn and

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PLATE 3. Procaryotic microbiotas from ~ 2 to ~ 0.7 Gyr BP (A–D) and some ~ 0.5 Gyr old eucaryotes (E).

A. Pokegama microbiota, ~ 2.1 to 2 Gyr BP (loc. 3 of 3/10/64, N. E. Minnesota).

FIGURE 1. Photomicrograph of mass of micro-filaments in thin section of chert. Arrow points to septate larger filament. Rare heterocyst-like structures found in such filaments not shown in this figure.

FIGURE 2. TEM micrograph of HF-isolated empty sheath of probable cyanophyte showing fibrillar meshwork structure.

B. Gunflint microbiota, ~ 2 Gyr BP (loc. 1 of 25/8/63, southern Ontario). Photomicrographs from thin sections of stromatolitic chert.

FIGURES 3 & 7. *Gunflintia minuta* Barghoorn, interpreted as a nostocacean BGA showing cellular differentiation (letters h and a suggest comparison with heterocysts and akinetes).

FIGURE 4. *Kakabekia umbellata* Barghoorn, a probable budding bacterium.

FIGURE 5–6. *Eosphaera tyleri* Barghoorn, affinities problematical.

FIGURE 8. Typical view of a Gunflint thin section from stromatolitic chert at this locality, showing abundant septate filaments of *Gunflintia minuta* Barghoorn and polymodal spheroids of uncertain affinity (*Huroniospora*).

C. Paradise Creek microbiota, ~ 1.6 Gyr BP (loc. 3 of 20/7/65, N. W. Queensland). Photomicrographs from thin sections of stromatolitic chert.

FIGURE 9. Probable cyanophytic septate filament.

FIGURE 10. Cubical *Eucapsis*-like colonies.

D. Hector microbiota ~ 0.7 Gyr BP (loc. 3 of 2/9/67, S. W. Alberta).

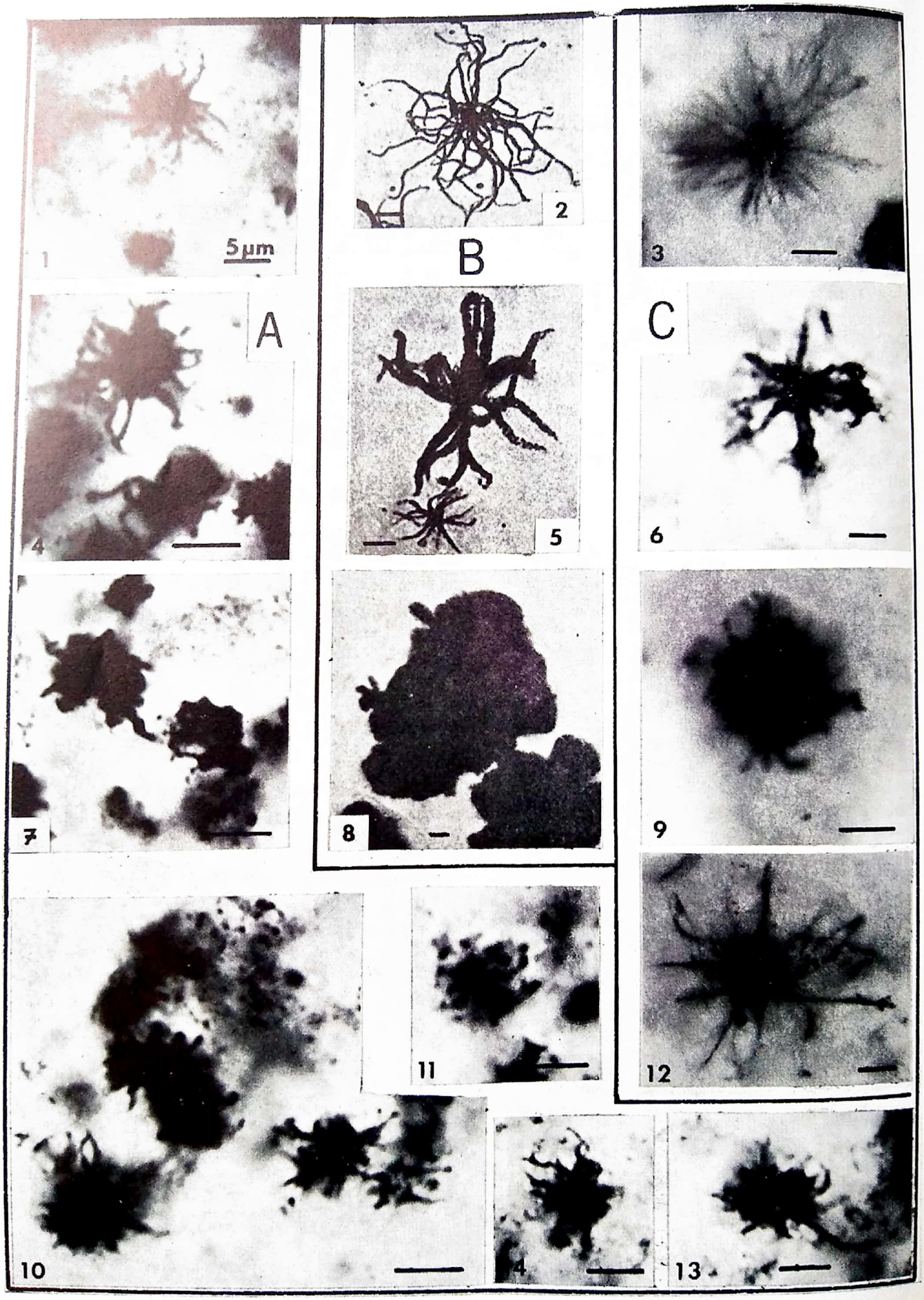
FIGURE 11–13. SEM (figure 11) and TEM (figures 12–13) micrographs of maceration isolates of *Sphaerocongregus variabilis* Moorman from black mudstone of Hector Formation; 11 = endosporangium, 13 = ultrathin section through center of clonal coenobium, 12 = detail of juncture of multi-laminate cell envelopes shown at lower edge of fig. 13 (arrows in figures 12 and 13 point to same location).

E. Sablino microbiota ~ 0.5 Gyr BP (loc. 3 of 10/9/71, ~ 30 km SE of Leningrad, USSR). Nomarski interference photomicrographs of maceration isolates from basal Ordovician (Tremadoc) siltstone.

FIGURE 14. *Trichosphaeridium annolovaense* Timofeev.

FIGURE 15. *Acanthodiacrodium* sp. (a probable dinophycean cyst).

FIGURE 16. *Archaeohystrichosphaeridium* sp. (probable dinophycean cyst showing open archeopyle at base).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Tyler 1965) called *Kakabekia* (Plate 3, figure 4) and *Eoastrion* (Plate 4), at the same time as Cloud (1965) was recognizing a striking morphological similarity between *Eoastrion* and the living Mn-oxidizing bacterium *Metallogenium* from Karelian lakes (Perfil'ev et al. 1965). Specimens from my collection have since been studied by Kline (1975), who kindly prepared Plate 4 of this work to show the detailed micromorphological resemblance between Gunflint *Eoastrion*, modern *Metallogenium*, and a similar organism from the ~ 1.6 Gyr old Paradise Creek microbiota of northwest Queensland (Licari et al. 1969; Licari and Cloud 1972). Figures 1–9 on Plate 4 compare the modern and ancient species at similar stages of development, while figures 10–12 and 14 show distal swellings on fossil trichomes similar to the terminal reproductive cells of the living *Metallogenium*. Similar forms, as well as other elements of the Gunflint microbiota have also recently been reported from the Frere Formation, Nabberu Basin, northeast edge of Yilgarn Block, Western Australia (Walter et al. 1976), of about the same age as the Gunflint. We need not pursue the question of whether *Metallogenium* and its ancient look-alikes might be actinomycetes, spirochaetes, or something else rather than a budding bacterium. The point of interest here is that there is no reasonable doubt that, whatever these structures may be, they are all remarkably similar over a range of matching and complicated morphotypes. If one is biogenic, it seems likely that all are, and the clearly biogenic one is at the procaryotic or non-mitosing and microaerophilic evolutionary level.

