

ARCHEAN PHOTOAUTOTROPHY: SOME ALTERNATIVES AND LIMITS*

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Abstract. From the Archean geological record, one can infer that photoautotrophy evolved early in earth history; however, the nature of this photosynthesis – whether it was predominantly bacterial or cyanobacterial – is less clearly understood. General agreement that the earth's atmosphere did not become oxygen rich before the Early Proterozoic era places constraints on theories concerning more ancient biotas. Accommodating this limitation in various ways, different workers have hypothesized (1) that blue-green algae first evolved in the Early Proterozoic; (2) that oxygen producing proto-cyanobacteria existed in the Archean, but had no biochemical mechanism for coping with ambient O₂; and (3) that true cyanobacteria flourished in the Archean, but did not oxygenate the atmosphere because of high rates of oxygen consumption caused, in part, by the emanation of reduced gases from widespread Archean volcanoes.

Inversion of hypothesis three leads to another, as yet unexplored, alternative. It is possible that physiologically modern blue-green algae existed in Archean times, but had low productivity. Increased rates of primary production in the Early Proterozoic era resulted in the atmospheric transition documented in strata of this age. An answer to the question of why productivity should have changed from the Archean to the Proterozoic may lie in the differing tectonic frameworks of the two areas. The earliest evidence of widespread, stable, shallow marine platforms is found in Lower Proterozoic sedimentary sequences. In such environments, productivity was, and is, high. In contrast, Archean shallow water environments are often characterized by rapid rates of clastic and pyroclastic influx – conditions that reduce rates of benthonic primary production.

This hypothesis suggests that the temporal correlation of major shifts in tectonic mode and atmospheric composition may not be fortuitous. It also suggests that sedimentary environments may have constituted a significant limit to the abundance and diversity of early life.

Nothing is harder, yet nothing is more necessary, than to speak of certain things whose existence is neither demonstrable nor probable.

Hermann Hesse

A *koan* is a riddle, usually in the form of a brief anecdote or aphorism, employed as a catechetical device in the discipline of Zen Buddhism. Initially the resolution of a *koan* may appear obvious, even trite; but as one continues to contemplate its subtleties, rolling them over in his mind, a variety of new and different interpretations suggest themselves. The riddle is an enigma. Each new insight leads down another path, and no two paths terminate at the same point. One example is the familiar paradox. "What is the sound of one hand clapping?" Another would be the somewhat more esoteric, "What is your face before your parents' birth?" The puzzle of Archean biology constitutes a *koan* of impressive complexity. Numerous lines of evidence, shaded by qualification or uncertainty, combine

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to reveal but a hazy picture of early evolution in which several widely varying scenarios seem possible.

It appears to be reasonably certain that life on earth did exist in Archean times. This statement can be justified, if for no other reason, by the recorded presence of stromatolites in sedimentary rocks up to 3000 m.y. in age (MacGregor, 1941; Joliffe, 1955; Schopf *et al.*, 1971; Bickle *et al.*, 1975; Henderson, 1976; Mason and von Brunn, 1977). However, the nature of early organisms – their abundance and diversity – is less clearly understood. The reasons for this lie in the nature of the evidence itself. Archean stromatolites provide a good example. Most modern microbial mats are built principally by cyanobacteria; therefore, it might seem logical to assume that the oldest known mat-building communities also contained blue-green algae. Unfortunately, the problem is not so simple – bacteria can also build stromatolites. Flexibacteria weave coherent mats in hot spring environments of Yellowstone Park (Walter *et al.*, 1972; Doemel and Brock, 1974), and it is possible that a bacterial community built the columnar stromatolites found in the 2000 m.y. old Gunflint Iron Formation (Walter, 1972). Thus, the presence of stromatolites in Archean sedimentary sequences does not in and of itself constitute proof that oxygen eliminating photoautotrophs existed more than 2500 m.y. ago.

