

Biospheric Evolution Is Coarsely Deterministic

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Abstract Starting with the origin of life, I argue that the general pattern of the tightly coupled evolution of biota and climate on Earth has been the very probable outcome from a relatively small number of possible histories at the macroscale, given the same initial conditions. Thus, the evolution of the biosphere self-selects a pattern of biotic evolution that is coarsely deterministic, with critical constraints likely including surface temperature as well as oxygen and carbon dioxide levels in the atmosphere. Environmental physics and chemistry drive the major events in biotic evolution, including photosynthesis and oxygenic photosynthesis, the emergence of new cell types (eucaryotes) from the merging of complementary metabolisms and finally multicellularity and even encephalization.

Revival of an Old Debate: "Playing the Tape Again," Contingency vs Predictability in Evolution

Here I revisit a provocation: that the evolution of the biota, embedded in the biosphere, has been coarsely deterministic (Schwartzman 1999, 2002; Schwartzman 2001; Lineweaver and Schwartzman 2004; Schwartzman and Lineweaver 2005). I obviously take sides in an old but still active debate. If the "tape were played again," would the outcome be roughly the same, or is biologic evolution non-repeatable given similar initial conditions and roughly similar solar/planetary/impact history? Stephen J. Gould in his exchange with Simon Conway Morris (Conway Morris and Gould 1998-1999) took the position that the origin of life is very probable, but biologic evolution is not predictable, while Conway Morris argued that the evolution of life is predictable, but the origin of life was an unlikely event.

I agree in part with both scientists on the side of coarse determinism, both are very probable given the Earth/Sun's initial conditions. Conway Morris's position is largely based on his case for strong convergence of morphologies and biochemistries in the history of life (Conway Morris 2003; 2010; 2015). The issue of contingency versus determinism in this history continues to be a focus of vigorous research (e.g., Blount 2017; Blount et al. 2018; Simoes 2019). Determinism almost certainly breaks down at finer levels; it is hard to imagine that giraffes and blue whales are on Earth-like planets around Sun-like stars in our galaxy, except in bad science fiction novels!

Cosmic Thermobiology, Emergence at the Edge of Stability

Returning to the likelihood of the origin of life on Earth, we can start with the observation that the cooling of the Earth and its climate and growing com-

plexity of lifeforms are correlated, consistent with the same trend for complexity in the universe since the Big Bang (Lineweaver and Schwartzman 2004; Chaisson 2009). A roughly deterministic cosmic thermobiology can be inferred from the evolution of life on Earth, enabling us to predict a potential similar pattern of growing complexity in biologic evolution on the surfaces of terrestrial planets around Sun-like stars. Of course, this pattern, indeed abiogenesis itself, is contingent on the context of the planetary system, i.e., stellar mass/luminosity history, distance of the terrestrial planet to its host star, and the initial conditions and impact history of the planet considered (see chapter 10, Schwartzman 1999 2002).

Starting with The Last Universal Common of Life (LUCA), I argue that the emergence of the main groups of living organisms occurred at their edge of

stability, at their upper temperature limits. LUCA emerged at thermophilic to hyperthermophilic temperatures in submarine alkaline hydrothermal vents (Martin and Russell 2007; Lane 2015; Weiss et al. 2016a; Sojo et al. 2016). This scenario is robustly supported, e.g., by the stereochemistry of FeS clusters in the cores of primitive enzymes such as ferredoxin, inferred to have been inherited from sulfide minerals deposited in the vents (Russell and Hall 1997) and the key role of iron catalysis and iron sulfide minerals in the origin of life (Camprubi et al. 2017; Li et al. 2018).

