

# THE PRECAMBRIAN EVOLUTION OF TERRESTRIAL LIFE

A. H. Knoll  
Department of Organismic and Evolutionary Biology  
Harvard University  
Cambridge, Massachusetts 02138  
U.S.A.

ABSTRACT. Paleontological evidence indicates that terrestrial life existed at least 3500 Ma ago, and it is quite possible that the earliest cells arose well before that time. The early appearance of life on Earth suggests that under appropriate environmental conditions the probability of chemical evolution proceeding to the point of biogenesis may be reasonably high. Most of biological history has been the history of microorganisms, with tissue-grade plants and animals characterizing only the most recent 15% or so of the fossil record. Intelligent life has occupied only the latest instant in geological time. The time table of terrestrial evolution is governed more by the particulars of our planet's physical and biological history than by some universal tempo of evolutionary change. One aspect of terrestrial life that is likely to be universal is the organization of populations into efficient biogeochemical systems.

## 1. INTRODUCTION

In the 1960's, enthusiasm over the explanatory powers of the newly emergent theory of plate tectonics led to the publication of numerous pronouncements on what is and is not possible in orogenesis. Exasperated by the failure of many authors to reconcile their models with known geological facts observable in the field, the late Marshall Kay coined what he termed the Zeroeth Law of Thermodynamics. Briefly stated, this law holds that anything that *did* happen, *can* happen.

Kay's tongue-in-cheek canon aptly captures the spirit in which the exobiologist must regard the evolution of life on Earth. Earth is the only known example of a planet containing life, so its history is immediately relevant to any discussion of life in the universe. Yet, we have no way of knowing to what extent Earth history may serve as an appropriate model for biological evolution in other solar systems. In the present context, it may in fact be most fruitful to examine Earth history for evidence of evolutionary roads not taken or for developments that need not have eventuated elsewhere in order to gain a greater appreciation of what, if any, elements of terrestrial evolution may

201

potentially be universal.

In this paper, I will examine briefly the geological evidence for early biological evolution, concentrating in particular on the timing of major evolutionary events. It is of some importance to the search for extraterrestrial life to ask whether this time scale is governed by some characteristic tempo of evolution that might be expected to obtain on other planets or whether it reflects a history of biological and environmental events particular to the Earth.

## 2. THE PALEONTOLOGICAL RECORD

### 2.1. The Emergence of Life

Of the many evolutionary events whose timing one would like to be able to document in the geological record, none is more central than the origin of life itself. Unfortunately, paleontology can provide only a minimum date for the emergence of biological systems because the oldest negligibly metamorphosed sedimentary rocks known at present already contain compelling evidence for the existence of life at the time of their deposition.

The rocks in question are volcanic-sedimentary sequences preserved in ancient cratonic areas of southern Africa and Western Australia dated at 3400-3500 million years (Ma) old. Silicified chemical sediments in both successions contain large populations of small (2-4  $\mu\text{m}$  diameter) organic walled spheroids, some preserved in various stages of binary division (Muir and Grant, 1976; Knoll and Barghoorn, 1977; Awramik et al., 1983). These microstructures are simple in organization and, consequently, are difficult to identify unequivocally as fossils; however, the regularity of their size frequency distributions, the spatial distribution of populations along bedding planes, surface and internal diagenetic features that compare closely with those characteristic of known microfossils in younger rocks, the absence of mineral grains that could have formed templates for the organic spheroids, and the evidence for binary division collectively suggest that at least some of these Archean microstructures are most parsimoniously interpreted as the remains of once-living microorganisms. This interpretation is strengthened by the recent discovery in both Africa and Australia of filamentous microfossil populations (Awramik et al., 1983; Walsh and Lowe, 1983). The few microfossils unearthed to date suggest a prokaryotic biota of limited morphological diversity, but the available sample is so small--and thus liable to sampling bias--that no strong conclusions can be drawn from these data alone.

Stromatolites can be considered as the trace fossils of microbial mat-building communities, and their presence in the two ancient sedimentary sequences provides further evidence for the early emergence of life. The microorganisms responsible for stromatolite accretion were presumably phototactic and, most likely, were photosynthetic (Walter, 1983). Independent evidence for the presence of photosynthesis is provided by stable isotope analyses of organic carbon preserved in the sequences (Schidlowski et al., 1983). Other geochemical evidence

indicates that very little free oxygen was present in the contemporary biosphere (Holland, 1984), from which one can conclude that early biotas were anaerobic.

