

10.14 Geology, Life, and Habitability

G Southam, The University of Queensland, Brisbane, QLD, Australia

F Westall, Centre de Biophysique Moléculaire, Orléans, France

T Spohn, German Aerospace Center (DLR), Berlin, Germany

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10.14.1 Introduction

10.14.1.1 The Requirements for an Origin of Life and 'Habitability'

Whether or not life originated on Earth, it was certainly present in abundance and at a relatively advanced level of evolution by about 3.5 billion years ago (Ga) (see reviews in Westall and Southam (2006) and Westall (2011)). At this time, the habitable environment of the Earth was very much different than the Earth of today – significantly hotter (Arndt, 1994; Knauth and Lowe, 2003) and more volcanically/hydrothermally active (Hofmann and Bolhar, 2007) and basically without oxygen (<0.2% present atmospheric levels, Catling and Claire, 2005; Kasting, 1993). The low levels of reactive oxygen produced by photolysis (Kasting, 1993) relative to the abundance of reduced chemical species would have resulted in a correspondingly reducing chemistry for the hydrosphere and lithosphere as well. Based on comparisons with the lunar cratering record, the environment was also affected by a short, sharp influx of bolides (the Late Heavy Bombardment (LHB); Gomes et al., 2005) about 3.9 Ga ago that may or may not have evaporated all the surface water (Sleep et al., 1989) and eliminated all life (Maher and Stevenson, 1988). It is commonly believed that the life on Earth today evolved from primitive cells that could only have appeared after the end of the LHB (Lowe and Byerly, 1986; Lowe et al., 2003), that is, after ~3.85 Ga. However, the last decade has seen an enormous advance in our understanding of the limits of life and it is clear that, once started, it is very difficult to eradicate prokaryotes from either the Bacteria or Archaea domains (Woese et al., 1990), especially the latter since they generally occur in environmental conditions that today are considered to be extreme but were common on the early Earth. It is possible, therefore, that life appeared on Earth before

~4.0 Ga and survived the catastrophic LHB in, for instance, a protected subsurface habitat (cf. Russell et al., 2010), to reappear and flourish at the surface once water had recondensed. They may represent the survivors of a 'hot bottleneck' through which the early forms of life had to pass, such as would have existed during a catastrophic impact event. However, whether or not they represent the last universal common ancestor (LUCA) is still debated (Brochier and Philippe, 2002). An alternative hypothesis is that life first appeared on another planet and was transported by panspermia to the Earth (e.g., Cockell, 2008) once habitable conditions had been reestablished at the end of the catastrophic bolide period. However, the other likely contender for an independent origin of life in the inner part of the solar system, Mars, also suffered from the same bolide bombardment.

In order to address the concept of life and habitability in the solar system, we start with a brief overview of the current thinking on the basic requirements for life to originate and the origin of life. In life as we know it, all cells need a source of energy and are composed of water and carbon molecules that include some essential elements (notably hydrogen, oxygen, nitrogen, phosphorus, and sulfur (HONPS)). These are therefore the minimum requirements on a planet (or other type of rocky body) for the appearance of life. Since organic carbon molecules occur in interstellar clouds, as well as in the materials forming the proto-solar system cloud (in the form of the planetesimals that formed the rocky planets, asteroids, meteorites, micrometeorites, and comets), they can be considered to be more or less ubiquitous. Endogenous sources of organic carbon included the primordial, slightly reducing atmosphere (Johnson et al., 2008; Miller, 1953) and active hydrothermal systems where organic carbon is primarily produced via Fischer–Tropsch synthesis (i.e., hydrocarbons containing up

to 29 carbon atoms have been produced from the Rainbow ultramafic hydrothermal system on the Mid-Atlantic Ridge; Holm and Charlou, 2001; see also Russell et al., 2010), which are believed to have been very active on the early Earth. A significant amount of the organic molecules (and other volatiles, such as water) were also delivered from extra-terrestrial sources (Chyba and Sagan, 1992; Sephton and Botta, 2008). Carbonaceous chondrite meteorites contain up to 5% organic carbon, and eight of the amino acids that have been identified in them are of the kind used in living cells today; they are the building blocks of life. The present-day flux of carbonaceous micrometeorites (to the Earth) containing up to 2% carbon is estimated between 50 and 100 tons per year, which implies an extraordinary amount equaling 10^{23} g carbon over a 300 My period during the LHB (Maurette et al., 2000; see also Brack, 2004, for a review). Thus, organic carbon on rocky bodies in the young solar system was readily available.

The sources of the other elements essential for an origin of life (HONPS) would likewise be readily available on any rocky planet. A rocky planet is also an excellent source of energy. Living organisms need energy in order to militate against the constant problem of entropy, the increase in disorder or dissipation of chemical energy within a closed system, their entire lives. From a simplistic, energy perspective then, any geologic system that provides geochemical energy, that is, a reaction that can be written possessing a negative ΔG_r , should conceivably have the capacity to support life. However, because water is a necessary ingredient of life as we know it and is therefore also necessary for life to emerge elsewhere in our solar system (or in the universe), this means that the target planetary body should be situated within the habitable zone around its star (see Franck et al., 2006; Kasting et al., 1993; Kopparapu et al., 2013). Habitable conditions are defined by the sum of the physical and chemical conditions, which support the presence of liquid water at the surface of a planetary body. This habitable zone around the Sun has moved outward since the formation of the solar system as luminosity, now about 25–30% > 4.6 Ga ago, has increased (Newman and Rood, 1977). While rocky planets within this zone represent ideal potential habitats, rocky bodies with liquid water in contact with rock do exist outside this zone and can thus be considered as being potentially habitable. In the early part of the history of the solar system, a number of planets and satellites had their own internal heat source from decaying radioactive elements, and in the case of Europa, there is convincing evidence that a liquid ocean exists underneath its icy crust (e.g., Hussmann et al., 2014; Chapter 10.18) with the energy required to keep the fluid liquid being impacted by the strong tidal forces from Jupiter (Chyba and Phillips, 2001; Hussmann et al. 2014) and the Laplace orbital resonance of the three inner Galilean satellites Io, Europa, and Ganymede. Analysis of the induced magnetic field (Khurana et al., 1998) as well as more recent spectral observation suggests that Europa's ocean is a brine containing Na, K, and Mg salts (Brown and Hand, 2013).

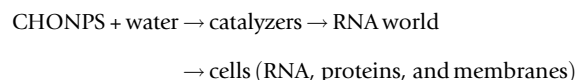
10.14.1.2 The Origin of Life and the First Cells

A working definition of a minimal life-form could be “a structure capable of auto-reproduction including errors that lead to evolution” (Brack, 2005). The basic structure consists of three

long chain carbon molecules that are necessary for the functioning of the cell: (1) a lipid membrane enclosing a (2) molecule capable of information transfer (RNA/DNA) and (3) a catalyzing molecule (enzyme) to provide the basic work of the cell. Despite the fact that it has not yet been possible to reproduce a life-form *ex novo* in the laboratory, the last 50 years has seen significant advances in understanding how these basic elements formed from inorganic components.