Other lines of evidence are similarly ambiguous. Microfossils preserved in Archean cherts (Muir and Grant, 1976; Knoll and Barghoorn, 1977; Dunlop *et al.*, 1978) are morphologically similar to *Aphanocapsa*-type cyanobacteria, but they also resemble any one of a variety of bacteria, both photosynthetic and heterotrophic. Indeed, from the simple morphology of these bodies, it is difficult to distinguish them unequivocally from hypothesized prebiotic or protobiotic ancestors. The significance of the hematitic iron formation found in many Archean greenstone belts is likewise unclear. The fundamental question in this instance is, "Can significant concentrations of oxygen be produced abiologically by the photodissociation of water vapor in the upper atmosphere?" Opinion has been divided on this issue, but a recent contribution of K. M. Towe (1978) suggests that the answer is "yes" – at least in terms of early earth. Towe points out that molecular oxygen is required for one step in the biosynthesis of chlorophyll *a*. From this he draws the reasonable, in fact necessary, conclusion that oxygen tolerance preceded biological oxygen production. Small concentrations of oxygen were produced abiologically prior to the evolution of aerobic photosynthesis. Does this mean that O₂ bound in the hematite grains of Archean iron formation originated by the photodissociation of water molecules? Not necessarily. Nothing in Towe's biochemical arguments precludes the Archean appearance of physiologically modern cyanobacteria. The jury is effectively hung.

Carbon isotope ratios and the sedimentological distribution of organic matter constitute presumptive evidence for photosynthetic activity in early seas, but again, what kind of photosynthesis was involved, bacterial or cyanobacterial? And is it possible that abiotic processes of chemical evolution could have mimicked biological patterns of isotope fractionation and organic detritus distribution?

1. Limits Imposed by the Early Proterozoic Record

Earliest Proterozoic (and older) continental and deltaic deposits – for example, those of the South African Witwatersrand Supergroup or the lower part of the Huronian Supergroup in Ontario – often contain detrital uraninite and pyrite, but lack red beds. In contrast, red beds are widespread in younger Early Proterozoic sequences. In these rocks, it is the detrital uraninite and pyrite that are missing. It is widely accepted that this temporal change in the constitution of continental sedimentary rocks reflects a contemporaneous shift in the composition of the earth's atmosphere. Specifically, Early Proterozoic sedimentary strata record the initial appearance of free oxygen in the atmosphere (Cloud, 1968, 1973, 1974, 1976).

This interpretation has recently been challenged by Dimroth and Kimberley (1976) who believe that geologic evidence does not support the concept of a pre-Proterozoic oxygen-free atmosphere. It is impossible, in this brief paper, to summarize adequately their arguments, but it should be noted that some of the evidence documented by Dimroth and Kimberley, such as the absence of kerogen in littoral sandstones and limestones, does strongly suggest that at least *some* O₂ was present in the Archean atmosphere. (In the absence of at least a weakly oxidizing atmosphere, it is likely that small amounts of organic matter would have been preserved in these types of sediments.) A similar conclusion seems to be necessitated by the biochemical arguments of Towe (1978), as well as by the very presence of hematite-rich banded iron formation in Archean greenstone belts. Therefore, the critical question is not “*Was* oxygen present?”; it is “*How much* oxygen existed in the pre-Proterozoic atmosphere?” Dimroth and Kimberley maintain that essentially present-day concentrations of oxygen may have been present for the past 3800 m.y., but it is difficult to reconcile this hypothesis with the observed temporal shifts in the abundance of certain important types of sediments. A single example suffices to illustrate the point. If the oxygen content of the earth's atmosphere has not changed significantly during the past 3800 m.y., then it is difficult to explain why detrital uraninite, a widespread component of earliest Proterozoic sedimentary sequences, ceases to be important after that time. If, on the other hand, atmospheric oxygen did increase substantially during the Early Proterozoic, then the dearth of detrital uraninite in younger Precambrian strata can be explained readily (Cloud, 1973). The most reasonable conclusion is that the Archean atmosphere contained very small (<1% PAL, approximately the concentration at which detrital uraninite begins to oxidize rapidly) concentrations of O₂, and that these concentrations rose significantly during the Early Proterozoic era.

Curiously, it is this conclusion, based largely on evidence from Proterozoic rocks, that most strongly constrains hypotheses about Archean life. The way in which one explains the initial rise of atmospheric oxygen determines how one can interpret the carbon isotopic ratios and sedimentary distributions, the banded iron formation, the stromatolites, and the microfossils present in Archean sedimentary sequences. J. W. Schopf (1978) has hypothesized that the Early Proterozoic atmospheric transition reflects the initial

appearance of the blue-green algae. In this view, green plant photosynthesis could have played no part in earlier microbial ecosystems. Thus, Archean stromatolites must be interpreted as the biosedimentary products of bacteria; carbon isotopic ratios and sedimentary distributions must be attributed to bacterial photosynthesis, to abiotic chemical syntheses, or to a combination of the two; and the hematite in early iron formations can only be related to the abiological production of O_2 via the photodissociation of water.

