

High-temperature life without photosynthesis as a model for Mars

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Abstract. Discoveries in biology and developments in geochemistry over the past two decades have lead to a radical revision of concepts relating to the upper temperature at which life thrives, the genetic relationships among all life on Earth, links between organic and inorganic compounds in geologic processes, and the geochemical supply of metabolic energy. It is now apparent that given a source of geochemical energy, in the form of a mixture of compounds that is far from thermodynamic equilibrium, microorganisms can take advantage of the energy and thrive without the need for photosynthesis as a means of primary productivity. This means that life can exist in the subsurface of a planet such as Mars without necessarily exhibiting a surface expression. Theoretical calculations quantify the geochemically provided metabolic energy available to hyperthermophilic organisms in submarine hydrothermal systems on the Earth, and help to explain the enormous biological productivity of these systems. Efforts to place these models in the context of the early Earth reveal that substantial geochemical energy would have been available and that organic synthesis would have been thermodynamically favored as hydrothermal fluids mix with seawater.

Life on Mars Two Decades After Viking

More than two decades ago, during the planning and execution of the Viking missions to Mars, the photosynthetic paradigm for microbial primary productivity was so well established that the search for evidence of life on Mars focused on surface soils. Since the 1970s, and largely in the past decade and a half, the discovery of microbial life at high temperatures, especially in the darkness of submarine hydrothermal systems, together with the evolutionary position of these organisms, provides a completely new paradigm for imagining how life could have emerged and evolved on Mars. In fact, knowing what we do about life on Earth, it is more appropriate to think of life in Mars rather than on the inhospitable surface of the planet. Two advances in biology combined with new developments in geochemical modeling open the possibility that geologic processes provide geochemical sources of energy that can drive early microbial metabolism in the absence of photosynthesis.

One of the advances in biology is the discovery since 1980 of microorganisms called hyperthermophiles, which thrive at, and demand, temperatures above 80°C (see Figure 1). Many hyperthermophiles have been isolated from hot springs on continents, and from submarine hydrothermal systems [Barns *et al.*, 1994; Adams and Kelly, 1995; Stetter, 1995; Karl, 1995]. Both heterotrophs and autotrophs are represented among the hyperthermophiles [Baross and Deming, 1995], and some of the autotrophs gain their energy from inorganic reactions such as sulfate reduction, sulfur reduction, and methanogenesis (CO₂ reduction to methane). The majority of these organisms are in an evolutionarily distinct group called Archaea, and the recognition of the Archaea and their place in the phylogenetic tree of life is the second advance in biology. A universal phylogenetic tree, modified from Woese [1987], is shown in Figure 2, where it can be seen that there are three major domains of

life: Bacteria, Archaea, and Eucarya. The lengths of the line segments between branch points correspond to the magnitude of evolutionary differences established by the comparison of genetic material [Woese, 1987; Woese *et al.*, 1990]. The thicker segments connect the hyperthermophilic organisms, and it can be seen that they populate the base of the phylogenetic tree. Some researchers draw from this that the first organism may have also been a hyperthermophile [Pace, 1991; Daniel, 1992; Seeger *et al.*, 1993]. The geochemical energy provided when submarine hydrothermal fluids mix with seawater has been recently quantified [McCollom and Shock, 1997], and other geochemical modeling has shown that organic synthesis from CO₂ is thermodynamically favorable within submarine hydrothermal systems [Shock, 1990a, 1992a] and in zones of fluid mixing [Shock and Schulte, 1997].

One purpose of this paper to illustrate how geologic processes provide geochemical energy that is tapped by present-day hyperthermophiles. Specifically, mixing of hydrothermal fluids with seawater provides a source of geochemical energy that is independent of photosynthesis at the surface. A second purpose is to summarize the arguments for potential organic synthesis in hydrothermal environments. It turns out that the conditions that allow hyperthermophiles to thrive also favor organic synthesis. The overall goal is to provide the evidence that there are many possible ways that hydrothermal processes could have provided the energy to sustain life and/or allow life to emerge at some point in the history of Mars. If life got started in this way, it need not ever have been at the surface. This raises that possibility that the Viking experiments looked in the least likely place for life. But first, what is the evidence that hydrothermal systems existed on Mars?

Evidence for Hydrothermal Systems on Mars

Ample photographic evidence supports the notion that there has been extensive volcanic activity on Mars [Wilson and Head, 1994], and there is abundant evidence indicating that water has been present on and below the surface of Mars [Carr, 1996].

