

## Hypothesis Paper

# Extremophiles May Be Irrelevant to the Origin of Life

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### ABSTRACT

In recent years, Bacteria and Archaea have been discovered living in practically every conceivable terrestrial environment, including some previously thought to be too extreme for survival. Exploration of our solar system has revealed a number of extraterrestrial bodies that harbor environments analogous to many of the terrestrial environments in which extremophiles flourish. The recent discovery of more than 105 extrasolar planets suggests that planetary systems are quite common. These three findings have led some to speculate that life is therefore common in the universe, as life as we know it can seemingly survive almost anywhere there is liquid water. It is suggested here that while environments capable of supporting life may be common, this does not in itself support the notion that life is common in the universe. Given that interplanetary transfer of life may be unlikely, the actual origin of life may require specific environmental and geological conditions that may be much less common than the mere existence of liquid water. **Key Words:** Extremophiles—Origin of life—Liquid water—Extraterrestrial life—Exobiology—Extreme environments. *Astrobiology* 4, 1–9.

**T**O BEGIN, IT MUST BE STATED that a demonstrated comprehensive theory for the origin of life is not presently available. Theories range from an origin of life in drying lagoons or sandy beaches (Miller and Orgel, 1974), on clay minerals (Bernal, 1951), near hydrothermal deep-sea vents (Corliss *et al.*, 1981), on sulfide minerals (Wächtershäuser, 1988), and as aerosols in clouds or vapor droplets (Woese, 1979; Oberbeck *et al.*, 1991; Dobson *et al.*, 2000). One thing these theories generally hold in common is that life began with organic matter that was either able to support its own metabolic propagation (Wächtershäuser, 1988; Morowitz *et al.*, 2000; Shapiro, 2000) or its own genetic replication (Belozerskii, 1959; Brachet, 1959; Buchanan, 1965;

Crick, 1968; Orgel, 1968), although there are other theories (Cairns-Smith, 1977).

Recently, the field of astrobiology has been invigorated by the discovery of at least 105 extrasolar planets (Lissauer, 2002; Schneider, 2003). Extrasolar planet detection is in its infancy, and it is likely that the inventory of new planets and our understanding of planet formation will be greatly expanded in the near future. It is becoming clear that planets are common in our galaxy, and this increases the likelihood that rocky planets in habitable zones where liquid surface water may exist are prevalent as well (Doyle, 1996). This increases the overall prospect for the abundance of life in the universe. Concurrently, exploration

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of extreme terrestrial environments has turned up a diverse assortment of microorganisms that not only live, but also thrive, at environmental extremes previously thought to be inhospitable to terrestrial life. These conditions include extremes of pH (pH 0.5 to pH >11), extremes of temperature ( $-20$  to  $113^{\circ}\text{C}$ ), extremes of pressure (1,000 atm, 100 MPa), high levels of ionizing radiation or UV light, low levels of nutrients, low water activity, and extremes of salinity (as high as 5.2 M) (Cavicchioli, 2002). These findings have extended the generally agreed-upon definition of a planetary habitable zone to include any place where liquid water, including water in subsurface reservoirs, can exist (Kasting *et al.*, 1993).

Exploration of our solar system has revealed a host of planetary environments in which it is now believed that life could survive. For example, Mars and Europa are now considered by some to be plausible environments for the existence of extremophiles (Davis and McKay, 1996; Chyba and Phillips, 2001).

Mars probably received a lower flux of large impactors and may have enjoyed more clement surface conditions early in its history. While life might have begun on Mars while the Earth was still subject to the late-heavy phase of meteoric bombardment, the likelihood that life forms sufficiently advanced to survive impacts that eject large amounts of debris, the high vacuum, UV flux and ionizing radiation of interplanetary space, and the heat and shock of arrival on the Earth is not high (Lindahl, 1993; Clark, 2001; Horneck *et al.*, 2002).