One alternative to this proposal is the scenario envisaged by Preston Cloud (1976). He also associates the Early Proterozoic rise of atmospheric O_2 concentrations with the evolution of physiologically modern cyanobacteria, but, unlike Schopf, he does not believe that the oxygen bound in Archean iron formations could have been produced abiologically. To accommodate the constraints of both atmospheric history and his interpretation of Archean oxygen production, Cloud has suggested that primitive cyanobacteria or protocyanobacteria flourished as early as 3800 m.y. B.P., but these *Uralgen* possessed no biochemical mechanism to cope with the oxygen released during photosynthesis and, thus, were restricted to environments in which ambient oxygen sinks could immediately combine with the toxic photosynthetic byproduct. Cloud regards ferrous iron in solution as a principle sink, and from this concludes that Archean iron formation is the product of primitive algal photosynthesis. According to this hypothesis, the exhaustion of available sinks early in the Proterozoic era created selective pressures that resulted in the evolution of oxygen tolerance and, ultimately, the rise of atmospheric oxygen. It follows from the tenets of this theory that the bulk of the organic carbon preserved in Archean strata must be a product of bacterial photosynthesis. Stromatolites may be viewed as either bacterial or blue-green algal.

Lynn Margulis and colleagues (1976) suggest that physiologically modern blue-green algae evolved early in earth history. In their discussion of atmospheric evolution, these authors note a simple but important feature of the terrestrial oxygen budget: free oxygen accumulates in the atmosphere when there is an excess of O_2 production *relative* to O_2 consumption. Thus, the apparent dearth of oxygen in the Archean atmosphere need not be ascribed to the absence or severe biochemical restriction of oxygen producing photoautotrophs; it could as easily have resulted from high rates of oxygen consumption. The abundance of lava and pyroclastic debris in Archean supracrustal sequences suggests that volcanism was extremely widespread in the early stages of crustal evolution. Margulis *et al.* hypothesize that it was the effusion of reduced gases from these volcanoes, coupled with such sinks as reduced minerals and organic matter, that kept Archean O_2 concentrations negligibly low, even though cyanobacteria were producing free oxygen. Waning volcanic intensity and oxygen saturation of surface minerals in the Early Proterozoic reduced rates of oxygen consumption to the point where they were lower than those of O_2 production. The result, an oxygen rich atmosphere. Under the terms of the argument advanced by Margulis *et al.*, stromatolites, microfossils, carbon isotope ratios and distributions, and banded iron formation can all be viewed as being predominantly the products of cyanobacterial photosynthetic activity. Schidlowski's (1976, 1977) theories

regarding the carbon budget of the Archean earth would also be compatible with this type of scenario.

2. An Additional Alternative

William Smith (the essayist, not the father of stratigraphy) wrote in 1859 that:

if man was to think beyond what the senses had given him, he must first throw some wild guesswork into the air, and then, by comparing it bit by bit with nature, improve and shape it into truth.

It is in this spirit that I suggest one more way of thinking about Archean photoautotrophy and the rise of atmospheric oxygen. Bacteria do not arise by spontaneous generation, and neither do ideas. Thus, the proposal outlined below owes much to previous published hypotheses. It is perhaps most similar in outlook to that of Margulis *et al.* (1976), but differs in emphasis. Where Margulis *et al.* focused on oxygen *consumption*, I will concentrate on oxygen *production*.

The Hypothesis: Communities of physiologically modern blue-green algae existed during the Archean era, but were characterized by low productivity. A significant increase in primary production during the Early Proterozoic era led to the oxygenation of the earth's atmosphere.

It is, of course, impossible to divine actual rates of photosynthesis for remote geological eras, but one can examine the environments available to early microbes and, by analogy to similar modern habitats, broadly categorize their potential for primary production. That is, one can apply a system of 'ecological uniformitarianism'. This approach has the same limitations as the physical uniformitarianism of Hutton (1795), but when applied to the Precambrian geological record, it yields results that are, at the very least, intriguing.

