SUBMARINE HYDROTHERMAL VENTS AND ASSOCIATED GRADIENT ENVIRONMENTS AS SITES FOR THE ORIGIN AND EVOLUTION OF LIFE

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Abstract. Submarine hydrothermal vents are the only comtemporary geological environment which may be called truly primeval; they continue to be a major source of gases and dissolved elements to the modern ocean as they were to the Archean ocean. Then, as now, they encompassed a multiplicity of physical and chemical gradients as a direct result of interactions between extensive hydrothermal activity in the Earth's crust and the overlying oceanic and atmospheric environments. We have proposed that these gradients provided the necessary multiple pathways for the abiotic synthesis of chemical compounds, origin and evolution of 'precells' and 'precell' communities and, ultimately, the evolution of free-living organisms. This hypothesis is consistent with the tectonic, paleontological, and degassing history of the earth and with the use of thermal energy sources in the laboratory to synthesize amino acids and complex organic compounds. In this paper, we expand upon the geophysical, chemical, and possible microbiological analogies between contemporary and Archean hydrothermal systems and suggest several hypotheses, related to our model for the origin and evolution of life at Archean vents, which can be tested in present-day hydrothermal systems.

1. Introduction

The discovery of submarine hydrothermal environments has resulted in a profoundly greater understanding of the Earth's geological, geochemical, and biological history. It has also provided new insights and renewed interest in the origin and evolution of life as processes that occurred on Earth (Corliss *et al.*, 1980, 1981; Berry and Wilde, 1983), rather than (or as well as) elsewhere in the Universe (Crick and Orgel, 1973).

Available hypotheses, as to how and where life originated and evolved do not account for: (1) the widely diverse set of physical and chemical conditions that would have been necessary for the sequential processes of chemical, biochemical, biological, and ecosystem evolution; (2) a continuous, concentrated source of energy to drive these evolutionary processes; (3) a source of biologically important trace elements, such as molybdenum (associated with nitrogen-cycling reactions); or (4) the geologically short time interval between formation of the Earth's oceans and appearance of microorganisms in the fossil record. Submarine hydrothermal systems, which operate today much as they are believed to have functioned in the Archean, meet all of these criteria. They encompass an expansive range of closely-linked gradients, in both physical and

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chemical conditions ultimately established through their direct link with magmatic heat. They produce, continuously, high concentrations of chemical precursors to organic compounds of biological importance, by circulated fluids through temperature gradients and across ample reactions surfaces. These environments would have provided an almost infinite set of conditions and variables, as well as combinations of conditions, effectively shortening the geologic time period required for random occurrence of a successful, life-generating series of events.

In a previous paper, we proposed submarine hydrothermal systems as general sites for the origin and evolution of life (Corliss *et al.*, 1981). At that time, we based our hypothesis on the available information concerning properties of present-day hydrothermal environments, lithological associations of the most ancient fossils, and use of thermal energy sources in the laboratory to synthesize amino acids and complex organic compounds. In this paper, we expand on our original hypothesis by considering new information on the geology and biology of present-day hydrothermal systems, inferred properties of the Archean ocean, and characteristics of Archean fossil-bearing sediments. We propose that life developed and evolved in a primeval, shallow ocean in association with the multiplicity of gradients established by what are now known to have been important features of the early Archean: the tectonism associated with seafloor spreading and the resultant hydrothermal alteration of the newly-emplaced oceanic crust and the composition of the ocean and atmosphere of the early Earth. We conclude with a discussion of specific hypotheses, related to the origin of life, which can be tested in present-day, submarine hydrothermal environments.

2. Hydrothermal Systems and the Archean Ocean

It has become increasingly apparent that the oldest sediments on Earth are marine and associated stratigraphically with sequences of crust that have been altered hydrothermally (Corliss *et al.*, 1980, 1981; Schopf, 1983; Hoffman, 1984; Abbott and Hoffman, 1984). The microfossil record in Precambrian sediments indicates that the earliest microbial communities on Earth were established in similar environments (see Corliss *et al.*, 1981, and Schopf, 1983, for references; Yun, 1984). It is important, therefore, to understand and model the sequence of geological, chemical, and biological changes that must have occurred in the Archean ocean and atmosphere. The relevance of present-day hydrothermal environments is that they have retained many of the characteristics of Precambrian systems and, therefore, represent 'primeval' sites suitable for studying a range of biogenic reactions and evolutionary processes.

Current ideas on the early history of the Earth have been discussed in a number of recent papers (e.g., Corliss *et al.*, 1981, and papers in Schopf, 1983). Physical and chemical characteristics of the Archean ocean and atmosphere, as well as the extent of tectonic activity and rate of continent formation, have been inferred from the geological and geochemical records of Precambrian strata. These inferred properties of the early ocean are summarized in Table I. Although some of the properties are still unclear (e.g., period of formation, depth). the available evidence indicates that the ancient ocean was

TABLE I

Inferred properties of the early ocean

Properties		References
1.	PERIOD OF FORMATION Early or delayed, rapid or gradual accumulation.	Towe, 1983; Schopf, 1980
2.	DEPTH Dependent on period of formation of continental masses, cooling history of oceanic crust, existence and extent of hotspot volcanism.	Towe, 1983; Abbott and Hoffman, 1984
3.	HYDROTHERMAL ACTIVITY Greater and more rapid seafloor spreading at 3.5 Ga than at present; ridge length 5 times the present and hydrothermal activity at least 3–4 times the present.	Bickle, 1978; Abbott and Hoffman, 1984; Hoffman and Baross, 1984
4.	TEMPERATURE Warm (< 30 °C) to hot (> 100 °C), depending on 1-3 above and atmospheric conditions such as presence and period of a greenhouse effect; earliest evidence of glaciation dates to 2.2 to 2.7 Ga.	Costa *et al.*, 1980; Fyfe, 1980, 1981; Hoyle and Wickramasinghe, 1979; Schopf, 1980; Stevenson, 1983; Walker *et al.*, 1983
5.	CHEMISTRY Reducing conditions with high concentrations of H_2S, H_2, CH_4, NH_3, metals, etc., and the possibility of organic compounds including condensing agents such as HCN and formaldehyde; surface water interaction with greenhouse atmosphere having high concentrations of CO_2 and H_2O; possible presence of significant concentrations of O_2 and other oxidized gases (CO, N_2O) produced by photolysis; aerobic conditions at ~1.7 Ga.	Schopf, 1980, 1983; Towe, 1983; Walker, 1983; Berry and Wilde, 1983
6.	CONTINENT FORMATION No discrete continental masses at 3.9 Ga; two periods of rapid continental accretion between 3.8 and 3.5 Ga and between 3.1 and 2.6 Ga; earliest sediments hydrothermal and marine.	Abbott and Hoffman, 1984; Corliss *et al.*, 1980, 1981

a chemically reducing environment (Berry and Wilde, 1983), probably warm or hot (> 30 °C to possibly greater than 100 °C; Costa *et al.*, 1980), shallow (maximum depth of ~1000–2000 m), and considerably more active tectonically and hydrothermally than it is today (Abbott and Hoffman, 1984; Hoffman and Baross, 1984). At the time the ocean was formed (4.2 Ga), it is likely that the whole Earth was covered with water and that hydrothermal activity was at least five times more prevalent that at present. This conclusion is based on a model in which the overall rate of seafloor creation and subduction has declined steadily over the history of the Earth (Abbott and Hoffman, 1984). The model indicates that the total oceanic ridge length at 3.5 to 4.2 Ga was between three and five times greater than at present (Abbott and Hoffman, 1984). Such an extended ridge length would have resulted in voluminous hydrothermal circulation