Authentic, probably microaerophilic, procaryotes thus were unequivocally extant by ~ 2 Gyr ago, but associated with them are also microorganisms that from time to time are suggested as possible eucaryotes (e.g. Kazmierczak 1976; Tappan 1976; Darby 1974; Edhorn 1973; Licari and Cloud 1968; Barghoorn and Tyler 1965). The most persuasive evidence for an eucaryotic presence is that of Kazmierczak (1976), who compares the Gunflint *Eosphaera* with a strikingly (but I believe superficially) similar Devonian form which he has named *Eovolvox* and compares with the living "colonial" (coenobial) Volvocales. *Eovolvox*, however, clearly displays internal daughter colonies which are absent or obscure in *Eosphaera*, lacks the well-defined thick-walled inner sphere of the latter, and has an external diameter of 42 to 135 μm, as compared to ~ 28 to 30 μm for *Eosphaera*. There may be eucaryotes in the Gunflint microbiota, but the evidence for them can hardly be considered stronger than permissive. Although Kazmierczak has argued skillfully that the photoorganotrophic coenobial Volvocales tolerate, or even prefer, low oxygen concentrations and that some have a high requirement for iron, the simplest explanation for the Gunflint microbiota, and that most consistent with contemporaneous geochemical evidence and evolutionary developments up the geological column, is that it is wholly procaryotic.

What then are the biogeochemical implications of the supposedly wholly procaryotic

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PLATE 4. *Metallogenium*-like budding bacteria ~ 1.6 Gyr old (A), modern (B), and ~ 2 Gyr old (C). Bar scales all 5 μm. Photomicrographs of thin sections (A & C) and cultures (B). (A) from chert of Paradise Creek Formation, N. W. Queensland (loc. 4 of 20/7/65). (B) from Perfil'ev et al. (1965). (C) from chert of Gunflint Formation, S. Ontario (figures 3 and 12 from S. Awramik loc. GF-69-4D and figure 6 from GF-69-4E; figure 9 from loc. 1 of 25/8/63 of Cloud). Plate presents some findings of a Master's thesis by Gary Kline and was prepared by him for this report.

FIGURES 1–9. Comparable morphological gradation (downward) from non-encrusted trichospheres to encrusted stages in fossil (A & C) and living (B) forms. Figures 1 to 3, trichospherical microcolonial stage, 4 to 6 mildly encrusted stage; 7 to 9, heavily encrusted stage.

FIGURE 10. Cluster of fossil trichospheres exhibiting gradation of associated microcolonies from lightly to heavily encrusted. Note terminal swellings on some filaments.

FIGURES 11–12. Fossil microspheres with enlarged terminal bodies analogous to terminal reproductive cells of living *Metallogenium*. Cells of living form may detach to form a new trichosphere or bud while attached (as at upper left of figure 14) to start a satellite trichosphere.

FIGURE 13. Branching of filament at top center is not from an enlarged terminal body, but instead resembles the "hyphal" branching characteristic of budding bacteria.

FIGURE 14. Filament trending to upper left shows a terminal body with two branches, starting the growth of a secondary trichospherical microcolony as in living *Metallogenium*.

microbiota that seems to have existed in several parts of Canada, the north-central United States, Australia, and probably wherever BIF is found, up to ~ 2 Gyr ago or later?

I have already outlined a hypothetical relation between cyanophytic or protocyanophytic O_2 production and the chemical sedimentation of BIF. In this model a critical feature is the nature of the advance of photoautotrophy beyond the stage of merely nascent O_2 production with immediate recombination (as in bacterial photosynthesis), to the actual release of extracellular free O_2. It seems unlikely that this step would have been accompanied by immediate full enzymatic protection against high levels of ambient O_2. Simple cytochromes, of course, or their antecedents, plus chlorophyll *a* and probably carotenoids would have been minimal prerequisites. But, as previously observed, at that stage of evolution cyanophytic metabolism may well have been microaerophilic and dependent on some mechanism for maintaining very low free O_2 levels, as apparently continues to be the case among some stromatolite-forming and other blue-green algae today (Stewart and Pearson 1970; Weller et al., in press).

Thus I see the prevalence of ferrous iron in solution in the older pre-Phanerozoic seas as one of the major O_2 sinks that assured the survival of the perhaps initially anaerobic but later microaerophilic protocyanophytes from their origin ~ 3.8 Gyr ago, until the appearance of efficient enzymatic protection against increasing levels of free O_2 perhaps 2 Gyr ago. As long as O_2 levels stayed low and oxygen sinks remained to be filled, there would have been no great selective pressure favoring the evolution of higher O_2 tolerance and a fully oxidative metabolism. For evolution, as noted above, is not so much a function of elapsed time as it is, given suitable ancestry, of opportunity; which would explain, among other things, why we were wrong so long in our guesses about the length of time required for the emergence of the Metazoa.

What could have stimulated greater O_2 tolerance among the early cyanophytes? Was it merely a chance mutation for the production of superoxide dismutase in the larger populations associated with the vast marine iron deposits between ~ 2.2 and 2 Gyr ago, or a selective consequence of the exhaustion of contemporaneous O_2 sinks? Whatever the cause, we may infer from the essential termination of BIF and onset of red beds about 2 Gyr ago that this was when enzymatic mediation of that particular early atmospheric pollutant (e.g. Fridovich 1975; Singer and Edmondson 1974; McCord et al. 1971) became efficient enough to tolerate free O_2 at levels above ~ 1% PAL.

The biogeochemical consequence of increased O_2 tolerance was the saturation in O_2 of the photic zone of the hydrosphere as the sedimentary segregation of carbon continued, initiating the growth of free O_2 in the atmosphere. This, in turn, initiated the growth of the ozone screen, the termination of BIF sedimentation, the retention of ferric oxides in the weathering profile, and the burial and preservation of oxidized sediments, of which the most conspicuous evidence is the formation of continental and marginal marine red beds throughout the last 2 Gyr.

The challenges that this collection of hypotheses have encountered since first proposed a decade ago (Cloud 1965) have produced constructive revisions but no major changes. On the contrary, relevant new or previously unfamiliar evidence has so far been either supportive or permissive of the model. As I have noted elsewhere for instance (Cloud 1974a), the prevalence among procaryotes of repair mechanisms for UV-disrupted DNA and of UV-shielding pigmentation suggests a response to the primitive absence of an ozone screen as a result of the rarity and evanescence of free O_2. Similarly the evolution of nitrogen-fixing enzymes, now limited to the anaerobic environment of heterocysts, may have occurred in response to the difficulty of achieving abiological nitrogen fixation in an atmosphere devoid of free O_2. And the ever more voluminous geochemical evidences for the earliest generally oxidative and latest generally anoxygenous environments converge toward the vicinity of 2 Gyr before the present (BP).

Here it is relevant to return to the earlier mentioned manganese-oxidizing bacterium *Metallogenium* and its fossil analogs (*Eoastrion*), now known also from other localities in probably ~ 2 to ~ 1.6 Gyr old rocks in Australia (Walter et al. 1976; Muir 1974). Perfil'ev, who has written, coauthored, or sponsored the most definitive works on living *Metallogenium*

(e.g. Perfil'ev et al. 1965), notes that its habitat is microaerophilic, with growth normally confined to zones of low O_2 tension. Hirsch (1974, p. 429) in his review of budding bacteria adds the observations that an "iron-oxidizing and -requiring, acid-tolerant *Metallogenium* has (now) been isolated from streams" and that a UV mutant has been obtained that proved incapable of manganese oxidation and deposition but still grew well. Although the association of the *Metallogenium*-like *Eoastrion* with dolomite and riebeckite implies a saline and presumably marine environment for pre-Phanerozoic forms, *Metallogenium* itself is a fresh water form. But euryhalinity is common among procaryotes, and the oxygen requirements and tolerances of the *Metallogenium*-like fossils may have been as similar to recent forms as is their micromorphology. If so, the presence of the fossils in rock-encrusting shallow-water stromatolites would support the hypothesized very low O_2 levels and probable exposure to UV irradiation ~ 2 Gyr ago. Their persistence in the shallow to intertidal stromatolitic habitat to as recently as ~ 1.6 Gyr ago in Australia might even suggest that the increase in free O_2 levels after the termination of BIF was for some time not much greater than was needed to account for red bed sedimentation, which would still go on at relatively low partial pressures of O_2—especially in the presence of small quantities of ozone and atomic oxygen.

In short, the model of interacting biospheric, atmospheric, and related geochemical evolution that I partially sketch above and summarize in Figure 1 has verifiable consequences, and enough of these have now been verified to justify some confidence in its approximation to reality.