In 1943, F. J. Pettijohn compared Archean sedimentary patterns to those of Phanerozoic eugeosynclines. More recently, Dimroth and Kimberley (1976) have noted that "most Archean sedimentation apparently occurred on tectonically active, steep slopes surrounding volcanic piles". In these two observations, we find the essence of Archean sedimentary environments: rapid deposition of clastic and pyroclastic debris in tectonically active basins. Conglomerates, greywackes, and shales are common, while quartzose sandstones and carbonates are relatively infrequently encountered.

It might be assumed from Pettijohn's analogy that the surviving Archean sedimentary record consists largely of strata deposited in relatively deep water, but this is not the case. A growing body of evidence suggests that shallow water deposits are well represented among ancient clastic and pyroclastic accumulations. In a detailed sedimentological analysis of strata from the 3400 m y. old Onverwacht Group in the Barberton Mountain Land, South Africa, Lowe and Knauth (1977) documented the presence of such sedimentary features as cross-bedding, ripple marks, and desiccation-type cracks. Such evidence points to the conclusion that some of the Onverwacht sediments were deposited in shallow marine environments adjacent to subaerially exposed volcanic islands. Quartz

arenites of the overlying Moodies Group, also located in the Barberton Mountain Land, contain numerous features associated with tidalities: cross stratification interference ripples, mudcracks, washouts and rill marks, and fining upward paleotidal range sequences (Eriksson, 1977; Klein and Ryer, 1978). Similar features characterize detrital deposits of the 3000 m.y. Pongola Supergroup, exposed south of the Barberton area (von Brunn and Hobday, 1977; Klein and Ryer, 1978). Coarse grained clastics characteristically occur in the marginal facies of Canadian Shield greenstone belts (Goodwin, 1973). Quiet water limestones and tidal flat mudstones do exist, and it is in these strata that the earth's oldest stromatolites are found. Such facies are rare however; perhaps half a dozen occurrences of stromatolites have been documented from an Archean geological record spanning more than 1000 million years.

Employing ecological uniformitarianism, one can speculate on the primary productivity of the Archean earth. Modern cyanobacterial mat communities have high rates of primary production - Bunt (1975) listed a value of $0.65\text{--}2.15 \text{ gC m}^{-2} \text{ d}^{-1}$ for intertidal blue-greens from Eniwetok, while Krumbein *et al.* (1977) recorded productivity rates as high as $12.0 \text{ gC m}^{-2} \text{ d}^{-1}$ from stromatolites from Solar Lake in the Sinai. It is reasonable to conclude that stromatolite building communities in Archean shallow, quiet water facies were also highly productive. But, as mentioned above, such habitats form only a very limited percentage of known early environments. More typical Archean shallow marine environments are characterized by high rates of clastic and pyroclastic influx, and in similar modern environments, benthonic productivity is relatively low - $0.08\text{--}0.53 \text{ gC m}^{-2} \text{ d}^{-1}$ for northern U.S. estuaries, $0.02\text{--}0.22 \text{ gC m}^{-2} \text{ d}^{-1}$ for tropical sediments, and $0.01\text{--}0.03 \text{ gC m}^{-2} \text{ d}^{-1}$ for Scottish shallow marine sediments (Bunt, 1975). Variation in methods of obtaining productivity data hinders attempts at detailed quantitative comparison of rates, but the data do establish that microbial mat communities in clastic-poor environments have higher rates of primary production per unit area than algae growing in regions of high clastic movement.

A significant problem arises in trying to assess the role of plankton in Archean primary production. Walker (in press) has offered the following intriguing statement:

It seems most unlikely that single-cell, freely floating organisms could have survived in surface waters before the rise of oxygen and the development of the ozone screen. The real significance of ultraviolet light in Precambrian evolution may have been to prevent the development of planktonic forms of life prior to the rise of atmospheric oxygen.

The oldest assuredly planktonic microfossils are found in rocks of Early Proterozoic age (Hofmann, 1976; Knoll *et al.*, 1978). The abundance of organic detritus in off-shore shale facies may suggest that the early ocean was populated by photosynthetic microorganisms, but this need not necessarily be the case. The organic matter contained in modern continental slope sediments is derived in part by transport from shallow water environments (Dow, 1977). Perhaps this also held true in Archean seas.

