

Microbial colonization in impact-generated hydrothermal sulphate deposits, Haughton impact structure, and implications for sulphates on Mars

J. Parnell¹, P. Lee², C.S. Cockell³ and G.R. Osinski⁴

¹Department of Geology, University of Aberdeen, Aberdeen AB24 3UE, UK
e-mail: J.Parnell@abdn.ac.uk

²Mars Institute, SETI Institute and NASA Ames Research Center, Moffett Field, CA 94035-1000, USA

³British Antarctic Survey, Madingley Road, Cambridge, CB3 0ET, UK

⁴Department of Planetary Sciences, University of Arizona, Tucson, AZ 85721-0077, USA

Abstract: Hydrothermal gypsum deposits in the Haughton impact structure, Devon Island, Canada, contain microbial communities in an endolithic habitat within individual gypsum crystals. Cyanobacterial colonies occur as masses along cleavage planes, up to 5 cm from crystal margins. The crystals are transparent, so allow transmission of light for photosynthesis, while affording protection from dehydration and wind. The colonies appear to have modified their mineral host to provide additional space as they expanded. The colonies are black due to UV-screening pigments. The relative ease with which microbial colonization may be detected and identified in impact-generated sulphate deposits at Haughton suggests that analogous settings on other planets might merit future searches for biosignatures. The proven occurrence of sulphates on the Martian surface suggests that sulphate minerals should be a priority target in the search for life on Mars.

Received 12 May 2004, accepted 7 July 2004

Key words: cyanobacteria, endoliths, gypsum, Haughton impact structure, impact craters, life on Mars, sulphates.

Introduction

Impact craters are of high interest in planetary exploration because they are viewed as possible sites for evidence of life (Cabrol *et al.* 1999; Newsom *et al.* 2001; Rathbun & Squyres 2002). Hydrothermal systems in craters are particularly regarded as sites where primitive life could evolve (Farmer & Des Marais 1999; Farmer 2000; Newsom *et al.* 2001). Evidence from the Miocene Haughton impact structure shows that not only should crater hydrothermal deposits be a priority target in seeking evidence for former thermophilic life (Farmer & Des Marais 1999), but they may be a preferred site for subsequent colonization and hence possible extant life: hydrothermal sulphate deposits in the Haughton structure are colonized by viable cyanobacteria.

The Haughton impact structure, Devon Island, Canadian High Arctic, is a 24 km diameter crater of Miocene (~23 Ma) age, which developed in a succession of 1750 m Lower Palaeozoic carbonates upon a Precambrian metamorphic basement (Frisch & Thorsteinsson (1978), Robertson & Sweeney (1983), see Fig. 1). The structure preserves an exceptional record of impact-induced hydrothermal activity, including sulphide, sulphate and carbonate mineralization (Osinski *et al.* 2001). The target rocks excavated at the site

included massive gypsum (calcium sulphate)-bearing carbonate rocks of Ordovician age (Robertson & Sweeney 1983). Impact-remobilized sulphates occur as metre-scale masses of intergrown crystals of the clear form of gypsum *selenite* in veins and cavity fillings within the crater's impact melt breccia deposits (see Fig. 2; Osinski & Spray (2003)). The selenite is observed to cross-cut both clasts of shocked target rock in the melt breccia and sulphate melt textures in which the primary mineral is anhydrite. Paragenetic studies of the hydrothermal mineral assemblage suggest that temperatures of precipitation were probably less than 100 °C (Osinski *et al.* 2001). Fluid inclusions in the Haughton selenite are monophasic, similarly suggesting low (<50 °C) temperatures (Goldstein & Reynolds 1994). However, the selenite is regarded as part of the hydrothermal assemblage as it was precipitated by cooling hot waters that were circulating as a result of the impact process. Further mobilization of the sulphate continues to the present day, such that it occurs in soil crusts (Fig. 3) ranging from relatively pure gypsum to sandy beds with a gypsum cement. The sulphate-cemented beds make an interesting comparison with the sulphate-bearing sandy beds encountered by the Opportunity Mars Exploration Rover (Moore 2004). During several Arctic summer field campaigns at Haughton, we have found that the impact-related selenite

