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Hydrothermal conditions and the origin of cellular life

(Hypothesis article)

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Running title: Hydrothermal vents vs. hydrothermal fields

Abstract

The conditions and properties of hydrothermal vents and hydrothermal fields are compared in terms of their ability to support processes related to the origin of life. The two sites can be considered as alternative hypotheses, and from this comparison we propose a series of experimental tests to distinguish between them, focusing on those that involve concentration of solutes, self-assembly of membranous compartments and synthesis of polymers.

Key words: hydrothermal systems

Introduction

In an often cited article in *Science* with the title *Strong Inference*, John Platt proposed that formulating alternative hypotheses was a preferred approach to testing new ideas (Platt, 1964). Here we will use this approach to consider two geophysical conditions that have been proposed as alternative sites conducive for the origin of life. The first condition is that of hydrothermal vents (Corliss *et al.*, 1981; Baross and Hoffman, 1985; Kelley *et al.*, 2001) that are characterized by a single interface between solid mineral surfaces and the aqueous phase of seawater. The second condition is associated with volcanoes emerging above sea level. Precipitation on volcanic landmasses produces fresh water hydrothermal fields characterized by geysers, hot springs and clay-lined fresh water pools. These more complex environments have three interfaces that undergo cyclic fluctuations: atmosphere/water, atmosphere/mineral and mineral/water. In the following discussion we will compare the two different hydrothermal systems in terms of their ability to permit the self-assembly and polymerization processes that were likely to be the initial stages on the pathway to cellular life. We will then propose experimental tests that may provide a weight of evidence favoring one of the two sites.

Self-assembly, concentration, and synthetic chemistry in hydrothermal conditions

For the purposes of this discussion, we will assume that the origin of life required systems of interacting molecules to be confined in some sort of compartment. Mineral compartments have been proposed to serve in this regard (Russell and Hall, 1997), but for cellular life to begin, a molecular system must be encapsulated by a fluid phase membranous compartment composed of amphiphilic compounds. The properties of the amphiphiles must be such that the membranes they form are both stable and fluid under the conditions of the environment ([Georgiou and Deamer, 2014](#)). These properties are related to chain length, unsaturation, branching and the hydrophilic groups of the amphiphiles. For instance, a fatty acid with a chain length of 10 carbons can form stable membranes at ordinary temperatures but would not be stable at the near boiling temperatures of hydrothermal sites. Common head groups of single chain amphiphiles include carboxylate, hydroxyl, phosphate and sulfate moieties, all of which can participate in membrane assembly (Hargreaves and Deamer, 1978).

The question we are addressing here concerns how amphiphiles and other organic compounds behave in hydrothermal conditions. In this regard, it is worth noting the misconception that all membranes are intrinsically fragile. It is true that

certain conditions can degrade the structural integrity of any given membrane system, but those same conditions can be ideal for another system. For instance, Mansy and Szostak (2008) demonstrated stable vesicles of oleic acid at near boiling temperatures, and we have investigated a variety of membrane-forming amphiphiles that can produce remarkably robust vesicles at high and low pH ranges, some even resistant to divalent cations (Namani and Deamer 2008; Monnard and Deamer 2002).

Although hydrothermal vents ("black smokers") were first to attract attention as potential sites for the origin of life (Baross and Hoffman, 1985; Russell *et al.*, 1993; Russell and Hall, 1997) so far this proposal remains largely speculative because of the difficulty in simulating the high pressures and temperatures in the laboratory (Imai *et al.*, 1999) or testing the idea *in situ*. The alternative alkaline hydrothermal vent sites (Lane and Martin, 2012), have recently been simulated in the laboratory (Herschy *et al.*, 2014). These occur at relatively low temperature ranges, are stable for thousands of years, and produce porous mineral structures composed of mineral membranes through which warm seawater comes into contact with cold seawater. The alkaline fluids are saturated with calcium carbonate that precipitates as porous mineral structures upon cooling.

In order for biologically relevant products to accumulate in a hydrothermal vent environment, there must be a process by which dilute organic compounds in seawater become sufficiently concentrated to undergo chemical reactions. Theoretical studies (Baaske *et al.*, 2007) predicted that small organic molecules such as nucleotides and nucleic acids originating from very dilute external reservoirs could be concentrated by the strong thermal gradients developed within the thin channels produced by mineral precipitates of hydrothermal vents. A laboratory simulation found that subcritical concentrations of fatty acids can be concentrated (>1000-fold enrichment) and self-assemble into vesicles at the bottom of capillary channels, with a parallel concentration of DNA oligonucleotides that were encapsulated within the vesicles (Budin *et al.*, 2009; Budin and Szostak, 2010). These results confirm the concentrating effects of thermal gradients in porous mineral structures.

