Sources of nutrients and energy for a deep biosphere on Mars

Martin R Fisk

College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis

Stephen J Giovannoni

Department of Microbiology, Oregon State University, Corvallis

Abstract. Hydrothermal vents appear to be the tip of the subsurface biosphere in the ocean crust. The primary prducers in this biosphere are prokaryotes that tolerate a wide variety of physical and chemical conditions and are versatile in their use of inorganic compounds to drive metabolism. A synthesis of chemical and mineralogical data from Martian meteorites and measurements of the Martian surface suggest that conditions similar to those that make life possible in Earth's oceanic crust, namely, water, carbon, nutrients, appropriate temperatures, and gradients in redox conditions, also occur within Mars. Chemolithoautotrophic microorganisms capable of living below the seafloor on Earth would probably survive in some regions of the Martian subsurface.

1. Introduction

The surface of Mars appears inhospitable to life because there is no liquid water, temperatures are well below freezing, solar ultraviolet radiation is intense, and the abundance of organic carbon is extremely low [*Klein et al.*, 1992; *Klein*, 1998]. Although metabolizing and growing organisms may have adapted to these conditions [*Clark*, 1998], it has been suggested life is relegated to the Martian subsurface [*Boston et al.*, 1992; *Carr*, 1996; *Nealson*, 1997; *Shock*, 1997]. Even though evidence for subsurface life in a Martian meteorite [*McKay et al.*, 1996, 1997] may not be substantiated [*Bradley et al.*, 1997; *Jull et al.*, 1998; *Bada et al.*, 1998], the question remains, "Are conditions inside Mars suitable for life?" On Earth some life in the deep biosphere is independent of conditions at the surface. Our comparison of conditions inside Mars and Earth based on primary and secondary mineralogy of igneous rocks suggests that several present subsurface environments on Mars are capable of supporting life.

2. Earth's Subsurface Biosphere

The existence of microorganisms living in the upper 2 km of Earth is now well established. This biosphere contains 5% to 50% of Earth's biomass [*Parkes et al.*, 1994; *Gold*, 1992; *Whitman et al.*, 1998]. Some of this biomass has been found in sediments and sedimentary rocks [*Balkwill*, 1989; *Tseng et al.*, 1998; *Liu et al.*, 1997; *Parkes et al.*, 1994], in subsurface aquifers [*Pederson*, 1993; *Stevens and McKinley*, 1995; *Pederson et al.*, 1997; *Deming and Baross*, 1993; *Juniper et al.*, 1995], in silicic volcanic rocks [*Haldeman and Amy*, 1993; *Haldeman et al.*, 1993; *Fisk et al.*, 1998a], and in basalts [*Thorseth et al.*, 1992; *Giovannoni et al.*, 1996; *Furnes et al.*, 1996; *Torsvik et al.*, 1998; *Fisk et al.*, 1994, 1998b]. In this paper we limit our analysis to basalts because Martian meteorites suggest that basalts are the

dominant rock type of the Martian surface [*Longhi et al.*, 1992; *Singer and McSween*, 1993], and basalts to basaltic andesites were found at the Pathfinder landing site [*Rieder et al.*, 1997].

In basaltic crust on land, microbial activity is associated with the weathering of volcanic rocks [*Thorseth et al.*, 1991, 1992, 1995a; *Stevens and McKinley*, 1995]. In experiments, microbes are known to attach to basaltic glass, cover it with a biofilm, and produce pits [*Thorseth et al.*, 1995b]. Aquifers in basalts are enriched in H_2 and harbor populations of anaerobic autotrophic methanogens or acetatogens that use H_2 as the electron donor and CO_2 as the electron acceptor for energy-yielding metabolism [*Stevens and McKinley*, 1995]. Other members of the microbial community found in basalt aquifers use Fe^{3+} or sulfate as electron acceptors. Theoretically, microbes such as these could also live in subsurface ocean crust.

Microbial communities in the oceanic basalts are inferred from the microbiology of vent waters. Hyperthermophylic, anaerobic Archaea above an eruption in the South Pacific [*Huber et al.*, 1990] and microbial floc (silica and iron in the shape of microbial filaments, coccoids, and rods) near eruptions on ocean ridges [*Haymon et al.*, 1993; *Juniper et al.*, 1995] have been attributed to a subsurface community. The floc may have been dislodged by high fluid flow in fissures created by magma movement. Alternatively, the floc resulted from a microbial bloom that was induced by the mixing of oxidized seawater and reduced hydrothermal fluids, as has been demonstrated experimentally with oxygenated and H_2S-rich fluids [*Taylor and Wirsen*, 1997].

Additional evidence for a deep biosphere comes from basalts drilled from the seafloor hundreds to thousands of kilometers from hydrothermal vents where fluid flow is a few meters per year [*Thorseth et al.*, 1995a; *Giovannoni et al.*, 1996; *Furnes et al.*, 1996; *Fisk et al.*, 1997, 1998b; *Torsvik et al.*, 1998). Here the weathering of volcanic rocks produces distinct styles of pits and channels (Figure 1) that are also the locations of nucleic acids, carbon, and phosphorus, and in some cases cell-like bodies. This distinct weathering appears to be a ubiquitous feature of the cool (less than 100°C) ocean crust [*Fisk et al.*, 1998b]. The substrates,
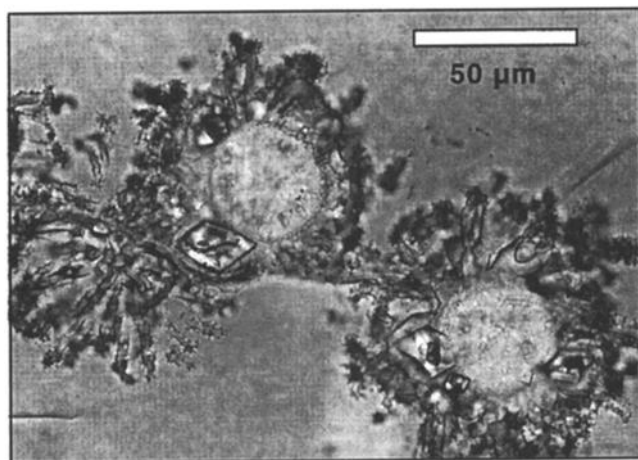
Figure 1. Transmitted light photomicrograph of weathering that is hypothesized to be created in association with microbial life. Radiating channels surround round vesicles and rhombohedral olivine grains along a fracture through the center of the figure. Channel tips commonly contain nucleic acids, carbon, and phosphorus. Sample 765D-5R-1-12 from the Ocean Drilling Program was collected in the Indian Ocean from 1.2 km below the seafloor at an *in situ* temperature of about 30°C.

metabolism, and phylogenetic origin of these organisms are being examined, and it is clear that the organisms can survive in low-oxygen environments with limited nutrients.

3. Metabolic Requirements of Subsurface Microbes

Many prokaryotes (Archaea and Bacteria) use inorganic compounds as substrates for the production of metabolic energy (chemolithotrophy), and many of these also are capable of growing autotrophically, using only CO_2 as a carbon source. Prokaryotes that couple autotrophy with chemolithotrophy can survive and grow in environments without sunlight or complex organic compounds. For organisms to grow in these environments, they must be supplied with C, N, P, S, and micronutrients as well as a source of chemical energy.

3.1. Sources of Carbon and Nutrients

In the ocean crust, carbon is found in basalts, circulating fluids, and calcite ($CaCO_3$) deposited in voids. Ocean basalt magmas typically contain about 0.02 wt % CO_2 [*Dixon et al.*, 1988], but equal amounts of CO_2 exsolve from magmas as they cool. Carbon dioxide is present in hydrothermal vent waters [*Von Damm*, 1995]. Calcite is a ubiquitous but minor component of the upper few hundred meters of the ocean crust [*Alt et al.*, 1996] and can be deposited by the circulation of fluids in the crust [*Griffith and Shock*, 1995]. Thus there are several sources of inorganic carbon for microbiological communities in the subsurface. In addition, methane and more complex organic compounds can be generated abiotically; these also may be a source of carbon [*Shock*, 1997].

Elemental or reduced nitrogen (N_2, NH_3, CN, or HCN) has concentrations of only 0.5 ppm in the basalts [*Marty et al.*, 1995] (Table 1). Even this low abundance, however, is sufficient to support about millions of microorganisms per gram of basalt, if the organisms are 6% N by weight (about 10 fg N per cell). Subsurface nitrogen can also be supplied by nitrates, nitrites, or ammonia derived from atmospheric N_2. Phosphorus, sulfur, as well as macronutrients (K, Mg, Ca, Fe) and micronutrients are present in basalt (Table 1) and thus can be supplied to circulating fluids by the weathering of these rocks [*Ehrlich*, 1996].