Combining geological evidence with newly available data on microbial phylogeny obtained by means of comparative molecular and physiological analyses (e.g., Fox et al., 1980; Gest, 1980), one can state with reasonable confidence that life originated early in our planet's history, that the initial diversification of anaerobic Eubacteria and Archaeobacteria was rapid, and that by 3400–3500 Ma ago, the Earth contained complex anaerobic ecosystems fueled by photosynthesis (see Knoll, 1985). In the Isua region of southwestern Greenland, still older (approximately 3800 Ma) sedimentary rocks are found. The distribution of reduced carbon in these rocks and, particularly, the evidence for isotopic fractionation in the carbon are consistent with an even earlier diversification of life (Schidlowski, 1984); however, the Greenland rocks are severely metamorphosed and, hence, their unequivocal biogeochemical interpretation is impossible.

Although no record of prebiotic chemical evolution is known to be preserved in Archean sedimentary successions, ancient rocks do fix some broad environmental constraints on the conditions under which life originated. The geological record also supplies one other very important fact about the origin of life--it occurred early. The various syntheses, polymerizations, and other reactions that comprise chemical evolution culminated in the emergence of living systems within a relatively short time, a few hundred million years at most and, conceivably, much more quickly. This suggests that given a physical environment similar to that which characterized the early Earth, the genesis of living systems from simple precursor molecules may not be the extremely low probability event that some have assumed.

## 2.2. The Emergence of Aerobic Metabolism

The evolution of cyanobacterial photosynthesis initiated profound changes in the Precambrian biosphere and made possible a second radiation of prokaryotic microorganisms, that of the aerobes. The time of origin of "green plant" photosynthesis is not known with any certainty, but John Hayes (1983) has interpreted temporal patterns in the stable carbon isotope ratios of Precambrian organic matter as indicating the presence of oxygen evolving photoautotrophs 2800 to 2900 Ma ago. This may well be a minimum estimate.

Although cyanobacterial photosynthesis may have originated early, it appears that the transition to an aerobic biosphere was a protracted process (e.g., Knoll, 1979; Schopf, 1983). Early oxygenic environments were probably local and short-lived, and organisms capable of exploiting these habitats may have been facultatively aerobic, or amphiaerobic (Schopf, 1983). Mineralogical, gaseous, and organic sinks for photosynthetically produced oxygen were sufficient to keep O<sub>2</sub> levels extremely low over much of the planet's surface. Some mineralogical and isotopic evidence suggests that oxygen grew in biogeochemical importance in the earliest Proterozoic Eon (Figure 1), concomitant with the appearance of large, stable continents (Knoll, 1979; Cameron, 1982,

1983). I have elsewhere discussed the ecological reasons for expecting cyanobacterial productivity to rise as large continental blocks stabilized (Knoll, 1979, 1984). Despite this increase, fully aerobic environmental conditions may not have been established on a stable basis throughout the world's oceans until the mid-Proterozoic (Schopf, 1983; Holland, 1984). Far better geochemical data on the rise of atmospheric oxygen are needed, and until such data become available, one can really only discuss this transition in broad terms. It is clear, however, that aerobic metabolism evolved during this period of environmental change and that the coupled aerobic/anaerobic biogeochemical pathways characteristic of the modern Earth's surface were established at this time.

### 2.3. Increasing Intra- and Intercellular Complexity

It is now widely accepted that the complex intracellular organization characteristic of eukaryotic organisms originated in part by means of microbial endosymbiosis. In particular, the principal energy-yielding organelles of eukaryotic cells, the mitochondria and plastids, are descended from purple non-sulfur bacteria and cyanobacteria, respectively, that lived symbiotically within a host cell whose genetic organization had differentiated from that of the Eubacteria extremely early in biological history (Margulis, 1981; Gray and Doolittle, 1982; Woese, 1983). Although the geological record can contribute little to the debate over how eukaryotic cells originated, it does provide an estimate of when nucleated cells evolved (e.g., Knoll, 1983). Once again, this is a minimum estimate. The oldest fossils that can plausibly be interpreted as the remains of eukaryotes are large (40-100  $\mu\text{m}$ ), thick walled organic vesicles found in sedimentary sequences up to approximately 1400 Ma old (e.g., Horodyski, 1980). These microfossils are similar in construction and distribution to the cysts and walls of planktonic algae that are commonly preserved in younger rocks, and they have been interpreted in comparable terms (e.g., Tappan, 1980; Vidal and Knoll, 1983). Such an interpretation is reasonable, but it is not entirely iron-clad, because the robust spheroidal envelopes of colonial cyanobacteria can exhibit somewhat comparable morphologic features. Perhaps the strongest evidence that can be marshalled in support of the interpretation of these large 1400 Ma old microfossils as eukaryotes is the observation that demonstrably eukaryotic microfossils become increasingly abundant and diverse in succeeding Late Proterozoic sequences (Vidal and Knoll, 1983). If this interpretation is correct, then the first appearance of eukaryotic microfossils in the fossil record represents not the initial evolution of eukaryotic cellular organization, nor even the origin of algae, but the emergence of algae capable of producing degradationally resistant walls and cysts. Thus, the first eukaryotic microfossils that are recognizable in the geological record may significantly post-date the origin of the group.

