# PALAEOBIOLOGY II

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To the memory of J.J.SepkoskiJr



considerable support to the idea that the primitive translation apparatus may have been shaped, at least in part, by interactions between amino acids of prebiotic origin and polyribonucleotides (Gesteland *et al.* 1999). If the current interpretation of the evolutionary significance of these and other properties of RNA molecules is correct, then one of the central issues that origin-of-life research must confront is the understanding of the processes that led from the primitive soup into RNA-based life forms. The search for simple organic replicating polymers will play a central role in this inquiry. Even if the appearance of life remains an elusive issue, redefining the questions that need to be addressed to understand how it took place is, in itself, an encouraging scientificachievement.

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# 1.1.2 Exploring for a Fossil Record of Extraterrestrial Life

J.D. FARMER

#### Introduction

While speculation about the possibility of life elsewhere in the Cosmos has been a persistent theme throughout the history of humankind, the last decade of the twentieth century has witnessed a number of important advances in our understanding of the nature and evolution of terrestrial life. These developments have opened up important new possibilities for the existence of living systems elsewhere in the Solar System (or beyond) and have spawned a new interdisciplinary science called 'astrobiology'-the study of the origin, evolution, distribution, and destiny of life in the Cosmos. This new discipline embraces the traditional field of exobiology, which focuses on the origin of life and early biosphere evolution, along with a newer sister discipline, exopalaeontology, which seeks evidence for a fossil record of ancient life or prebiotic chemistry in extraterrestrial materials, or from other planets in the Solar System.

An important legacy of the Apollo space missions was the development of a detailed cratering history for the moon. This led to the view that during early accretion, prior to =4.4Ga, surface conditions on Earth were unfavourable for the origin of life (Chang 1994). As a consequence of frequent giant impacts, magma oceans could have been widespread over the Earth's surface, and volatile compounds, including water and the biogenic elements needed for life's origin, would have been lost to space. Models of early accretion suggest that during the interval 4.4-4.2Ga impact rates and object sizes declined to a point where the water (and associated organics) delivered to the Earth by volatilerich impactors (e.g. comets) was retained. A stable atmosphere and oceans probably developed during this time, providing the first suitable environments for prebiotic chemical evolution and the origin of life.

Models also suggest that early biosphere development overlapped with one or more late, giant impacts that were large enough to volatilize the oceans and perhaps sterilize surface environments (Sleep *et al.* 1989). Such events would have frustrated the development of the early biosphere and may have even required that life originate more than once. The most protected habitat during this early period would have been the deep subsurface.

Discoveries of  $\sim 3.4$  Ga cellular microfossils from cherts in volcanic sequences in Western Australia (Schopf 1993), and possible 3.86 Ga chemofossils (carbon isotopic signatures) from phosphate-rich metasediments in Greenland (Mojzsis *et nl.* 1996) indicate that once the conditions necessary for life's origin were in place, life arose very quickly, perhaps in a few hundred million years or less. This observation significantly improves the possibility that life originated on Mars, or elsewhere in the Solar System where habitable zones of liquid surface water were more ephemeral features of early planetary evolution.

While recent discoveries in Precambrian palaeontology have pushed back the dates for the oldest fossils, molecular phylogenies have also provided important clues about the origin and early evolution of life on Earth, based on the historical record preserved in the genomes of living organisms. Comparisons of genetic sequences in 16 Sribosomal RNA indicate that terrestrial life is subdivided into three major domains: the Archaea, the Bacteria, and the Eukarya. It is also apparent that the vast proportion of biodiversity on Earth is microbial. Higher forms of multicellular life appeared quite late in Earth history and make up only a tiny fraction of the total number of species. The deepest branchng lineages in the RNA tree are high-temperature forms that utilize reduced inorganic substrates, like sulphur \_\_\_\_or hydrogen. This suggests that the last common ancestor of life on Earth was a high-temperature ('thermophilic') chemotroph, a view that is consistent with the higher rates of heat flow, volcanism, and frequent impacts that prevailed on the early Earth. However, the RNA tree may reveal little about life's origin (see Section 1.1.1). The thermophilic properties of the most deeply rooted lineages may simply be a legacy of late giant impacts that eliminated all but the highest temperature species.