Table 1. Composition of Ocean Floor and Mars Basalts

Oxide	Ocean Floor, wt %		Mars, wt %		
	MORB*	MORB (High Iron)*	Shergotty[†]	A-3	A-7
SiO_2	49.3	49.0	49.5	58.6	55.5
TiO_2	1.45	3.71	10.87	0.8	0.9
Al_2O_3	16.2	11.5	7.59	10.8	9.1
FeO	8.5	18.4	19.8	12.9	13.1
MnO	0.12	0.29	0.52	0.9[‡]	0.5[‡]
MgO	8.66	4.31	8.95	3.0	5.9
CaO	12.2	9.13	9.63	5.3	6.6
Na_2O	2.91	2.00	1.29	3.2	1.7
K_2O	0.06	0.20	0.19	0.7	0.5
P_2O_5	0.06	0.31	0.72	2.1[‡]	2.1[‡]
Cr_2O_3	0.05	0.01	0.20	0.0	0.1
SO_3	0.18[§]	0.62 [‖]	0.16	2.2	3.9
CO_2	0.03[¶]	0.005[¶]	0.16	nd	nd
N_2	0.5 ppm**	nd	4 ppm[††]	nd	nd

MORB, mid-ocean ridge basalt; nd, not determined.
* *Fisk et al.* [1982]
[†] Basaltic Mars meteorite [*Laul*, 1986] A-3 and A-7 from *Rieder et al.* [1997]
[‡] From NASA website http://mars.sgi.com/science/apxs_elemental.html
[§] Reported as S [*Byers et al.* 1986]
[‖] Reported as S by *Perfit et al.* [1983]
[¶] *Dixon et al.* [1988]
** *Marty et al.* [1995]
[††] Released from shergottite Zagami above 600°C [*Grady et al.* 1997] Chassigny and two nakhlites have from 2.4 to 17 ppm N_2 [*Wright et al.* 1992]

Table 2. Mineralogy of Oceanic Crust and Mantle, Mars Meteorites, and Chondrite

Rock	Percent of Major Minerals					Description	Reference
	ol	en	di	pl	sp		
Basaltic rocks							
MORB	1	0	2	8	0	86% quench minerals, TR154 21D-3	1
Ocean diabase	1	0	46	49	0	ODP 148-504B-250R-1-57-60 cm	2
Shergotty	<1	0	72	23	2	basaltic SNC meteorite	3
EETA79001	9	5	65	17	0	basaltic SNC meteorite	4
Olivine rich rocks							
Peridotite	69	17	3	11	0.3	ultramafic rock from Indian Ocean	5
Chassigny	88	0	4	1	1.4	olivine-rich SNC meteorite	6
ALH77005	60	10	4	10	2.1	Martian meteorite	7
Chondrite	47	23	5	11	0.6	most common type of meteorite	8
EETA79001	9	5	65	17	0	basaltic SNC meteorite	4

Minerals are ol, olivine; en, enstatite; di, diopside; pl, plagioclase; and sp, spinel. Total minerals sum to less than 100% because minor phases are not tabulated. MORB, mid-ocean ridge basalt. References are 1, *Schilling et al.* [1983]; 2, *Alt et al.* [1993]; 3, *Stolper and McSween* [1979]; 4, *McSween and Jarosewich* [1983]; 5, *Dick* [1989]; 6, *Prinz et al.* [1974]; 7, *Treiman et al.* [1994]; 8, *Dodd* [1981].

3.2. Sources of Chemical Energy

Electron donors that are used or that can potentially be used by chemolithoautotrophs and that are relevant to this study are H_2, H_2S, S, CH_4, CO, Fe^{2+}, and Mn^{2+}. Some of these, H_2, H_2S, and CH_4, are generated abiotically in Earth by the reaction of water with rocks of the upper mantle [*Berndt et al.*, 1996] and by the reaction of water with basalt [*Stevens and McKinley*, 1995]. *Berndt et al.* [1996] found that both H_2 and CH_4 were generated by the reaction of a CO_2-bearing, NaCl aqueous fluid with the common igneous mineral olivine, $(Mg,Fe)_2SiO_4$, at 300°C and 500 bars. (Olivine typically makes up 1 to 5 vol % of ocean basalts [*Schilling et al.*, 1983] and 60 to 90 vol % of the oceanic upper mantle [*Michael and Bonatti*, 1985; *Dick*, 1989] (Table 2)) .

Evidence for this H_2-producing reaction in the oceanic lithosphere is the relatively high levels of H_2 and CH_4 in hydrothermal fluids from vents on mantle rocks compared to vent waters from basalts [*Lilley et al.*, 1983; *Welhan and Craig*, 1983; *Evans et al.*, 1988; *Kadko et al.*, 1990; *Donval et al.*, 1997].

Other electron donors (Fe^{2+}, Mn^{2+}, and S) are constituents of volcanic rocks (Table 1) and could be released by weathering. Electron donors can be coupled with the electron acceptors CO_2, Fe^{3+}, and Mn^{4+} that are also in basalts, or SO_4^{2-} and O_2 that are present in fluids to drive metabolic reactions. Additional acceptors (such as NO_3^-, and NO_2^-) are used by microbes on Earth but are not considered here because they have not been detected in the atmosphere or rocks of Mars. Examples of microbes capable of using these chemical substrates are given below.

Thiobacillus ferrooxidans and other species derive energy from reduced iron, reduced forms of sulfur, and metal sulfides, and obtain their carbon from CO_2. One Mn^{2+} oxidizing bacterium (SI95-9A1) has the genes for the key enzyme for fixing CO_2, but chemolithoautotrophy has not been confirmed [*Caspi et al.*, 1996]. The aerobic chemolithoautotroph *Alcaligenes eutrophus* and anaerobic methanogens and acetogens all oxidize H_2 and reduce CO_2. Although autotrophs have not been identified with the reduction (by H_2) of all of the electron acceptors listed above, the investigation of microbial consortia from new ecosystems

will probably reveal additional examples of redox couples that can be used advantageously by microbes. One potential mechanism identified by theorists using thermodynamic calculations is based on the reaction

$$FeS + H_2S => FeS_2 + H_2 \ (\Delta G = -41.9 \ kJ)$$
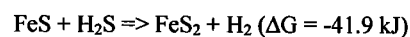
[*Koch and Schmidt*, 1991]. Although organisms with the capacity to catalyze this reaction have not been found, a simple series of biochemical reactions by which the energy from this reaction could be transduced to biological molecules has been postulated. This reaction does not require oxygen and, theoretically, could proceed in low O_2 environments.

3.3. Microbial Mineral Production and Degradation

Some metabolic reactions produce inorganic minerals such as hydroxides, oxides, carbonates, and sulfates inside cells, on the cell walls, and in the medium near the cell [*Schultze-Lam et al.*, 1996]. In hypersaline soils magnesium carbonate can be precipitated [*Rivadeneyra et al.*, 1993]; and magnetite (Fe_3O_4), maghemite (Fe_2O_3), and siderite ($FeCO_3$) are formed by thermophilic bacteria [*Liu et al.*, 1997]. Oxidation of Mn^{2+} to form insoluble Mn^{4+} oxides is carried out by a variety of bacteria and fungi [*Tebo et al.*, 1997]. The hydrous silicates, palagonite and clay, are derived from volcanic glass by microbial action [*Thorseth et al.*, 1991, 1992]. Disimilitory iron-reducing bacteria (that use Fe^{3+} as an electron acceptor) are known from sedimentary basins [*Liu et al.*, 1997]; these thermophilic bacteria (living at 45 to 75°C) generate magnetite (Fe_3O_4), maghemite (Fe_2O_3), and siderite ($FeCO_3$) as by-products. Additional references for microbially mediated mineral formation are given in Table 3.

Microbes also transform igneous minerals into secondary minerals and in the process release metabolic substrates, nutrients, or micronutrients. The three most abundant igneous minerals in the crusts of Earth and Mars (pyroxene, olivine, and feldspar), as well as silicate glass, are all weathered biologically on Earth [*Silverman*, 1979]. Agents associated with weathering are organic acids, bases, and chelators [*Berthelin*, 1983], compounds, such as siderophores [*Adams et al.*, 1992], and extracellular

polysaccharides [*Welch and Vandevivere*, 1994], but weathering could also be promoted by the reduction of insoluble species such as Fe^{3+} and Mn^{4+} to more mobile species.

3.4. Microbial Environments Are Maintained by Fluid Flow

A major driving force for life inside Earth is the difference in the oxidation state of Earth's surface and the reduced interior. Earth's deep interior has oxygen activities that are roughly 8 orders of magnitude less than the atmosphere [*Balhaus et al.*, 1990]. Chemical gradients caused by transport of reduced compounds from the interior of Earth to the surface, or of oxidized substances from the surface to the interior provide the nonequilibrium conditions needed by chemolithoautotrophs. Hydraulically driven downward flow can carry electron acceptors into the reduced subsurface [*Lovley and Chapelle*, 1995], and thermally or hydraulically driven flow can carry electron donors to the oxidized surface, such as at deep-sea hydrothermal vents, continental hotsprings, or deep basalt aquifers [*Stevens and McKinley*, 1995]. On Earth, hot springs provide a spectacular confluence of electron donors from the subsurface with electron acceptors from the surface. Most hot springs are driven by volcanism that occurs predominantly at convergent and divergent plate tectonic boundaries, but some thermal springs are also found in stable continental areas at great distances from plate boundaries and hotspot volcanoes (for example Bath, England, and Hot Springs, Arkansas).