Even if meteors or dust particles containing viable microorganisms could be transferred between planets of our solar system or between stellar systems (Nicholson, 2003; Napier, 2004; Wallis and Wickramasinghe, 2004), there is still the problem that the majority of terrestrial microorganisms cannot be isolated and grown in pure culture. Rather, they require unknown growth factors or pheromones produced by other organisms (Kaeberlein *et al.*, 2002). Most microorganisms apparently live and grow in consortia of several species, and it seems unlikely that an intact community would survive transfer to a new planetary environment. Experimental data for extant terrestrial organisms show great differences in survival under outer space conditions (Clark, 2001; Horneck *et al.*, 2002; Nicholson, 2003), and one would assume that this would be true for early life forms as well.

Finally, although there are reports of spore-forming bacteria surviving in ancient salt deposits, ice, fossils, amber, etc., for times consistent with interplanetary transfer (Kennedy and Reader, 1992; Vreeland *et al.*, 2000; Nicholson, 2003), these concern complex organisms preadapted to harsh conditions and not primitive life forms. Moreover, some of the oldest reportedly viable organisms appear to be mesophiles, and hence unlikely to have survived the long periods at the predicted temperatures even as spores (Nicholson, 2003). It would appear that there was slow growth and low-level metabolism, which would permit DNA repair as lethal mutations would otherwise accumulate (Lindahl, 1993; Hofreiter *et al.*, 2001).

It is thus unlikely that terrestrial life originated on Mars and even less so that it originated on Europa. Conversely, the probability of the transfer of viable organisms from the early Earth to Mars or Europa has always been much lower and would have decreased greatly by the time advanced microorganisms that were capable of surviving transfer and growing in the extreme environments postulated on these bodies had evolved.

If the interplanetary transport of microorganisms is improbable, then all life must originate independently. This being the case, the conditions for the origin of life must have at one time been present on the body where life originates. We do not yet know what the necessary conditions are, but they are possibly much more restrictive than the existence of liquid water.

Life as we know it is based on carbon chemistry. If life began with organic compounds, then a prebiological source of these compounds would have been essential. There are three main theories for the source of these compounds. First is the synthesis from atmospheric gases by energy sources such as UV radiation, gamma rays, electric discharges, shock waves, and other forms of high-energy radiation (for a review, see Miller, 1987). Second is the delivery of organic compounds synthesized in space via mechanisms similar to the atmospheric syntheses, and delivered via cosmic dust, meteorites, and comets (Chyba and Sagan, 1992). Third is the mineral-catalyzed hydrothermal synthesis from Fischer-Tropsch-like mechanisms (Hayatsu *et al.*, 1972) near undersea hydrothermal vents (Corliss *et al.*, 1981; Wächtershäuser, 1988). An exhaustive comparison of the relative merits of these sources is

beyond the scope of this discussion. All three sources may contribute to a planet's or moon's organic inventory, depending on environmental conditions at the time of synthesis or delivery.

Assuming there is a sufficient supply of organic compounds and that the compounds synthesized by the three types of synthesis are all equally conducive to self-organization to form a living entity (which may not be true), the organic compounds must be concentrated sufficiently so that they may react to form more complex structures. There are several methods by which this may be accomplished.

First, the compounds may be synthesized so robustly that they saturate any body of water in which they are deposited. This seems unlikely. For example, calculations based on favorable atmospheric syntheses or extraterrestrial delivery on the primitive Earth reach low concentrations at steady state (Miller, 1987; Chyba and Sagan, 1992). Second, they may be adsorbed to minerals (Bernal, 1951). Third, they may be concentrated by evaporation (Miller and Orgel, 1974). Fourth, they may be concentrated by eutectic freezing (Sanchez *et al.*, 1966). Fifth, they may be concentrated by partitioning between organic and aqueous phases, which might occur in a primordial oil slick, as has been suggested by some authors (Lasaga and Holland, 1971; Nilson, 2002). Sixth, they could be concentrated at the air–water interface in spray from which excess water evaporates before being returned to oceanic or fresh water environments (Dobson *et al.*, 2000). Seventh is lyophilization as the water in organic-containing ice is sublimed.

A schematic representing the various possible combinations of sources of organic compounds and the methods by which they may have been concentrated, ultimately leading to the origin of life and its diversification thereafter, is shown in Fig. 1.

It is possible that all of these synthesis and concentration mechanisms contributed significantly to the origin of life. However, lacking detailed knowledge about the physical conditions on the primitive Earth and the early solar system, it is premature to conclude that the mere presence of liquid water is sufficient to guarantee the existence of life on extraterrestrial bodies.