In the modern cell, membranes are primarily composed of amphipathic phospholipids that are stable in water. These lipids can be formed from fatty acids found in carbonaceous chondrites like the Murchison meteorite (Deamer, 1998). Catalytic reactions in modern, living cells are performed by proteinaceous enzymes, themselves made of homochiral amino acids. As we have noted earlier, these were abundantly available on the early Earth. There are, however, a number of scenarios regarding the condensation or assemblage of simple amino acids into longer chain molecules, such as peptides. These include condensation on mineral surfaces, such as clays (Ferris et al., 1996), thermal condensation (Fox and Dose, 1977), and chemical reactions (Barbier and Brack, 2002). Likewise, the origin of the first information transfer molecules is highly debated. Nucleic acids in modern cells are composed of bases (purine and pyrimidine), sugars (ribose or deoxyribose), and phosphate groups. RNA (ribonucleic acid) is considered to be a likely, primitive replicating molecule because it also has catalytic properties (representing self-replication, mutation, and evolution) and can act as a polymerization template (Zaug and Cech, 1986). However, even RNA is too complicated to have been the first replicating molecule (Schwartz and Orgel, 1985). Nonenzymatic replication has been demonstrated (Inoue and Orgel, 1982), as have autocatalytic reactions involving the reaction of FeS and H₂S on the surface of pyrite (Wächtershäuser, 1988). In the latter scenario, organic molecules forming a network on the surface of the mineral evolve. Other candidates for precursor replication molecules include pyranosyl-RNA and threo furanosyl nucleic acid, though the latter is considered to be more likely because of the greater availability of the carbon precursors of tetrose than ribose on the primitive Earth.

The basic process leading to an origin of life can be envisaged thus (Brack, 2004):



10.14.2 Geology, Life, and Habitability

Based on the previously described criteria for habitability and the origin of life, the key to understanding the potential for the emergence of life, that is, habitability, is the understanding of the history of liquid water on any terrestrial planet or icy moon. Given the necessity of disequilibria conditions in the emergence of life, liquid water needs to be in contact with minerals/rocks, implying liquid water on a rocky planet. The capacity to support life may be transient, that is, it will not be constant for a particular planet over time but will vary based on a wide range of geologic and planetary factors (e.g., Westall et al., 2013). We only have terrestrial life to use as a basis for

discussion of the relationship between geology (including aqueous geochemistry), life, and habitability. Assuming water is available, there is a wide diversity of metabolic strategies that have been developed by terrestrial microorganisms (Barns and Nierzwicki-Bauer, 1997; Pace, 1997; Reysenbach and Shock, 2002), so that they can successfully colonize almost all geologic environments.

In this chapter, we focus on the interaction between geology and prokaryotic life as a way to address the subject of habitability, both from our perspective and from that of the prokaryotes, which have inhabited Earth for far longer than we have. Today, prokaryotic organisms are ubiquitous on Earth, being found in a wide variety of surface and subsurface environments (Colwell et al., 1997; Lovley and Chapelle, 1995; Onstott et al., 2006; Parkes et al., 1994; Stevens et al., 1993), where they are only limited by the availability of water (Navarro-Gonzalez et al., 2003) and temperatures $< 121^{\circ}\text{C}$ (Kashefi and Lovley, 2003). In these natural environments, prokaryotes typically grow as biofilms on mineral surfaces (Marshall, 1988; Wanger et al., 2006). This intimate association of life with its geologic substrate is thought to have occurred for at least the last ~ 3.5 billion years (see Westall and Southam, 2006; Westall, 2011, for a review) producing molecular to global-scale by-products. During the initial stages of this interaction, the physical and chemical conditions of the early Earth would have controlled the biosphere. However, over time, life exerted an increasing influence over the geosphere. Life serves as a catalyst for a wide array of reactions at geologically low temperatures, doing them faster than would happen abiotically (e.g., Singer and Stumm, 1970).

10.14.2.1 Habitability as Defined by the Physical and Chemical Environmental Constraints on Life

The growth of prokaryotes is affected by the various physical and chemical constraints of the environments in which they are growing (Figure 1). They, in turn, can have a profound

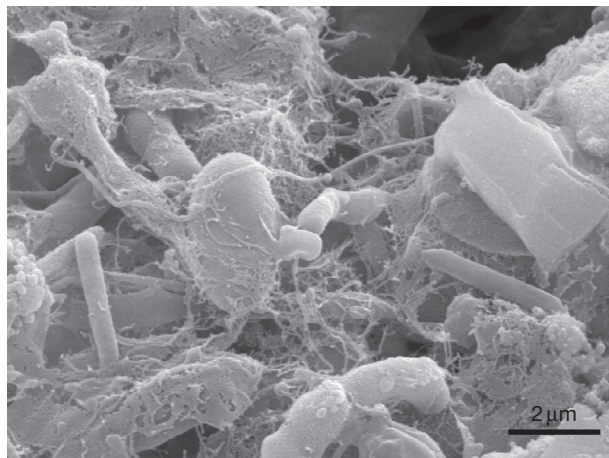


Figure 1 A scanning electron micrograph of a bacterial biofilm collected from a groundwater outflow into an oxygenated mining environment, 3.1 km below land surface in the Witwatersrand Basin, Republic of South Africa. Note the spiderweb-like appearance of the bacterial exopolymer material.

effect on their surrounding environment. Understanding the physical and chemical limits of bacteria and their environmental influences allows us to predict the types and distribution of microorganisms that could occur in natural systems.

The range of (and optimum) growth temperatures differentiate prokaryotes into broad groups (Stetter et al., 1990). Psychrophiles grow optimally at or below 15°C and have even demonstrated activity down to -20°C (Mykytczuk et al., 2013); viable prokaryotes have been recovered from million-year-old permafrost (Gilichinsky et al., 2007). Psychrotolerant prokaryotes grow optimally between 20 and 40°C but will grow at temperatures as low as 0°C . Mesophiles grow optimally between 15 and 45°C . Thermophiles have optimum growth temperatures above 45°C and hyperthermophiles grow optimally above 80°C (Figure 2). While no single microorganism can withstand the full range of temperatures described here, as a group, prokaryotes can be found across any thermal gradient, from ice or permafrost regions all the way up to hydrothermal fluids (121°C).

In all environments, prokaryotes concentrate solutes within their cell envelopes and obtain water through osmosis, thus enabling them to maintain intra-cell turgor pressure (Kunte, 2006). The prokaryote cell envelope is designed to withstand this turgor pressure, which can measure between 2-3 atmospheres in gram-negative bacteria and up to 15 atmospheres in gram-positive bacteria (Beveridge, 1981). The accumulation of water represents a challenge for prokaryotes in the Archaea domain in contemporary (e.g., the Great Salt Lake) and paleo-evaporitic (Bechtel et al., 1996), hypersaline systems. Some of these environments are continually under stress due to low water activity and are therefore considered to be examples of extreme environments, which will only support halophilic (or halotolerant) microorganisms (see Figure 3).

Most natural environments occur as circumneutral pH systems. Therefore, most prokaryotes exhibit optimal activity in the pH range of 6–8. At pH 7, the hydrogen ion concentration is 100 nM. Extreme environments possessing acidic (e.g., pH 2) or alkaline (e.g., pH 11) pH conditions will contain



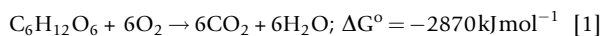
Figure 2 A photograph of a hydrothermal spring in Norris Geyser Basin, Yellowstone National Park. Extreme environments, such as this, are dominated by prokaryotic organisms representing both the Archaea and Bacteria domains. The field of view is ~ 8 m across.