4. Mars and SNC Meteorites

In section 3 we identified the key requirements for subsurface microbial habitats on Earth. This section uses results of Martian landers, orbiters, and Earth-based observations, as well as studies of the Martian SNC meteorites to show that the subsurface of Mars meets all the requirements for microbial life: appropriate temperatures, water, carbon, nutrients, metabolic substrates, and fluid flow. (SNC is the acronym for Shergotty, Nakhla, and Chassigny; namesakes for the shergottite, nakhlite, and chassignite groups of meteorites. There is firm evidence that they came from Mars [*Becker and Pepin*, 1984; *Pepin*, 1985; *McSween*, 1994; *Marti et al.*, 1995]. The meteorite ALH84001 also appears to be from Mars although it is distinct from the SNC groups [*Mittlefehldt*, 1994].)

4.1. Rock Types, Chemistry, and Mineralogy

The Martian crust appears to be basalts and basaltic andesites [*Singer and McSween*, 1993; *Rieder et al.*, 1997]. These rocks have 50% to 60 wt % SiO_2, 12 to 15 wt % FeO, and Al_2O_3, MgO, CaO, and Na_2O are additional major constituents. K_2O, P_2O_5, and MnO are minor components (Table 1). The silicate mineralogy of Mars rocks also appears to be the same as on Earth [*McSween*, 1994]. Of particular interest is the presence of the iron-magnesium silicate, olivine, in SNC meteorites (Table 2) and its presumed presence as the dominant mineral of the Martian mantle [*Longhi et al.*, 1992]. The presence of iron-bearing olivine is significant because of its reaction with water at the appropriate conditions to produce H_2 [*Berndt et al.*, 1996].

Remote sensing and SNC meteorites also indicate a wide variety of minor and secondary minerals on Mars (Table 3).

The Martian interior (as revealed from SNCs) contains clay, palagonite, hydrous minerals, carbonates, sulfates, sulfides, iron oxides, and amorphous silica (numbers in columns S, N, C, and A of Table 3 are references to the occurrence of these minerals). On the Martian surface, iron oxides are probably present, and magnesian clay, iron-rich palagonite, and sulfate are possibly present, [*Soderblom*, 1992; *Banin et al.*, 1992].

The secondary minerals in Table 3 are considered to be products of abiotic reactions, but their occurrence indicates that free energy favors their formation. Consequently, the formation of some minerals in Table 3 can be used by chemolithotrophs to sustain metabolic activity, so environments where these minerals form could, in theory, support subsurface life. Other minerals in Table 3 are microbial by-products, so in environments where they form naturally, microbes would not have to expend energy for their production [*Shock*, 1997].

4.2. Temperature and Water

Water was present on the surface of Mars and is probably present below the surface now [*Carr*, 1996]. SNC meteorites and ALH84001 all appear to have been exposed to aqueous solutions [*Wentworth and Gooding*, 1994]. The presence of hydrous minerals in some meteorites (Table 3) indicates that fluids were present in the rocks prior to the meteorites reaching Earth. The amount of H_2O that could be held in the pore space of the regolith is equivalent to a global ocean 500 to 1400 m deep, of which 60% to 70% is ice [*Clifford*, 1993]. This frozen zone of Mars (cryosphere) is estimated to be a minimum of 1 km and a maximum of 8 km thick [*Squyers et al.*, 1992; *Clifford*, 1993]. Below the cryosphere, water equivalent to a global ocean 200 m deep could exist [*Clifford*, 1993]. The zone suitable for life could extend 8 to 25 km below the cryosphere if the thermal gradients are between 5 and 15°C/km [*Solomon and Head*, 1990]. As the Martian crust is at least 8 km thick [*Longhi et al.*, 1992; *Bills and Ferrari*, 1978], subsurface water would be in contact with basaltic or mantle rocks, as it is in Earth's oceanic lithosphere.

4.3. Carbon

Dissolved inorganic or organic carbon is likely to be available to microorganisms from subsurface fluids on Mars. The Martian atmosphere is 95% carbon dioxide (pressure of 7 to 10 mbar), so it would be present in fluids exposed to the atmosphere. Mars probably had a more substantial CO_2-rich atmosphere in the past, much of which was lost to space [*Jakosky and Jones*, 1997], but thermodynamic calculations suggest some of the CO2 could be sequestered in the Martian interior as carbonate [*Griffith and Shock*, 1995] or as complex organic molecules [*Shock*, 1997]. These calculations are consistent with the small amount of carbonate found in SNC meteorites and the conclusion that carbon was present in the fluids that circulated through the SNC meteorites prior to their arrival on Earth [*Wentworth and Gooding*, 1994]. The isotopic ratio of carbon isotopes in SNC meteorites and the atmosphere suggest that there are two reservoirs for CO_2; one in the atmosphere and one in the Martian interior [*Jakosky and Jones*, 1997].

4.4. Nutrients

Nutrients are available from Martian rocks and, in the case of nitrogen, possibly from the atmosphere, which has 2.7% N_2

Table 3. Secondary Minerals and Compounds of Mars

Chemical Type	Mineral Name	Formula	Observed*					Microbially Mediated†	Possible Precursors	Conditions‡	
			S	N	C	A	R			Redox	pH
Carbonate	calcite	$CaCO_3$	9	10	11	1	13	b	CO_2, Ca^{2+}_{aq}	high	high
	magnesite	$MgCO_3$	12		11	1	19	b	CO_2, Mg^{2+}_{aq}	high	high
	siderite	$FeCO_3$		6		1		a	CO_2, Fe^{2+}_{aq}	high	high
Sulfate	gypsum	$CaSO_4 \cdot 2H_2O$	9	10	11	14	13	a	nd	high	nd
	iron sulfate	$FeSO_4$				14		d	nd	high	nd
	epsomite	$MgSO_4$		10					nd	high	nd
Iron oxide	magnetite	Fe_3O_4	§	15		1		c	Fe_2O_3	low	nd
	ferrihydrite	$Fe_2O_3 \cdot nH_2O$		15				a	FeO	high	nd
	goethite	$FeO(OH)$	18	5				a	pyrite	high	nd
	hematite	Fe_2O_3		4			8	a	nd	high	nd
Phosphate	Mg phosphate?		9					d	nd	high	nd
Hydrous	iddingsite			16					olivine	high	nd
	palagonite						8	e	glass	high	nd
	serpentine			4					olivine	high	nd
	smectite			15			13	f	olivine	high	nd
Sulfides	greigite?	Fe_3S_4				1		c	FeS_2, SO_3	low	high
	pyrite	FeS_2				17		a	nd	low	nd
	pyrrhotite	$Fe_{1-x}S$				1		c	nd	low	nd
Organic compounds			2			1			nd	low	nd

nd, not determined.

* Occurrences of the secondary minerals in meteorite groups or regolith are indicated by a reference number.

S, shergottite; N, nakhlite; C, Chassigny; A, ALH84001; R, regolith.

† Microbially mediated occurrences of secondary minerals on Earth are indicated by letter references.

‡ High or low redox indicates that the secondary mineral was formed by the addition or removal of O_2; some minerals also require high pH.

§ Magnetite occurs as a primary igneous mineral but not as a secondary mineral.

References for secondary mineral occurrence from columns S, N, C, A, R: 1, McKay et al. [1996]; 2, Wright et al. [1989]; 3, Gooding and Muenow [1986]; 4, Treiman and Gooding [1991]; 5, Boctor et al. [1976]; 6, (Mn,Fe)CO3 [Chatzitheodoridis and Turner, 1990]; 7, Bunch and Reid [1975]; 8, Soderblom [1992]; 9, Gooding et al. [1988]; 10, Gooding et al. [1991]; 11, Wentworth and Gooding [1994]; 12, Mg bearing CaCO3 [Gooding and Wentworth, 1991]; 13, inferred [Gooding, 1992]; 14, Wentworth and Gooding [1995]; 15, Treiman et al. [1993]; 16, Berkley et al. [1980]; 17, Mittlefehldt [1994]; 18, McSween et al. [1979]; 19, inferred to make up as much as 10% of the regolith based on infrared absorption [Calvin et al., 1994].

References for microbial production of minerals: a, Brown et al. [1994]; b, Ferris et al. [1994]; c, Frankel [1991]; d, Lowenstam [1986]; e, Thorseth et al. [1992]; f, Furnes et al. [1996].

[Owen, 1992]. Atmospheric N_2 could be transformed to nitrogen compounds that are useful to microorganisms by electrical discharge or ultraviolet radiation, but it is not known how much of these compounds are presently produced in the atmosphere of Mars [McKay et al., 1992; Barth et al., 1992], and so far they have not been detected [Owen, 1992]. The atmosphere may have had more N_2 in the past which was lost to space or to the crust by the formation of nitrogen compounds [Mancinelli, 1996]. Although sequestered nitrogen compounds have not been found in SNC meteorites, N_2 (as N_2, NH_3, CN, or HCN) is present in similar amounts in basalts on Earth and Mars (Table 1). This nitrogen is sufficiently concentrated to support microbial life. Another source of reduced nitrogen (ammonia) is abiotically produced by the reaction of N_2 with metal, or by the reaction of water with reduced minerals to produce H_2, followed by the reduction of N_2 by H_2 [Brandes et al., 1998].

Phosphorus, sulfur, and macronutrients (Ca, K, Mg, and Fe) and micronutrients have abundances in Martian rocks that are similar to oceanic basalts (Table 1), so it appears that all nutrients required by microorganisms are present on Mars basalts. Aqueous weathering of these basalts (as seen in some SNC meteorites) would release nutrients to fluids where they would be available to microorganisms.

