



THERMOPHILES, ORIGIN OF

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GLOSSARY

Archaea One of three domains of life; from the Greek *archaios* (ancient, primitive); prokaryotic cells; membrane lipids predominantly isoprenoid glycerol diethers or diglycerol tetraethers; formerly called archaeobacteria.

Bacteria One of three domains of life; from the Greek *bacterion* (staff, rod); prokaryotic cells; membrane lipids predominantly diacyl glycerol diesters; formerly called eubacteria.

biomarker A macromolecule unique to a particular organisms or group of organisms such that its detection alone would suggest the presence of the organism or group of organisms.

chemolithotroph Organism deriving its energy from the oxidation of inorganic compounds.

Eukarya One of three domains of life; from the Greek *eu-* (good, true) and *karion* (nut; refers to the nucleus); eukaryotic cells; cell membrane lipids predominantly glycerol fatty acyl diesters.

heterotroph Organism deriving its energy from the oxidation of organic compounds.

hyperthermophiles From the Greek *hyper-* (over), *therme-* (heat), and *philos* (loving); includes organisms that grow best at temperatures warmer than 80°C.

photoautotroph Organism that uses light as its source of energy (photosynthesis) and inorganic carbon (CO₂) as its sole carbon source.

planetesimals Small, solid bodies similar to meteors in composition but revolving in orbit around a central gaseous nucleus, as do planets around the sun.

small subunit ribosomal RNA RNA (about 1500 bases in prokaryotes) that functions as part of the ribosome and the sequence permits the inference of evolutionary relationships among organisms.

thermophiles From the Greek *therme-* (heat) and *philos* (loving); includes organisms that grow best at temperatures between 50° and 80°C.

AT THE TIME when liquid water—a prerequisite for life as we know it—appears in the geological record (3.8 billion years ago), Earth was a hot, anoxic environment and under constant bombardment by meteors, many of which could have virtually vaporized the oceans. Early Earth, therefore, would have been an attractive home to heat-loving thermophiles and their extreme cousins, the hyperthermophiles, where thermophily would have offered a great selective advantage.

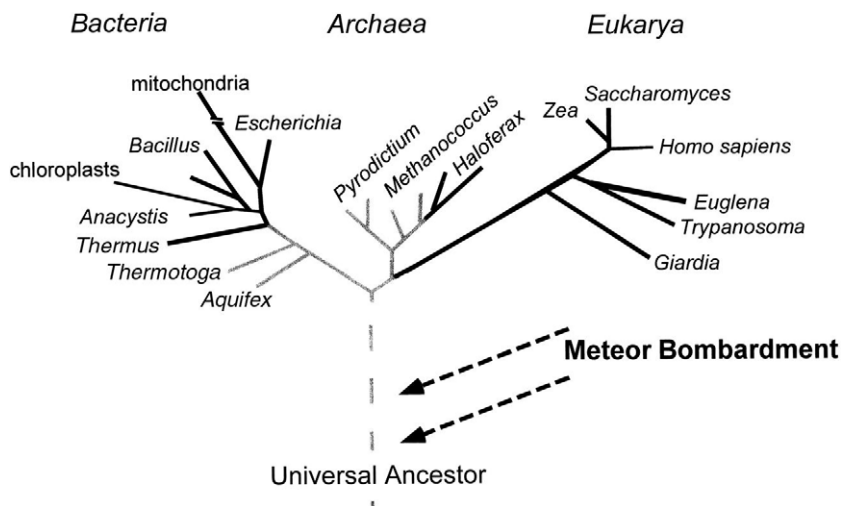


FIGURE 1 Rooted phylogenetic tree based on the small subunit rRNA molecule. The tree is not drawn to scale.