The potential for alkaline hydrothermal vents to support the chemical reduction of carbon dioxide was simulated in a reaction vessel in which an alkaline solution of K_2HPO_4 , $Na_2Si_3O_7$ and Na_2S (pH 11) were slowly mixed with a larger volume of an acidic solution (pH 5) of $FeCl_2$, $NaHCO_3$ and $NiCl_2$ (Herschy *et al.*, 2014). Microscopic precipitates of ferrous silicates and phosphates formed, and these appeared to be hollow tubes when examined by scanning electron microscopy. Because carbon dioxide is in equilibrium with bicarbonate at pH 5, and Fe^{2+} was present as a reducing agent, the authors expected that some fraction of the carbon dioxide might be reduced under these

conditions. After several hours small amounts of formic acid were detected (50 μM), and in some of the runs traces of formaldehyde (~ 100 nM).

The authors also tested whether thermal gradients in a porous alumina ceramic could concentrate otherwise dilute solutes. A warm hydrothermal fluid with dilute fluorescein dye was slowly pumped into a ceramic foam in a reactor vessel that was cooled to produce a thermal gradient of 50°C from the interior of the foam to the exterior. After several hours, UV illumination showed that the fluorescein had become visibly concentrated by as much as 5000-fold in cooler regions of the foam. No concentrating effect was observed in the absence of a thermal gradient.

Although thermal gradient concentration works under laboratory conditions with relatively dilute aqueous solutions, marine environments are characterized by high salt concentration (0.5 M NaCl in today's ocean water) that may not support concentration of solutes by thermal gradients. Furthermore, divalent cations (10 mM Ca^{2+} and 54 mM Mg^{2+}) are present in seawater, and at even higher concentrations in alkaline hydrothermal vents composed of calcium carbonate. High salt concentrations and divalent cations tend to inhibit membrane assembly from amphiphilic compounds like monocarboxylic acids (Monnard and Deamer, 2002). Therefore, the effect of sea water on concentration and self-assembly of amphiphilic compounds should be investigated as an experimental test of the alkaline vent hypothesis.

Hydrothermal fields

Localized areas characterized by hot springs, boiling pools, geysers and fumaroles are commonly associated with volcanic activity. One well-known example is Yellowstone National Park, and similar less extensive sites can be found in Iceland, Kamchatka and active volcanoes in the Pacific coastal ranges of north and south America. We will refer to such sites as hydrothermal fields (Mulkidjanian *et al.*, 2012).

In contrast to hydrothermal vents, hydrothermal fields have three interfaces: atmosphere/water, atmosphere/mineral and mineral/water. Because the interfaces are constantly fluctuating due to evaporation and precipitation, cycles of dehydration and rehydration occur that are not possible in hydrothermal vents. Furthermore, the aqueous phases are relatively low in ionic solutes, typically in the range of a few millimolar in concentration.

The wet-dry cycles lead to physical effects that are conducive to processes of self-assembly. For instance, the cycling is a continuous process with periodicity measured in minutes to weeks as water levels fluctuate due to evaporation and refilling around edges of small pools. This means that reactions do not occur just once and then approach equilibrium, but instead reaction products accumulate and

can undergo increasingly complex interactions (Damer and Deamer, 2015).

A second effect is that any organic compounds that are present as solutes become highly concentrated films on mineral surfaces during the dry phase of a cycle. Furthermore, under these conditions amphiphilic compounds present as micelles or vesicles assemble into multilamellar structures on the surface, and any solutes that are present are concentrated and organized between lamellae (Toppozini *et al.*, 2013). A subsequent rehydration cycle produces large lipid vesicles that have encapsulated a significant fraction of the solutes (Shew and Deamer, 1985). This observation gave rise to the hypothesis that chemical reactions could be promoted in concentrated films. That is, when the dehydrated amphiphiles self-assemble into multilamellar layers that trap concentrated monomers between the bilayers, condensation reactions have the potential to link the monomers into polymers (Deamer, 2012). The elevated temperature of the hydrothermal site would provide essential activation energy for the reaction.