4.5. Metabolic Substrates on Mars

One likely electron donor is H_2, which is produced by the reaction of water and olivine. Olivine comprises as much as 88% of the Martian meteorite Chassigny, and olivine is present in other meteorites (Table 2), so it is likely to be a major component of the interior of Mars. Thermodynamic calculations [Griffith and Shock, 1997] indicate that weathering of Chassigny at 150°C will produce about 15% serpentine, $Mg_6(Si_4O_{10})(OH)_8$. Serpentine formation was accompanied with H_2 production in water-olivine reaction experiments [Berndt et al., 1996]. The presence of serpentine in nahklites indicates that hydrogen-producing reactions have occurred in the Martian subsurface.

With H_2 as the electron donor, a number of oxidized components of the Martian interior could act as electron acceptors; Fe^{3+}, SO_4^{2-}, CO_2, CO, and possibly Mn^{4+} and O_2. These are all known to be present at the Martian surface or in SNC meteorites. Fe^{3+} can be released by weathering pyroxene in the Martian subsurface. CO_2, and SO_4^{2-}, are likely to be present in subsurface fluids based on the observation of secondary carbonate and sulfate minerals in SNC meteorites (Table 3). Mn^{4+} is an energetic electron acceptor that may also be present in the Martian surface, based on its abundance in Mars rocks and the relatively oxidized surface of Mars.

Other electron donors (Fe^{2+} and Mn^{2+} and S) are available from the weathering of the minerals that make up basalts (pyroxene, olivine, magnetite, sulfides) or from the abiotic production (H_2S and CH_4). CO is a minor constituent of the Martian atmosphere (0.07%) and potentially could be an electron donor. These electron donors are typically coupled with O_2, which would require sufficient O_2 on Mars to support microaerophilic metabolism.

The small amount of O_2 (0.13%; 0.01 mbar) in the atmosphere is probably due to photolysis of CO_2 [Barth et al., 1992]. Brine in equilibrium with the atmosphere would have 0.3 to 0.7 μg/L of O_2 at a temperature of 260°K [Clegg and Brimblecombe, 1990]. This is well below the level required by E. coli, which needs about 9 μg/L to maintain metabolism at half of the full rate [Kita et al., 1984]. However, the hydrogen-oxidizing hyperthermophilic bacteria of the genus Aquifex use oxygen concentrations as low as 7.5 ppm [Deckert et al., 1998], which is slightly less than 0.01 mbar of O_2. Organisms with similar microaerophilic requirements may be able to use free oxygen as the electron acceptor for H_2, Fe^{2+}, Mn^{2+}, H_2S, CH_4, and S. Farquhar et al. [1998] find evidence for the storage of 0.1 g/cm^2 of oxygen in the regolith, so if there is a net production of O_2 in the atmosphere, it could be balanced by microbial consumption of O_2 in the subsurface.

Other sources of O_2 may also be available on Mars [Clark, 1979]. O_2 was released from Martian soil that was moistened and heated, probably from the decomposition of superoxides [Oyama and Berdahl, 1977]. Even, if there is insufficient O_2 for autotrophic oxidation of reduced inorganic compounds, other metabolic pathways discussed above such as the reduction of CO_2, CO, SO, Fe^{3+}, or Mn^{4+} by H_2 are suitable to the subsurface of Mars [Boston et al., 1992; Nealson, 1997, Jakosky and Shock, 1998]. Yet to be documented reactions may also be possible.

5. Discussion

The ingredients for life (H_2O, C, N, P, macronutrients, micronutrients, and chemical substrates) all appear to be present on Mars. In addition to these chemical ingredients, fluid flow or diffusion in the subsurface is needed to maintain chemolithoautotrophic metabolism. Secondary minerals in some SNCs reveal that there were fluxes of both oxidized and reduced fluids inside Mars (Table 3). For example, the weathering of sulfate to sulfide in ALH84001 [McKay et al., 1996] suggests that the fluids interacting with the meteorite were reducing. In the other SNC meteorites there is oxidative weathering of sulfide to sulfate (Table 3). Previously, attention was given to hydrothermal forcing of fluid flow on Mars [Boston et al., 1992; Shock, 1997; Nealson, 1997; Jakosky and Shock, 1998; Gulick, 1998], possibly because

much of Earth's thermally driven flow and subsurface biology are associated with volcanic activity; however, other mechanisms of fluid flow should be considered.

On Earth, volcanoes at diverging and converging plates provide much of the heat to drive hydrothermal flow, but a few percent of Earth's heat flux is from isolated hotspot volcanoes. Mars lacks plate tectonics, so hydrothermal flow would be confined to isolated volcanoes [Gulick, 1998]. Fluid flow on Mars may also result from (1) thermal springs unrelated to volcanoes, such as are sometimes found on Earth; (2) water vapor transport through moist, porous material driven by a thermal gradient [Clifford 1993]; (3) pumping of water by impacts or earthquakes [Clifford, 1993]; (4) hydraulic flow of meltwater from the base of the polar caps [Carr, 1996]; and (5) circulation of brines from the base of the cryosphere (Figure 2).

Mars does not have as much water as Earth, but on Earth microbes have adapted to extremely dry environments, such as the dry valleys of Antarctica [Friedmann, 1982; Friedmann et al., 1987], where water is available a few days a year. In other dry environments such as temperate deserts, microorganisms live in deep soils [Monger et al., 1991], and they are associated with the formation of the dark coatings of Fe and Mn oxides and hydroxides known as desert varnish [Adams et al., 1992]. In hyperarid deserts, water is supplied by rare fog or dew, so perhaps on Mars, only occasional wetting is sufficient to maintain life. For sustained microbial activity, the water must be part of a hydrologic cycle.

On Mars a hydrologic cycle could be maintained by the evaporation of subsurface ice at low latitudes, its condensation at the north pole [Zurek, 1992], and by melting of the base of the polar deposit to resupply aquifers (cycle I-I', Figure 2). It has been suggested that at an interconnected groundwater system could exist [Clifford, 1993] to transport water from the base of the northern polar deposit toward the equator. Another cycle (II, Figure 2) may be maintained by circulating brines at the base of the cryosphere. Dense, cold, residual brines would form by vapor transport to the cryosphere. Sinking brines would be replaced by less saline, warmer and more reduced brines from below.

Fluids in equilibrium with the atmosphere and oxidized surface rocks would transport CO_2, SO_3, and O_2 into the planet at the poles (reducing zone 1, Figure 2). This flux of oxidized components into H_2-generating crust or mantle could produce a zone that maintains sulfide, methane, or acetate producing bacteria. Electron acceptors, Fe^{3+} (and probably Mn^{4+}), are present on the Martian surface, but they are unlikely to be transported by water because of their insolubility. Therefore they would tend to accumulate on the surface. Downward flow of relatively oxidized brines may also occur at the base of the cryosphere (zone 6, Figure 2).

Upward fluxes of reduced fluids could be driven thermally (zones 2 and 3, Figure 2), as they are on Earth, or by the transport of vapor to the cryosphere (zone 4, Figure 2) due to the thermal gradient [Clifford, 1993]. Convective replacement of sinking brines (zone 5, Figure 2) is also possible. In these upflow zones, H_2 could react with CO_2, SO_3, or O_2, but also with Fe^{3+} and Mn^{4+}, which are likely to be present near the surface. If there is sufficient O_2 to support metabolic activity, H_2S, S, Fe^{2+}, Mn^{2+}, and CH_4 in rising reduced fluids would be oxidized near the surface. In the absence of fluid flow, diffusion of H_2 along fractures in the mantle and crust could potentially reduce insoluble oxides
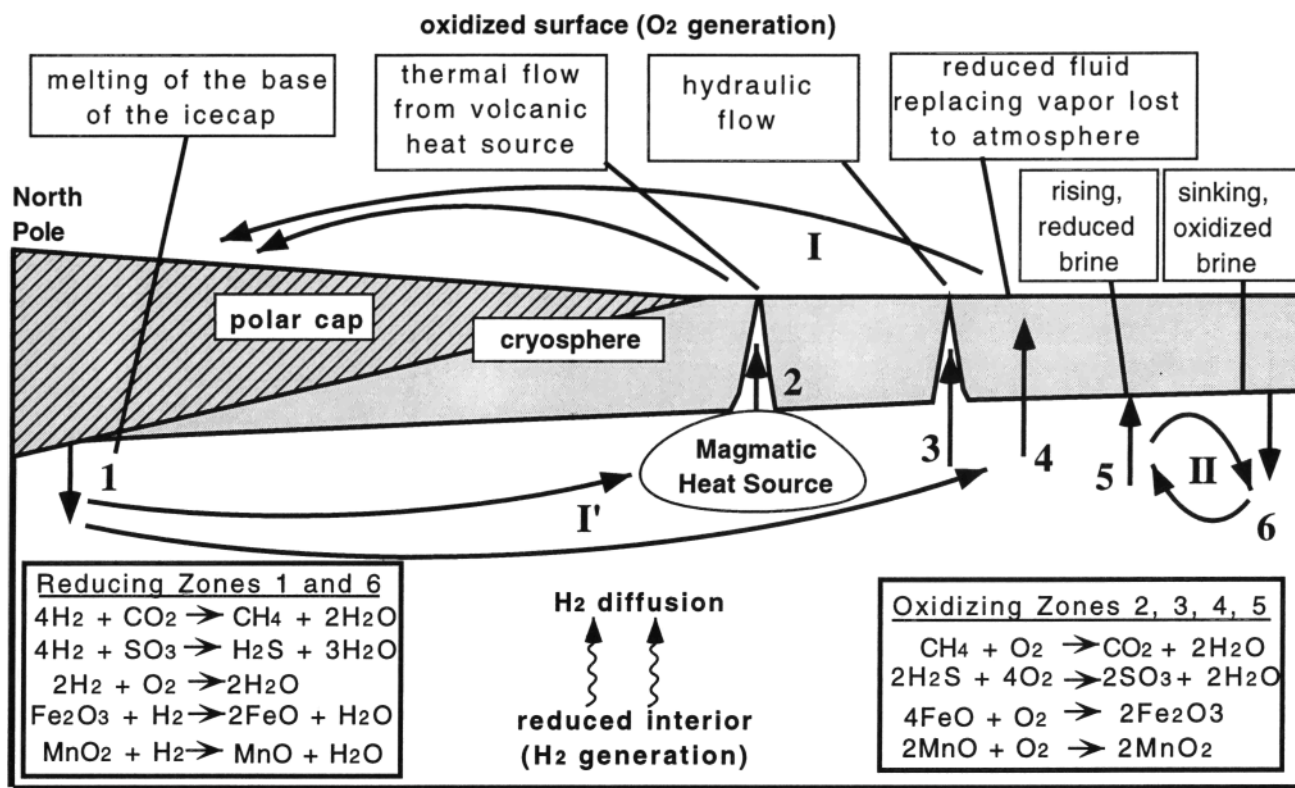
oxidized surface (O₂ generation)