Figure 3 A photograph of Basque Lake #2, in central BC, Canada. The evaporite minerals in this basin are dominated by epsomite, indicating the hypersaline nature of this environment.

indigenous microorganisms, that is, acidophilic (acidotolerant) or alkaliphilic (alkalitolerant) prokaryotes, respectively, whose growth parameters are adapted to these extremes in environmental pH (Goodwin and Zeikus, 1987). Note that the word ‘extremophile’ is an anthropocentric term because for many microorganisms, thiobacilli, an ambient pH of 2 is optimum.

Our modern habitat is characterized by an atmosphere rich in oxygen (which was not the case on the early Earth). The capacity to utilize oxygen as a terminal electron acceptor creates a competitive advantage as well as a challenge for prokaryotes, which are subdivided into aerobic and anaerobic groups based on their oxygen requirements and detoxification strategies (Chapelle, 1993). There are also facultatively anaerobic prokaryotes that utilize oxygen if it is available, becoming anaerobes when the oxygen runs out, that is, they can grow with or without oxygen. The utilization of oxygen as a terminal electron acceptor enables organisms to fully oxidize their respective source(s) of energy and thereby maximize their energy gain from reaction [1]:



Any organism that is capable of growing in the presence of oxygen, whether or not it utilizes oxygen as a terminal electron acceptor, must also have the capacity to detoxify the chemically reactive oxygen compounds produced through the stepwise reduction of oxygen to water (hydrogen peroxide, superoxide radical, and the hydroxyl radical; Atlas and Bartha, 1997). Detoxification of these oxygen radicals requires a series of enzymes including superoxide dismutase, catalase, and peroxidase. The ability to tolerate oxygen relates to the presence or absence of each of these enzymes. Measurements of dissolved oxygen and redox potential, which represents the sum reactivity of oxidants and reductants, are important in determining which microbial processes are functioning within natural systems.

Analyses of the physical and chemical limits on prokaryote growth and survival typically focus on one ‘stressor’ at a time, for example, pH (acidophile vs. neutrophile vs. alkaliphile),



Figure 4 A photograph of a hydrothermal acid hot spring in Shimabara, Japan. In these extreme environments, the geosphere dominates the biosphere.

temperature (psychrophile vs. mesophile vs. thermophile), salinity (freshwater vs. halophile), or oxygen availability (aerobe vs. anaerobe). On the other hand, there are many examples of prokaryotes that can withstand multiple ‘stressors’ (see de Vera et al., 2013), for example, thermoacidophiles. It is in these environments (see Figure 4) that the diversity of prokaryotes and the limits of life are truly appreciated (see Table 1). Nevertheless, other combinations of ‘stressors’ will be deadly to microorganisms, such as low water activity together with high UV radiation, as on the surface of Mars today (Cockell and Raven, 2004).

10.14.2.2 Building Cells

Modern prokaryotes use a wide range of organic and inorganic nutrients. Organic nutrients, for example, carbohydrates, amino acids, nucleic acids, and hydrocarbons, include nearly every organic monomer or polymer found in the living or diagenetically altered biosphere. Inorganic nutrients include dissolved gases (carbon monoxide, carbon dioxide, hydrogen, nitrogen, and dihydrogen sulfide), soluble cations (sodium, calcium, magnesium, ammonium, and ferrous and ferric iron), base metals (chromium, nickel, copper, cobalt, zinc, lead, and mercury), and soluble anions (chloride, nitrite, nitrate, hydrogen sulfide, sulfite, sulfate, phosphate, selenate, and arsenate). Depending on nutrient requirements, these compounds can be used in assimilation reactions, that is, building new cells, or in dissimilatory processes to generate the energy needed to construct new biomass (discussed in the succeeding text).

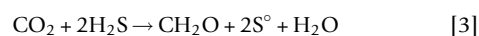
Carbon utilization is one of the most important criteria by which prokaryotes are characterized. Heterotrophic prokaryotes require organic carbon for their metabolism and typically couple the oxidation of organic carbon to CO_2 with the reduction of dissolved inorganic species or minerals. The sources of carbon and energy for heterotrophs can range from simple organics such as glucose and asparagine, an amino acid (Goldman and Wilson, 1977), to macromolecular materials such as cellulose (Ljungdahl and Eriksson, 1985).

Table 1 Classification and examples of extremophiles

Environmental parameter	Type	Definition	Examples
Temperature	Hyperthermophile	Growth >80 °C	<i>Pyrolobus fumarii</i> , 113 °C
	Thermophile	Growth 60–80 °C	<i>Synechococcus lividis</i>
	Mesophile	15–60 °C	<i>Homo sapiens</i>
	Psychrophile	<15 °C	<i>Psychrobacter</i> , some insects
Radiation			<i>Deinococcus radiodurans</i>
Pressure	Barophile	Weight loving	Unknown
	Piezophile	Pressure loving	For microbe, 130 MPa
Gravity	Hypergravity	>1 g	None known
	Hypogravity	<1 g	None known
Vacuum		Tolerates vacuum (space devoid of matter)	Tardigrades, insects, microbes, seeds
Desiccation	Xerophiles	Anhydrobiotic	<i>Artemia salina</i> ; nematodes, microbes, fungi, lichens
Salinity	Halophile	Salt loving (2–5 M NaCl)	<i>Halobacteriaceae</i> , <i>Dunaliella salina</i>
pH	Alkaliphile	pH >9	<i>Natronobacterium</i> , <i>Bacillus firmus</i> OF4, <i>Spirulina spp.</i> (all pH 10.5)
	Acidophile	Low pH loving	<i>Cyanidium caldarium</i> , <i>Ferroplasma sp.</i> (both pH 0)
Oxygen tension	Anaerobe	Cannot tolerate O ₂	<i>Methanococcus jannaschii</i>
	microaerophile	Tolerates some O ₂	<i>Clostridium</i>
	aerobe	requires O ₂	<i>Homo sapiens</i>
Chemical extremes	Gases metals	Can tolerate high concentrations of metal (metalotolerant)	<i>Cyanidium caldarium</i> (pure CO ₂) <i>Ferroplasma acidarmanus</i> (Cu, As, Cd, Zn); <i>Ralstonia sp.</i> CH34 (Zn, Co, Cd, Hg, Pb)

Reproduced from Rothschild and Mancinelli (2001).

Autotrophs are able to obtain their cellular carbon for biomass from inorganic sources (dissolved CO₂/HCO₃⁻). Autotrophic organisms direct most of their energy toward the fixation (reduction) of CO₂ into organic carbon, that is, biomass production, and therefore tend to grow at slower rates than heterotrophic organisms. However, autotrophs are extremely important since they serve as the basis of the food chain upon which 'we' heterotrophs thrive. For example, autotrophic bacteria oxidize sulfur (reaction [2]) and synthesize carbohydrates at seafloor hot springs (reaction [3]):



They are the base of the 'food chain' in these lightless, extreme environments (Cavanaugh et al., 1981).

