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Organic host analogues and the search for life on Mars

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Abstract: Mars analogue sites represent vital tools in our continued study of the Red Planet; the similar physico-chemical processes that shape a given analogue environment on Earth allow researchers to both prepare for known Martian conditions and uncover presently unknown relationships. This review of organic host analogues – sites on Earth that mimic the putatively low organic content of Mars – examines specific locations that present particular Mars-like obstacles to biological processes. Low temperatures, aridity, high radiation and oxidizing soils characterise modern-day Mars, while acid–saline waters would have presented their own challenges during the planet's warmer and wetter past. By studying each of these hurdles to life on Earth, scientists can prepare instruments headed for Mars and identify the best locations and approaches with which to look for biological signatures. As our use of organic host analogues becomes increasingly sophisticated, researchers will work to identify terrestrial sites exhibiting multiple Mars-like conditions that are tailored to the distinct mineralogical and physical characteristics of Martian locations. Making use of organic host analogues in these ways will enhance the search for signs of past or present life on Mars.

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Introduction

The search for life beyond Earth remains one of the most far-reaching and provocative scientific endeavours of our time. With five spacecraft currently operating on or around Mars (Mars Express, the Mars Exploration Rovers Spirit and Opportunity, the Mars Reconnaissance Orbiter and Mars Odyssey), we find ourselves in a golden age of Mars exploration. As future missions, such as the National Aeronautics and Space Administration's (NASA's) Mars Science Laboratory and the European Space Agency's (ESA's) ExoMars prepare to carry the baton, it is vital that current knowledge be used to inform the preparation and planning of this next generation of rovers and landers.

Our information from Mars spacecraft is valuable but limited. Much greater volumes of knowledge can be obtained by studying not only data acquired from Mars but also information from Mars-like materials on Earth. This can be achieved through the use of analogue sites – terrestrial locations that resemble Mars in certain ways. There are several varieties of Mars analogues, which can be categorised by the Martian characteristics they best mimic (Table 1). Such Mars analogues are diverse and can be employed to take advantage of a variety features. An attempt at rationalisation and categorisation of Mars analogues and their respective uses is described below.

Composition

Promising Mars analogue sites exhibit compositional traits that are as similar as possible to Martian soils in terms of mineralogy, elemental abundances, volatiles and organic content. Elemental and mineralogical analyses are the most direct and well-understood paths towards the provision of geological context (Squyres *et al.* 2004a; Bibring *et al.* 2006). All of these chemical parameters play important roles in establishing the broader context of a given environment on Mars.

Electrochemical

Properties such as dielectric constant, redox potential, pH, and magnetism influence the interactions of soil constituents and have important implications for organic substances. The dielectric constant is an important parameter in determining subsurface ice purity – a factor that could reveal potential water and nutrient sources and affect instruments, such as ground-penetrating radars (Grimm *et al.* 2007; Watters *et al.* 2007; Grima *et al.* 2008). The redox state of a given geochemical environment provides clues to the local geological history (Kilinc *et al.* 1983; Christie *et al.* 1986) and dictates the energy yield from chemical reactions that may be exploited by life (Lovley 1991; Fetzer & Conrad 1993; Rivkina *et al.* 1998). Soil pH levels are known to influence the

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Table 1. *Parameters by which potential analogue environments can be categorised and compared to environments on Mars. Highest-level attributes are on the left and more detailed measurables progress to the right of the table*

Hierarchy of Mars analogue attributes		
Compositional	Mineralogical distribution	
	Elemental abundances	
	Presence of volatiles	Water content
		Dissolved gases
	Organic content	
Electrochemical	Dielectric constant	
	Redox potential	
	pH	
	Magnetic	Magnetic susceptibility
		Saturation magnetization
Physical	Thermophysical	Albedo
		Thermal inertia
	Mechanical	Shear strength
		Slope stability
	Bulk physical	Particle size distribution
		Particle shape
		Density
		Porosity
Environmental	Temperature	
	Aridity	
	Wind	
	Radiation	

chemical absorption of ions (Farrah & Pickering 1979; Burt 1981; Yong *et al.* 1998). Magnetic properties of the Martian surface, reflected by magnetic susceptibility (a quantitative measure of the extent to which a material may be magnetised) and saturation magnetism (the maximum possible magnetization of a material), influence how electrical space craft equipment can be operated and offer useful information about the local geology, including the potential involvement of water (Hviid *et al.* 1997; Bertelsen *et al.* 2004; Rochette *et al.* 2004). By identifying suitable electrochemical analogues on Earth, not only can relevant instruments, such as radar and spectrometers, be tested and calibrated, but also analysts can apply systems-based knowledge from analogue sites to less rigorously studied Martian environments.

Physical

Soil properties, such as thermophysical, mechanical and bulk physical characteristics, influence both small- and regional-scale processes. The interaction of a rover with the surface material (via slope stability, soil strength, porosity, etc.) determines the ease and manner of mobility and thereby fundamentally influences overall mission success. Particle sizes and shapes must be taken into account when evaluating the physical effects of Martian soil on mechanical components, such as spacesuit joints, robotic hinges and soil samplers (Young *et al.* 2005). A detailed understanding of soil mechanical parameters, such as cohesion and internal friction angle, is crucial in order to optimise roving capability and minimise lost time during active mission phases (Kemurdjian 1998; Shibly *et al.* 2005). On a larger scale, Mellon & Jakosky (1993) demonstrated that thermophysical properties are the primary determinants of ground ice stability on Mars, and spacecraft engineers must consider such parameters when designing electronic and structural components (Kirschman *et al.* 2001; Birur *et al.* 2002). Locating analogue sites on Earth that mimic these physical properties of Mars allows for more robust rover and spacecraft construction and greater understanding of the broader physical and scientific influences that will influence robotic missions.

Environmental

Martian soils are also shaped by a range of broader environmental parameters, such as the temperature regime, atmospheric composition, wind, and radiation. Therefore, useful analogue sites on Earth must take into account the environmental aspects of the particular time and place on Mars that is of interest. Environmental parameters are particularly important for organic host analogues, because they represent mechanisms by which organic matter is destroyed and successful detection precluded.

Organic host analogues

In the context of Table 1, organic host analogues are particularly dependent upon environmental variables that create Mars-like challenges for biological processes. Many organic host analogues are soils and this paper will review the current state of Mars organic host analogue research by summarizing the utility of these soils, highlighting relevant analogues, and discussing their continued application to future missions.

Organic host analogues are vital tools in the preparation of Mars missions seeking signs of past or present life (Cabane *et al.* 2004; Mattingly *et al.* 2004; Bada *et al.* 2007). Testing instruments in a setting of limited organic content allows scientists and engineers to evaluate instrument sensitivity and functionality in a field environment. Pullan *et al.* (2008), for example, used a range of samples from organic host analogue sites to test a suite of instruments, promoting the use of multiple techniques when analysing organic molecules.