| melting of the base of the icecap | thermal flow from volcanic heat source | hydraulic flow | reduced fluid replacing vapor lost to atmosphere |

rising, reduced brine | sinking, oxidized brine

North Pole

polar cap

cryosphere

Magmatic Heat Source

Reducing Zones 1 and 6
$4H_2 + CO_2 \rightarrow CH_4 + 2H_2O$
$4H_2 + SO_3 \rightarrow H_2S + 3H_2O$
$2H_2 + O_2 \rightarrow 2H_2O$
$Fe_2O_3 + H_2 \rightarrow 2FeO + H_2O$
$MnO_2 + H_2 \rightarrow MnO + H_2O$

H₂ diffusion

reduced interior (H₂ generation)

Oxidizing Zones 2, 3, 4, 5
$CH_4 + O_2 \rightarrow CO_2 + 2H_2O$
$2H_2S + 4O_2 \rightarrow 2SO_3 + 2H_2O$
$4FeO + O_2 \rightarrow 2Fe_2O_3$
$2MnO + O_2 \rightarrow 2MnO_2$

Figure 2. Schematic shallow cross section of the north polar region of Mars (not to scale) with six oxidation-reduction zones that could support life. The cryosphere is gray, and the north polar deposit is indicated with diagonal rule. The surface is oxidized relative to the planet interior due to oxygen production in the atmosphere. Hydrologic cycles I and II are indicated by solid arrows. The six oxidation-reduction zones are created by (1) oxidized fluids generated by melting at the base of the polar deposit sinking into the reduced regions of the crust and mantle; (2) reduced fluids driven by magmatic heat convecting upward; (3) hydraulically driven flow; (4) water replacing vapor lost to the base of the cryosphere [Clifford, 1993]; and by (5) warm brines convecting upward to replace (6) dense, oxidized brines. The lower left box indicates a number of redox reactions that could be catalyzed by microbes in regions 1 and 6. The lower right box indicates reactions that can be catalyzed by microbes in the oxidized surface of Mars if there is sufficient oxygen. All the reactions in zones 1 and 6 could also occur in zones 2, 3, 4, and 5 if H₂ is present in the rising fluid. Fluxes in zones 2 and 3 could produce isolated thermal oases.

Fe_2O_3 or MnO_2. Also, as yet undocumented metabolic reactions, such as the reduction of FeS by H₂, could occur in the subsurface.

It is noteworthy that primitive hydrogen-oxidizing bacteria on Earth are capable of utilizing O₂ at partial pressures very similar to those found in the Martian atmosphere. The total biomass that could be supported on Mars by aerobic chemolithotrophy would be limited by the abiotic production of O₂ in the atmosphere. Therefore, in theory, the presence of large populations of aerobic chemolithotrophic microorganisms, similar to *Aquifex*, in the Martian subsurface could affect the accumulation of O₂ in the atmosphere. If there is a net production of O₂ in the Martian atmosphere, it is likely to be small, and a net flux of O₂ from the atmosphere to the regolith would generate less biomass than the energy available from weathering of basalt [*Jakosky and Shock*, 1998]. H₂-producing reactions could have generated about 20 g of biomass per cm² of Martian surface over the life of the planet [*Jakosky and Shock*, 1998].

Methane is produced by autotrophic organisms that use H₂ and CO₂. CH₄ has not been detected in the Martian atmosphere (the upper limit is 0.02 ppm of CH₄ [*Owen*, 1992]), so the rate of methane transport to the atmosphere would have to be less than the rate of its photodissociation to CO₂ and H₂ or its oxidation to compounds such as formaldehyde [*Moreau et al.*, 1997]. CH₄ could be stored as gas hydrate in the cryosphere over regions of focused upflow (zones 2 to 5, Figure 2). Catastrophic decomposition of these gas hydrates may create chaotic terranes.

Table 3 lists some inferred and confirmed secondary minerals that are present in SNC meteorites or Martian regolith. These minerals can be produced by microbial weathering of the primary minerals or by microbial activity in aqueous fluids. This does not mean that microbes were involved in formation of these minerals because these reactions are favored by thermodynamics and can proceed abiotically. Microbes, however, are able to extract metabolic energy from some mineral transformations, and the occurrence

of these transformations in SNC meteorites suggests that they could also provide the driving force of subsurface life on Mars.

6. Conclusions

We conclude that the major conditions are satisfied for a biosphere in Mars that is similar to the biosphere observed in silicate rocks in aqueous environments on Earth. These requirements are (1) water, (2) a source of carbon, (3) temperatures above freezing and below 120°C, (4) basaltic crust as a source of nutrients, (5) gradients in oxidation state, (6) chemical energy for metabolism of chemolithotrophs, and (7) fluid flow. Observations of the Martian surface and SNC meteorites indicate that the first five requirements are satisfied. Chemical energy could be derived from the reaction of oxidized compounds (Fe^{3+}, SO_4^{2-}, CO_2 and possibly Mn^{4+}) with H_2. The production of H_2 inside Mars seems assured given the olivine content and the occurrence of serpentine in some SNC meteorites. Abiotically produced O_2 in the atmosphere may be abundant enough to support the metabolism of aerobic chemolithotrophs that oxidize H_2 and other reduced molecules (Fe^{2+}, H_2S, CH_4, and Mn^{2+}). Mechanisms of fluid flow have been proposed for Mars that could bring reduced and oxidized molecules together, thereby providing the conditions needed to sustain microbial life. Thermally and hydrolically driven upflow zones (fluxes 2 and 3 in Figure 2) may be expressed on the surface. Recharge zones (flux 1 in Figure 2) may not have any surface expression. Methanogenesis could occur in regions of high olivine content in the crust and in the mantle resulting in the formation of methane hydrates in the cryosphere.

The mass of Martian life will be constrained by the production and flux of compounds that can serve as energy sources for chemolithoautotrophic primary production. A Martian biosphere might well resemble Earth's earliest biosphere and, conceivably, could harbor a diverse assemblage of species in subsurface habitats that vary in oxygen availability, temperature, and sources of chemical energy available for metabolism.

References

Adams, J. B., F. Palmer, and J. T. Staley, Rock weathering in deserts, mobilization and concentration of ferric iron by microorganisms, Geomicrobiol. J., 10, 99-114, 1992.

Alt, J. C., et al., (Eds.) Proceedings Ocean Drilling Program, vol. 148, Ocean Drill. Program, College Station Tex., 1993.

Alt, J. C., D. A. H. Teagle, C. Laverne, D. A. Vanko, W. Bach, J. Honnerez, K. Becker, M. Ayadi, and P. A. Pezard, Ridge flank alteration of upper oceanic crust in the eastern Pacific, synthesis of results for volcanic rocks of holes 504B and 896A, Proc. Ocean Drill. Program, Sci. Results,148, 435-450, 1996.

Bada, J. L., D. P. Glavin, G. D. McDonald, and L. Becker, A search for endogenous amino acids in martian meteorite ALH84001, Science, 279, 362-365, 1998.

Balhaus, C., R. F. Berry, and D. H. Green, Oxygen fugacity controls in the Earth's upper mantle, Nature, 348, 437-440, 1990.

Balkwill, D. L., Numbers, diversity, and morphological characteristics of aerobic, chemoheterotrophic bacteria in deep subsurface

sediments from a site in South Carolina, Geomicrobiol. J., 7, 33-51, 1989.

Banin, A., B. C. Clark, and H. Wänke, Surface chemistry and mineralogy, in Mars, edited by H. H. Kieffer, B. M. Jakosky, C.W. Snyder, and M. S. Matthews, pp. 594-625, Univ. of Ariz. Press, Tucson, 1992.