With time, some populations of nucleated cells became organized into multicellular clonal aggregates, and from these evolved tissue-grade seaweeds and animals. Macroscopic carbonaceous compressions are found throughout the Proterozoic geologic record, but

many of these may be ripped up fragments of microbial mats. Among the oldest fossils that are incontestably the remains of multicellular organisms are large populations of morphologically regular carbonaceous ribbons preserved in siltstones and shales from northwestern Canada, China, and Svalbard estimated to be approximately 850 to 900 Ma old (Hofmann and Aitken, 1979). The phylogenetic affinities of these earliest megafossils are not clear, but the remains of demonstrable metazoans are found in latest Precambrian (650-600 Ma) sedimentary rocks from several continents (Glaessner, 1979). The oldest animal fossils are casts and molds of large, flat, soft-bodied invertebrates, but preserved tracks, trails, and burrows found in the same sequences indicate that a diversity of small bottom dwelling animals also inhabited latest Precambrian coastal environments.

The evolution of mineralized skeletons, which occurred independently in a number of algal and animal phyla, marks the beginning of the Phanerozoic Eon (literally, the age of visible animals). It has been during this latest approximately 570 Ma interval of biological history that many of the events traditionally discussed as the "history of life" occurred--the diversification of animal structure, the invasion of the land surface by plants and animals, the dramatic increase in global biomass and primary productivity that accompanied the radiation of woody vascular plants, and the recent appearance of a species capable of changing the course of evolution by means of technology.

### 3. THE TIMING OF TERRESTRIAL EVOLUTION

Figure 1 summarizes the timing of major evolutionary events in Earth history. Microorganisms of prokaryotic ultrastructural organization were the sole inhabitants of our planet for the first 50% or more of biological history, and tissue-grade metazoans have been present for only the last 15 to 20%. In Figure 1, hominid history corresponds to the last 130  $\mu\text{m}$  of the time axis, *Homo sapiens* the last 2  $\mu\text{m}$ , and the Industrial Revolution a mere 60  $\text{\AA}$  at the top of the figure.

On Earth, intelligent life emerged 3500 to 4000 Ma after the initial radiation of living systems. Can one justifiably infer from this that terrestrial history reflects some characteristic time scale for the evolution of intelligent life? Both tacit and explicit support for this view can be found in the literature. For example, more than two decades ago, S. S. Huang (1959) wrote, "One may question the wisdom of using  $3 \times 10^9$  years for  $t_b$  [the duration of biological evolution necessary to produce intelligent life] in general, because this value is based on a single case--that of the earth. However, we can argue that the time scale,  $t_b$  cannot be greatly shortened because, according to current ideas in biology, the natural selection and evolution of organisms is the result of mutations which are of a random nature and are therefore slow." More recently, M. Cohen (1981) has reiterated this view, stating flatly that "there seems to be a consensus that the

