

Earth's Early Biosphere

David J. Des Marais

Space Science Division, Ames Research Center, Moffett Field, CA

ABSTRACT

Understanding our own early biosphere is essential to our search for life elsewhere, because life arose on Earth very early and rocky planets shared similar early histories. The biosphere arose before 3.8 Ga ago, was exclusively unicellular and was dominated by hyperthermophiles that utilized chemical sources of energy and employed a range of metabolic pathways for CO₂ assimilation. Photosynthesis also arose very early. Oxygenic photosynthesis arose later but still prior to 2.7 Ga. The transition toward the modern global environment was paced by a decline in volcanic and hydrothermal activity. These developments allowed atmospheric O₂ levels to increase. The O₂ increase created new niches for aerobic life, most notably the more advanced Eukarya that eventually spawned the megascopic fauna and flora of our modern biosphere.

INTRODUCTION

The search for the origin, evolution and distribution of life in the universe benefits from studies of early life on earth. For example, the discovery that our biosphere is more than 3.8 billion years (Ga) old (Mojzsis et al., 1996) indicates that perhaps only a few 100 million years or less are required for life to begin on planets that sustained liquid water near their surfaces. Also, the rocky planets Earth, Venus, Mars, Mercury and our own Moon all experienced core formation, an early global episode of crustal differentiation, heavy meteor bombardment, and a second crustal differentiation characterized by basaltic overplating (Lowman, 1989). These planets all sustained these processes for perhaps as long as 1 to 2 billion years, therefore they shared similar geologic histories for time intervals longer than the time required for life to begin on Earth. Furthermore, the evolution of Earth's habitable environments and the biosphere are probably inextricably related (see, e.g., Bengtson, 1994), therefore an understanding of this relationship offers perspectives for assessing the prospects for life's existence elsewhere.

GEOCHEMICAL EVIDENCE OF THE EARLY BIOSPHERE

The fossil record in rocks and the record within the macromolecules of living cells offers insights into the nature of the early biosphere. Evidence of life in ancient rocks can be grouped into the following categories: morphological remains of individual cells, rock structures and textures produced by microbial communities (e.g., the laminations in stromatolites), biogenic organic matter, minerals whose formation was influenced by biological processes, and stable isotopic patterns among biogenic elements such as carbon, nitrogen and sulfur. All of these lines of evidence indicate that life existed prior to 3.4 billion years ago (Ga). Evidence for life existing prior to 3.8 Ga is much more sparse but is still strongly consistent

with a biological interpretation. The great antiquity of this evidence reminds us that our biosphere consisted solely of single celled life for more than three-fourths of its existence.

The earliest record of life consists of reduced carbon (C) that has a very diagnostic stable isotopic composition (Mojzsis et al., 1996). This isotopic composition is most clearly understood in the context of a network which describes the processing of C by the Earth and its oceans, atmosphere and biosphere. This network is termed the biogeochemical C cycle and is illustrated in Fig. 1 as an assemblage of C reservoirs (boxes) connected by processes (arrows) (Des Marais, 1997a). As the word "cycle" implies, a major dynamic is the movement of C around any of several cyclical pathways. For example, the "habitable zone" subcycle moves C between the oceans, atmosphere and biosphere (the "fresh organic matter"). The "sedimentary" subcycle moves C between the surface environment and the sedimentary organic matter and carbonate reservoirs. The other subcycles include more deeply-situated C reservoirs. Although these cyclic pathways differ from each other regarding some of the reservoirs and processes involved, they share common ground in the hydrosphere and atmosphere. It is this common ground that unites the entire C cycle and allows even its most remote components to influence the surface environment and the biosphere. The processes linking the reservoirs are represented by labelled arrows, and the arrays of boxes and arrows delineate the various subcycles. The timescales typically required for C to traverse each of the subcycles are indicated by the vertical bars at right. Note that crustal C occupies two principal reservoirs, namely reduced biogenic organic C and carbonate. This organic C enters Earth's crust by sedimentation and burial. Biogenic organic C is vastly more abundant in crustal sediments and rocks ($>10^{21}$ moles) than in the living biosphere (1.3×10^{10} moles), and therefore reflects the integrated effects of biological and geological processes that have acted over hundreds of millions to billions of years (Des Marais, 1997a).