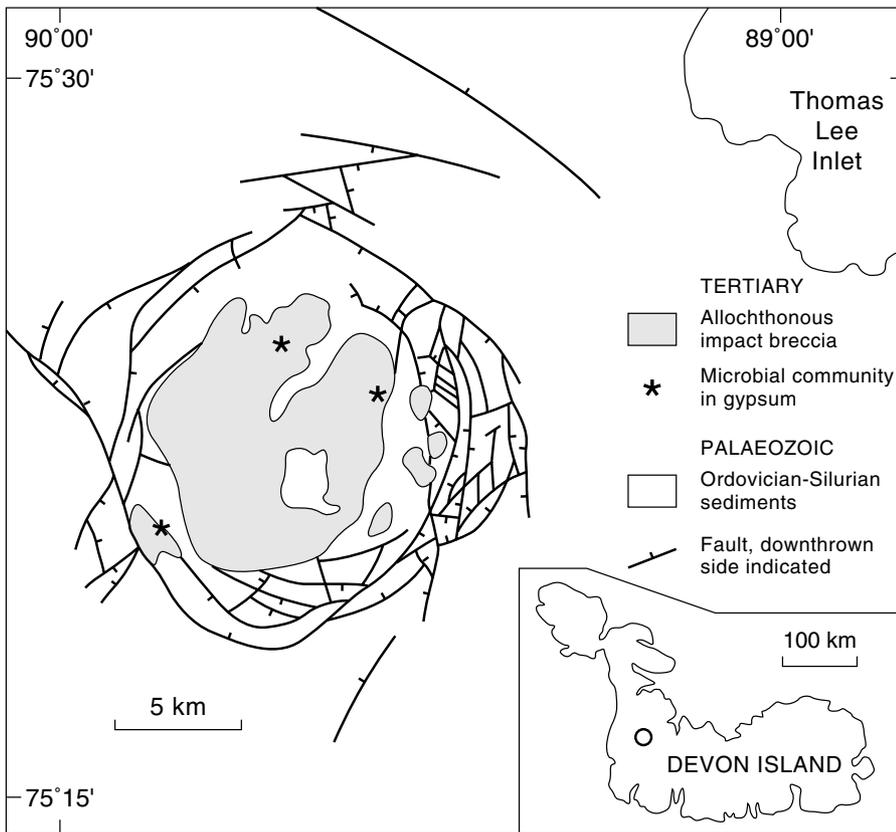


Fig. 1. A map of the Haughton Impact Structure, Devon Island, Canada, showing the location of gypsum samples exhibiting microbial communities. The Insert shows the site on Devon Island.



Fig. 2. Field exposure of a coalesced mass of clear gypsum crystals, within melt breccia deposits.

