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**Hadean geodynamic  
and metabolic cycles**

M. J. Russell and N. T.  
Arndt

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# Geodynamic and metabolic cycles in the Hadean

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## Abstract

High-degree melting of hot dry Hadean mantle at ocean ridges and plumes resulted in a crust about 30 km thick, overlain in places by extensive and thick mafic volcanic plateaus. Continental crust, by contrast, was relatively thin and mostly submarine. At constructive and destructive plate boundaries, and above the many mantle plumes, acidic hydrothermal springs at  $\sim 400^\circ\text{C}$  contributed Fe and other transition elements as well as P and  $\text{H}_2$  to the deep ocean made acidulous by dissolved  $\text{CO}_2$  and minor HCl derived from volcanoes. Away from ocean ridges, submarine hydrothermal fluids were cool ( $\leq 100^\circ\text{C}$ ), alkaline (pH  $\sim 10$ ), highly reduced and also  $\text{H}_2$ -rich. Reaction of solvents in this fluid with those in ocean water was catalyzed in a hydrothermal mound, a natural self-restoring flow reactor and fractionation column made up of carbonates and freshly precipitated Fe-Ni sulfide and greenrust pores and bubbles, developed above the alkaline spring. Acetate and the amino acetate glycine were the main products, much of which was eluted to the ocean. Other organic byproducts were retained, concentrated and reacted within the compartments. These compartments comprising the natural hydrothermal reactor consisted partly of greigite ( $\text{Fe}_5\text{NiS}_8$ ). It was from reactions between organic modules confined within these inorganic compartments that the first prokaryotic organism evolved. These acetogenic precursors to the Bacteria diversified and migrated down the mound and into the ocean floor to inaugurate the 'deep biosphere'. Once there the Bacteria, and the recently differentiated Archaea, were protected from cataclysmic heating events caused by large bolide impacts. Geodynamic forces led to the eventual obduction of the deep biosphere into the photic zone where, initially protected by a thin veneer of sediment, the use of solar energy was mastered and photosynthesis emerged. The further evolution to oxygenic photosynthesis was effected as catalytic  $[\text{CaMn}^{4+}]$ -bearing molecules that otherwise would have been interred in the mineral ranciéite in the shallow marine manganiferous sediments, were sequestered and invaginated within the cyanobacterial precursor where, energized by light, they could oxidize water with greater efficiency. Thus, chemical sediments were

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required both for the emergence of chemosynthesis and of oxygenic photosynthesis, the two innovations that did most to change the nature of our planet.

## 1. Introduction

The Earth's internal thermal energy is mainly degraded through convection. Heat is transferred to the surface by a convecting mantle, to be discharged through volcanoes and hydrothermal springs into the ocean and atmosphere (the volatisphere). Chemical disequilibrium between reduced mantle and oxidized volatisphere is focused at springs and seepages on land or on the ocean floor. In turn this chemical energy is degraded through metabolism. Today metabolism relies on convection for supply of nutrients in the ocean and on convection in the atmosphere for irrigation and chemical weathering of the land. The springs and seepages are oases of life in both realms.

At a broader scale and at slower rates, global geodynamic processes generate fresh, reduced rock surfaces that provide energy and supply nutrients to life. This coupling of metabolism to convection was directly implicated in the onset of life, which probably emerged at least 4 Ga ago at moderate temperature seepages (Russell et al., 1988, 1994).

Reconstruction of the conditions that drove life to emerge and evolve its metabolic cycles is the main task of this paper. We begin by considering what present-day processes offer to the understanding of the conditions on the surface and in the interior of the Hadean/Archaean Earth, then suggest a scenario for the onset of life and its colonization of the ocean floor. This journey from geodynamics, through geochemistry to biochemistry leads us to conclude that obduction of oceanic crust facilitated the evolutionary jump to photosynthesis.

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## 2. The modern oceanic crust

### 2.1. Birth and death of oceanic crust

A complete plate tectonic cycle starts with the formation of crust at a ridge and ends with its recycling to the mantle at a subduction zone. Continental crust forms above subduction zones, a direct result of the dehydration of subducting oceanic crust which triggers partial melting in the overlying mantle and the development of hydrous magmas. Superimposed on the plate tectonic cycle is the formation of oceanic islands and oceanic plateaus, which are generated by partial melting in mantle plumes.

### 2.2. Modern hydrothermal systems – how they work

Five main types of hydrothermal fluids circulate through modern oceanic crust. Three high temperature types ( $\leq 4^\circ\text{C}$ ) operate at oceanic ridges, above plumes or in back arc basins; an intermediate type occurs on ridge flanks ( $\leq 75^\circ\text{C}$ ); and the last, far cooler, on the deep ocean floor (Anderson et al., 1977; Von Damm, 1990, Cathles, 1990; Sedwick et al., 1994; Kelley et al., 2001; Wheat et al., 2002) (Table 1).

The temperature of the very hot springs, driven by magmatic intrusion, is controlled largely by the two-phase boundary of water and its critical point (Bischoff and Rosenbauer, 1984). Temperatures in modern hydrothermal convective systems, which bottom at an overall water column depth of 4 km or so, tend to peak at  $\sim 4^\circ\text{C}$ . The fluids in the downdrafts become acidic (pH  $\sim 3$ ) through the release of protons as  $\text{Mg}^{2+}$  is fixed as serpentine and brucite (Janecky and Seyfried, 1983; Douville et al., 2002). These acidic solutions dissolve, transport and exhale the transition metals, some phosphate,  $\text{H}_2\text{S}$  and  $\text{H}_2$ , at black smokers (Table 1) (Von Damm, 1990; Kakegawa et al., 2002).