At present, prokaryotic photoautotrophs account for only a small fraction of the total primary production of open ocean ecosystems. In fact, only one taxon of cyanobacteria, the oscillatorioid genus *Trichodesmium*, is commonly found among the oceanic plankton (Dawson, 1966). Does this situation reflect the competitive exclusion of blue-greens from

pelagic environments by eukaryotic algae? Or was the oceanic habitat underexploited prior to the evolution of nucleated organisms? Here the limits of uniformitarian methodology became clear. However, if Walker is correct, then the problem of Archean productivity can be discussed completely in terms of benthonic communities. I will return to the question of planktonic productivity.

One can also infer from the preserved record of early sedimentation that the total area occupied by shallow marine environments was limited during the Archean era. Shallow water habitats were situated predominantly in narrow zones adjacent to volcanic arcs; extensive continental platform and miogeosynclinal shelf deposits are unknown in Archean supracrustal sequences.

Thus, while bearing in mind the obvious uncertainties involved, I suspect (but cannot prove) that whatever the dominant form of photoautotrophy in Archean seas, primary production was low relative to that of the succeeding Proterozoic era. The limited extent of shallow water marine environments and the common coupling of such regions to rapidly eroding land areas in active tectonic settings must have influenced the abundance and diversity of early biotas.

3. Early Proterozoic Environments

The geological differences between the Archean and Proterozoic are as fundamental as the biological dissimilarities between prokaryotic and eukaryotic cells. Table I summarizes the major features of Early Proterozoic sedimentary sequences. From this compilation emerges a picture of stable continental blocks flooded by epicontinental seas and bordered by geosynclines similar in size and developmental pattern to their Phanerozoic counterparts. This contrasts strongly with the granite-greenstone pattern of Archean rocks and represents the initial appearance of a more or less modern global sedimentary/tectonic regime in earth history (Windley, 1977). In terms of biological evolution, two features of this geological evolutionary transition seem particularly important:

1. The area available for colonization by benthic photoautotrophs must have increased substantially. Engel *et al.* (1974) have calculated that the ratio of quartzite plus carbonate to other sediments shifts from 1:100 in the Archean to about 1:5 in the Proterozoic. Windley (1977, p. 335) regards this as an approximate estimate of the increase in stable shelf and platform environments at this time, suggesting a twenty-fold increase in area.

2. The ecological rigor of these shallow water environments decreased significantly — again, one can contrast the thick sequences of carbonates that accumulated throughout wide stretches of the Early Proterozoic sea floor to the highly clastic habitats of the Archean.

Stromatolites first become widespread in rocks approximately 2200–2300 m.y. old (Schopf, 1975; Knoll, 1978). We know from preserved microfossils that at least some of

TABLE I
Lower proterozoic sedimentary sequences

Geologic unit	Location	Age (m.y.)	Tectonic setting	Iron formation ±	Red beds ±	Detrital uraninite ±	Carbonates	Stromatolites	Other notable features	Reference
1. Witwatersrand supergroup	South Africa	2600–2380	Continental basin	+	— ^a	+	—	—	Gold, thucolite	Pretorius (1974)
2. Huronian supergroup	Ontario, Canada	2300	Continental margin	—	+	+	+	—	Glaciogenic features	Young (1973a)
3. Montgomery lake beds	N.W.T., Canada	2300	Continental	—	—	+	—	—	—	Bell (1970)
4. Chibougamau and Otish mountain groups	Quebec, Canada	2300	Continental platform	—	—	+	—	—	Glaciogenic features	Young (1973b)
5. Jacobina group	Brazil	>2300	Continental	—	—	+	—	—	Gold	Cox (1967)
6. Mistassini group	Quebec, Canada	2200–1800	Continental platform or miogeosyncline	+	+	—	+	+	—	Chown and Caty (1973)
7. Animikie group	Lake Superior, U.S.A. & Canada	2000	Miogeosyncline	+	—	—	+	+	Coal	Goodwin (1956) Cannon (1973)
8. Circum-Ungava geosyncline	NE Canada	2000	Mio- and eugeo-syncline	+	+	—	+	+	Evaporites	Dimroth <i>et al.</i> (1970)
9. Coronation geosyncline	N.W.T., Canada	2200–1800	Mio- and eugeo-syncline, platform	—	+	—	+	+	—	Hoffman <i>et al.</i> (1970)
10. Hurwitz group	N.W.T., Canada	2300–1800	Geosyncline	+	+	—	+	+	—	Hoffman (1973)
11. Sutton Lake group	Ontario, Canada	2000–1800	Miogeosyncline	+	?	—	+	+	—	Bell (1970) Goodwin (1974)
12. Penhyn and Piling grps.	Arctic Canada	2340–1950	Miogeosyncline	—	?	?	+	?	Metamorphosed	Heywood (1968)
13. Yavapai group	Arizona, U.S.A.	1820–1725	Variable pre- and synorogenic facies	+	—	—	—	—	Metamorphosed	King (1976)
14. Mt. Bruce supergroup	W. Australia	2200–1900	Miogeosyncline, platform	+	—	—	+	+	—	Daniels (1966) Horwitz and Smith (1977)
15. Nalheru group	W. Australia	2200–1900	Platform	+	?	—	+	+	—	Walter <i>et al.</i> (1976) Horwitz and Smith (1977)
16. Pine Creek Geosyncline	Australia	2200–1900	Geosyncline	—	+	—	+	+	—	Walpole <i>et al.</i> (1968)
17. Kimberley group	Australia	>1800	Continental margin or taphrogeosyncline	—	+	—	—	—	All clastics	Canavan and Edwards (1938)