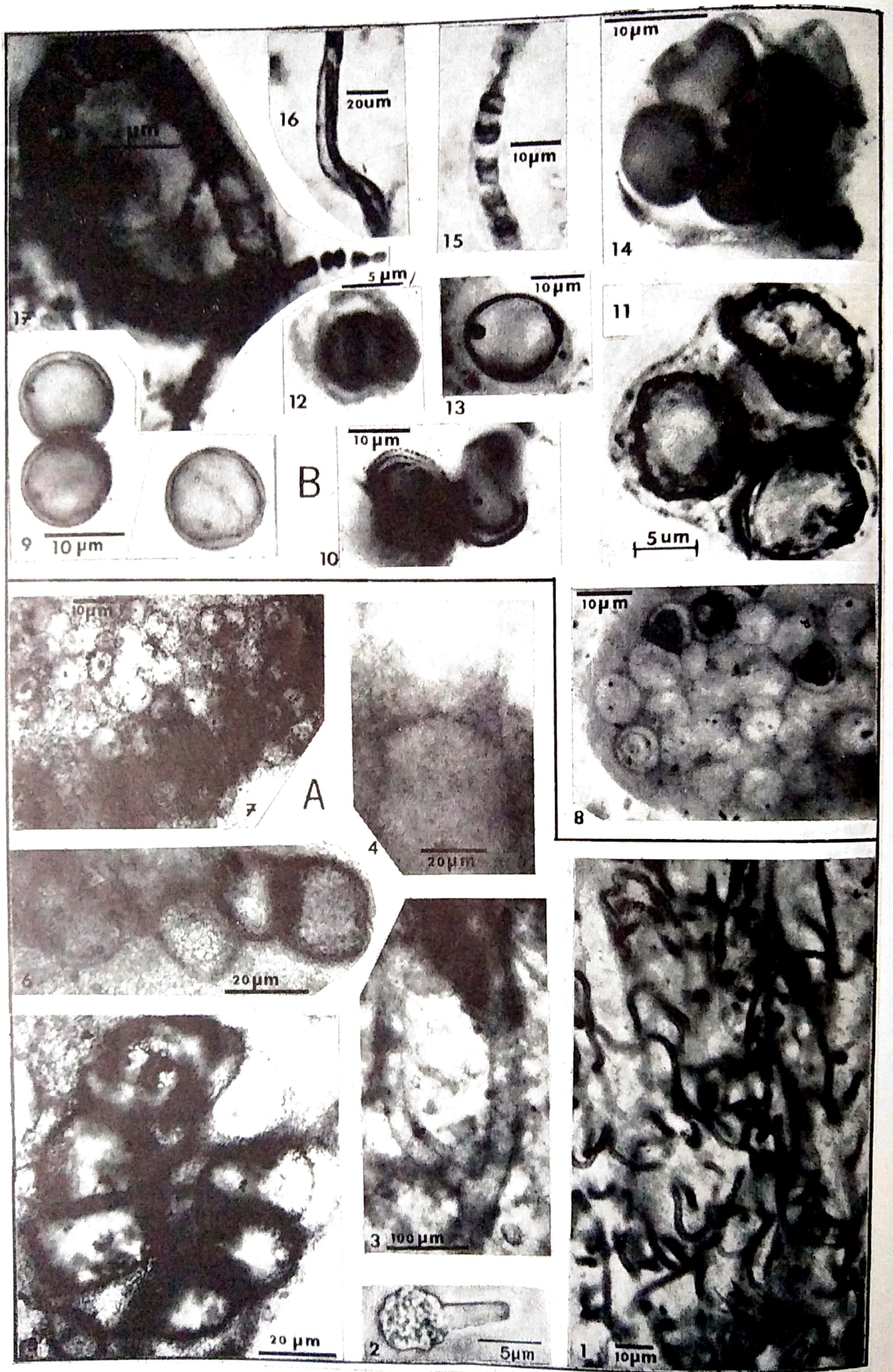
Oldest Eucaryotes and Their Biogeochemical Consequences

With the inferred evolution of efficient enzymatic O_2 mediating systems ~ 2 Gyr ago and the resultant rapid increase of atmospheric O_2 to above 1% PAL, intracellular isolation of anaerobic vital processes would become essential. For, as Wald (1964) has emphasized, the most basic metabolic processes are anaerobic in all organisms, and biochemical evolution has gone to great lengths to see that most biological oxidation is carried out by removal of hydrogen rather than by addition of oxygen.

At any time after ~ 2 Gyr ago, or whenever thereafter O_2 reached 1% PAL, the mitosing or eucaryotic cell might have arisen as a result of the breakup of the single circular procaryotic chromosome into several linear chromosomes, their enclosure within a double nuclear membrane, and the origin of mitochondria, peroxisomes, other membrane-bound organelles, and, except in red algae, the 9 + 2 flagellum. A currently popular view holds that the eucaryotic cell arose from anaerobic, protoeucaryotic ancestors as a result of a succession of endosymbiotic events (Merechkowsky 1905; Echlin 1966; Margulis 1970). Others have argued for emergence from a procaryotic ancestor by normal selective processes (Allsopp 1969; Klein 1970; Raff and Mahler 1972). And Taylor (1974) sees virtues in both processes.

The most articulate and imaginative recent advocate of serial endosymbiosis is Margulis (1970 and elsewhere), who, with fine disdain for Occam's Razor, calls on up to 5 separate endosymbiotic events for the ancestral eucaryote and 27 independent transitions from mitotic to meiotic cell division (her fig. 2–6, p. 62). The fascination of the endosymbiotic hypothesis is that it is a known process that could explain the transition if one is willing to accept the many coincidences required. The difficulty is that the number of independent events called for strains credibility.

The most effective counter-arguments are those of Cavalier-Smith (1975). He points out that the presence of polyunsaturated fatty acids in blue-green algae and eucaryotes but not in bacteria implies a cyanophytic ancestor for the eucaryotes (although I must disagree about it being "unable to fix nitrogen"). With Stanier, he sees phagocytosis (and pinocytosis) as of key importance in eucaryote evolution and endosymbiosis as an almost inevitable consequence of phagocytosis. But endosymbiosis is seen as unable to explain the central feature of the eucaryotic state—the membrane-bound nucleus—and unnecessary for the origin of its other characteristics. Most importantly, Cavalier-Smith provides a logical alternative mechanism—in simplest terms comprising initial loss of cell wall, leading to endocytosis, budding and cleavage, chromosome fractiona-


16
20um
15
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8
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6
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1
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tion, microtubules, and the rest. An interesting corollary of Cavalier-Smith's model is that it envisages the evolution of mitosis and meiosis as essentially simultaneous—"the most distinctive feature of eukaryotic [*sic*] chromosomes, mitosis, meiosis and sex probably all evolved in a very short space of time."

As with the origin of life itself, we will never *know* the answers to exactly how the eucaryotes arose. In fact, even the spelling is disputed, although Chatton (1938), who coined the terms eucaryote and procaryote used c's rather than k's, and I do not find kosmos or kosmology, even as alternate spellings, in either Webster or the *Oxford English Dictionary*. Fortunately we are not here concerned with the problem of origin or transliteration, but with the more tractable one of *when* the eucaryotic cell arose.

Although Barghoorn and Tyler (1965), Licari and Cloud (1968), Edhorn (1973), Darby (1974), Tappan (1976), and Kazmierczak (1976) have all suggested that some of the ~ 2 Gyr old Gunflint nannofossils *could* be eucaryotes, the evidence cited remains unimpressive. Kazmierczak's arguments, as noted above, are interesting and may be true but are inconclusive. Edhorn's "desmid-like" and "radiolarian-like" organisms are simply fuzzy images of the probable budding bacterium *Kakabekia* and perhaps *Eoastrion* (Barghoorn and Tyler 1965). Darby's comparisons involve superficial resemblances that could as well be procaryotic. And Barghoorn and Cloud have retreated from their earlier tentative suggestions. It has also been proposed by Tappan (1976) that the *Eucapsis*-like organism from the indirectly dated ~ 1.6 Gyr old Paradise Creek microbiota (Plate 3, figure 10; Licari et al. 1969) could be an eucaryote, but the sizes of the cells and shapes of the cell-packets do not support such an interpretation. Thus, although it would suit the geochemical evidence perfectly well for the eucaryotic cell to have emerged at any time from about 2 Gyr onward, the oldest really persuasive morphological evidence for that development is not found until about 1.3 Gyr ago.

I refer to microorganisms preserved in locally chertified stromatolites at the top of the indirectly dated Beck Spring Dolomite of

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PLATE 5. Eucaryotes (figures 3–6, and perhaps 2, 7, and 9–14) and other microbial forms from cherts ~ 1.3 Gyr (A) and ~ 0.8 Gyr (B) old. All figures are photomicrographs of thin sections.