The temperatures and compositions of intermediate-temperature hydrothermal convection cells are controlled by exothermic reactions and the rheology of the newly serpentinized mafic to ultramafic rock of the conduits. So far the fluid from only one entirely submarine example of ultramafic interaction has been sampled, the “Lost City” field, 15

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km from the Mid Atlantic Ridge (Kelley et al., 2001). The pH of this water approaches 10 as  $\text{Ca}(\text{OH})_2$ ,  $\text{HCO}_3^-$  and  $\text{H}_2$  are eluted, and the temperature is 70–75°C (Table 1) (Kelley et al., 2001). A cooler (72°C) alkaline (pH 10) fresh-water submarine spring in a fjord off the north coast of Iceland (Marteinsson et al., 2001; Geptner et al., 2002) is characterized by porous cones of Mg-rich clay (saponite) some tens of metres high (Table 1).

Still farther from ridges, even cooler circulation is driven by heat within the uppermost crust. Small closed convection cells are evenly spaced with a periodicity of about 7 km, with thermal cusps around 20°C (Anderson et al., 1977).

Data for columns 1 to 4 from Von Damm (1990), Douville et al. (2002), Kelley et al. (2001) and Marteinson et al. (2001). Elemental and molecular concentrations are in millimoles. Temperatures at the base of the convection cells developed at oceanic spreading centres and the off-ridge systems are presumed to be ~400°C and ~100°C, respectively.

### 3. Hadean/Archaean ocean/atmosphere, oceanic crust and global dynamics

#### 3.1. The volatisphere

According to oxygen isotope analysis of the oldest known zircons, an ocean is assumed to have condensed on Earth by 4.4 Ga (Wilde et al., 2001). The atmosphere contained  $\text{CO}_2$  and  $\text{N}_2$ , some HCl,  $\text{SO}_2$ ,  $\text{S}^0$  and minor amounts of  $\text{H}_2$  and Ar (Kasting, 1993; Kasting and Brown, 1998; Pavlov and Kasting, 2002). Volcanogenic  $\text{CO}_2$  and HCl, augmented by output from high temperature acid springs, rendered the early ocean acidulous (pH 5–6) (Maisonneuve, 1982; Sedwick et al., 1994; Kasting, 1993; Macleod et al., 1994). The proportion of  $\text{CO}_2$  depended on the balance between inputs from volcanic emissions and redissolution in the deep ocean, and outputs via carbonation of the crust and of the dust thrown up by meteorite impacts (Alt and Teagle, 1999; Nisbet and Sleep, 2001). Transition metals and phosphate contributed by very hot springs

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remained in solution in this acidulous ocean (Kakegawa et al., 2002). Particularly important is  $\text{Fe}^{2+}$ , some of which was photo-oxidized to insoluble flocs of  $\text{FeOOH}$  at the ocean's surface (Braterman et al., 1983; Gaffey, 1997; Russell and Hall, 2002).

### 3.2. Crustal structure and composition

5 Heat production in the Hadean was at least 5 times that of the present day and it is probable that the mantle was several hundred degrees hotter than today's mantle (Turcotte, 1980). Because the dehydration reactions that control the amount of water recycled to the mantle are temperature dependent, the Hadean mantle was drier than its modern counterpart. The ocean contained most of the Earth's water and its volume  
10 may have been up to twice that of today's oceans (Bounama et al., 2001). Upwelling of hot, dry mantle at oceanic spreading centres generated an early Archaean crust about 30 km thick (Sleep and Windley, 1982) (Fig. 1). Oceanic plateaus more extensive than Ontong Java covered large parts of the oceanic crust with an additional 30 km of mafic and ultramafic igneous rock. Both oceanic crust and plateaus were internally  
15 differentiated into an upper ~5 km-thick layer of magnesian basalt underlain by ~10 km of gabbros and troctolites and 10 km or more of ultramafic cumulates (Francis et al., 1999; Foley et al., 2003).

The volume of continental crust in the early Archaean was a subject of intense debate in the 1980's. Geochemists tended to the interpretation that continental crust  
20 started to appear only around 3.8 Ga, the age of the oldest rocks known at that time. Since then several important discoveries have been made. The pre 4.2 Ga zircons provide evidence for the existence of granitic rocks in the Hadean (Froude et al., 1983; Compston and Pidgeon, 1986). Direct or indirect evidence for continental crust is becoming more abundant: the 4 Ga Acasta gneisses (Bowring and Williams, 1999) and  
25 the recently discovered 3.8 Ga Porpoise Cove supracrustal rocks (Stevenson et al., 2003). Ultra-high-pressure metamorphic rocks indicate that portions of the continental crust are routinely cycled deep into the mantle. These discoveries provide mounting support for Armstrong's (1981, 1991) model of rapid early continental growth. In this

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model, granitic continental crust was abundant by the end of the Hadean.

The topography of the Hadean planet differed radically from that of the modern Earth. Because Hadean granitic crust contained higher concentrations of radioactive elements it was hotter, less viscous, and thinner than modern continental crust (Sandiford and McLaren, 2004). And because the mantle also was hotter, the continental lithosphere was thinner. Oceanic crust, in contrast, was much thicker than modern oceanic crust; as thick or thicker than the early Archaean continental crust. The oceans were more voluminous and they flooded a greater portion of the Earth's surface. Most of the continents were submerged and only mountain ranges at convergent margins and vast volcanic plateaus occasionally breached the ocean surface (Arndt, 1999). Thus there was little subaerial weathering and erosion of the mainly submerged continental masses and therefore comparatively little clastic sedimentation.

