# 16 Temperature, Biogenesis, and Biospheric Self-Organization

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**Summary.** We argue that the biosphere has evolved deterministically as a self-organized system, given the initial conditions of the Sun-Earth system. With temperature as a critical constraint, biogenesis and the overall patterns of biotic evolution were the highly probable outcomes of this deterministic process. Emergence of life and its major evolutionary innovations occurred as soon as the temperature decreased to their upper temperature limits. These innovations include phototrophy, oxygenic photosynthesis, and the emergence of Eukarya ("complex" life) and its Kingdoms.

## 16.1 Introduction

Tim Lenton (1998) raised a fundamental question: How can self-regulation at all levels of the biosphere emerge from natural selection at the individual level? A seemingly unrelated but deeply connected debate centers around a challenge to a long held view of evolutionary biology, namely that if the "tape" of life's history were played again, the results would be radically different owing to the stochastic nature of evolutionary emergence. The alternative is that the evolution of the biosphere is deterministic, i.e., its history and the general pattern of biotic evolution is very probable, given the same initial conditions. Likewise the evolution of self-regulating biospheres on Earth-like planets around Sun-like stars is deterministic. We would reverse Tim Lenton's question: was the pattern of natural selection determined by the self-regulating history of the biosphere? As Conway Morris (1998–1999) put it, "[biotic] history is constrained, and not all things are possible".

More precisely, we argue that the evolution of life and the biosphere is quasi-deterministic, i.e., the general pattern of the tightly coupled evolution of biota and climate was very probable and self-selected from a relatively small number of possible histories at the macroscale, given the same initial conditions (see also discussion on macroscopic reproducibility in Lineweaver, this volume). Major events in biotic evolution were likely forced by environmental physics and chemistry, including photosynthesis as well as the merging of complementary metabolisms that resulted in new types of cells (such as eucaryotes) and multicellularity. Determinism likely breaks down at finer levels. Critical constraints on this deterministic aspect of biotic evolution have likely included surface temperature, along with oxygen and carbon dioxide levels (see Catling, this volume).

Why quasi-deterministic? In addition to events that were probably inevitable, it is likely there is a role for randomness in both abiotic and biotic evolution even on the coarsest scale. For example, this randomness may include the influence of large impacts on the history of life, the possible multiple attractor states in mantle convection and therefore plate tectonic history, even multiple attractors for steady-state climatic regimes. Thus, there are a finite number of histories, for the same initial conditions and cosmic background, hence "quasi"- deterministic evolution.

Evolution of procaryotes and complex life on terrestrial planets around Sun-like stars are expected to have similar geochemical and climatic consequences. Thus, the main patterns would be conserved if "the tape were played twice", a theory argued from computer simulations by Fontana and Buss (1994). The width of the habitable zone for Earth-like planets around Sun-like stars for complex life may be substantially smaller than that for the appearance of biota, constrained only by the presence of liquid water. Surface temperature history on terrestrial planets may be critical to the time needed to evolve complex life and intelligence. For Earth-like planets within the habitable zone of stars less massive than the Sun, the earlier emergence of complex life is expected, all other factors being the same, since its upper temperature limit is reached earlier as a result of the lower rate of luminosity increase (Schwartzman 1999).

### 16.1.1 Cosmology and Temperature

Big Bang cosmology has given us an abiotic, deterministic model for the evolution of the Universe in which, as the Universe expanded and cooled from arbitrarily high temperature, an increasingly complex series of structures emerged including life and biospheres at least on terrestrial planets around Sun-like stars (see Lineweaver and Schwartzman, in press; Chaisson, this volume; Lineweaver, this volume). A deterministic origin of life is now a virtual astrobiological paradigm, whether the preferred scenario invokes the primordial broth, hydrothermal regime or some variation with or without a significant extraterrestrial organic supply.

Here we examine the hypothesis that temperature has not only played the dominant deterministic role in cosmology and planet formation but also in biogenesis and biological evolution. That the diversification of life is strongly constrained by temperature and that as the temperature on the surface of the Earth decreased, this allowed the first life to appear but also determined what kind of life could appear.