Nitrogen and phosphorus are the limiting nutrients in most natural systems. However, prokaryotes can easily assimilate all forms of water-soluble inorganic nitrogen, and when the availability of nitrogen is limited, a wide range of prokaryotes possess a nitrogenase enzyme that allows them to fix atmospheric nitrogen (Brill, 1975). Regarding phosphorus-limiting conditions, microorganisms can produce a wide array of organic and inorganic acids that can enhance the weathering of silicate minerals in rocks and thus assimilate phosphate (Rogers et al., 1998; discussed in Section 10.14.3.1).

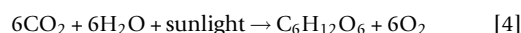
10.14.2.3 Generating Energy

In natural systems, prokaryotes exploit a wide range of redox reactions having negative ΔG_r to support metabolism (Nealson and Stahl, 1997). The requirement of energy for biosynthetic reactions is described according to the electron donor or source of reducing power and by the electron acceptor, that is, a redox

couple. Current research on the diversity of life focuses on phenotypic and genotypic studies of geochemical gradients, where thermodynamic calculations highlight possible biogeochemical reactions that could support life, for example, anaerobic methane oxidation at deep-sea cold clathrate vents (Thomsen et al., 2001).

In natural systems, microbially catalyzed redox processes are established through competition for available nutrients (assimilation) and through the efficiency of their respective energy generation mechanisms (Lovley and Klug, 1983). As geochemical conditions become increasingly reducing, the amount of energy (as expressed by ΔG_r) available from each of the predominant biogeochemical reactions (i.e., redox zones) decreases (Lovley and Chapelle, 1995; Lovley and Phillips, 1988) resulting in a concomitant reduction in biomass (Onstott et al., 2006).

Phototrophs utilize sunlight to produce ATP (adenosine triphosphate, the principal energy carrier of all cells) from otherwise chemically stable reduced compounds. Anoxygenic phototrophs were probably already present on the Earth by 3.5 Ga (see reviews in Westall and Southam, 2006; Westall, 2011); contemporary representatives of this group are anaerobic green and purple sulfur bacteria that derive their energy for growth from light and H₂S or Fe²⁺ (Heising and Schink, 1998; Kappler and Newman, 2004), producing elemental sulfur, sulfate, or Fe³⁺ as end products of their metabolism (van Gemerden, 1986). The later-evolved oxygenic phototrophs use light in combination with H₂O as their source of energy (reaction [4]):



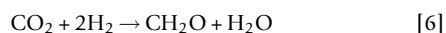
Chemolithotrophs (hydrogen, ammonia, or sulfur oxidizers and methylotrophs) are prokaryotes that utilize inorganic chemicals (H₂, NH₄⁺, H₂S, and CH₄) as their energy

sources (electron donors). Lithotrophs grow more slowly than heterotrophs owing to the relatively low levels of chemical energy present in inorganic versus organic compounds (Nealson and Stahl, 1997) (Figure 5). Chemoorganotrophs, which utilize organic carbon as their source of reducing power and cellular carbon, include both aerobic and anaerobic prokaryotes.

Prior to the evolution of oxygenic photosynthesis (Dismukes et al., 2001; Kasting, 1993), the extremely low levels of oxygen in the atmosphere (<0.2% of present atmospheric levels, Kasting, 1993) would have resulted in lower overall biological activity (Des Marais, 2000). The capacity of oxygen to help provide abundant energy directly via aerobic respiration would simply not have existed. The small amount of oxygen produced by photolysis of H₂O vapor in the upper atmosphere or by radiolysis of water molecules at the surface of the oceans would have been immediately scavenged by the abundant reduced mineral species that covered the Earth, thus indirectly providing some oxidized inorganic electron acceptors, although nowhere near the quantity that was available ever since the atmosphere was oxidized.

Today, because of the presence of oxygen in our atmosphere and dissolved oxygen in surface and near-surface groundwater (Figure 6), aerobic microorganisms dominate the Earth's surface with anaerobic prokaryotes becoming increasingly important with depth below the surface. During the early to mid-Archean, prior to the evolution of oxygenic photosynthetic bacteria, or presumably, on any geochemically reducing planetary body possessing an 'early stage' biosphere, anaerobic organisms would have been the dominant group (Kasting, 1993).

Below the aerobic zone (or at the surface of an anaerobic planet), a progression of different anaerobes (e.g., metal reducers, sulfate reducers, and methanogens) exists (would exist), most of which (from Earth's lessons) utilize organic matter for their metabolism (Lovley and Chapelle, 1995; Lovley and Klug, 1983). Under moderately reducing conditions, Fe- and Mn-reducing bacteria couple the oxidation of organic matter to the reductive dissolution of high-surface-area Fe and Mn oxyhydroxides (Lovley and Phillips, 1988; Myers and Nealson, 1988). At increasingly reduced conditions, sulfate-reducing bacteria oxidize low-molecular-weight organic compounds, utilizing sulfate as the terminal electron acceptor, forming and releasing hydrogen sulfide as a by-product of metabolism (Anderson et al., 1998; Donald and Southam, 1999). Bacterial methane production occurs under even more reducing conditions than microbial sulfate reduction. Methanogenesis (reaction [5]) is also the dominant anaerobic prokaryotic process that cycles inorganic carbon back into the organic carbon pool (reaction [6]):



Biogenic methane can migrate out of the zone of methanogenesis and become an organic carbon source (electron donor) for heterotrophic bacteria elsewhere. This redox zonation going from aerobic → Fe–Mn–oxide reduction → sulfate reduction → methanogenesis is a universal phenomenon on the present-day Earth, as demonstrated, for example, in marine sediment pore waters (e.g., Drever, 1997).

Since prokaryotes can only transport soluble compounds across their cell envelopes, they have evolved various metabolic ways in which to obtain nutrients from solid substrates, for example, Fe or Mn oxides, to support their growth. The ability to alter the chemistry of their surrounding environment on the scale of 10s to 100s of nanometers (Purcell, 1977) is what enables prokaryotes to promote the dissolution of otherwise 'stable' mineral phases (based on bulk fluid chemistry) or the precipitation of minerals under apparently undersaturated conditions. Remarkably, it has been recently demonstrated that prokaryotes can produce electrically conductive nanowires under electron acceptor-limiting conditions (Gorby et al., 2006), thus demonstrating that biogeochemical cycling, which is not directly evident from fluid chemistry or mineralogy, may still be possible via interspecies electron transfer (Gorby et al., 2006).

10.14.2.4 The Growth of Microorganisms

Their small size (submicrometer to micrometer-scale) and resulting high surface area to volume ratio of bacteria help facilitate their growth. Since access to nutrients is based on diffusion and active uptake transporters at the cell surface, the greater the surface to volume ratio, the greater the capacity to obtain nutrients (Koch, 1996; Pirie, 1973; Purcell, 1977). Also, since individual prokaryotes only possess a mass of $\sim 1 \times 10^{-12}$ g (wet weight; Neidhardt et al., 1990), extremely low amounts of dissolved nutrients can support their growth and survival. On Earth, prokaryotes are critical components of the food chain because they utilize dilute concentrations of inorganic and organic nutrients that are unavailable directly to higher eukaryotic organisms (Fenchel and Jorgensen, 1977). The ability of prokaryotes to metabolize organic compounds in natural systems is dependent on the chemical properties and the composition and mineralogy of the soil (Knaebel et al., 1994). For example, Scow and Hutson (1992) found significant decreases in microbial degradation of organic carbon in the presence of kaolinite, owing to the effects of sorption and reduced diffusion from the clay surface.

