The habitat and nature of early life

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Earth is over 4,500 million years old. Massive bombardment of the planet took place for the first 500–700 million years, and the largest impacts would have been capable of sterilizing the planet. Probably until 4,000 million years ago or later, occasional impacts might have heated the ocean over 100 °C. Life on Earth dates from before about 3,800 million years ago, and is likely to have gone through one or more hot-ocean 'bottlenecks'. Only hyperthermophiles (organisms optimally living in water at 80–110 °C) would have survived. It is possible that early life diversified near hydrothermal vents, but hypotheses that life first occupied other pre-bottleneck habitats are tenable (including transfer from Mars on ejecta from impacts there). Early hyperthermophile life, probably near hydrothermal systems, may have been non-photosynthetic, and many housekeeping proteins and biochemical processes may have an original hydrothermal heritage. The development of anoxygenic and then oxygenic photosynthesis would have allowed life to escape the hydrothermal setting. By about 3,500 million years ago, most of the principal biochemical pathways that sustain the modern biosphere had evolved, and were global in scope.

What is life? Natural science has never found a satisfactory definition. Cardinal Newman[1], following Thomas Scott, lived by the parable "Growth is life". This is not the answer to the puzzle, but it reduces the problem by providing a useful working tool to the geologist. Life can be recognized by its deeds — life is disequilibrium, leaving behind the signatures of disequilibrium such as fractionated isotopes or complex molecules. It is more besides, but the larger question 'what is life?' is perhaps beyond natural science. Continuum exists between chemistry, autocatalysis and what every one would agree is life. But defining the point at which autocatalysis becomes life is like searching for the world's smallest giant.

The prebiotic Hadean environment

The Solar System began after one or more local supernova explosions about 4,600 million years (4.6 Gyr) ago. In one widely accepted scenario of the later stages of accretion of the Solar System it is thought that there were 500 or so planetesimals, bodies about the size of the Moon, in the region now occupied by the inner planets[2,3]. Collision between planetesimals produced the inner planets. Venus, Earth and Mars all received inventories of water vapour and carbon, perhaps with early oceans on all three. But other models are also possible[4]. The fate of the volatile inventory[5] in each planet was completely different: Venus is dry, with a surface now at around 500 °C under 90 bar (9×10^6 Pa) of carbon dioxide (CO_2). Mars is in permafrost. Earth has approximately the same external inventory of CO_2 as Venus, and both planets radiate heat to space at very similar 'effective' temperatures (in some senses Earth is hotter), but for us the CO_2 is tied up in carbonate minerals (for example, limestone). The blanket is less and so the oceans can exist.
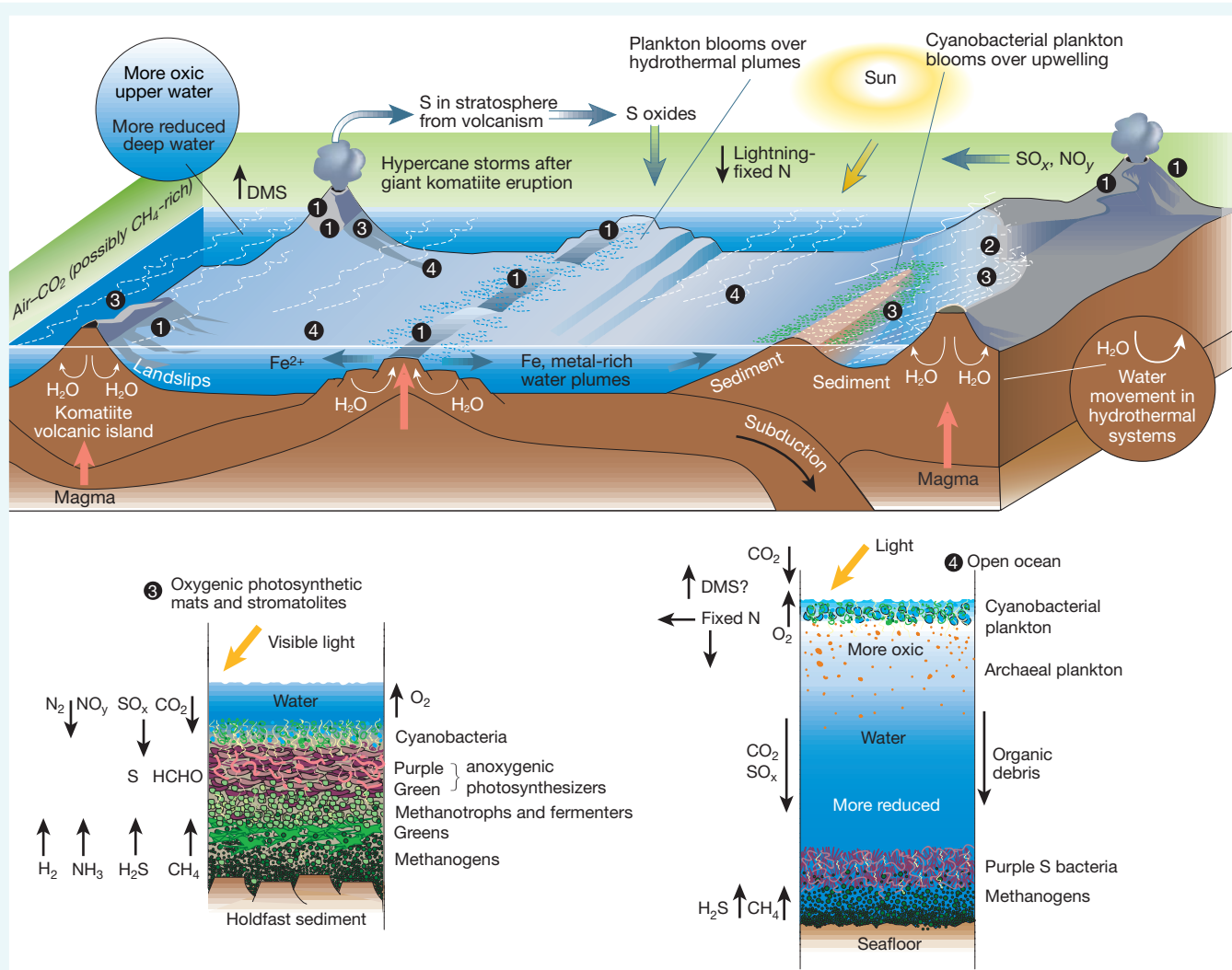
Water is a strong greenhouse gas and, at some stages early in the history of Venus and Earth, water vapour was probably present high in the atmosphere. Such water vapour would have been photolysed into hydrogen and oxygen, and the hydrogen present in the upper atmosphere would have been lost rapidly to space. Deuterium would have been lost also, but being more massive, would have been lost more slowly. In comparison to the D:H ratio of hydrogen that is thought to have been originally in the planetary mix, the residual hydrogen in Venus's atmosphere has a strong deuterium enrichment. The simplest explanation is that Venus lost its water early in its history when a runaway greenhouse developed. In this model, initially Venus had oceans and a warm (>75 °C) surface; water was partitioned into the high atmosphere, photolysed, and hydrogen was lost and the planet dehydrated[6], leaving a more oxidized planet. Alternately, if Venus has or had a molten magma ocean in its mantle it may there too have sequestered 'light' hydrogen as OH. Mantle minerals are typically 'light', or depleted in deuterium relative to sea water[7].