The geochemical and thermal characteristics of deep-sea hydrothermal vents and terrestrial hot springs are thought to approximate conditions on Earth at the earliest possible time that it could have supported life, providing modern analogs for testing early evolution of life hypotheses. In addition, the relatively recent use of the evolutionarily conserved molecules such as the small subunit ribosomal RNA (ss rRNA) sequences in phylogenetic analyses of all life has placed the thermophiles closest to the root of the universal tree of life (Fig. 1). On this tree, hyperthermophiles decidedly monopolize the lowest and shortest branches, suggesting that they may be related to the earliest microbes to inhabit Earth. However, the proposal that thermophiles may have originated early in Earth's history is much debated. Therefore, this article also considers alternative scenarios for the origins of thermophiles.

I. THERMOPHILES AND HYPERTHERMOPHILES DEFINED

All life can be placed in one of the three domains of life: the Archaea, Bacteria, or Eukarya. Archaea and Bacteria are prokaryotes, and the Eukarya are eukaryotes. However, phylogenetically, the Archaea are as different from the Bacteria as the Bacteria are from the Eukarya. Thermophiles are found in all domains as multicellular and unicellular organisms, such as fungi, algae, cyanobacteria, and protozoa, and they grow best at temperatures higher than 45°C. In contrast, the ex-

treme thermophiles, or hyperthermophiles, grow best at temperatures higher than 80°C and are almost exclusively restricted to the Archaea, with only two hyperthermophilic orders in the Bacteria, namely, the Thermotogales and Aquificales. Commonly, thermophiles and hyperthermophiles are found associated with deep-sea and terrestrial hydrothermal vents. Thermophiles have also been obtained from deep (up to 3500 m), hot, subterranean areas, Jurassic oil-bearing sandstone and limestone formations, and suitable manmade environments such as smoldering coal refuse piles, coal-containing uranium mines, and boiling wastewaters from geothermal power plants.

II. ECOLOGICAL NICHE AND METABOLIC DIVERSITY OF HYPERTHERMOPHILES

Deep-sea hydrothermal and terrestrial hydrothermal vents form primarily as the result of plate tectonics, either as a result of seafloor spreading or as a tectonic plate moves across a hot spot. In both scenarios, fissures and faulting occur in the earth's crust, permitting water (seawater, groundwater, or rainwater) to percolate downward. As the fluid moves through the earth's crust and approaches the magma chamber, the fluid heats and reacts with the surrounding rocks, adding some minerals and gases (e.g., iron, manganese, carbon dioxide, hydrogen, and hydrogen sulfide) and removing others (e.g., sulfate and magnesium in seawater). The

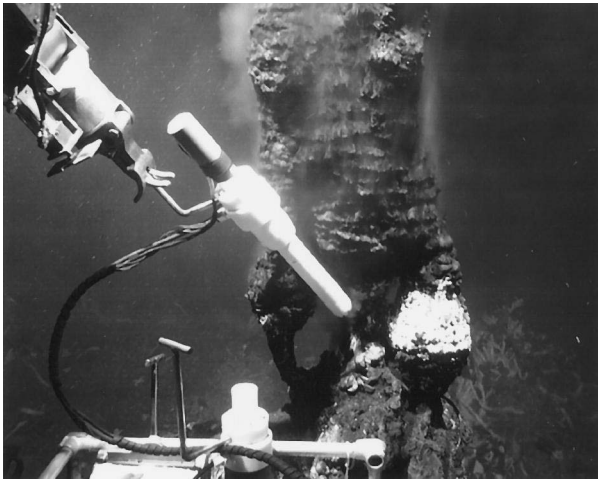


FIGURE 2 Sampling a deep-sea hydrothermal vent chimney from the eastern Pacific Ocean. The porous sulfide chimney structures can reach several meters high and are ideal habitats for hyperthermophiles.

fluid is finally forced back to the surface as a highly altered hot fluid, its chemistry representing a history of its travels through the earth's crust. At deep-sea hydrothermal vents, this fluid can reach temperatures of 400°C , remaining in a liquid state due to the hydrostatic pressures at these depths (>2000 m). It rapidly mixes with cold, oxygenated water, and the minerals rapidly precipitate, giving the fluid a smoky appearance (Fig. 2). These vents are aptly named "black smokers." As the minerals precipitate they create porous sulfide-mineral structures called "chimneys." At terrestrial hot springs, the fluid may be ejected forcefully as a geyser or simply bubble into a thermal spring or mudpot (Fig. 3).