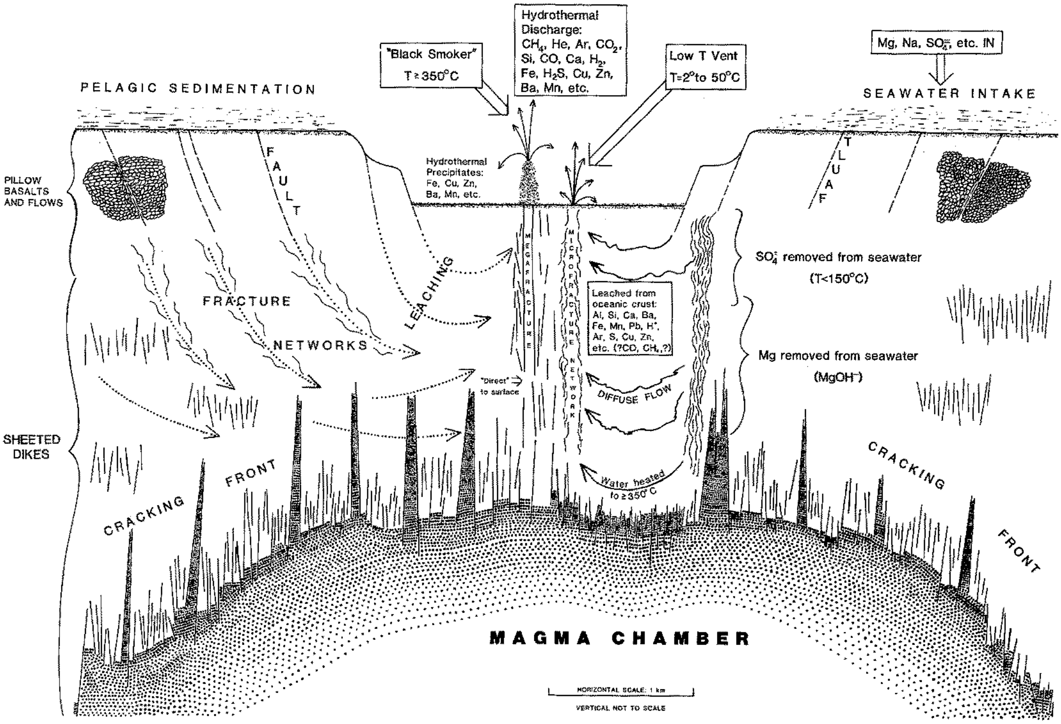

Fig. 1. Cross-section of the central 6 km of a seafloor spreading center with schematic diagrams of hydrothermal circulation superimposed (vertical not to scale). Tectonic and structural features are indicated on the left; chemical features on the right. A system of listric faults (heavy broken lines) controls seawater intake which occurs along a network of interconnected fractures (wavy lines). Arrows show direction of seawater transport. Dotted region above magma chamber represents the emplacement of diabasic sheeted dikes. 'Smoker' vents (on left in diagram) discharge end member hydrothermal fluids (no measurable contamination by ambient seawater) at temperatures ≥ 350 °C and flow rates of m s^{-1}. Polymetallic sulfide mounds are associated with this type of vent. Galapagos-type vents (on right in diagram) discharge hydrothermal fluid mixed with varying proportions of ambient seawater during ascent. Water temperatures in these vents range from 2 °C to about 50 °C and flow rates are measured in cm s^{-1}. The chemical characteristics of hydrothermal systems are the result of water-rock interactions at high temperatures. See text for further details.

of reduced elements and gases. Hydrothermal systems, such as the one shown in Figure 1, would have been very common features of the Archean ocean floor (Abbott and Hoffman, 1984; Hoffman and Baross, 1984).

Figure 1 shows, schematically, the geological and geochemical features of hydrothermal circulation systems which occur along the central rift zone of modern spreading ridges (based in part on Gregory and Taylor, 1981). It summarizes the chemical reactions associated with hydrothermal vents, indicates sites of hot water extraction of chemical species from basalt and consequent gas formation, and illustrates the circulation patterns resulting in smoker (high temperature) and Galapagos-type (low-temperature) vents. Seawater intake occurs off-center of the spreading ridge. Water percolates downward, through accumulated sediments and underlying basalts, along zones of weakness created by a system of listric faults. Faulting and fracturing are facilitated by the movement of seawater. Seawater is believed to penetrate to the 'cracking front', a zone of incipient crystallization directly overlying the roof of the magma chamber. The crystallization and hydrothermal cooling which occur along the cracking front cause further fracturing which leads to the emplacement of magmatic dikes. Thus, a continuous heat source is essentially assured by an almost self-perpetuating system. As long as magma is supplied to the magma chamber, the hydrothermal circulation system is inevitably active. Ambient seawater circulates through cracks in the crust, reacts at depth with basalts and diabasic dikes at temperatures of at least 350 °C, and ascends back to the seafloor in altered form, enriched to varying degrees with magmatically-derived elements, gases, and inorganic compounds (Figure 1).