## THE TIME SCALE OF TERRESTRIAL EVOLUTION

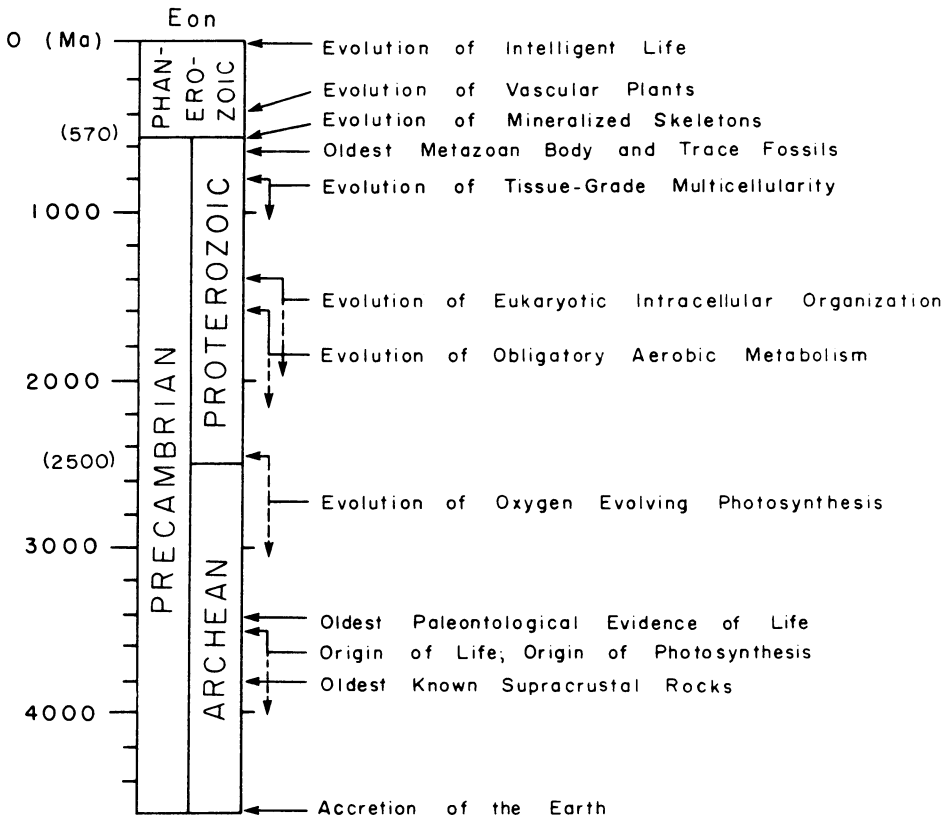


Figure 1. Chart showing the chronology of biological evolution on Earth. For events whose timing is not known with certainty, the horizontal arrow points to the youngest time of origin consistent with the geological record while the vertical arrow indicates that an earlier origin is probable. For a discussion of dates, see text and references cited therein.

emergence of intelligence on a planet requires about three billion years of relative constancy of stellar output."

Despite these expressions of faith, there is really little basis



for the supposition that evolution on Earth has proceeded at some universal rate. In fact, there is little evidence to support the underlying assumption that rates of macroevolutionary change correspond closely to rates of mutation. Clearly, the time scale for the emergence of intelligent life on Earth is governed not so much by the relatively rapid changes in multicellular organisms that have occurred during the Phanerozoic Eon as by the evolutionary events of the long Precambrian era, events such as the evolution of aerobic metabolism, the radiation of eukaryotic cells, and the evolution of regulatory systems to control the expression of different genes in daughter cells within a single colony--a major step in the evolution of tissue-grade multicellular organisms. Of course, one must bear in mind a point argued forcefully by G. G. Simpson (1964), namely that there is no good reason to assume that intelligence is the inevitable product of biological evolution (see also Cloud, 1983).

Controls on the timing of major evolutionary innovations are complex. Each event reflects the influence of previous biological history, as well as the constraints and opportunities presented by the physical environment and other organisms. The relative importance of different factors may vary from one event to another, making generalizations about large scale evolutionary tempo impossible. As a single example, one can consider the emergence of aerobic metabolism. An obvious precondition for the evolution of aerobic physiological pathways was the appearance of environments containing metabolically useful concentrations of oxygen. The required oxygen was produced by cyanobacteria, but it is apparent from the geological record that the establishment of stable oxygenic environments long post-dates the physiological evolution of cyanobacterial photosynthesis (see section 2.2 and references cited therein). The growth of atmospheric and oceanic oxygen levels occurred when levels of O<sub>2</sub> production increased to a point where they exceeded those of oxygen consumption. This, in turn, may well have been a consequence of the physical evolution of the Earth, as large, stable continents flanked by broad shallow shelves and zones of upwelling appeared and, concomitantly, rates of production of reduced gases and minerals by volcanoes abated. Laboratory experiments have repeatedly demonstrated the ability of bacteria to adapt rapidly to environments containing novel substrates and altered environmental conditions, and so it is likely that when oxygenic conditions appeared, microbial populations quickly evolved the capacity to exploit them metabolically. Thus, following the evolution of cyanobacterial photosynthesis, the timing of evolution of aerobic pathways was probably controlled most strongly by the tectonic development of the planet. On Earth, surface environments became oxygenic about 1500 to 2000 Ma after the origin of life. All other factors being equal, under different tectonic conditions, the same event might have happened 1000 Ma earlier, 2000 Ma later, or not at all.