Additional insights into the biogeochemical C cycle are revealed by $\delta^{13}\text{C}$ values of carbonate (δ_{carb}) and reduced organic C (δ_{org}) in the various C reservoirs (for the definition of $\delta^{13}\text{C}$, see Fig. 1 caption). To the extent that sedimentary rocks have avoided deep burial and alteration, their δ_{carb} and δ_{org} values reflect the status of the C cycle at the time of their deposition. Ranges in $\delta^{13}\text{C}$ which represent the bulk of δ_{carb} and δ_{org} values for the various C reservoirs are depicted in Fig. 1 (Deines, 1980; Weber, 1967). The $\delta^{13}\text{C}$ values of recently-deposited sedimentary organic C are created by those processes and reservoirs associated with erosion and outgassing of C, the transport and chemical transformation of C within the hydrosphere and atmosphere, and the sedimentation and burial of C. Organisms that assimilate compounds having single C

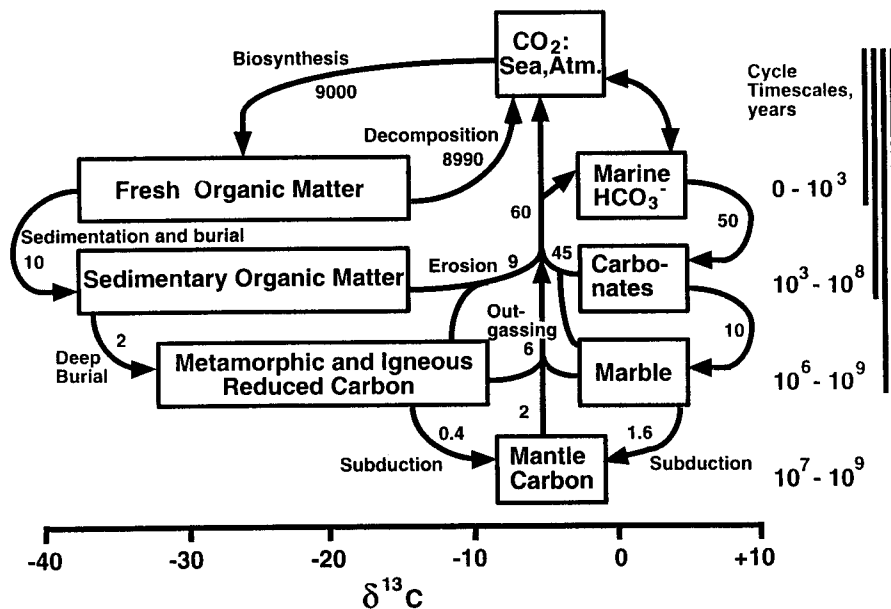


Figure 1. Biogeochemical C Cycle (Des Marais, 1997a). Shown are principal C reservoirs in the mantle, crust, oceans and atmosphere (boxes) and also the processes which unite these reservoirs (arrows). The range of each of these reservoir boxes along the horizontal axis gives a visual estimate of $\delta^{13}\text{C}$ values most typical of each reservoir. These $\delta^{13}\text{C}$ values are defined as follows: $\delta^{13}\text{C} = ((R_{\text{sample}}/R_{\text{standard}}) - 1)1000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ and R_{standard} refers to the Peedee Belemnite C isotope standard. Numbers adjacent to the arrows give estimates of present-day fluxes, expressed in the units $10^{12} \text{ mol yr}^{-1}$. The vertical bars at right indicate the timeframes within which C typically completely traverses each of the four C subcycles. For example, C traverses the subcycle having the hydrosphere, atmosphere and biosphere reservoirs in 0 to 1000 years.

atoms (e.g., CO_2 or CH_4) virtually always prefer ${}^{12}\text{C}$ over ${}^{13}\text{C}$, thus they form organic matter having $\delta^{13}\text{C}$ values lower than the that of the inorganic C source. The net isotopic difference ($\delta_{\text{carb}} - \delta_{\text{org}} = \Delta\text{C}$) reflects both (1) the metabolic pathways of CO_2 fixation and C metabolism by the biota which make organic matter (these biota are called autotrophs), and (2) the pathways and mechanisms by which organic C is transformed and/or destroyed. The δ_{carb} values are nearly identical to the $\delta^{13}\text{C}$ values of dissolved inorganic C (DIC) in seawater. Carbonates deposited in open marine environments have δ_{carb} values which are typically representative of the global marine DIC.