Fracturing in the central rift zone and at the cracking front influences the upward transport of these altered fluids. Large fractures, as shown on the left of Figure 1, deliver pure 'end member' (defined below) hydrothermal fluids directly to the seafloor. Interconnecting networks of small fractures, as shown on the right in Figure 1, allow ambient (2 °C) seawater to mix with hot ($>$ 350 °C) hydrothermal fluids at subsurface depths. As a result of these different structures, two general types of vent systems occur on the seafloor: hot 'smoker' vents, in which there is little or no subsurface mixing of colder seawater with hydrothermal fluid; and cool Galapagos-type vents, in which varying amounts of ambient seawater penetrate through cracks and mix with the hydrothermal fluid prior to its venting at the seafloor. Both types of vents have been found to occur along spreading ridge crests of the East Pacific Rise and Juan de Fuca Ridge in the Pacific (Rona *et al.*, 1984). Hydrothermal fluids exiting from the first 'smoker' vents to be explored registered a temperature of 350 °C. The chemistries of these waters indicate their direct transport via conduits from the point at which seawater is heated (to at least 350 °C) to the seafloor. The 350 °C waters were found to be enriched to the maximum extent with magmatically-derived elements and compounds and, thus, to serve as an 'end member' for determining the extent to which various Galapagos-type vent waters ($<$ 50 °C) have been diluted with ambient seawater (Edmond *et al.*, 1982). Since the discovery of 'black smokers' venting 350 °C to 400 °C end-member fluids (Delaney *et al.*, 1984, measured 400 °C water at the Juan de Fuca Ridge) 'white smokers' venting more mixed waters at lower temperatures and altered chemical composition have also been described (Hekinian *et al.*, 1984). Depending on this degree of mixing, concentrations of the major components of potential importance to biological processes in venting fluids have been found to range from 0 to $>$ 4 mM for H_2S, 1 to $>$ 1000 μM for Mn, and from $<$ 1 to $>$ 200 μM for Fe. Concentrations of gases were also higher than saturation in some cases and ranged from 0.1 to 50 μM for CH_4, 1 nM to $>$ 600 μM for H_2, and 10 to 100 nM for CO (Lilley *et al.*, 1982, 1984). Together, these chemical components are believed to serve as the primary energy sources for the extensive microbial communities (see Figures 2 and 3) associated with present-day vent environments (Lilley *et al.*, 1984; Jannasch, 1984). All of the biologically important trace elements are also known to be associated with submarine hydrothermal vents.

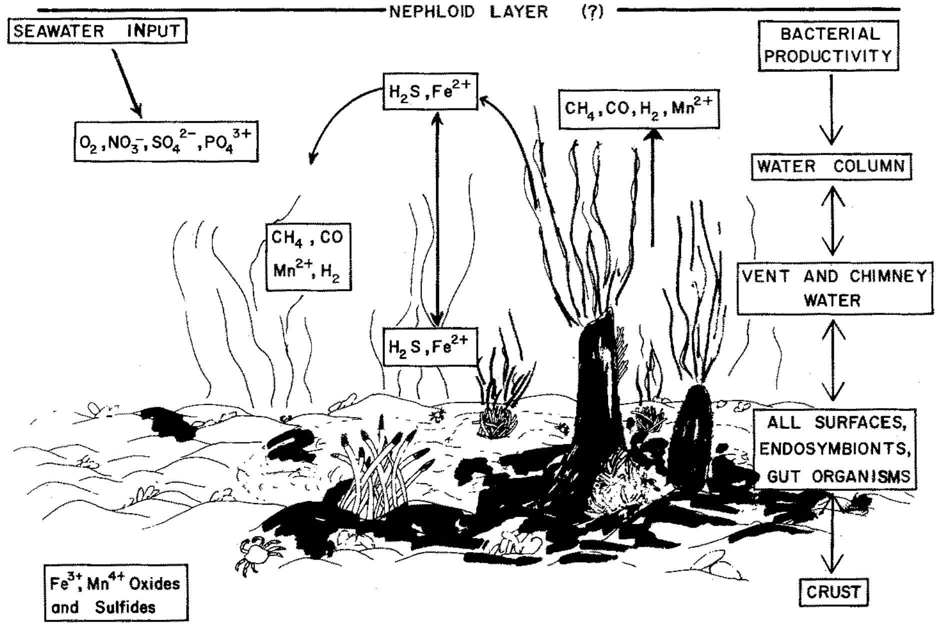

Fig. 2. Diagram of submarine hydrothermal vent environment showing discharges of the most abundant carbon and energy sources used by vent bacteria. The 'primary producers' in these environments are chemosynthetic bacteria which are present in discharging hydrothermal fluids, on all surfaces, in the surrounding seawater, and as animal endosymbionts. The most important environmental energy sources for these bacteria are H_2S, H_2, CH_4, Mn^{2+}, Fe^{2+}, and CO.

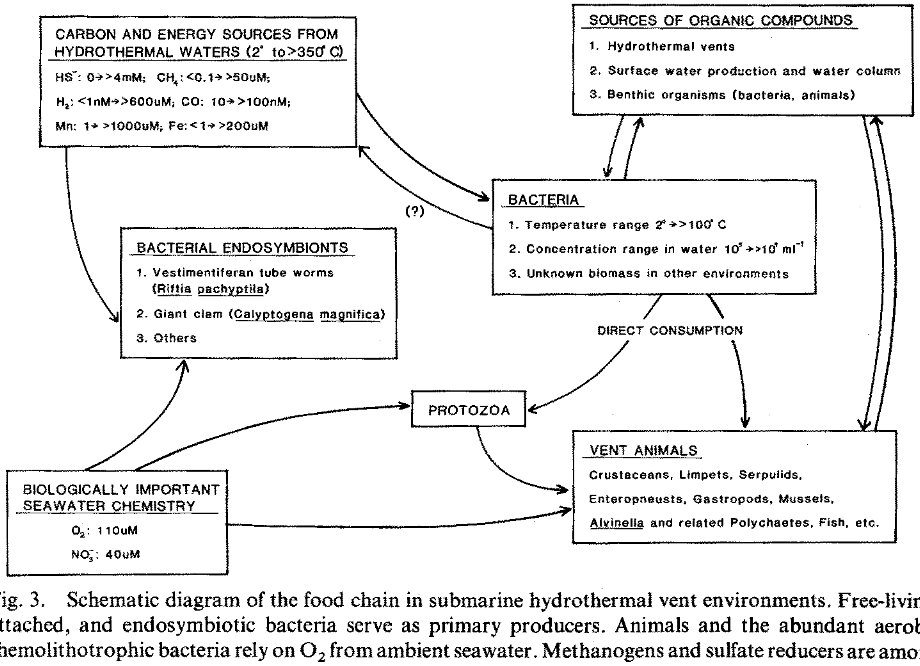

Fig. 3. Schematic diagram of the food chain in submarine hydrothermal vent environments. Free-living, attached, and endosymbiotic bacteria serve as primary producers. Animals and the abundant aerobic chemolithotrophic bacteria rely on O_2 from ambient seawater. Methanogens and sulfate reducers are among the more abundant anaerobes.

The major chemical components of exiting hydrothermal fluids are derived from water/rock reactions at high temperatures. It has been shown that the principal source of H_2S–S in the end-member smoker vents is basalt and not seawater sulfate (Shanks *et al.*, 1981; Styrt *et al.*, 1981). Thus, part of the H_2S measured in Galapagos-type vents comes from basalt. However, it is also possible that in these cooler vents a significant proportion of the H_2S results from microbial sulfate reduction, occurring at temperatures from ambient (2 °C) to greater than 100 °C. All waters sampled from the Galapagos vents contained sulfate-reducing bacteria (Lilley *et al.*, 1984). Some of the waters sampled from 350 °C vents at 21 °N also contained sulfate reducers which could grow and reduce sulfate, as well as other oxidized forms of sulfur, at 110 °C and 1 atm pressure, using H_2 or C_1- or C_2-organic compounds (Lilley *et al.*, 1984; Baross, unpublished data).

