

Interactive comment on “Geodynamic and metabolic cycles in the Hadean” by M. J. Russell and N. T. Arndt

M. J. Russell and N. T. Arndt

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Response to the comments of C. Blank (Referee)

Blank concludes the first paragraph of the review with the statement “*Russell and Arndt make their case on how these transitions happened with firm, declarative statements which I believe, cannot be solidly made given the controversial and poorly understood nature of many of these statements. For example, their claim that the oldest zircons show the presence of an ocean by 4.4 Ga is one that is highly controversial where much more theoretical and experimental work needs to be done in order to explain the observations (e.g., Whitehouse Kamber, 2002). I believe that the authors would have been better served if they would take their declarative statements, examine and explain the controversies, and then formulate their statements as hypotheses that need to be tested in order to support their own model regarding the transition between the inorganic and the organic worlds. When the controversies are not pointed out*

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or discussed (granted this is difficult to do given space constraints), the declarative statements may appear one-sided." (In the following text the reviewer's are given in italics)

We had indeed overlooked the Whitehouse Kamber paper. We appreciate the reference and have now incorporated it in our manuscript. Whitehouse and Kamber's work does not directly address the suggestion of an early ocean, but does challenge early subduction. Regarding the general criticism, surely, that this it is a theoretical manuscript is taken as read. Such a manuscript should be bold and parsimonious so that points made may be refuted, a view fully endorsed by the reviewer. Indeed the manuscript highlights the major controversy regarding the onset of oxygenic photosynthesis.

"I do not have sufficient expertise to make any specific comments about the first part of the manuscript and will leave this for others. However, I do have several comments on the declarative statements that the authors have made which are biological in nature: 1. The authors state (pg. 599; line 7) that "...because of the fragility of RNA we recognise that life is unlikely to have emerged at temperatures much above 40oC". This statement contains a number of underlying assumptions. First, it assumes that there was an RNA world (which is hypothetical and not universally accepted). "

We do not assume there was an RNA world - merely an RNA era (we consider peptides predated RNA (Milner-White and Russell, 2005). The view that RNA emerged as the first coding molecule is widely accepted (Poole et al., 1999, BioEssays; Moulton et al. 2000 JME 51, 416; Aravind and other references supplied). Nor do we accept that an RNA world must have existed at high temperatures

"Perhaps the origin of life did occur at high temperatures, and then moved into lower temperature environments once it reached the stage of the RNA world (if, in fact, the RNA world existed in the first place)".

We argue that acetate was likely to have been the first waste product as argued in

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Russell and Martin 2004 in Trends in Biochemical Sciences (which passed the ordeal of 5 international referees and an editor). There are no hyperthermophilic acetogens, as to be expected from the thermodynamic calculations of Schink, (1999), Shock et al. (1998), Amend and Shock (2001).

“Ē there are many RNA molecules that have high G+C content and in their stems and therefore can maintain their secondary structures at high temperatures (even with several breaks in the sugarphosphate backbone).”

That may be, but this doesn't argue either way. Moreover, we suggest that the first RNAs, being adsorbed to a mackinawite surface, presented their codons directly to the ambient amino acids and subordinate RNA monomers, i.e., they were not folded upon themselves into double strands.

“With this information, one can then hypothesize that the RNA world indeed could have existed at moderately high temperatures if natural selection resulted in chemical and G+C content adaptations that conferred thermostability upon the molecules.”

One may hypothesize in this way, but this is not what we mean to do. The metabolic argument is the most important one here because all else will rely on it, and we reiterate our metabolic argument in favour of a mesophilic onset of life.

“I do not understand the statement made (600;4) that ferredoxins are "proteins with the longest pedigree" (are the authors implying either that these proteins are more ancient than others in the cell, or that these proteins have the longest branch lengths and therefore fastest rate of evolution?).”

This is standard knowledge since Eck and Dayhoff (Science 1966), Hall et al. (Nature 1971) and many recent papers by Trifonov.