A. Beck Spring microbiota, eastern California (loc. 3 of 8/11/68, except figure 2).

FIGURE 1. The dominant mat-forming nostocacean cyanophyte responsible for stromatolite construction.

FIGURE 2. Highly refractive spheroidal structure with central plug similar to mineralized cysts of chrysophycean algae such as *Uroglena* (e.g. Huber-Pestalozzi 1962, pp. 179–181). Loc. 3 of 24/11/66, a nonstromatolitic chert.

FIGURES 3–4. Large diameter, dichotomously and laterally branched, sparingly but unequivocally septate, probably eucaryotic filaments with similarities to siphonaceous chlorophytes and chrysophytes. These specimens 30–50 μm in diameter; range for form 15–60 μm. Note fungus-like septum in figure 4. From stromatolitic chert.

FIGURES 5–6. Large diameter unicells interpreted as probable chlorococcalean (and chlorosarcinacean) chlorophytes. Diameter these specimens 20–45 μm; range for form 19–62 μm.

FIGURE 7. Unicells of possible chlorosarcinacean affinity embedded in sheath-like brownish residue. These specimens ~ 8–12 μm, but range for form 6–25 μm. Note dark subcentrally located spots which Licari (1971) observed in 134 of 165 unicells of this type counted.

B. Bitter Springs microbiota, central Australia (from gift collection by Alistair Stewart at locality about 65 km ENE of Alice Springs except for Figure 11; see Schopf 1968 for details).

FIGURE 8. Cluster of smooth chroococcacean cyanophytes (*Myxococcoides minor* Schopf) embedded in common sheath. Note dark shrunken cell contents in three cells at top and similar but light cell contents of one cell at lower left.

FIGURES 9–10, 12–14. Unicells with peripheral dark inclusions interpreted as probable chlorosarcinacean chlorophytes (*Glenobotrydium*). Note punctate multiple sheaths in figure 10 and common sheath around just-divided cells of figures 12 & 14. Cell diameter these specimens 7–10 μm, range of 129 cells counted by Schopf 7–12 μm.

FIGURE 11. Tetrahedral tetrad of *Eotetrahedrion princeps* Schopf & Blacic (after Schopf 1972, Fig. 38b).

FIGURES 15–16. Degraded cyanophycean filaments within well-defined sheaths.

FIGURE 17. Probable nostocalean cyanophytes *Anabaenidium johnsonii* Schopf and *Caudiculophycus rivularioides* Schopf.

eastern California (Plate 5A). The conclusion that eucaryotes are represented in this microbiota is based on micromorphological evidence first noted by Cloud et al. (1969) and explored in detail by Licari (1971). The two main features that strongly imply an eucaryotic component in the Beck Spring microbiota are:

(1) Apparently smooth, *dichotomously and laterally branched*, organic walled, *filaments with diameters from 30 to 60 μm and rare septa or cross-walls* (Plate 5, figures 3–4)—resembling certain siphonaceous chlorophytes (e.g. *Derbesia*) and chrysophytes (e.g. *Vaucheria*).

(2) Reticulate to granular, organic walled, subsphaeroidal *unicells that commonly exceed 40 μm and range up to 62 μm in diameter* (Plate 5, figures 5–6), locally crowded or dispersed in a common matrix of sheath-like matter. Showing probable binary cell division reminiscent of the chlorophyte family Chlorosarcinaceae.

Additional evidence that may be supportive but is possibly spurious includes:

(3) Small (~ 5μm diameter), mineralized, cyst-like structures with crystalline spikes and plugs (Plate 5, figure 2) reminiscent of the resting spores of chrysophycean algae such as *Uroglena*.

(4) Abundant subspheroidal unicells 6–25 μm (mean 14.5 μm) in diameter that are typically crowded, strung out in linear aggregates, or dispersed within what appears as a common sheath-like material (Plate 5, figure 7). A count of such cells by Licari showed that 134 out of 165 cells had subcentrally located dark spots or aggregates of spots that differ from the usual collapsed cell contents (e.g. Plate 5, figure 8) in their much smaller size and regular location. Their prevalence would be consistent with an interpretation as ghosts or pyritic replacements of organelles of some sort, and at least six well-authenticated instances of the preservation of cell organelles as fossils are known (Schopf 1974). In addition the manner of dispersal of the cells within a common sheathlike matrix looks suggestively eucaryotic. Nevertheless, as Knoll and Barghoorn (1975) have properly insisted, a case for eucaryotic affiliation cannot be made on such evidence alone. If these "spotted" cells were to prove to be eucaryotes, however, their apparent binary cell division would suggest assignment to the chlorosarcinacean Chlorophyta.

I hasten to qualify the 2d and 3d lines of evidence mentioned in the paragraphs above—relating to cell size and chrysophycean-like cysts. Although the large-diameter unicells are much larger than nearly all known procaryotes, one living coccoidal cyanophyte *Anacystis dimidiata*, is reported to attain a diameter as great as 50 μm (Drouet and Daily 1956, p. 71). It is also reported, though not confirmed by published records with which I am familiar, that diameters up to 60 and even 80 μm are now known among several different cyanophyte species (Lynn Margulis, oral communication, 8 July, 1975). In the case of the chrysophycean-like structures we do not observe plausible active stages or microcytological data that would clinch the suggested affinities, and other characteristics of these bodies suggest that they *could* be diagenetic or secondary artifacts of some sort.

Despite these qualifications, as well as the absence of diagnostic ultramicroscopical or biochemical data on cell organelles, it is statistically much more probable that unicells with diameters of 40 to 62 μm are eucaryotes than that they are procaryotes, particularly if we allow for shrinkage on fossilization. In addition the large-diameter, branching, sparingly but unquestionably septate tubes come close to compelling evidence for an eucaryotic affiliation. The suggestion by Schopf (1975) that they might be boring cyanophytes or abandoned cyanophytic sheaths is simply not tenable for structures displaying such cross walls (Plate 5, figure 4) no matter how uncommon the cross walls may be.

In dealing with the fossil record it doesn't make sense either to argue that we must demonstrate electron-microscopically the existence of membrane bound organelles, 9 + 2 flagella, basal bodies, etc., before an eucaryotic affinity can be considered likely in the face of the large dimensions and distinctive micromorphology noted above.

On the subject of cell size and eucaryotic affinities, it has long been realized by Soviet

workers that the individual members of their "sphaeromorph" assemblages increase in size with decreasing age and that maximum cell size in an assemblage might have stratigraphic significance, as recently summarized by Timofeev (1973b). Indeed it was the Soviet data, plus my own confirmation and extension of it in both unicells and filaments, that initially caused me to question the alleged biological affinities of aberrantly large microstructures described by various authors from Archean rocks in the Barberton Mountain Land and by Gowda and Sreenivasa (1969) from the Archean of south India. The limited data available, in fact, indicates that the prevalent size of cells and filaments in authentic microbiotas ~ 1.6 Gyr old and older ranges from barely 1 to rarely as much as 30 μm. In the ~ 1.3 Gyr old Beck Spring and microbiotas of equivalent or younger age, unicells and filaments > 40 μm and even > 60 μm in diameter are added. This shift in size has recently been quantitatively evaluated by Schopf and Oehler (1976), who place it at 1.4 Gyr and correlate it with the appearance of the eucaryotic cell. This is certainly a defensible working hypothesis, even though the dating is shaky on all counts and the actual transition from procaryote to eucaryote *may* have occurred as early as ~ or > 1.5 Gyr (Oehler et al. 1976) or possibly earlier (although probably not before ~ 1.8 to perhaps 2 Gyr ago, when atmospheric O_2 concentrations first reached or exceeded ~ 1% PAL).

On up the geological column above the Beck Spring Dolomite we encounter younger microbiotas that probably also contain eucaryotes. The most impressive of these so far is the perhaps 800 to 900 Myr old Bitter Springs microbiota described by Schopf (1968), by Schopf and Blacic (1971), and recently, in ultrastructural detail, by Oehler (1976). That will be discussed in the next section. Here it suffices to note that, although I would not rule out completely the *possibility* of an eucaryotic component in the ~ 2 Gyr old Gunflint microbiota, the oldest convincing eucaryotes are, in fact, those from the ~ 1.3 Gyr old Beck Spring microbiota. By convincing I do not mean to imply that there is no room for argument, but that the probability of their being eucaryotes is so high that the burden of proof rests on those who would claim a procaryotic affinity.