The dichotomy in C isotopic abundance (Figs. 1 and 2) persists in rocks as old as 3.8 Ga (Schidlowski et al., 1983; Hayes, 1994; Mojzsis et al., 1996), indicating that biological isotopic discrimination during organic biosynthesis is at least 3.8 Ga old. Both the magnitude and the pattern of isotopic composition of reduced C in >3.8 Ga rocks strongly resemble corresponding compositions in younger, more demonstrably fossiliferous rocks, therefore strengthening the interpretation that the isotopic patterns in the >3.8 Ga-old rocks are indeed biogenic. The biogenic reduced C in these older rocks occurs as coatings on grains of the mineral apatite. Even the formation of the apatite grains themselves is consistent with biological processes in ancient sediments (Mojzsis et al., 1996).

MORPHOLOGICAL EVIDENCE OF EARLY MICROBIAL COMMUNITIES

Records of morphological remains of individual microbial cells and communities extend back to approximately 3.4 Ga, however the record prior to 2.5 Ga is extremely sparse. For example, whereas hundreds of fossiliferous rock formations and thousands of microfossil occurrences have been described in rocks between 2.5 Ga and 0.55 Ga (0.55 Ga is just prior to the "explosion" of the animal and plant fossil record in the Cambrian period), only about two dozen occurrences of stromatolites have been reported in rocks >2.5Ga (Schopf, 1994). A stromatolite is a laminated rock representing a "reef" or pavement constructed by microbial mat communities that became mineralized and preserved. For example, Byerly et al. (Byerly et al., 1986) described wavy-laminated flat-laminated and columnar stromatolites in a chert deposit in the 3.2 Ga-old Fig Tree Group of sedimentary rocks in the Barberton Mountains in eastern South Africa. Flat-lying, domical and conical stromatolites were reported in 3.5 to 3.3 Ga-old sediments in northwestern Australia (Lowe, 1980; Walter et al., 1980). Although actual cellular remains of microorganisms were not found in these stromatolites, their textures indicate that microbial mat communities were involved in their construction.

Authentic microfossils have been reported in Archean rocks from South Africa and western Australia.

THE RECORD WITHIN LIVING CELLS

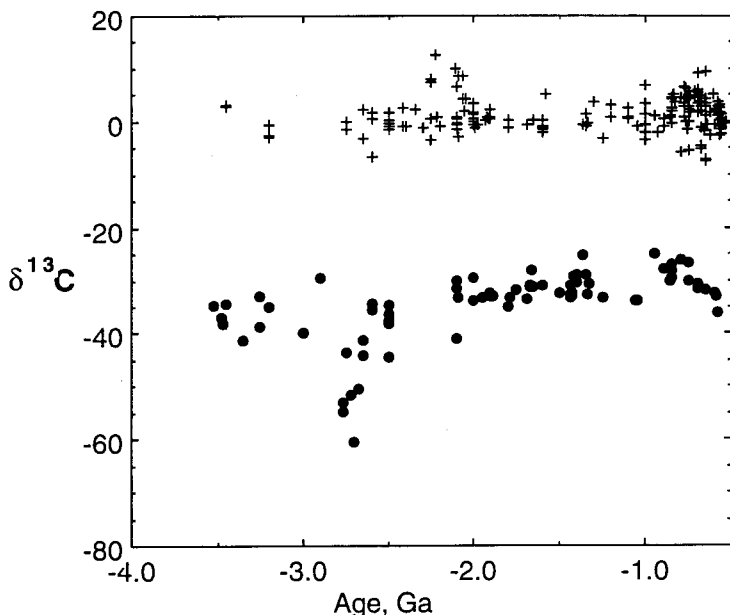


Figure 2. Plot of Age Versus δ_{carb} (crosses) and δ_{org} (filled circles) for Sedimentary Rocks Having Ages in the Range 3.4 to 0.55 Ga. Data for reduced C are corrected for the effects of thermal alteration (Des Marais, 1997b). Between 2.2 to 2.0 billion years ago, note the high δ_{carb} values and the virtual disappearance thereafter of δ_{org} values more negative than -36. Other evidence indicates that atmospheric O_2 increased substantially at this time (see text).