Barth, C. A., A. I. F. Stewart, S. W. Bougher, D. M. Hunten, S. J. Bauer, and A. F. Nagy, Aeronomy of the current martian atmosphere, in Mars, edited by H. H. Kieffer, B. M. Jakosky, C.W. Snyder, and M. S. Matthews, pp.1054-1089, Univ. of Ariz. Press, Tucson, 1992.

Becker, R. H., and R. O. Pepin, The case for a Martian origin of the shergottites, nitrogen and noble gases in EETA 79001, Earth Planet. Sci. Lett., 69, 225-242,1984.

Berkley, J. L., K. Keil, and M. Prinz, Comparative petrology and origin of Governador Valadares and other nakhlites, Proc. Lunar Planet. Sci. Conf., 11th, 1089-1102,1980.

Berndt, M. E., D. E. Allen, and W. E. Seyfried, Reduction of CO2 during serpentinization of olivine at 300°C and 500 bar, Geology, 24, 351-354, 1996.

Berthelin, J., Microbial weathering processes, in Microbial Geochemistry, edited by W. E. Krumbein, pp. 223-262, Blackwell Sci., Cambridge, Mass., 1983.

Bills, B. G., and A. J. Ferrari, Mars topography, harmonics, and geophysical implications, J. Geophys. Res., 83, 3497-3508,1978.

Boctor, N. W., H. O. Meyer, and G. Kullerud, Lafayette meteorite, petrology and opaque mineralogy, Earth Planet. Sci. Lett., 32, 69-76,1976.

Boston, P. J., M. V. Ivanov, and C. P. McKay, On the possibility of chemosynthetic ecosystems in subsurface habitats on Mars, Icarus, 95, 300-308, 1992.

Bradley, J. P., R. P. Harvey, and H. Y. McSween Jr., No "nanofossils" in martian meteorite orpthopyroxene, Nature, 390, 454, 1997.

Brandes, J. A., N. Z. Boctor, G. D. Cody, B. A. Cooper, R. M. Hazen, and H. S. Yoder Jr., Abiotic nitrogen reduction on the early Earth, Nature, 395, 365-367,1998.

Brown, D. A., D. C. Kamineni, J. A. Sawicki, and T. J Beveridge, Minerals associated with biofilms occurring on exposed rock in a granitic underground research laboratory, Appl. Environ. Microbiol., 60, 3182-3191,1994.

Bunch, T. E., and A. M. Reid, The nakhlites, I, Petrography and mineral chemistry, Meteoritics, 10, 303-315,1975.

Byers, C. D., M. O. Garcia, and D. W. Muenow, Volatiles in basaltic glasses from the East Pacific Rise at 21°N, implications for MORB sources and submarine lava flow morphology, Earth Planet. Sci. Lett., 79, 9-20,1986.

Calvin, W. M., T. V. V. King, and R. N. Clark, Hydrous carbonates on Mars?, Evidence from mariner 6/7 infrared spectrometer and ground-based telescopic spectra, J. Geophys. Res., 99, 14,659-14,675,1994.

Carr, M. H., Water on Mars, Oxford Univ. Press, New York, 1996.

Caspi, R., B. M. Haygood, and B. M. Tebo, Unusual ribulose-1,5-bisphosphate carboxylase/oxygenase genes from marine manganese-oxidizing bacterium, Microbiology, 142, 2548-2559, 1996.

Chatzitheodoridis, E., and G., Turner, Secondary minerals in the Nakhla meteorite, Meteoritics, 25, 354,1990.

Clark, B. D., Solar-driven chemical energy sources for a Martian biota, Origins Life, 9, 241-249, 1979.

Clark, B. D., Surviving the limits to life at the surface of Mars, J. Geophys. Res., 103, 28,545-28,555, 1998.

Clegg, S. L., and P. Brimblecombe, The solubility and activity coefficient of oxygen in salt solutions and brines, Geochim. Cosmochim. Acta, 54, 3315-3328,1990.

Clifford, S. M., A model for the hydrologic and climatic behavior of water on Mars, J. Geophys. Res., 98, 10,973-11,016, 1993.

Deckert, G., et al., The complete genome of the hyperthermophilic bacterium Aquifex aeolicus, Nature, 392, 353-358,1998.

Deming, J. W., and J. A. Baross, Deep-sea smokers,windows to a subsurface biosphere?, Geochim. Cosmochim. Acta, 57, 3219-3230, 1993.

Dick, H. J. B., Abyssal peridotites, very slow spreading ridges and ocean ridge magmatism. in Magmatism in the Ocean Basins, edited by A. D. Saunders, and M. J. Norry, pp. 71-98, Geol. Soc., London, 1989.

Dixon, J. E., E. Stolper, and J. R. Delaney, Infrared spectroscopic

measurements of CO_2 and H_2O in Juan de Fuca Ridge basaltic glasses, *Earth Planet. Sci. Lett., 90*, 87-104, 1988.

Dodd, R. T., *Meteorites, A Petrologic-Chemical Synthesis*, Cambridge Univ. Press, New York, 1981.

Donval, J. P., J. L. Charlou, E. Douville, J. Knoery, Y. Fouquet, E. Poncevera, P. Jean Baptiste, M. Stievenard, and C. German, High H_2 and CH_4 content in hydrothermal fluids from Rainbow site newly sampled at 36°14'N on the AMAR segment, Mid-Atlantic Ridge, diving FLORES cruise, July (1997). Comparison with other MAR sites (abstract), *Eos Trans. AGU, 78*, Fall Meet. Suppl., 832, 1997.

Ehrlich, H. L., How microbes influence mineral growth and dissolution, *Chem. Geol., 132*, 5-9, 1996.

Evans, W. C., L. D. White, and J. B. Rapp, Geochemistry of some gases in hydrothermal fluids from the southern Juan de Fuca Ridge, *J. Geophys. Res., 93*, 15,305-15,313, 1988.

Farquhar, J., M. H. Thiemens, and T. Jackson, Atmosphere-surface interactions in Mars $\Delta^{17}O$ measurements of carbonate from ALH 84001, *Science, 280*, 1580-1582, 1998.

Ferris, F. G., R. G. Wiese, and W. S. Fyfe, Precipitation of carbonate minerals by microorganisms: Implications for silicate weathering and the global carbon dioxide budget, *Geomicrobiol. J., 12*, 1-13, 1994.

Fisk, M.R., A. E. Bence, and J-G. Schilling, Major-element chemistry of Galapagos Rift Zone magmas and their phenocrysts, *Earth Planet. Sci. Lett., 61*, 171-189, 1982.

Fisk, M. R., S. J. Giovannoni, and T. D. Mullins, Microbial alteration of ocean ridge basalt glass (abstract), *Eos Trans. AGU, 78*, Fall Meet. Suppl., 706, 1994.

Fisk, M. R., S. J. Giovannoni, E. Urbach, and I. H. Thorseth, Microbial weathering of the volcanic ocean crust (abstract), *Eos Trans. AGU, 78*, Fall Meet. Suppl., 740, 1997.

Fisk, M. R., I. H. Thorseth, S. J. Giovannoni, E. Urbach, and M. J. Streck, Endolithic microbes in the Rattlesnake tuff, Oregon Blue Mountains (abstract), *Eos Trans. AGU, 78*, Fall Meet. Suppl., 58, 1998a.

Fisk, M. R., S. J. Giovannoni, and I. H. Thorseth, Alteration of oceanic volcanic glass: Textural evidence of microbial activity, *Science, 281*, 978-980, 1998b.

Frankel, R. B., Iron biominerals, an overview, in *Iron Biominerals*, edited by R. B. Frankel and R. P. Blakemore, 1-6, Plenum, New York, 1991.

Friedmann, E. I., Endolithic microorganisms in the Antarctic cold desert, *Science, 215*, 1045-1053, 1982.

Friedmann, E. I., C. P. McKay, and J. A. Nienow, The cryptoendolithic microenvironment in the Ross Desert of Antarctica: Nanoclimate data, 1984 to 1986, *Polar Biol., 7*, 272-287, 1987.

Furnes, H., I. Thorseth, O. Tumyr, T. Torsvik, and M. Fisk, Microbial activity in the alteration of glass from pillow lavas from ODP Hole 8968, Leg 148, *Proc. Ocean Drill. Program, Sci. Results,148*, 191-206, 1996.

Giovannoni, S. J., M. R. Fisk, T. D. Mullins, and H. Furnes, Genetic evidence for endolithic microbial life colonizing basaltic glass/seawater interfaces, *Proc. Ocean Drill. Program, Sci. Results,148*, 207-214, 1996.

Gold, T., The deep, hot biosphere, *Proc. Natl. Acad. Sci. USA, 89*, 6045-6049, 1992.

Gooding, J. L., Soil mineralogy and chemistry on Mars: Possible clues from salts and clays in SNC meteorites, *Icarus, 99*, 28-41, 1992.

Gooding, J. L., and D. W. Muenow, Martian volatiles in shergottite EETA79001: New evidence from oxidized sulfur and sulfur-rich aluminosilicates, *Geochim. Cosmochim. Acta, 50*, 1049-1059, 1986.

Gooding, J. L., and S. J. Wentworth, Origin of "white druse" salts in the EETA79001 meteorite (abstract), *Lunar Planet. Sci., XXII*, 461-462, 1991.