Understanding if and how organic molecules are preserved under Mars-like conditions can inform the search for analogous substances on the Red Planet. For example, the periodic field seasons carried out under the Arctic Mars Analog Svalbard Expeditions (AMASE) have provided a platform from which instruments can be tested in an analogous macro-environment in an iterative fashion (Jorge-Villar *et al.* 2006; Steele *et al.* 2006; Botta *et al.* 2007; Jorge-Villar *et al.* 2007; Sarrazin *et al.* 2007). The resulting data not only enhance instrument development, but also increases scientific knowledge about Earth-based systems that can be applied to organically relevant questions on Mars. This function means that through the use of organic host analogues, scientists can

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Table 2. *Analogue sites examined in the review, divided by their characteristics most threatening to life*

Analogous environmental parameters	Organic host analogue sites
Salinity & acidity	Acid–saline lakes of Western Australia Rio Tinto, Spain
Low temperature	Antarctic ice Arctic permafrost Sea ice
Aridity	Mojave Desert, California Atacama Desert, Chile
Radiation & oxidizing soil	Atacama Desert, Chile Antarctic dry valleys

both improve planned mission machinery and use relevant findings to adjust course in the search for life.

Modern-day Mars is a harsh place for life as we know it, where frigid temperatures, intense radiation, highly oxidizing soil and extreme aridity combine to present significant obstacles to any potential extant life forms. The planet was once warm and wet (Pollack *et al.* 1987; Carr 1996; Baker 2001; Bibring *et al.* 2005; Golombek *et al.* 2005), but even under such relatively balmy conditions, acidic waters and high salt concentrations presented their own formidable challenges (Tosca *et al.* 2008). Although the search for signs of life will occur in the harsh conditions of modern Mars, the use of analogues must take into account both past and present Martian environmental conditions. Understanding the conditions on ancient Mars (such as high salinity and acidity) will help to reveal the types of organic compounds that should be targeted and the likely mineralogical hosts of these materials. Moreover, appreciating life's limits in today's harsh Mars-like conditions on Earth (low temperatures, aridity, high radiation and highly oxidizing soils) could help suggest potential refuges of viable Martian organisms.

Given the need to understand the habitats and associated stresses on potential Martian biology, six characteristics of modern and/or ancient Mars, divided into four environmental regimes, have been identified as challenging but tolerable for life as we know it: high acidity and salinity, low temperatures, aridity and intense radiation and oxidizing soil. For each of these four parameters, the most Mars-like/best-characterised analogue sites are described (Table 2) and relevant organic data is reviewed below.

This review is not an exhaustive list of all sites on Earth that have been or are similar to parts of past or present Mars; to accumulate such a compilation is beyond the scope of this document. Rather, by focusing on and promoting the use of well-characterised analogue sites, mission planners and scientists alike can achieve synergies by testing both equipment and hypotheses in the same environments. By studying how life on Earth responds to specific biologically challenging conditions in analogue environments, future life-detection instruments will be better prepared to achieve their objectives.

Salinity and acidity

The past presence of liquid water on Mars has been confirmed (Squyres *et al.* 2004a), and although the precise geochemical nature of the ancient bodies of water remains unclear, most recent findings suggest a highly acidic and saline hydrochemistry. The rover Opportunity's detection of jarosite, magnesium sulphates and calcium sulphates (Klingelhofer *et al.* 2004; Squyres *et al.* 2004a) point to the ephemeral percolation of acidic, saline groundwater (Grotzinger *et al.* 2005; McLennan *et al.* 2005). Morris *et al.* (2008) suggest that the SiO_2- and TiO_2-enriched soils at Home Plate in the Gusev Crater result from acid sulphate leaching.

The temporal extent of this aqueous environment, as well as its degree of salinity and acidity, is not certain, but the detection of hydrous minerals in Noachian rocks by OMEGA implies that wet conditions were present in Noachian times (Bibring *et al.* 2005). Atmospheric and oceanic chemistry would have been affected in late Noachian times by increased volcanism, which formed the Tharsis and Elysium volcanic features. This volcanism released substantial amounts of sulphur, which interacted with water to produce the highly acidic and saline conditions detected by Opportunity at Meridiani Planum (Squyres *et al.* 2004b). Such conditions were probably prevalent in late Noachian and early Hesperian times (Bibring *et al.* 2006) and suggest that osmotically challenging conditions were present on Mars for extended periods of time.

Discussions of water salinity are best illustrated with the water activity parameter (a_w). a_w, a quantification of the chemical availability of water, is defined as the vapour pressure of water in a given material divided by the vapour pressure of pure water at the same temperature. Values range from 0 (absolutely no water) to 1 (pure water). This parameter moves beyond the concept of moisture content and seeks to quantify the water that is available to microbial organisms, taking into account other chemical interactions, such as pH and salinity. The magnesium sulphates identified at Meridiani Planum can only precipitate under a_w ranges between 0.51 and 0.78 (Tosca *et al.* 2008). From orbit, the OMEGA instrument on Mars Express and the Compact Reconnaissance Imaging Spectrometer for Mars, or 'CRISM', on the Mars Reconnaissance Orbiter have located extensive deposits of the same sulphate salt (Gendrin *et al.* 2005). Tosca *et al.* (2008) estimate that localised water deposits in Meridiani were 10–100 times more saline than terrestrial seawater. These models and the presence of salt minerals imply a saline past, and other studies suggest that if liquid solutions persist in isolated niches today, they would also be characterised by high salinity and halophiles would be the most likely inhabitants (Christensen 2003; Mancinelli *et al.* 2004).

Most bacteria require a a_w from 0.9 to 1 for growth, but other species are hardier (Nealson 1999). Halophilic organisms can thrive in a a_w of 0.7, *Saccharomyces* and *Xeromyces* fungi grow down to a a_w of 0.6 (Nealson 1999) and some spores can survive (although not in a state of

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active growth) in conditions with a_w down to 0 (Horneck 2000). Potts & Friedmann (1981) demonstrated that *Chroococcidiopsis* microbes could withstand a_w values of 0.83 for 24 hours, employing trehalose as a stand-in for water molecules, which prevents protein denaturation by stabilizing membranes (Crowe *et al.* 2001). Other halophilic and halotrophic organisms withstand intense osmotic pressure (produced by a difference in salt concentrations between solutions on either side of a cell membrane) by gathering substances, such as potassium ions (K^+) or glycine-betaine, collectively termed osmotica, in their cytosol to balance the osmotic pressure (Le Rudulier & Bouillard 1983; Mohammad *et al.* 1983; Galinski 1995).

Acidophiles are equally remarkable, having evolved strategies to avoid acid-induced injury. Some organisms pump protons out of the intracellular space to maintain a neutral pH while others, including *Acetobacter aceti*, have developed acid-stable proteins that minimise the harmful accumulation of cations (Menzel & Gottschalk 1985). One of the most impressive acidophiles is *Picrophilus oshimae*, an archaeal species that grows best at a pH of 0.7 (Schleper *et al.* 1995; Johnson 1998).

The high acidity and salinity of past and present aqueous solutions on Mars is a significant obstacle to the development of life. Some organisms on Earth have adapted to similarly low a_w values, but these extremophiles all evolved from less-tolerant organisms, indicating that acidic brines were not necessarily conducive to the origin of life (Oren 2002; Knoll *et al.* 2005). Because acid–saline conditions on Mars appear to be a constant challenge throughout the lifetime of the hydrosphere, any Martian life would require unprecedented adaptations to not only persist, but to originate. With this dilemma in mind, the study of acidophilic and halophilic organisms on Earth can help scientists understand how life may have dealt with high salinity conditions on Mars. This objective is most efficiently and realistically achieved by examining sites that exhibit or have exhibited both highly acidic and salty properties, such as the lakes of Western Australia and the ancient terraces of Rio Tinto.