For example, Walsh and Lowe (Walsh and Lowe, 1985) observed threadlike filamentous microfossils in 3.4 to 3.5 Ga-old chert rocks which had been deposited in subtidal to intertidal marine environments. Moreover, these 1.0 to 2.5 micron-diameter filaments occur in association with wavy flat-laminated layers such as those frequently found within stromatolites. The filaments resemble any of several groups of filamentous bacteria, therefore it is difficult to attribute any specific biochemical capabilities to them. In contrast, rather more elaborate cellular remains were found in bedded cherts within the ~3.4 Ga-old Apex basalt sequence of northwestern Australia (Schopf and Packer, 1987). Most convincing are segmented filaments whose individual segments consist of well-defined barrel-shaped, discoidal or quadrate medial cells (Schopf, 1994). Some cells appear to have been preserved while in the process of cell division. The biological origin of the filaments is established by their morphological complexity, by the degree of regularity of cell shape and size of numerous specimens, by their resemblance to modern photosynthetic bacteria (particularly oxygenic-photosynthetic cyanobacteria), and by their carbonaceous composition. The close resemblance of these microfossils to living cyanobacteria indicates further that photosynthesis, perhaps even O_2 -producing photosynthesis, existed as early as 3.4 Ga ago (Schopf and Packer, 1987).

Living cells harbor a record of their ancestry within the sequence order of monomers within macromolecules such as DNA, RNA and proteins. The most thoroughly-studied example of this record to date has been the 16s ribosomal RNA molecule (rRNA), which is involved in the translation of information from DNA to proteins and is therefore an ancient, essential molecule utilized by all living organisms. Differences between rRNA monomer sequences have been interpreted to indicate similarities of ancestry among lineages of biota, where less similar molecules indicate more distant relationships and therefore more ancient common ancestry. This analysis led to the construction of a "tree of life" (Fig. 3) whose major branches represent the most ancient observable diversifications of lineages and whose smaller branches and twigs represent subsequent evolutionary diversifications leading to the modern biosphere. The reconstruction of the rRNA tree revealed that all extant life can be grouped into the following three domains: Archaea, Bacteria and Eukarya (Woese et al., 1990). To the extent that the various lineages currently can be associated with specific microbial physiologies, we can infer the metabolic capabilities of the early biosphere.

Several lineages that form the deepest subdivisions within the domains Archea and Bacteria consist of hyperthermophiles, namely microorganisms that grow optimally above 80°C (Stetter et al., 1990). Furthermore, many of these hyperthermophiles synthesize organic matter from CO_2 and utilize other chemical reactions as a source of energy. For example, they can react H_2 with CO_2 , O_2 or SO_4^{2-} , or they can react H_2S with O_2 in order to obtain energy. Some hyperthermophiles can utilize organic matter by fermentation or by respiration of sulfur. The precise timing of origin of anoxygenic photosynthesis is not yet clear (note P designations in Fig. 3). However, modern oxygenic photosynthesis did not arise until later diversifications occurred among the Bacteria. These observations indicate that, for a substantial interval early in earth history, our biosphere occupied thermal environments and obtained its sources of reducing power exclusively from chemical (hydrothermal?) sources.

Regarding modes of organic matter synthesis from CO_2 , the earliest microorganisms utilized the reductive tricarboxylic acid cycle or modifications thereof: the reductive acetyl-CoA or the reductive malonyl-CoA pathways (e.g., Fuchs, 1989; Fuchs et al., 1992). In contrast, the Calvin-Benson cycle (see "C" designations in Fig. 3), which is employed by all oxygenic photosynthetic bacteria, algae and plants, several anoxygenic photosynthetic bacteria and also some aerobic bacteria, perhaps arose later, later even than some forms of photosynthesis (Kandler, 1994).