Hydrated oceanic crust continually cycled back into the mantle. At the base of the thickest sections, where oceanic plateaus had erupted onto the oceanic crust, pressures were sufficient to convert plagioclase to garnet. The downward drag of these dense eclogitised segments and the underlying dense Fe-rich ultramafic cumulates initiated subduction. Once started, the entire basaltic and gabbroic portion of the crust converted to eclogite, and plunged into the mantle (cf. Holmes, 1931). The earliest subduction zones probably were steeply dipping, rather than shallow, as is commonly assumed (Fig. 1) (Karsten et al., 1996). The upper layers of the crust dehydrated and triggered the melting in the over-riding mantle that gave rise to the magmas parental to continental crust. The uppermost parts of the oceanic crust obducted to form accretionary prisms of the type discussed by Maruyama (1997) and Foley et al. (2003). These prisms obliterated any nascent oceanic trenches, a process that was highly significant, as we shall see, to the development of photosynthesis.

### 3.3. Hydrothermal circulation

If we assume that the 400°C springs developed at constructive plate margins were comparable to those emanating from the ultramafic crust at the Rainbow field, the highly

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reduced acidic fluids would have carried about 20 mM of  $\text{Fe}^{2+}$  to the ocean (Von Damm, 2000; Douville et al., 2002; Allen and Seyfried, 2003) (Table 1). With negligible marine sulfate in the Hadean (Farquar et al., 2000) there were no spontaneously precipitated protective anhydrite chimneys, and no black smokers. Hydrogen sulfide, reacting first with zinc, produced soluble but stable  $\text{ZnS}$  clusters as the solutions cooled on exhalation (Luther et al., 1999). Given the high remaining metal to sulfide ratio (Walker and Brimblecombe, 1985), much of the Fe and minor Ni stayed in solution in the acidulous ocean, though photo-oxidation of a proportion of the  $\text{Fe}^{2+}$  generated flocs of  $\text{FeOOH}$  (Braterman et al., 1983).

In marked contrast, off-ridge springs had a similar temperature and chemistry to those of the present day ( $<100^\circ\text{C}$  and pH 9–10, Table 1) (Shock, 1992; Macleod et al., 1994; Kelley et al., 2001; Russell and Hall, 2002; Foley et al., 2003). Similar solutions may have exhaled from faulted zones within the oceanic plateaus. Such alkaline solutions could have provided  $\sim 10$  mM of  $\text{HS}^-$  to the seepage site (Macleod et al., 1994; Rahman, 2003). A mound of precipitates formed where these seepage waters met the acidulous ocean. The main precipitates were of iron, calcium and magnesium carbonates, with subsidiary ferrous and ferric oxyhydroxides and iron>nickel sulfides (Russell et al., 1988, 1998).

### 3.4. Ocean temperatures

The temperature of the Hadean ocean is uncertain. The effective radiative temperature of the Sun was about 70% of its present output (Bahcall et al., 2001) and only the presence of atmospheric  $\text{CO}_2$  prevented the Earth from completely freezing over (Kasting, 1993). Indeed, temperatures may, on occasion, have approached  $100^\circ\text{C}$ . There were several effective sinks for  $\text{CO}_2$  including the extensive volcanic plateaus and the dust raised by major bolide impacts (Nisbet and Sleep, 2001). These impacts may also have vapourised the ocean from time to time, though temperatures were never so high that a Venus-like atmosphere persisted. Very likely there were frequent oscillations from

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hot (impact and green-house induced), to cold and partially frozen, a consequence of solar radiation masking by local or galactic dust clouds (Kasting, 1993; Kasting and Brown, 1998; Alt and Teagle, 1999; Nisbet and Sleep, 2001). Very cold conditions were short-lived because of continuous and widespread volcanicity and exhalations of CO<sub>2</sub>.

Notwithstanding our earlier suggestion for a thermophilic start to life (Russell and Hall, 1997), because of the fragility of RNA we recognise that life is unlikely to have emerged at temperatures much above 40°C (Forterre, 1996; Moulton et al., 2000; Brochier and Philippe, 2002). And because a thermal gradient is required to drive convection, we suggest that life's emergence had to await a period, or "window of opportunity" when oceanic temperatures were low, perhaps around 20°C (but see Schwartzman and Lineweaver, 2004, for a contrary view). However, once life had emerged it had to survive the Hadean periods of high temperature. How this was done will have to be addressed in our hypothesis of life's emergence and early evolution.

## 4. Chemical contribution to the onset of life

### 4.1. The hydrothermal mound

Haeckel (1892, p. 414) considered life to have emerged from an "inorganic formative fluid" and Leduc (1911, p xv) suggested that "the chain of life is . . . a continuous one, from the mineral at one end to the most complicated organism at the other". In Leduc's view, the first compartments to store the potential energy that drove life to emerge were also inorganic. These prescient ideas were ignored, partly because they seemed to hark back to theories of spontaneous generation put paid to famously by Pasteur, and partly because scientists were loath to consider anything but an organic origin for any organic being. Although this organic view held sway for 75 years, the inorganic hypothesis has since been disinterred. Here we suggest that a stable, long-lived alkaline submarine seepage of moderate temperature satisfies Haeckel's expectations (Rus-

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sell et al., 1988, 2003) and that Leduc's inorganic compartments may have comprised catalytic iron(nickel) sulfides generated at this same seepage, a suggestion given significance by the recognition that iron and sulfur comprise the active centres to proteins with the longest pedigree, the electron transfer agents known as the ferredoxins (Eck and Dayhoff, 1966; Hall et al., 1971; Russell et al., 1994).