The actual reactions involved in the production of gases is not clear. Both H_2 and CO are common gases associated with volcanic activity. The major source of H_2 is believed to be the oxidation of magnetite ($Fe^{+2}Fe^{+3}{}_2O_4$) to hematite(Fe_2O_3), while CO is believed to originate within the magma from C-O-H-S equilibria (see Baross *et al.*, 1984, for references). Presently, there is some disagreement as to the source and levels of CH_4 entrapped in the mantle (Gold, 1982). In some studies of hydrothermal systems, concentrations of CH_4 have been found to parallel concentrations of ^3He (a conserved gas of magmatic origin) to an extrapolated end member of 350 °C (Lupton *et al.*, 1977). However, concentrations of CH_4 and H_2 in Galapagos vent waters indicate that the biological processes of gas production and consumption are occurring (Lilley *et al.*, 1984).

Surface deposits associated with present-day vent fluids consist predominantly of Fe-, Cu-, and Zn-sulfides. In the case of smoker vents, these deposits take the form of mounds or chimneys that can exceed 15 m in height. Similar sulfide chimneys have been observed in Cretaceous sulfide deposits at Cyprus (Oudin and Constantinou, 1984) and in the Oman ophiolite (Haymon *et al.*, 1984). Such deposits would have been common occurrences on the seafloor once the ocean became oxygenated. During the early Precambrian, the reduced elements, gases, and other compounds in vent fluids would have remained in solution, keeping the ocean environment chemically reduced until the influences of continent formation, decreased hydrothermal activity, abiogenic and biogenic oxygen production, bacterial oxidative processes, and an altered atmosphere began the sequence of changes leading to present-day conditions. Thus, although present-day hydrothermal systems are geologically and geochemically very similar to their Archean counterparts, the surrounding oceanic environments differ markedly. In the modern ocean, O_2, other electron acceptors ($NO_3{}^-$, $SO_4{}^{2-}$, and $PO_4{}^{3-}$), and a variety of additonal compounds have allowed for the abundant growth of a physiologically diverse community of vent microorganisms and complex assemblages of a variety of vent animals (Corliss *et al.*, 1979; Cavanough *et al.*, 1981; Baross *et al.*, 1984; Jannasch, 1984; Hessler and Smithey, 1984), as discussed in the next section.

Some inferences have been made concerning the first groups of microorganisms to have evolved on Earth, given the model of an Archean ocean that was warm or hot, hydrothermally-driven, and anoxic (Corliss *et al.*, 1981; Berry and Wilde, 1983). The catalytic reactions of these microorganisms would have changed the geochemical characteristics of Archean environments which, in turn, would have increased the diversity of subsequent microbial communities. At the present time, we find physical-chemical conditions most resembling those in the Archean ocean only in the immediate vicinity of hydrothermal activity. It is at these sites that we might expect to find microbial communities having morphological and physiological characteristics analogous to fossilized communities that have been observed in Archean oceanic sediments.

3. Food Chains and Archean Biology

In general, present-day ecosystems are based on photosynthesis and the consequent production of oxygen. Only in extreme environments, having temperatures above 55 °C, acidic pH, or saturated levels of solute, do we see simple ecosystems based on bacteria (Brock, 1978; Kushner, 1978). That photosynthetically-based food chains were established in the Precambrian has frequently been inferred from the morphology of filamentous microfossils in ancient sedimentary strata and from evidence that significant levels of oxygen may have been present in the Precambrian atmosphere (Schopf, 1975; Margulis *et al.*, 1976; Towe, 1978, 1983).

In present-day environments associated with submarine hydrothermal vents, the food chain is based upon chemosynthetic bacterial processes rather than photosynthesis. A variety of physiologically diverse bacteria from these environments have been identified. They include sulfur and metal oxidizers, methane producers and consumers, hydrogen producers and consumers, and sulfate reducers (Lilley *et al.*, 1984; Jannasch, 1984). Total numbers of bacteria in samples of vent water have ranged from 10^5 to greater than 10^9 ml^{-1}. Their productivity levels have been measured at 100–1000 times that in surrounding, deep-sea water and at least three to four times that in overlying surface water (Karl *et al.*, 1980). Abundant bacteria have also been found on all surfaces at vents, as endosymbionts associated with some animals, and in the most extreme of smoker environments (Figures 2 and 3; Jannasch and Wirsen, 1981; Baross and Deming, 1983; 1985; Baross *et al.*, 1984; Jannasch, 1984; Lilley *et al.*, 1984).

A representative vent community supported by these bacteria, and associated geological and geochemical features, is portrayed in Figure 2. The large vestimentiferan tube worm, *Riftia pachyptila* Jones, and the giant clam, *Calyptogena magnifica*, have endosymbiotic bacteria (Cavanaugh *et al.*, 1981) and live close to warm water vents (Hessler and Smithey, 1984). The polychaete tube worm, *Alvinella pompejana*, lives on the outer surfaces of chimneys at temperatures to at least 45 °C (Desbruyeres *et al.*, 1983; Baross, unpublished observations). Fossilized remnants of similar polychaetes have been found in association with metalliferous deposits of Cretaceous sulfide chimneys on Cyprus (Oudin and Constantinou, 1984) and in the Oman ophiolite (Haymon *et al.*, 1984).

One of the implications of our hypothesis that the earliest groups of microorganisms were associated with hydrothermal systems and surrounding environments is that the earliest microbial habitats were volcanic and anoxic, evolving in temperature over the first 2 billion years from hot (> 70 °C) to warm (< 30 °C). Temperature and, eventually, O_2 gradients would have been the major parameters regulating the evolution of ecosystems. This evolution would have proceeded from simple systems, dominated by anaerobic, extremely thermophilic prokaryotes, to more diverse communities of thermophilic prokaryotes including anaerobic and aerobic photosynthesizers (Photosystems 1 and 2), and eventually to complex systems including eukaryotic green algea (temperatures below approximately 50 °C). These temperature-regulated demarcations in community structure can be observed today in smoker and other thermal environments, such as the crater and thermal streams of Mt. St. Helens (Brock, 1978; Baross *et al.*, 1982b).

In terrestrial environments with temperatures of 50 to 70 °C, cyanobacteria and chemolithotrophic bacteria dominate. As previously discussed, members of the latter group of microorganisms also dominate at submarine vent environments where they have access to a variety of energy sources. However, some microbial processes, such as nitrogen fixation, nitrification, and methane oxidation, are not known to occur at temperatures above 55 °C. The absence of nitrogen fixation at higher temperatures raises the question of source and speciation of nitrogen used by thermophiles in both present-day volcanic and Archean aquatic environments. Although source reactions for nitrogen in Archean systems are unknown, it is presumed that NH_3-N was the most abundant form, as it is in contemporary vent ecosystems (Lilley, unpublished data).