## 16.2 Biogenesis at Life's Upper Temperature Limit: A Hyperthermophilic Origin of Life

The case for a high temperature origin of life was made by Wachtershauser (1998), who argued that biogenesis and microbial evolution proceeded deterministically from hyperthermophiles to mesophiles. We have likewise argued

(Schwartzman 1999; Lineweaver and Schwartzman 2004) that biogenesis and the emergence of the three domains of life was likely thermally inevitable, given the abiotic initial conditions of our planet. The chemical evolution research program continues to generate support for determinism, for example, in arguments for the likely universality of intermediary autotrophic metabolism (Morowitz et al. 2000) and the genetic code (Vogel 1998).

A hyperthermophilic last common ancestor of life (LCA) has long been thought implied by the rRNA phylogenetic tree (Fig. 16.1) (Woese 1987; Pace 1997). While the deep-rootedness of hyperthermophilic Archaea still appears to be robust (Matte-Tailliez et al. 2002; Caetano-Anolles 2002), some researchers argue that even deeply – rooted Bacteria acquired their hyperthermophily by horizontal gene transfer (*hgt*) from Archaea (Aravind et al. 1998; Forterre et al. 2000; Brochier and Philippe 2002), a view under challenge (Di Giulio 2003a,b,c). All known hyperthermophiles apparently have reverse gyrase (*rg*) in a fused gene (Forterre 2002), with the exception of the newly discovered Nanoarchaeota (Waters et al. 2003). The latter discovery suggests that fusion of separate genes to reverse gyrase occurred at hyperthermophilic, not moderately thermophilic or mesophilic conditions as previously argued (Lopez-Garcia 1999; Declais et al. 2000). Alternatively, another protective mechanism was present in a hyperthermophilic LCA and early organisms (Baross 1998; Musgrave et al. 2002).

An objection to a hyperthermophilic LCA based on G + C content of rRNA of extant organisms (Galtier et al. 1999) has been challenged (Di Giulio 2000a,b 2003). In addition to G + C content, Di Giulio used a thermophily index based on the propensity of amino acids to enter more frequently into (hyper)thermophile proteins, concluding that the late stage of genetic code structuring took place in a (hyper)thermophilic organism. These studies have used the correlation of the optimal growth temperature with the above measures to infer the temperature of the LCA, but the maximum temperature for growth ($T_{MAX}$) is plausibly closer to the temperature of emergence, giving a stronger inference of a hyperthermophilic LCA. Similarly, a hyperthermophilic LCA is inferred from the robust correlation of $T_{MAX}$ with the rRNA phylogenetic distance from the LCA for (hyper)thermophilic procaryotes (Fig. 16.2) (Schwartzman and Lineweaver 2003), with an inferred temperature exceeding 120° C, consistent with the newly discovered record $T_{MAX}$ of 121° C for life (an Archaea close to Pyrodictium; Kashefi and Lovley 2003), although this reported $T_{MAX}$ is now being challenged (Stetter 2003).

Other recent support for a hyperthermophilic LCA comes from expanded sequence and secondary structure data of rRNA (Shepard et al. 2003), the tRNA sequence tree (Tong et al. 2003) and experimental tests using modified enzyme residues (Miyazaki et al. 2001; Yamagishi et al. 2003). If future phylogenetic trees based on greater sampling and better understood genomes confirm the apparent near universal absence of hyperthermophiles with mesophilic ancestors (Fig. 16.1), the asymmetric evolution of hyperthermophiles to mesophiles would be confirmed. This asymmetry is supported for example, by the absence of any living eucaryote with a $T_{MAX}$ exceeding a few degrees above 60° C, in spite of at least 2 billion years of opportunity to adapt to hyperthermophily.

A hyperthermophilic LCA does not of course require an origin of life at similar high temperatures. In particular, biogenesis could have occurred at mesophilic temperatures to be followed by a major impact event sterilizing the surface and leaving a subsurface hyperthermophilic LCA survivor or primitive procaryotes close to the LCA (Gogarten-Boekels et al. 1995), although a recent reinterpretation of the lunar impact record argues that such sterilizing events may well have been absent (Ryder 2003). Nevertheless, the possibility that biogenesis did indeed occur at hyperthermophilic temperatures should be reexamined in light of recent research. A plausible scenario for the origin of life requiring the presence of a hydrothermal regime and thus a proximate hyperthermophilic environment is outlined by Martin and Russell (2003), with the locus being FeS compartments produced by reaction of contrasting pH solutions reacting at the seafloor. They postulate a temperature for this origin at about 50° C, argued from the assumed constraint of RNA instability at higher temperatures (Moulton et al. 2000). However saline solutions, readily available in this environment, appear to stabilize DNA/RNA at hyperthermophilic temperatures (Marguet and Forterre 1998; Tehi et al. 2002). Therefore, the possibility of an RNA/DNA world (Dworkin et al. 2003) that is hyperthermophilic should be revisited. Other objections to a hot origin of life including the instability of amino acids and ribose at hyperthermophilic temperatures (Levy and Miller 1998; Islas et al. 2003) have been addressed by supporters of a hydrothermal scenario, citing evidence for the thermodynamic favorability (Shock et al. 1998) and actual synthesis of amino acids under hydrothermal conditions (Hennet et al. 1992; Marshall 1994).