As to the broader biogeochemical consequences of the Eucaryota, they are extensive. Because such organisms cope well with oxygen, and because the level of O_2 required for eucaryotic metabolism would assure the presence of an ozone screen, they could grow abundantly under higher levels of O_2 and in a wide spectrum of shallow aquatic habitats that had previously been excluded as permanent sites of life because of high energy UV irradiation. The probable consequences of this are that sedimentary segregation of carbon increased, more O_2 accumulated, more CO_3^{-2} and SO_4^{-2} became available for formation of carbonate sediments and later sedimentary sulfate, and the stage was set for the origin of sexuality (if it did not originate at the same time as the eucaryotes themselves), of Metazoa, and of advanced plants.

In addition, the biogenic precipitation of silica becomes possible and perhaps probable with the appearance of eucaryotes (no procaryotes are known to precipitate silica). That could lead (after silica precipitators arose) to the reduction of dissolved silica in the oceans toward present undersaturated levels, with the result (among others) that direct chemical precipitation of silica from open marine waters, such as is associated with the deposition of the typical BIF, would come to an end.

Less obvious is the implication that cytochrome-*c*, superoxidase dismutase, and the oxygenases, the latter essential for the oxidation of cell membrane steroids and implying a *minimum* O_2 pressure of 10^{-5} PAL (M. Ycas, personal communication), had to have existed before the eucaryotic cell itself, although the common occurrence of red beds in rocks as old as 1.8 Gyr or more suggests that such an O_2 level of 10^{-5} PAL was exceeded long before the Beck Spring eucaryotes.

In brief, the appearance on Earth of a biologically generated level of free $O_2 > 10^{-2}$ PAL, followed by or accompanied by the emergence of an eucaryotic level of organization was, after initial outgassing and the origin of life itself, the most important set of related events, not only in the history of life, but also of biogeochemical, atmospheric, and sedimentary evolution. The timing and circumstances of eucaryotic origin are subjects whose surpassing interest is exceeded only by the need for further research on them.

Origin of Sexuality and its Consequences

Given the presence of eucaryotic ancestors, the next big step on the evolutionary path to Metazoa and vascular plants—unless it happened simultaneously with the eucaryotic state (Cavalier-Smith 1975)—was the origin of sexuality, as manifested by meiotic cell division, with all its potentiality for subsequent evolutionary diversification via sexual recombination and selection (Table 1). Again we do not know how or precisely when it happened, but we know that sexuality was already prevalent by about 680 to 700 Myr ago, because that is the age of the oldest known Metazoa (Ford 1958; Cloud 1968b).

As the development of eucaryotic sexuality was a prerequisite to the metazoan level of evolution, it must have originated before ~ 700 Myr ago, in pre-Phanerozoic time. One late pre-Phanerozoic record of probably sexual organisms is provided by the dasycladalean-like *Papillomembrana*, described from rocks beneath the Moelv glaciogene deposits of southern Norway by Spjeldnaes (1963). Another comprises megascopic, probably brown algae (*Vendotaenia* and *Tryrasotaenia*) described from sediments of similar stratigraphic position near Leningrad by Gnilovskaja (1971). And a third may be the suggested limber megascopic algae that made curvate dragmarks in central Australian deposits estimated to be ~ 760 Myr old (Milton 1966).

Thus one is prepared to consider favorably evidence advanced by Schopf (1970, pp. 340–341, 1972, 1975) for an eucaryotic component in the perhaps 800 to 900 Myr old Bitter Springs microbiota of central Australia. His key points concern the presence of (1) regularly located internal bodies in many cells of the genera *Glenobotrydium* and *Caryosphaeroides* that can be interpreted to suggest nuclei or other cell organelles (Plate 5, figures 9–10, 12–14), (2) triradiate surface markings and one tetrahedral tetrad (Plate 5, figure 11) suggesting the tetradal spore formation of eucaryotes, most commonly resulting from meiotic cell division, (3) forms that generally resemble pleurococcacean, chlorosphaeracean, and chlorellacean chlorophytes, and (4) unbranched, predominantly nonseptate filaments 2 to 4.5 μm in diameter (*Eomycetopsis*) interpreted by Schopf as probable fungi. Altogether 9 out of 50 named Bitter Springs species have been assigned to the Eucaryota (Schopf 1970, 1972; Schopf et al. 1973).

Unlike Knoll and Barghoorn (1975), I find the total effect of the evidence summarized strongly persuasive for the presence of eucaryotes in the Bitter Springs microbiota, especially in view of the highly probable presence of an eucaryotic component in the much older Beck Spring microbiota discussed above. Although disagreement has arisen about the likelihood of preservation of cell organelles in fossils, such preservation is well documented by the work of Bradley (1962) and others cited by Schopf (1974), and Schopf's data is highly suggestive, presented with appropriate reservation, and backed up by the ultrastructural studies of Oehler (1976) and a recent review of the problem by Schopf and Oehler (1976). Thus, although the evidence may not be as airtight as a molecular biologist or biochemist might like, I hold serious reservations only about the affinities of the proposed fungi and the strength of the argument that triradiate markings and tetrahedral tetrads are sufficient evidence of meiotic cell-division and thus of sexuality.

The problem with a fungal presence is that *Eomycetopsis*, either from Australia or from much older rocks in the Belcher Islands (Hofmann and Jackson 1969), shows no features suggestive of fungi beyond the fact that it is a sparingly septate tube with constrictions at the sites of the septa. It may, to be sure, be a fungus, but it might also be a siphonaceous alga of some type, perhaps even a cyanophyte. To interpret it as a fungus is not only to hypothesize the existence of fungi at a time when O_2 was probably still barely 1% PAL or less (Belcher Islands record) and without an obvious host or symbiotic organism, but also to take issue on slender grounds with the growing judgement that "the derivation of the fungi from the algae presents more difficulties than does a theory of protozoan origin" (Martin 1968, p. 639; summarized by Broda 1970, pp. 191–192). In this connection, it is perhaps also noteworthy that Protozoa have not yet been observed in pre-Phanerozoic rocks and probably did not long antedate the appearance of the Metazoa. Thus, a protozoan ancestry for the fungi would not only eliminate *Eomycetopsis* as a fungus, but also *Archaeorestis* Barg-

hoorn and the lopsided division pairs from Gunflint strata suggested by Darby (1974) as advanced yeast-like fungi. Even if the fungi were polyphyletic we lack convincing evidence for their pre-Phanerozoic presence.

That leaves the triradiate markings and the tetrad (Schopf 1970, 1972; Schopf and Blacic 1971; Schopf et al. 1973). Brown and Bold (1964), however, find the formation of tetrads to be common in the chlorosarcinacean green algae *Tetracystis*, while Y-shaped triradiate scars defining ~120° angles are common among living coccogonophycean (Cloud et al. 1975) cyanophytes and easily produced in abiogenic microspheres (Plate 1, figure 16). In a comprehensive review of this matter, Oehler et al. (1976) have noted some 8 additional coccoid cyanophytes that form non-meiotic tetrahedral tetrads in one of which (*Mycacanthacoccus cellaris*) they are thickly ensheathed. They also note the formation of non-tetrahedral tetrads by accidental clustering or division (as in Plate 5, figure 14) and the formation of real tetrahedral tetrads even in the procaryotic *Synechocystis* (per S. Golubic). They point out that enveloped tetrahedral tetrads of *algal* cells are mainly the product of mitotic reproduction among coccoid chlorophytes.

That seems to dispose of the argument for meiosis and sexuality in the Bitter Springs microflora based on evidence presented, and perhaps that was the main extrapolation to which Knoll and Barghoorn (1975) objected. Indeed, Schopf (1975, p. 232) now concedes *that* point, although still finding the tetrahedral tetrads of *Eotetrahedrion* (Plate 5, figure 11) "strongly suggestive of the existence of eucaryotes" (letter of 1 April, 1976, to Cloud).

However, the existence of meiotic, sexual, reproduction long before the wave of metazoan diversity that initiated the Phanerozoic Eon is supported by other evidence. That evidence is not compelling by any means, but sufficiently strongly suggestive to warrant serious consideration by anyone not already committed to the view that meiosis was the trigger for metazoan evolution and therefore necessarily barely preceded the oldest Metazoa. Although scarcely in the realm of hard evidence, the views of Cavalier-Smith (1975) about eucaryote origins (summarized above) contradict those of Schopf et al. (1973) that so many steps are involved in the transition from simple haploid-dominant mitosing cells to mainly diploid-dominant meiotic cell division that the process may have consumed much time (i.e. from ~1.3 Gyr or more ago to ~0.8 to 0.9 Gyr ago), and that attainment of meiosis may be the evolutionary trigger that set off the burst of multicellular evolution for which we see evidence in rocks younger than about 700 Myr.