In terrestrial environments with temperatures greater than 70 °C, microbial diversity decreases, with methanogens, anaerobic sulfur metabolizers, thermoacidophiles, and some sulfur- and metal-oxidizers dominating. Many bacteria that have become established in the most extreme environments, and particularly in environments having temperatures greater than 80 °C and/or acidic pH, have proven to be members of the Archaebacteria. This heterogeneous group of bacteria includes methanogens, halobacteria, and extremely thermophilic acidophiles. They have been characterized by their unusual ribosomal RNA sequences, ribosome structure, membrane lipids and other macromolecules, as well as their physiology and ecology (Woese, 1982). Extremely thermophilic Archaebacteria bave been isolated from volcanic environments where they grow at temperatures above 90 °C (Stetter, 1982; Baross *et al.*, 1982b; Jones *et al.*, 1983). Bacterial communities have also been obtained from samples of 'black smoker' fluid, originally at temperatures of 195–306 °C. They were shown to produce H_2, CH_4, and CO at 100 °C (Baross *et al.*, 1982a) and, in separate study, to incorporate ^{3}H-adenine at 90 °C (Karl *et al.*, 1983). Additional evidence indicates that one of these thermophilic microbial communities grew at 250 °C when recompressed to *in situ* pressures of 265 atm (Baross and Deming, 1983; Baross *et al.*, 1984). Their physiological and temperature growth characteristics indicate that they, too, are Archaebacteria, possibly living in the crust at very elevated temperatures and pressures. We have already suggested that these bacterial communities may be analogous, physiologically

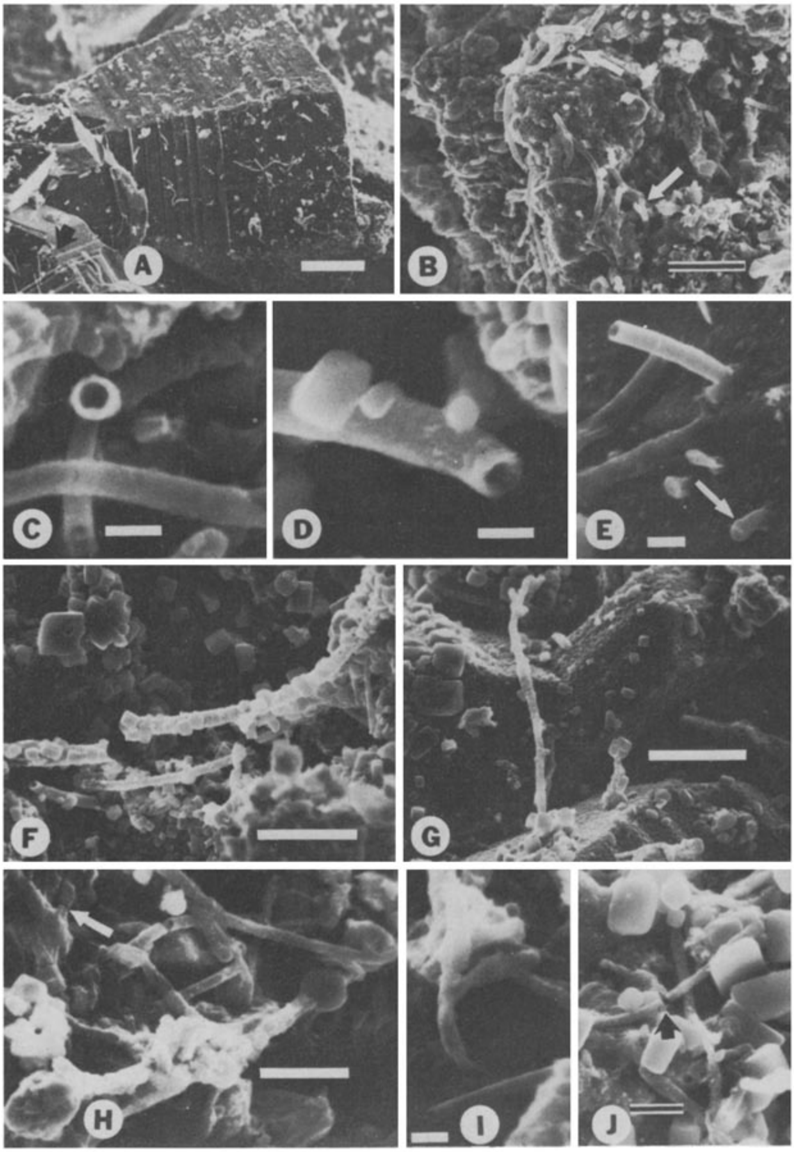

Fig. 4. (A–J). Scanning electron micrographs of tube-forming microorganisms on sulfide chimney rocks obtained from hydrothermal vents along the East Pacific Rise at 21 °N. (A) Sulfide crystal colonized by filamentous microorganisms. Arrow indicates vertical filaments. Bar is 25 μm. (B) Extensive colony of tube structures with hollow openings at many of the ends. Top arrow indicates a hollow end; bottom arrow, a branching point. Bar is 10 μm. (C) High magnification of the tube structure denoted by the top arrow in Figure 4B. Bar is 1 μm. (D) Side view of tube showing tapering end. Bar is *1* μm. (E) Hollow tube extending from the sulfide crystal with apparent bands around the tube. Arrow indicates what may be 'immature' organism. Bar is 1 μm. (F, G) Tubes that have accumulated small sulfide crystals and other precipitated salts, significantly increasing the width of the tubes. Bar in both figures is 10 μm. (H, I) Swollen or bulblike structures, commonly observed along the tubes, and occasionally seen as single structures or pairs at the end of tubes (Figure 4I; lower arrow in 4B). Bar in Figure 4H is 5 μm; bar in Figure 4I is 1 μm. (J) Dark band