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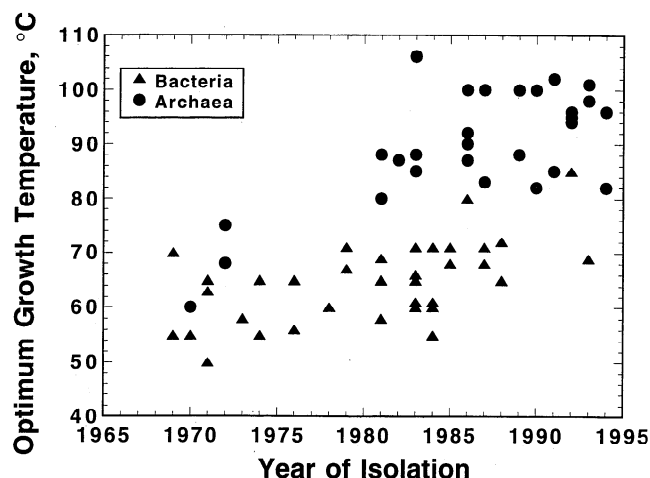


Figure 1. Plot of the optimum growth temperatures at laboratory conditions for newly discovered microorganisms against the year of discovery. Note the enormous increase in the number of organisms found that grow at temperatures above 80°C (hyperthermophiles) since 1980. A vast majority of the hyperthermophiles are classified among the Archaea, but a few Bacteria are represented [after Adams and Kelly, 1995].

Volcanic rocks shrink and crack when they cool, providing pathways for water to infiltrate to regions of elevated temperatures. Heating water causes it to decrease in density, become buoyant, and move upward and away from the source of heat, thus establishing a circulating hydrothermal system that acts like coolant in a refrigerator to remove heat from the volcanic rocks and efficiently transport it to space. The combination of volcanoes and liquid water on any planet leads inevitably to hydrothermal systems [Shock and McKinnon, 1993; Griffith and Shock, 1995, 1997].

On Earth, these systems can have surface expressions, like hot springs and geysers on the continents and black smoker vents at the mid-ocean ridges, or they can remain completely

internal to the crust like many of the huge circulation systems responsible for cooling granitic intrusions and generating ore deposits [Norton, 1984; Criss and Taylor, 1986]. In either event, reactions between hydrothermal fluids and the rocks that host them alter the rocks and change the composition of the fluid. Cooling of a hydrothermal solution or mixing it with another cooler fluid tends to generate a chemical system that is out of thermodynamic equilibrium. Dramatic consequences of this disequilibrium, and the enormous drive it provides toward an equilibrium state, are witnessed in massive hydrothermal ore deposits and in the black, iron sulfide “smoke” precipitating at submarine hydrothermal systems. The abundant life surrounding submarine hydrothermal vents is another manifestation of this geologically supplied geochemical energy.

On Mars there is evidence showing outflow channels which may be the surface expression of hydrothermal systems [Brakenridge *et al.*, 1985]. There is also geochemical and isotopic evidence in the purported Martian meteorites that can be explained by hydrothermal alteration [Watson *et al.*, 1994; Romanek *et al.*, 1994; McSween, 1994; Treiman, 1995]. Results of geochemical model calculations [Griffith and Shock, 1995, 1997] show that Martian hydrothermal systems have the potential to store water as hydrous minerals and sequester CO₂ in the crust as carbonate minerals. These models also illustrate the effects of rock composition, temperature, oxidation state, and ratio of water to rock in dictating the assemblage of minerals that can form. At present, the general lack of knowledge about the distribution of hydrothermal systems on Mars, as well as the composition of the host rocks or the initial fluids, renders moot the type of detailed modeling done for terrestrial hydrothermal systems. Nevertheless, many general features are found to be similar between Martian and terrestrial hydrothermal systems [Griffith and Shock, 1995, 1997], and it seems likely that Martian systems would be capable of generating the same types of geochemical disequilibrium as terrestrial systems. It follows that Martian hydrothermal systems may have been able to support life but that life may have existed below the surface.