Laboratory simulations have tested whether polymerization of monomers can occur in the fluctuating hydrothermal conditions. Small volumes of reaction mixtures containing millimolar concentrations of 5'-mononucleotides were exposed to multiple cycles of hydration and dehydration at elevated temperatures to simulate the wetting, evaporation and drying processes that are characteristic of small pools in hydrothermal fields. **Rajamani** *et al.*, 2008, and DeGuzman *et al.*, 2014, used phospholipids as organizing agents to promote polymerization under these conditions, while Da Silva *et al.*, 2015, reported that monovalent salts such as KCl, NaCl and NH₄Cl were also efficient promoters of polymerization. During dehydration, the monomers become increasingly concentrated and at some point water activity is sufficiently low so that condensation reactions form ester bonds between the phosphate and hydroxyl groups attached to the ribose moiety of the nucleotides. Typical yields of RNA-like polymers were a few percent of the monomers in a single cycle, with further increments as the number of cycles increased. Yields as high as 50% were achieved after multiple cycles in the presence of monovalent salts (Da Silva *et al.*, 2015). Nanopore analysis of the products revealed that linear polyanions were present, as expected if RNA-like products had been synthesized. Furthermore, the products were stained by ethidium bromide in a non-denaturing agarose gel. This dye becomes highly fluorescent when it intercalates into stacked bases, suggesting that the products had partially folded into duplex hairpin structures by hydrogen bonding between base pairs. The products also exhibited temperature-dependent hyperchromicity, which occurs when duplex strands melt into single-stranded polymers that have stronger absorbance at 260 nm. The authors concluded that polymerization reactions relevant to the origin of nucleic acids can be driven by conditions simulating those in hydrothermal fields.

In a recent report, Forsythe *et al.* (2015) demonstrated that wet-dry cycles

at elevated temperatures can also promote the polymerization of amino acids and alpha-hydroxy acids into oligopeptides. In this case, the enhancement was primarily due to the concentrating effect of evaporation, and the synthesis of peptide bonds was presumably spontaneous rather than driven by reduced water activity.

Intracellular ions and early photosynthesis

Another argument featuring hydrothermal fields was presented by Mulkidjanian *et al.*, 2012. This comes from the proposal that the ionic composition of modern cells might reflect the inorganic ion composition of the original habitats of protocells. By combining geochemical data with phylogenetic analysis of the inorganic ion requirements of life today, it was suggested that protocells evolved in habitats with a high K^+/Na^+ ratio and relatively high concentrations of Zn, Mn, and phosphate. Geochemical reconstructions in the absence of oxygen and in a CO_2 -rich atmosphere suggest that an ionic composition favoring the origin of cells could not have existed in marine settings. Instead, this is compatible with inland geothermal systems with ionic compositions resembling the internal environment of modern cells. In this scenario, pre-cellular stages of life developed in shallow ponds lined with porous silicate minerals and enriched in K^+ , Zn^{2+} , and phosphate.

A final contrast between hydrothermal vents and hydrothermal fields is that light is an abundant energy source used by cyanobacteria and other prokaryotes capable of photosynthesis. It has been suggested that early life quickly evolved mechanisms to capture and transduce light-driven chemiosmotic energy for reactions (Deamer, 1997; Deamer and Weber, 2010). In principle, such processes would involve light-absorbing pigments either encapsulated as solutes or partitioned into boundary lipid membranes. For instance, encapsulated TiO_2 particles have been shown to reduce the redox indicator MV^{+2} or NAD^+ (to $NADH$) upon irradiation (Summers *et al.*, 2009; Summers *et al.*, 2010). Moreover, aqueous suspensions of the mineral sphalerite (ZnS) can photo-reduce CO_2 to formate when illuminated with near-UV light (Zhou and Guzman, 2014), providing a mechanism of prebiotic carbon fixation. Certain photochemical reactions incorporating polycyclic aromatic hydrocarbons also release or take up protons, producing a proton gradient across the membrane that captures a portion of the original light energy (Deamer, 1992). At some point in early evolution such gradients could be coupled to biochemical processes to initiate a primitive version of chemiosmosis (Koch, 1985; Lane and Martin, 2012). How this came about remains a major gap in our understanding of early life, but it is relevant to this review that a hydrothermal field would be bathed in abundant light energy, while life in deep alkaline vents would necessarily be entirely chemotrophic with no

potential to develop photosynthetic pigment systems.