“Is this a deduction based on the observation that iron and sulfur are thought to have been plentiful on the early earth and therefore it follows that proteins with Fe-S clusters (like ferredoxins as well as a large number of other redox proteins) are primitive?”

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No, Eck and Dayhoff (1966) and Hall et al. (1971) argue the reverse.

“Or is this statement made because of the unique role that ferredoxins play in the cell (harvesting reducing equivalents at one location in the cell and then delivering them to wherever they are needed)?

No, it is based on parsimonious and bottom-up considerations of the simplest early code (Eck and Dayhoff (Science 1966), Hall et al. (Nature 1971), Trifonov 1999, 2003, 2004)).

“If the latter is the case, then I do not understand the point that the authors are trying to make. As far as I am aware, there is no phylogenetic evidence that these proteins are more ancient than any others that are currently found in the cell. Please see sited references.

“The authors state (600;25) "Indeed, acetate is the product of what is known as the acetyl coenzyme-A pathway - the most ancient for all metabolic pathways". I assume they mean the reductive acetyl Co-A pathway, which is reversible (and therefore could be used as an unusual form of respiration) and contains the enzyme carbon monoxide dehydrogenase (CODH). A quick BLAST search of sequenced genomes shows that the CODH enzyme is found in all the methanogen genomes (including Methanopyrus), as well as genomes from the Low G+C Gram Positive bacteria. Thus, one can infer that CODH (and the reverse acetyl Co-A pathway) was present in the ancestor to the Euryarchaeota, and then was later transferred laterally into the Low G+C Gram Positives. The enzyme is not in any of the Crenarchaeota or in any of the deeply branching bacteria, and therefore it is safe to conclude that this enzyme or this pathway was also not present in the last universal common ancestor (LUCA).

There is absolutely no evidence that CODH was later transferred laterally from the Euryarchaeota into the Low G+C Gram Positives. Please see Martin and Russell 2003, Trans R. Soc and Russell and Martin (Tibs 2004) and the many references sited therein.

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“So, I have to disagree with the statement made by the authors that this is the most primitive of metabolic pathways.

A letter from the referee to TIBS is called for challenging our model and outlining the disagreement.

“There have been many papers in the last decade trying to infer the ancestral metabolic traits of the LUCA, and many of them contradict each other (some even claim it was totipotent, others not). Therefore, our picture of the nature of the LUCA’s metabolic capability is somewhat murky at present and the claim of the authors premature.

We are trying to rectify this - see above.

“The authors state (602;8) “Most prokaryotes near the root of the evolutionary tree can use Fe(III) as an electron acceptor, supporting the notion that this element was the first to fulfill this vital role”. Statements similar to this are commonly seen in the microbiological literature. However, presence of a trait in the deep lineages does not necessarily mean that these traits are ancient, because these organisms have been around for a very long time and therefore contain many adaptive traits (such as adaptation to the presence of oxygen in the atmosphere, or adaptation to the presence of oxidized energy sources such as sulfate and thiosulfate) in addition to primitive traits. Therefore, in order to show that iron reduction is a primitive trait, the evolutionary history of iron reduction needs to be studied in detail in the deeply branching lineages.

We take our views from the well-sited papers by the Lovley, Phelps and other groups. Obviously it is an area that requires further research but is not our task.

“The authors need to be very careful about their terminology when they talk about methanogens and methanogenesis (603;12) in the context of pre LUCA metabolisms. The methanogens share a complex, highly evolved pathway with a large number of unique enzymes and co-factors. Most methanogens reduce CO₂ with H₂ completely to form methane, and this is likely the ancestral type of methanogenesis that existe-

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din the ancestor to the Euryarchaeota. Methanogenesis using more complex organic compounds (e.g., formate, acetate, and alcohols) appeared only in late branches in the euryarchaeal tree. As such, methanogenesis using acetate (by the methanogenesis pathway) could not have been an ancestral metabolic energy source for the Euryarchaeota. However, one could hypothesize that some distant ancestor, long before the LUCA, could have used acetate as an energy source. However, the organism cannot be called a methanogen, or be equated with the modern form of methanogenesis.