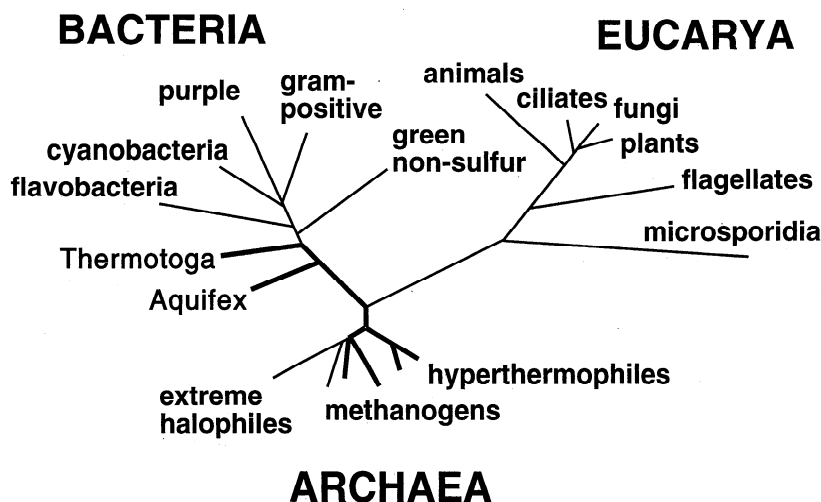


Figure 2. A universal phylogenetic tree based on genetic data (sequencing of 16S ribosomal RNA). The lengths of the line segments correspond to evolutionary distance among the organisms. Bold segments connect the hyperthermophiles among the Archaea and Bacteria. The inference is that a common ancestor of all three lineages is also a hyperthermophile. More recent efforts [Woese *et al.*, 1990] place a root to the tree between the Bacteria and the Archaea, indicating the closer genetic relationship of Eucarya to Archaea than to the Bacteria [after Woese, 1987].

It is also possible that life could have emerged in Martian hydrothermal systems following paths that many investigators propose for the hydrothermal emergence of life on Earth [Baross and Hoffman, 1985; Russell et al., 1988, 1989, 1993, 1994; Shock, 1990a, 1992a; Shock et al., 1995; Russell and Hall, 1997].

Geochemical Constraints on Life in Hydrothermal Systems

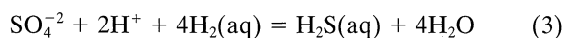
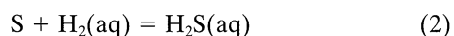
The enormous biological productivity of present-day submarine vent environments occurs because life can lower the Gibbs free energy of the chemical system that results when hydrothermal fluids mix with seawater. Primary productivity in the vent environment acts as a catalyst, which enables adventitious use of thermodynamically favored reactions that are allowed, but kinetically inhibited, by geochemical processes. In this sense, productivity surrounding vents differs from that of photosynthetic systems at the surface, where special mechanisms are needed to fix carbon into organic compounds by capturing solar energy and performing work against the chemical system in the oxidized atmosphere. Nowhere else on Earth is the connection between geochemical and biological processes as profoundly evident as in hydrothermal systems.

In an effort to quantify the energy available to microorganisms in submarine hydrothermal systems, and to begin to explain the enormous biological productivity of submarine hydrothermal vent environments, McCollom and Shock [1997] evaluated the geochemical energy provided by disequilibrium between seawater and submarine hydrothermal fluids. Some of those results are summarized here. It is important to emphasize that the mixing of seawater and hydrothermal fluids provides the geochemical energy that is tapped by hyperthermophiles and other microorganisms in hydrothermal systems. The relative abundance of cold seawater and hot hydrothermal fluid in the mixed fluid controls the temperature and composition of the mixture.

A major conclusion of this work is that H_2S oxidation via the reaction



can provide energy only at temperatures less than about 40°C and that above this temperature sulfur and sulfate reduction, and methanogenesis, are the energy-yielding reactions. The appropriate reactions are given by



On early Earth, or on Mars, the O_2 concentration would be severely limiting and probably preclude the availability of any energy from reaction (1). Nevertheless, the reductive reactions (2)–(4) are all possible energy suppliers for the first hyperthermophilic organisms. In the following discussion, methanogenesis from CO_2 (reaction (4)) will be used to illustrate the geochemical supply of metabolic energy.

The mixing calculations start with fluid compositions corresponding to seawater and an end-member hydrothermal vent fluid from the East Pacific Rise (21°N [Von Damm et al., 1985; Von Damm, 1990].) It was assumed that conductive cooling is minimal. As a result, the temperature of the mixture is fully