The geological and molecular biological evidence indicates that, prior to 3.0 Ga, the biosphere was

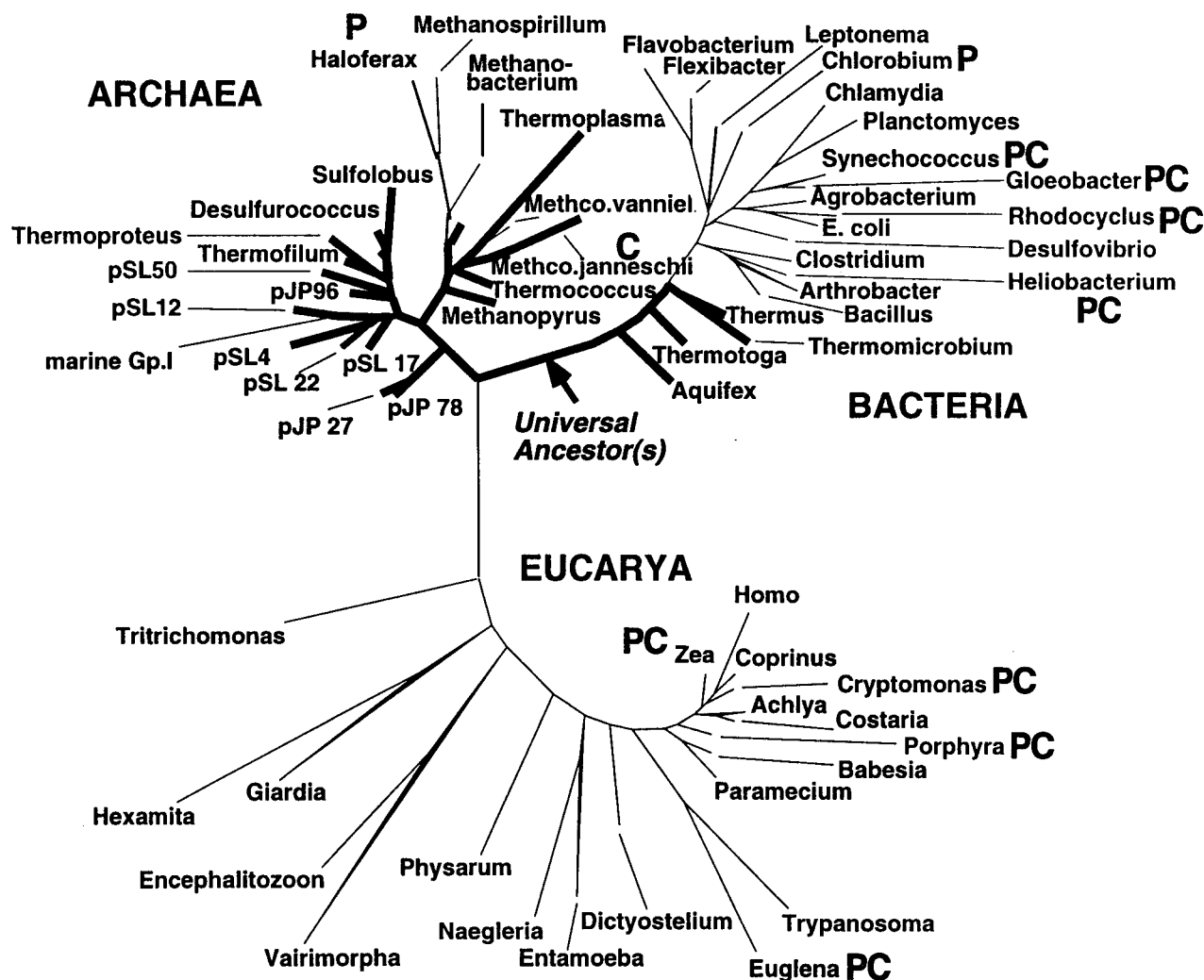


Figure 3. Phylogenetic Tree of Life, Inferred by Maximum Likelihood Analysis of Ribosomal RNA Sequences Representing 64 Taxa from the Domains Archaea, Bacteria and Eukarya (Barnes et al., 1996). *The locations of the inferred root of the tree is indicated by the arrow. Lineages having hyperthermophilic microorganisms are designed by the bold lines. Lineages having photosynthesis are designed with a P; lineages having the Calvin-Benson cycle for CO₂ assimilation are designed with a C.*