Western Australia

Benison & Bowen (2006) argued that the acid–saline lakes of the Yilgarn Craton of Western Australia are sedimentologically and mineralogically more similar to depositional environments on Mars than anywhere else on Earth. The lakes boast salinities up to 28 % total dissolved solids (or TDS, the cumulative amount of inorganic and organic molecules in liquid water) and pHs as low as 1.5. The Yilgarn Craton contains hundreds of ephemeral lakes hosted in Jurassic to Eocene fluvial inset valleys (Clarke *et al.* 1996; de Broekert & Sandiford 2005). Sulphate-rich brines contain a range of cations, and the highly acidic hydrochemistry is maintained by ferrolysis, evapoconcentration and biological activity (Bowen *et al.* 2008).

Sedimentary features of the acid–saline lakes bear particular resemblance to those of the Burns formation in Meridiani Planum (Grotzinger *et al.* 2005; Bowen *et al.* 2008). In the Australian lakes, most notably Lake Brown and Lake Aerodrome, bedded fine-to-medium grained quartz and gypsum sands predominate, and interbedded laminations and thin beds are made up of siliciclastic components, evaporites and decayed organic matter (Benison & Bowen 2006; Bowen *et al.* 2008). External forces also influence sedimentary features. Small ripples, which can be preserved in soft sediments, are generated by wind and flood-induced turbulence; mudcracks pattern the lake-bed as mud dries out and, as minerals precipitate, 'bathtub rings' of salt minerals signal the high-water mark. At Meridiani Planum, the Opportunity rover found fine-to-medium grains, cross-bedding and preserved mudcracks and ripple marks, all of which suggest a shallow, ephemeral, wind-stirred body of water (Squyres *et al.* 2004a; Grotzinger *et al.* 2005). The sedimentary similarities are helping scientists determine the temporal and spatial extent of acid–saline conditions, important details that go a long way toward establishing habitability.

Mineralogies observed in both the Western Australian lakes and Meridiani Planum are strikingly similar. Benison & Bowen (2006) report precipitation of gypsum, halite, hematite, goethite and jarosite in the Australian lakes, all of which have been identified on Mars (Klingelhofer *et al.* 2004; Clark *et al.* 2005; Gendrin *et al.* 2005; Yen *et al.* 2006). Hematite and goethite even form spheroidal concretions that are morphologically similar to Martian 'blueberries' (Benison & Bowen 2006). Squyres *et al.* (2004b) note that the remains of precipitated dried salts at Eagle crater, potentially including magnesium sulphates, calcium sulphates and halite, would have made for a highly saline hydrosphere. By the presence of jarosite alone, a number of teams has concluded that the sulphate salt outcrops at Eagle crater have not been exposed to waters with a pH greater than 4–5 since their formation (Madden *et al.* 2004; Tosca *et al.* 2005). In both locations, products of the acid–saline system exist very close to phyllosilicates, reflecting an interface of neutral–acidic geochemical regimes (Baldridge *et al.* 2008).

Because of these sedimentary and mineralogical similarities, the acid–saline lakes of Western Australia may represent a window into the Martian past, and any biological activity in these harsh conditions could offer important clues to how Martian life may have persisted under similar conditions.

Bacteria and archaea have been identified in the acid–saline lakes of Western Australia (Hong *et al.* 2006; Mormile *et al.* 2007), and other manifestations of microbial life, including slimy mats and gas release, are readily visible (Bowen *et al.* 2008). Bowen *et al.* (2008) putatively identified the remains of acidophilic microbial colonies in 'hairy blobs' from several lakes. These organic masses grew in fluids with pH values of 2.5–3.0 and were encapsulated in evaporite salts, such as halite, continuing to grow even after salt precipitation. Identification of these structures via Laser Raman microspectroscopy and scanning electron microscopy suggests that evaporites may be effective preservation environments and potential targets for the search for microbial remnants on Mars (Bowen *et al.* 2008).

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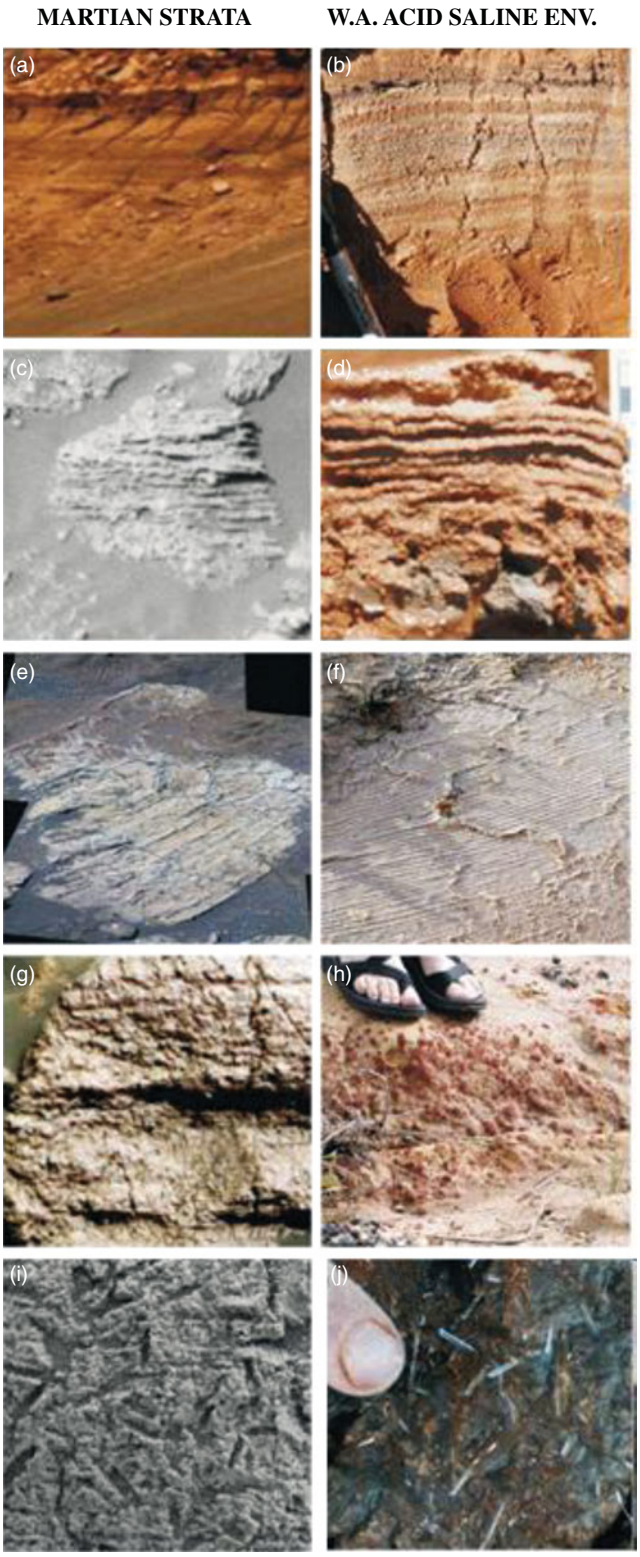