This single example shows that, were all other features of terrestrial evolution left unchanged, a more rapid development of the crust-mantle system could have almost halved the time required for biology to proceed from biogenesis to intelligence. A slower development could have doubled the time, and under some tectonic

regimes, oxygen production might never have outstripped consumption. Generally similar arguments could be made for most major evolutionary events of the Precambrian era. The point is that the time scale of terrestrial evolution appears to have been governed less by some intrinsic evolutionary metronome than by the particulars of our planet's physical and biological history, including such extrinsic agencies as directional environmental change and mass extinction.

In a stimulating paper, Carter (1983) recently argued on the basis of what he terms the anthropic principle that the intrinsically expected average time for the evolution of intelligence must be far longer than the period actually required on Earth and, therefore, far longer than the main sequence lifetimes of life supporting stars. If this argument is correct, then the universe probably contains few intelligent civilizations. However, in light of geological observations, it is not at all clear that one can reject the alternative hypothesis that because of constraints related to the particular course of Earth history, evolution on this planet has proceeded slowly relative to rates that might be possible elsewhere (see Maddox, 1984). Indeed, the history of our own planet leads one to entertain the idea that the timescale determining early events of biological evolution are significantly constrained by the physical evolution of planets. If this is true, and if, as seems reasonable, planetary development is related to the larger scale evolution of solar systems, then the observed similarity in the time required for the evolution of intelligence on Earth and the main sequence lifetime of the Sun may have a physical basis and, therefore, not be a coincidence that can be dismissed as being *a priori* improbable. If this possibility can be admitted, then according to the probability equations of Carter (1983), intelligent life may be widespread in the universe. The fact is, of course, that without any knowledge of evolutionary rates and trends on even a single other planet, one cannot determine whether the appearance of intelligent life midway through our Sun's main sequence lifetime should be regarded as unusually early, unusually late, or unusual at all.

#### 4. ARE THERE UNIVERSAL FEATURES OF TERRESTRIAL EVOLUTION?

Having sided with those who argue that both the tempo and products of evolution may vary on different planets, I close by asking whether any features of terrestrial life are likely to be universal. I would argue that the answer is "yes", but that the universal features do not necessarily include biochemical pathways, morphological designs, or specific taxa. More likely the universal aspects of life on Earth include the organization of metabolically disparate populations into biogeochemical systems capable of transferring energy and cycling biologically important elements. It is only by means of these systems that life can be maintained for evolutionarily long periods of time. Therefore, it is likely that any planet that sustains life will contain series of taxa having biogeochemically complementary metabolisms for the rapid biological cycling of materials, as well as a tectonically



active planetary surface capable of maintaining the longer term biogeochemical balance of biospheres.

## 5. ACKNOWLEDGMENTS

My research on problems of Precambrian biological evolution has been supported by NSF Grant BSR 82-13682. S. Goldberg drafted the evolutionary timescale figure.

## 6. REFERENCES

- Awramik, S. M., Schopf, J. W., and M. R. Walter. 1983. 'Filamentous fossil bacteria from the Archean of Western Australia' Precambrian Res. 20: 357-374.
- Cameron, E. M. 1982. 'Sulphate and sulphate reduction in early Precambrian oceans' Nature 296: 145-148.
- Cameron, E. M. 1983. 'The start of sulfur oxidation in continental environments about  $2.2 \times 10^9$  years ago' Science 221: 549-551.
- Carter, B. 1983. 'The anthropic principle and its implications for biological evolution' Phil. Trans. R. Soc. Lond. A310: 347-363.
- Cloud, P. E. 1983. 'Cosmobiology' Quart. Rev. Biol. 58: 57-60.
- Cohen, M. 1981. 'Stellar influences on the emergence of intelligent life' Pp. 115-118. In: Billingham, J., ed., Life in the Universe. MIT Press; Cambridge, Massachusetts.
- Fox, G. E., et. al. 1980. 'The phylogeny of prokaryotes' Science 209: 457-463.
- Gest, H. 1980. 'The evolution of biological energy-transducing systems' FEMS Microbiol. Lett. 7: 73-77.
- Glaessner, M. F. 1979. 'Precambrian' Pp. A79-A118. In: Robison, R. A., and C. Teichert, eds., Treatise on Invertebrate Paleontology, Part A: Introduction. Geol. Soc. Amer. and Univ. Kansas Press; Boulder, Colorado, and Lawrence, Kansas.
- Gray, M. W., and W. F. Doolittle. 1982. 'Has the endosymbiont hypothesis been proven?' Microbiol. Rev. 46: 1-42.
- Hayes, J. M. 1983. 'Geochemical evidence bearing on the origin of aerobiosis, a speculative hypothesis. Pp. 292-301. In: Schopf, J. W., ed., Earth's Earliest Biosphere, Its Origin and Evolution. Princeton Univ. Press; Princeton, New Jersey.