18. Middleback group	S. Australia	>1800	?		Metamorphosed BIF	+			Parkin (1969)
19. Ketildian supergroup	S. Greenland	>1800	Shallow basins, tectonically controlled	+	-	+	Coal		Bondesen (1970) Appel (1974)
20. Ventersdorp supergroup	South Africa	2300	Volcanic basin with intercalated sediments	-	-	+			Winter (1963)
21. Transvaal supergroup	South Africa, Botswana	2300-2100	Platform	+	-	+			Beukes (1973)
22. Lomagundi group	Rhodesia	2300-2000	Platform	+	+	+			Swift (1961)
23. Waterberg system	South Africa	1900-1800	Non-marine in part	-	+	-	All clastics		Houghton (1969)
24. Roraima formation	Guyana Shield, South America	1800	Continental basin	-	+	-	All clastics		Grabert (1969)
25. Minas series	Brazil	2700-1300	Miogeosyncline and platform				Metamorphosed and heavily weathered BIF		Dorr (1969, 1973)
26. Carajas formation	Brazil	>1800	Platform				Heavily weathered BIF alternating with clastics		Dorr (1973)
27. Karelian supergroup	Soviet Karelia and adjacent Finland	2500-2000	Miogeosyncline, platform	+	+	+	Shungite (coal)		Salop (1977)
28. Tampere group	Finland	>1900	Eugeosyncline	-	-	-			Salop (1977)
29. Burzyan group	Southern Urals, U.S.S.R.	2470 ± 500	Miogeosyncline, platform	-	+	+	Metamorphosed equivalents in N. Urals		Salop (1977)
30. Krivoi Rog group and equivalents	Ukrainian S.S.R.	2200-1900	Miogeosyncline	+	-	+	'Coaly' phyllite		Salop (1977)
31. Udokan group, Muya group	Baikal region, U.S.S.R.	2600-1900	Platform, Miogeosyncline	+	+	+			Salop (1977)
32. Charodokan to Kebetka formations	Aldan Shield, U.S.S.R.	2200-2000	Platform, eugeosyncline	-	+	+			Salop (1977)
33. Khariton Laptev coast group and equivalents	Taymyr Belt, U.S.S.R.	>1900	Miogeosyncline, eugeosyncline	-	-	-	Metamorphosed clastics		Salop (1977)
34. Liao Ho and Huto groups	China	2600-1860	Metamorphosed clastics and carbonates (some stromatolitic)	+	+	+			Salop (1977)
35. Upper Dharwar and Aravalli groups	India	2600-2100	Geosyncline	+	-	+			Radhakrishna and Vasudev (1977) Salop (1977)

^a The Witwatersrand red beds discussed by Dimroth and Kimberley (1976) are of secondary origin (Beukes, 1973).

^b Detrital uraninite is found only in the basal beds of the Karelian sequence. Upper units contain red beds.