Modern Earth does not lose significant amounts of water to space. Today, the top of Earth's troposphere is cold and water falls back to the surface: the stratosphere is extremely dry, and relatively little hydrogen reaches the top of the atmosphere. It is possible that on the early Earth, as probably on early Venus, there was a substantial hydrogen loss to space, but to a lesser extent, losing only up to a little over a third of the ocean[8]. If so, the residual oxygen (up to 100 bar) would have meant that the outer part of the young Earth was significantly enriched in oxidant compared to the interior. The noble gases of Earth's atmosphere have a complex history[9], in part recording primordial accretion in planetesimals, but perhaps also recording the early onset of subduction.

On Mars, residual water is today present as subsurface brine aquifers subject to rare break-out floods; there is evidence for earlier events when water was free on the surface[10]. Mars also had early volcanic activity. With water and volcanoes, early Mars may have been an eminently habitable place, perhaps more so than Earth.

Earth is unique among the inner planets in possessing a disproportionate Moon. Of the explanations for the origin of the Moon, the most persuasive is that proto-Earth was struck, around 4.5 Gyr, by another inner planet about the size of Mars or even larger[11]. This impact spun and tilted the Earth[12]. The heat of the impact would have been enough to melt the Earth, even if it were not already molten from infall heat and the heat from radioactive decay. The impact (the 'big splat') would have ejected enormous amounts of molten mantle into orbit, some of which coalesced to form the Moon. The consequences of the impact are wide. The spin and tilt of the Earth have evolved from that event, dissipated by tides, to give us the present day–night cycle and the seasons, both crucial in distributing heat around the planet and making the Earth habitable by

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The figure shows a diagram of an early Earth ocean environment with the following labels:

More oxic upper water / More reduced deep water

Plankton blooms over hydrothermal plumes

Cyanobacterial plankton blooms over upwelling

Sun

S in stratosphere from volcanism → S oxides

Lightning-fixed N

SO_x, NO_y

Air–CO_2 (possibly CH_4-rich)

↑DMS

Hypercane storms after giant komatiite eruption

H_2O H_2O Komatiite volcanic island

Landslips Fe^{2+} H_2O H_2O Fe, metal-rich water plumes   Sediment   Sediment H_2O H_2O

Subduction

Magma   Magma

H_2O Water movement in hydrothermal systems

❸ Oxygenic photosynthetic mats and stromatolites

Visible light

N_2 ↓ NO_y SO_x CO_2 ↓   Water   ↑O_2

S   HCHO

Cyanobacteria

Purple / Green anoxygenic photosynthesizers

Methanotrophs and fermenters

Greens

H_2 NH_3 H_2S CH_4 Methanogens

Holdfast sediment

CO_2 ↓   Light   ↑DMS?   ← Fixed N O_2 ↓   ❹ Open ocean

Cyanobacterial plankton

More oxic

Archaeal plankton

CO_2 SO_x ↓   Water   Organic debris

More reduced

Purple S bacteria

H_2S ↑CH_4 Methanogens

Seafloor

biology. The heat that powers modern plate tectonics and volcanism originates in approximately equal measures from the primordial impact heat of accretion and early radioactivity, and from the long-term decay of uranium, thorium and potassium. Were it not for the continual renewal of the erosion cycle driven by this heat, and the supply of new volcanic cations and reduction power, the productivity of the biosphere would have slowly died from shortage of essential elements. Instead, nature remains unimpaired by time[13].

Immediately after the Moon-forming impact, a rock vapour atmosphere would have formed. As this cooled it would have formed an optically thick layer of dust in the high atmosphere. After about 2,000 years, a rind would have begun to form on the magma ocean of the mantle, and for perhaps 2 million years surface temperatures lingered near 100 °C, with a steam greenhouse, before beginning to cool. Bombardment on a lesser scale was ongoing, but gradually decaying. Until about 3.8 Gyr, the Earth would have suffered frequent massive meteorite impacts, some sufficiently large to heat the oceans to >110 °C, or even to the ~350 °C needed to convert the whole ocean to steam. Impacting bodies of a diameter of 500 km or more would have been capable of vaporizing the ocean; bodies of 200 km could have heated it above 100 °C. Impacts would have ejected huge quantities of debris, made of basalt or komatiite (a magnesium-rich lava). Planets are active, and the Earth's ocean is not simply an unchanging puddle. Seawater chemistry would have been controlled by volcanism and by reaction with this debris, such that it is improbable that a long-lived global 'primeval soup' could have collected from impacts of organic-rich meteorites and comets.

The oldest minerals known on Earth are 4.4-Gyr zircons from Western Australia[14]. These zircons are recycled — they now occur in a younger rock that eroded from a Hadean parent (see Box 1 for the aeons). The oldest rock (coherent assemblage of minerals) is the 4-Gyr Acasta gneiss from northwest Canada[15]. That it is a gneiss suggests that silica-rich rocks and possibly subduction existed at the close of the Hadean and the start of the Archaean. Perhaps water oceans existed, which were needed to provide cool, hydrated lithospheric plate for subduction and hence to create continental rocks[14,16].

The meteorite bombardment, heaviest until about 3.8 Gyr but to an extent continuing to the present (it remains a danger), was capable initially of ejecting matter into orbit from any of the inner planets. In rare cases, ejecta could have suffered very low stresses. Life, once begun, spreads rapidly into any available habitat. Thus if life were present on any inner planet with liquid water, it could have spread quickly across that planet, such that cells were present everywhere that conditions were suitable. Thereafter, each significant impact event producing huge numbers of ejecta would have been likely to have thrown into space a few rocks that carried undamaged cells. Some of these ejecta would have crossed to other inner planets: material from Mars still falls on Earth[17]. Had life existed on Mars, these ejecta could have carried one or more cells, quick frozen in space and held safe from ultraviolet (UV) light in rock crevices. Even if they survived ejection, nearly all cells on a rock would have perished in space, but it takes only one cell to infect a planet.