While prokaryotes can be planktonic, attachment to a mineral surface is advantageous in that it allows them to persist or hold their position within a presumably, favorable geochemical flow, letting the nutrients come to them (Figure 5; Emerson and Revsbech, 1994; Purcell, 1977). Individual prokaryote species often grow as microcolonies (Hall-Stoodley et al., 2004), tens of microns in diameter, and can occur in association with other microcolonies within biofilms. Where freshwater--hypersaline aquatic conditions are stable for a long periods of time and, where nutrients and favorable redox conditions exist for rapid growth, these 'biofilms' can reach large dimensions, up to centimeters or even meters in plan view and a mm or more in thickness, forming significant microbial mats on sediment/rock surfaces (Figure 4; Nealson and Stahl, 1997).

These mats are characterized by the microbial production of copious quantities of extracellular polymeric substances (EPS or capsule, Figure 1; Moser et al., 2003; Wanger et al., 2006). EPS serve many purposes, including protecting the colonies from the 'external' environment and providing a unique micro-environment or habitable zone in which the organisms can control the redox and pH conditions (Roden et al., 2004).

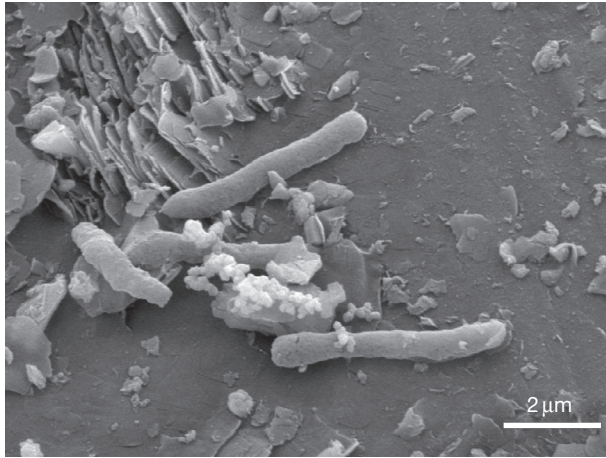


Figure 5 A scanning electron micrograph of a natural fracture face collected 2.8 km below land surface demonstrated that the deep subsurface possesses very sparse bacterial 'biofilms' (see [Wanger et al., 2006](#)).

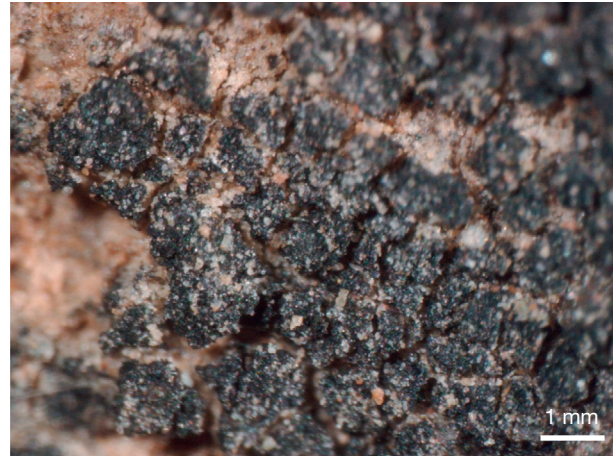


Figure 7 A photograph of an endolithic bacterial colonization (the blackening) of aeolian sandstone in potholes at Bartlett Wash, near Moab, NM (see [Chan et al., 2005](#)).



Figure 6 A photograph of microbial mats growing near Atlin, BC, Canada. Prior to the evolutionary development of predators, approximately one-half billion years ago, much of the photic biosphere on Earth presumably looked similar to this.

EPS-rich biofilms can also play an important role in the stabilization of sediment surfaces by cementing mineral particles together (see [Figures 1 and 3](#); [Stahl, 1994](#)), thus prolonging the stability of a particular habitat.

Under arid environmental conditions where water activity is limited, for example, hot and cold desert environments ([Friedmann and Ocampo, 1976](#)), habitable endolithic micro-environments are found within soil or within rock. Endolithic microbial communities display an intimate relationship with the substrate they inhabit, also producing protective and nutritive EPS ([Figure 7](#)).

10.14.3 Geology and Life

10.14.3.1 Lithotrophy

Lithotrophic or 'rock-eating' prokaryotes are broadly characterized as organisms capable of utilizing inorganic compounds,

for example, H_2S or minerals to generate energy, and can produce geologically significant phenomena. For instance, metal sulfide oxidation produces acidic environments as in acid mine drainage systems ([Nordstrom and Southam, 1997](#); [Singer and Stumm, 1970](#)) and supergene copper deposits ([Enders et al., 2006](#)).

Microorganisms are also active agents of chemical weathering of silicate minerals (e.g., [Brantley et al., 2001](#); [Hiebert and Bennett, 1992](#); [Rogers et al., 1998](#); [Figure 3](#)), and if reactive organic matter is abundant, mineral dissolution can occur very rapidly. Silica weathering (both as grains and as cement) is a general phenomenon resulting from microbial corrosion in order to concentrate elements limited in their environment, for example, iron and phosphate ([Banerjee et al., 2000](#)), and micronutrients, such as Fe, Co, Zn, Mo, Cu, and Ni, which are represented in trace amounts in most terrestrial materials ([Bennett et al., 1996](#)). Moreover, if apatite occurs in a silicate rock, it will be the first mineral to be dissolved out because phosphate is a biolimiting nutrient ([Taunton et al., 2000](#)). An added advantage of silicate weathering is the creation of suitable habitats for the growth of endolithic microbial communities in water-limited ecosystems ([Chan et al., 2005](#); [Friedmann, 1980, 1982](#)). This process also results in the exfoliation of silicate rocks that is typical of hot or cold desert environments, whereby the metabolic activity of microbes inhabiting the protective microhabitat beneath the exposed surface of the rocks weakens the rock in layers parallel to its surface ([Parnell et al., 2004](#)).

The importance of mineral weathering in supporting the biosphere has led to the general hypothesis that life on Earth or any other rocky planetary body would ultimately be limited in the long term without some form of plate tectonics or lithospheric renewal providing nutrients from the more reduced lithosphere below. However, once established, subsurface colonization of planetary bodies would extend life for much longer periods of time as the planet cools, allowing the deeper penetration of life into the lithosphere. For example, [Hoening et al. \(2013\)](#) modeled the evolution of the continental surface coverage and the mantle water content with and without

biologically enhanced weathering rates. These authors speculated that the mantle would be significantly drier and the aerial surface coverage by continents smaller than observed if the Earth had no biosphere. The Earth may even lack plate tectonics altogether under these circumstances!