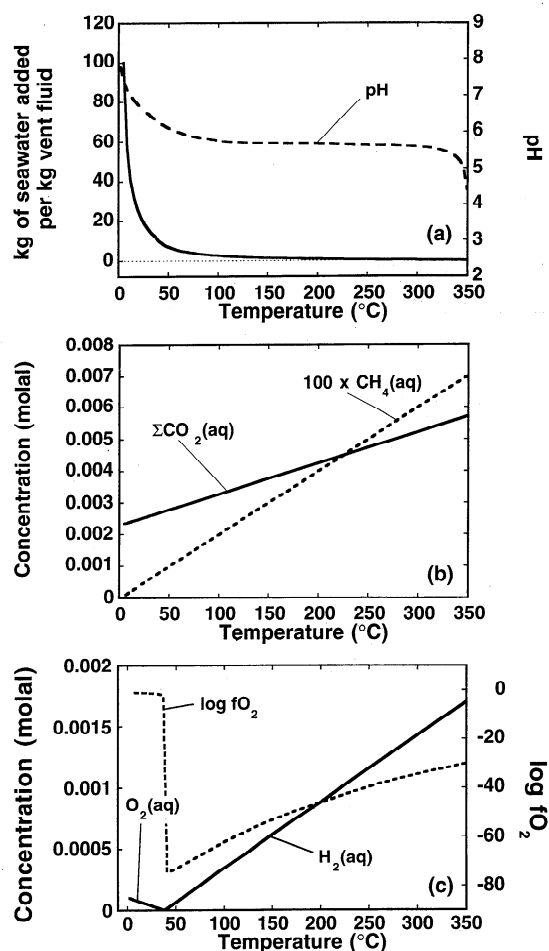


Figure 3. Results of calculations to determine the consequences of mixing between hydrothermal fluid and seawater on the potential for methanogenesis and methanotrophy [McCollom and Shock, 1997]. Mixing ratios and pH are shown in Figure 3a, and concentrations of aqueous methane, total aqueous carbonate, aqueous oxygen, and aqueous hydrogen are depicted in Figures 3b and 3c. Note that the concentration shown for aqueous methane has been multiplied by a factor of 100. It is important to emphasize that the mixed fluid has a different composition at each temperature.

determined by the mass of each of the two fluids in the mixture. Temperatures resulting from mixing progressive kilograms of 2°C seawater into 1 kg of 350°C vent fluid are shown in Figure 3a, together with the calculated pH of the mixture. It should be emphasized that the mixed fluid has a different composition at each temperature. The calculated concentrations of aqueous methane and carbonate species ($CO_2(aq) + HCO_3^- + CO_3^{2-}$, designated $\Sigma CO_2(aq)$) are shown in Figure 3b. These values are calculated with the assumption that the oxidation/reduction reactions between CO_2 and CH_4 (like reaction (4)) are kinetically inhibited, which is a necessary prerequisite if the reaction can provide metabolic energy. Calculated values of the concentrations of aqueous O_2 and H_2 are plotted in Figure 3c, together with calculated values of the log of the fugacity of O_2 (fO_2), one variable which can be used to express to oxidation state of the system.

Although efficiencies are never perfect, the metabolic energy that is potentially available from a chemical reaction is