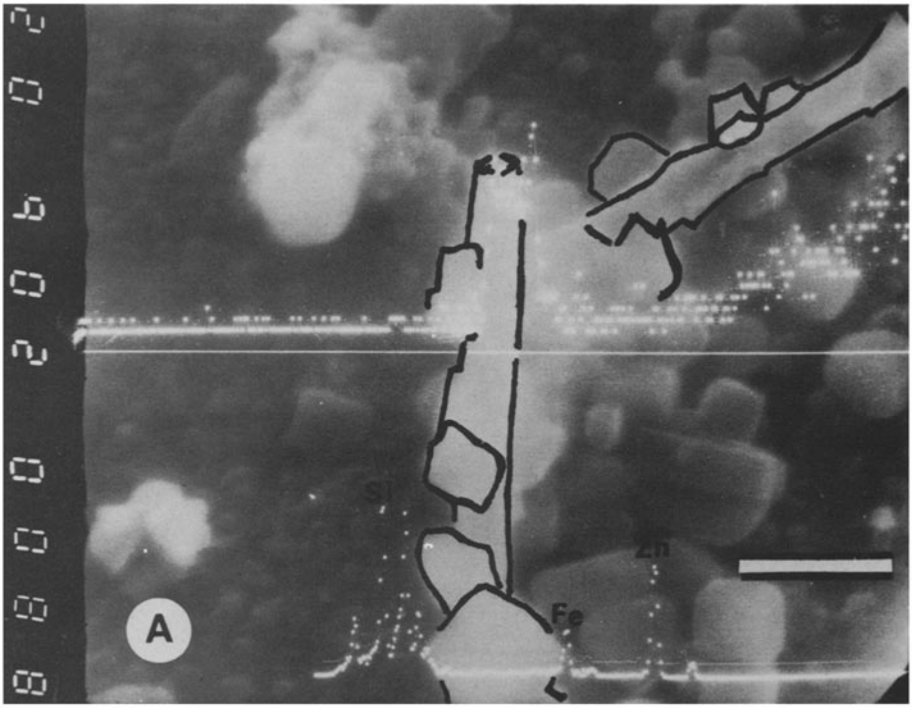

Fig. 5. Scanning electron microscopic and energy dispersive x-ray spectroscopic (EDS) analyses of the tube structures shown in Figure 4. The top curve is a line scan of silicon over one of the tube structures from Figure 4. The uninterrupted line represents the area of x-ray analysis. The bottom scan is a total elemental analysis of the tube revealing Si, Fe, and Zn. The relatively low levels of Fe and Zn were comparable to those found in surrounding sulfide crystals. Bar is 2 μm. Samples were observed and analyzed using a JEOL JSM-35 scanning electron microscope with EDS capability.

and biochemically, to the earliest group of microorganisms to have evolved on Earth (Baross *et al.*, 1984).

Further analogy can be made between present-day volcanic environments and ancient microbial habitats based on the fossil record. The earliest evidence of unicellular fossils and stromatolites has been found in the 3.5 Ga Warrawoona Group (Pilbara Block, Western Australia) (Walter *et al.*, 1980) and in the 3.5 to 3.3 Ga Swaziland Sequence (Barberton Mountain Land, South Africa) (Knoll and Barghoorn, 1977). The fossil-bearing strata in both localities are part of submarine sequences that include lava flows, pillow basalts, and chemical sediments, probably derived from volcanic sources via hydrothermal activity (Corliss *et al.*, 1981; Hoffman, 1984). Complex microfossil assemblages have also been reported in the middle

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(arrow) frequently observed on filamentous tubes (see also Figure 4H, arrow). Bar is 2 μm. All samples were fixed in sterile artificial seawater containing 2% gluteraldehyde minutes after the ALVIN surfaced. Aseptic techniques were used during all manipulations. Fixed samples were dried by the critical point method, mounted on aluminium stubs, and coated under a vacuum with a layer of gold 10–20 μm thick. Samples were viewed using an International Scientific Instruments Mini-SEM, Model MSM-2 scanning electron microscope.

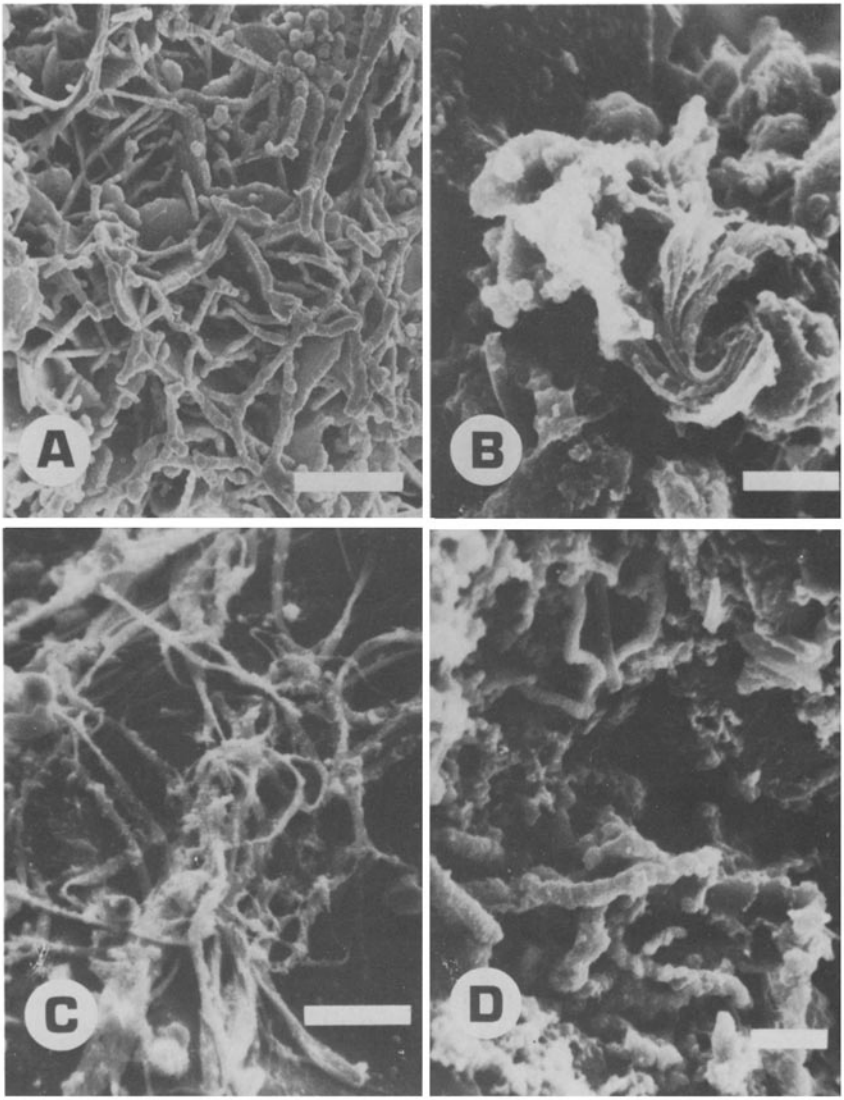

Fig. 6 (A–D). Scanning electron micrographs showing metal-encrusted bacteria on the outer surfaces and inner surfaces (exposed by crushing) of rocks obtained from active 'black smokers' at 21°N along the East Pacific Rise in November of 1979 (Figures B, C, and D) and April of 1982 (Figure A). Bar in A is 25 μm; in B and D, 5 μm; and in C, 10 μm. Samples were prepared as described in the caption of Figure 4.