A critical driver of determinism in evolutionary history has been the strong coupling of biologic evolution with climate history as a result of the long-term biogeochemical carbon cycle. A key process in this cycle is the progressive increase of the biotic enhancement of weathering resulting from the increase of terrestrial productivity and evolution of the land biota in the history of life (Schwartzman 1999, 2002; 2015). In the case of the Earth, the trend to present of decreasing volcanic outgassing, increasing continental area and biotic enhancement of weathering has outweighed the warming influence of rising solar luminosity, but the latter will overwhelm cooling influences in the future (e.g., Caldeira and Kasting 1992). Further, considering the astrobiological implications, if biospheres emerge in a strongly habitable context, their survival is likely enhanced by analogous strong coevolutionary mechanisms (Nicholson et al. 2018; Lenton et al. 2018).

The following is a test of the difficulty for steps in major evolutionary emergences: If a potential constraint is released at the time of emergence, then it was virtually inevitable (“easy”). The upper

temperature limits of growth of the main groups of living organisms corresponds to the approximate climatic temperature at the times of their first emergence, assuming a very warm Archean climate (Schwartzman 1999, 2002; Schwartzman and Knauth 2009; Garcia et al. 2017; Schwartzman 2017). The case for a very warm Archean climate will be outlined shortly. These

emergences are illustrated in Figure 1 on the climatic temperature curve consistent with the hot early climate scenario, as well in Table 1.

The Earth’s climate went from a “Hothouse” to an “Icehouse” in the last 4 billion years. The numbers on the curve correspond to the ratio of the present biotic enhancement of weathering to that at the indicated time in the