Gooding, J. L., S. J. Wentworth, and M. E. Zolensky, Calcium carbonate and sulfate of possible extraterrestrial origin in the EETA79001 meteorite, *Geochim. Cosmochim. Acta, 52*, 909-915, 1988.

Gooding J. L., S. J. Wentworth, and M. E. Zolensky, Aqueous alteration of the Nakhla meteorite, *Meteoritics, 26*, 135-143, 1991.

Grady, M. M., I. P. Wright, and C. T. Pillinger, A carbon and nitrogen study of Zagami, *J. Geophys. Res., 102*, 9165-9173, 1997.

Griffith, L. L., and E. L. Shock, A geochemical model for the formation of hydrothermal carbonate on Mars, *Nature, 377*, 406-408, 1995.

Griffith, L. L., and E. L. Shock, Hydrothermal hydration of Martian crust: Illustration via geochemical model calculations, *J. Geophys. Res., 102*, 9135-9143, 1997.

Gulick, V. C., Magmatic intrusions and a hydrothermal origin of fluvial valleys on Mars, *J. Geophys. Res., 103*, 19,365-19,387, 1998.

Haldeman, D. L., and P. S. Amy, Bacterial heterogeneity in deep subsurface tunnels of Rainer Mesa, Nevada Test Site, *Microbiol. Ecol., 25*, 183-194, 1993.

Haldeman, D. L., P. S. Amy, D. Ringleberg, and D. C. White, Characterization of the microbiology within a 21 m^3 section of rock from the deep subsurface, *Microbiol. Ecol., 26*, 145-159, 1993.

Haymon, R. M., et al., Volcanic eruption of the mid-ocean ridge along the East Pacific Rise crest at 9°45-52'N: Direct submersible observations of seafloor phenomena associated with an eruption event in April 1991, *Earth Planet. Sci. Lett., 119*, 85-101, 1993.

Huber, R., P. Stoffers, J. L. Cheminee, H. H. Richnow, and K. O. Stetter, Hyperthermophylic archaebacteria within the crater and open-sea plume of erupting Macdonald Seamount, *Nature, 345*, 179-182, 1990.

Jakosky, B. M., and J. H. Jones, The history of Martian volatiles, *Rev. Geophys., 35*, 1-16, 1997.

Jakosky, B. M., and E. L. Shock, The biological potential of Mars, the early Earth, and Europa, *J. Geophys. Res., 103*, 19,359-19,364, 1998.

Jull, A. J. T., C. Courtney, D. A. Jeffrey, and J. W. Beck, Isotopic evidence for a terrestrial source of organic compounds found in Martian meteorite Allan Hills 84001 and Elephant Moraine 79001, *Science, 279*, 366-369, 1998.

Juniper, S. K., P. Martineau, J. Sarrazin, and Y. Gélinas, Microbial-mineral floc associated with the nascent hydrothermal activity on CoAxial segment, Juan de Fuca Ridge, *Geophys. Res. Lett., 22*, 179-182, 1995.

Kadko, D. C., N. D. Rosenberg, J. E. Lupton, R. W. Collier, and M. D. Lilley, Chemical reaction rates and entrainment within the Endeavour Ridge hydrothermal plume, *Earth Planet. Sci. Lett., 99*, 315-335, 1990.

Kita, K., K. Konishi, and Y. Anraku, Terminal oxidases of *Escherichia coli* aerobic respiratory chain, II, Purification and properties of cytochrome b558-d complex from cells grown with limited oxygen and evidence of branched electron carrying systems, *J. Biol. Chem., 259*, 3375-3381, 1984.

Klein, H. P., The search for life on Mars: What we learned from Viking, *J. Geophys. Res., 103*, 28,463-28,466, 1998.

Klein, H. P., N. H. Horowitz, and K. Biemann, The search for extant life on Mars, in *Mars*, edited by H. H. Kieffer, B. M. Jakosky, C. W. Snyder, and M. S. Matthews, pp. 1221-1233, Univ. of Ariz. Press, Tucson, 1992.

Koch, A. L., and T. M. Schmidt, The first cellular bioenergetic process: A primitive generation of proton-motive force, *J. Mol. Evol., 33*, 297-304, 1991.

Laul, J. C., The Shergotty consortium and SNC meteorites: An overview, *Geochim. Cosmochim. Acta, 50*, 875-888, 1986.

Lilley, M. D., J. A. Baross, and L. I. Gordon, Reduced gases and bacteria in hydrothermal fluids: The Galapagos Spreading Center and 21°N East Pacific Rise, in *Hydrothermal Processes at Seafloor Spreading Centers*, edited by P. A. Rona, K. Boström, L. Laubier, and K. L. Smith Jr., pp. 411-449, Plenum, New York, 1983.

Liu, S. V., J. Zhou, C. Zhang, D. R. Cole, M. Gajdarziska-Josifovska, and T. J. Phelps, Thermophilic Fe(III)-reducing bacteria from the deep subsurface: The evolutionary implications, *Science, 277*, 1106-1109, 1997.

Longhi, J., E. Knittle, J. R. Holloway, and H. Wänke, The bulk composition and internal structure of Mars, in *Mars*, edited by H. H. Kieffer, B. M. Jakosky, C.W. Snyder, and M. S. Matthews, pp. 184-208, Univ. of Ariz. Press, Tucson, 1992.

Lovley, D. R., and F. H. Chapelle, Deep subsurface microbial processes, *Rev. Geophys., 33*, 365-381, 1995.

Lowenstam, H. A., Mineralization processes in monerans and protoctists, in *Biomineralizaton in Lower Plants and Animals*, edited by B. S. C. Leadbeater and R. Riding, pp. 1-17, Clarendon, Oxford, England, 1986.

Mancinelli, R. L., The search for nitrogen compounds on the surface of Mars, *Adv. Space Res., 18*, 241-248, 1996.

Marti, K., J. S. Kim, A. N. Thakur, T. J. McCoy, and K. Keil, Signatures of the Martian atmosphere in glass of the Zagami meteorite, *Science, 27*, 1981-1984, 1995.

Marty, B., M. Lenoble, and N. Vassard, Nitrogen, helium and argon in basalt: A static mass spectrometry study, *Chem. Geol., 120*, 183-195, 1995.

McKay, C. P., R.L. Mancinelli, C. R. Stoker, and R. A. Wharton Jr., The possibility of life on Mars during a water-rich past, in *Mars*, edited by H. H. Kieffer, B. M. Jakosky, C.W. Snyder, and M. S. Matthews, pp. 1234-1245, Univ. of Ariz. Press, Tucson, 1992.

McKay, D. S., E. K. Gibson Jr., K. L. Thomas-Keprta, H. Vali, C. S. Romanek, S. J. Clemett, X. D. F. Chillier, C. R. Maechling, and R. N. Zare, Search for life on Mars: Possible relic biogenic activity in Martian meteorite ALH84001, *Science, 273*, 924-930, 1996.

McKay, D. S., E. K. Gibson Jr., K. Thomas-Keprta, and H. Vali, Reply to No "nanofossils" in martian meteorite orthopyroxene, *Nature, 390*, 455-456, 1997.

McSween, H. Y., Jr., What we have learned about Mars from SNC meteorites?, *Meteoritics, 29*, 757-779, 1994.

McSween, H. Y., Jr., and E. Jarosewich, Petrogenesis of the Elephant Moraine A79001 meteorite: Multiple magma pulses on the shergottite parent body, *Geochim. Cosmochim. Acta, 47*, 1501-1513, 1983.

McSween, H. Y., Jr., L. A. Taylor, and E. M. Stolper, Allan Hills 77005: A new meteorite type found in Antarctica, *Science, 204*, 1201-1203, 1979.

Michael, P. J., and E. Bonatti, Peridotite composition from the north Atlantic: Regional and tectonic variations and implications for partial melting, *Earth Planet. Sci. Lett., 73*, 91-104, 1985.

Mittlefehldt, D. W., ALH84001: A cumulate orthopyroxenite member of the martian meteorite clan, *Meteoritics, 29*, 214-221, 1994.

Mittlefehldt, D. W., Survey of carbonates in ALH84001, *Curator's Report*, Johnson Space Cent., Houston, Tex., 1996.

Monger, H. C., L. A. Daugherty, W. C. Lindemann, and C. M. Liddell, Microbial precipitation of pedogenic calcite, *Geology, 19*, 997-1000, 1991.

Moreau, D., A. Marten, Y. Biraud, and C. Muller, Two-dimensional modeling of distribution of reduced carbon species in the current Martian atmosphere (abstract), *Eos Trans. AGU, 78*, Fall Meet. Suppl., 410-411, 1997.

Nealson, K. H., The limits of life on Earth and searching for life on Mars, *J. Geophys. Res., 102*, 23,675-23,686, 1997.

Owen, T., Composition and early history of the atmosphere, in *Mars*, edited by H. H. Kieffer, B. M. Jakosky, C.W. Snyder, and M. S. Matthews, pp. 818-834, Univ. of Ariz. Press, Tucson, 1992.

Oyama, V. I., and B. J. Berdahl, The Viking gas exchange experiment results from Chryse and Utopia surface samples, *J. Geophys. Res., 82*, 4669-4676, 1977.