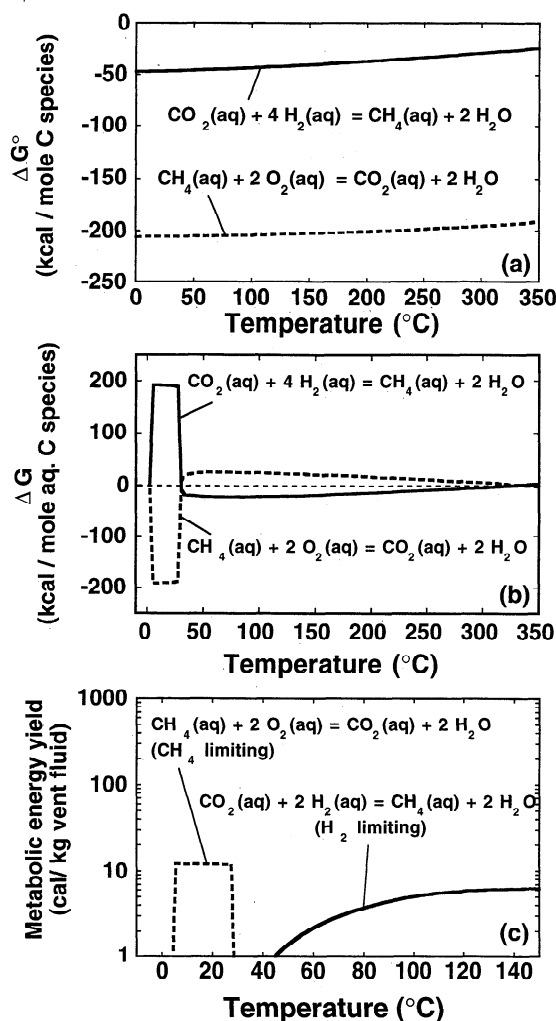


Figure 4. Thermodynamic calculations related to the microbial processes of methanogenesis (reaction (4)) and methanotrophy (reaction (6)) in hydrothermal vent environments [McCorm and Shock, 1997]. Figure 4a shows the standard Gibbs free energies of the reactions as functions of temperature. Figure 4b depicts the total Gibbs free energies of the reactions evaluated with (5) by taking account of the compositional constraints illustrated in Figure 3. Note that energy from methanotrophy is only available at temperatures $< \sim 45^\circ\text{C}$, but that energy from methanogenesis is available at temperatures above 45°C and as high as about 325°C . Figure 4c illustrates the potential metabolic energy yield, which is limited by the chemical species at the lowest concentration in the mixture.

equivalent to the total Gibbs free energy of the reaction (ΔG_r), which can be calculated using the relation

$$\Delta G_r = \Delta G_r^\circ + RT \ln Q_r \quad (5)$$

where ΔG_r° represents the standard state Gibbs free energy of the reaction, T indicates the temperature in Kelvin, R designates the gas constant, and Q_r stands for the product of the activities of all of the chemical species involved in the reaction. It has to be emphasized that it is the total Gibbs free energy (ΔG_r) and not the standard state contribution (ΔG_r°) that reflects the amount of energy available to an organism from a chemical reaction. Although this is overlooked in many analyses of microbial energetics that use only the standard Gibbs

free energy to determine the amount of energy available from potential food sources, such analyses can lead to serious misinterpretations of the availability of metabolic energy sources in a geologic environment [Shock et al., 1995; McCollom and Shock, 1997].

Reactions with negative values of ΔG_r are termed exergonic because they give off energy as they proceed. These reactions are able to provide energy for metabolism because the energy released can be transferred to the organism and used for cellular synthesis. Heterotrophs, like humans, depend on exergonic reactions involving organic compounds generated by other organisms. Autotrophs, on the other hand, generate their own energy, and chemolithoautotrophs like hyperthermophilic methanogens take advantage of chemical energy present as inorganic compounds. McCorm and Shock [1997] estimated the metabolic energy available for all of the chemolithoautotrophic reactions during mixing of hydrothermal fluids and seawater in submarine vent environments with (5) by taking into account the standard Gibbs free energies of the reactions, which are functions of temperature, together with the changing composition of the fluid during mixing, which is accounted for by Q_r . Some of the energetic consequences for the corresponding geochemical mixture are detailed in Figure 4.

Values of the standard state Gibbs free energy are shown in Figure 4a for the methanogenic reaction (4) and its opposite metabolic process, methanotrophy, given by



These values can be combined with the activities of $\text{CO}_2(\text{aq})$, $\text{CH}_4(\text{aq})$, and other pertinent species in the mixed fluid (see Figure 3) to evaluate the total Gibbs free energies shown in Figure 4b. Negative values of ΔG_r correspond to conditions at which a reaction is favored to proceed spontaneously from left to right as written, and positive values indicate that the reaction is favored to proceed from right to left. Therefore energy is available to methane oxidizers at temperatures below $\sim 45^\circ\text{C}$, but energy is available to methanogens at all temperatures $> 45^\circ\text{C}$. Shown in Figure 4c is a plot of the metabolic energy yield from methane oxidation and methanogenesis in calories per kilogram of vent fluid. This is evaluated by determining which of the species in the reaction is present at the lowest concentration and will therefore limit the progress of the reaction. Note that the energy available from methanogenesis is at a maximum in the $100\text{--}150^\circ\text{C}$ range, where hyperthermophilic methanogens are known or suspected to thrive [Daniel, 1992; Karl, 1995].

If a hyperthermophile is capable of reducing CO_2 , then it can combine H_2 from the vent fluid with CO_2 from seawater (both of which are present and out of equilibrium in the mixed fluid) to form methane and H_2O , capture some of the energy released by this reaction, and use it for its various energy-demanding metabolic processes. The number of calories depicted in Figure 4c are deceptively small. The energy from methanogenesis at $\sim 100^\circ\text{C}$ is capable of producing ~ 5 mg of cells per kilogram of vent fluid, or anywhere from 10^6 to 10^{10} cells, depending on size [McCorm and Shock, 1997]. Given the average flow of 5.4×10^5 kg fluid/h from the vent field at 21°N East Pacific Rise [Converse et al., 1984], the small amount of energy shown in Figure 4c can generate ~ 2.5 kilograms of biomass per hour in this one location.