Fig. 1. Comparisons of sedimentary features between Martian strata at Meridiani Planum and the acid–saline environment in Western Australia. (a) and (b) Cross beds are clearly visible in both (a) Burn's Cliff and (b) the Sandflat formation at Lake Aerodrome. (e) and (f) Ripple marks and mudcracks from (e) Escher rock at Endurance Crater and (f) Cumulate Raceway, Lake Cowan basin. (g) and (h) Hematite concretions (g) in El Capitan rock at Meridiani and (h) in recent sandstone near Bandee Lakes. (i) and (j) Displacive crystals and moulds in (i) El Capitan rock at Meridiani and (j) in quartz and hematite-rich sand underneath Twin Lake West. Image details. (a) Image courtesy of NASA/Jet Propulsion Laboratory (JPL)/Cornell. Vertical field of view is 3.5 m. (b) Image courtesy of Benison & Bowen (2006), pen for scale. (c) Image courtesy of NASA/JPL/Cornell, centre of rock is 12 cm across. (d) Image courtesy of Benison & Bowen (2006), field of view is 1 m across. (e) Image courtesy of NASA/JPL/Cornell; centre rock is 12 cm across. (f) Image courtesy of Benison & Bowen (2006); field of view is 1 m across. (g) Image courtesy of NASA/JPL/US Geological Survey (USGS), field of view is 32 cm across. (h) Image courtesy of Benison & Bowen (2006), feet for scale. (i) Image courtesy of NASA/JPL/USGS, field of view is 9 cm across. (j) Image courtesy of Benison & Bowen (2006), finger for scale.

Rio Tinto

The Rio Tinto in southwestern Spain is an active aqueous system that operates within well-preserved deposits from past sedimentary periods (Fig. 1). At its headwaters, the active river is a bright red, low-pH (1–3) stream that carries iron, sulphate and other ions. During seasonal evaporation events, minerals from the flowing river are deposited as evaporite efflorescent salts, such as copiapite and gypsum (Osburn *et al.* 2007). On a longer timescale, thin pink coats of jarosite form as transient pools dry up; this active system overlays and cuts through two distinct goethite and hematite terraces that are approximately one thousand and two million years old (Fernandez-Remolar *et al.* 2003). Many recent findings from the Mars Exploration Rovers (Arvidson 2007; Morris *et al.* 2008), OMEGA (Arvidson *et al.* 2005; Bibring *et al.* 2005; Gendrin *et al.* 2005) and CRISM (Swayze *et al.* 2008) suggest that aqueous deposition and modification of acid-sulphate salt systems, such as those at Rio Tinto, have played an important role in the Martian geological record. Rio Tinto is a particularly important analogue, because it contains well-preserved ancient deposits of a geochemically similar hydrological system, effectively providing a time-lapse and showing how the precipitated minerals are altered by diagenesis.

To draw any meaningful comparisons from the ancient terraces, the modern biology must first be characterised. Despite the challenging environment, the river maintains a surprisingly diverse array of acidotolerant and halotolerant prokaryotic and eukaryotic organisms: photosynthetic eukaryotes, chemolithotrophic bacteria, various heterotrophs, algae and fungi populate the Rio Tinto (Amaral Zettler *et al.* 2002; Sabater *et al.* 2003; Aguilera & Amils 2004). The chemolithotrophs in particular, comprising mainly the iron oxidisers *Leptospirillum ferrooxidans* and *Acidithiobacillus ferrooxidans*, play an important role in creating the region's highly acidic chemistry by oxidizing subsurface iron sulphides to generate sulphuric acid (Fernández-Remolar *et al.* 2005). In addition to the diverse microbial population, remains of macroorganisms, such as plants and animals, often enter the Rio Tinto system, making for a range of biological material available for preservation.

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In the short term, crustal precipitates and sediments trap microbes, plant fragments and insects, incorporating bacteria and preserving macrostructures where present. Nanophase iron oxide coatings best initiate the preservation of organic material, while efflorescent salts are much less effective. In the younger terraces (700–800 years old), nanophase iron oxides become nanophase goethite following diagenesis (Fernandez-Remolar *et al.* 2003). Spatial relationships among fossilised organisms are maintained, and biological material is replicated by minerals that retain morphological and anatomical details, but not the original organic matter. The older terraces show the same trends: material initially encapsulated in nanophase iron oxide fares better than its sulphate-deposited contemporaries, goethite crystallization maintains structure, and subsequent iron oxide deposition ensures long-term preservation (Fernandez-Remolar *et al.* 2003). One of the primary advantages of Rio Tinto is the continuity of the acid–saline biological system, which allows for a detailed assessment of both the modern biological and preserved systems. Rio Tinto evidence thus demonstrates that even microscopic organisms can be preserved and recognised after significant diagenesis and remineralization, both focusing and bolstering optimism surrounding the search for signs of life on Mars.

Low temperature

Modern Mars is a frigid environment and Carr (1996) reports surface temperatures ranging from -123 °C to 25 °C, with diurnal swings of up to 100 °C. The Thermal Emission Spectrometer aboard the Mars Global Surveyor chronicled temperature variations on Mars over one Martian year, providing a relatively comprehensive picture of the planet's thermal conditions. The data show a range from -132 °C (winter night-time minimum at the northern pole) to 36 °C (summer day-time maximum at 30° S latitude). It is important to note, however, that the subsurface, the most likely habitat for extant life, would almost certainly be significantly below the freezing point of pure water. At 15–20 cm below the surface, temperatures quickly converge to the mean diurnal value and exhibit smaller seasonal fluctuations (Carr 1996). Thus, any modern life at or near the surface would need to be well adapted to cold-weather conditions.

Encouragingly, a number of biological processes have been chronicled at remarkably cold temperatures. Researchers have detected metabolic activity at -20 °C (Rivkina *et al.* 2000) and electron transfer at -80 °C (Junge *et al.* 2006). Microorganisms are able to survive, if not actively metabolise, at even colder temperatures: Weber & Greenberg (1985) reported viable spores after exposing them to -263 °C. Price & Sowers (2004) suggest that there may be no lower temperature limit for cell growth after all, provided the presence of a suitable solvent.

Although these extreme lab-based conditions help us understand the capabilities and limits of biological systems, low-temperature ecosystems serve as more useful Mars analogues for mission planners. It is in these natural environments that instruments can be tested, conditions can be monitored over time, and life-based processes can be understood from a systems-based perspective. Established cold-temperature Martian analogues include Antarctica, Arctic permafrost and sea ice.

Antarctic ice

Antarctic ice, varied in structure and composition, has been the site of many biological surveys, and life has been shown to be pervasive, if not overly abundant. The ice sheet over Lake Vostok is among the best-characterised Antarctic sites. Priscu *et al.* (1999) reported 2.8×10^3 to 3.6×10^4 cells ml^{-1} of melted ice, although organisms were not culturable and failed to incorporate radiolabelled carbon over a 52-hour period. Karl *et al.* (1999) found $0.2-8 \times 10^3$ cells ml^{-1} at -3 °C in the Vostok ice sheet and noted slow uptake of $^{14}CO_2$; a small proportion of ice-bound organisms are likely viable but unable to reproduce given the accumulated physiological damage and extremely slow metabolic rates (Abyzov *et al.* 1998). At a similar site, up to $0.1-4 \times 10^5$ cells ml^{-1} have been detected in particle-rich inclusions within the -5 °C ice in Lake Bonney (Priscu & Christner 2004). Carpenter *et al.* (2000) detected metabolic activity in South Pole snow at temperatures down to -17 °C, while Friedman *et al.* (1999) observed growth at -20 °C with a doubling time of 180 days. Abyzov *et al.* (1998) found viable cells that have persisted for approximately 240 000 years embedded in an Antarctic glacier 2.8 km beneath the surface.