Numerous geologically plausible syntheses of biologically relevant compounds have been investigated over the years (Miller, 1987). As has been pointed out, many such schemes disregard

the necessary geological continuum from synthesis to concentration to oligomerization and self-organization (Schwartz *et al.*, 1975; Shapiro, 1986). Extreme environments place severe constraints on both prebiotic chemistry and supramolecular organization. A brief summary of some of these is provided in Table 1.

It is also important to recognize the limitations of the various concentration mechanisms with regard to the source of the organic material and the geological conditions in which they are deposited. For example, in any wholly aqueous environment (i.e., Europa's subsurface ocean), concentration by evaporation is precluded. It is likewise difficult to imagine how extraterrestrial materials delivered to an ice-covered body such as Europa could be transported at sufficient rates through a kilometers-thick ice layer to the subsurface ocean and possibly adsorb to minerals on the seafloor. On completely frozen bodies, eutectic freezing seems unlikely, as subsequent thawing of the solution would be difficult. Even if organic compounds were synthesized by hydrothermal systems on such planets, condensation reactions and, thus, the origin of life would be improbable without a concentration mechanism.

Polypeptides have been synthesized from drying lagoon simulations (Fox and Harada, 1958; Bujdak and Rode, 1996) as well as in hydrothermal vent simulations (Imai *et al.*, 1999). While amino acids can be concentrated by evaporation and oligomerized under some of the conditions investigated (conditions that are not implausible for a planet with some dry land), it is unclear how these could have been attained in marine environments such as hydrothermal vents, where water activity is high and reactant concentrations would be low. The already low yields of such hydrothermal syntheses would be expected to drop off as the inverse square of the concentration of reactants. Synthesis of simple metabolites, such as acetate (Huber and Wächtershäuser, 1997), under hydrothermal vent conditions is likely to suffer from the same difficulties. The ability of compounds such as amino acids to be concentrated by mineral adsorption in such scenarios has not been demonstrated; however, it is likely that adsorption would be weaker at high temperatures. In regions where the temperature was low enough to permit binding, the barrier to reaction might not then be overcome. In addition, most bioorganic compounds are much less stable at