Thus, we argue that the chemical evolution to the LCA of Bacteria and Archaea could have occurred at hyperthermophilic conditions in Martin and Russell's scenario as Russell himself argued previously (Russell et al. 1998). Hence, the divergent chemical evolution leading to Archaeal and Bacterial free-living cells as proposed by Martin and Russell (2003) can be accommodated in a temperature gradient between the hydrothermal source and ambient climatic temperature, with the upper temperature limits of Archaea (greater or equal to about 120° C) and Bacteria (at 95° C if not higher) corresponding to the first possible self-organization of each cell type with cell membranes and walls. In this scenario, biogenesis occurred with the emergence of protocells with minimal metabolism and replication at the "edge of stability" to use the phrase in Musgrave et al. (2002). The differences between Archaeal and Bacterial membrane lipid biosynthesis and cell wall biochemistry is central to Martin and Russell's hypothesis. Their thermal stability might be clues to the temperature regimes prior to the emergence of free-living cells.

The deep nesting of primitive metabolisms inferred from extant hyperthermophiles (Ronimus and Morgan 2002; Berry 2002) can be readily explained by this scenario. The emergence of Archaea has been linked to the metabolism of methanogenesis (Koch 1994; Kral et al. 1998), a plausible

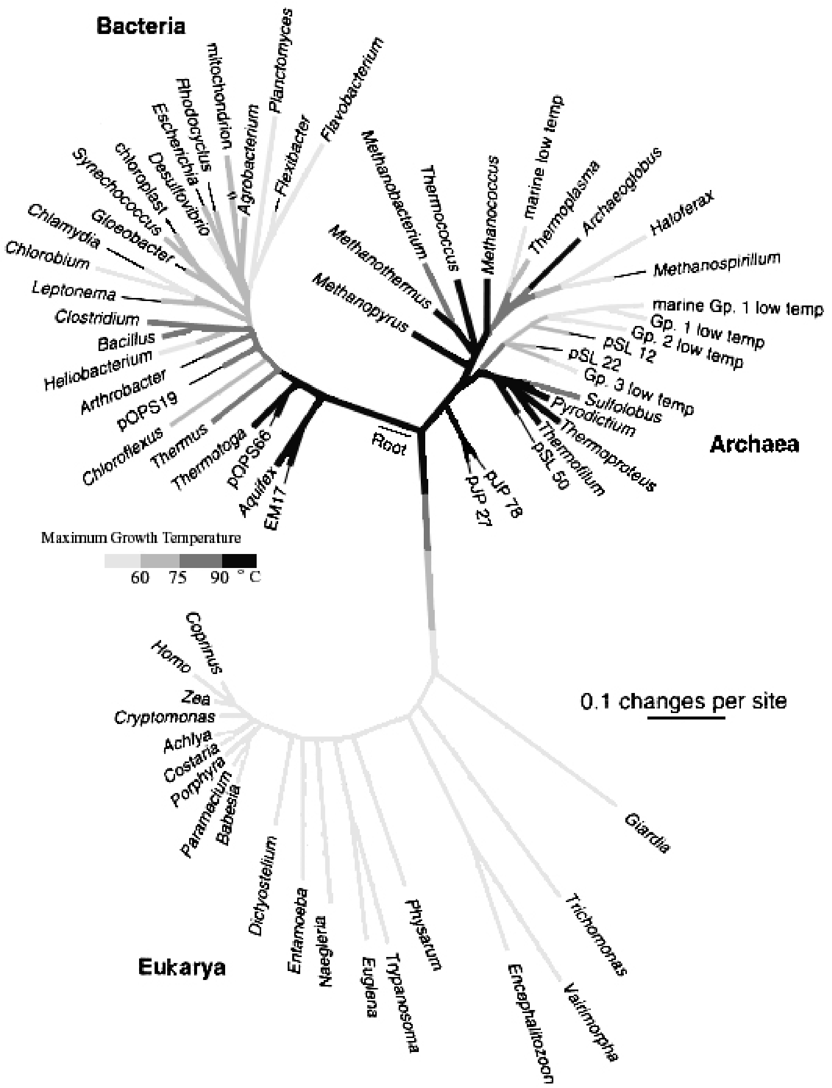

**Fig. 16.1.** Phylogenetic Tree based on rRNA sequences (after Pace, 1997). The scale bar corresponds to 0.1 changes per nucleotide. The last common ancestor (LCA) is located on the bacterial line between the node to Aquifex and the Y intersection of the three domains (Barns et al., 1996). Maximal growth temperatures ($T_{MAX}$) have been used to assign shades of grey to the branches (Lineweaver and Schwartzman, 2004). A thin black ending line indicates $T_{MAX}$ data is lacking for this organism

natural exploitation of abundant carbon dioxide and hydrogen by early life (see Catling, this volume). The other primitive metabolisms found in deeply rooted Archaea can likewise be explained as the exploitation of available raw materials (sulfur, trace metals such as Fe, Ni, Cr, W and As; see Lebrun et al. 2003) readily available on early Earth, particularly in the hydrothermal regime environment (see Russell et al. 1998), first by chemoautotrophs soon followed by heterotrophs, in the chemoautotropic scenario for biogenesis. Plausibly the origin of these metabolisms occurred before 3.7 Ga, the age of metasedimentary rocks from Greenland containing the earliest known evidence for life, $^{13}$C depleted carbon (Rosing 1999).