This opens the question: on which planet did life begin? Mercury is improbable, being sunward of the habitable zone and too extreme[18]. Venus, being large, would have had less planet-leaving ejecta, and events
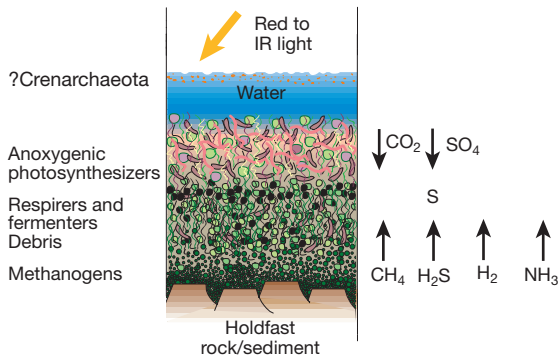
Figure 1 Late-Archaean biosphere — the living communities and their chemical products. The upper part of the left panel shows a model of possible habitats of microbial communities. Field and isotopic evidence exists for many of these settings, but the presence of plankton is inferred from sediment record and molecular interpretation, and the mid-ocean ridge community is inferred. (Figure not to scale.) Microbial mat communities are illustrated in the lower part of the left panel and the right panel. Columns show possible mat communities and biofilms (numbers refer to typical settings in the habitat model). Evolutionary heritage follows standard model.
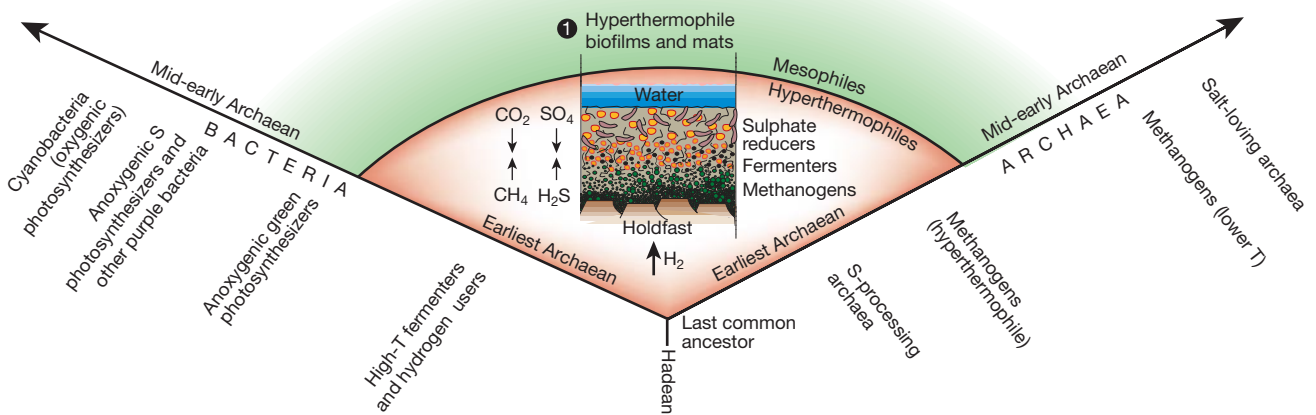
capable of ejecting undamaged cells into space would have been rare. However, a Perelandrian[19] origin of life in early Cytherean oceans is not impossible. Mars is more suitable: it is a smaller planet and could have provided a suitable nurturing place given its possible early shallow seas under a CO_2-rich air, into which volcanoes would have been erupting[20]. Being small in comparison to Venus, major impacts would have ejected rocks relatively frequently that were capable of reaching Earth. Impact sterilization would have been a significant danger to life on any inner planet. Overall, early Mars may have been safer than the early Earth, and Mars was possibly habitable in the Hadean[21]. The 'giant impactor' that hit Earth is also a possible although improbable birthplace, with a small chance that cells survived the impact by being ejected into orbit until the Earth's surface cooled or were transferred to Mars or Venus by the collision. Exchange between the inner planets is ~10^6 times easier than exchange between the inner planets and outer planet satellites. Transfer from shallow interiors of large asteroids to inner planets is possible, but soft landing of debris on asteroids is unlikely. Finally, it is worth noting that if life did originate on Earth, rather than being carried here from Mars or another planet, it is possible that a meteorite impact could have ejected terrestrial living cells to infect Mars or Venus, despite the difficulty of leaving our relatively large planet.

The 'faint young Sun' puzzle

If the modern Earth were an airless, rapidly rotating planet of its present colour, its surface temperature — the 'effective temperature' T_e — would be 255 K (the effective temperature of modern Venus is similar)[4]. Because of the H_2O–CO_2 greenhouse, the actual surface is 33 K warmer

and thus sustains liquid water (which in turn allows abundant water vapour in the air, the main component of the greenhouse). The early Sun was fainter by a factor of roughly a quarter to a third[22], and if such a sun shone on the present-day Earth there would be global glaciation. On the early Earth, therefore, the possibilities are either that there was indeed global glaciation, or that warmth was sustained by a massive global CO_2 greenhouse: a 10–100-bar CO_2–CO atmosphere over liquid ocean, with the CO_2 content of the air declining as the Sun warmed.

A CO_2 greenhouse would imply CO_2-rich oceans, which would react with basalt to form carbonates, especially with the huge supply of basalt fragments from impact ejecta. A CO_2 greenhouse would also have evolved to lower temperatures until volcanic outgassing of CO_2 matched the carbonate precipitation. This would take millions of years, during which the water temperature would linger near 100 °C. Thereafter, surface temperature may have been cool, even glacial. It is possible that the Hadean between 4.4 and 4.0 Gyr was mostly a Norse Ice-Hades, with intervals of Inferno after major impacts occurred when the Earth's surface was a lake of fire and brimstone. A glacial Earth in the Hadean would not lose much hydrogen to space, as so little water would be present in the high atmosphere. On Venus, being closer to the Sun, the slightly warmer temperatures may have allowed a moist greenhouse to be sustained in the long gaps between impacts, and the planet was consequently dehydrated.

Alternative hypotheses can be proposed. Ammonia and methane are strong greenhouse gases, and if their mixing ratio were high enough, they could have sustained liquid oceans. However, ammonia photodissociates quickly in solar UV. It is possible that methane in the

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Box 1
Geological timescales
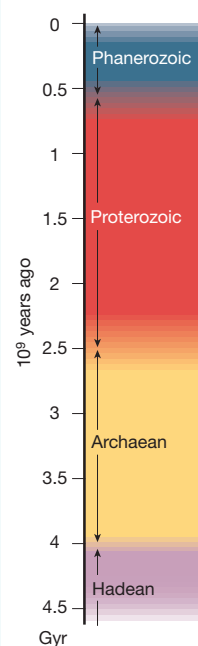
In discussing geological time, 1 Gyr is 10^9 years, 1 Myr is 10^6 years (the 'ago' is implicit and often omitted, such that Gyr and Myr refer to both time before present and duration). There are four aeons. The Hadean is taken here as the time from the formation of the Solar System and early accretion of the planet (4.6–4.5 Gyr), to the origin of life (probably sometime around 4.0 ± 0.2 Gyr). The Archaean, or time of the beginning of life, is from about 4–2.5 Gyr; the Proterozoic from 2.5 Gyr to about 0.56 Gyr; and the Phanerozoic since then.

atmosphere could have produced a high-altitude organic smog that absorbed UV, allowing ammonia to exist below[22,23]. In such circumstances, a liquid ocean could exist. However, for a methane smog to screen the planet, the CH_4:CO_2 ratio of the air must have been high (above unity[24]). Methane can be produced after impact fireballs[25], but a long-lived methane atmosphere is perhaps unlikely on a prebiotic planet if surplus oxidation power comes from hydrogen loss[8], but might have been possible later after methanogens (methane-generating organisms) had evolved. Reaction between a hydrous mantle magma shell and a reduced core[26] could also have provided oxidation power, through mantle-derived volcanic output.