Parkes, R. J., B. A. Cragg, S. J. Bale, J. M. Getliff, K. Goodman, P. A. Rochelle, J. C. Fry, A. J. Weightman, and S. M. Harvey, Deep bacterial biosphere in Pacific Ocean sediments, *Nature, 371*, 410-413, 1994.

Pedersen, K., The deep subterranean biosphere, *Earth Sci. Rev., 34*, 243-260, 1993.

Pederson, K., S. Ekendahl, E. Tulborg, H. Furnes, I. Thorseth, and O. Tumyr, Evidence of ancient life at 207 m depth in a granitic aquifer, *Geology, 25*, 827-830, 1997.

Pepin, R. O., Evidence of Martian origins, *Nature, 317*, 473-375, 1985.

Perfit, M. R., D. J. Fornari, A. Malahoff, and R. W. Embley, Geochemical studies of abyssal lavas recovered from DSRV *Alvin* from eastern Galapagos Rift, Inca Transform, and Ecuador Rift, 3, Trace element abundances and petrogenesis, *J. Geophys. Res., 88*, 10,551-10,572, 1983.

Prinz, M., P. H. Hlava, and K. Keil, The Chassigny meteorite: A relatively iron-rich cumulate dunite, *Meteoritics, 9*, 393-394, 1974.

Rieder, R., T. Economou, H. Wänke, A. Turkevich, J. Crisp, J. Brükner, G. Dreibus, and H. Y. McSween Jr., The chemical composition of Martian soil and rocks returned by the mobile alpha proton X-ray sepectrometer: Preliminary results from the X-ray mode, *Science, 278*, 1771-1774, 1997.

Rivadeneyra, M. A., R. Delgado, G. Delgado, A. Del Moral, M. R. Ferrer, and A. Ramos-Cormenzana, Precipitation of carbonates by *Bacillus sp.* isolated from saline soils, *Geomicrobiol. J., 11*, 175-184, 1993.

Schilling, J-G., M. Zajac, R. Evans, T. Johnston, W. White, J. D. Devine, and R. Kingsley, Petrologic and geochemical variations along the mid-Atlantic Ridge from 29°N to 73°N, *Am. J. Sci., 283*, 510-586, 1983.

Schultze-Lam, S., D. Fortin, B. S. Davis, and T. J. Beveridge,

Mineralization of bacterial surfaces, *Chem. Geol., 132*, 171-181, 1996.

Shock, E. L., High-temperature life without photosynthesis as a model for Mars, *J. Geophys. Res., 102*, 23,687-23,694, 1997.

Silverman, M. P., Biological and organic chemical decomposition of silicates, in *Biogeochemical Cycling of Mineral-Forming Elements*, edited by P. A. Trudinger, and D. J. Swaine, pp. 445-465, Elsevier, New York, 1979.

Singer, R. B., and H. Y. McSween Jr., The igneous crust of Mars: Compositional evidence from remote sensing and SNC meteorites, in *Resources of Near-Earth Space*, edited by J. S. Lewis, M. S. Mattews, and M. M. L. Guerrieri, pp. 709-736, Univ. of Ariz. Press, Tucson, 1993.

Soderblom, L. A., The composition and mineralogy of the Martian surface from spectrographic observations, 0.3 μm to 50 μm, in *Mars*, edited by H. H. Kieffer, B. M. Jakosky, C.W. Snyder, and M. S. Matthews, pp. 557-593, Univ. of Ariz. Press, Tucson, 1992.

Solomon, S. C., and J. W. Head, Heterogeneities in the thickness of the elastic lithosphere of Mars: Constraints on the flow and internal dynamics, *J. Geophys. Res., 95*, 11,073-11,083, 1990.

Squyers, S. W., S. M. Clifford, S. M. Kuzmin, J. R. Zimbelman, and F. M. Costard, Ice in the Martian regolith, in *Mars*, edited by H. H. Kieffer, B. M. Jakosky, C. W. Snyder, and M. S. Matthews, pp. 523-554, Univ. of Ariz. Press, Tucson, 1992.

Stevens, T. O., and J. P. McKinley, Lithoautotrophic microbial ecosystems in deep basalt aquifers, *Science, 270*, 450-454, 1995.

Stolper, E., and H. Y. McSween Jr., Petrology and origin of shergottite meteorites, *Geochim. Cosmochim. Acta, 43*, 1475-1498, 1979.

Taylor, C. D., and C. O. Wirsen, Microbiology and ecology of filamentous sulfur formation, *Science, 277*, 1483-1485, 1997.

Tebo, B. M., W. C. Ghiorse, L. G. van Waasbergen, P. L. Siering, and R. Caspi, Bacterially mediated mineral formation: Insights into manganese, II, Oxidation from molecular genetic and biochemical studies, in *Geomicrobiology: Interactions Between Microbes and Minerals*, edited by J. F. Banfield, and K. H. Nealson, *Rev. Mineral.*, 35, 225-266, 1997.

Thorseth, I. H., H. Furnes, and O. Tumyr, A textural and chemcal study of Icelandic palagonite of varied compositions and its bearing on the mechanism of glass-palagonite transformation, *Geochim. Cosmochim. Acta, 55*, 731-749, 1991.

Thorseth, I. H., H. Furnes, and M. Heldal, The importance of microbiological activity in the alteration of natural basaltic glass, *Geochim. Cosmochim. Acta, 56*, 845-850, 1992.

Thorseth, I. H., T. Torsvik, H. Furnes, and K. Muehlenbachs, Microbes play an important role in the alteration of oceanic crust, *Chem. Geol., 126*, 137-146, 1995a.

Thorseth, I. H., H. Furnes, and O. Tumyr, Textural and chemical effects of bacterial activity in basaltic glass: An experimental approach, *Chem. Geol., 119*, 139-160, 1995b.

Torsvik, T., H. Furnes, K. Muehlenbachs, I. H. Thorseth, and O. Tumyr, Evidence for microbial activity at the glass-alteration interface in oceanic basalts, *Earth Planet. Sci. Lett., 162*, 165-172, 1998.

Treiman, A. H., and J. L. Gooding, Iddingsite in the Nakhla meteorite, TEM study of mineralogy and texture of pre-terrestrial, Martian? Alterations, *Meteoritics, 26*, 402, 1991.

Treiman, A. H., R. A. Barrett, and J. L. Gooding, Preterrestrial aqueous alteration of the Lafayette, SNC meteorite, *Meteoritics, 28*, 86-97, 1993.

Treiman, A. H., G. A. McKay, D. D. Bogard, D. W. Mittlefehldt, M. S. Wang, I. Keller, M. E. Lipschutz, M. M. Lindstrom, and D. Garrison, Comparison of the LEW88516 and ALHA77005 Martian meteorites: Similar but distinct, *Meteoritics, 29*, 581-592, 1994.

Tseng, H-Y., M. Person, and T. C. Onstott, Hydrogeologic constraint on the origin of deep subsurface microorganisms within a Triassic basin, *Water Resour. Res., 34*, 937-948, 1998.

Von Damm, K. L., Controls on the chemistry and temporal variability of seafloor hydrothermal fluids, in *Seafloor Hydrothermal Systems*, *Geophys. Monogr. Ser.*, vol. 91, edited by S. E. Humphris, R. A. Zierenberg, L. S. Mullineaux, R. E. Land, and R. E. Thomson, pp. 222-247, AGU, Washington, D. C., 1995.

Welch, S. A., and P. Vandevivere, Effect of microbial and other naturally occurring polymers in mineral dissolution, *Geomicrobiol. J., 12*, 227-238, 1994.

Welhan, J. A., and H., Craig, Methane, hydrogen, and helium in hydrothermal fluids at 21°N on the East Pacific Rise, in

Hydrothermal Processes at Seafloor Spreading Centers, edited by P. A. Rona, K. Boström, L. Laubier, and K. L. Smith Jr., pp. 391-409, Plenum, New York, 1983.

Wentworth, S. J., and J. L. Gooding, Carbonates and sulfates in the Chassigny meteorite: Further evidence for aqueous chemistry on the SNC parent planet, *Meteoritics, 29*, 860-863, 1994.

Wentworth, S. J., and J. L. Gooding, Carbonates in the Martian meteorite, ALH84001: Water-borne but not like the SNCs (abstract), *Lunar Planet. Sci., XXVI*, 1489-1490, 1995.

Whitman, W. B., D. C. Coleman, and W. J. Wiebe, Prokaryotes: The unseen majority, *Proc. Natl. Acad. Sci., USA, 95*, 6578-6583, 1998.

Wright, I. P., M. M. Grady, and C. T. Pillinger, Organic materials in a Martian meteorite, *Nature, 340*, 220-222, 1989.

Wright, I. P., M. M. Grady, and C. T. Pillinger, Chassigny and the nakhlites: Carbon-bearing components and their relationship to Martian environmental conditions, *Geochim. Cosmochim. Acta, 56*, 817-826, 1992.

Zurek, R. W., Comparative aspects of the climate of Mars: An introduction to the current atmosphere, in *Mars*, edited by H. H. Kieffer, B. M. Jakosky, C. W. Snyder, and M. S. Matthews, pp. 799-817, Univ. of Ariz. Press, Tucson, 1992.

M. R. Fisk, College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331. (mfisk@oce.orst.edu)

S. J. Giovannoni, Department of Microbiology, Oregon State University, Corvallis, OR 97331. (giovanns@bcc.orst.edu)