While the climatic temperature for the Hadean is not well constrained other than an inference of liquid water at 4.4 Ga (Valley et al. 2002), temperatures of 80° C at 3.8 Ga (Knauth 1992) and 70 (+/- 15)° C at 3.5 Ga (Knauth and Lowe 2003) have been derived from the oxygen isotopic record of marine cherts. Thus, while biogenesis plausibly occurred above late Hadean/early Archean climatic temperatures, a climatic temperature constraint on microbial evolution prevailed through the Precambrian with a temperature constraint on microbial evolution (Schwartzman 1999). The robust correlation of $T_{MAX}$ with distance of the rRNA phylogenetic distance from the LCA (Figs. 16.1 and 16.2) is consistent with the maximum growth temperature of thermophiles, if not hyperthermophiles, being close to the climatic temperature of each organism at emergence.

## 16.3 The Temperature Constraint on Biologic Evolution

A temperature constraint on biologic evolution was first apparently proposed by Hoyle (1972) who suggested that a warm early Earth held back the emergence of low-temperature life. We argue that climatic (surface) temperature was the determining constraint with respect to the timing of major events in microbial evolution (e.g., emergence of photosynthesis, eucaryotes and Metazoa/Fungi/Plants), with thermophily prevailing for the first two-thirds of biospheric history. The biosphere evolved from a “hothouse” at its birth some 4 Ga ago to an “icehouse” for the last billion years, producing a biotic evolutionary explosion filling the myriad of new habitats created in the process.

However, surface temperature on Earth is not a fixed boundary condition for life, but it is affected by the biota. Surface temperature is regulated on a geological time scale by the carbonate-silicate biogeochemical cycle (Berner 1999; Schwartzman 1999). While on short time scales of less than $10^4$ years the cycling between the atmosphere/ocean and surface pools such as organic carbon can have significant impact on atmospheric carbon dioxide levels (witness the glacial/interglacial cycles of the last 2 million years, anthropogenic impacts etc.), the long-term cycle on time scales greater than $10^5$ years is controlled by the silicate-carbonate geochemical cycle. This cycle entails transfers of carbon to and from the crust and mantle. In the modern era, this cycle was first described by Urey in 1952:

$$CO_2 + CaSiO_3 = CaCO_3 + SiO_2 \tag{16.1}$$

The reaction to the right corresponds to chemical weathering of Ca silicates on land ($CaSiO_3$ is a simplified proxy for the diversity of rock-forming CaMg silicates such as plagioclase and pyroxene which have more complicated formulas, e.g., Ca plagioclase: $CaAl_2Si_2O_8$), while the reaction to the left corresponds to metamorphism ("decarbonation") and degassing returning carbon dioxide to the atmosphere.