Fig. 1. Map showing the location of Lower Proterozoic sedimentary sequences of the world. Numbers indicating individual sequences refer to Table II.

these structures were built by essentially modern taxa of cyanobacteria (Hofmann, 1976; Nagy, 1978), and it is reasonable to suppose that *most* Early Proterozoic stromatolites are the product of blue-green algal activity. The sedimentary sequences containing these structures constitute the earliest record of extensive 'Proterozoic-type' platform carbonates. It is evident, then, that the blue-green algae rapidly took advantage of the appearance of new environments.

It is also in rock units of this age that we find the first evidence for the build-up of atmospheric oxygen. As mentioned earlier and documented in Table I, the youngest continental sediments containing detrital uraninite and pyrite are of earliest Proterozoic age (2600–2300 m.y.). Continental red beds appear soon afterward. In North America, for example, oxidized sediments fill grabens formed in the initial stages of the evolution of the Labrador Trough (Dimroth *et al.*, 1970). Supratidal red beds, sometimes dotted by casts of halite and gypsum crystals, also occur near the base of the Lower Proterozoic sequence of the Belcher Islands (Jackson, 1960; Bell and Jackson, 1974). Other red beds can be found in the Hurwitz Group, the Mistassini Group, and in several horizons in the Coronation Geosyncline (see Table II for references), but the most important red beds in terms of fixing a date for the transition to an oxygen-rich environment are those present in the Huronian Supergroup of Ontario. This sequence contains detrital pyrite and uraninite in its lower half and oxidized sandstones in the upper. I see no reason to dispute S. M. Roscoe's hypothesis that the Huronian sedimentary deposits record the establishment of an oxygen-rich atmosphere (Frarey and Roscoe, 1970; Roscoe, 1973). Folding of

the Huronian Supergroup 2200–2300 m y. ago fixes a minimum age for the atmospheric transition (Morris, 1977).

It has been common practice to assume that red beds did not appear until after the deposition of the world's great deposits of sedimentary iron formation, but it should be clear from the above arguments that this type of sediment was deposited contemporaneously with, and in some cases earlier than, the prodigious accumulations of Early Proterozoic iron formation. It is true that sedimentary sequences immediately overlying the great iron formations often contain thick red bed units – these deposits constitute the detritus eroded from continents uplifted during widespread orogenic episodes 2000–1800 m.y. ago. The red beds contained in these clastic blankets are conspicuous (the Roraima Formation, the Waterberg Group, the Athabasca and associated formations, and others); however, they are not the oldest deposits of their kind. The temporal overlap of red bed and iron formation deposition may reflect a brief but geologically resolvable period during which transport of ferrous iron in solution was possible in oceans lying beneath an increasingly aerobic atmosphere.

The important point to be gleaned from the above discussion is that the earliest evidence for extensive Proterozoic-type shallow carbonate seas, widespread stromatolitic communities, and oxygen-rich atmospheric conditions are all found in the same rock sequences. How does one explain this coincidence in the timing of fundamental geological, biological, and atmospheric changes? Following Cloud and Schopf, one can assume that important physiological innovations arose at or near the beginning of the Proterozoic era, *but one need not make this assumption*. Again applying the principle of ecological uniformitarianism one can assess the impact of the Archean/Proterozoic tectonic transition on a *pre-existing* cyanobacterial flora. The establishment of blue-green algal mat communities over the vast new areas of shallow sea floor open to them would have had two important consequences:

1. Morphologic and perhaps biochemical diversity would have increased as cyanobacteria became more and more specialized to exploit smaller niches more successfully. Some evidence for this can be seen in the tremendous diversity of stromatolite types found in Early Proterozoic carbonates (Hoffman, 1976; Donaldson, 1976; Hofmann, 1976; Truswell and Eriksson, 1972, 1973).

2. Benthic productivity would have increased as a function both of increased area and of increased rates of production per unit area.

The extensive cratonization that ushered in the Proterozoic era also carries implications for increased upwelling and erosional run-off, the net effect of which would have been an increase in the productivity of oceanic plankton communities (Chamberlain and Marland, 1977). Increased rates of primary production, coupled with decreasing rates of oxygen consumption by reduced volcanic gases and progressively more oxidized surface sediments (Margulis *et al.*, 1976), would have resulted in a rise in atmospheric oxygen concentrations. If Walker (in press) is correct that photosynthetic plankton could not have proliferated until the establishment of an ozone shield in the stratosphere, then this initiation of aerobic atmospheric conditions would have permitted the occupation of the

vast ocean surface habitat. This, in turn, would also greatly increase the total primary production by O_2 eliminating microbes. In short, the superimposition of a change in the earth's tectonic framework upon a pre-existing cyanobacteria dominated biota would produce an Early Proterozoic record identical to that which really exists.