More generally, a strongly reduced prebiotic atmosphere rich in methane and ammonia seems unlikely, given the probable oxidation state of lavas, and of the rock debris ejected from the mantle after major impacts, especially after differentiation of the iron-rich core. Perhaps abiotic Earth was indeed glacial, with occasional meteor-impact melting events, and pools of water around volcanoes. The ocean may have been covered with sea ice, with some open leads and thin ice where ablation occurred. Possibly on Venus a much warmer clime prevailed with early liquid oceans and a moist CO_2 greenhouse, but at the price of losing hydrogen to space. On Mars, further away but with a gentler impact history, a CO_2 greenhouse (or even a CH_4–NH_3 atmosphere) may have been sustainable for some time.

Summary of the geological evidence for early life on Earth
Earlier Archaean (4–3.6 Gyr)
Geological evidence[27–29] shows that it is certain that life has been present on Earth for at least 3.5 Gyr, and it is probable that life began before 3.8 Gyr. Early evidence for life comes from southwest Greenland, especially the Isua belt which contains rocks up to 3.8 Gyr old that show clear evidence of deposition on the planet's surface, including what may be the oldest known water-lain sediment[30]. There has long been a suspicion that inorganic carbonate in the rocks shows a ^{13}C 'heavy' enrichment that is the necessary counterpart of the light carbon extracted by the biosphere[31,32]. But dating is controversial, and the carbonate is not necessarily the age of the host rock. In rocks from Isua and also from Akilia island, both in southwest Greenland, isotopically 'light' (that is, probably biologically reduced) carbon occurs in carbonaceous

inclusions in apatite (calcium phosphate)[33]. A different line of evidence comes from sedimentary rocks in Isua that contain minute graphite globules with a ^{13}C content of about 19‰ (ref. 34). These may have been derived from early Archaean plankton. Controversy continues.

Mid-Archaean successions (3.6–3.3 Gyr)
In rocks around 3.5 Gyr old there have been many claims of fossil microbial biofilms and stromatolites (organosedimentary structures produced by microbial trapping, binding and precipitation, usually but not always photosynthetic)[35]. Although some of these features can be interpreted equally as non-biological in origin[36], others possess all the diagnostic features of biogenic structures[37]. Carbonate that is isotopically similar to modern carbonate is known throughout the past 3.5 Gyr, as is reduced carbon that shows isotopic fractionation that can only be explained as biological[31,32]. The most obvious explanation is that throughout this time large-scale photosynthetic carbon fractionation (that is, oxygenic photosynthesis) by the enzyme ribulose-1,5-bisphosphate carboxylase–oxygenase or 'Rubisco' had operated — on a global scale. This removed about one-fifth of carbon released from the Earth's interior as 'light' biological carbon, leaving the counterpart 'heavier' four-fifths to precipitate as carbonate.

The evidence is not just isotopic. In rocks of about 3.3–2.5 Gyr in the Barberton Mountain Land in South Africa and the Pilbara in Western Australia there are carbonaceous microstructures that may have been microbial in origin[38–40]. Filamentous microfossils are known in a 3.2-Gyr volcanogenic massive sulphide (deep-water) deposit in Western Australia[41], implying that life existed on Archaean mid-ocean ridges[42]. There is thus reasonable ground to suppose microbial life was widespread in the mid-Archaean, probably present both on coastal fringes and as photosynthetic plankton in deeper water, as well as in both shallow and deep hydrothermal habitats.

Late-Archaean successions (3.0–2.5 Gyr)
In late-Archaean rocks there is abundant evidence for life[28,42]. Stromatolites are well developed at Steep Rock, Ontario[43], and in the Pongola Supergroup, South Africa[44], which are both nearly 3.0 Gyr old. Well developed stromatolites from 2.7-Gyr successions are found in many places[28,45,46]. Figure 1 shows various habitats of microbial mats and biofilms in the late-Archaean biosphere.

Textural evidence for late-Archaean bacteria depends on the assumption that similarity to modern microbial sedimentary structures implies similar ancient biota. Poorly preserved microfossils[39] and indirect geochemical arguments[47] supported the case, but it remained circumstantial. More direct evidence has now come from molecular fossils — biological lipids are preserved in 2.7-Gyr rocks from the Pilbara, Western Australia[48]. Hydrocarbon biomarkers, including 2α-methylhopanes which are characteristic of cyanobacteria[49], imply oxygenic photosynthesis was occurring. Steranes, derived from chemicals characteristic of eukaryotes, are also present. Whether the sulphur cycle was similarly modern in aspect is at present controversial[50].

The universal ancestor and the last common ancestor
Insight into the descent of life has come from molecular palaeontology[51]. The 'standard model' of microbial descent[52,53] is based on small-subunit ribosomal RNA. One hypothesis[54,55] is of an early population of replicating organisms of uncomplicated design, possessing simple modular structures and functions, and mutually exchanging genes — the 'universal ancestor' was not one cell but a community sharing information. As evolution selected proteins to become more specific and efficient, genes became less exchangeable and divergence crystallized. From this 'universal ancestor' the 'standard' view[51,56] is that the two domains Bacteria and Archaea arose, and that later on, further along the 'universal phylogenetic tree', symbiosis produced the domain Eucarya[57,58].

The standard view[52] clearly implies (but does not prove) that in the early microbial community in which the last common ancestor lived, life was hot and chemotrophic[59] — the 'hyperthermophile Eden' hypothesis — although evidence for a hyperthermophile

Box 2
Hydrothermal systems

Hydrothermal systems occur wherever magma reaches the surface. Water is heated by the magma, becomes less dense, and rises to be replaced by incoming cool fluid. As it moves it interacts chemically with the rock matrix, leaching metals. When it emerges and suddenly cools, these are redeposited. Around volcanoes on land, rainwater-fed systems form hot pools and fumaroles of varying pH. At mid-ocean ridges, in water 2.5–3 km deep, vigorous circulation includes 'black smokers' emitting jets of very acid water at temperatures up to 400 °C, which are crucial in ocean chemistry, especially metal supply and pH control[106,107]. Many minerals offer internal surfaces that are organophilic and catalytic[108].