This cycle is really biogeochemical. While decarbonation and outgassing is surely abiotic, taking place at volcanoes associated with subduction zones and oceanic ridges, chemical weathering involves biotic mediation, which entails soil stabilization by biotic cover on land along with the multifold processes induced by biological activity in the soil itself. The critical role of biology entails the progressive increase in the biotic enhancement of chemical weathering, the critical sink of carbon dioxide with respect to the atmosphere involving deposition of calcium carbonate on the ocean floor. This biotic enhancement of weathering generates a weathering flux balancing the volcanic source resulting in a steady-state level of atmospheric carbon dioxide (and temperature) at a lower level than on an abiotic Earth (see full discussion in Schwartzman 1999). On a global scale, the stabilization of thick soils by vascular plants makes possible the multifold accelerating effects of the rhizosphere, resulting in the estimated present biotic enhancement of weathering on the order of 10–100 times the abiotic regime. This biotically-mediated cooling increases the width of the habitable zone for the possible occurrence and evolutionary time frame of complex life.

If surface temperature was the critical constraint on microbial evolution, then the approximate upper temperature limit for viable growth of a microbial group should equal the actual surface temperature at time of emergence, assuming an ancient and necessary biochemical character determines the presently determined upper temperature limit $T_{MAX}$ of each group (see Table 16.1, Fig. 16.3). The latter assumption is supported by an extensive data base of living thermophilic organisms. No phototroph has been found to grow above about 70° C, in spite of a likely $\geq 3.5$ Ga age for this metabolism, similarly for eucaryotes with an upper limit of just over 60° C, with at least 2 Ga for the possibility of adaptation to life at higher temperatures. (Note: The report of the Pompeii worm living in hydrothermal vents with its attachment reaching 80° C is not good evidence that the upper temperature limit for metazoan growth exceeds 60 or even 50° C. Note that their head emerges from the vent chimney at 22° C (Cary et al. 1998)).

The upper temperature limit for viable growth is apparently determined by the thermolability of biomolecules (e.g., nucleic acids), organellar membranes and enzyme systems. For example, the mitochondrial membrane is particularly thermolabile, apparently resulting in an upper temperature limit of about 60° C for aerobic eucaryotes (note that the presumed ancestor of the mitochondrion, the Proteobacteria, have an upper temperature limit of 60° C).