More explicit evidence is found in a recent restudy by Walter et al. (1976) of long ribbon-like megafossils referred by Walcott to "*Helminthoidichnites*" and a second megascopic form, *Beltina*, from the ~1.3 Gyr old Greyson Shale (Belt Supergroup) of Montana. Walter et al. reasonably conclude, on grounds of size and complexity, that the forms in question are eucaryotic multicellular algae. This would support the idea that not only eucaryotes but also sexuality were extant much earlier than has previously been directly suggested by anyone. If their interpretation is correct, and I see no reason at this time to dispute it, Cavalier-Smith's conjecture about the essential simultaneity of origin of mitotic and meiotic cell division would be consistent with the biogeological evidence to date that mitosis almost certainly and meiosis probably were both extant by 1.3 Gyr BP. I say probably rather than possibly on theoretical grounds highlighted by Cavalier-Smith (1975). If too long a space of time is allowed between the origin of mitosis and that of meiosis, one is forced to hypothesize (as Margulis 1970 did) multiple independent origins of eucaryotic sexuality. Indeed, *if* a tetrahedral tetrad from the Amelia Dolomite of northern Australia is a meiotic product and is correctly dated at ~1.5 Gyr old (Oehler et al. 1976), eucaryotes, and, consistent with Cavalier-Smith, sexuality *may* both have been present by ~1.5 Gyr ago.

Whatever the timing, an interesting consequence of eucaryotic sexuality is that it fulfills one of the two essential preconditions for the advance from a cellular to the tissue and organ level of somatic complexity observed in the subsequent origin of differentiated multicellular animals and plants. The other precondition is a sufficient level of free O_2, seen at the onset of Phanerozoic time. Apart from this we would expect that, with the genetic diversity generated by sexuality, evolution

generally might be speeded up; that later-deposited fine-grained or chemical sediments would eventually come to contain a diversity of Protista (including Protozoa), some ancestral to Metazoa; and that biogenic concentration of trace elements might become a more prevalent aspect of sedimentation. All of these effects should be sought in the rocks as additional clues to the time of origin of eucaryotic sexuality.

Metazoa, Exoskeletons, and Early Land Plants

The origin of multicellularity in the sense of cellular differentiation into function-specific tissues, and later organs, is the last step in early evolution, antecedent to Phanerozoic metazoan diversification and the advanced land plants, culminating in tracheophytes with roots and vascular tissue.

The oldest known metazoan fauna is the soft-bodied Ediacarian fauna, now recorded from South Australia, S. W. Africa, England, Sweden and both the European and Asiatic parts of the USSR (Glaessner and Daily 1959; Glaessner 1966, 1971; Germs 1974; Ford 1958; Krylov in Rosanov et al. 1969, pp. 258–264; Sokolov 1972; Keller et al. 1974; Stanley 1976, pp. 58–60). It may also be represented by soft-bodied metazoans from Newfoundland (Anderson and Misra 1968) and perhaps by large wormlike imprints from North Carolina (Cloud et al. 1976), as well as British Columbian trace fossils of unknown affinity (Young 1972). The age of this fauna appears to be ~ or slightly > 680 Myr in England, where it is well dated on essentially coeval porphyroids (Evans et al. 1968). A similar age is suggested for the Soviet occurrences (e.g. Sokolov 1972). The volcaniclastic sediments that contain the wormlike imprints from North Carolina are correlated with volcanics that give a Pb-U zircon concordia age of 620 ± 20 Myr, and Anderson (1972) reasonably estimates from indirect evidence that the age of the Newfoundland material is about the same. The Edicarian-like fauna from S. W. Africa is bracketed between ~ 700 and ~ 550 Myr (H. L. Allsopp, letter of 7 October, 1975) and probably lies high in that range, as it is associated with shelly cribricyathids of Early Cambrian aspect (Germs 1972). Thus, rounding off, the interval from ~ 700 to ~ 600 Gyr ago is the approximate age range of the rather impoverished but highly significant, mainly soft-bodied, initial Metazoan fauna—the Ediacarian fauna, used in a somewhat sweeping sense.

What is the nature of this basal Phanerozoic, soft-bodied, Ediacarian fauna and its relation to the succeeding shelly faunas of Cambrian and younger age? The most recent tabulation of the type Ediacarian fauna (Stanley 1976) lists only 27 species, of which fully 19 are cnidaria ("coelenterates") and 5 are flat-bodied annelid-like forms, two of which may be transitional to arthropods. The remaining 3 are oddities that may be ancestral arthropods and echinoderms. A few trace fossils of possibly annelidan or molluscan affinities may be added to round off the diversity at maybe 30 species. Forms described from other continents add a bit of specific diversity but no significant change in the general picture beyond the cribricyathids mentioned.

This reads, not unexpectedly, like the earliest metazoan fauna predicted either from considerations of oxygen supply and diffusion mechanisms (Raff and Raff 1970) or from conventional zoological phylogenies, with perhaps one surprise. Some of these organisms, although thin and flimsy as predicted, had very large surface areas. I have collected fragments of the sheetlike annelid *Dickinsonia* that imply the whole animal would have attained a length of perhaps 40 to 50 cm and a width 65 to 75% as great. Specimens and fragments of *Dickinsonia*, however, are commonly wrinkled and folded on themselves, indicating inconsequential thickness. The cnidarians are jellyfish-like or frondose. Some S. W. African forms bulk larger in the rock but apparently had flimsy walls and large central cavities. Thin walled but large wormlike organisms from ~ 620 Myr old rocks in North Carolina (Cloud et al. 1976) attained lengths of more than a meter and diameters of around 1.2 cm. They seem to have been large but flimsy organisms, as do the Ediacarian-age trace fossils from British Columbia (Young 1972) and the Conception Group imprints from Newfoundland (Anderson and Misra 1968).

The matter of size, of course, is a critical one because many have argued that the initial metazoans must have been so tiny as to have a low probability of being found or recognized if found. On the face of it that sounds likely,

but is it? In the initial phases of metazoan evolution the only factors limiting size would have been mechanical support and oxygen supply. In the marine aqueous medium, in which the body chemistry of organisms tells us life originated (Banin et al. 1975), and in which the oldest Metazoa we know lived and presumably evolved, oxygen would have been a critical factor. The first Metazoa, before the evolution of advanced respiratory systems, would have been limited in tissue thickness, but not in area by their dependence for oxygen on its diffusion from the ambient hydrosphere to their cytochrome oxidase systems. They were necessarily soft-bodied because a skeletal cover would have vitiated the essential diffusion process.

Raff and Raff (1970) have employed a Taylor series expansion method to solve the steady state diffusion equation governing tissue thickness at different pressures of O_2 and rates of O_2 consumption. Their graphs indicate that at 1% present atmospheric level of O_2 (PAL = ~ 160 mm of Hg) maximum thickness of whole animal or of cellular or tissue sheets surrounding a freely circulating body cavity could have been only ~ 0.1 mm. But studies cited by the Raffs show that the modern polychaete *Arenicola marina* is able to operate at oxygen tensions as low as 4.2 to 8.4% PAL, while the cytochrome oxidase respiratory system of *Siphonosoma ingens* can operate at 1.9 to 6.2% PAL (3–10 mm Hg). At the latter level, which may have been high enough for the evolution of a respiratory system more advanced than diffusion systems, tissues ~ 1 mm thick are possible at low rates of O_2 consumption.

It is fair to hypothesize therefore, that the first Metazoa may have arisen from protozoan ancestors when, as a result of photosynthesis accompanied by sedimentary segregation of carbon, O_2 tension approached or attained ~ 6.2% PAL—corresponding to 10 mm Hg in the atmosphere and 0.6 to 0.3 ml/l dissolved O_2 in seawater of normal salinity over a temperature range of 2 to 30°. That is consistent with but refines previous suggestions by Cloud (e.g. 1968a, 1968b, 1974a) and by Rhoads and Morse (1971). It is, however, six times the frequently quoted O_2 level proposed by Berkner and Marshall (1964 and later) as suitable for metazoan emergence in their seminal pioneering assessment of the problem.