Modern subaerial hydrothermal pools are widely colonized by hyperthermophile bacteria and archaea. Subaerial systems are very diverse, with a wide range of pH possible. Near-surface magma can heat steam to >600 °C, with highly acidic, vigorously boiling hot springs. Fluids heated by basaltic magmas degassing at depth can form near neutral to alkaline springs. If the country rock is ultramafic (magnesium-rich), very alkaline systems can occur. Komatiite shield volcanoes may have produced many alkaline systems. At high levels in the volcano both fluid and vapour phases can occur. Country rock is altered to clay, and sulphide deposition (usually iron sulphide) is widespread. Komatiites host nickel sulphide deposits[28].

Submarine systems[107] include diffuse vents as well as black smokers, which emit iron and manganese oxides. Typically, hydrothermal fluids that have interacted with magma in some way are more reduced than overlying sea water. Sulphur has a key role. Some is volcanic, but in modern systems much of the sulphur is from seawater sulphate (which derives from sulphur gases via photosynthetic oxidation). The sulphate is reduced bacterially (for example, against organic matter, or against more reduced chemical species) as the water enters the hydrothermal circulation, further reduced in the circulation system, and then reoxidized by bacteria as the water leaves vents and mixes with ambient oxidized water. Similarly, nitrate is reduced, such that ammonium minerals are found in deposits. Before photosynthesis, the supply of sulphate and nitrate (that is, oxidized species of sulphur and nitrogen) to oceanic water was probably far less than today, coming from, respectively, oxidation of sulphur gases by OH in the upper air, and lightning fixation of nitrogen, and returned by volcanism.
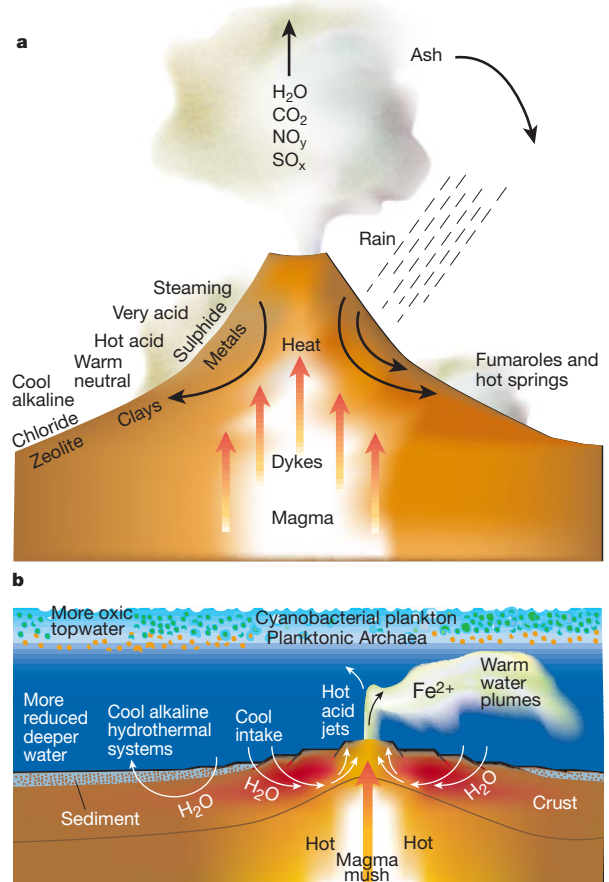
Box 2 Figure Hydrothermal systems. **a**, On land, around a volcano. **b**, On seafloor, at a mid-ocean ridge. (Not to scale.)

ancestry has been challenged[60]. Several geological settings could have hosted the Eden community. It could have lived in a brief (up to 1 million years) period of hot (~100 °C) ocean after a major meteor impact, or possibly could have existed in a hydrothermal system (see Box 2). In the transient hot-ocean case, hydrothermal systems would have offered protective settings even after the ocean cooled.

An alternate version (the 'hyperthermophile Noah' hypothesis) is that the universal ancestor was not necessarily hyperthermophile, but diversified from an unknown Eden into an early population that included some hyperthermophiles near hydrothermal systems. During the earliest Archaean, it would have been likely that a major meteorite impact capable of heating the ocean to 100 °C would have hit the earliest community[61,62]. Only hyperthermophiles could survive an impact catastrophe — the 'impact bottleneck'[63]. Perhaps two by-then-distinct lineages of descendants survived the bottleneck, one to lead to the bacteria and the other to the archaea. The 'Noah' was the last common pre-impact ancestor of those organisms that survived, except possibly some viruses[64]. Since then, the rainbow has shone over cool waters.

A third alternative is that the earliest evolution took place on Mars. There is no consensus whether life exists, or ever existed, on Mars, but early Mars, with then-vigorous volcanism, may have been a kinder, gentler habitat than Earth[62]. Large impacts would have occurred here too, but there was no deep ocean which could be vaporized to maintain a global steambath. Major impacts would have ejected many fragments from the surface of Mars, some of which would have landed on Earth. If

Mars did have life, possibly one or more cells survived impact on Mars, ejection, freezing in space, and transfer to and landing on Earth, where the cell line then survived later ocean-heating bottlenecks associated with impacts. Gene transfer is potential signal rather than noise as parts of the tree on the same planet would exchange with each other. A tenable 'martian' explanation of the origin of the Eucarya is that the ancestral eukaryote was a later, second martian transfer. In this hypothesis, the ancestors of the eukaryote stem cell continued to evolve on Mars, after the time the ancestor of the archaea and bacteria had been ejected to Earth. If a cell from this line were later ejected to Earth, the newly arrived distant cousin could have hosted a symbiotic union with the bacteria.

Both the notional 'hyperthermophile Eden' and 'Noah' last common ancestors discussed here must have been DNA-based and chemically sophisticated, possessing many of the basic housekeeping proteins. But these might not have been the original replicating organisms. The variety of suggestions about the setting of the origin of life is wide and unconstrained, beyond the scope of this review. Where was Eden? Possible birthplaces and first habitats range from ancestry in an aerosol, to a cold pond under a glacier, to a small, warm pond near a hydrothermal system[65], and many other alternatives.