#### Possible extant life on Mars and Europa

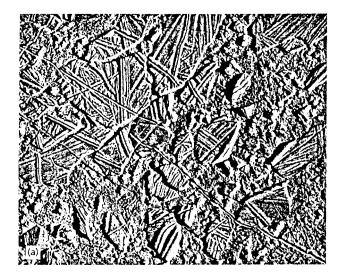
The discovery of an extensive subsurface biosphere on the Earth opened up exciting new possibilities for the existence of habitable zones elsewhere in the Solar System. On Earth, subsurface habitats harbour many species that are capable of synthesizing organic molecules from simple inorganic substrates. The subsurface

is the most compelling environment for extant Martian life because of the possibility that a deep subsurface ground water system may exist at several kilometres depth (Carr 1996). In addition, results from the Galileo mission provide support for the existence of a subsurface ocean beneath the crust of Europa, one of Jupiter's moons. It is postulated that heating of the moon's interior by tidal friction could sustain a subcrustal ocean of liquid water, and sea floor hydrothermal systems (Belton et al. 1996). Indeed, the complexly fractured and largely uncratered surface of Europa (Fig. 1.1.2.1) indicates an active ice 'tectonics' involving the periodic upflow of icebrines from beneath the Europan crust. It is possible that where water welled up from below, it carried life forms or prebiotic chemistry from the underlying ocean and incorporated these materials into surface ices. Terrestrial microbes are known to retain viability at subzero temperatures by exploiting thin films of brine on grain surfaces in permafrost soils. Could viable organisms be present within similar ice-brine environments on Europa? Viability arguments aside, ice could also provide a means for the prolonged cryopreservation of organic materials, accessible to robotic landers.

#### **Exploring for an ancient Martian biosphere**

The Viking lander missions showed the present surface environment of Mars to be unfavourable for life due to the absence of liquid water, intense UVradiation, and oxidizing soils. At the same time, images obtained from Mars orbit revealed the early planet to be more Earthlike, with a broad range of surface environments suitable for life. It is likely that habitable environments disappeared from the surface =3.8Ga as Mars began to lose its atmosphere (Fanner and Des Marais 1999). If extant life exists on Mars today, it is likely to be in deep subsurface environments that will be inaccessible to robotic platforms. Deep subsurface drilling will likely require a human presence. However, if life once existed in surface environments, it is likely to have left behind a fossil record in ancient sediments now exposed at the surface. Such deposits could be accessed during the robotic phase of exploration. This simple concept underlies the basic rationale of the present Mars exploration programme.

Studies of the Precambrian fossil record on Earth, and of modern microbial systems that are analogues for those on the early Earth and Mars, provide a conceptual framework for guiding the search for a fossil record on Mars. An understanding of how preservation vanes between different groups of microorganisms over extremes of the environment, and how postdepositional, diagenetic changes affect the long-term preservation of microbial biosignatures in rocks, is crucial (Farmer and Des Marais 1999). Such studies allow the formulation of



**Fig. 1.1.2.1** (a)Galileo orbiter image of the surface of Europa, one of the moons of Jupiter. The surface crust is composed of water ice that has been fractured into irregular blocks. The fracture patterns suggest that the crust was mobilized by a layer of subsurface water which flowed up from below, filling fractures between blocks as they separated. Such observations support the view that Europa once had, and perhaps still has, a subcrustal ocean of liquid water that could sustain life or

'rules' of preservation that help optimize strategies to explore for past life on Mars and other planetary bodies, such as Europa.