Botta *et al.* (2008) analysed the Antarctic ice from the LaPaz ice field to determine the amino acid and polycyclic aromatic hydrocarbon (PAH) composition and they found that most amino acids were near blank levels, but glycine (7.2 parts per trillion (ppt)) and L-alanine (4.1 ppt) were measureable. α-Aminoisobutyric acid (AIB) – a non-protein amino acid derived from extraterrestrial sources – was also detected at abundances of up to 33.1 ppt, and it was likely extracted from Antarctic micrometeorites during the concentration procedure applied to the ice samples (Botta *et al.* 2008). Two-step laser mass spectrometry (L2MS) results of ice-bound particulate matter demonstrated that the Antarctic ice was very depleted in PAHs, and only phenanthrene/anthracene (as well as their alkylated homologues) at levels below the L2MS 10–80 pg l^{-1} detection limit were detected (Botta *et al.* 2008). These results agree with previous studies of amino acids (McDonald & Bada 1995; Bada *et al.* 1998; Glavin *et al.* 2006) and PAHs (Becker *et al.* 1997; Clemmett *et al.* 1998) in the Antarctic ice.

Other researchers have clarified the survival strategies of these ice-bound organisms. Priscu *et al.* (1998) discovered ice-bound sediment particles that, when heated by the Sun, produce localised melts for approximately 150 days per year. Microbes gather around these nutrient-rich oases, and well-developed ecosystems capable of nitrogen fixation, photosynthesis and decomposition can form. Reid *et al.* (2006) found methanogenic and halophilic archaea at –2 °C that formed multicellular aggregate communities bound together by extracellular polymeric material. It is believed that these

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community structures allow for optimal nutrient exchange and protection in the harsh nutrient-poor environment. The ability to understand the nature of psychrophile distributions around nutrient-rich nodes will help planners and analysts who search for life in metabolically constrained systems, such as the frigid Martian subsurface.

Permafrost

Arctic permafrost is perhaps a more realistic analogue for Mars due to its frozen land-water ice interface; an environment that has gained further relevance with the Phoenix Lander's observation of water ice several centimetres beneath the Martian surface (Smith 2009; Smith *et al.* 2009). High latitude sites on Earth serve as valuable models for the northern plains of Mars, and many of the physico-chemical factors controlling these geomorphological similarities create similar biological stresses. These limitations include a consistently subfreezing environment (−12 °C to −20 °C throughout much of the Arctic), a low water activity ($a_w = 0.8$–0.85) and limited organic matter (Deming 2002; Vishnivetskaya *et al.* 2006). Despite these challenges, permafrost environments support the greatest diversity of bacteria and archaea of all low-temperature analogues, because there are many metabolic niches that allow a more varied range of organisms to persevere (Jakosky *et al.* 2003).

Studies of the Siberian permafrost have detected 5×10^4 cells ml^{-1} in −1.5 °C conditions (Gilichinsky *et al.* 2003). Optimal psychrophilic growth occurred at 4–5 °C, but metabolic activity persisted in liquid brines down to −15 °C (Gilichinsky *et al.* 2003). Rivkina *et al.* (2000) have pushed this limit even lower, detecting the incorporation of isotopically labelled acetate into metabolically active cells in −20 °C Siberian permafrost. Doubling times increased from 1 day at 5 °C to 20 days at −10 °C and 160 days at −20 °C (Rivkina *et al.* 2000), and become even longer as cells enter deep resting states. Whether such slow rates of metabolism can sustain an actively growing community rather than a few tenacious microbes clinging to life remains an open question.

Permafrost environments also serve as a useful testing ground for the long-term cryogenic preservation of organisms, and a number of investigators have found viable cells from samples dating back millions of years (Vorobyova *et al.* 1997; Vishnivetskaya *et al.* 2006). Understanding the long-term patterns of preservation for both viable organisms and remnant organic molecules, including the role of freeze–thaw cycles, is another key area of investigation. Further research in permafrost-rich environments will help determine how water stresses and nutrient fluxes associated with thermal cycles affect microbial survival.

Sea ice

Sea ice seems to be an unlikely Mars simulant, but given its lowered freezing point (resulting from the incorporation of salt water) and psychrophilic inhabitants, it is among the most widely used low-temperature organic host analogues. Life in ice is possible only because of the persistence of thin films of liquid water brines. Junge *et al.* (2004) detected viable organisms at temperatures from −2 °C to −20 °C, conditions corresponding to salinities of 38–209 parts per thousand, respectively. They describe a network of interconnected tubes, veins, and junctures within the ice matrix that allow fluid to deliver nutrients and remove waste. As interstices shrink with ice compression, water thin films can remain in a liquid state due to surface charges and water molecule polarity interactions (Junge *et al.* 2001). Saltwater-based ice is more habitable than freshwater ice because it contains more varied liquid solutions, more connections between pores and larger pores (Deming & Eicken 2007).

Icebergs or ice shelves are often the best places to isolate psychrophiles, because 'tourist' organisms derived from local impurities or soil inclusions are absent (Deming & Eicken 2007). Despite the increased selective pressures, both archaea and bacteria have been found in actively metabolizing states, providing evidence of low-temperature adaptations across domains (Staley & Gosink 1999; Sheridan *et al.* 2003). During the winter, arctic sea ice becomes the coldest ice-based environment on Earth; microbial diversity decreases (Junge *et al.* 2004) and the metabolic activity of the remaining cells is extremely low (Deming & Eicken 2007). Water-based brines have been detected at temperatures as low as −35 °C (Herborg *et al.* 2001), although some researchers believe life could persist at even lower temperatures (Price & Sowers 2004).

Aridity

Modern conditions on Mars preclude surficial liquid water, but recent evidence of ancient river channels (Ivanov *et al.* 2005; Hynek & Phillips 2008), evaporites (Squyres & Knoll 2005), concretions (Squyres *et al.* 2004a) and aqueously deposited minerals (Christensen *et al.* 2004; Squyres & Knoll 2005) strongly suggests a watery past. Researchers believe that there was enough liquid water to cover the planet with a several-hundred metre-deep ocean during the Hesperian and Amazonian epochs (Parker *et al.* 1989; Baker *et al.* 1991). As the Martian atmosphere deteriorated and the planet cooled, much of the surface- and atmosphere-based water evaporated into space, but substantial quantities passed into the subsurface (Clifford & Parker 2001). In 2001, the Mars Odyssey spacecraft detected subterranean water ice in the high northern latitudes (Feldman *et al.* 2002); NASA's Phoenix Lander has since provided direct physical evidence of the ice (Smith 2009; Smith *et al.* 2009) and most recently Mars Reconnaissance Orbiter studies of recent meteorite impact craters have exposed a white material that fades over time, suggesting the presence of subsurface ice on Mars (Byrne *et al.* 2009).