The high temperatures and unusual geochemical characteristics of deep-sea and terrestrial hydrothermal vents create ecological niches that are exploited by hyperthermophilic Bacteria and Archaea. The geochemical milieu provides different energy sources (electron donors) and carbon dioxide for a chemolithotrophic existence. The porous chimney structures provide temperature gradients along which thermophiles can situate themselves, and thermal springs create temperature gradients as the fluid moves away from the source. Comparable to photoautotrophs that harvest light energy to fix inorganic carbon, these chemolithotrophs harvest inorganic chemical energy to fix inorganic carbon. It has been calculated that the mixing of superheated thermal fluids at deep-sea vents with cold, oxygenated seawater causes a significant geochemical disequilibrium, significant enough to lower the Gibbs

free energy and help drive biologically mediated redox reactions (Shock, 1996). The food chain does not stop there, though. Many thermophiles are heterotrophs, consuming organic carbon produced from biological activity. Additionally, at terrestrial vents, due to the available light energy, the springs are often colonized by a rich diversity of thermophilic phototrophs, including the cyanobacteria, which are oxygenic phototrophs that use water as the reductant and evolving oxygen in the process. Anoxygenic phototrophs are also found at terrestrial vents, primarily using the readily available hydrogen sulfide as the reductant in photosynthesis, releasing elemental sulfur in the process. Both of these types of phototrophs are part of a complex community with heterotrophs, and together they form thick green, purple, and orange microbial mats typical of many terrestrial thermal areas throughout the world.

The majority of hyperthermophiles are anaerobes, with a few exceptions that are microaerophilic, requiring low oxygen concentrations for growth. In contrast, aerobiosis is more common among the thermophiles because oxygen dissolves more readily in the lower temperatures of the cooler thermal springs. The thermophiles that have been isolated from deep-sea vents generally grow at pH values near neutrality. However, thermophiles from terrestrial hot springs have been grown at pH values from 1 to 10.

Although the highest temperature for life has not been determined, it has been suggested that 150°C may represent that threshold. In contrast, the lower temperature limit for most hyperthermophiles is 60°C , a temper-



FIGURE 3 Moose Pool, Yellowstone National Park, Wyoming. This acidic thermal spring contains elemental sulfur that accumulates on the gas bubbles (see inset). The archeon *Sulfolobus acidocaldarius* was isolated from this spring in the late 1960s by Thomas Brock.

ature fatally hot for most other organisms. Even 90°C is too low for one of the more extreme hyperthermophiles, *Pyrolobus fumarii*, which has a maximum temperature for growth of 113°C. However, for these thermophiles, the inability to grow does not result in death; they are capable of entering a dormant state when exposed to cold conditions and will thrive again when returned to favorable temperatures. Thermophiles are therefore very well suited to the deep-sea hydrothermal vent environment, in which the hot fluids are continually being mixed with cold, oxygenated seawater.

III. MOLECULAR MECHANISMS FOR THERMOPHILY

On a molecular level, thermophily is accomplished in many ways, contributing together to overall stability and success of life at high temperatures. In general, the amino acid composition of hyperthermophilic enzymes is surprisingly similar to that of homologous mesophilic enzymes. Because of the amino acid sequence similarity, it has been proposed that heat resistance is explained, instead, by the manner in which the polypeptide chains are folded on themselves, forming their tertiary conformational stability. It is a polypeptide's three-dimensional or tertiary shape in critical locations on the polymer that permits an enzyme to function. Proteins do not spontaneously fold into their active form after synthesis. Instead, many require the assistance of molecular chaperones for proper folding. A specialized form of molecular chaperone, called a thermosome, is of particular importance to hyperthermophiles because it assists proteins in refolding correctly after denaturation due to heat exposure. Also called heat shock proteins, thermosomes effectively increase heat tolerance of organisms so they can function at higher temperatures. For instance, at 108°C, approximately 80% of the protein of *Pyrodictium occultum* consists of a heat-induced thermosome, allowing it to survive 1 h of autoclaving at 121°C (Stetter, 1998).