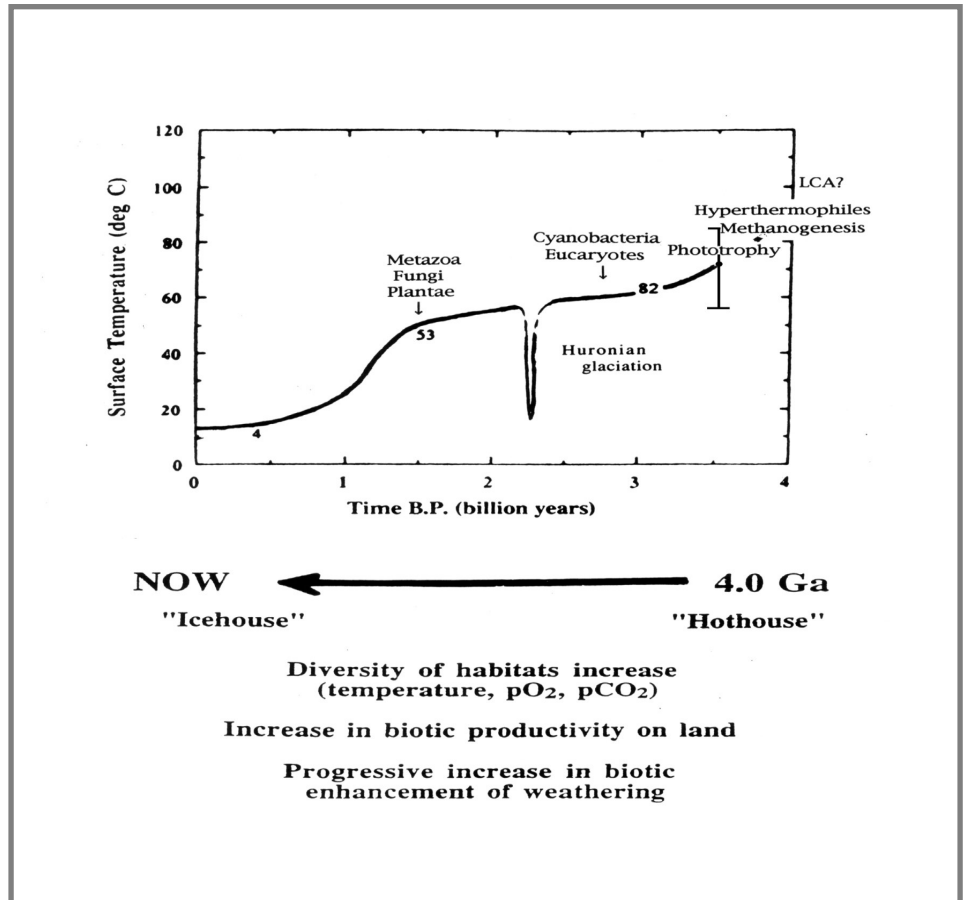


Figure 1. Temperature History of Biosphere

Group	Approximate upper temperature limit (°C)	Time of Emergence (Ga)
<i>“Higher” kingdoms:</i>		
Plants	50	0.5-1.5
Metazoans (Animals)	50	0.6-1.5
Fungi	60	0.6-2.4 (?)
Eukaryotes	60	2.1-2.8
<i>Prokaryotes</i>		
Phototrophs	70	>3.5
Hyperthermophiles	>100	>3.8

(Temperatures from Brock et al. 1994)

Table 1. Upper temperature limits for growth of living organisms, approximate times of their emergence

past, as derived from modeling in Schwartzman (1999; 2002); see update in Schwartzman (2017). This curve leaves out Temperature excursions in the last billion years, including major glacial episodes.

The upper temperature limits are very likely primitive characters determined by the intrinsic biochemistry/biophysics of cellular components, for example, the nuclear and mitochondrial membranes. Phototrophic organisms had over three billion years to adapt to hyperthermophilic temperatures (above 80°C) but never succeeded; likewise during at least two billion years, eucaryotes did not succeed in adapting to temperatures above about 65°C; there are no living hyperthermophilic phototrophs or eucaryotes. The empirical foundation for this temperature history is derived from the sedimentary chert oxygen isotopic record, specifically from the highest O^{18}/O^{16} ratio at any age, as well as other evidence summarized as follows:

1) The oxygen isotope record in sedimentary chert and the compelling case for a near constant isotopic oxygen composition of seawater over geologic time support thermophilic surface temperatures prevailing in the Archean, with some support for hot conditions lasting until about 1.5 billion years ago, aside from lower temperatures during the glacial episodes at 2.2- 2.4 Ga and a problematic one at 2.9 Ga (Pongola).

2) Melting temperatures of proteins resurrected from sequences inferred from robust molecular phylogenies give paleotemperatures at emergence consistent with a very warm early climate (see discussion below).

3) High atmospheric pCO_2 levels in the Archean are consistent with high climatic temperatures near the triple point of primary iron minerals in

banded iron formations and the formation of Mn-bicarbonate clusters leading to oxygenic photosynthesis.

4) Higher weathering intensities on land in the Archean would not have occurred if seafloor weathering dominated the carbon sink, pulling down the temperature; hence, this empirical evidence supports a hot climate and high carbon dioxide levels, likewise consistent with 50-60 bars of CO_2 in the crust as carbonate and reduced organic carbon.

5) The inferred viscosity of seawater at 2.7 Ga is consistent with a hot Archean climate.

6) A cold Archean is difficult to explain taking into account the higher outgassing rates of carbon dioxide, significantly smaller land areas and weaker biotic enhancement of weathering than present in the context of the long-term carbon cycle, taking into account the fainter Archean sun in climate modeling.

This case is discussed in more detail, including references with support for the arguments and evidence presented in the above list in Schwartzman, 2015; 2017; 2018.

Critique of Recent Challenges to a Hot Archean Climate

Re: Galili et al. (2019)

In their study of oxygen isotopic composition of marine iron oxides, they conclude that seawater has become isotopically lighter from the early Paleozoic to Archean time. However, their case rests on an inference of a non-uniformitarian variation in the seawater oxygen isotopic ratio for the sake of undermining a hot Archean climate. For a rebuttal of their interpretation of the chert Archean oxygen isotopic record see Knauth and Lowe (2003). Critically, their trend to lighter oxygen isotopic ratios of parent fluids

for Fe oxides going back to 1.88 Ga (their Fig. 2 D) is consistent with a meteoric water influence in diagenesis in the continental shelf or an estuarine environment (see, e.g., Fralick et al. 2017, noting that the oldest Fe oxides sampled by Galili et al. (2019) come from the Gibraltar Iron Formation, a Canadian deposit of the same age as the Gunflint Formation).