10.14.3.2 Microorganisms and Mineral Formation

Given sufficient mineral ions in the aqueous medium, microorganisms and their biofilms or mats can be rapidly fossilized (Figure 2; Schultze-Lam et al., 1995; Westall et al., 1995). Fossilization takes place either (i) by the complexation of mineral ions to functional groups in the organic material, gradually replacing the organic structure and, at the same time, trapping the degrading organic molecules in the polymerizing mineral matrix, or (ii) when amorphous minerals formed in the aqueous phase bind to the cell envelope (Konhauser et al., 2003; Rancourt et al., 2005). The organic matter in the fossilized microorganisms becomes rapidly degraded (e.g., Orange et al., 2013), but the degradation products may remain trapped in the encapsulating mineral matrix. Alternatively, in modern oxidizing hydrothermal environments, the organic matter can be completely oxidized, although the microbial cast still remains (Konhauser, 1998).

The formation of many secondary minerals catalyzed by microorganisms occurs in both natural and laboratory systems (Figure 8; see Lowenstam, 1981). Metal sorption and mineral nucleation onto microbial cell envelopes are two different passive mineralization processes. Metal sorption occurs via ion-exchange reactions through competition between hydronium ions, alkaline earth ions, and heavy metals for anionic reactive sites on microbial surfaces (Beveridge, 1981; Urrutia and Beveridge, 1994). Many cell envelope polymers have a demonstrated capacity to bind metallic ions and promote mineral nucleation (Beveridge, 1981; Fein et al., 1997).

Active surface-mediated mineralization occurs either by the direct transformation of metals into unstable forms (Lovley

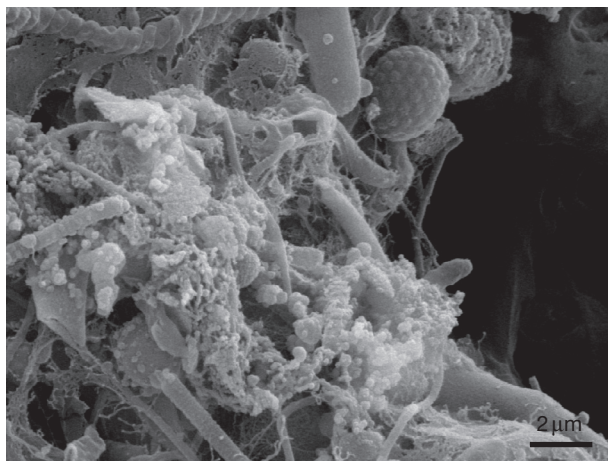
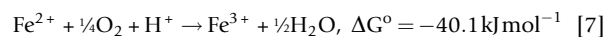
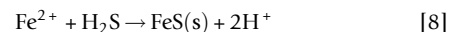


Figure 8 A scanning electron micrograph of a biofilm collected from a borehole flowing from the deep subsurface, 3.1 km below land surface in the Witwatersrand Basin, Republic of South Africa. Note the fine-grained, amorphous iron silicate minerals that have precipitated within the biofilm.

et al., 1991) or by the formation of metal-reactive by-products (Fortin et al., 1994). For example, cyanobacteria have the capacity to precipitate carbonates (Thompson and Ferris, 1990; Thompson et al., 1997) via the creation of alkaline conditions immediately around the cell from photosynthetic activity (Figure 6). However, the formation of unstable forms or metal-reactive by-products depends on the geochemical environment in which they are formed. One hypothesis for the deposition of banded iron formations in the late Archean is that iron oxide precipitation was mediated by the metabolic activity of oxygenic photosynthetic cyanobacteria (although there are a number of BIFs that formed by abiotic processes on the early, anoxic Earth before the advent of oxygenic photosynthesis). Today and since the oxygenation of Earth's atmosphere, the oxidation of iron (reaction [7]) occurs within the aerobic/anaerobic interface of the Earth surface where the reduced iron encounters oxidizing conditions:



(Edwards, et al., 2004; Ehrlich, 1975; Emerson and Revsbech, 1994; Little et al., 2004). Dissimilatory metal-reducing prokaryotes are best known for their ability to utilize minerals for their electron acceptors resulting in the solubilization of Fe (Lovley and Phillips, 1988) and Mn (Myers and Neelson, 1988) oxides and any coprecipitated base metals, as well as the formation of magnetite, siderite, chromium hydroxide, and uraninite (Ishibashi et al., 1990; Lovley et al., 1991; Pedersen and Ekendahl, 1990). The most common metal sulfide attributed to biogenic activity is iron sulfide (Tuttle et al., 1969; reaction [8]):



These dissimilatory processes combined with bacterial surface catalysis are responsible for mineral formation on cell surfaces in these systems.

Although individual bacteria are extremely small, bacteria have played a role in the formation of geologically significant deposits of carbonate, banded iron formations, and phosphorites (Konhauser et al., 2002; Riding, 2000; Youssef, 1965; see Figure 9). From a geochemical perspective, the contribution of bacteria to the formation of ancient deposits is often inferred by the enrichment of stable light isotopes by microbial mineral-forming processes (Kakegawa, 2001; Schidlowski, 1988). Mineral signatures then can serve as biomarkers when they are associated with fossils (Cady et al., 2003; Rasmussen, 2000; Southam et al., 2001; Tazaki et al., 1992), when they possess isotopic signatures that point to biochemical (enzymatic) processing of dissolved solutes, or when realistic, abiotic geologic phenomena cannot explain their occurrence (see review in Westall and Southam, 2006).

10.14.3.3 Habitable Conditions on Early Earth (and Other Rocky Planets)

As we saw briefly in the Introduction, the early Earth would have presented a very different habitat compared with the modern planet (see reviews in Nisbet and Fowler, 2004; Nisbet and Sleep, 2001). The hotter mantle meant that there was a greater amount of volcanic and hydrothermal activity (perhaps similar

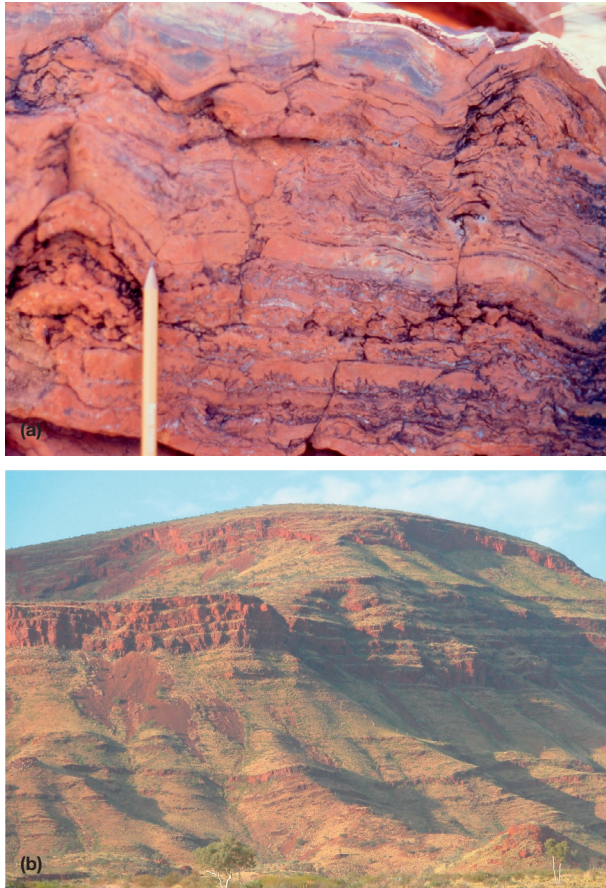


Figure 9 (a) Small, conical stromatolites from the early Archean (>3.46 billion years old) North Pole Dome of the Pilbara (photograph D. Marchesini). (b) A photograph of the Brockman Formation, a banded iron formation found in the Hamersley Range, Pilbara, Western Australia.