- Hofmann, H. J., and J. D. Aitken. 1979. 'Precambrian biota from the Little Dal Group, Mackenzie Mountains, northwestern Canada' Can. J. Earth Sci. 16: 150-166.
- Holland, H. D., 1984. The Chemical Evolution of the Atmosphere and Oceans. Princeton Univ. Press; Princeton, New Jersey.
- Horodyski, R. J. 1980. 'Middle Proterozoic shale-facies microbiota from the lower Belt Supergroup, Little Belt Mountains, Montana' J. Paleontol. 54: 649-663.
- Huang, S. S. 1959. 'The occurrence of life in the universe' Amer. Sci. 47: 397-402.
- Knoll, A. H. 1979. 'Archean photoautotrophy: some alternatives and limits' Origins of Life 9: 313-327.
- Knoll, A. H. 1983. 'Biological interactions and Precambrian eukaryotes' Pp. 251-283. In: Tevesz, M. J. S., and P. L. McCall, eds., Biotic Interactions in Recent and Fossil Benthic Communities. Plenum Publ. Corp.; New York.
- Knoll, A. H. 1984. 'The Archean/Proterozoic transition: a sedimentary and paleobiological perspective' Pp. 221-242. In: Holland, H. D., A. F. Trendall, eds., Patterns of Change in Earth Evolution. Dahlem Konferenzen. Springer Verlag; Berlin.
- Knoll, A. H. 1985. 'Patterns of Evolution in the Precambrian Era' Paleobiology. In Press.
- Knoll, A. H., and E. S. Barghoorn. 1977. 'Archean microfossils showing cell division from the Swaziland System of South Africa' Science 198: 396-398.
- Maddox, J. 1984. 'New twist for anthropic principle' Nature 307: 409.
- Margulis, L. 1981. Symbiosis and Cell Evolution. W. H. Freeman and Co.; San Francisco.
- Muir, M. D., and P. R. Grant. 1976. 'Micropaleontological evidence from the Onverwacht Group, South Africa' Pp. 595-604. In: Windley, B. F., ed., The Early History of the Earth. Wiley; London.
- Schidlowski, M. 1983. 'Evolution of photoautotrophy and early atmospheric oxygen levels' Precambrian Res. 20: 319-335.
- Schidlowski, M., Hayes, J. M., and I. R. Kaplan. 1983. 'Isotopic inferences of ancient biochemistries: carbon, sulfur, hydrogen, and nitrogen' Pp. 149-186. In: Schopf, J. W., ed., Earth's Earliest Biosphere, Its Origin and Evolution. Princeton Univ. Press; Princeton, New Jersey.

- Schopf, J. W., ed. 1983. Earth's Earliest Biosphere, Its Origin and Evolution. Princeton Univ. Press; Princeton, New Jersey.
- Simpson, G. G. 1964. 'The non-prevalence of humanoids' Science 143: 769-775.
- Tappan, H. 1980. The Paleobiology of Plant Protists. W. H. Freeman and Co.; San Francisco.
- Vidal, G., and A. H. Knoll. 1983. 'Proterozoic plankton' Geol. Soc. Amer. Mem. 161: 265-277.
- Walsh, M. M., and D. R. Lowe. 1983. 'Filamentous microfossils from the 3.1-3.5 billion-year-old Swaziland Supergroup, Barberton Mountain Land, South Africa' Lunar and Planetary Sci. XIV, Abstr. Pp. 814-815.
- Walter, M. R., 1983. 'Archean stromatolites: evidence of the Earth's earliest benthos' Pp. 187-213. In: Schopf, J. W., ed., Earth's Earliest Biosphere, Its Origin and Evolution. Princeton Univ. Press; Princeton, New Jersey.
- Woese, C. R. 1983. 'The primary lines of descent and the universal ancestor' Pp. 209-233. In: Bendall, D. S., ed., Evolution from Molecules to Men. Cambridge Univ. Press; Cambridge, U.K.