Portions of a hydrothermal mound comprising freshly precipitated films of iron sulfide in the form of disordered nanometric mackinawite ( $\text{Fe}_{1+x}\text{S}$ ) and minor greigite ( $\text{Fe}_5\text{NiS}_8$ ) offered semipermeable and semiconducting containers for the synthesis and retainment of organic molecules (Russell and Hall, 1997; Filtner et al., 2003; Wolthers et al., 2003). Strong gradients developed at the outer margins of such a mound where the reduced alkaline hydrothermal solution interfaces with the cooler, more oxidized Hadean ocean. Potentials focused across the iron sulfide membranes were hydrodynamic (between buoyant hydrothermal solution and ocean), thermal ( $<20^\circ$  to  $100^\circ\text{C}$ ), chemical (between hydrothermal  $\text{H}_2$  and  $\text{CO}_2$ ) and electrochemical (between redox couples  $\text{H}^+/\text{H}_2$  and  $\text{Fe}^{3+}/\text{Fe}^{2+}$ ) (Russell and Martin, 2004). Electrons could also be gained from  $\text{H}_2\text{S}$ .

Reduction of  $\text{HCO}_3^-$  to  $\text{CO}$  with activated  $[\text{H}]$  is assumed to take place on nanocrystals of mackinawite and greigite (Russell et al., 1998; Russell and Martin, 2004). Further reduction to methane thiol ( $\text{CH}_3\text{SH}$ ), involving activated  $[\text{H}]$  and  $\text{HS}^-$ , is thermodynamically favoured (Schulte and Rogers, 2004) and has been demonstrated by Heinen and Lauwers (1996). Huber and Wächtershäuser (1997) reacted at  $100^\circ\text{C}$  and at a pH of 6.4 the two products  $\text{CO}$  and  $\text{CH}_3\text{SH}$  to produce acetate ( $\text{H}_3\text{C.COO}^-$ ) in yields of 40% with respect to the thiol. These chemical and physical states can be met in the hydrothermal mound. It appears then that the first product of reaction between an alkaline hydrothermal fluid and carbonic ocean water will be acetate. Indeed, acetate is the product of what is known as the acetyl coenzyme-A pathway – the most ancient of all metabolic pathways (Peretó et al., 1999; Russell and Martin, 2004).

In their experiments Huber and Wächtershäuser (1997) used a slurry of iron sulfide and nickel sulfide. However, Russell et al. (1998) pointed out that greigite and violar-

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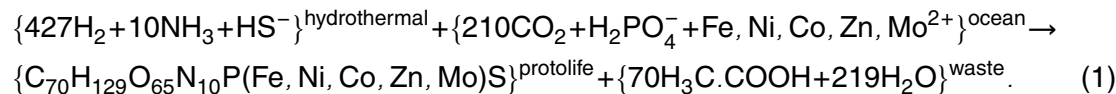
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ite ( $\text{Fe}_2\text{Ni}_4\text{S}_8$ ) are more likely to have been the catalysts. The high acetate yields are consistent with the thermodynamic calculations of Shock et al. (1998), who showed the reaction between of  $\text{CO}_2$  and  $\text{H}_2$  with the production of acetate to be extremely favourable (exergonic). The structure of greigite ( $\text{Fe}_5\text{NiS}_8$ ) is strikingly similar to the active centres (e.g.  $\text{Fe}_4\text{NiS}_5$ ) of the enzymes carbon monoxide dehydrogenase/acetyl co-enzyme-A synthase (CODH/ACS) (Dobbeck et al., 2001; Drennan et al., 2001; Darnault et al., 2003) that are presently involved in the reduction of  $\text{CO}_2$  and the formation of acetate (Vaughan and Craig, 1978; Russell et al., 1994, 1998). The same enzymes have the facility to activate  $\text{H}_2$  (Menon and Ragsdale, 2000).

The first microbes therefore used the energy and materials within the hydrothermal solution and the ocean to generate acetate (with water) as a waste product, i.e. it was an “acetogen” (Russell and Martin, 2004). The emergence of life and the generation of acetate waste within the natural hydrothermal reactor resembled mineral precipitation at a hot spring. As soon as organic molecules are formed in the process they have the effect of inhibiting mineral growth (e.g. Rickard et al., 2001): the active centres of the metalloproteins can be thought of as “still-born” mineral clusters. The approximate and highly simplified formula for “proto-life” used here [ $\text{C}_{70}\text{H}_{129}\text{O}_{65}\text{N}_{10}\text{P}(\text{Fe},\text{Ni},\text{Co},\text{Zn},\text{Mo})\text{S}$ ] is gleaned from Redfield et al. (1963), Orr (1978), Morel and Hudson (1985), Faggebakke et al. (1996) and Macalady and Banfield (2003). The trace metal contents are exaggerated in keeping with their likely contribution to the first living cells. The reactions that generated this proto-life and waste can be put notionally as:



Note the high waste-to-protolife molecular ratio.

In this explanation, the hydrothermal mound can be viewed as a self-restoring catalytic flow reactor that synthesized acetate (Russell and Martin, 2004). More complex organic molecules were a minor by-product of the reaction, a by-product that optimized acetate production. Of particular significance was the amino acetic acid glycine

(H<sub>2</sub>N.CH<sub>2</sub>.COOH), which has been produced in hydrothermal experiments by Hennet et al. (1992). Once glycine appeared in the sulfide compartments, redox and pH gradients came into effect (Russell and Hall, 1997, 2002). The alkaline mounds constituted the hydrogen electrode, or cathode, and the photolytic Fe<sup>III</sup> flocculants aggregated at the mound's exterior acted as a positive electrode. It is the Fe<sup>III</sup> that provides the potential, augmented by the exterior protons, that results in polymerization (Russell and Hall, 1997, 2002). Fe<sup>III</sup> accepted the electrons ultimately contributed by hydrothermal H<sub>2</sub>. Most prokaryotes near the root of the evolutionary tree can use Fe<sup>III</sup> as an electron acceptor, supporting the notion that this element was the first to fulfill this vital role (McFadden and Shively, 1991; Liu et al., 1997; Pace, 1997; Russell and Hall, 1997; Vargas et al., 1998; Reysenbach and Lovley, 2002).