Additional thermal resistance of DNA is conferred by the presence of DNA topoisomerases and histones and, to a lesser extent, by the base composition of the genome. All hyperthermophiles known to date have been shown to possess reverse gyrase, a unique type I DNA topoisomerase that causes stabilizing, positive superwists in the DNA helix. Additionally, archaeal (but not bacterial) hyperthermophiles possess histones which significantly increase the temperature at which DNA denatures.

Because an increased guanine + cytosine (G + C) nucleic acid content increases the melting temperature of DNA, one would predict that hyperthermophiles have a higher G + C content in their genomes. In many cases, the opposite is true. However, analysis of the genome reveals that certain genes essential to survival, such as the ss rRNA gene, have higher G + C contents.

The presence of ethers instead of esters in cellular membranes also contributes to the stability of hyperthermophiles at high temperatures. Cell membranes of Bacteria and Archaea are generally distinguished by the presence of glycerol-linked ether lipid moieties in Archaea and ester lipid moieties in Bacteria. An exception to this rule is the presence of a glycerol ether lipid in *Thermotoga maritima*, one of the few bacterial hyperthermophiles. The presence of the ether lipids probably increases stability of cellular membranes against hydrolysis at high temperatures. Membranes of the archaeal hyperthermophiles contain lipids derived from diethers or tetraethers and are highly resistant against hydrolysis at high temperatures.

IV. ORIGIN OF THERMOPHILES: FOSSIL RECORD AND UNIVERSAL PHYLOGENETIC TREE

Were thermophiles the original ancestors to all life? Much of the debate about origins of life and early evolution of life on Earth centers on this question. Is thermophily an acquired feature derived from adaptation? As more information accumulates, the resolution of these questions becomes less clear. However, many different scenarios are emerging based on fossil record analyses, RNA and protein phylogenies, and our understanding of the conditions that prevailed on early Earth.

A. Early Earth and Its Hyperthermophilic Niche

Perhaps the most compelling evidence supporting the proposal that hyperthermophiles are living fossils of the first life that arose on Earth is that modern ecological niches of hyperthermophiles fit our current view of the conditions on primitive Earth, which was anoxic, hot, and volcanically active. During its first half billion years of existence (4.6–4.0 billion years ago), the temperature of the surface of Earth probably exceeded 100°C. From recent studies of ancient sedimentary rocks of the Isua formation in Greenland, traces of biologically produced carbon were detected, suggesting that the invention of

life had already taken place 3.8 billion years ago. Thus, sometime prior to 3.8 billion years ago, it is likely that the first living organisms appeared at a time when Earth, although cooling, was much hotter than it is now, and all the essential geochemical energy sources were present for a chemolithotrophic and thermophilic existence. Heat-tolerant organisms such as hyperthermophiles would have been at a distinct advantage over heat-sensitive organisms.

In addition to the generally hot and anoxic conditions on early Earth, the bombardment of early Earth by meteors may have caused a bottleneck event that favored survival of hyperthermophilic organisms. An examination of the impact craters on Earth's geologically inactive moon strongly suggests that the earth was heavily bombarded by meteors from its formation 4.6 billion years ago until about 3.8 billion years ago. A large meteor impact, of which there were many, would have caused intense local heat and sent sufficient debris into the atmosphere to cause global cooling and a reduction in light intensity, detrimentally impacting photosynthesizing organisms. There is also evidence of extremely large meteor impacts that would have generated enough energy to heat the earth's surface to 2000 K and virtually vaporize the world's oceans. In either scenario, hyperthermophiles would have been uniquely adapted to survive. They could have tolerated lower light levels because many are chemolithotrophs, making a living independent of photosynthesis. Any life adapted to live near ocean-floor volcanic centers would have had the greatest chance of surviving one of these ocean-evaporating events.