We find this hard to follow. If we look at Amend and Shock (2001) for anaerobic core metabolic reactions that involve the reduction of CO₂ (or CO) using H₂ as an electron donor, acetogenesis is a pathway found only in eubacteria to date, and methanogenesis, is a pathway found only in archaeobacteria to date. They have in common the acetyl-CoA pathway of CO₂ fixation that utilizes ACS/CODH (Müller, 2003). The catalytic/enzymetic machinery required for part of both processes is also similar (Fontecilla-Camps and Ragsdale 1999). Despite overall similarity in design and in the energy producing reactions of acetogens and methanogen involving chemiosmosis, it is true that the basis of chemiosmosis in the two groups differs, involving different co-factors (THF vs MP; quinols vs. Mpz), in membranes composed of different lipids (FA vs IPE). Yet they utilize homologous ATPases. Thermodynamic considerations alone would lead us to expect methanogenesis to be the first route taken by an incipient metabolist (Schink, 1997) but the kinetic barriers are too high at moderate temperature, so the less energetically favourable genesis of acetate is the likely first metabolic process at around 40°C (Russell and Martin TIBS 2004). Notwithstanding these points, such detail is not called for in this paper.

“With regard to differentiation into the bacterial and archaeal domains (603;20) - there is no particular reason (or evidence), that I am aware of, that they should have diversified in the same location and in the same location as the LUCA. The hypothesis that they diversified in two different locations is equally parsimonious at this point, due to lack of evidence supporting one of these hypotheses over the other.

Logically it doesn't make sense that an unargued speculation be just as parsimonious as our hypothesis. Nor does it explain commonalities of the universal genetic code, tRNA and ribosomes, ribosomal proteins (most of which are encoded in a conserved superoperon that is present and conserved in gene order across many genomes). The LUCA also possessed DNA, DNA polymerases, RNA polymerases, and a battery of accessory translation factors such as EF-Tu and EF-G that are present in all prokaryotes, probably along with F1-F0 type ATPases as well as prokaryotic forms of the signal recognition particle, an accessory to translation. Furthermore it had to have had all of the pathways necessary for efficient nucleotide and amino acid biosyntheses, a core carbon metabolism to provide the biosynthetic precursors, and for the cofactors required for those biosynthetic pathways (Martin and Russell, 2003).

"I am not aware of any phylogenetic data showing that Mn reduction and sulfur reduction arose after iron and carbon dioxide reduction (603;27). In fact, it has long been argued (e.g., in Woese, 1987) that sulfur reduction is an ancestral trait in the tree of life. My own work supports this, and suggests that heterotrophy is just as ancient as autotrophy in the tree of life (and thus autotrophy is not necessarily more ancient).

Sulfur is not so easily accessed by bacteria and manganese would only be accessed after lower potential Fe(III) (and see Klein et al., 2001, Journal of Bacteriology, 183, 6028). Heterotrophs would soon run out of food and material in the absence of autotrophs as pointed out by Haeckel in 1892. Moreover, the writers cannot be expected to indulge the referee's unpublished work.

"Also, there are at least 5 known ways that prokaryotes fix carbon dioxide, and thus this trait has arisen convergently a large number of times. This alone suggests that this is not an ancient trait, but one that is more derived (Blank, in prep.)

We simply can't see the logic of this statement but do look forward to seeing this work and its logical basis in print. Meanwhile we cannot be expected to alter our argument on this unsubstantiated declaration.

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"The authors state (604;1) that "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. 550°C). But the propensity to live well above 40°C was passed back to the nascent bacteria through genetic transfer." They the authors go on to explain that an impact could explain why the LUCA was a thermophile. These statements do not follow each other logically nor do they make sense, and the claims should be backed up with appropriate citations. Most would agree that the deepest branches in both the bacterial and archaeal domains live at very high temperatures, and therefore it is safe to infer that the LUCA as well as the ancestors that gave rise to the archaeal and bacterial domains were not just thermophiles, but hyperthermophiles.