Precambrian chert environments, which are believed to be marine and volcanic in origin, (Barghoorn and Tyler, 1965; Walter *et al.*, 1976; Awramik and Barghoorn, 1977; Yun, 1984). Complex communities of microorganisms, bearing morphological resemblances to these microfossil assemblages, have now been found in modern hydrothermal environments. Examples of the modern assemblages are shown in Figures 4 and 6.

A composite of scanning electron micrographs, showing one of the microbial assemblages found on sulfide chimney rocks is shown in Figure 4. The assemblage is dominated by filamentous structures, many of which appear as hollow tubes or sheaths with an inside diameter of about 0.5 μm. EDS analyses of the tubes showed that they were composed mainly of silicon, with low levels of Fe, Mn, and Cu (Figure 5). Most of the other microbial mats observed on the sulfide chimneys, many of which were extremely dense (Figure 6C), were also heavily encrusted with metals (Figures 6, A–D). The dominant metal deposited in the mats shown in Figure 6C was iron (Figure 7). Many of these features suggest a relationship to known metal-oxidizing, sheath-forming bacteria, such at *Leptothrix* and *Sphaerotilis* spp. (Caldwell and Caldwell, 1980). However, the evidence of branching, swollen segments (Figures 4B, I, J), and akinite-like structures (Figures 4H and 4J), seen especially in the silicon tube structures, would usually be indicative of eukaryotic organisms such as fungi.

Although it is not known whether the silicon tubes were formed biotically or abiotically, the physical conditions in the environment around the chimneys are

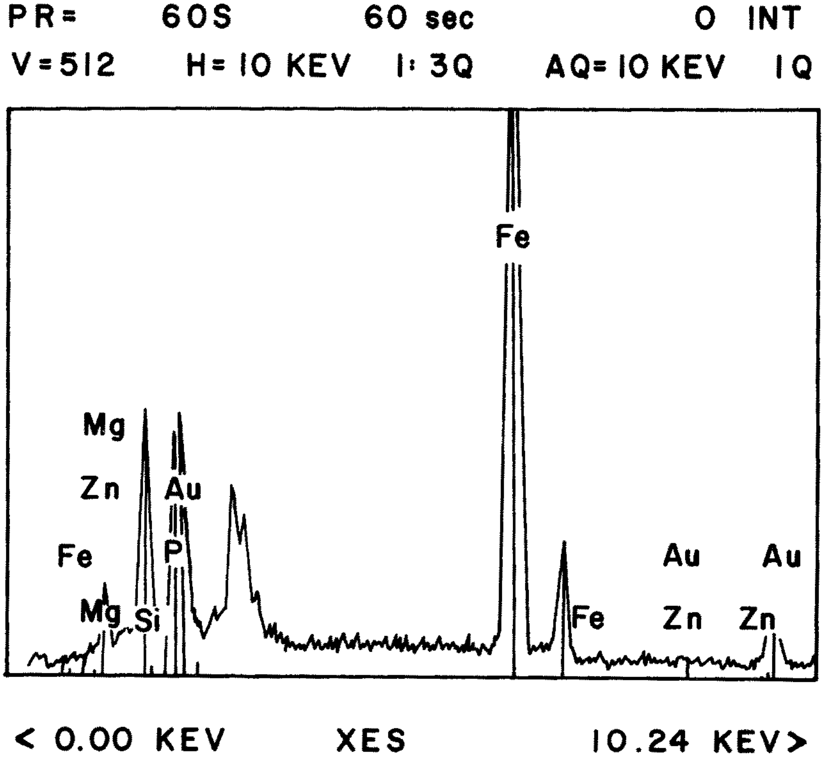

Fig. 7. Line drawing of energy dispersive x-ray spectroscopic (EDS) analysis of the organisms shown in Figure 6A, indicating Fe deposition. Similar scans were observed for organisms shown in Figures 7A, B, and D. EDS analyses of uncolonized sections of chimney material showed greatly reduced levels of Fe and high levels of S, Zn, Cu, and Si.

definitely conducive to abiotic silicification. Hot vent waters enriched in silica are expelled into the cold ambient waters where the moderate hydrostatic pressures and alkaline pH of seawater favor precipitation of silica (Oehler and Schopf, 1971). Amorphous silica deposits, not associated with organisms, were a common feature of vent mounds and chimneys along the East Pacific Rise (Spiess *et al.*, 1980). The abiotic precipitation of silica sheaths around bacteria is also known to occur in the somewhat related environments of alkaline hot springs at Yellowstone National Park where modern silica stromatolites have been observed (Walter *et al.*, 1972). It is interesting to note that the silicification of prokaryotic cells often increases the apparent size of an organism and can result in the formation of distinct morphological characteristics more indicative of eukaryotic organisms (Francis *et al.*, 1978a). Thus, the interpretation of microfossils having a coating or sheath of silica or carbonate can be quite difficult (Francis *et al.*, 1978b). We invoke this same phenomenon to explain the eukaryotic features of the contemporary vent organisms described above.

A variety of fossil microorganisms, resembling both cyanobacteria and fungi in size and morphology, have been described from samples of early Precambrian pyritic and siliceous rocks (Schopf, 1975, 1983). The existence of these comparatively advanced organisms in early environments, believed to be deficient in oxygen and organic material, has always been difficult to explain. If, however, these organisms were chemosynthetic bacteria living in or near submarine hydrothermal vents, the source of their nutrients is no longer a problem. We believe that epiphytic chemosynthetic bacteria evolved in hydrothermal environments before the formation of organic-rich stromatolites and that the filamentous tube-forming microorganisms and metal-associated microbial mats, found attached to surfaces in present-day hydrothermal environments, represent living replicas of some of the fossil organisms found in hydrothermally-derived Precambrian strata. The organisms observed on contemporary sulfide mounds are definitely not photosynthetic and probably not heterotrophic, yet they have morphologies similar to those of Precambrian fossils and particularly to those observed in the Gunflint (approximately 2 Ga) and other middle Precambrian cherts (Schopf, 1983). We believe that detailed studies of epiphytic bacteria at present-day vents as well as the extremely thermophilic Archaebacteria cultured from hot hydrothermal fluids, will lead to a better understanding of the physiological groups of microorganisms that existed in Precambrian hydrothermal environments and, thus, preceded mat- and stromatolite-forming microbial communities.

4. Summary View of the Origin and Evolution of Life in the Archean Ocean

We have hypothesized that submarine hydrothermal environments provide all of the necessary conditions for abiotic synthesis of organic compounds, macromolecules, and 'precells' leading to the development of living organisms (Corliss *et al.*, 1980, 1981). In our model, heat derived from the hydrothermal cooling of newly-emplaced oceanic crust provides the energy source for converting inorganic precursors into organic compounds. The characteristic convective flow in submarine hydrothermal systems (refer to Figure 1) results in both the removal and addition of precursors and products from the sites of reaction through gradients of temperature, pH, and chemical composition. By expanding this model to include the Archean ocean and atmosphere, an almost infinite multiplicity of gradients becomes available as potential sites for the variety of abiotic and biotic processes necessary for the eventual evolution of ecosystems. These gradients are summarized in Table II.