Further, they ignore the evidence for near present seawater O^{18}/O^{16} ratio going back into the Archean including the following.

1) There are direct measurements of fossil seawater from salt inclusions for Paleozoic seawater (Knauth and Roberts 1991). The same conclusion comes from clumped isotope studies (Bergmann et al. 2017; Henkes et al. 2018; Ryb and Eiler 2018).

2) Likewise, the same conclusion comes from the inferred seawater ratio in the Neoproterozoic (760 Ma: Hodel et al. 2018) and Early Proterozoic (2.4 Ga: Zakharov and Bindeman 2019).

3) Again, the same conclusion is inferred from the geologic record of ancient seawater- altered oceanic crust (ophiolites, their eclogite proxies, greenstones). Aside from their problematic interpretation of this geologic record, Galili et al. (2019) fail to confront the evidence from Archean eclogite proxies for depleted/enriched seawater-altered oceanic crust (Jacob 2004) with abundant depleted values, clear evidence of high temperature interaction with seawater, an O^{18} source for seawater during the buffering process, noting that a favorite way to generate lighter ratios has been to argue this process was not happening back in the early Precambrian.

Re: Krissansen-Totton et al. (2018)

They model the long-term carbon cycle, concluding that current best knowledge of this cycle precludes a hot Archean. However, rather than actually critiquing the robust empirical case for a hot Archean climate they cite, they make a model to refute it by generating a Sleep and Zahnle (2001) model with sufficient seafloor weathering to keep Archean temperatures below 50 deg C. Ignored is evidence for high Hadean/Archean pCO₂ levels in the atmosphere/ocean as well as higher weathering intensities on land.

Re: Charnay et al. (2017)

From their 3D climate-carbon model, they “favor cold or temperate climates with global mean temperatures between around 8°C (281 K) and 30° C (303 K) and with 0.1–0.36 bar of CO₂ for the late Hadean and early Archean.” However, the much lower biotic enhancement of weathering on land in this early time was not included in their modeling of the long-term carbon cycle; further, the recycling of CO₂ back in subduction zones in Archean was likely close to 100% efficient because of a hotter upper mantle rather than the lower value they assume.

Temperature History from Molecular Phylogeny

More evidence for this temperature history comes from molecular phylogeny of organisms belonging to the three main domains of life, Bacteria, Archaea and Eukarya, noting the apparent absence on the rRNA phylogenetic tree of deeply-rooted mesophiles/psychrophiles (see, e.g., Figure 1 in Schwartzman and Lineweaver 2004). If Archean temperatures were similar to the Phanerozoic, then some of the low-temperature prokaryotes should be grouped near the root with the hyperthermophiles/thermophiles. While some more recent phylogenetic trees

are more ambiguous regarding this conclusion (e.g., see Lineweaver and Chopra 2019 citing Hug et al. 2016), Weiss et al.'s (2016a) research supports a thermophilic LUCA:

The concept of a last universal common ancestor of all cells (LUCA, or the progenote) is central to the study of early evolution and life's origin, yet information about how and where LUCA lived is lacking. We investigated all clusters and phylogenetic trees for 6.1 million protein coding genes from sequenced prokaryotic genomes in order to reconstruct the microbial ecology of LUCA. Among 286,514 protein clusters, we identified 355 protein families (0.1%) that trace to LUCA by phylogenetic criteria. Because these proteins are not universally distributed, they can shed light on LUCA's physiology. Their functions, properties and prosthetic groups depict LUCA as anaerobic, CO₂-fixing, H₂-dependent with a Wood-Ljungdahl pathway, N₂-fixing and thermophilic. LUCA's biochemistry was replete with FeS clusters and radical reaction mechanisms... The 355 phylogenies identify clostridia and methanogens, whose modern lifestyles resemble that of LUCA, as basal among their respective domains. LUCA inhabited a geochemically active environment rich in H₂, CO₂ and iron. The data support the theory of an autotrophic origin of life involving the Wood-Ljungdahl pathway in a hydrothermal setting.” (Abstract)