B. The Fossil Record

Additional evidence for early ancestors of microbial life can be found in the rock record. Rocks older than 3.5 billion years are highly metamorphosed and deformed, precluding the preservation of morphological fossils. However, the 3.8-billion-year-old Isua rocks from Greenland, mentioned previously, offer indirect evidence that life existed earlier than 3.5 billion years ago. These sedimentary rock formations are associated with liquid water, a prerequisite for life as we know it. The rocks contain geochemical evidence of past biotic activity preserved within the minerals. Grains of apatite (calcium phosphate) contain a significant portion of carbonaceous inclusions that are isotopically "light," suggesting biological activity. Microorganisms preferentially incorporate the lighter carbon-12 isotope over the carbon-13 isotope when inorganic carbon is fixed into organic carbon using the enzyme ribulose bisphos-

phate carboxylase/oxygenase (Rubisco). This isotopic evidence suggests these putative life-forms were carbon-fixing chemolithotrophs or phototrophs and not heterotrophs.

Three hundred million years later, the first microfossils appear in rocks (about 3.5 billion years old) from Western Australia and South Africa. The fossils are simple rod-shaped and filamentous bacteria, indistinguishable morphologically from any similar-shaped bacteria today. Many are reminiscent of photosynthetic bacteria, such as modern cyanobacteria. However, there is some doubt that much oxygen evolved from photosynthesis into early Earth's atmosphere. Isotopic signatures associated with these fossils do suggest a lighter carbon preference, similar to that observed in the 3.8-billion-year-old rocks. Were these first fossils perhaps thermophiles? Unless we are able to identify specific thermophilic biomarkers in these fossils, we may never know the answer.

C. The Molecular Fossils

Although they are not a substitute for the existence of microfossils, evolutionarily conserved macromolecules within living organisms function as "molecular fossils," permitting an inference of relatedness to other organisms and of evolutionary distance from a hypothetical common ancestor. Carl Woese's pioneering work with the ss rRNA molecule (16S rRNA in prokaryotes) led to the generation of the universal phylogenetic tree (Fig. 1), in which life falls within three domains: the Archaea, Bacteria, and Eukarya. The suitability of ss rRNA as the macromolecule for evolutionary comparisons is based on several critical reasons. The ss rRNA exists in every living organism, its function in every living organism is constant, it is an ancient molecule (assuming protein synthesis was necessary in the earliest of life), it has undergone only moderate changes in nucleic acid sequence when compared between diverse biological domains, and the size of the molecule is large enough to contain considerable information but small enough to be manageable.

1. Molecular Phylogenies

The relatedness of organisms to each other as suggested by the universal phylogenetic tree is markedly different than the previously proposed phylogenies. Most notably, the three domains of biological life (the Bacteria, Archaea, and Eukarya) replace the five kingdoms (animals, plants, fungi, protista, and monera). The Eukarya domain includes the multicellular animals, plants, fungi, and protista. Distributed throughout the Bacteria

and Archaea are the unicellular prokaryotes. Using alternative markers, such as 23S rRNA, RNA polymerase, elongation factor Tu, F_1F_0 ATPase β -subunit, RecA protein, and HSP60 heat shock protein, reveals general agreement with the major lineages in the ss rRNA tree. However, some discrepancies are evident.

One can root the ss rRNA tree by comparing it with a paralogous marker that arose from gene duplications (such as EF-Tu or ATPase) prior to the diversification of the three primary domains. This rooted tree reveals that all hyperthermophiles, whether bacterial or archaeal, comprise the deepest and earliest lineages within the tree (Fig. 1). In other words, they may be the closest living relatives to a common universal ancestor. However, mutational rates of ss rRNA and their associated base sequence changes are not consistent enough through time nor within lineages to assign a specific date to branching events, and so one cannot assign a clock to this tree. Nonetheless, the shorter branches leading to the hyperthermophiles indicate a slower evolutionary rate, whereas the longer branches leading to their mesophilic relatives suggest a faster evolutionary rate. It is possible that the hyperthermophiles have short lineages because they are so highly adapted to their ecological niche that they have no need for further adaptation. It is also possible that certain evolutionary constraints are imposed on thermophiles due to the extreme selectivity of the high-temperature environment. Nevertheless, the placement of thermophiles at the base of the universal phylogenetic tree strongly suggests that they are most closely related to the common ancestor of all life. In this sense, they are not unlike other "living fossils," or organisms whose morphology has changed very little based on comparisons of modern and ancient fossilized specimens, such as horseshoe crabs, club mosses, *Welwitschia*, and *Ginkgo bilboa*.