Despite the presence of water ice on Mars, near-surface soils are extremely arid. Several robotic missions have measured soil water content, which includes structurally bound water (i.e., hydrate minerals), structurally adsorbed water (H_2O molecules between sheets of clays, for example) and water adsorbed from the atmosphere. Mariners 6 and 7 showed an increase in water content with increasing latitudes (Pimentel *et al.* 1974). The Viking landers measured 1–2 wt. %

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water (Biemann *et al.* 1977) and Yen *et al.* (1998) found $\leqslant 4$ wt.% from orbital data, but both studies have uncertainties of several wt.%. Most recently, using water's 3 μm spectral feature to quantify the absolute water content of the uppermost few hundred microns of Martian soil, OMEGA team members have provided a new level of detail and global coverage of surface-based water mapping. They report an increase from 2–5 wt.% water in low-latitude regions (0–45° N) to 5–15 wt.% northward of 45° N (Jouglet *et al.* 2007).

Desiccation leads to DNA strand breaks, lipid phase changes and protein crystallization, denaturation and condensation (Billi & Potts 2002; Potts 1994). In the face of these challenges, microbes have evolved a number of mechanisms that allow for survival in extremely arid conditions. The challenges of water acquisition and utilization are similar for inhabitants of both very arid and saline environments, and details regarding relevant adaptations will be discussed below.

In search of an arid organic host analogue for Martian soil, researchers have made use of Earth's deserts. Among the most important arid analogue sites are the Mojave Desert and, increasingly, the Atacama Desert. These locations serve as important testing grounds for future life-detection missions.

Mojave Desert

The Mojave Desert of eastern California has been used extensively as a physical and chemical analogue for Mars given its volcanic geology (Greeley *et al.* 2002; Byrnes *et al.* 2006), but its inclusion as an organic host analogue is equally justifiable. The Mojave is the driest region of North America, with a precipitation range from 6 cm per year in Death Valley to 23 cm per year in the Tehachapi Mountains (Bryant & Rech 2008). Researchers detected 2.66×10^4 colony forming units (CFUs) of microbes gm^{-1} of Death Valley soil and 3.3×10^6 CFUs gm^{-1} of Tehachapi soil (Bryant & Rech 2008). For purposes of comparison, average soil microbial content is roughly 1×10^7 CFUs gm^{-1} (Ketch *et al.* 2001); the Death Valley sample exhibited a roughly 1000-fold decrease in microbial content relative to average soil.

The Mojave Desert is also noteworthy because of its desert varnish, a shiny black rock coating approximately 5–500 μm thick that is characteristic of hot desert environments. The nature of desert varnish formation has long proved enigmatic (Dorn 1998; Broecker & Liu 2001), with claims of both biotic (Dorn & Oberlander 1981) and abiotic (Potter & Rossman 1977; Glasby *et al.* 1981) mechanisms. Recent work strongly suggests an abiotic precipitation model whereby silicic acid condenses through evaporation to form a coating, incorporating airborne particles and organic molecules in the process (Perry *et al.* 2006). These exogenous molecules, which include amino acids, lipids and DNA, provide faithful representations of paleo-environments, including a window into the biological past of a given environment (Liu 2003; Perry *et al.* 2003; Perry *et al.* 2006).

Desert varnish-like coatings have been observed on Mars (DiGregorio 2002; Murchie *et al.* 2004) and may contain signs of past biological activity like their analogues on Earth. Some hypothesise that Martian varnish could be an even more effective preservation environment for biomarkers, given lower levels of chemical and physical weathering (Perry & Sephton 2006). This possibility makes the Mojave Desert a valuable organic host analogue and an ideal location to further examine the relationship between biomarker preservation and desert varnish.

Atacama Desert

Recently, the most sought-after arid organic host analogue location has been the Atacama Desert, a desolate stretch of land in northern Chile, where the offshore Humboldt Current, the Pacific anticyclone and the Andes mountains conspire to maintain hyper-arid conditions (Miller 1976). The Atacama is the driest place on Earth, 50 times drier than other arid and hyperarid regions (McKay *et al.* 2003; Navarro-Gonzalez *et al.* 2003; Warren-Rhodes *et al.* 2006; Bonaccorsi & McKay 2008). Although the entire desert is arid and receives minimal precipitation, some locations experience marine fog, which is capable of supporting hypolithic algae, lichens and some hardy cacti (Rundel *et al.* 1991; Warren-Rhodes *et al.* 2006). The hyperarid core of the Atacama, however, is in a 'fog shadow' created by the coastal mountain range and receives virtually no rain – in four years of meteorological monitoring, just one precipitation event of 2.4 mm was reported (McKay *et al.* 2003). Similarly dry conditions have dominated for approximately 15 million years, providing a useful opportunity to study long-term microbial adaptation and preservation (Ericksen 1983).

Organic content is very low throughout the Atacama, and is particularly sparse at Yungay, the desert's hyperarid core. Bonaccorsi & McKay (2008) found 0.026–0.056 wt.% organic carbon, carbon to nitrogen ratios (C:N) from 1.6–5.5 and cell counts of $5–8 \times 10^6$ cells g^{-1} soil. For comparison, the same study reported 0.093–2.24 wt.% organic carbon, a C:N ratio ranging from 7.4 to 36.6, and cell counts from 0.85 to 4.06×10^8 cells g^{-1} soil south of Yungay in slightly less arid locations. Among organic molecules, only formic acid (1 μmol g^{-1}) and benzene (0.01 umol g^{-1}) were detected; these molecules can result from thermal degradation of a number of cellular components, including carboxylic acids, carbohydrates, polysaccharides and proteins (Navarro-Gonzalez *et al.* 2003). At some Yungay sites, amino acids were not found above detection limits, while samples nearby produced abundances from 10 to 200 parts per billion (ppb), suggesting significant regional variability (Peeters *et al.* 2009). The number and diversity of microbes increased along a precipitation gradient, but at Yungay no cells were cultured by serial dilution plating and no DNA was recovered, suggesting that researchers had identified the dry limit of life (Navarro-Gonzalez *et al.* 2003). What is more, any organics that are produced are destroyed via oxidation processes, another condition that is analogous to Mars, as discussed below.

Researchers have descended on the Atacama to test organic detection technology (Skelley *et al.* 2005). The Mars Organic Analyser (MOA), a microfluidic instrument, was

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tested in the Atacama. Three locations along a North–South transect (with annual precipitation increasing southward) were sampled by both high-performance liquid chromatography (HPLC) and the more sensitive capillary electrophoresis (CE) method. CE alanine/serine levels increased from 0.009 to 0.17 parts per million (ppm) southward along the transect, glycine increased from 0.03 to 0.32 ppm, aspartic acid increased from 0.01 to 0.04 ppm and glutamic acid, undetectable at the northern site, reached 0.36 ppm at the more hospitable southern site (Skelley *et al*. 2005). Based on amino acid measurements, Amashukeli *et al*. (2007) calculated a concentration of roughly 10^5 cell equivalents per gram of soil. As technology continues to improve, the hyper-arid Atacama remains a fruitful testing ground for scientists probing the dry limits of life, as well as instruments headed to Mars.

