Origin of first cells at terrestrial, anoxic geothermal fields

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Table P1. Comparison of geological settings potentially conducive to the early evolution of life

Setting	Shallow sea waters	Deep-sea hydrothermal vents (3)	Geothermal fields over vapor-dominated zones of inland geothermal systems (present study)
Stability/duration	$>10^9$ y	$\leq 10^5$ y	$\geq 10^6$ y
Steady thermodynamic driving force for continuous supply of organic precursors	+, Solar UV photochemistry	+, Serpentinization	++, Solar UV photochemistry, hydrothermal alteration
Continuous supply of phosphorous compounds	Unlikely	−/+, <0.5 μM in hydrothermal fluids	+, Up to 1 mM in geothermal fluids
Opportunity for reagent concentration	Modest (wet/dry cycles in tidal zones)	Modest (concentration at mineral surfaces)	High (concentration at mineral surfaces combined with wet/dry cycles, evaporation, freezing)
Selection force for abiotically formed, photostable (poly)nucleotides	Solar UV light	−	Solar UV light
Probability of spontaneous condensation reactions, polymerization and replication	Modest (only during wet/dry cycles in tidal zones)	Low	High (wet/dry cycles, evaporation, freezing, high amide levels)
Protection of first replicators from UV damage	Modest (low in tidal zones)	High (no UV light)	High (protection by UV-absorbing metal sulfides and silica minerals)
Continuous supply of ammonia	−/+	+	+
Continuous supply of reduced sulfurous compounds	−/+	+	+
Enrichment in transition metals, particularly Zn	−	+	+
Enrichment in boron compounds	−	−	+
K^+/Na^+ ratio > 1	−	−	+

Little is known about the conditions under which the first life forms and cells evolved. As life is most likely older than the oldest known rocks, the geological record offers few clues. The best window into the earliest stages of life evolution might therefore be the internal chemical composition of cells, which can be expected to reflect the composition of the primordial environment (1). Here, we attempted to reconstruct the "hatcheries" of the first cells by combining geochemical analysis with an examination of the universal, inorganic ion requirements of modern cells. Our results support a hypothesis in which life first evolved at anoxic geothermal fields.

All modern cells contain much more potassium, phosphate, and transition metals than modern or reconstructed primeval oceans, lakes, or rivers do. Cells maintain ion gradients by using sophisticated energy-dependent membrane pumps that are embedded in elaborate ion-tight membranes, which the first cells would have lacked. Therefore, the concentrations of small, inorganic molecules and ions within protocells and in their environment would equilibrate. Hence, the inorganic ion composition of modern cells is expected to reflect the ion composition of the habitats of protocells (1). The ubiquitous, and, by inference, primordial proteins and functional systems of modern cells (2) show affinity to and functional requirement for potas-

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sium, zinc, manganese, and phosphate. Thus, protocells must have evolved in habitats with a high K^+/Na^+ ratio and relatively high concentrations of transition metals and phosphorous compounds.

Geochemical reconstruction shows that the ionic composition found in the modern cells and apparently conducive to the origin of the first cellular life forms could not have existed in marine settings. In contrast, the inorganic ion composition of cells is compatible with emissions of vapor-dominated zones of modern inland geothermal systems. The geothermal vapor, which results from the boiling of ascending geothermal fluids, can carry metal ions to the earth's surface and is particularly enriched in potassium, carbon dioxide, ammonia, borate, as well as organic and phosphorous compounds. Geochemical considerations indicate that, in the absence of oxygen and at high carbon dioxide concentration, which were the salient features of the primordial atmosphere, the chemistry of basins at anoxic (i.e., lacking oxygen) geothermal fields would resemble the internal milieu of modern cells and could be the most suitable hatcheries for protocells. Under this scenario, the first cells are envisaged to have evolved in shallow ponds of condensed, cool geothermal vapor; these pools probably were lined with porous silicate minerals mixed with metal sulfides and enriched in potassium, zinc, and phosphorous compounds.

The major biochemical building blocks are derivatives of those molecules that preferably partition to the vapor phase upon geothermal separation, namely simple carbonaceous and phosphorous compounds, ammonia, and sulfide. Hence, anoxic geothermal fields could also provide crucial chemical conditions for the emergence of life. As summarized in Table P1, primordial, anoxic geothermal fields, as putative cradles of life, share all the advantages of the deep-sea hydrothermal vents that have been previously proposed to play the same role (3), including the presence of inorganic compartments, versatile catalysts, and sources of organic matter. However, in contrast to deep-sea vents, terrestrial geothermal fields are conducive to crucial condensation reactions and enable the involvement of solar light as an energy source and selective factor that would have favored the accumulation of nucleotides, important eventual components of RNA and, thereafter, DNA, because nucleotides are particularly photostable (4). Additionally, in contrast to the fluids of deep-sea vents, geothermal vapor is enriched in phosphorous and boron compounds that would be essential for the emergence of the first RNA-like polymers (5).

Clearly, this model for the origin of cells—and potentially life itself—is consonant, at least conceptually, with Charles Darwin's famous vision of a primordial "little warm pond" as the cradle of life. The hypothesis described here implies that cells invaded the oceans at a relatively late, advanced stage of evolution, after elaborate, modern-type membranes capable of efficiently maintaining ion gradients had evolved. Thus, life might have originated locally, being initially confined to a long-lasting inland geothermal field or to a network of such fields at a continental volcanic system and becoming a planetary phenomenon only after colonizing the oceans. Further experimental exploration of models mimicking terrestrial, anoxic geothermal fields might shed more light on precellular evolution.

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