The abiotic synthesis of organic compounds is ascribed to subsurface hydrothermal gradients, while other gradients in surface waters and at interfaces would have provided an extensive variety of chemical and physical conditions in support of an equally diverse array of biologically-catalyzed reactions. The earliest microbial processes in Precambrian ocean gradients would have included the anaerobic utilization of H_2 and S°, production and consumption of CH_4, anaerobic photosynthesis, and possibly some

TABLE II

Hydrothermal vents and associated ocean gradients: variables important for studying the origin of life and related evolutionary processes (adapted from Hoffman and Baross, 1984).

Environment		Variables	
I.	Submarine hydrothermal vents (open and geologically continuous)	1.	Temperature ($\sim$500 °C to $\sim$2 °C at present; $\sim$500 °C to $>$ 30 °C in the Archean)
		2.	Pressure ($<$ 1500 to $>$ 3000 m at present; ? in Archean – dependent upon depth of the ridge)
		3.	Concentrations of reduced metals (microbial energy sources), trace metals, and gases (H_2S, CH_4,H_2, CO, N_2, NH_3 etc.)
		4.	Organic compounds (?)
		5.	Condensing agents (CN, CH_2O, polyphosphates, etc.)
		6.	pH ($<$ 4 to $>$ 7) at present; Archean ocean reducing
		7.	Reaction surfaces (clays, zeolites)
II.	Surface waters Archean ocean	1.	Light
		2.	Temperature (?); greenhouse atmosphere in Archean (Towe, 1983; Walker, 1983)
		3.	Pressure (dependent on partial pressure of atmospheric CO_2)
		4.	Oxygen (? from photolysis)
		5.	N_2O, NO, other biologically important gases
		6.	Carbon and microbial energy sources (see I-3 above)
III.	Other associated environments	1.	Submarine rock/water interfaces
		2.	Subaerial rock/water interfaces
		3.	Atmosphere/ocean interfaces
		4.	Temperature and hydrostatic pressure gradients; possible two phase separation of water (brine and nonbrine phases).
		5.	Brine gradients associated with phase separation of water (III, 4), or in evaporating aquatic environments.

oxidative reactions in shallow surface waters having significant levels of oxygen produced photolytically. Banded iron formations could have developed from these environments as a result of the absence of an active oxygen-producing photosynthetic community (Towe, 1983). From the delayed ocean model of Towe (1983), we can deduce that the early Archean ocean (pre-3.5 Ga) was relatively shallow and, consequently, that atmospheric conditions would have exerted an important influence on microbial influence in microbial evolution. Furthermore, in a shallow ocean where hydrothermal activity was 3–5 times greater than in the present day ocean, concentrations of magmatically-derived chemical species would have been correspondingly greater as well. The development of biological diversity in these environments would have been influenced by the availability of light, oxygen and other photolytically-produced electron acceptors, CO_2 partial pressure, and UV radiation. The variety of available gradients would have enhanced biological diversity by providing many different paths for evolution to follow.

TABLE III

Some hypotheses related to the origin and evolution of life that can be tested in present-day submarine hydrothermal environments

1. Heat from ridge crest magmatic activity was a primary energy source for abiotic synthesis of amino acids, purines and pyrimidines, macromolecules, and 'protocells'. Suitable conditions for each of these reactions were provided by the many different gradients and large surface areas characteristic of submarine hydrothermal vents (Table II).

2. The earliest sediments containing fossilized microorganisms were volcanic and marine. Microorganisms at present-day hydrothermal environments have morphologies similar to some of the fossil microbial assemblages in Archean sediments and are thus analogues (morphologically as well as physiologically) to Precambrian microflora.

3. The earliest microorganisms used magma-derived energy and carbon sources, including HS^-, H_2, reduced metals, organic gases (CH_4, CO_2), and possibly other organic compounds synthesized abiotically.

4. Specific microbial processes in the Archean were methanogenesis, sulfate reduction, elemental sulfur reduction (as by contemporary *Pyrodictum occultum* and *Thermodiscus* sp., for example), anaerobic photosynthesis (Photosystem 1), and possibly nitrogen fixation. Limited oxidative microbial reactions occurred in shallow waters (see 5).

5. Microbial oxidation reactions occurred during the early Precambrian in surface waters having significant concentrations of photolytically-derived oxygen and in all anoxic aquatic environments with alternate electron acceptors (N_2O), magnetite, and related compounds (MnO_2).

6. The earliest groups of microorganisms were thermophilic (40–> 100 °C), chemolithotrophic, and thus physiologically related to present-day Archaebacteria which include the thermoacidophiles, methanogens, and metabolizers of elemental sulfur. Greater prokaryotic and eukaryotic diversity coincided with decreases in ocean temperatures below 30–50 °C.

7. The earliest forms of life (and predecessors to free-living, single-celled organisms) were symbiotic communities of 'precells' each containing only limited amounts of nucleic acid. Various mechanisms for genetic exchange, such as the contemporary transposition of genetic elements, were the rule.

Our model for the origin and evolution of life in hydrothermal vent environments suggests several hypotheses that can be tested in present-day systems. The foregoing sections have alluded to all but the last of these hypotheses, as listed in Table III. Hypothesis number 7 further addresses the question of how complex microbial communities could have formed in such a short period of time (less than 500 million years) after the formation of the ocean. It is impossible to think of a single organism having appeared and evolved through some single-stepwise accumulation of genetic information by coordinated sequences of rare events within this time frame. It has been easier for some to imagine that life originated elsewhere and contaminated the early Earth (Crick and Orgel, 1973). In our overall hypothesis, the evolutionary time necessary for free-living organisms to evolve from complex organic compounds is reduced by the simultaneous availability of a vast number of environmental conditions (provided by gradients) under which the ultimately successful series of life-generating events could have occurred. The time-scale can be compressed even further by assuming as we do in hypothesis number 7, that the precursor to the first free-living cell was actually a community of 'precells' that contained small fragments of genetic material which, collectively and in an interdependent manner, provided for the complete panoply of metabolic, synthetic, and replicative functions. This hypothesis draws from the views of Margulis (1981), who proposed that eukaryotes evolved from prokaryotes through a series of symbioses. We are suggesting that prokaryotes evolved from communities of symbiotic 'precells'. The first self-replicating single cell(s) would have developed not through an internal step-wise progression of rare events, but rather through prolific genetic exchange with other 'precells' in the community, perhaps involving structures resembling transposable genetic elements and viral-like particles. This scenario allows for many different 'trial' combinations of sizeable genetic segments to have arisen rapidly and for the more successful combinations to have evolved into more complex entities and, ultimately, the first free-living organism.

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