As with Earth-based palaeontology, site selection is crucial for the successful implementation of Mars missions designed to explore for past life. Preservation is a selective process that is strongly dependent upon the biogeological environment. Studies of microbial fossilization reveal that the rapid entombment of microorganisms and their by-products by fine-grained, clay-rich sediments and/or chemical precipitates is of singular importance in enhancing preservation. Favourable geological environments are those where microbial systems coexist with high rates of fine-grained detrital sedimentation, and/or aqueous mineral precipitation. Examples include rapidly mineralizing hydrothermal systems (below the upper temperature limit for life), terminal lake basins (where chemical sediments such as evaporites, fine-grained lacustrine sediments, and sublacustrine cold spring tufas are deposited), and mineralizing soils (e.g. hard-pans, including calcretes, ferracretes, and silcretes). Even if life did not develop on Mars, this exploration strategy is still important because the same sedimentary environments could preserve a record of prebiotic chemistry similar to that which spawned the development of life on Earth. This early prebiotic history has been lost from the terrestrial record.

Mars may preserve the most complete record of early



prebiotic chemistry. The smallest features visible in this image are about 20 m across. (b)Close-up of the surface of Europa showing a complex network of ridged fractures originally formed when plates of ice crust pulled apart. Many ridge segments were later offset along strike—slip faults. The large ridge in the lower right corner of the image is about 1km across. (Photographs by courtesy of NASA.)

events of planetary evolution anywhere in the Solar System. The 4.56Ga age of Martian meteorite ALH 84001 (McKay et al. 1996) indicates that the ancient, heavily cratered highlands of Mars contain a crustal record extending back to the earliest period of planetary evolution. On Earth, comparably aged crustal sequences have been destroyed by tectonic cycling, metamorphism, weathering, and erosion. In contrast, Mars never developed a plate tectonic cycle and extensive watermediated weathering and erosion was probably limited to the first billion years or so of the planet's history. Geomorphic features suggest that surface hydrological systems were active until near the end of heavy bombardment (=3.8Ga), after which time liquid water quickly disappeared from the surface, presumably as a result of the loss of the Martian atmosphere (Carr 1996).

The preservation of fossil biosignatures is favoured when organisms or their by-products are incorporated into low permeability sedimentary deposits (producing a closed chemical system during diagenesis) of stable mineralogy (promoting a prolonged residence time in the crust). Chemical sediments composed of silica, phosphate, and carbonate, along with fine-grained, clay-rich detrital sediments and water-deposited volcanic ash, are especially favourable lithologies for long-term preservation. This is illustrated by the fact that on Earth most of the Precambrian record is preserved in such lithologies.

Many potential sites for a fossil record have been

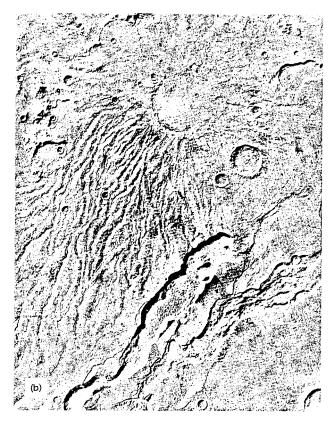


**Fig. 1.1.2.2** (a) Gusev Crater, Mars. A large river canyon to the south (Ma'adim Vallisdrained into this = 150km diameter crater, depositing a delta where it entered the crater. Geological studies suggest a prolonged hydrological history for this region of Mars, with the Gusev Crater being the site of an ancient palaeolake system. (b) The slopes of Hadriaca Patera, an ancient Martian volcano, show channels radiating downslope, away from the caldera rim (caldera = **7 s**km across). These small channels are interpreted to be the result of

identified on Mars using orbital photographs obtained by Viking (e.g. Fig. 1.1.2.2). However, information about the mineralogical composition of the Martian surface is still lacking. Mineralogy provides important clues about the palaeoenvironment, information needed to determine the best sites for detailed surface exploration. An important exploration goal is to identify aqueous mineral assemblages (of the types that commonly capture and preserve fossil biosignatures) from orbit using spectral mapping methods prior to landed missions. In targeting sites for sample return, evaporative lake basins and hydrothermal sites are given a high priority. In terrestrial settings, the deposits formed in these environments frequently provide optimal conditions for preservation.