Today the power of light drives metabolism. In the Hadean, photolytic Fe<sup>III</sup> represented "borrowed light" that energized and helped drive life's emergence (Cairns-Smith et al., 1992; Russell and Hall, 2002). In theory, the electrochemical potential approaches one volt (Russell and Hall, 1997; Russell et al., 1998); in practice, Russell and Hall (2002) and Filtner et al. (2003) have demonstrated that an FeS membrane, spontaneously precipitated at the interface between solutions containing 10mM of Fe<sup>2+</sup> >>Fe<sup>III</sup> on the one side, and 10mM HS<sup>-</sup> on the other, can hold a tension of 600 to 700 mV for several hours. The gradients had the potential to polymerize inorganic phosphate if water activity was low (Baltscheffsky, 1996). Polymerization may have taken place on the surfaces of closely packed mackinawite nanoclusters making up the inorganic membrane. In turn, and on the same surfaces, pyrophosphate might have polymerized glycine to form homopeptides. That amino acids may be polymerized on saponite clay has been demonstrated by Ferris et al. (1996).

Once formed the primitive peptides coordinated the building blocks of greigite (e.g. [Fe<sub>2</sub>S<sub>2</sub>]<sup>+</sup>, [Fe<sub>4</sub>S<sub>4</sub>]<sup>2+</sup> and perhaps [Fe<sub>4</sub>S<sub>6</sub>Ni]<sup>+</sup>) that had been inhibited from further growth by organic sulfides such as ethane thiol (CH<sub>3</sub>CH<sub>2</sub>S<sup>-</sup>) (Bonomi et al., 1985; Stevens and Kurtz, 1985). This started the organic take-over of the mineral-based prebiotic chemistry (Milner-White and Russell, 2004). These peptides also formed a

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proteinaceous membrane, more stable and flexible than its inorganic precursor, yet with sequestered sulfides and phosphate that were still able to gain electrochemical energy and nutrients from outside the individual cells.

#### 4.2. Evolution in the mound

5 Evolution in the mound extended beyond mere optimization of the chemotrophic acetate reaction (Martin and Russell, 2003). The first step was adaptation to organotrophy, the digestion of the reduced carbon and energy to be found in dead cells. Newly evolved acetogens were the forerunners of the true Bacteria. A minority of cells, derived from those that emerged at around 40°C, exploited the potential offered at higher  
10 temperatures deeper in the mound where the kinetic energy was greater and the activation energy required for reduction, through acetate all the way to methane, was lower. These first so-called methanogens may have evolved while still in the mound, where they exploited the greater energy to be had in the full reduction of CO<sub>2</sub> (Amend and Shock, 2001). Methanogenic Archaea derived energy by generating methane from the  
15 acetate waste from neighbouring acetogens (Madigan et al., 2000):



Russell and Hall (2002) suggested that such methanogenic cells were the precursors of the Archaea, the sturdy but slowly evolving second domain of the prokaryotes (Woese et al., 1990). If so, the last common ancestor of life occupied the very hatchery in  
20 which life first emerged, and the most significant of all cellular differentiations, that between the Bacteria and the Archaea, probably took place before the mound was evacuated (Koga et al., 1998; Martin and Russell, 2003). Up till this time of divergence, genes were shared like software in what may be called a cellular cooperative. Eventually the cells differentiated as opportunities for exploratory evolution in this previously  
25 empty habitat presented themselves, a differentiation partly driven by entropy. Random changes in genes eventually gave mutually exclusive phenotypes (Wicken, 1987) and by this stage Mn<sup>IV</sup> and S<sup>0</sup> had joined Fe<sup>III</sup> and CO<sub>2</sub> as electron sinks.

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In summary we can say that Bacteria were initially suited to low to moderate temperatures, and the Archaea originally evolved to withstand the shock of relatively high temperatures (i.e.  $\sim 55^{\circ}\text{C}$ ). But the propensity to live well above  $40^{\circ}\text{C}$  was passed back to the nascent bacteria through genetic transfer. A period of high ambient temperature, caused either by a bolide impact or a  $\text{CO}_2$  greenhouse (Kasting and Akerman, 1986; Kasting and Brown, 1998; Nisbet and Sleep, 2001) could explain why the last common ancestor of all life may have been a thermophile, perhaps living at  $50^{\circ}$  to  $60^{\circ}\text{C}$  (Gaucher et al., 2003 but see Brochier and Philippe, 2002). Whatever the heating event, it was from the surviving community that the evolutionary tree was seeded.

Representatives of both domains found it advantageous to live syntrophically. Cells relied upon their neighbours to swap genes, provide some of the nutrients and to remove some of the waste. Unfortunates that were entrained within the hydrothermal solution and dispersed to the ocean could not have survived such dilution of nutrient (e.g. Bjerrum and Canfield, 2002). The only way out was down – down onto the ocean floor and into the warm chemical sediments and permeable basalts below.