Hydrothermal Organic Synthesis

Calculations like those summarized in Figures 3 and 4 provide insight into the metabolic strategies of hyperthermophilic organisms and help explain the vast biological productivity of hydrothermal systems. Similar calculations can be used to evaluate the energetic demands for fixing carbon into organic compounds. Those summarized in this section reflect efforts to evaluate the potential for hydrothermal organic synthesis during fluid mixing on early Earth [Shock and Schulte, 1997]. The surprising result is that there is a thermodynamic drive to form simple organic compounds from dissolved CO_2 or HCO_3^- and that organisms can actually gain energy by conducting simple organic synthesis because it lowers the free energy of the unstable mixture of seawater and hydrothermal fluid.

In much the same way that the total Gibbs free energy of the methanogenesis reaction becomes negative during mixing of seawater and hydrothermal fluids, the total Gibbs free energies of organic synthesis reactions are also negative. The underlying reason is that bicarbonate present in seawater is out of equilibrium with the dissolved H_2 in the hydrothermal fluid. In addition, any dissolved CO_2 in the hydrothermal fluid will be out of equilibrium with the dissolved H_2 as the temperature is lowered [Shock, 1990a, 1992a]. To illustrate this point, mixing calculations of the type conducted by McCollom and Shock [1997] can be modified to include organic synthesis reactions. Organic compounds considered in these calculations include carboxylic acids, alcohols, aldehydes, ketones, and alkenes. Alkanes and aromatic hydrocarbons are excluded from the calculations to remain consistent with observations about metastable equilibrium in natural systems [Shock, 1988, 1989, 1994; Helgeson et al., 1993]. Thermodynamic data and revised Helgeson-Kirkham-Flowers equation-of-state parameters are taken from Shock and Helgeson [1990] and Schulte and Shock [1993] who provide values for straight-chain compounds with carbon numbers up to 8, except for organic acids, which come from Shock [1995], who gives values for aqueous monocarboxylic, dicarboxylic, and hydroxy acid compounds with carbon numbers up to 12.

Results of mixing calculations that involve organic synthesis are shown in Figures 5 and 6. There are two major differences between the calculations shown in these figures and those discussed above. One is the oxidation state of the mixture. In this case, the oxidation state of the hydrothermal fluid is set by equilibrium with the assemblage fayalite-magnetite-quartz (FMQ) to reflect more closely redox control by basalt in a rock-dominated hydrothermal system. Also, because the model is designed for early Earth, the concentration of dissolved O_2 in seawater has been removed. The other difference is the provision for metastable equilibrium between dissolved carbonate species ($\Sigma\text{CO}_2(\text{aq})$) and aqueous organic compounds. Arguments for this and other metastable equilibrium states in natural aqueous solutions and experiments are given by Shock [1988, 1989, 1990a, b, 1992a, 1994], Helgeson et al. [1993], Seewald [1994], and T. M. McCollom et al. (Reactivity of polycyclic aromatic hydrocarbons under hydrothermal conditions: Implications for alteration of organic matter and generation of hydrothermal petroleum, submitted to *Organic Geochemistry*, 1997a; Reactivity of monocyclic aromatic compounds in hydrothermal experiments and geologic fluids, submitted to *Geochimica Cosmochimica Acta*, 1997b). Two salient points from these studies are (1) that reversible reactions between aqueous organic compounds are possible and