#### Putative signs of life in a Martian meteorite

The report of possible fossil signatures in Martian met-



pyroclastic flows, the channels being subsequently enlarged by sapping flow. The basal slope of Hadriaca Patera was later eroded by outfloods of subsurface water which carved Dao Vallis, a large channel located near the bottom of the photograph (channel = 45 k m ide). The association of subsurface water and a heat source (the subsurface magma that produced the volcano) suggests the potential for sustained hydrothermal activity in this region. (Photographs by courtesy of NASA.)

eorite Allan Hills 84001 (McKay *et al.* 1996) generated an intense, ongoing debate over the usefulness of a variety of morphological, mineralogical, and geochemical data for detecting biosignatures in ancient rocks. Subsequent work by the broader scientific community indicates that the major lines of evidence used to support the biological hypothesis for ALH 84001 are more easily explained by inorganic processes.

Polycyclic aromatic hydrocarbons (PAHs), such as those found in ALH 84001, are not generally regarded as being diagnostic of life. In addition, it has been shown that a major fraction of the organic matter present in the meteorite exhibits radiocarbon activity, indicating that it originated through terrestrial contamination after reaching the Earth (Jullet a/. 1998). Although a small fraction of remaining organic matter could be Martian, it has not yet been characterized.

A key test of the biological hypothesis for ALH 84001 is the formation temperature of the carbonates that

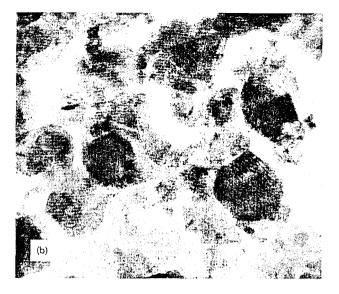


**Fig. 1.1.2.3** (a)Scanning electron micrograph of nanostructures found on fracture surfaces of carbonate minerals in Martian meteorite, ALH 84001. The elongated structure in the centre of the image is =2 u mlong and consists of a series of smaller segments each =0.1 u mwide. (b) Transmission electron micrograph showing small magnetite

contain the putative fossil evidence. Carbon and oxygen isotope measurements obtained for carbonates in the Alan Hills meteorite indicate a wide range of formation temperatures, the lowest falling within the range for life (<120°C). Because the carbonates experienced multiple shock events, each with highly localized effects, the spread of isotopic values is perhaps not surprising. However, the lowest temperature estimates are likely to be primary, having been least affected by shock metamorphism (Treimanand Romanek 1998).

Magnetite grains present in the rims of the ALH 84001 carbonates (Fig. 1.1.2.3b) were compared to intracellular magnetite crystals ('magnetosomes') formed by terrestrial magnetotactic bacteria. However, ultrastructural features (spiral defects) discovered in some of the ALH 84001 magnetites suggest that they were formed by vapour deposition at high temperatures. In addition, the ALH 84001 magnetites exhibit epitaxial growth relationships with the host carbonate, and are therefore unlikely to have formed within the cells of bacteria (Bradley et *al.* 1998).

Nanometre-scale morphologies having shapes similar to microbes were observed on some fracture surfaces of carbonates in the ALH 84001 meteorite (Fig. 1.1.2.3a). These were compared to terrestrial 'nanobacteria'. This is an informal term used to describe small (<0.1um)rods and spheroids found in rocks which resemble spores or resting stages of microorganisms (see Kirklandet *al.* 1999). At this observational scale, problems often arise in distinguishing biological structures from inorganic



grains found within carbonate minerals of ALH 54001. The magnetite grains average 15-20 nm wide. Magnetite crystallites in ALH 54001 exhibit epitaxial relationships with the host carbonate grains and screw dislocations suggestive of vapour-phase deposition. (Photographs by courtesy of the Lunar Planetary Institute.)

forms which originate by self-organizing crystal growth, or as artefacts created during the application of crystalline metal coatings used to prepare samples for scanning electron microscopy SEM). The putative microfossils in the ALH 84001 meteorite have subsequently been explained by a combination of the above processes. At the nanometre scale, shape is clearly a poor criterion for biogenicity. In the absence of other types of compelling evidence, it is probably best to avoid the use of the term 'nanobacteria', and adopt instead a non-genetic descriptive term, like 'nanostructures', which does not imply an origin.