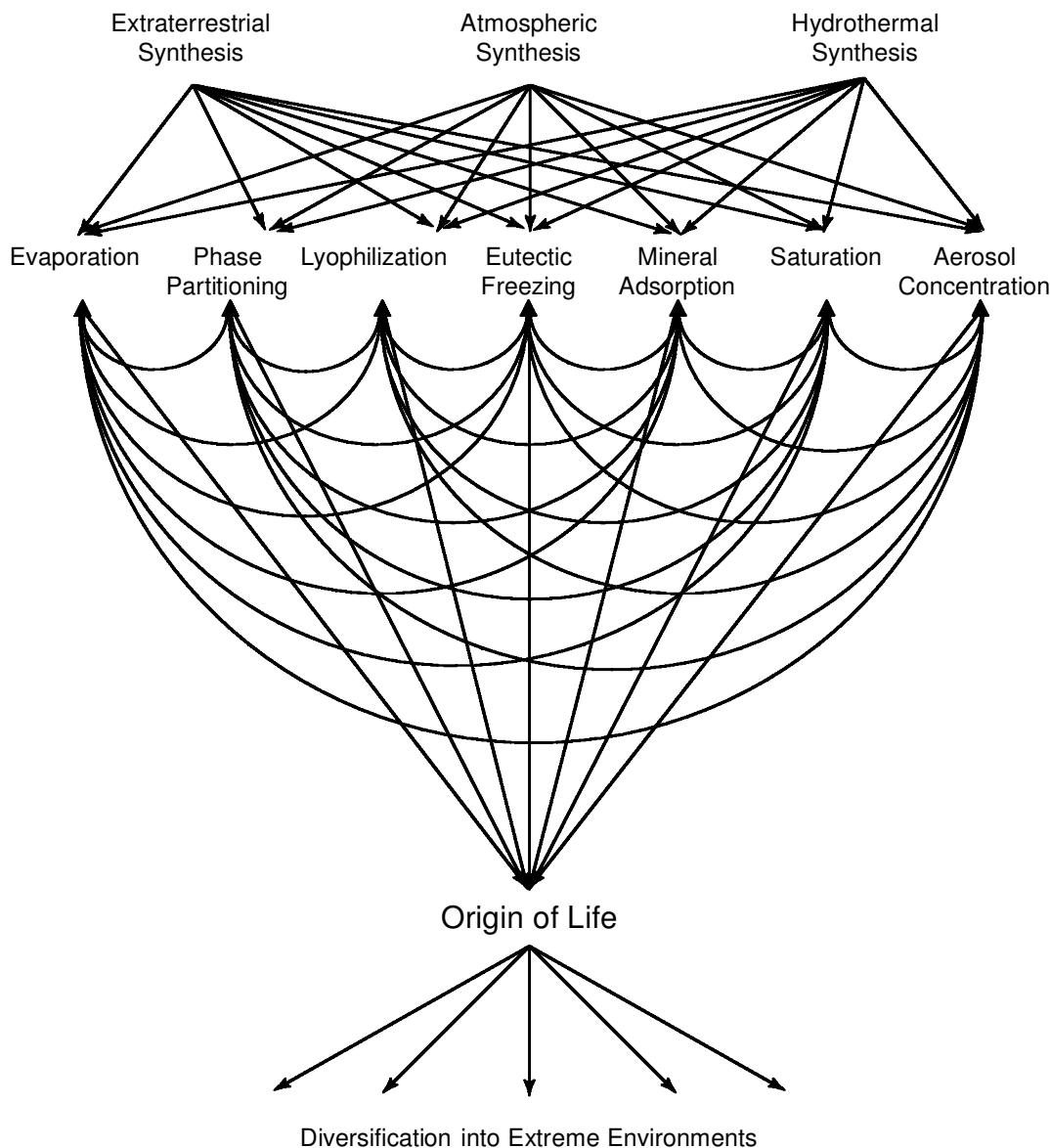


FIG. 1. Schematic diagram of the presumed sources of prebiotic compounds, the origin(s) of life, and its subsequent diversification into extreme environments.

high temperatures (Bada *et al.*, 1995). For example, the rate of adenine hydrolysis at pH 7 is some  $10^4$  times faster at  $100^\circ\text{C}$  than at  $25^\circ\text{C}$  (Levy and Miller, 1998), and the rate of deamination of aspartic acid between pH 5 and 8 is some  $2.6 \times 10^5$  times faster at  $100^\circ\text{C}$  than at  $25^\circ\text{C}$  (Bada and Miller, 1968). The weak interactions that govern many important biological processes, such as hydrogen bonding (Jeffrey and Saenger, 1994), are also likely to be disrupted by high temperatures.

Drying syntheses are problematic in that many precursor organic compounds are volatile and unable to be concentrated by this mechanism (for

example, HCN and HCHO). Some are also quite unstable, for example, ribose (Larralde *et al.*, 1995), and thus would be mostly degraded even during moderate temperature evaporation from low concentrations. It is possible that borate ions might have stabilized ribose and increased its concentration relative to other sugars (Prieur, 2001; Cimpoiasu and Scorei, 2002; Ricardo *et al.*, 2004). However, boron is a somewhat rare element and might not have been present in high concentration in the same microenvironments as the precursors to ribose.