to that observed in the central portion of [Figure 2](#)), as well as faster recycling of the crust ([Arndt, 1994](#)). The atmosphere was composed of mostly CO_2 , together with CO , NH_3 , N_2 , and probably a certain amount of CH_4 (the latter possibly at least partly biological; [Pavlov et al., 2001](#); [Zahnle et al., 2010](#)). Oxygen levels were low (<0.2% of present atmospheric levels, [Kasting, 1993](#)), the oxygen being produced by photolysis of water vapor in the upper atmosphere. Based on the high CO_2 concentrations in the atmosphere ([Rye et al., 1995](#)), the oceans were probably slightly acidic, pH 6–7 ([Grotzinger and Kasting, 1993](#)). These acidic conditions, combined with the rapid cycling of hydrothermal fluids ([Duchač and Hanor, 1987](#); [Hofmann and Bolhar, 2007](#); [Paris et al., 1985](#)), would have resulted in extensive mineral weathering. Higher salinity ([de Ronde et al., 1997](#)) and somewhat higher temperatures ($\leq 40^\circ\text{C}$ according to [Hren et al., 2009](#)) were also characteristic of the early to mid-Archean oceans. However, isotopic studies of fluid inclusions in Archean rocks have found that the composition of the oceans has remained somewhat constant over time ([Holland, 1984](#); [Kasting et al., 1993](#)). The lack of significant oxygen in the atmosphere meant that UV radiation levels were high, that is, up to 50 times present levels and up to 1000 times in a

worst-case scenario ([Cockell and Raven, 2004](#)). However, the deleterious effects of UV radiation on the biosphere may have been mitigated by large amounts of dust and aerosols in the atmosphere from volcanic eruptions, meteoritic impacts ([Lowe et al., 2003](#)), and possibly water vapor ([Lammer et al., 2005](#)) or CH_4 smog ([Lovelock, 1988](#)).

The coexistence of reducing and oxidized gases in the prebiotic atmosphere, combined with the input of extraterrestrial organic carbon (e.g., [Brown et al., 2000](#)), would have provided abundant untapped chemical energy for early life-forms ([Catling and Claire, 2005](#)), for example, methanogens that utilize the redox disequilibrium by combining H_2 and CO_2 to make methane (reaction [4]).

10.14.3.4 The Earliest Traces of Life

We would describe the early life-forms on Earth as being anaerobic, halotolerant, UV-resistant (see [Daly et al., 1994](#)), and thermophilic (see [Stetter et al., 1990](#)). What is intriguing about the remnants of the oldest life on Earth is (1) the modern-looking aspect of the individual microorganisms, their colonies, and growth as biofilms and mats ([Figure 10](#)), (2) their diversity, and (3) their wide environmental distribution (see review in [Westall and Southam, 2006](#); [Westall, 2011](#)). While stromatolitic structures and shallow water microbial mats of presumably anaerobic photosynthetic origin have been described from the early Archean period ([Allwood et al., 2006](#); [Hofmann et al., 1999](#); [Tice and Lowe, 2004](#); [Walsh, 1992](#); [Westall et al., 2006b, 2011](#)), they are orders of magnitude smaller ([Figure 9\(a\)](#)) than the aerobic bioconstructions of the late Archean/Proterozoic epochs ([Figure 9\(b\)](#); [Awramik and Sprinkle, 1999](#)). Other carbon-rich sediments from this period testify to a relatively abundant input of carbonaceous material from shallower water environments ([Tice and Lowe, 2004](#); [Walsh and Lowe, 1999](#)) or from the planktonic photic zone ([Javaux et al., 2010](#); [Walsh and Lowe, 1999](#)). However, the main limitation to early Archean productivity appears to be the fact that oxygenic photosynthesis and the corresponding aerobic heterotrophs had not yet developed ([Des Marais, 2000](#)).

The advanced level of evolution demonstrated by the remnants of life at 3.5 Ga has implications for the timing of the origin of life. Did the predicted planet-sterilizing impacts ([Nisbet and Sleep, 2001](#); [Ryder, 2002](#); [Sleep et al., 1989](#)) during the LHB between 4.0 and 3.85 Ga ([Maher and Stevenson, 1988](#)) completely wipe out all traces of life, if it had evolved before, or was life able to survive in protected subsurface ecosystems? Note that an alternative hypothesis proposes that only the topmost 400 m of the oceans would have been evaporated during the worst of the impact events ([Ryder, 2002](#)). The occurrence of hyperthermophilic microorganisms in the lowest branches of the evolutionary tree of life ([Pace, 1997](#)) is generally considered to imply that early life must have passed through severe (catastrophic) environmental conditions, such as an almost planet-sterilizing impact and that life-forms in protected habitats, such as deep-sea hydrothermal vents, survived, whereas life-forms in the more exposed habitats did not. Whatever the timing necessary for life to appear ([Lazcano and Miller, 1996](#), suggested 10 My), a rocky planet with a hydrosphere can support prokaryote life-forms.