The apparent refutation of the biological hypothesis for the ALH 84001 meteorite leaves the question of Martian life unresolved. Answering this question is likely to require the careful in situ study of Martian samples that formed under aqueous conditions that were favourable for the rapid capture and long-term preservation of biosignatures. Given the difficulty of recognizing ancient microbial signatures in rocks, the return of samples to the Earth for analysis in specialized laboratories may be required for an adequate test of the life hypothesis. The careful re-examination of biological evidence for the ALH 84001 meteorite has improved the basis for interpreting the Precambrian record on Earth by establishing more rigorous standards for biogenicity in ancient materials. The broadly based effort has also helped to prepare the scientific community for a series of Mars sample return missions tentatively scheduled to begin in 2009.

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#### 1.1.3 Life in the Archaean

R. BUICK

#### Introduction

When did life on Earth first appear? What were primordial organisms like? How and where did they live? Though these are age-old philosophical and theological questions, they also have scientific significance. Clearly, Earth's history would have been different if abundant, diverse life had arisen when the crust solidified, perhaps 4.5 billion years ago, rather than halfway through geological time, at the end of the Archaean (2.5Ga).

To answer these questions empirically, palaeontological and geochemical relics of an Archaean biota are required, but finding such evidence can be difficult. Archaean rocks are rare because the exposed rock mass diminishes markedly with age due to erosion, burial, and subduction. Many that remain are poorly preserved because the probability of destructive deformation or metamorphism increases with age. However, in a few ancient cratons, relatively untraumatized Archaean supracrustal rocks still exist in reasonable abundance, permitting palaeobiological investigation of suitable facies. These consist mainly of kerogenous cherts and shales, banded ironstones, and carbonates of various compositions, but more exotic lithologies (sandstones, palaeosols, hydrothermal deposits) can also yield useful data.

As even the most pristine Archaean rocks have complex histories, their sedimentary environment, stratigraphic relationships, postdepositional evolution, and geochronology must be fully understood to ascertain whether any biological remains are indeed ancient and not younger contamination. However, these basic geological data are rarely available in many Archaean terrains. Furthermore, as early organisms were probably small, simple, and subtle in their environmental impact, the biogenicity of putative Archaean fossils is often ambiguous. More studies of modern microbes, their biogeochemical interactions, and their inorganic mimics are needed to resolve this issue. Perhaps most importantly, it is essential to approach Archaean palaeobiology from first principles, because the nature of the early fossil record is unpredictable, and to subject all data to severe scrutiny, because real discoveries are of such significance.

#### How are relics of Archaean life preserved?

#### **Microfossils**

The ideal form of Archaean palaeobiological evidence is the preserved remains of the organisms themselves (see Section 3.4.2). As no macrofossils have ever been found in rocks older than 2.1 Ga, the search for Archaean fossils has been largely conducted by microscopy. The most cenvincing are barely of Archaean age, =2.52 Ga from the Transvaal Supergroup of South Africa (Lanier 1986; Klein *et al.* 1987; Altermann and Schopf 1995). The assemblages (Fig. 1.1.3.1)contain solitary or paired ellipsoids (0.2–2.5um), solitary, paired or clustered spheroids (1.5–20um), solitary tubular filaments (diameter 0.5-3 um)and interwoven mats of tubular filaments (diameter 10-30 um) ll composed of kerogen that is isotopically