The notion of a universal phylogenetic tree that crystallized into distinct branches has been criticized[53,66] on the grounds that lateral gene transfer between contemporaneous organisms may have been on a much wider scale than is implied by a tree. There is clear evidence today for lateral transfers of genetic information. However, such

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transfers between widely separated organisms would rarely be advantageous: for example, gaining information about photosynthesis would be of little use to a bacterium that lived deep in mud. Perhaps a better model is not a tree, even a mangrove, but a braided stream delta, with much cross-over, yet still clearly defined flows from the main distributaries. A closer analogy is the origin of languages: there are many parallels between the evolution of eukaryotes and the chimaera that amalgamated a Saxon root with French, Latin and Greek implants, and added doses of Arabic to Zulu, to make English.

Molecular phylogeny can be calibrated by reference to the geological record[29,67]. To summarize, given the scale of the early bombardment, it is unlikely that Earth could have been a permanent habitation before about 4.2 or even 4.0 Gyr or less[61]. If the evidence from the Isua belt[34] does indeed record life, and the age is interpreted correctly, then life is perhaps up to 3.8 Gyr old, or more; moreover, this life possibly existed by anoxygenic photosynthesis, implying that considerable speciation had taken place by then. The last common ancestor would have existed long before that. By about 3.5 Gyr the Rubisco signature necessarily implies global oxygenic photosynthesis[32] and the evolution of cyanobacteria. Ancestral eukaryotes appear to predate 2.7 Gyr (refs 48, 49).

Habitat occupation

It is possible that the earliest replicating system was an RNA molecule, capable of acting as a ribozyme and in some way self-assembling, which was ancestor of the ribosome. This RNA-world hypothesis[68] deserves special attention, especially as the 30S ribosomal subunit, which lies at the heart of the cell, is in effect a giant ribozyme supported by a scaffold of caring proteins[69,70]. An RNA world may have lived in pores in rock around a hot spring where both vapour and liquid phases were present[28,71]. Possibly the setting was subaerial, allowing both gas and fluid chemistry. The environment was presumably rich in phosphate, to allow a self-replicating molecule to gain access to essential phosphorus. Geologically, such environments tend to occur around alkaline volcanics, mainly but not all on continents. One possibility is an alkaline hot spring drawing fluid from an alkaline ultramafic body. Phosphates are associated with rocks such as carbonatites that are typically intruded in continental settings, but hydroxylapatite is known from rocks such as serpentinites[72], which are similar to ocean-floor material and to altered komatiite, a lava common in the Archaean[28]. Komatiite volcanoes would have built large Hawaii-like shields, perhaps hosting alkaline hydrothermal systems around subaerial volcanoes.

Many of the basic components of biochemical housekeeping may reflect ancestry in a hydrothermal system[73]. These may include many of the metal proteins, especially those involving iron–sulphur, nickel, molybdenum, copper, cobalt and zinc, some of which, such as metal–nitrogen structures, may have condensed in alkaline settings. Heat-shock proteins possibly date from the time when the community before the last common ancestor lived on the fine line between starving (being too cold, and too far from the hot vent) and being cooked. Any property that could repair damage would be highly advantageous. The shaping properties of heat-shock proteins would preadapt them for use as chaperonins, helping protein folding.

The phylogenetic tree implies strongly that the first living community was not photosynthetic. It seems improbable that the sophisticated biochemistry needed for photosynthesis should spring out of nothing. Early Archaean life would have had access to redox contrast between a more oxidized atmosphere–ocean system, open at the top to space, and the more reduced fluids in contact with mantle-derived magmas. Sulphur offers the best opportunities. An early atmosphere rich in sulphur gases, with CO_2 partial pressure exceeding 2 bar, could have provided some warmth and protection against UV radiation[74]. With water present in the air, and hence probably OH, volcanic sulphur dioxide would have been oxidized to sulphate[75], although this may have been slow on a glacial planet. Dissolved in water, sulphate would provide oxidation power for organisms to react against reduced species in hydrothermal fluids, such as hydrogen and methane, and in rock surfaces.

Perhaps the last common ancestor lived in a thin biofilm of cells near

Gaia in the Archaean?

In the modern atmosphere, nitrogen is managed biologically by nitrifying and denitrifying bacteria, and has a lifetime of tens of millions of years. Carbon dioxide in air has a lifetime of centuries, whereas the lifetime of oxygen in the air is many millions of years, but they are obverse and reverse. The reduced carbon reservoir is on the surface (for example, in plants, peat and soil) and in sediment (in gas, oil and coal). Oxygen in the air is only a small store of the total oxidation power that has been created by the biological use of light[109]. More oxidation power is stored in the long-term heritage of oxidized minerals in sediment, crust and mantle. Tectonic control on carbon storage can be important[110]. In one view, most of the modern atmosphere can be seen as a biological construct[111], although the basic geochemical controls should not be forgotten[112]. Only argon is not managed by biological processes.

Although microbial and less productive than today, Archaean ecology[113] used the same basic biochemical cycles as on the modern Earth. Purple bacteria and cyanobacteria did then what mitochondria and chloroplasts do today. Archaean methanogens did then what they do in bovine stomachs today. There may have been significant emission of dimethylsulphide by microbial plankton, important in the sulphur cycle then as today. Moreover, below the surface the sedimentary biosphere has always been microbial. From this comes the hypothesis that the Archaean atmosphere and greenhouse feedback loops were also biologically cycled[28,111]. It is possible, however, that for periods the Archaean biosphere was 'upside-down', with the store of reductant in the air, and oxidant stored in the sediment (for example, as iron oxide)[114]. Prior to the oxic transition, hydrogen loss to space from methane photolysis could have been important in oxidant supply to the surface environment. After the transition the reduction in CH_4 and hence greenhouse warming could have caused global cooling[115].

Hydrothermal water from liquid oceans cools plates, and the presence of this water in oceanic crust, when driven off during subduction into overlying mantle, causes melting and ultimately the formation of the granitoid rocks that, collectively, are the continents. No water, no continents[16]. If there is too little water so that the mid-oceanic ridge is exposed, oxygen is consumed in weathering. Too much water, and the flooded continents never get weathered. Liquid water, maintained by the regulation of the atmospheric greenhouse, has controlled the presence of continents and the functioning of plate tectonics. Has the day-to-day regulator of the greenhouse, and hence water, been life?

a hot vent, surviving on the redox contrast between slightly more oxidized water and slightly more reduced substrate, and on the difference between warm reduced water from vents and slightly more oxidized ambient water. Dead and dying cells would inevitably accumulate under the biofilm, creating a potential habitat-niche in recycling the reduced organic matter. Thus once a biofilm existed, niches would inevitably form and be filled by evolutionary divergence. Evolution works by tinkering with the available equipment[76], adapting existing organs to new purposes.