Although hyperthermophiles may be most closely related to the universal ancestor of all life, their metabolic machinery is anything but primitive. Viewed independently of the rooted ss rRNA universal phylogenetic tree, their heat-tolerant adaptations appear sophisticated or even highly evolved. If an analysis of another universal and highly conserved macromolecule placed hyperthermophiles away from the root of its phylogenetic tree, it would severely shake the topology of the phylogenetic tree discussed previously. A phylogenetic analysis of the conserved DNA-directed RNA polymerase has done just that (Klenk *et al.*, 1999). Although overall the RNA polymerase-based phylogeny corresponds very well with the ss rRNA-based phylogeny, the positions of the hyperthermophilic bacteria *A. pyro-*

philus and *Thermotoga maritima* are in the middle of the RNA polymerase tree instead of in the most deeply rooted branch in the Bacteria as suggested by ss rRNA phylogeny. Other examples also exist in which the ss rRNA tree does not quite hold true. Additional analyses of universal and highly conserved macromolecules such as DNA-directed RNA polymerases or whole genomes may one day provide a comprehensive universal phylogenetic tree that may or may not place hyperthermophiles near its root.

The debate continues, and evidence against an early origin of thermophily accumulates. If mesophily preceded thermophily, then versions of heat-tolerant mechanisms that characterize hyperthermophiles would have evolved first in mesophiles and been exploited by hyperthermophiles to open up new ecological niches. Structural analysis of reverse gyrase and *Taq* polymerase support such a proposal, suggesting they evolved from mesophilic ancestors (Forte, 1996). Additionally, the lipid moieties in hyperthermophilic Bacteria are not homologs of the lipid moieties in hyperthermophilic Archaea. Instead, they are analogs with opposite stereochemistry, suggesting the ether-based lipid moiety feature evolved independently in the Bacteria and Archaea instead of from a common ancestor (Forte, 1996).

2. Lateral Gene Transfer and the Genetic Annealing Model

Lateral (horizontal) gene transfer and variable rates of evolution and mutation may have played a significant role in the evolution of life and may offer an explanation for the confusing results of the analyses of non-ss rRNA molecules (Woese, 1998; Doolittle, 1999). Lateral gene transfer refers to the exchange of genetic material from one organism to another. It is contrasted against vertical gene transfer, in which genetic information is passed vertically from parent to offspring. Bacteria and Archaea, which as a general rule have simpler cell designs, exhibit considerable horizontal gene transfer. In contrast, the Eukarya, which contain highly evolved cell designs, generally do not engage in horizontal gene transfer. Woese proposed in his "genetic annealing model" that the universal ancestor was not a discrete entity but rather a diverse community of primitive cells that evolved as a unit, engaging in horizontal gene transfer on a scale even greater than that occurring in Bacteria and Archaea today and developing into three different communities, which in turn gave rise to the three primary lines of descent as defined by the ss rRNA tree (Woese, 1998).

The ss rRNA universal tree, then, is not a conven-

tional organismal phylogenetic tree but rather a history of the evolution of central components of the ribosome, with the deeply rooted branches of the universal tree representing a “gene tree” and not an “organismal tree.” In other words, by the time the three primary lines of descent emerged, and the tree started to take form, self-replicating organisms had not yet taken form. Instead, “life,” with its associated exchange of genetic information, existed in communal entities by way of lateral gene transfer. Additional cell complexity and function needed to evolve before there was life as we envision it today. Nonetheless, these communal entities could have evolved in the conditions on early Earth.