#### 4.3. Inauguration of the deep biosphere

Growth and expansion of the colonies of acetogens and methanogens followed the redox front laterally out of the mound and into the surrounding sediments. Colonization of the entire seafloor and upper crust was relatively rapid as microbial colonies were entrained in aqueous advection currents.  $\text{H}_2$  continued to be the available fuel, diffusing into the sediments from hydrating crust and mantle (Apps and van der Kamp, 1993).  $\text{H}_2$  was also provided by fellow metabolizing cells within the syntrophic communities (Wolin, 1982; Towe, 1996).  $\text{CO}_2$  for biosynthesis was provided by downward percolating ocean water, and photolytic  $\text{Fe}^{\text{III}}$ , already deposited on the ocean floor, acted as the terminal electron acceptor to maintain electrochemical potential. At some stage fatty acids and lipids started to replace much of the protein in the membrane (Martin and Russell, 2003).

Once life had gained a foothold in the sediments and hydrated volcanics of the ocean

bottom, it would have been extremely hard to eradicate. Strong Earth tides resulting from the shorter day and lunar cycle and the closer moon continuously pumped the required nutrients from above and below (Davis and Becker, 1999). Only Fe<sup>III</sup>, the main electron acceptor in the chemical sediments, may have been in short supply. Even so, a small flux of H<sub>2</sub> was enough to prevent decay of cellular material and racemization of peptides (Morita, 2000).

Thus the deep biosphere was born (Parkes et al., 1990, 1994; Pedersen, 1993; Thorseth et al., 1995; Wellsbury et al., 1997; Whitman et al., 1998; Kotelnikova and Pedersen, 1997; Furness et al., 2004). At this depth, as the thermal conductivity of saturated sediment and basalt is so low, the prokaryotes were well protected by a layer of insulating sediment and basalt from the effects of impacts, even of those that may have caused the entire ocean to volatilize.

## 5. Obduction and the emergence of photosynthesis

Given that conditions for life in the open sea were most inhospitable, how do we explain the emergence of photosynthetic organisms in the full glare of hard UV from the young sun (Canuto et al., 1982)? We suggest that obduction brought microbial consortia from the deep ocean floor into the photic zone. Because of the particular geometry of Hadean oceanic crust, chemical sediment overlying hydrated basaltic crust was obducted over the subducting, delaminated, eclogitised lower parts of the slab. Obduction of oceanic sediments, particularly of carbonates and hydrated oxyhydroxides precipitated on the margins of volcanic chains, and of the hydrated basalt beneath, passively transported the bacterial colonies into shallow water and into the photic zone. Cells were protected from deleterious solar radiation beneath a mineral coating, perhaps within a biofilm (Cockell and Knowland, 1999). In these conditions some Bacteria near the surface augmented their protective shield by developing a UV pigment protector from a ring of organic bases. Pigments comprising macrocyclic aromatic rings probably date back to at least 4 Ga (Pratt, 1993). Single ions of Fe, Mg, Zn, Co, and Ni can be

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sequestered individually in variants of what is known as the corrin or tetrapyrrole ring, itself comprising four C/N rings (Eschenmoser, 1988; Allen, 2004). Pigments developed for photoprotection could then have been adapted as electron transfer agents, as photosynthetic reaction centres and antenna proteins (Mulikidjanian and Junge, 1997; Allen, 2004).

### 5.1. The first photosynthesisers

The process of photosynthesis was mastered at least by the early Archaean (Westall et al. 2001). The first photosynthesizing bacterium may have been a precursor to the green sulfur bacteria (Baymann et al., 2001). Like some pre-photosynthetic bacteria, these bacteria relied lithotrophically on H<sub>2</sub>S as an electron donor. Just as in modern island arcs and accretionary prisms, hydrothermal H<sub>2</sub>S of magmatic or metasomatic derivation would have circulated through the sediments in the obducted pile (Fig. 2). In these conditions, a photosynthetic reaction centre (RC1) could have developed that generated elemental sulfur as waste, and gained electrons in the process (Eq. 3).



As we might expect of gradualistic evolution, the green sulfur bacteria continued to rely on iron sulfide clusters as electron transfer agents (Blankenship, 2002).

An evolutionary variant – a photosynthetic precursor of the heliobacteria bacteria – was able to fix CO<sub>2</sub> with electrons supplied indirectly by organic detritus (Vermaas, 1994). This change of electron source echoes the early evolution of biosynthesis, beginning with lithotrophs, followed by rapid and opportunistic adaptation to organotrophy (Sect. 4.2). The heliobacteria substituted a pigment as an electron transfer agent in place of some of the iron-sulfur centres (Allen, 2004). But they retained the use of photosynthetic reaction centre 1 (RC1) (Dismukes et al., 2001; Blankenship, 2002).

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## 5.2. Oxygenic photosynthesis

The photosystem (PC2) employed by all cyanobacteria and plants to oxidize water used gene duplication and gene splitting to descend from RC1 (Baymann et al., 2001). These genes probably came from green sulfur bacteria and heliobacteria (Michel and Deisenhofer, 1988; Baymann et al., 2001). PC2 works in conjunction with photosystem 1 (PS1), itself also probably evolved from the first reaction centre (RC1) (Baymann et al., 2001). PS2 is capable of oxidizing two molecules of H<sub>2</sub>O during the generation of a single molecule of O<sub>2</sub>, gaining incrementally four electrons and four protons for the fixation of carbon from CO<sub>2</sub> or HCO<sub>3</sub><sup>-</sup> for biosynthesis (Hansson and Wydrzynski, 1990) (Eqs. 4 and 5).