Archaean hydrothermal settings (Fig. 1) would have been varied[42,73]. In deep water, mid-ocean ridge volcanism may have been much more active than today, with abundant vent fields including 'black smokers' and hydrothermal deposits rich in, for example, manganese, iron, copper, zinc and sulphur. Widespread volcanoes erupted komatiite, possibly forming shields similar to Hawaii today, but lower and much wider, hosting subaerial hot springs. If plate tectonics operated, subduction volcanism (comparable to that in Japan today) would also have occurred, hosting subaerial and subaqueous hydrothermal systems, with fluids containing, for example, copper, molybdenum and zinc.

Methanogens are deeply rooted on the standard tree, and it is possible to imagine an early biosphere inhabited by sulphate reducers that exploited the oxidation contrast between the air–water system and more reduced rock-derived fluids. These primary producers would be underlain by methanogenic recyclers[77,78]. Such a biota would have produced surplus methane, which may, if the system was productive enough, have had global consequences by greenhouse warming. If the $CH_4:CO_2$ ratio were high enough, a biogenic, methane-rich smog layer[23,24] might have formed that blocked UV light.

Origin of photosynthesis

There are various hypotheses for the evolution of photosynthesis[79–83]. One plausible model is a sequence starting with accidental use of pigments by simple organisms living in a setting where local chemical disequilibrium is easily and accidentally exploited, leading to preadaptation that allowed cells to exploit light as an additional source of energy in anoxygenic photosynthesis, and finally the transition to full dependence on photosynthesis.

It was thought, on biochemical grounds, that chlorophyll biosynthesis predated bacteriochlorophyll, but recent evidence disputes this[83]. The appearance of anoxygenic (bacteriochlorophyll) photosynthesis would have made shallow-level and subaerial hydrothermal systems much more productive. Anoxygenic photosynthesis exploits light in the longer visible and near-infrared spectrum. The specific light wavelengths used depend on the type of bacterium and setting in a mat[79,84]. Purple bacteria have a wide spectrum of absorption, including bacteriochlorophylls absorbing at 900 or >1,000 nm, whereas green bacteria use bacteriochlorophylls that have absorption maxima around 750 nm in living cells. Anoxygenic photosynthesis uses a variety of electron donors in different bacteria, including hydrogen, hydrogen sulphide, sulphur and various organic chemicals. Some cyanobacteria can use sulphide in anoxygenic photosynthesis[85]. Anoxygenic photosynthesis could have evolved in a bacterium using infrared thermotaxis[82]. This preadaptation, useful in a deep-water setting near hot hydrothermal vents, could have allowed a bacterium that drifted into shallow water to utilize sunlight and occupy mesothermophile habitats.

In contrast, oxygenic photosynthesis uses visible light in more energetic wavelengths, and has H_2O as the electron donor; Rubisco then helps capture carbon from CO_2 in the atmosphere–ocean system. The family of photosystem II reaction centres, using pigments and quinones as electron acceptors, is found in purple bacteria and in *Chloroflexus aurantiacus,* a green bacterium that may be from a line of great antiquity, as well as in cyanobacteria and chloroplasts. The photosystem I family of reaction centres, using iron–sulphur centres as electron acceptors, occurs in green sulphur bacteria, cyanobacteria and chloroplasts. The involvement of both photosystems in oxygenic photosynthesis indicates an origin from genetic transfer between cooperating or closely juxtaposed cells, each using anoxygenic photosynthesis.

A key component in oxygenic photosynthesis is the oxygen-evolving complex that is based on a manganese complex exploiting a transition from Mn_4O_4 to Mn_4O_6. To the geologist, the involvement of manganese immediately suggests the vicinity of a vent of a hydrothermal system, but the environment needs to be oxygen-rich. The complex might have developed in a photosynthetic mat from manganese–catalase, perhaps to handle excess peroxide[81], or as a toxic weapon to use against competitors, or both.

The evolution of the structure of microbial mats may have paralleled the evolution of photosynthesis, with newer forms progressively claiming occupation of the more productive but more dangerous uppermost level in the mats, where light was brighter[86]. In this model, early pre-photosynthetic biofilms that were hyperthermophile and chemotrophic would have had bacterial sulphate-processers on top, underlain by archaea that recycled redox power. Anoxygenic photosynthetic mats would have added a top layer of bacterial photosynthesizers, introducing a new source of reduction power. This would have allowed occupation of the mesothermal outer perimeters of hydrothermal pools, and then the open environment away from

volcanism (Fig. 1). Finally in this model, before 3.5 Gyr, cyanobacteria brought a new occupant to the top layer. Their evolution, possibly as a bacterial chimaera formed from a genetic exchange between inter-dependent purple and green bacteria living on the redox boundary of a microbial mat, created an organism that could live freely on the planet, wherever water, light and CO_2 were present (Fig. 1). Coupled with their nitrogen-fixing ability, this would have allowed an enormous expansion of the biosphere. Whereas before the community away from hydrothermal systems was limited probably to sulphate-reducers depending on available sulphate, now life could spread widely (and the sulphate supply would rise too).

Is Rubisco a 'qwerty' enzyme?

Where CO_2 is in excess, as in the air, Rubisco[87] preferentially selects ^{12}C. For 3.5 Gyr, this isotopic signature in organic carbon, and the reciprocal signature in inorganic carbonate, has recorded Rubisco's role in oxygenic photosynthesis as the main link between atmospheric and biomass carbon[32]. But Rubisco itself may long predate oxygenic photosynthesis, as many non-photosynthetic microaerobic and aerobic bacteria use it. Unlike the many enzymes whose efficiency has been so honed by the aeons as to approach 100% (for example, catalase), Rubisco works either as carboxylase or oxygenase in photosynthesis and photorespiration[88]. This apparent 'inefficiency', capable of undoing the work of the photosynthetic process, is paradoxical, yet fundamental to the function of the carbon cycle in the biosphere. Without it, the amount of CO_2 in the air would probably be much lower.

It is possible that Rubisco is not subject to evolutionary pressures because it has a monopoly. The qwerty keyboard, which is the main present link between humanity and the silicon chip, may be a parallel: legend is that qwerty was designed to slow typists' fingers so that the arms of early mechanical typewriters would not jam. It is among the worst, not the best, of layouts, and only minor evolution occurred (English has Y where German has Z). Perhaps the same applies to Rubisco: if so, genetic engineering to improve Rubisco might lead to a productivity runaway that removes all atmospheric CO_2.