Homoacetogens, thought by many to be the first prokaryotes (e.g., Pereto et al. 1999), out-compete methanogens completely at low temperature in acidulous waters (pH 6.1) (Phelps and Zeikus 1984). Acetogens tend to takeover below 20°C, a bacteriogenic process that is even more marked at 10°C or less. Acetogenesis is less energetically viable at temperatures at which methanogens can operate (Schink, 1999; Amend and Shock, 2001). Indeed, today acetate has been syntrophically oxidised to produce CH₄ and CO₂ at 58°C (Zinder and Koch 1984), a reversal of acetogenesis. Acetate conversion to methane at higher T is carried out by an acetoclastic bacterium, Methanosarcina thermophila (Schink, 1999). These are just some of the considerations that have led to our hypothesis of a mesophilic onset of life (though not of the LCC or LUCA) - ones that it is inappropriate to detail in this context.

"The French hypothesis and the work in Benner's lab (as indeed is correctly cited by the authors) are in the minority in claiming that the LUCA was not a hyperthermophile.

As critical scientists we cannot be expected to toe the majority's line. We think the arguments of Moulton, Penny and others to be the more cogent.

"Second, there are many instances where hyperthermophilic lineages independently diverged into low temperature environments.

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We do not see why this is important

“There are also instances where mesophilic ancestors diverged into high temperature environments (e.g., in the Cyanobacteria), however these secondary adaptations back to high temperatures never quite made it back into the realm of hyperthermophily.

Indisputably

“Ē The genome itself also has to be stabilized, either with supercoiling or with protective proteins, to eliminate thermal denaturation, double strand breaks, and chemical damage to the bases which can occur at more frequently higher temperatures. Hyperthermophiles also have some unique adaptations, like reverse gyrase, which help them survive at very high temperatures. Thus, it is doubtful that thermophily is a discrete trait that could be laterally transferred between distantly related lineages, as the authors propose.

We agree that it is difficult to follow evolution to thermophily and hyperthermophily; so difficult indeed as to beggar belief that the first organism could master all these (e.g a reverse gyrase) traits at once!

“Lastly, yes it is agreed that one hypothesis to explain why the LUCA is a hyperthermophile is that it survived a meteorite impact. However, there are plenty of other hypotheses, which at this time should carry equal weight as the first in the face of a lack of evidence, such as that perhaps there were also mesophiles early on, but they were out-competed with organisms with hyperthermophilic ancestry.

We give the only other likely reason.

“Or, the LUCA could have been seeded from another planet, such as Venus, Mars, or Europa, upon which the origin of life occurred (rather than the Earth).

This begs the question. Whatever idea may be considered for the “origin of life” it had to “emerge” somewhere. Europa appears to us unlikely for lack of an electrochemical potential of half a volt on that planet. We have argued elsewhere that life may have

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emerged on Mars independently (Russell and Hall 1999). The Venus hypothesis is untestable

“It is not clear to me why the authors need to postulate some physical means (obduction of oceanic crust) in order to transfer microbes from the hydrothermal mounds on the oceanic floor to shallow water environments (605). The authors claim that their rationale for this hypothesis is that the ocean at the time was “inhospitable”. It is not clear why the early oceans would have been inhospitable (or less hospitable than the hydrothermal mounds which are at the interface of a hydrothermal cell and the ocean).

Nutrients (e.g., would be hard to come by (little organic material for heterotrophs and no focus of a hydrogen (energy) supply for autotrophs). The ocean, even more so then, would have been a nutritional desert.

“Perhaps they are referring to the near surface environments which are also part of the ocean but bombarded with intense uv?”

That is only a minor aspect, but meteoritic bombardment heating the ocean to 200°C+ is more of a concern for the early Earth (Maher and Stevenson 1988 now included).

“Perhaps the authors are implying that there would have been a general lack of energy sources in the early ocean?”

Yes

“In general, microbes that are in stationary phase (where they are not actively growing) can exist for very long periods of time. They also take on traits that render them resistant to environmental stresses like heat shock, cold shock, desiccation, as well as exposure to uv, ionizing radiation and peroxides.