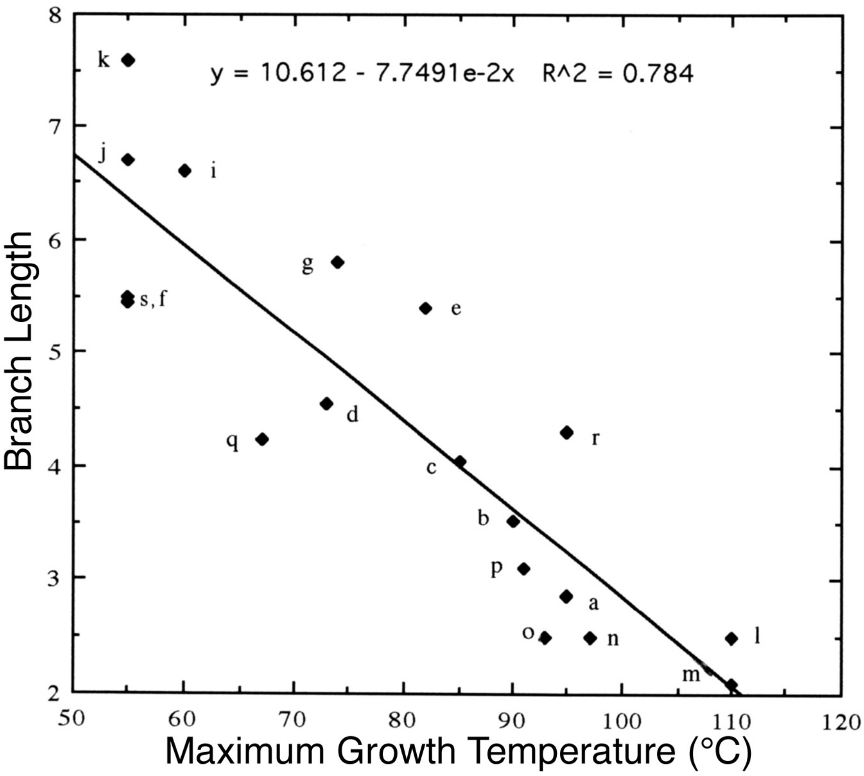

**Fig. 16.2.** The maximum growth temperature of (Hyper)Thermophiles versus their Phylogenetic Distance (Branch Length) from the LCA using rRNA phylogenetic tree (Fig. 16.1). The correlation coefficient $r^2$ for Archaea and Bacteria is $r^2 = 0.755$ and $r^2 = 0.777$ respectively. a Aquifex; b Thermotoga; c Thermus; d Chloroflexus; e Bacillus; f Chlorobium; g Synechococcus; i Agrobacterium; j Plantomyctes; k Flavobacterium; l Pyrodictium; m Methanopyrus; n Methanothermus; o Thermococcus; p Methanococcus; q Thermoplasma; r Archaeoglobus; s Haloferax For further details see Schwartzman and Lineweaver (2003)

Now let us return to the contention that the actual surface temperatures were thermophilic (greater than 50°C) for the first two-thirds of the history of the biosphere, i.e., from 4 Ga to about 1.5 Ga. This high temperature scenario for the Earth's climatic history remains controversial (see extensive discussion in Schwartzman 1999). The strongest evidence for this temperature scenario comes from the inferred paleotemperatures from the oxygen isotopic record of ancient chert and carbonates. Paleotemperatures have been derived from the oxygen isotope record of pristine cherts (Knauth and Lowe 1978; Knauth 1992; Knauth and Lowe 2003). The fractionation of the stable isotopes of oxygen is a function of the phases involved and temperature. A necessary assumption for these temperature calculations, that the Precambrian oxygen isotopic composition of seawater was close to the present, received recent support from studies of ancient seawater-altered oceanic crust. Robust new evidence for a very warm Archean comes from Knauth and Lowe's (2003) detailed study of the Onverwacht cherts, South Africa, centering on their oxygen isotopic record in the context of their geologic characteristics. The inferred paleotemperatures of ancient seawater are consistent with the inferred Precambrian temperature history illustrated in Fig. 16.3.

**Table 16.1.** Upper temperature limits for growth of living organisms and approximate times of their emergence. Temperatures from Brock et al. 1994

| Group | Approximate upper temperature limit | Time of Emergence |
|---|---|---|
| | (°C) | (Ga) |
| Plants | 50 | $0.5^{\wedge}$–$1.5^{*}$ |
| Metazoa | 50 | $0.6^{\wedge}$–$1.5^{**}$ |
| Fungi | 60 | $0.4^{\wedge}$–$1.5^{*}$ |
| Eucaryotes | 60 | $2.1^{**}$–$2.8^{\wedge\wedge}$ |
| Procaryotic microbes | | |
| Phototrophy | 70 | $\geq 3.5^{\wedge\#}$ |
| Hyperthermophiles | $\geq 80$ | $\geq 3.7^{\#}$ |

$^{\wedge}$ Fossil evidence
$^{*}$ Molecular phylogeny
$^{**}$ Problematic fossil evidence, molecular phylogeny
$^{\#}$ Biogenic carbon isotopic signature
$^{\wedge\wedge}$ Organic geochemistry

We presume eucaryotes emerged as the endosymbiogenic product of Archaeal and Bacterial cells associating because of complementary metabolisms, with the acquisition of the mitochondrion close in time with the initial emergence of the eucaryotic cell (Martin and Russell 2003). Others have argued for a later acquisition of the mitochondrion (see e.g., Gupta 1998; Hedges et al. 2001) or even a primordial ancestor (the "Chronocyte") of the eucaryotic cell (Hartman and Fedorov 2002).

If the Chronocyte and amitochondrial eucaryotes arose earlier than the mitochondrial, then higher upper temperature limits are expected for both, with the Chronocyte perhaps in the hyperthermophilic range. In the two-step scenario for the origin of the mitochondrial eucaryotic cell, gram-negative bacteria are postulated to be fused with an archaeon, followed by the incorporation of the mitochondrion from a proteobacterium (Lang et al. 1999). If the $T_{MAX}$ of at least 80°C of presently cultured gram-negative bacteria (e.g., Bacillus) is primitive then the emergence of amitochondrial eucaryotes may reach back into the early Archean.