Origin of Eucarya

Late-Archaean (2.7 Gyr) rocks contain molecules that suggest not only the presence of cyanobacteria but also eukaryotes[48,49]. Eukaryotes may have evolved slowly, from a parental stem that symbiotically incorporated chloroplasts (which are descended from cyanobacteria) and then mitochondria (probably descended from α-proteobacteria). In this model the amitochondrial eukaryotes would be primitive. However, it is possible that the incorporation of mitochondria was synchronous with the origin of the eukaryote nucleus[89]. In the 'hydrogen hypothesis'[90], a symbiotic partnership may have become a union between anaerobic hydrogen-dependent archaea and heterotrophic proteobacteria capable of producing molecular hydrogen through anaerobic fermentation. An alternative, but not necessarily exclusive, hypothesis[91] is that an anaerobic archaeon could have evolved the ability to survive in more oxidizing environments (for example, near to oxygenic cyanobacteria) by incorporating symbiotic respiring proteobacteria. The origin of chloroplasts may have been a single ancestral cyanobacterium, but this is not proven[92]. Perhaps the eukaryote-creating event also incorporated mitochondria and chloroplasts simultaneously, in a single accident, possibly in a symbiotic consortium living on the redox boundary in a microbial mat.

The oxygen debate

The debate about the oxidation state of the Archaean atmosphere is vigorous, with strong proponents both of the 'oxic'[93] and not-oxic[94] viewpoints. Certain facts are available. In the early geological record, sulphate, although rare, does occur. Apparently evaporitic at first, it is present in ~3.5-Gyr rocks[95,96]. Deposition of sulphate implies localized non-reducing conditions (although not necessarily the presence of free oxygen), at least at 3.5 Gyr. But many Archaean rocks contain apparently detrital pyrite, siderite and uraninite[94,97], minerals that are

difficult to transport far in oxidizing settings. Rocks widely recognized as redbeds do not exist before about 2.2 Gyr (there are some older exceptions, but these may have been oxidized later under Cretaceous or Tertiary erosion surfaces), and interpretation of palaeosoils also suggests oxidizing conditions after this time.

Models of the chemistry of the early atmosphere, into which abundant CO_2 and sulphur gases would have been emitted by volcanism, suggest that oxygen was present, but at low partial pressures[98]. Given the probable oxidation state of the mantle and thus the degassing of SO_x gases and subsequent presence of oxidant in the high atmosphere[75], as well as a possible supply of relict oxygen after hydrogen loss to space, it is likely that the supply of sulphur gases was adequate to support early chemotrophic life. Such life would have reacted chemical species from the relatively oxidized atmosphere–ocean system, bombarded by light and open to space, with more reduced mantle-exchanged hydrothermal fluids[98]. The planet may have been covered mainly in ice, except for open-water leads[99], unless the CH_4 content of the air was high enough to sustain a methane greenhouse[24].

The appearance of oxygenic photosynthesis before 3.5 Gyr (ref. 32) provided a source of atmospheric oxidation power that would have increased the productivity of chemotrophic life. The nitrogen cycle may be of similar antiquity. Nitrogenase, which after Rubisco is the next most important enzyme (and is perhaps also a qwerty enzyme), consists of an iron protein and a molybdenum–iron protein that includes a 4Fe–4S cluster and a Mo–3Fe–3S cluster. The presence of molybdenum, iron and sulphur suggest a hydrothermal heritage, perhaps originally for dealing with ammonia in a reducing setting, as nitrogenase is inhibited rapidly by oxygen.

Life spreads instantly on a geological timescale, and immediately the modern carbon and nitrogen cycles were in place the atmosphere would have become biologically ruled by kinetics and disequilibrium, not sustainable equilibrium (see Box 3). There were huge reservoirs of reductant (for example, reduced iron, sulphide and organic debris in sediment), but the biosphere is inflationary in that it sequesters oxidant and reductant and exploits the possibilities of cycling between them. A thin layer of life can divide sharply contrasted redox reservoirs.

The abundance of Archaean ironstones implies that transport of iron took place from the source to the place of deposition. But only Fe^{2+} species are soluble, indicating that reducing conditions were required. Vast bacterial blooms could have produced ironstones, perhaps where deep, reduced water met shallow-level, oxidized water. The objection to this idea is that there is little organic carbon in ironstones: deposition may have been inorganic. However, biological iron transport could have been important in a microbial world. Bacteria could acquire iron in local reducing settings, such as near hydrothermal vents or in soil, and then pass the iron through the biomass by predation or by recycling dead bodies (but see Box 3 for Walker-world, the upside-down biosphere).

Global oxygen production has probably been of the same order of magnitude as today (to a factor of 10) for at least 3.5 Gyr, but the oxygen level in the atmosphere does not depend on production alone. Consider a bathtub (the atmosphere) with a running tap (oxygen production by photosynthesis). The level in the tub depends not so much on the flow from the tap but on the plug. If the plug is out, there will be little water in the tub even if the tap is full on; if it is in, the tub will eventually fill to the overflow limit, even if the tap only drips. The air may be similarly regulated. If the oxygen level increased sharply around 2.2 Gyr, possibly the appearance of complex eukaryotes may have been involved. The cellular cybernetic switch between mitochondria and chloroplasts[100] may control the link between photosynthesis, CO_2 and nitrogen fixation, in partnership with the ability of Rubisco to reverse its function[87,88,101] as CO_2/O_2 ratios change. There may have been major excursions from this simple picture of a planet with a microaerobic early atmosphere that switched to oxic air after 2.2 Gyr. For example, at times global methane production by archaea may have been highly significant, with events when the atmospheric methane burden was high[23,24,102].

The evolution of the sulphur cycle remains controversial. Some isotopic evidence[103,104] suggests that microbial fractionation of sulphur was limited in the Archaean, implying that sulphate concentrations were low. But other isotopic evidence[50] implies that the full sulphur cycle evolved earlier, which would be expected if the 'standard' molecular phylogeny[52] is correct with respect to sulphur processing. It is possible that the microbial diversity of sulphur handlers was present early on, but only became widespread much later[105].

Afterview

On Earth, life probably dates from 3.8 Gyr or before, but life may have existed earlier on Mars or even on Venus or an outer moon and been translated to Earth by meteorite. We still have little idea how, when or where life began. The notion that life began in a hydrothermal setting is extremely attractive, but the evidence is circumstantial and can be compared with delving into such records as there are in Massachusetts of the Mayflower, to discern the origins of the English language.

The debate about life's origins has deep resonance in our society. Those who work in this field frequently find their search challenged in assaults on empirical natural science. Judaeo–Christian thought must accept convincing evidence from nature; denial is both destructive of faith and dangerous to science. To find the fragments of fact, and to attempt to understand them, is a powerful response to the Creationist heresy. Not only fact and honest interpretation, but also orthodox theological argument reject Creationism: much Jewish and Christian thinking agrees with the anonymous writer of the epistle to the Hebrews, Peter and Augustine in the view that the Biblical Day is a wider concept than the 24-hour rotation of the Earth. The Seventh Day is lasting. The author of Job and Paul both challenge us to search nature, although we may not find the answer.

In summary, the best evidence is that life has been present on Earth since about 3.8 Gyr or earlier, and for at least the past 3.5 Gyr the main biochemical carbon cycle has been operating. But whether Earth is alone as a planet of life remains an open question. □

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