biochemically sophisticated and diverse. It utilized both a broad array of chemical substrates and as well as light for energy. It deployed multiple strategies for the biosynthesis and degradation of organic compounds. Diverse microbial mat communities dwelled in thermal waters as well as in subtidal and intertidal coastal marine environments. These communities coped successfully with periodic desiccation and with harsh ultraviolet radiation (an effective O₂-sustained O₃ ultraviolet screen had yet to materialize). Perhaps most remarkable is the fact that the pre-3.0 Ga biosphere was quite sophisticated biochemically, yet the development of plants and animals did not occur until more than two billion years later.

INTERACTIONS BETWEEN THE ATMOSPHERE, GEOSPHERE AND BIOSPHERE DURING THE ARCHEAN

Prior to 3.8 Ga, the atmosphere was likely dominated by CO₂, N₂ and H₂O, with lesser amounts of CO, H₂ and reduced sulfur gases (Kasting, 1993). This composition was sustained by rates of volcanic outgassing that exceeded modern rates (Holland, 1984; Veizer et al., 1982; Des Marais, 1985).

As atmospheric composition ultimately reflects the balance between sources and sinks of the components, it is useful to consider how climate might have affected weathering rates. The substantial volcanic inputs of CO₂ to

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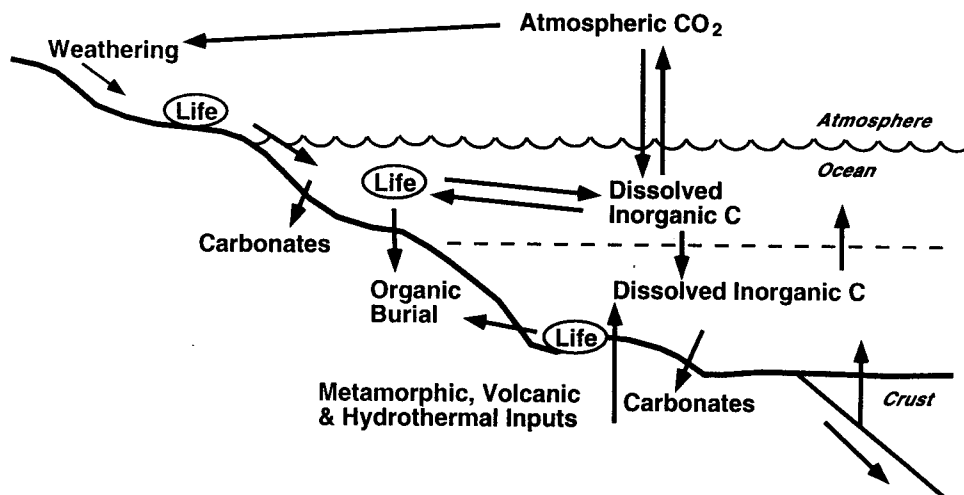


Figure 4. Schematic Representation of C Pathways in the Atmosphere, Ocean and Crust. *The oval symbols depicting life represent the following three communities of primary producers: terrestrial photosynthetic, shallow water photosynthetic (both benthic and planktonic), and deep water and subsurface chemosynthetic (associated principally with hydrothermal activity and the alteration of basaltic crust).*

the atmosphere (Fig. 1; Des Marais, 1997a) ultimately were balanced by the rate of CO₂ removal by weathering (Fig. 4). Because increasing CO₂ concentrations intensify greenhouse warming that, in turn, increases the rate of CO₂ removal by weathering, CO₂ participates in a negative feedback mechanism that apparently has stabilized Earth's climate (Walker et al., 1981). To sustain liquid water within surface environments 3.8 Ga ago (Schopf, 1983), despite the predicted lower solar luminosity at that time (Newman and Rood, 1977), the Archean atmosphere must have contained higher-than-modern concentrations of CO₂ and/or other greenhouse gases. An atmospheric CO₂ inventory of approximately 0.2 to 2 bars could have maintained temperatures in the range 5 to 20°C during the early Archean (Kasting, 1987). This CO₂ inventory declined as the solar constant increased over time, thus stabilizing global temperatures.