Testing alternative hypotheses

Hydrothermal fields and alkaline hydrothermal vents are attractive ideas for sites that would be conducive to the origin of life. The following predictions can guide experimental tests that will allow a choice between the two sites in terms of plausibility.

1. Dilute solutes will become sufficiently concentrated to undergo chemical reactions. To test this prediction, monomers such as amino acids or nucleotides can be exposed to laboratory simulations of hydrothermal fields and vents, with the expectation that one of the two simulations will be more conducive to concentrating effects.

2. Self-assembly of amphiphiles into membranous compartments will occur over a range of temperatures, salt concentrations and pH ranges related to each site. Again in laboratory simulations, the assembly of amphiphilic compounds into membranous vesicles is likely to be favored by one of the two conditions

3. Chemicals available in the environment will drive reactions such as carbon fixation or polymerization. If the first prediction above passes experimental tests, activated monomers can be added to the simulation to test whether polymerization is promoted.

4. Products of reactions will accumulate within the site rather than dispersing into the local environment. This prediction can be tested in the field by injecting a simulated mixture of reaction products into the mineral matrix of an alkaline hydrothermal vent, or by adding such a mixture to a small pool within a volcanic hydrothermal field.

5. Biologically relevant polymers will be synthesized with chain lengths sufficient to act as catalysts or carry genetic information. If the first and third predictions are confirmed experimentally, it would not be sufficient just to synthesize short oligomers such as dimers, trimers or tetramers. The results will only be significant if the chains have 50 – 100 nucleotides, a length at which they become capable of folding into a catalytic configuration.

Table 1 summarizes the points that we consider to be pertinent to both alternatives, based on what is currently known from previous publications related to this topic. We note that none of the predictions listed above has ever been tested *in situ* in freshwater hydrothermal fields or alkaline hydrothermal vents in seawater. Rather than confining experiments to laboratory simulations, we recommend that such studies should be undertaken in the field because the results will provide additional evidence for comparing the relative plausibility of the two alternative sites for the origin of life.

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Table 1. Merits and limitations of alkaline hydrothermal vents and hydrothermal fields	
Submarine hydrothermal vents	Volcanic hydrothermal fields
Favorable properties	
A source of chemical energy is available from solutes and minerals at different redox states and pH ranges (Wächtershäuser, 1992; Zierenberg <i>et al.</i> , 2000).	A source of chemical potential is available from reduced water activity during dehydration.
Alkaline vents last up to ~30,000 years, providing a constant supply of chemical energy at life-compatible temperature ranges (50-90°C).	Self-assembly of amphiphilic compounds readily occurs in low ionic strength aqueous phases (Monnard and Deamer, 2002).
Vent minerals are a source of transition metals with potential catalytic activity when incorporated into peptides (Zierenberg <i>et al.</i> , 2000).	Concentration of dilute solutes on mineral surfaces occurs naturally upon drying (Robertson and Miller, 1995).
Dissolved carbon dioxide can be reduced to formic acid (Herschey <i>et al.</i> , 2014).	Condensation reactions and polymerization have been demonstrated in laboratory simulations (Da Silva <i>et al.</i> , 2015; DeGuzman <i>et al.</i> , 2014; Rajamani <i>et al.</i> , 2008).
A mechanism for concentrating dilute solutes has been demonstrated in laboratory simulations of alkaline vents (Budin <i>et al.</i> , 2009; Herschey <i>et al.</i> , 2014).	Cycles of hydration and dehydration drive increased complexity as products accumulate in closed systems of hydrothermal pools (Damer and Deamer, 2015).
	Light energy is abundant, so photosynthesis can develop.
Limitations	
Self-assembly of amphiphiles into membranes is inhibited by high salt concentration and divalent cations present in alkaline vents (Monnard and Deamer, 2002).	Low pH ranges may inhibit polymer accumulation by hydrolyzing ester bonds and peptide bonds.
Polymerization by condensation reactions in an aqueous medium like seawater requires activated substrates. Activation of solutes has not been demonstrated experimentally in hydrothermal vent conditions.	Undesirable cross linking reactions may produce insoluble by-products (Benner <i>et al.</i> , 2012).
Hydration-dehydration cycles do not occur in hydrothermal vent conditions	Extensive clay deposits adsorb organic solutes and reduce their availability as reactants

	(Deamer <i>et al.</i> , 2006).
Photosynthesis could not develop in vent conditions.	Exposure to the ultraviolet component of sunlight can damage some molecules.