PS2 oxidizes water using what is known as the oxygen-evolving complex (OEC). Its active centre is a [CaMn<sub>4</sub>O<sub>4</sub>] cubane containing one Ca atom and three Mn atoms coordinated to a peripheral Mn (Ferreira et al., 2004). To explain such an extraordinary innovation, Russell and Hall (2002) and Russell et al. (2003) suggested that a small cluster, which otherwise would have been interred in the mineral ranciéite [(Ca,Mn<sup>2+</sup>)Mn<sub>4</sub><sup>4+</sup>O<sub>9</sub>.3H<sub>2</sub>O], was co-opted on the outer surface of the membrane of the photosynthetic precursor, and from there sequestered into a protein complex as a 'ready-made' catalytic centre. Ranciéite readily participates in redox reactions and Mn<sup>4+</sup> is reduced by organic molecules (Sunda et al., 1983; Post, 1999). We now imagine the precursors to cyanobacteria embedded at the top of shallow water manganese precipitates with "catalase" activity. Here the precursors exploited the protons and electrons released to them from [CaMn<sup>4+</sup>] structures by photons to reduce bicarbonate ions in the pores space (Dismukes et al., 2001). Eventually these [CaMn<sup>4+</sup>] molecules with photolytic function were invaginated to become a primitive OEC.

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In ranciéite,  $\text{Ca}^{2+}$  or a diadochic reduced  $\text{Mn}^{2+}$ , is coordinated with three oxygens and with the oxygens of three water molecules (cf. Post and Veblen, 1990; Manceau et al., 2002). Calcium and the distal manganese have the same role in the OEC where they ligate two molecules of water prior to their oxidation (Ferreira et al., 2004). However, thus-coordinated, the electrons and protons are stripped from the bonded water in the OEC and transferred separately to take part in biosynthesis, while the two remaining oxide ions bond covalently to form waste  $\text{O}_2$ .

### 5.3. The appearance of oxygenic photosynthesis

We do not know when oxygenic photosynthesis started. Did it appear in the Hadean or at the end of the Archaean, over a billion years later? Geochemical evidence from the Isua Banded Iron Formation (Dymek and Klein 1988), from radio- and stable isotopes in rocks of the same age (Rosing and Frei, 2003), and 16sRNA evolutionary trees (Pace, 2002), suggest that it emerged before 3.75 Ga. Yet soil profiles lacking  $\text{Fe}^{\text{III}}$  and the absence prior to 2.7 Ga of morphological or molecular fossils (the polysaccharide-rich sheaths of cyanobacteria make them particularly prone to fossilization) point to a later age (Westall, 2001, 2004; Blank, 2004).

In the absence of discriminatory evidence, our own preference – based on our plate tectonic scenario, the rapidity with which dynamic structures evolve and emerge in the Universe, the pedigree of PS2 founded in the antecedent RC1, and the likely ubiquity of  $[\text{CaMn}^{4+}]$  molecules in shallow water sediments – is for an early onset of oxygenic photosynthesis. The absence of atmospheric oxygen prior to 2.7 Ga is then explained by the buffering effects of reduced iron and sulfide in the ocean and crust, the flooding of the atmosphere with methane from the deep biosphere, the relatively low productivity in the oceans, and by the reduction of  $\text{O}_2$  by ambient bacteria in microbial mats (Lécuyer and Ricard, 1999; Farquar et al., 2000; Timmins et al., 2001; Bjerrum and Canfield, 2002; Arnold et al., 2004).

## 6. Conclusions

1. Geodynamic and metabolic cycles are closely coupled on our planet, a coupling even more direct the first metabolizing systems emerged in moderate-temperature alkaline submarine seepages (Russell and Martin, 2004). Within catalytic iron sulfide cells in the hydrothermal mound, these “metabolists” gained genetic machinery and differentiated into the two prokaryotic domains, the Bacteria and the Archaea (Martin and Russell, 2003). It is likely that life had emerged on the planet at least by 4.2 Ga (Russell and Hall, 1997).
2. Gradual expansion of colonies of prokaryotes from the mound into surrounding sediments on the ocean floor provided a protected environment. From here the colonies were entrained in migrating fluids to depth in the oceanic crust to inaugurate the deep biosphere (Parkes et al., 1990, 1994; Pedersen, 1993; Thorseth et al., 1995). A continual draft of H<sub>2</sub> from the crust and mantle prevented bacterial decay.
3. Because of the relatively low conductivity of mafic rock, the deep biosphere could remain immune from bolide-induced heating events.
4. Obduction of the deep biosphere into the photic zone allowed evolution within shallow-water chemical sediments. Photoprotective molecules first developed from aromatic ring compounds previously employed in group and electron transfer, and from these the photosynthetic reaction centres and antenna proteins evolved (Mulkidjanian et al., 1997; Baymann et al., 2001; Allen, 2004).
5. The first photosynthesists, probable precursors of the green sulfur bacteria, used hydrothermal H<sub>2</sub>S as an electron donor and produced S<sup>0</sup> as waste. The precursors of the heliobacteria then used organic waste as the electron donor (Vermaas, 1994). The biggest evolutionary leap involved the heterodimerization of the reaction centres (RC1) of the green sulfur bacteria and the heliobacteria, and resulted

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in the combined cyanobacterial PS1 and PS2 (Blankenship, 2002).

6. Both chemosynthesis and oxygenic photosynthesis emerged within mineral constituents (greigite [NiFe<sub>5</sub>S<sub>8</sub>] and ranciéite [CaMn<sub>4</sub>O<sub>9</sub>.3H<sub>2</sub>O]) with catalytic propensity, moieties of which are employed as reactive centres in protein complexes to this day.

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**Table 1.** Comparison between types of modern high submarine springs.