Radiation and oxidizing soil

With minimal protection from its atmosphere, the Martian surface is bombarded with intense radiation, a hazard that causes direct biological damage and creates indirect photochemical dangers. Incoming radiation consists of ultraviolet (UV) radiation, whose intensity corresponds to its wavelength, and ionizing radiation in the form of solar energetic protons (SEPs) and galactic cosmic rays (GCRs), whose cumulative effect is quantified in J kg^{-1}, or Grays (Gy).

The greatest threat posed to potential organisms on the Martian surface comes from UV radiation, which is up to three orders of magnitude more harmful to DNA than on Earth (Cockell & Raven 2004). UV rays can be subdivided by wavelength into UVA (315–400 nm), UVB (280–315 nm) and UVC (200–280 nm), with the lower wavelength UVC component posing the greatest danger. Because Mars lacks an UV-absorbing atmosphere, surface fluxes of UVC are high, and even the most robust organisms have little chance of survival. Under simulated Martian conditions, Schuerger *et al*. (2003) show that viability of *B. subtilis* spores was reduced by $>99\%$ after 15 seconds, and Cockell *et al*. (2005) demonstrated that 99% of *Chroococcidiopsis* cells die within 5 minutes. Although UV radiation is extremely harmful, it has a limited penetration depth. Rettberg *et al*. (2004) showed that just 5 mm of soil cover maintains full viability, while Nienow *et al*. (1988) are slightly more conservative in estimating a 90% attenuation in 5 cm of soil.

UV radiation has similarly deleterious indirect effects, as borne out by interpretation of Viking data (Oyama & Berdahl 1977; Klein 1979; Oró & Holzer 1979; Zent & McKay 1994; Klein 1998). UV photolysis of water in the atmosphere creates oxidizing species, such as OH, HO_2, H_2O_2, O and O_3, which diffuse through the soil and react with any organic molecules along the way (McElroy *et al*. 1977; Hunten 1979; Bullock *et al*. 1994). Oxidants may also be produced on soil surfaces independent of atmospheric composition. Chun *et al*. (1978) demonstrated that organic degradation could result from the superoxide radicals that form on titanium oxide surfaces, while Yen *et al*. (2000) suggest that such reactive species could form within soil silicate matrices. Soil mixing processes and diffusion may sustain an oxidizing regime up to tens of centimetres or a few metres beneath the surface (Stoker & Bullock 1997; Zent 2000), while other geochemical mechanisms may produce local sources for subsurface oxidation (Davila *et al*. 2008).

Below the first few centimetres of soil, SEP and GCR ionizing radiation predominate, exciting and ionizing biomolecules and generating radicals from water that attack organic molecules (Baumstark-Khan & Facius 2001; Nelson 2003). These particles are less lethal than UV radiation over the short term, but pose the most serious threat to long-term survival or preservation because of their deeper penetration and cumulative oxidation effects (Rettberg *et al*. 2004). Dartnell *et al*. (2007) model a maximum dose of ~ 0.85 Gy $year^{-1}$ of ionizing radiation, which is manageable for even radiation-sensitive organisms. However, cells must be active in order to mitigate damage caused by radiation, and once repair activity ceases, due to long-term environmental changes or unsustained defence against radiation, biomolecules are slowly but inexorably destroyed. Even a 2-metre deep community of inactive *D. radiodurans*, the most radiation-tolerant organism on Earth, would suffer a million-fold population reduction in 450 000 years, leaving little hope for preservation over a geological timescale (Dartnell *et al*. 2007).

Kminek & Bada (2006) provide some useful constraints on the likely survival and detectability of organics on Mars with respect to radiation-induced damage. For example, they show that amino acids from organisms active 3 billion years ago would only be detectible today below 2 m: a detection limit of 10 ppt would allow instruments to detect the biological production of 10^3 cells $gram^{-1}$ below this depth. Any amino acids remaining in the upper 50 cm would need to be less than 100–500 years old.

Radiation presents a challenge to the prospects of both extant and extinct life. UV radiation and oxidizing soils make surface-based life a near impossibility, while ionizing radiation degrades biomolecules significantly over geological time. Studying Earth-based analogues with radiation stress and oxidizing conditions helps expose survival strategies, as well as successful preservation mechanisms and detection techniques.

Atacama Desert

As discussed above, the Atacama Desert of northern Chile is one of the most inhospitable places on Earth for microbial life (Navarro-Gonzalez *et al*. 2003). The extreme aridity of the site is largely to blame, but oxidizing soil chemistry also plays a role (Quinn *et al*. 2005). In field tests with the Mars Oxidation Instrument (MOI), Quinn *et al*. (2005) discovered a regime of dry acid deposition that is fundamentally rooted in UV photochemistry. Hydroxyl (OH) radicals are produced photochemically in the atmosphere and react with SO_2 and NO_2 to produce dry sulphuric acid and nitric acid, respectively. Overnight, as relative humidity increases, the acids are solvated and the soil becomes oxidizing, stripping electrons from any organic molecules that may be present. The same

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processes may pertain to Mars: acidic hydrochemistries existed in the past (Klingelhofer *et al.* 2004), and even modern surfaces may contain soil acids (Horowitz *et al.* 1977). Moreover, the Phoenix lander has detected the presence of perchlorate on Mars (Hecht *et al.* 2009), a substance that has a highly oxidizing nature, and the Atacama Desert represents a terrestrial location that has elevated concentrations of perchlorate as revealed by analysis of Chilean nitrates (Ericksen 1983). The preferential preservation of organisms at depth, likely resulting from surface hazards, such as oxidative damage, has been demonstrated in the Atacama. Amashukeli *et al.* (2007) calculated 10^5 cells per gram near the surface, while Skelley *et al.* (2007) estimated 10^6 cells per gram from 2–5 cm beneath the duracrust. Navarro-Gonzalez *et al.* (2003) sampled from a depth of <10 cm and detected no DNA and fewer than 10 colonies on 100 plates. Maier *et al.* (2004), on the other hand, examined soil between 20 and 30 cm deep and were successful in extracting DNA and plating 1–2 colonies per plate.

The Atacama is slightly limited as an analogue of highly oxidizing Martian soil because, to the best of our knowledge, no biological community has developed sufficient adaptations that allow us to speculate about the efficacy of similar strategies employed on Mars. However, the region can be useful as a testing ground for organic detectors, as in the case of the MOI, and as a crucible for organic decomposition studies (Zent *et al.* 2003; Quinn *et al.* 2005). Learning how soil-based organic molecules selectively respond to various oxidation mechanisms will help direct our pursuit of similar compounds on Mars.

Dry Valleys of Antarctica

Antarctica receives very high levels of both UVB and UVC radiation, particularly during the spring-time depletion maximum (Wynn-Williams 1994; Russell *et al.* 1998). Some biological effects have been observed, such as a 6–12% decrease in phytoplankton photosynthetic activity during spring and summer months, but ecosystem-wide catastrophes have been averted thanks to the seasonality of UV incidence and biological adaptations (Palmer 1990; Solomon 1999). One such adaptation is seen in the Antarctic Dry Valleys, where microbes have sought refuge from the harsh conditions by colonizing rocks. A subgroup of these organisms, known as cryptoendoliths, grow within porous quartzite sandstones of the Beacon Supergroup, which provide nutrients, a substrate and a layer of protection from radiation (Friedmann 1982; Edwards *et al.* 1997; Russell *et al.* 1998). Cryptoendolithic communities can be comprised of a variety of species: some are exclusively prokaryotic, others are largely eukaryotic, but most systems are lichens, i.e., a symbiotic collaboration between photosynthetic cyanobacteria and fungi (Friedmann *et al.* 1988).