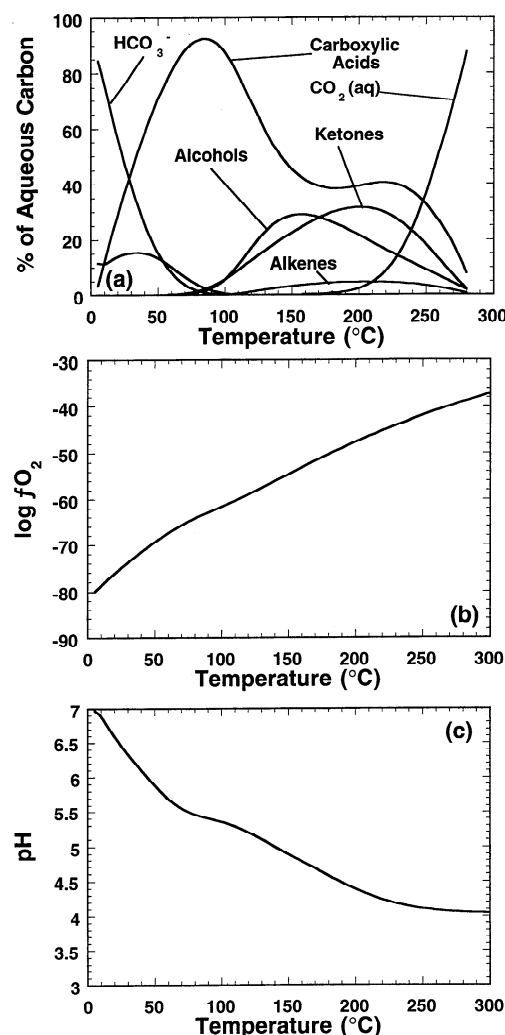


Figure 5. (a) Calculated distribution of carbon, (b) \log fugacity of O_2 , and (c) pH as functions of temperature at metastable equilibrium for mixing between a hydrothermal fluid initially at an oxidation state set by FMQ, and seawater that is missing its dissolved oxygen [Shock and Schulte, 1997]. This mixing calculation is meant to represent a possibility for early Earth. Note that the carbon in this calculation is predominantly inorganic at temperatures $< \sim 30^\circ\text{C}$ and $> \sim 250^\circ\text{C}$. In between these temperatures, organic acids, alcohols, ketones, and alkenes are the predominant organic compounds in the calculated distribution, with the greatest diversity of compounds occurring in the range $100\text{--}225^\circ\text{C}$.

(2) that thermodynamic equilibrium between several groups of organic compounds and CO_2 is likely at the redox conditions and elevated temperatures encountered in sedimentary basins and hydrothermal systems. In contrast, equilibrium between CO_2 and light hydrocarbons, including methane, is not attained in these systems. It is the kinetic barrier between CO_2 and methane that allows methanogenesis and petroleum generation, as well as organic synthesis by hyperthermophiles.

The distribution of carbon is shown in Figure 5a for fluid mixing calculations in which metastable equilibrium is allowed. In this figure the curves indicate the percent of carbon in the mixed fluid which is present as each family of organic compounds. Note the shifts in the relative abundances of the various groups as the overall redox state changes during the mix-

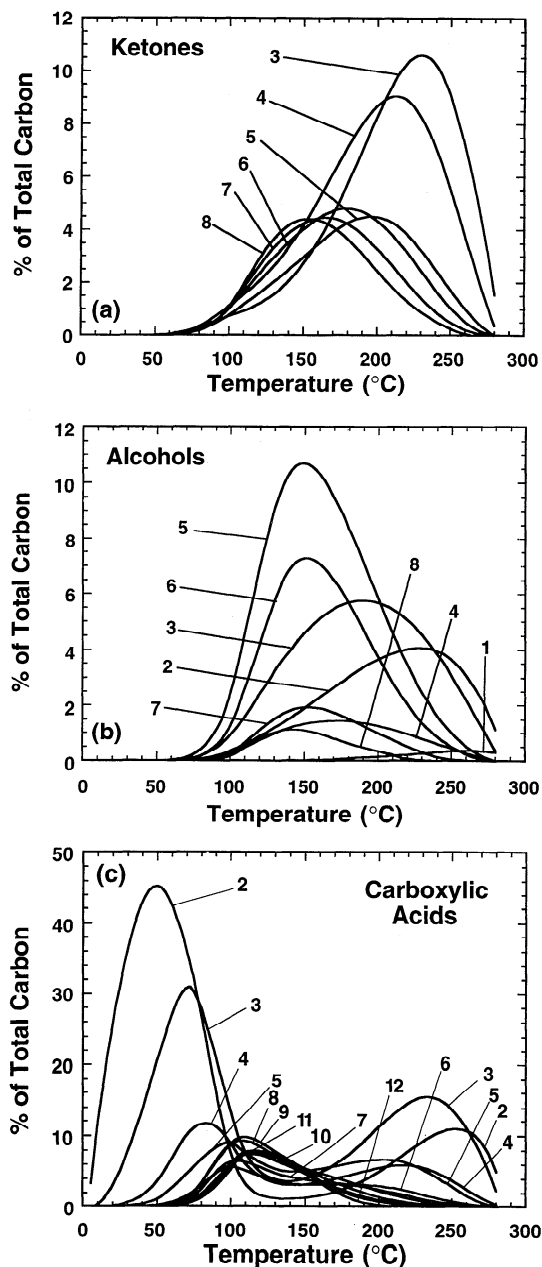


Figure 6. Calculated distributions of (a) ketones, (b) alcohols, and (c) carboxylic acids (acids + anions) as functions of temperature. Number labels refer to the number of atoms of carbon in one molecule of each compound. Note that in each case, smaller compounds are favored at higher temperatures, and larger compounds are favored for each group as temperature decreases. The greatest potential diversity of large organic compounds is found in the temperature range 100°–150°C, where Gibbs free energy minimization can lead to the formation of octanone, pentanol, and nonanoic acid, among many other compounds. These calculations help identify conditions which are most favorable for hydrothermal organic synthesis and also help explain the enormous biological productivity of hydrothermal ecosystems.