I suggest, in effect, that the 1% PAL level of free O_2 was first exceeded around the time of the onset of red beds or the possible emergence of eucaryotes. As eucaryotes, and probably eucaryotic sexuality, however, were already present hundreds of millions of years before the first Metazoa, it then becomes attractive to hypothesize that the trigger for metazoan emergence may have been the (probably gradual) attainment of a level of O_2 sufficient to bring on first the evolution of improved diffusion systems, and then systems advanced beyond simple diffusion. From the above, that would appear to have been ~ 6% PAL, and the geologic record seems to tell us that it happened ~ 700 Myr ago.

Because of their dependence on diffusion for their O_2 supply, primitive metazoans were thin and weak-bodied but some of them had large surface areas. As many of them were floaters, and others probably had planktonic larvae, they became widely distributed and are now found, although rarely, in suitable facies of marine sedimentary rocks over a large part of the planet. In addition to their cytochrome oxidase respiratory systems, another metazoan biochemical innovation probably was the enzyme DNA polymerase-β (Chang 1976), although how this might be reflected in biogeochemistry is hard to imagine.

The step in metazoan evolution that for reasons perhaps related to preservation and abundance seems to impress Phanerozoic paleontologists as more significant than the origin of the Metazoa themselves is the evolution of a calcareous exoskeleton. Many explanations have been offered for this, but we owe to Raff and Raff (1970) the clue to the probable one. As O_2 levels continued to increase and circulatory systems evolved, body surfaces no longer needed to be in contact with an external source of O_2. Thus mutations toward integumentary shielding and stiffening, previously lethal, would be viable, and the way would be open for the evolution of calcareous, calcareophosphatic, and chitinous exoskeletons, along with the more complicated and diverse forms of life that became possible with hard parts for leverage and articulation. This may have happened ~ 600 Myr ago, perhaps at ~ 10% PAL free O_2, as suggested by Rhoads and Morse (1971) from their analysis of faunal

types at different dissolved O_2 levels in existing marine basins. And that would closely approximate the time of first appearance of the currently conventional basal Cambrian skeletal biotas (e.g. Rosanov 1967, Rosanov et al. 1969; Zhuravleva 1970; Semikhatov 1974; Cowie and Rozanov 1973).

Indeed, as Stanley (1976) has stressed, there is really nothing mysterious about the appearance of skeletal biotas when viewed in biological context—"Major skeletal taxa appeared sequentially, not simultaneously, as one aspect of the initial divergence of the Metazoa. The appearance of a skeletal record in the Cambrian was simply part of the general diversification." What remains as the "Cambrian problem," as Stanley aptly puts it "is the delay of the origin of multicellularity"—a delay that I would relate first to the suppressed and then to the gradual accumulation of free O_2 in the face of thermodynamic forces that makes it a biogeochemical anomaly of first magnitude. The hypothesized relationships of O_2 to metazoan and other aspects of biospheric evolution are indicated in Figure 2.

The biogeochemical consequences of skeletonization are, of course, enormous. Skeletonized Metazoa, in combination with algae, have been reef-builders from Early Cambrian to the present. And, they, in combination with the Protozoa and calcareous algae, have tended to suppress dissolved $CaCO_3$ in the surface waters of the earth to levels such that the balance in the formation of carbonate rocks was shifted to the biosphere. From processes perhaps mainly physicochemical during sub-Cambrian history (with some assistance from CO_2 assimilation by algae), the formation of carbonate sediments seems to have become increasingly a function of the accumulation of skeletal debris and the biologically induced precipitation of $CaCO_3$ from the Cambrian onward.

At last we come to the early plants. As observed previously, available evidence says that multicellular eucaryotic algae were present by 700 Myr ago and possibly much earlier. Such plants show an alternation of sporophyte and gametophyte generations and may be expected to have further differentiated into reproductive and somatic tissues in the gametophyte generation.

The consequences of this could have been far reaching. At any time thereafter, given suitable mutational stimuli, mosses, liverworts, and vascular plants may have arisen, and any of these could have colonized the land, with profound effects on rock weathering, soil formation, stream regimens, and fluviatile sedimentation. Although the oldest body fossils definitely assignable to tracheophytic plants are still late Silurian (Banks 1970, pp. 56–59; Kevan et al. 1975) and thus only ~ 400 Myr old, and although bryophytes are not surely identified until later, we should not be surprised if it turns out that these records do not represent the first appearance of the levels of plant evolution represented, let alone the oldest land plants. Studies of Paleozoic spores by Gray and Boucot (1971, 1972), for instance, have revealed tetrahedral tetrads of early Silurian and late Ordovician age (~ 450 Myr) that these authors believe to represent the spores of vascular land (or semiaquatic) plants, although "a bryophyte origin cannot be precluded" (nor, I dare say, an advanced algal origin).

In any event, somewhere between ~ 400 and ~ 700 or more Myr ago, a terrestrial vegetation came into being; probably, according to current convention, from polyphyletic sources. It was most likely a wetland vegetation to begin with, located along estuaries, rias, and their upstream continuations, but spreading *via* wind transport of spores to wet sites inland. And it may have started from things like the probable dasycladalean *Papillomembrana* from the late pre-Phanerozoic of Norway (Spjeldnaes 1963). With time and evolutionary advancement, the lands generally became colonized and prepared for the later invasion of Metazoa.

Clues to the timing of such changes might come from sufficiently perceptive geochemical, textural and structural studies of older Phanerozoic and younger pre-Phanerozoic terrestrial sediments. Uncommon though the latter are, they do exist, and the ion-exchange effects of plant acids on feldspars and micas ought to show up in the chemistry and crystallography of paleosols, terrestrial sediments, and perhaps even marine clays. The effects of a land flora, even a primitive flora, in stabilizing stream courses and retaining sediments from overbank floods ought to show up in the local segregation and channeling of fluviatile sediments.

It is a happy aspect of our times that, even

as specializations proliferate, sciences once considered separate grow closer to one another and new interdisciplinary pursuits like biogeology arise. Given a continuing healthy interplay between related aspects of biology, paleontology, chemistry, and geology, we may yet come to apprehend and perhaps even to understand the beginnings of biospheric evolution and to perceive more clearly their biogeochemical consequences.

Summary

Biogeochemical consequences of biospheric evolution react upon their generative base, and both interact with the related evolutions of atmosphere, hydrosphere, and lithosphere. Such mutual feedbacks provide the evidence from which historical biogeology is reconstructed. This evidence is beset with pitfalls. Both biogenicity and primary origin need to be demonstrated, or confidence ratings estimated, for each supposed geochemical and micromorphological fossil. Relevance to biospheric or related evolutions must be critically evaluated for every geochemical and sedimentological anomaly.

The highest level of confidence rests on distinctive cytological or microstuctural differentiation, comparable with that of living organisms and implying a similarity of function and a continuity of evolution between them. Post-depositional introduction of microbiological and geochemical contaminants, and a variety of pseudofossils and dubiofossils are ubiquitous hazards.

Suggestive, if not compelling, indirect evidence (banded iron formation, stromatolites, red beds, and other data bearing on likely types of microbiological activity and ambient O_2 levels) offers important clues to both microbiological and biochemical evolution. Such data imply that the first presumably anaerobic and heterotrophic forms of life had already appeared and evolved to protocyanophytic photoautotrophs by ~ 3.8 Gyr (years $\times 10^9$ or gigayears) ago. Free O_2, on the other hand, first began to accumulate as a conspicuous atmospheric and hydrospheric gas only ~ 2 Gyr ago. Meanwhile ferrous iron in solution was probably an important acceptor for biogenic O_2 produced in excess of primitive anaerobic or microaerophilic tolerances.

The oldest demonstrable biogenic and primary fossils are cyanophytes, probably budding bacteria, and forms of uncertain affinities from rocks of the ~ or > 2 Gyr old Gunflint, Biwabik, and Pokegama strata of southern Ontario and northeastern Minnesota (microorganisms from the > 2.25 Gyr old Transvaal carbonates from South Africa are clearly biogenic and seemingly indigenous, but reservation has arisen concerning their primary origin). Advances in enzymatic O_2 mediation, with continued segregation of carbon, led to final filling of O_2 sinks, the beginning of large-scale evasion of O_2 to the atmosphere, and the development of an ozone screen about or shortly after 2 Gyr ago. Biogeochemical consequences were the termination of banded iron formation as a common sedimentary rock, initiation of widespread red-bed sedimentation, and the need for biological shielding of essential intracellular anaerobic processes—evolving toward membrane-bound cellular organelles and the eucaryotic cell.