Some of the polymerization processes that

TABLE 1. DELETERIOUS EFFECTS OF EXTREME ENVIRONMENTS

<i>Environments</i>	<i>Effects on prebiotic chemistry</i>	<i>Effects on protobiotic or supramolecular chemistry</i>
High pH (10–14)	Degrades ribose and other sugars, inhibits some prebiotic reaction, precipitates transition metal ions	Hydrolyzes RNA, proteins, phosphate esters, and other constituents, saponifies proton lipids, denatures proteins, prevents translocation and ATP synthesis
Low pH (<0.5)	Inhibits formose reaction, Strecker synthesis of amino acids, and HCN polymerization to adenine, guanine, and amino acids	Depurinates DNA, denatures and hydrolyzes proteins, saponifies lipids, hydrolyzes phosphate esters
High salt (5.2 M NaCl, other ions), may be highly alkaline as well	Disrupts proto-membrane formation, may precipitate or denature prebiotic polymers. Prevents concentration by eutectic freezing and inhibits evaporative concentration	Low water activity may denature proteins and prevent nutrient uptake. High ionic strength may precipitate or denature other biopolymers
High temperature (<100°C under hydrostatic pressure in deep ocean)	Degrades ribose and other sugars, hydrolyzes phosphate esters, peptides and nucleobases, racemizes amino acids	Disrupts membranes, denatures proteins and nucleic acids, depurinates DNA
Low temperature (–20°C or lower)	Reduces reaction rates, prevents evaporative concentration, may increase salt and ion concentrations and may change pH	Solidifies membrane lipids, lowers metabolic rates, may raise salt concentrations by eutectic freezing and increase osmotic stress
Ionizing radiation	Creates oxidants, which degrade purines, pyrimidines and other prebiotic compounds	Causes point mutations, deletions, and chain breaks in DNA and RNA. Degrades proteins and lipids. Creates toxic lipid peroxides
Ultraviolet radiation	Degrades aromatic amino acids, sugars, and nucleobases. May produce oxidants in regolith, which destroy organic compounds and generates reactive free radicals	Cross-links DNA and RNA at pyrimidine bases and hydrates pyrimidines. Degrades nucleic acids, proteins, and co-enzymes. Causes mutations in RNA and DNA genomics

have been investigated also require fairly low ambient humidity (Tohidi and Orgel, 1990), which may be unattainable even on bodies harboring dry land environments.

Salts hinder the ultimate concentration that may be obtained by eutectic freezing syntheses (Sanchez *et al.*, 1966; Stribling and Miller, 1991) and may thus limit the types of environments where these syntheses are possible. For example, a salty ocean may not be conducive to this type of synthesis.

Many origin of life theories require that the proto-organisms be sequestered from the environment by membranes. However, even moderate concentrations of salt inhibit the formation of micelles from lipid-like precursors (Monnard *et al.*, 2002). Thus, if micelle formation is crucial for the origin of life, then highly saline environments may be precluded as sites where life could arise. There may be, of course, other as yet undescribed compartmentalization mecha-

nisms that are not inhibited by hypersaline conditions. Such systems may warrant further investigation.

Problems also exist with high pH environments as sugars in particular are unstable in alkali [ $t_{1/2}$  for ribose decomposition is  $\sim 2$  days at 60°C and pH 9 (Larralde *et al.*, 1995)] and lipid membranes are disrupted. RNA is degraded quickly in alkaline solutions [ $t_{1/2}$  for inactivation of the single-stranded RNA virus R17 at 70°C and pH 10 is <1 day (Ginoza *et al.*, 1964)] and might not survive even in a lipid envelope.

Highly acidic environments would not allow for many of the fundamental prebiotic syntheses, including the formose reaction, the Strecker synthesis, or HCN polymerization. Low pH is also detrimental to most biopolymers, including DNA, which rapidly depurinates (Lindahl and Nyberg, 1972) [ $t_{1/2}$  for depurination of the single-stranded DNA virus  $\Phi$ X174 at pH 4 and 70°C is <1 day (Ginoza *et al.*, 1964)].

Terrestrial extremophiles have numerous special adaptations that allow them to survive in harsh environments. For example, the desiccation- and radiation-resistant bacterium *Deinococcus radiodurans*, in addition to having efficient repair enzymes, segregates copies of its DNA in tightly packed toroidal structures (Levin-Zaidman *et al.*, 2003). Some thermophilic bacteria have the more thermally stable  $N^4$ -methylcytosine, rather than 5-methylcytosine, in their DNA (Ehrlich *et al.*, 1985), and the tRNA of hyperthermophilic *Methanococcales* contains 2'-O-methylribose (McCloskey *et al.*, 2001). In general, the ribosomal RNAs of thermophilic and hyperthermophilic organisms have higher G-C contents than those of mesophiles (Galtier *et al.*, 1999).