4. A Summary, Two Assumptions, and a Limit to Early Life

Consider two brief statements:

1. Organisms living in an aqueous environment evolved the capacity to utilize water in the photosynthetic process early in the course of biological history.
2. The rise of atmospheric oxygen was an early consequence of the evolution of cyanobacterial photoautotrophy.

Both statements are logical, and both can be found woven into the fabric of many discussions of early evolution, but only one of them can be true. The hypothesis explored in this paper assumes the validity of sentence number one and presents environmental/ecological reasons for suspecting that Archean blue-green algae existed for hundred of millions of years before they transformed the atmosphere into an oxygen-rich medium. A reiteration of major points of this arguments runs as follows:

1. While Precambrian organisms are most commonly treated as taxonomic entities, they can also be viewed from an ecologic perspective. The foci of such a treatment are the sedimentary environments available to early biotas.
2. Because of the limited extent and often rigorous nature of early shallow water environments, the primary production levels of an Archean cyanobacterial flora would have been low. Sinks for the O_2 produced by these organisms were present in great supply; thus, it is reasonable to expect that Archean atmospheric oxygen concentrations remained low – not because oxygen was not being produced, but because rates of production did not exceed rates of consumption.
3. The change in the earth's tectonic framework manifested in the Archean/Proterozoic boundary resulted in the initial appearance of widespread shallow platform and shelf environments. Blue-green algae rapidly covered those sea floors, resulting in the evolution of increasingly specialized biologically accommodated algal communities characterized by relatively high rates of photosynthetic production. For the first time in earth history O_2 production exceeded O_2 consumption, and the excess oxygen accumulated in the atmosphere.
4. The hypothesized production rates for Archean and Proterozoic biotas are consistent with what is known of the early geological record. In Proterozoic and Phanerozoic rock sequences, stromatolites, organic carbon isotope ratios, the distribution of carbon in sediments, and the oxygen bound in sedimentary iron formations are all routinely considered as products of cyanobacterial (and in younger sequences, higher algal) activity. This theory affords one the opportunity to consider Archean stromatolites, carbon

isotope ratios, carbon distribution patterns, and iron formations in the same light.

5. The hypothesis outlined in this paper allows one to consider the differences between Archean and Proterozoic biotas primarily in terms of ecological differences directly related to sedimentary/tectonic styles, thus avoiding the necessity of hypothesizing a major physiological advance coincident with the erathem boundary.

Two major assumptions underlie the arguments summarized in the preceding paragraph. The first is that the contribution of benthonic photoautotrophs to early ecosystems was significant with respect to total productivity. Recast in another fashion, this assumption suggests that if Archean planktonic microbes existed, their total primary production was low relative to the production of Proterozoic and younger plankters. The second assumption is that the preserved Archean sedimentary record is reasonably representative of the early earth as it actually existed. (In *The Origins of Species* (1859), Charles Darwin discussed at length the reasons why one should not expect to find forms transitional between species in the fossil record. Summarizing his arguments, Darwin states that anyone who does not believe that the geological record is really as he has described it "will rightly reject the whole theory". It is clear that my hypothesis also stands or falls on the interpretation of the rock record.)

Because we understand so little about the true nature of the Archean biosphere, it would be foolish of me to argue that the proposal advanced in this paper provides a better description of early biology than do other models. Quite honestly, I have not written this essay with that thought in mind. Rather, I have penned these thoughts in the belief that we need to be open to as many working hypotheses as possible. My hypothesis and all previously published theories have both strengths and weaknesses, and as new data become available we will be able to select the strong points and discard the weak. In this way it may indeed be possible to arrive eventually at some clear comprehension of the biological workings of the Archean earth.

A corollary of the ideas presented here ties directly into the theme of this symposium. I believe that no matter what type of phototrophs populated Archean environments, the availability and sedimentological nature of shallow marine habitats must have constituted important limits to the abundance and diversity of early life.

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