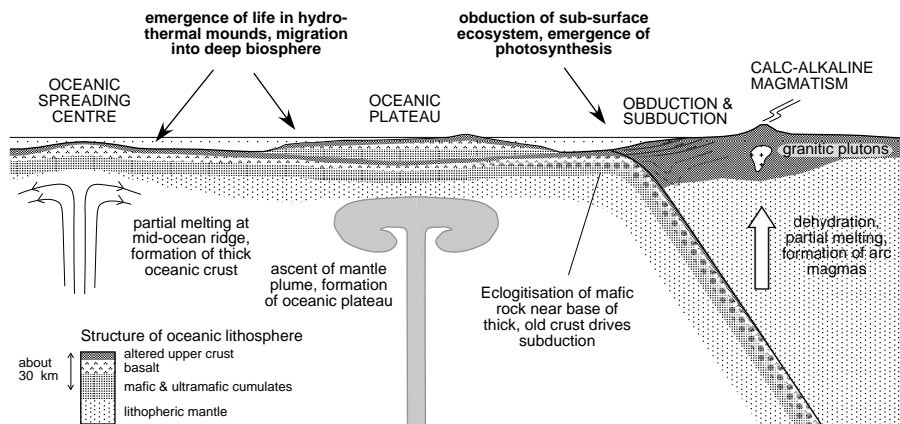
Parameter	J da Fuca <sup>1</sup>	Rainbow <sup>2</sup>	Lost City <sup>3</sup>	Eyjafjordur <sup>4</sup>
T°C	224°	365°	40°–75°	71.4°
pH	3.2	2.8	≤9.8	10.03 (24°C)
age yr	na	na	na	11 000
H <sub>2</sub>	na	13	0.43	na
H <sub>2</sub> S	3.5	1.0	0.064	0.01
SO <sub>4</sub>	0	(0)	5.9–12.9	0.2
Fe	18.74	24	na	0.00014
Mn	3.58	2.25	na	0.0000018
Mg	0	0	9–19	0.01
Ca	96.4	67	22	0.061
Na	796	553	482	3.4
K	51.6	20	na	4.2
SiO <sub>2</sub>	23.3	6.9	na	1.6
CO <sub>2</sub>	≤4.46	na	na	0.57
Cl	1087	380	548	1.26
Co	na	0.013	na	na
Ni	na	0.003	na	na
Zn	0.9	0.16	na	na
Mo	na	0.000002	na	na

Data for columns <sup>1</sup> to <sup>4</sup> from Von Damm (1990), Douville et al. (2002), Kelley et al. (2001) and Marteinsson et al. (2001). Elemental and molecular concentrations are in millimoles. Temperatures at the base of the convection cells developed at oceanic spreading centres and the off-ridge systems are presumed to be ~400°C and ~100°C, respectively.



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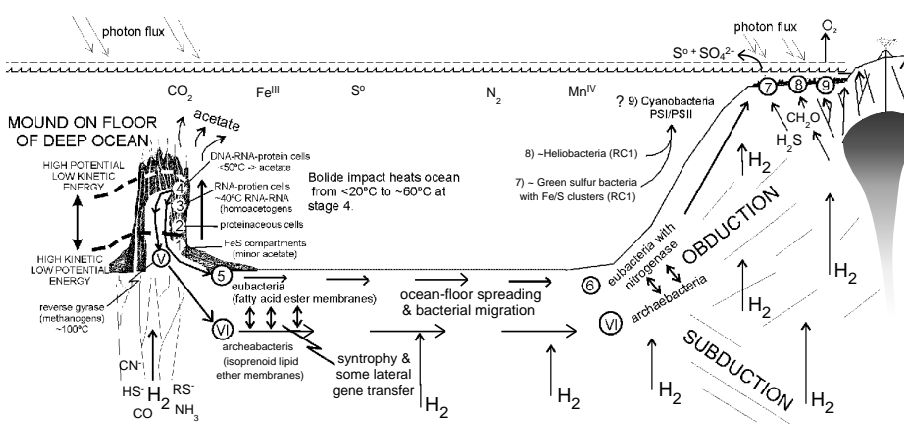


**Fig. 1.** Cross-section of mantle convection cell for the Earth at the Hadean/Archaean boundary (Campbell et al., 1989; Davies, 1992; Foley et al., 2003). Life is held to have emerged at an alkaline seepage site. An early batch of prokaryotic colonies comprising the “deep biosphere” were conveyed toward a plate margin where they were obducted into the photic zone, facilitating the onset of photosynthesis. (At times and in places plume-type convective mass transfer may have involved the whole mantle.)

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**Fig. 2.** Chemosynthetic life emerges at a warm alkaline seepage, differentiates into the precursors of the bacteria and archaea, and expands into the surrounding sediments and crust (Martin and Russell, 2003; Russell and Martin, 2004). From here a proportion is conveyed by ocean floor spreading toward a constructive margin produced largely by obduction. Once at the margin some of the cells happen to invade sediments in the photic zone where, at a sulfurous spring, some evolve to exploit solar photons. Numbers 1–3 relate to life’s emergence, 4 marks the point of differentiation of the Archaea from the Bacteria. Roman numerals V–VII mark evolutionary stages of the Archaea, and 5 and 6 show stages of evolution of the bacteria in the deep biosphere. Photon energy was first mastered by the green sulfur bacteria (7), followed by the heliobacteria (8). These photosynthesizing bacteria had probable appeared by the early Archaean (Westall et al., 2001). Oxygenic photosynthesis (9) is a further evolutionary development, though the age of its emergence is controversial. Photosynthetic bacteria embedded within calcium manganate hydrates, precursors to the cyanobacteria, found that the electrons and protons released from the hydrate, driven by photons, could contribute to biosynthesis. Oxygen was released as a waste gas. (Not to scale).

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