V. THEORIES OF THE ORIGIN OF LIFE

Theories of the origin of life are highly debated. Did life originate here on Earth, or did it develop on another planet, such as Mars, which shared similar planetary conditions 4.0 billion years ago? Did life originate in environments analogous to deep-sea hydrothermal vents, or did the first biological molecules form as a result of the reaction of electrical discharges within a prebiotic soup of chemicals? Closely tied to much of this debate are models pertaining to early Earth's atmosphere and the possible energy carbon sources (organic and inorganic). Given that this article deals with the origins of thermophiles, we focus our discussion on a possible high-temperature origin of life, highlighting some arguments that do not support this hypothesis.

In light of Earth's hot, reduced, and anoxic origins, it has been proposed that life may have arisen in environments very similar to present-day deep-sea hydrothermal vents. Here, life could take refuge and survive the planetesimal bombardment of early Earth in an environment rich in redox energy and inorganic carbon. The first biological entities could evolve rapidly as anaerobic, hyperthermophilic chemolithotrophs. The rapid mixing of superheated hydrothermal fluid, rich in reduced minerals, with cold oxygenated sulfate-rich seawater at deep-sea hydrothermal vents creates thermodynamic disequilibrium conditions that favor the production of organic molecules (Shock, 1996). The abundance of charged minerals associated with deep-sea vents led to the proposal by Gunter Wächtershäuser that the original source of reducing power for carbon fixation (and therefore a chemolithotrophic origin of life) may have come from exergonic “pyrite-pulled reactions”—the oxidative formation of pyrite (FeS_2) from ferrous sulfide (FeS) and hydrogen sulfide (H_2S or SH^-). Charged surfaces such as pyrite would attract and bind

any negatively charged molecule in solution, such as carbonate, phosphate, and sulfide. These molecules would be maintained in sufficient proximity for subsequent metabolic interactions by “surface bonding,” or anionic bonding to the positively charged pyrite surface, resulting in the formation of the first biomolecules on a charged surface. Many are skeptical of these high-temperature scenarios for the origin of life, offering evidence that many of the biomolecules of life, such as RNA, are not stable at high temperature and therefore would not support the proposal that RNA arose prior to DNA in an early RNA world (Miller and Bada, 1988). Furthermore, others have generated models to show that the ancestral rRNA would have a moderate G + C content, contrary to all thermophilic rRNAs which are generally rich in G + C contents (Galtier *et al.*, 1999).

The “panspermia” hypothesis offers another scenario for the origin of life. It holds that life originated elsewhere in the galaxy and that microorganisms were propelled through space to Earth or, alternatively, that exogenous organic carbon arriving on planetesimals fueled a heterotrophic origin of life on Earth. Chyba and Sagan (1992) estimate that approximately 4 billion years ago about 100,000,000 kg/year of organic carbon was delivered by interplanetary dust particles, and about 10,000,000,000 kg/year of organic carbon was produced by postimpact plumes caused by meteor, asteroid, and comet bombardment. From what is known about the hostile environment on early Earth and the timing of the appearance of the first microfossils, life became considerably complex within a relatively short period of time. Therefore, life either evolved very rapidly after its inception or, consistent with the panspermia hypothesis, it was raining down on Earth from elsewhere in the galaxy. Because the panspermia hypothesis involves high temperatures as particles enter the earth's galaxy, it embraces, at the very least, a thermotolerant origin of life.

VI. CONCLUSION

Morphological features of early microfossils generally offer little information about their relatedness to extant microbes. Consequently, microbiologists have come to rely on the molecular record to define phylogenetic relationships and infer the history of microorganisms. The absence of a good microbial fossil record prevents the assignment of a time line on the molecular record. The ss rRNA universal phylogenetic tree places hyperthermophiles in the deepest and shortest branches of the tree, implying that they are the closest living relative

to the common universal ancestor of life. However, as we sequence more microbial genomes and create detailed phylogenies from other molecules, the situation becomes increasingly confusing, with lateral gene transfer perhaps “muddying” the phylogenetic record. However, high-temperature conditions that prevailed on early Earth and its subsequent cooling favor the likelihood that at some time during Earth’s early history thermophiles took advantage of the geochemical energy supplied by the hydrothermal fluid and evolved into the highly adapted chemolithotrophic and heterotrophic life that is found at high temperatures.

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