Cryptoendolithic lichens interact with and modify their environments in ways that could prove fruitful for astrobiological investigations. Perhaps most obviously, cryptoendolithic communities display a black, white and green banded pattern just beneath the rock's outer crust, attributable to the pigmentation of various organisms, as well as biochemical alterations (Friedmann *et al.* 1988; Sterflinger 2000). Biological activity is also responsible for the generation of inorganic biomarkers, creation of microbial fossils, and dissolution and formation of rock crusts via oxalic acid production (Freidmann & Weed 1987; Sun & Friedmann 1999; Acasco & Wierzchos 2002; Wierzchos *et al.* 2003). Raman spectroscopy can be used to detect photosynthetic pigments and UV protectants, such as chlorophyll, β-carotene, scytonemin and anthraquinone parietin (Edwards *et al.* 1997; Russell *et al.* 1998; Wynn-Williams & Edwards 2000). Hand *et al.* (2005) successfully detected organic functional groups in cryptoendoliths using a mid-infrared Fourier transform micro-spectrometer that could potentially be used on a future mission to Mars. Inductively coupled plasma atomic emission spectroscopic (ICP-AES) measurements indicate that colonised sandstones have lower concentrations of both major and minor elements than their uncolonised counterparts, suggesting that microbes solubilise, utilise and ultimately remove elements from the substrate (Blackhurst *et al.* 2004). All of these physical characteristics could, if detected, point to the presence of similar communities on Mars.

Cryptoendoliths have found a way to survive amid high-radiation conditions, but there is one significant difference between the Antarctic communities and potential Martian endoliths. The majority of Martian rocks are volcanic in nature and exhibit low porosity, possibly minimizing the likelihood of rock colonization (Parnell 2004; Blackhurst *et al.* 2005), although counter-examples have been described (Jorge Villar *et al.* 2006). The cyanobacteria and fungi of the Dry Valleys, on the other hand, depend upon a porous substrate, such as the Beacon sandstones, in order to mobilise nutrients and access liquid water (Palmer 1990; Hughes & Lawley 2003). Other cryptoendoliths, such as those found in the high Arctic, inhabit the fissures of metamorphosed shocked gneiss (Fike *et al.* 2003). In order to bolster the analogous relationship between cryptoendoliths and potential Martian biology, future studies should prioritise the characterization of endoliths hosted in Mars-like substrates.

The future of organic Mars analogues

Analogue sites, at their best, exhibit the physical, chemical and environmental traits of a given time and place on Mars. Organic host analogues, which ideally demonstrate how life is maintained or preserved under Martian conditions, are employed differently depending on the details of the investigation.

Investigators hopeful of present life are most interested in sites that offer living organisms the greatest challenges of modern Mars: frigid temperatures, extreme aridity and high radiation (and its derivative, oxidizing soil). No one site exhibits all of these traits at Martian levels, but by studying life's adaptations to a particular stressor through comparisons to more amenable terrestrial locations, biological limits can be assessed and the search for life on Mars can be better managed. However, it is unclear what an organism's ability to

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withstand one extreme trait indicates about its ability to survive a different one. For this reason, and to develop a better sense of how organisms might adapt to the combined stresses of the Martian environment, it will become increasingly important to study biological adaptations to multiple Mars-like conditions. As highlighted above, a couple of sites appear particularly promising for this work. The Dry Valleys of Antarctica receive little water, but high levels of radiation, and the Atacama Desert is both arid and highly oxidizing.

Encouragingly, there is some evidence that biochemical adaptations to one challenge may help organisms cope with other obstacles. Radiation-tolerant organisms, for example, likely developed the capability from dealing with strand breaks caused by desiccation (Cox & Battista 2005). The ability to obtain water from dry environments is a key skill for both cryptoendoliths and organisms living in hot deserts (Navarro-Gonzalez *et al*. 2003; Blackhurst *et al*. 2004). Using organic host analogues to study how life deals with multiple stresses at the same time, rather than isolating a single condition, will help clarify the potential survivability of microbial life on modern Mars.

Scientists looking for evidence of past life on Mars are focused on modern or ancient terrestrial systems that best mimic the warmer, wetter Mars of the past, when the emergence of life was most probable. In this context, it is important to realise that Mars is a heterogeneous planet, and conditions were likely very different in distinct places at various times. Two of the most promising time- and place-specific analogues are the Western Australian acid–saline lakes and Rio Tinto, where acidic hydrochemistry and sulphur salt deposits closely resemble our emerging picture of an ancient Meridiani Planum (Fernandez-Remolar *et al*. 2003). Figure 1 provides convincing photographic evidence linking the Australian lakes to Meridiani, suggesting that the site may be a promising chemical and physical analogue, in addition to its role as an organic host analogue.

Analogues that are selected to reflect a particular time and place on Mars are particularly useful in answering specific questions about the preservation or detectability of organic substances. The use of such organic host analogues will gain traction as our knowledge of past physico-chemical conditions on Mars becomes more detailed and more widespread. One recent example of this paradigm is the study by Aubrey *et al*. (2006), which seeks Earth-based analogues to the evaporitic sulphate minerals found at Meridiani in order to evaluate how organic compounds are preserved over geological time scales. The investigation examines 4–40 million-year-old sulphates from California's Anza-Borrego Desert, the Haughton impact crater in Canada and Panoche Valley, California. Significant levels of amino acids were detected in all samples, equivalent to 10^6–10^7 cells g^{-1} of *E. coil*.

The broader environmental parameters at the time of sulphate deposition are not precisely known on Earth or on Mars, making it difficult to extrapolate the specifics to a Martian context, but the use of an analogue does effectively answer more narrowly focused questions. In this particular case, Aubrey *et al*. (2006) have established that amino acids can effectively survive tens of millions of years of diagenesis and degradation. Specifying preservation patterns will provide usable information to help future mission planners target the search for signs of past life. As scientists continue to characterise past Martian environments, novel organic host analogue sites must continually be considered, evaluated and assessed for their suitability.

Conclusion

Organic host analogues represent a crucial component in the search for signs of past or present life on Mars. Present life faces challenges from low temperatures, aridity and high radiation – dangers posed by a number of analogue sites, such as polar ice, permafrost, the Mojave Desert, the Atacama Desert and the Dry Valleys of Antarctica. Past life would have faced varying conditions depending on particular times and locations, but data from Meridiani Planum paints the picture of a highly acidic and salty Mars – conditions that are observed in the acid–saline lakes of Western Australian and Spain's Rio Tinto. Optimal use of organic host analogues in the future will consider life's response to multiple simultaneous challenges and will absorb and reflect new environmental interpretations of ancient Mars as they become apparent. In doing so, organic host analogues will continue to serve as important testing grounds for future robotic exploration. Missions, such as ExoMars and more distant sample return projects will benefit greatly from the prescriptive and predictive power of organic host analogues as they advance the search for life on Mars.

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