Really: are the first prokaryotes that sturdy. Doesn't it take evolutionary time to develop these traits?

“While in this state they are capable of acquiring mutations, so they can still evolve

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even if net population growth is not occurring. In this manner, cells released from their native environments (such as the mound) should be able to persist in a semi dormant, resistant state until they come in contact with growth conditions and energy sources they can survive in/on. For example, Thomas Brock showed several decades ago that one could culture thermophiles normally found in hot springs from samples of the Firehole River kilometers outside of Yellowstone National Park (despite their numbers being swamped out by simple dilution along with a vast number of actively growing low temperature biomass in the river).

We have read the literature and do refer to Morita (2000) but consider the best place for dormancy is in the deep biosphere, not in a rapidly circulating and occasionally vaporized Hadean ocean.

“Thus, it is not immediately clear to me why an unusual event such as obduction of oceanic crust is needed to account for the transport of microbial cells from the deep ocean to shallow water environments on the early Earth.

We argue that obduction was not an unusual event on the early earth, where oceanic crust was thick, hot and not easily subductable. Slices of the upper part of this crust probably were thrust onto growing continents as a normal part of the tectonic cycle.

“The details of the evolutionary history of photosynthesis are poorly understood at this stage, despite decades of work by a large number of researchers. This is, no doubt, because that evolutionary history has been very complex, and was likely a combination of divergent as well as horizontal evolution with different sets of components having different evolutionary histories (see Olsen and Blankenship, 2004).

We have read this and discussed our ideas with Blankenship at length. Sauer and Yachandra (2002, 2004) have sited our idea with approval.

“Also, many of the genes in photosynthesis have fast evolutionary rates and therefore long branch lengths, so phylogenetic trees with these proteins are not easily resolved

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(requiring a large amount of data). At this time, it is not clear which photosystem came first (PS1 or PS2), particularly since it has been proposed that the Green Non-sulfur bacteria, which branch somewhat deep in the bacterial domain and therefore has been long assumed to be primitively photosynthetic may have acquired photosynthesis laterally. It should be noted that PS2 is also found in the Proteobacteria and in the Green Non-Sulfur bacteria, and none of these groups are capable of splitting water to produce oxygen. Therefore, it is technically incorrect to say that "PS2 oxidizes water using what is known as the oxygen-evolving complex (OEC; 607;13)". Rather, what is unique is the combination of the OEC and PS2 in the cyanobacteria which led to using water as the electron source for oxygenic photosynthesis which is the key evolutionary innovation. We are aware of different origins and have discussed these with John Allen and Wolfgang Nitschke and reference their papers. Our point is to explain a geochemically and geologically plausible origin of the OEC.

"Ě the best evidence for the early presence of cyanobacteria is the hopanoid geolipids (Brocks et al., 1999; Summons et al., 1999; Brocks et al., 2003).

We include Brocks et al. (2003) in the revised manuscript; thank you for this reference. We do recognize the uncertainties but are alerting the intended readership to the immensity of this unresolved dichotomy.

"To conclude briefly: I believe that there are some important contributions in this work, such as the articulation of the hydrothermal mound as the cradle of life, what sort of inorganic and fledgling bio(in)organic processes could have occurred on the mound, and how organisms then moved from the mound to diverge into other environments with other phenotypes.

Thank you

"Unfortunately, I have to disagree with a large number of the declarative statements that the authors make about evolutionary processes that would have occurred toward the later part of their scenario. Given that remark, it must be stated that there is a

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great deal to be learned in the early evolution of life on Earth, that this is a field seeing rapid progress, particularly given whole genome sequences, and that we should see a number of the controversies and problems better illuminated in the near future.

We look forward to these better illuminations but meanwhile we are glad to bring these controversies to the fore. However, we cannot, on these grounds, consider our hypothesis disproven, but merely admit to a different thinking scheme to that of our critic.

Interactive comment on Biogeosciences Discussions, 1, 591, 2004.

BGD

1, S482–S494, 2004

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