## ARCHAEA



(photo: Seth Shostak)



Malcolm Walter (photo: Seth Shostak)



Rose Grymes (photo: Seth Shostak)

# Precambrian Surface Temperatures and Molecular Phylogeny

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Abstract. The timing of emergence of major organismal groups is consistent with the climatic temperature being equal to their upper temperature limit of growth  $(T_{max})$ , implying a temperature constraint on the evolution of each group, with the climatic temperature inferred from the oxygen isotope record of marine cherts. Support for this constraint comes from the correlation of  $T_{max}$  with the rRNA molecular phylogenetic distance from the last common ancestor (LCA) for both thermophilic Archaea and Bacteria. In particular, this correlation for hyperthermophilic Archaea suggests a climatic temperature of about 120°C at the time of the LCA, likely in the Hadean.

### 1. Introduction

The deterministic origin of life is now a virtual astrobiological paradigm. This contrasts with the long held view of evolutionary biology 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., the general pattern of the tightly coupled evolution of biota and climate was very probable, given the same initial conditions, with major events in biotic evolution forced by environmental physics and chemistry and the merging of complementary metabolisms (Schwartzman 1999). In particular, a critical constraint on biotic evolution was surface temperature in this alternative interpretation. Here we show that this constraint is supported by the correlation between molecular phylogenetic distance of thermophilic procaryotes from the last common ancestor and their maximum growth temperature. A temperature constraint on microbial evolution implies the equality of the upper temperature limit for viable growth  $(T_{max})$  of a microbial group and the actual surface temperature at the time of emergence. This predicted equality is consistent with the history of climatic temperature, notably for the emergence of phototrophy, eucaryotes and Metazoa with climatic temperatures inferred from the oxygen isotopic record of ancient chert (e.g., Knauth 1992;



Figure 1. Phylogenetic Tree based on rRNA sequences (after Pace 1997). The LCA is located on the bacterial line between the node to Aquifex and the Y intersection of the three domains.

Knauth & Lowe 2001). The implicit assumption that an ancient and necessary biochemical character determines the presently determined  $T_{max}$  of each group is supported by the best estimates of emergence times. For example, no phototroph has been found to grow above about 75°C, in spite of a likely 3.5 billion year old or more ancestry of this metabolism, similarly for eucaryotes with  $T_{max}$  of 60°C, with at least 2 billion years for the possibility of adaptation to life at higher temperatures. 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 mitochondrion, the Proteobacteria, have the same  $T_{max}$ ).

#### 2. Molecular phylogeny and climatic temperature

The deep rootedness of hyperthermophilic Archaea as inferred from molecular phylogeny appears to remain robust (Matte-Tailliez et al 2002), while new evidence is emerging for the acquisition of bacterial hyperthermophily by gene transfer from hyperthermophilic Archaea (Aravind et al. 1998). Nevertheless, recent work supports a thermophilic, even hyperthermophilic last common ancestor (LCA) of all life (Di Guilio 2000; Berry 2002).

Using Pace's (1997) rRNA phylogeny for hyperthermophilic/thermophilic procaryotes (Fig. 1) we note a good correlation of  $T_{max}$  with the branch length, an assumed measure of evolutionary distance from the LCA (Fig. 2). Likely



Maximum Growth Temperature (deg C)

The growth temperature of (Hy-Figure 2. maximum per)thermophilic Archaea/Bacteria versus their branchlength from Fig. 1. Archaea/Bacteria labelled "a" through "s" in Fig. 1 are plotted.  $T_{max}$  values are mainly from Kristjansson (1992) and Stetter (1999). We assume the distance of the intersection of the branch to the tree line of the domain to the LCA, the "branch length", is a measure of the evolutionary distance of the given organism. For a side branch from each domain, this corresponds to the distance from the intersection to domain tree line to the LCA. The LCA is assumed to be at the node in the "Y" in Fig. 1. The uncertainty in the location of the LCA only changes the relative branching lengths between the two domains, not the correlation. For Archaea,  $R^2 = 0.755$ , for Bacteria. 0.777. R is correlation coefficient.

sources of scatter include horizontal gene transfer since emergence. We argue that the inverse correlation shown in Fig. 2 is robust evidence of  $T_{max}$  being close to the climatic temperature of each organism at emergence at thermophilic conditions.

If molecular phylogeny can be interpretated to give significant time gaps in the emergence of deeply-rooted hyperthermophiles, assuming they are primitive, then their  $T_{max}$  values probably correspond to ambient climatic temperatures rather than the gradient between their locus of origin in hydrothermal vents and ambient aqueous media (ocean or fresh water). THis is because microbial evolution should take place on a shorter time scale than is resolvable on a molecular phylogenetic tree if the necessary environmental conditions are present. Hence if there was a gradient of about  $40^{\circ}$ C between the upper temperature limit of life (assumed  $120^{\circ}$ C) and the ambient sea water at 3.8-4.4 Ga (oceans at 4.4 Ga; Valley et al. 2002), then emergence of the hyperthermophiles should be nearly simultaneous at that time resolution rather than being spaced out. Therefore the climatic temperature was plausibly near 120°C at the LCA. For a substitution rate an order of magnitude higher in the hyperthermophilic realm close to the LCA (Gogarten-Boekels et al. 1995), the inferred time of emergence of these Archaea are spaced out on a  $10^7$  year timescale. This higher substitution rate was estimated for genes that underwent an ancient gene duplication which may not be true for rRNA. One chert-derived climatic temperature of 80°C at 3.8 Ga implies the LCA was further back in the Hadean. A plausible scenario is that the LCA was left after a major impact event (Gogarten-Boekels et al. 1995).

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