The atmospheric O₂ inventory reflects a balance between volcanic, atmospheric, biologic and tectonic processes (Fig. 5). For example, before life began, H₂ from volcanoes and H from the photodissociation of water vapor could have been lost to space (Walker, 1977). This loss would have caused the crust and the mantle slowly to become more oxidized (Kasting, 1993). However, once bacteria became widespread, they consumed H₂ emanating from the many undersea volcanoes. Virtually all bacteria, including nonphotosynthetic varieties, have a high affinity for ¹³C as an electron donor in biosynthesis (Fenchel and Blackburn, 1979). Thus the early biosphere would have captured ¹³C from this volcanic source of reducing power, cycled much of it as organic matter, and substantially curtailed its rate of escape to space.

The history of O₂ has been the most extensively studied aspect of the atmospheric redox budget. Only very

small amounts of abiotic O₂ were produced by the photodissociation of ¹³CO and the escape of H to space (Kasting and Walker, 1981). Oxygenic photosynthesis has been a much more robust O₂ source, and it arose certainly by the Late Archean (Buick, 1992; Beukes and Lowe, 1989), and perhaps earlier (Schopf and Packer, 1987). The evidence, summarized above, that shallow ocean waters were at least mildly oxidizing, is perhaps the most compelling indication that oxygenic photosynthesis existed during the Archean. The shallow seawater regime would have become anoxic had there not been a source of oxidizing power stronger than the abiotic photodissociation of water. Even at today's lower-than-Archean hydrothermal circulation rates, substantial inventories of O₂ and seawater sulfate in today's oceans and atmosphere would be consumed in less than 60 million years in the absence of oxygenic photosynthesis (Wollery and Sleep, 1989).

The availability of nutrients to biota living in the shallow seas and coastal environments of the Early to Mid-Archean would have been limited by the combination of a strongly stratified ocean (Beukes and Klein, 1992; Lowe, 1994), and relatively low global rates of subaerial weathering and continental runoff. These conditions favored benthic photosynthetic microbial mat communities over planktonic communities, because microbial mats are highly efficient at recycling and retaining nutrients (Canfield and Des Marais, 1993; Canfield and Des Marais, 1994). However, organic matter is efficiently recycled within microbial mats (Canfield and Des Marais, 1993), especially if sedimentation rates are low. This recycling would have led to low net organic productivity (e.g., low rates of organic matter burial), which is supported by the observation that shallow water Archean sediments are

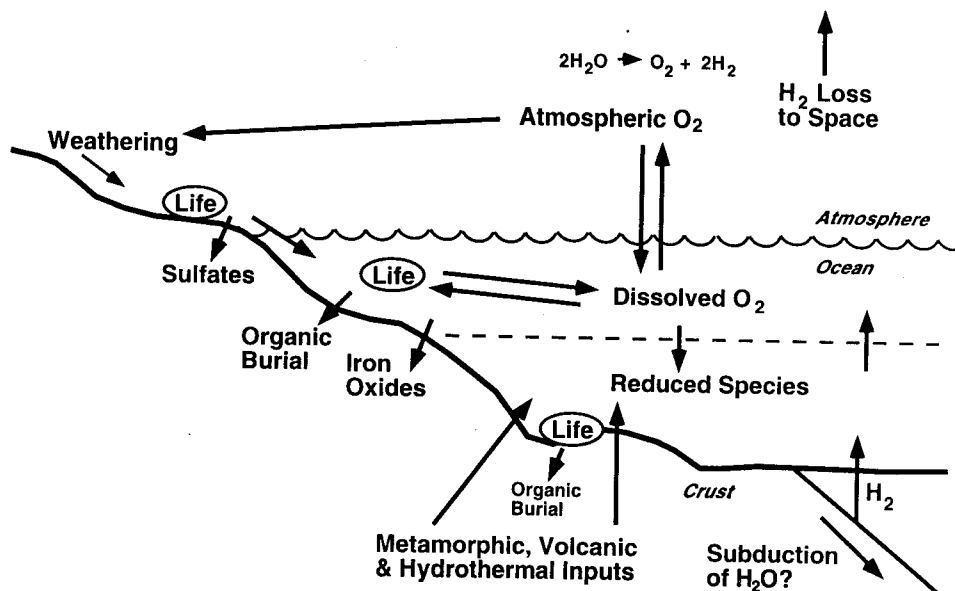


Figure 5. Schematic Representation of the O₂ Budget in the Atmosphere, Ocean and Crust. *The oval symbols depicting life represent the following three communities of primary producers: terrestrial photosynthetic, shallow water photosynthetic (both benthic and planktonic), and deep water and subsurface chemosynthetic (associated principally with hydrothermal activity and the alteration of basaltic crust).*