For more views on the concept of LUCA and its identification, see, for example, the following papers: Gogarten and Deamer (2016) with a reply by Weiss et al. (2016b), Di Giulio (2019) and Lineweaver (in press).

The inferred paleotemperatures from resurrected (elongation) proteins of cyanobacteria are consistent with a hot Archean climate, with cyanobacteria emerging at about 60° C at 2.8 Ga. (Garcia et al. 2017, as proposed by Schwartzman et al. 2008 and Gaucher et al. 2008; also see Fournier and Alm 2015; Romero-Romero et al. 2016; Bous-sau et al. 2008).

The Burst of Encephalization in the Late Cenozoic

For warm-blooded animals, the body temperature T_{body} is close to the upper limit of 40° C for vertebrates, thereby providing for the energy-intensive brain while the differential between body and climatic temperature, T_{body} - T_{climate}, determines the efficiency of heat loss from brain, recognizing that humidity and the evolution of sweating and hair distribution on the body also impact heat loss. Hence, we have proposed that climatic cooling is a *prime releaser* for encephalization (Schwartzman et al. 2009), with the window of opportunity for maximum encephalization shown in Figure 2. Thus, I argue that an intelligence niche, among other solutions to reproductive survival, exists on our planet and by implication potentially on other Earth-like planets around Sun-like stars. On Earth we have an intelligence niche for lineages in birds

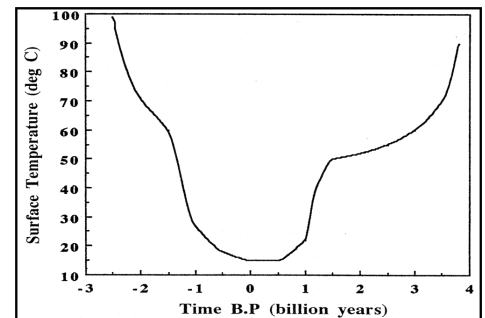


Figure 2. The surface temperature of the Earth in the past and projected for the future (positive and negative respectively on the x-axis), noting that 0 is the present and the temperature curve of the past approximates and compresses what is seen in Figure 1. A window for maximum encephalization is generated between +1 and -1 billion years B.P.

(e.g., corvids), marine mammals (e.g., dolphins) and terrestrial mammals (e.g., elephants, anthropoid apes, hominins) in the Cenozoic. Dunbar's (2016) strong case for sociality driving the evolution of big brains in mammals is the context for climate cooling reducing the constraint of inefficient heat loss from bigger brains. Thus, social animals are an apparent attractor niche for encephalization, and for warm blooded animals heat loss from an energy-intensive brain is a constraint. For primates in particular, Street et al. (2017) have made a convincing case that brain expansion and high reliance on culturally transmitted behavior coevolved with sociality and extended lifespan.

Conclusion

The case outlined here points to an important conclusion regarding biological evolution, namely,

to the critical role of a temperature constraint holding back the emergence of major organismal groups, starting with phototrophs in the Archean, culminating with eucaryotes, then metazoans in the Proterozoic and the burst of encephalization in the late Cenozoic. (It is important also to acknowledge that the constraints on biotic evolution have included atmospheric oxygen levels on macroeucaryotes, including metazoans in the Phanerozoic, along with atmospheric carbon dioxide levels on emergence of lichens and leaves (megaphylls) in the Devonian).

The pattern of biospheric evolution argued here raises the potential of similar coevolutionary relationships of life and its environment on Earth-like planets around Sun-like stars.

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