ing of seawater and hydrothermal fluid. The oxidation state of the system, shown in Figure 5b, is not buffered in these calculations, but controlled by the initial composition of the two fluids and the relative masses of the fluids at any given temperature. The predominance of carboxylic acids at lower tem-

peratures is also influenced by changes in pH (see Figure 5c), which help to stabilize the acids and their anions relative to other compounds. It should be noted that organic compounds dominate the speciation of carbon between ~250° and ~30°C and that in the range between 150° and 225°C, the three predominant groups, carboxylic acids, alcohols, and ketones, account for roughly 40%, 30%, and 30% of the total carbon, respectively.

The results shown in Figure 5 indicate that there is an enormous thermodynamic drive to form organic compounds as seawater and hydrothermal fluid, which are far from equilibrium, mix and move toward a more stable state. Hyperthermophiles take advantage of this situation by fixing carbon at no energetic cost. In fact, unlike photosynthetic organisms, they can gain energy from the organic synthesis process. As a consequence, respiration may not be necessary. In addition, minimizing the Gibbs free energy of the system favors organic compounds that are constituents of cells as shown in Figure 6, where the distributions of alcohols, ketones, and carboxylic acids are plotted as functions of temperature for the mixing calculation summarized in Figure 5. The sums of the curves shown in these plots correspond to the curves in Figure 5. The numbers which label the curves refer to the number of carbon atoms in a molecule of the indicated compound. It follows that carboxylic acid 2 is acetic, 3 is propanoic, 12 is dodecanoic, etc.

Note that the distribution of ketones (Figure 6a) is dominated by acetone at high temperatures, but that larger ketones dominate the ketone distribution at temperatures <150°C. The alcohols, which have a peak concentration near this temperature, show a similar shift in distribution (see Figure 6b), with ethanol and propanol dominating at temperatures above ~200°C, and pentanol and hexanol becoming dominant at lower temperatures. The distribution of carboxylic acids in Figure 6c is somewhat more complicated, in part, because there are thermodynamic data for more of these compounds [Shock, 1995] and, in part, because pH changes affect the distribution of species through dissociation reactions. Each curve shown in this figure represents the sum of an acid and its anion (i.e., curve 2 is the sum of the acetic acid and acetate percentages). Once again, the smaller compounds, in this case acetic and propanoic, dominate at high temperatures, and larger compounds account for the majority of the carbon as carboxylic acids in the temperature range ~100° to ~175°C. Unlike the ketones and alcohols, the smaller carboxylic acids again dominate the distribution of species at low temperatures.

One remarkable consequence of the interplay between changing temperature and oxidation state as the fluids mix is that larger compounds are favored as temperature decreases, at least down to ~100°C in the calculations shown here. In addition, there is an enormous variety of compounds that can potentially be produced at similar concentrations in the range from 100° to 150°C. Small fluctuations in temperature in this region will have a major impact on the distribution of species. For example, energy minimization at 80°C would produce acetic acid and propanoic acid, but an increase to 110°C would favor production of octanoic, nonanoic, and other long-chain acids instead of acetic and propanoic in order to minimize the energy. This suggests that the monomeric constituents of cell membranes and other biomolecules can be synthesized by hyperthermophiles at no energetic cost. In fact, it might be possible for organisms to use the energy gained through organic synthesis to drive other reactions. As an example, polymerization requires energy at elevated temperatures as it does at

room temperature, but in the case of peptide bonds, increasing temperature lowers the energy required to make the bond [Shock, 1992b].

These calculations indicate that organic synthesis is thermodynamically favored in hydrothermal vent environments, and additional studies show that similar systems on early Earth were likely environments for the emergence of simple metabolism driven by geochemical disequilibrium [Russell *et al.*, 1988, 1989, 1993, 1994; Shock, 1990a, 1992a, 1996; MacLeod *et al.*, 1994; Russell and Hall, 1995, 1997]. It follows that similar conditions could have existed on Mars at some time in the past when volcanism and circulation of hydrothermal fluids occurred. In any event, the fact that geochemical sources of energy are capable of sustaining life, and nurturing it with a steady supply of organic compounds at no energetic cost to the living system, provides a new impetus for exploring the subsurface of Mars (and the Earth) for the biological consequences.

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