Unicells up to 62 μm in diameter and large-diameter, branching, sparingly but definitely septate filaments imply an eucaryotic origin for elements of the ~ 1.3 Gyr old Beck Spring microbiota of eastern California. Thus the eucaryotic level of development appears to have been reached by ~ 1.3 Gyr ago. Indeed from inferred O_2 tensions, it could have appeared at any time after ~ 1.8 to perhaps as much as 2 Gyr ago (Figure 2). The biogeochemical consequences of this crucial biological innovation, itself subordinate in importance only to the origin of life, were probably increases in atmospheric O_2, carbonate and sulfate ion in the sea, carbonate rocks, and eventually the deposition of sedimentary sulfates, coupled with the stabilization of the ozone screen and the rise of sexuality.

Since sexuality had to precede the origin of the Metazoa, it necessarily evolved before the oldest known Metazoa ~ 680 to perhaps 700 Myr (years $\times 10^6$ or megayears) ago. Older advanced algae imply sexuality well before 700 Myr ago. And, as separate origins for meiosis in different mitosing ancestors complicates the evolutionary model beyond belief, it seems likely that sexuality may have originated with or soon after mitosis itself. The origin of sexuality completed the evolution of the eucaryotic hereditary mechanism. This important development, along with the growth of

atmospheric oxygen, paved the way for multicellular differentiation into tissues and organs, with all its potentialities for subsequent biological elaboration and biogeochemical feedback to the evolution of hydrosphere, sedimentary and diagenetic processes, and even the formation of some of the ore deposits that have allowed mankind to charter new modes and directions of evolution.

The earliest Metazoa were thin and soft-bodied because they obtained their oxygen by diffusion alone. Skeletons would have blocked the diffusion of O_2 and hampered a floating existence in the better aerated surface waters. Some of these primitive Metazoa, however, had large surface areas. With further increase of O_2 and the evolution of more advanced respiratory systems, skeletonization became possible, and, with it, new opportunities for increasing complexity and protection. Subsequent biospheric evolution is common knowledge.

Data and ideas central to this model of early biogeology are summarized in Table I and Figures 1 and 2.

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MICROFLORAL LOCALITIES

The following collections were made by the writer on the dates indicated (day/month/year as in international usage):

1 of 25/8/63 Animikie Group, Gunflint Iron Formation, basal stromatolitic chert; age ~ 2 Gyr (Goldich in James and Sims 1973). About 4 km west of Schreiber Beach and 6.5 km west-southwest of the town of Schreiber, Ontario, Canada, north shore of Lake Superior opposite a small island called Slate or Flint Island. Nb. 34, p. 20.

3 of 3/10/64 Animikie Group, Pokegama Quartzite, basal cherty facies; age ~ 2 Gyr (Goldich in James and Sims 1973). About 670 to 740 m N 60° E from prominent water tower near center of Eveleth, northeastern Minnesota, USA. Nb. 35, p. 17. Fossiliferous chert taken from a crack-filling in underlying Archean metasediments that apparently comprised a low rocky coast at the time of basal Pokegama sedimentation.

3 of 20/7/65 Paradise Creek Formation, lower Alpha zone of Robertson (1960); age ~ 1.6 Gyr (Licari et al. 1969). About 113 km airline N of Mt. Isa and downstream from Lady Annie Mine on south bank of Paradise Creek, 1/250,000 Camooweal Sheet, northwest Queensland, Australia. Nb. 36, pp. 23–24. Early chert replacement of small, branching, columnar stromatolites (*Eucapsiphora*) coating prior dolomitic pinnacle to make small stromatolitic dome.

4 of 20/7/65 Paradise Creek Formation, Beta zone of Robertson (1960), age and locality as 3 of 20/7/65 but ~ 15 m lower in section. Nb. 36, p. 25. Sample taken within large chert-replaced domal bioherm.

2 of 2/8/65 Tolmer Group, Hinde Dolomite; age 600–700 Myr (Dunn et al. 1966). East slope of Mt. Hinde, ~.15 m above surrounding flats, 1/63,360 Burnside Quadrangle, Northern Territory, Australia. Nb. 36, pp. 42–43.

1 of 9/9/65 Transvaal System, Dolomite (or Oliphants River) Group, ~ 100 m below top in cherty stromatolites of "main stromatolite horizon," age > 1.95 (Nicolaysen et al. 1958; Davies et al. 1970) and probably > 2.25 Gyr based on new Rb/Sr whole rock ages on the overlying Pretoria Group (A. Button, oral communication). About 8 km north of Lime Acres at north boundary of Farm Adams, N. Cape Province, S. Africa. Nb. 37, p. 36.

2 of 16/9/65 Onverwacht Group, Swartkoppie Formation, chert at top; age ~ 3.4 Gyr (Hurley et al. 1971). From Sheba Mine, ~ 20 km northeast of Barberton, Transvaal, S. Africa. Nb. 37, p. 45.

3 of 24/11/66 Pahrump Group, Beck Spring Dolomite, nonstromatolitic chert ~ 12 m below contact with overlying Kingston Peak Formation; age ~ 1.3 Gyr (Cloud et al. 1969). Ridge ~ 1.5 km east-southeast of Acme Talc Mine, 1/62,500 Tecopa Quadrangle, southeastern California, USA. Nb. 38, p. 29.

3 of 2/9/67 Miette Group, Hector Formation, Black mudstone 7.5 cm below contact with overlying St. Piran Quartzite (Lower Cambrian); age ~ or > 700 Myr (Moorman 1974). At 2370 m elevation on north slope of northeast spur of Mt. Bell, just south of Taylor Lake, 1/50,000 Lake Louise East Quadrangle, southwest Alberta, Canada. Nb. 38, p. 13.

3 of 8/11/68 Pahrump Group, Beck Spring Dolomite, stromatolitic chert in uppermost bed of unit; age ~ 1.3 Gyr (Cloud et al. 1969). South side of Tecopa Pass Road, ~ 0.8 km east of Horse Thief Spring, at 1230 m elevation along base of spur on east Kingston Range, 1/62,500 Horse Thief Spring Quadrangle, southeastern California, USA. Nb. 38, p. 33.

3 of 10/9/71 Basal Ordovician, Tremadoc age siltstone and shale; age ~ 500 Myr. Small borrow pit on east side of road to Leningrad, at northwest edge of village of Sablino, on left bank of Sablinka River, ~ 30 km southeast of Leningrad, USSR. Nb. 41, p. 91.

1 of 8/12/71 Dharwar System, Guddadarangappanahalli beds; age > 2.34 Gyr (Crawford 1969), probably 2.6 Gyr (Aswathanaryana 1968), and possibly > 3 Gyr BP (Pichamuthu 1971). Collected at an elevation of ~ 830 m, at crest of small spur extending east from 945 m ridge ~ 11 km N 10° E from Chitradurga, Mysore, south India. Nb. 42, p. 21. The rock at this place was pointed out by T. N. Sreenivasa, who guided me to the locality, as the "shale" from which material illustrated by Gowda and Sreenivasa (1969) was obtained. It is a deeply weathered and caliche-infiltrated impure clastic sediment heavily coated with lichens and a black algal growth. I expected it to be contaminated with algal cells from the surface and infiltrating caliche but found instead that the common spheroidal cell-like structures observed in thin section were bubble-like features mainly associated with porous caliche. Particulate matter on the surface and interior gives the appearance of poorly preserved cell wall and internal bodies. The outer surfaces of these bubbles are or were tough enough to bend and rupture. Specimens illustrated by Gowda and Sreenivasa, although said to be entirely from maceration slides, include forms similar to the coated bubbles and other patterns of clustered debris. Others, more cell-like, are considerably larger than one would expect from rocks as old as the basic outcrop appears to be, and, *if biologic*, are probably modern contaminants

that came in with the infiltrating caliche. See Plate 1, figures 8–15.

of 27/8/74 Isua supracrustals; age ~ 3.8 Gyr (Moorbath et al. 1973). Banded iron formation on west slope of hill just north of Kryolitselskabet's Greenmines camp, edge of inland ice, Isua area, Godthåbsfjord region, southwest Greenland. Nb. 44, p. 10.

In addition to above, materials are illustrated from two thin sections loaned by S. M. Awramik: GF-69-4D and 4E. Both from same sample of bedded, non-stromatolitic chert from unit shown as upper Gunflint on Map 1960p (Loon Lake Area) of Ontario Department of Mines; age ~ 2 Gyr (Goldich in James and Sims 1973). About 1.6 km due east of O'Conner Point and west of Sibley Peninsula, north shore of Lake Superior, Ontario, Canada.

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