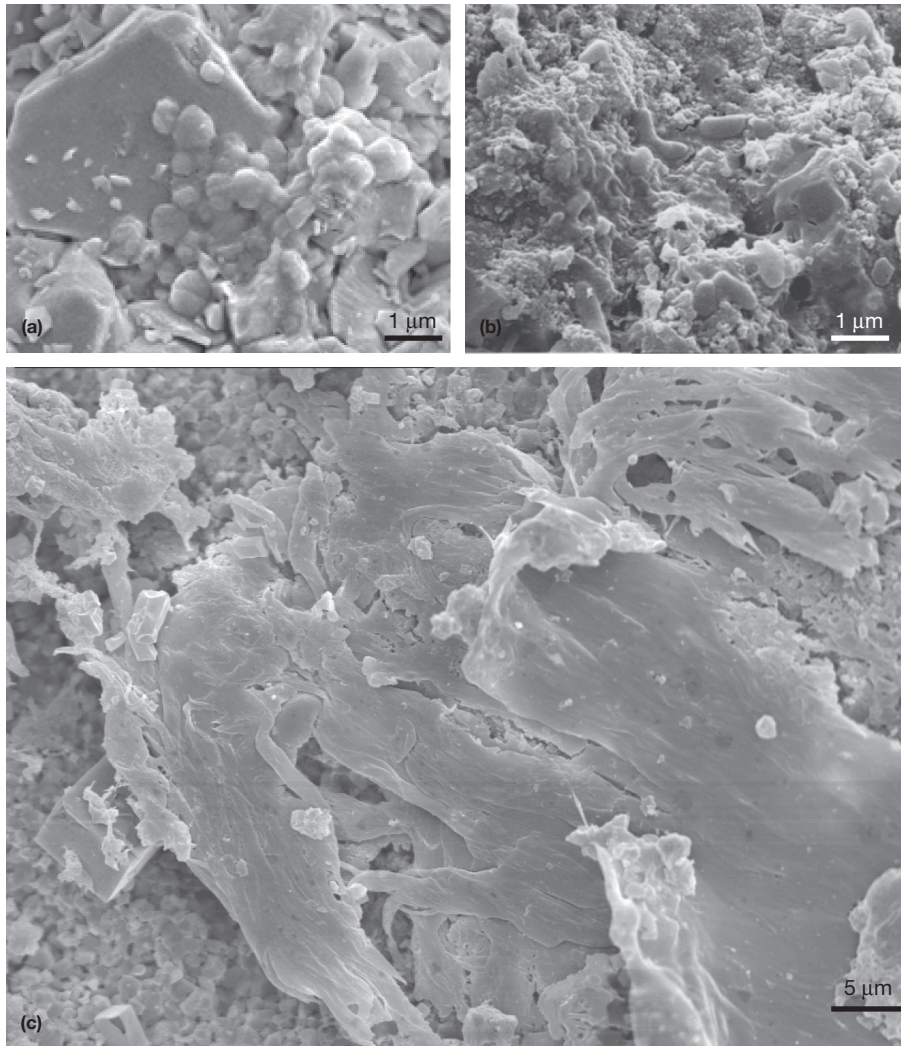


Figure 10 Fossilized early Archean microorganisms (3.47–3.34 billion years) (a) small colony of small coccoid microfossils (arrow) that colonized a marine, subsurface sedimentary habitat (see Westall et al., 2006a); (b) small colony of rod-shaped to vibrioid-shaped microfossils (arrow) that were closely associated with anaerobic, photosynthetic filaments forming a well-developed microbial mat (c) on beach sediments in an evaporitic environment (see Westall et al., 2006b).

10.14.4 Conclusions for Geology, Life, and Habitability Beyond the Earth

The ingredients necessary for life to originate (liquid water in contact with rocks/minerals; abundant organic molecules (exogenous or endogenous); elements such as hydrogen, oxygen, nitrogen, phosphorous, and sulfur; and energy sources (geochemical and sunlight)) were abundant on the early Earth. They were also abundant elsewhere in the early solar system and presumably in the universe. It is therefore legitimate to surmise that life could have arisen independently wherever these initial conditions are stable for the length of time that is necessary for the process. Once started, from a microbiological point of view, these ‘primitive’ life-forms can exist wherever there are the essential nutrients and potential redox reactions (providing chemical energy) that could support growth. Apart from the classical terrestrial planets in the solar system (Venus and Mars), Europa has also recently

excited interest because of the potential for liquid water in contact with a rocky core (Bhattacharjee and Chela-Flores, 2004; Greenberg, 2005), and the presence of water ice on Enceladus is equally stimulating (Brown et al., 2006).

The possibility of extraterrestrial life on Mars has fascinated humans for over a hundred years: Percival Lowell (1910) started the ball rolling with an account of Martian life based on Schiaparelli’s (1879) drawing of what he thought were channels (or intersecting straight lines) on the surface of Mars. Although various missions over the last 30 years have discounted these fanciful theories, it is clear that, early in its history, there was a significant inventory of water on the surface of the planet as documented by geomorphological features (e.g., Di Achille and Hynek, 2010; Jaumann et al., 2002) and the presence of minerals produced by aqueous alteration and deposition (e.g., Bibring et al., 2006; Loizeau et al., 2012), albeit probably not sufficient for an ocean covering the northern hemisphere (Clifford and Parker, 2001;

Mouginot et al., 2012), that is, Mars possessed an active hydrosphere during the time when life originated on Earth. As we have seen earlier, microbial life does not require oceans of water in order to function: Once it has got going, it just requires continual access to a very small amount of carbon, nutrients, and energy. Given the access to the basic requirements for an origin of life (liquid water, organics, and rocks/minerals), it is possible that life did arise independently on the red planet (Westall et al., 2013). Indeed, the first results from the Mars Science Laboratory mission with its rover Curiosity in the 3.6-Ga-old Gale crater indicate that there is evidence for habitable conditions in the crater (http://www.nasa.gov/mission_pages/msl/news/msl20130312.html). Therefore, Mars may contain a record of fossilized primitive microorganisms or their associated mineralogical biomarkers, similar to those that are found on Earth. These traces of early Martian life will likely occur in the rocks of the southern hemisphere, which are largely Noachian in age and have apparently undergone aqueous alteration. Of course, boulders or meteorites of southern hemisphere material could be found elsewhere on Mars or even on the moons of Mars, Phobos, and Demos, since Mars, together with the other inner solar system planets, experienced a period of late bombardment between 4.0 and 3.8 billion years ago. It is equally possible that the Noachian-age rocks will contain traces of the prebiotic stage of life and the appearance of the first cells, that is, the critical period of life on Earth's history that is missing on Earth – if we are capable of recognizing these traces (Westall et al., 2013).

If life established itself on Mars during the Noachian age, could it still be present today and, if so, where? The loss of liquid water on Mars' surface and the cessation of any sort of plate tectonic activity (if there ever was any) due to the rapid cooling of the planet limit one of the important criteria for life, that is, a flux of reduced or energetic redox species, although Curiosity did find evidence of the redox couple sulfide and sulfate in Gale crater (Grotzinger et al., 2014; McLennan et al., 2014). As we noted earlier, microorganisms can survive a wide range of extreme conditions, but there are certain combinations that are lethal, and it appears that the combined low water activity, high UV radiation, and the presence of some kind of oxidant species that oxidizes labile organic components (i.e., those that are necessary for life) makes the surface of the planet hostile to any long-term survival. However, Mars is not completely volcanically inactive (Neukum et al., 2004), and there could be hydrothermal activity in its subsurface, as indicated by occasional surface exposure (Malin and Edgett, 1996) and with subsequent implications for life (Farmer, 1996; Schwenger et al., 2012). Previous identifications of methane on Mars (e.g., Formisano et al., 2004) gave rise to hypotheses of a subsurface origin related to biological activity (Tung et al., 2005) although an alternative hypothesis related to hydrothermal melting of CH₄ clathrates was also postulated (Prieto-Ballesteros et al., 2006). However, it now appears that the detections of methane were erroneous (Zahnle et al., 2011). Whether or not methane has been detected, this activity would provide the necessary criteria/conditions for life, at least in the subsurface of Mars, similar to that provided to bacteria in Earth's subsurface (Boston et al., 1992; Wanger et al., 2006).

While we do not know the exact conditions necessary to create life, the basic requirements of a habitable extraterrestrial

body (assuming Earth is a representative sample) are fairly well understood. Habitable locations in our solar system today, that is, places where life can be sustained, are not as restrictive as those where life could originate and include Mars' subsurface (Boston et al., 1992), as well as the ocean on Europa (Chyba and Phillips, 2001). It is also intriguing to realize that, in the future as the Sun gets hotter and comes into the red giant phase of its history, these planets and possibly others in the outer solar system will be able to host life, if not see it appear independently. Thus, the possibility of finding traces of extinct or extant life on other planets in the solar system is strong, and the future for life in the solar system is optimistic, even though the habitability of our own planet will slowly decrease starting in another c.1.5 Ga (Franck et al., 2006).

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