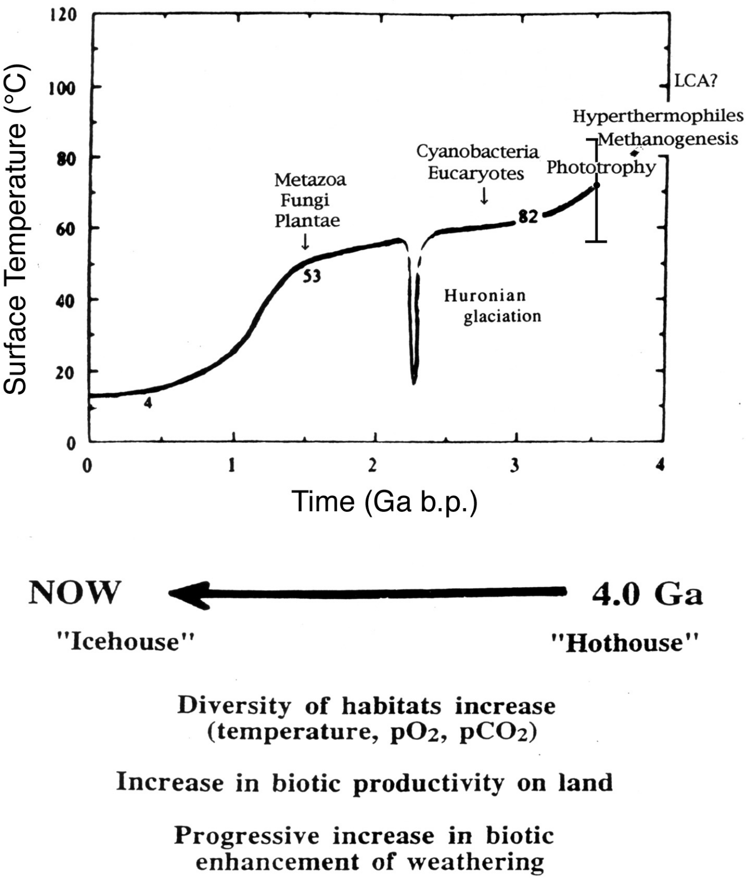

**Fig. 16.3.** Temperature of the surface of the Earth as a function of time. Emergence times of major organismal groups and long-term trends in biospheric evolution shown. Numbers near curve are the computed model ratios of the present biotic enhancement of weathering to the value at that time (Schwartzman, 1999). The temperature for 3.5 Ga is from Knauth and Lowe (2003)

A deterministic emergence of the so-called higher kingdoms (Fungi, Metazoa and Plantae) is consistent with Szathmary and Maynard Smith's (1995) contention that epigenetic inheritance had already existed in protists prior to the emergence of these kingdoms. The inferred emergence time from molecular phylogeny (Heckman et al. 2001; Wang et al. 1999) and problematic metazoan trace fossils (e.g., Rasmussen et al. 2002a,b) are consistent with our temperature curve (Fig. 16.3).

The biogeochemical carbon cycle is linked to the oxygen cycle. Space precludes a full discussion of atmospheric levels of oxygen and carbon dioxide as constraints on evolution (see Catling, this volume). Aerobic microenvironments in the Archean apparently preceded the emergence of aerobic eucaryotes, which in turn preceded their first likely presence in the fossil record. Aerobic respiration may have emerged very early (Castresana and Saraste 1995). The rise of atmospheric oxygen by 1.9 Ga (15% present atmospheric level (PAL) according to Holland (1994) predated the emergence of Metazoa, which may require less than $\sim 2\%$ PAL (e.g., mud-dwelling nematodes; see Runnegar 1991). On the other hand, the atmospheric oxygen level plausibly constrained the emergence of megascopic eucaryotes, particularly Metazoa, as originally argued by Cloud (1976), with the explanation being the diffusion barrier of larger organisms (Raff 1996). The rise of a methane-dominated greenhouse and concomitant drop in atmospheric carbon dioxide level at about 2.8 Ga has been proposed as the trigger for the emergence of cyanobacteria (Schwartzman and Caldeira 2002).

## 16.4 Future Directions

Tests for (quasi-)deterministic evolution include further confirmation of the apparent close correspondence of organismal emergence times to the times that necessary environmental conditions are reached as inferred from the fossil, organic geochemical and paleoclimatic record, future discovery and characterization of alien biospheres (e.g., detection of atmospheric methane, oxygen and water) and computer simulations of biospheric evolution.

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