Halophilic organisms may accumulate KCl, glycerol, glycine, betaine, mannitol, trehalose, and other highly soluble compounds to offset the high osmolarities of their environments. DNA reverse gyrase and histone-like proteins have been found in hyperthermophiles, which have subtle changes in amino acid sequence that seem to stabilize the proteins at high temperatures (reviewed in Zierenberg, 2000). Other adaptations are known, but somewhat surprisingly, DNA G-C content does not correlate with optimal growth temperature (Cavicchioli, 2002). The only organism whose DNA is known to contain 2,6-diaminopurine in place of adenine, which is capable of making three rather than two H-bonds to thymine, is a cyanophage isolated near Leningrad (Kirnos *et al.*, 1977).

Although it has been argued that the transition from the origin of life to fairly sophisticated microorganisms may have occurred rather quickly (Lazcano and Miller, 1994), it does not seem likely that the first organisms, whether on Earth, Mars, or Europa, were especially complex. Thus they would not have had these sophisticated adaptations.

Despite the diversity of life on Earth and the diversity of habitats in which it exists, molecular biological evidence supports the notion that all living things on Earth are descendants of a common ancestor, itself the result of a unique event. It is possible that there exist numerous solutions to the origin of life, and life may have originated several times on the primitive Earth, perhaps simultaneously. Such events undoubtedly would have taken place in discrete environments where conditions allowed for life's development,

though it is unknown what those conditions might have been (Arrhenius *et al.*, 1999).

Comparative studies of the rRNA genes of prokaryotes strongly suggest that their putative ancestor was not hyperthermophilic (Galtier *et al.*, 1999; Brochier and Philippe, 2002), and studies on the folding of model RNA sequences suggest that RNA world organisms were mesophilic (Moulton *et al.*, 2000). Di Giulio (2003) has argued that the last universal common ancestor was either a thermophile or a hyperthermophile. Gaucher *et al.* (2003) suggested that the primordial elongation factor EF-Tu had a temperature optimum of about 60°C, which is thermophilic rather than mesophilic or hyperthermophilic. This hypothesis is based on the reconstruction of a DNA consensus sequence that was inserted into an expression vector to generate a "resurrected" protein whose ability to bind GDP at various temperatures was measured. On the balance, the data suggest that the common ancestor of Archaea and Bacteria passed through a stage in which it was thermophilic rather than mesophilic or hyperthermophilic.

Unfortunately, genomic reconstruction of the ancestor may be obscured by subsequent extensive lateral gene transfer among descendants with specialized adaptations (Doolittle, 2000; Hartman and Fedorov, 2002; Raymond *et al.*, 2002; Woese, 2002). Regardless, these arguments apply to organisms that are quite sophisticated with respect to the origin of life (Arrhenius *et al.*, 1999).

The principal appeal of the idea that extremophiles are closer to the last common ancestor of all extant terrestrial life is based on molecular biological evidence, which suggests that the Archaea have evolved less rapidly than the Eucarya and the non-hyperthermophilic Eubacteria. However, this may simply reflect the stability of certain environments over geological time, the lack of competition for these niches, and functional constraints on the structure of cellular components that allow extremophiles to flourish under such unfavorable conditions.

The argument has been made that the development of life is an almost inevitable consequence of planetary geochemistry (De Duve, 1995) or even the thermal history of the universe (Lineweaver and Schwartzman, 2003). While this may be so, the converse may also be true: The origin of life may require extremely spe-

cialized conditions (Shapiro, 1986). The diversity of life in extreme environments should not be interpreted as evidence that all extreme environments are plausible candidates for the origin of life. Environments compatible with the origin of life may be extremely common (undersea or underground hydrothermal systems of any pH), or extremely rare (environments with some dry land, exposed to periodic drying, freezing, and thawing cycles at a narrowly defined pH value where a reducing atmosphere exists). Once a functioning biology capable of Darwinian evolution arises, its diversification to inhabit all potential environments is possible. If this is true, then some planetary bodies, despite possessing environments compatible with the existence of life, do not or never did harbor environments compatible with the origin of life, and thus are likely to be sterile.

Our present understanding of the origin of life does not allow inferences to be drawn regarding the likelihood of extraterrestrial life based on extrapolation of the lifestyles of terrestrial extremophiles.

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