relatively poor in organic matter (Lowe, 1994). Thus, even though Archean deeper-water shales do contain some organic matter (Lowe, 1994), global rates of burial of organic matter from oxygenic photosynthesis were probably low by modern standards. Low rates of organic burial correspond to low net rates of O₂ accumulation (Bernier and Canfield, 1989). Furthermore, it has been proposed (Kasting et al., 1993) that the oxidation state of the upper mantle increased since the Archean. If so, then volcanic emanations during the Archean and Early Proterozoic would have been even more reduced, and atmospheric O₂ levels even lower than currently estimated. The combination of low net O₂ production and higher inputs of reduced volcanic gases seem consistent with the interpretation that Archean O₂ levels were substantially below modern levels.

THE TRANSITION TOWARDS THE MODERN BIOSPHERE

As mentioned above, the fossil record of life becomes much more robust after 2.5 Ga, indicating both that fossil preservation in marine sediments was enhanced by the assembly and stabilization of broad continental platforms, and that life had become widespread and diverse by that time. These shallow-water microbial communities were likely sustained by oxygenic photosynthesizers, presumably cyanobacteria, yet atmospheric O₂ levels were still low, perhaps only 1 to 2 percent of modern values.

Conditions were altered substantially during the

interval 2.2 to 1.9 billion years ago. Atmospheric [O₂] levels rose to more than 15% PAL (Holland, 1994; Knoll and Holland, 1995). Sedimentary sulfide δ³⁴S values became more variable and ranged to include substantially lower values (Cameron, 1982). This evidence for enhanced isotopic discrimination during bacterial reduction of SO₄²⁻ to sulfide in shallow marine sediments indicated that SO₄²⁻ concentrations in seawater had increased significantly. Microfossils (Han and Runnegar, 1992) and organic biomarker compounds (Summons and Walter, 1990) appeared, indicating that O₂-requiring eukaryotes had become globally prominent. By virtually all accounts, the global surface environment had become substantially more oxidized.

OXYGEN-UTILIZING EUKARYA: PROGENITORS OF PLANTS AND ANIMALS

The Eukarya domain of life responded substantially to the major environmental changes that occurred after 2.2 Ga. The oldest known Eukarya are spirally-coiled, megascopic fossils in 2.1 Ga-old shales (Han and Runnegar, 1992). A major increase in the diversity of Eukarya is observed in rocks approximately 1.0 Ga in age (Knoll and Walter, 1992). Indeed, the "crown group" of Eukarya, which includes the lineages leading to algae, fungi, plants, and animals, probably arose around this time. The diversification which led to plants and animals occurred between 0.53 and 0.59 Ga ago.

Evolutionary innovations within the Eukarya lineage (Fig. 3) might be linked to the history of O₂ levels (e.g., Knoll and Holland, 1995). Molecular O₂ is required by virtually all Eukarya having organelles (e.g., algae, fungi, plants and animals have mitochondria; plants also have chloroplasts). To the extent that certain subgroups of Eukarya require specific minimum O₂ levels, specific groups perhaps appeared soon after their required O₂ levels were first attained. The earliest fossils of Eukarya appeared during the oxidation event between 2.2 and 2.0 Ga ago (see above). Another event at the end of the Proterozoic immediately preceded the earliest well-documented occurrence of multicellular life (Kaufman and Knoll, 1995). The coincidence in timing between these atmospheric O₂ increases and the evolutionary events in Eukarya indicates that important biogeochemical linkages might exist between the biosphere, atmosphere and geosphere (Knoll and Holland, 1995). It falls to future investigators to discover conclusive evidence of these linkages and, along with them, evidence for the origins of our modern biosphere.

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