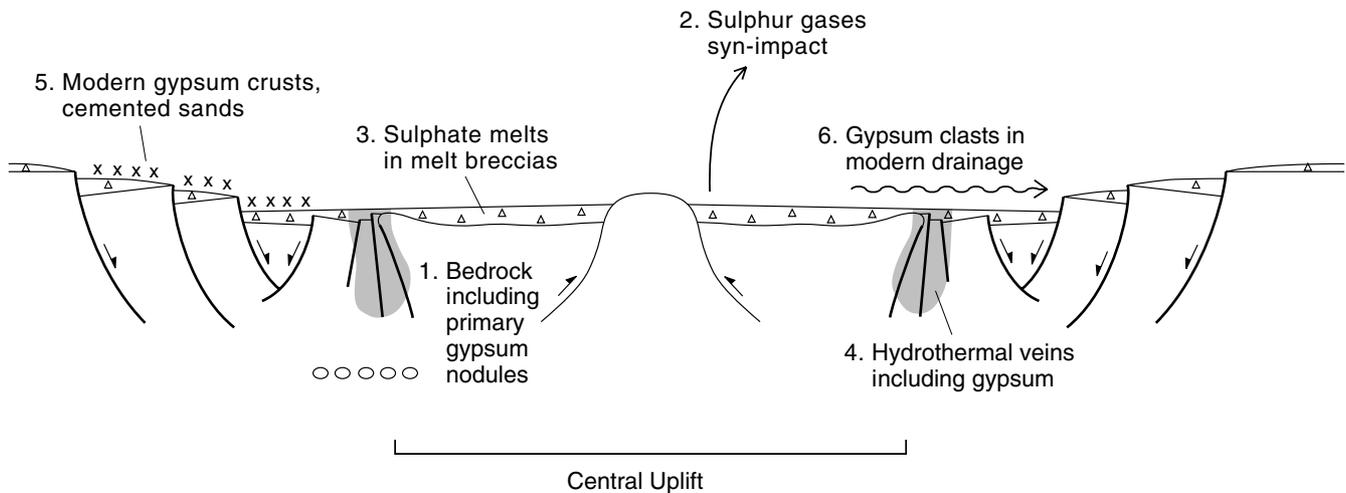


Fig. 3. A schematic cross-section showing the range of sulphate components in the Haughton crater. Numbers indicate time sequence.

at Haughton is colonized by cyanobacteria. The colonies are visible to the naked eye, so can be readily sampled for study.

Methodology

Selenite crystals were sampled from several localities within the impact melt breccias (Fig. 1). After cleaning off surface detritus, they were examined by a combination of transmitted light microscopy (Olympus BH-2 microscope), scanning electron microscopy (SEM) (JEOL 6400 instrument in secondary electron and backscattered modes, at 15 kV) and fluorescence microscopy (Olympus BX-51 universal microscope fitted with mercury-arc lamp epifluorescence assembly). They were characterized for ultraviolet absorption using a UV-1 Unicam spectrometer. Culturing experiments were undertaken using 2% BG-11 agar. The response of crystals to frost was determined by overnight outdoor exposure in Aberdeen at temperatures of -5 to 0 °C.

Microbe-bearing gypsum

The selenite crystals are up to 0.3 m in width and, in general, are of high purity and transparent (Fig. 4a). They do not show evidence for the incorporation of other mineral matter during growth. The crystals are compact, but locally exhibit frayed margins where some cleavage surfaces have separated. This is only evident in the outermost few millimetres, and not in all cases. This exfoliation may be a response to freeze-thaw weathering which affects Haughton for about 20 days each year at present (Cockell *et al.* 2002). Microscopic examination shows that the selenite contains traces of four components: rock detritus, newly precipitated gypsum, other authigenic (new) mineral growths and microbial colonies (Fig. 4). The rock detritus consists of sediment particles which have penetrated the opened cleavage surfaces by up to 2 cm from the crystal margins. Some of the detritus is cemented into place by gypsum, which must have been dissolved and reprecipitated from the host selenite.

Crystals at three of five localities sampled were found to be colonized by microbial communities. The microbial colonies occur up to 5 cm from the crystal margins, i.e. they have penetrated more deeply than the rock detritus. The communities identified within the selenite are primarily composed of two species of cyanobacteria, *Gloeocapsa alpine* (Nägeli) Brand and *Nostoc commune* Vaucher. Some samples were cultured and after several weeks other minor components were identified, including filamentous components resembling *Scytonema*. The compositions of these endolithic communities within the selenite are similar to those observed as epilithic communities on rocks and in cryptogamic crusts in this region of the Arctic (Dickson 2000; Cockell *et al.* 2002) and imply that they have been dispersed from the surrounding environment.

We have not yet observed microbial colonization in the other types of sulphate occurrence in the crater (Fig. 3).

Mode of occurrence

The *Gloeocapsa* colonies consist of several hundred adjoining cells, which exhibit all stages of cell division and have clearly grown *in situ*. The colonies form sheets, a single cell thick, and equidimensional masses of cells, all coloured black (see Figs 4a and b). *Nostoc* occurs as yellow ball-like masses of cells, both intermixed with, and separate from, the *Gloeocapsa*. The *Gloeocapsa* sheets occur along cleavage surfaces. The masses occur within cavities in the selenite distributed along cleavage surfaces (see Fig. 4c). The cleavage surfaces open to the outside, permitting penetration of water, but are no more than a few micrometres wide. The cavities are up to 1.5 mm across. Empty cavities have not been observed, suggesting a causal relationship between the cavities and their microbial colonies. This relationship could either involve microbial occupation of cavities or the formation of cavities around microbial colonies. Cavity development must involve water to dissolve away the selenite. Experiments exposing dry selenite crystals to cold, moisture-rich (frost-forming) conditions overnight show that moisture condenses around the microbial colonies.

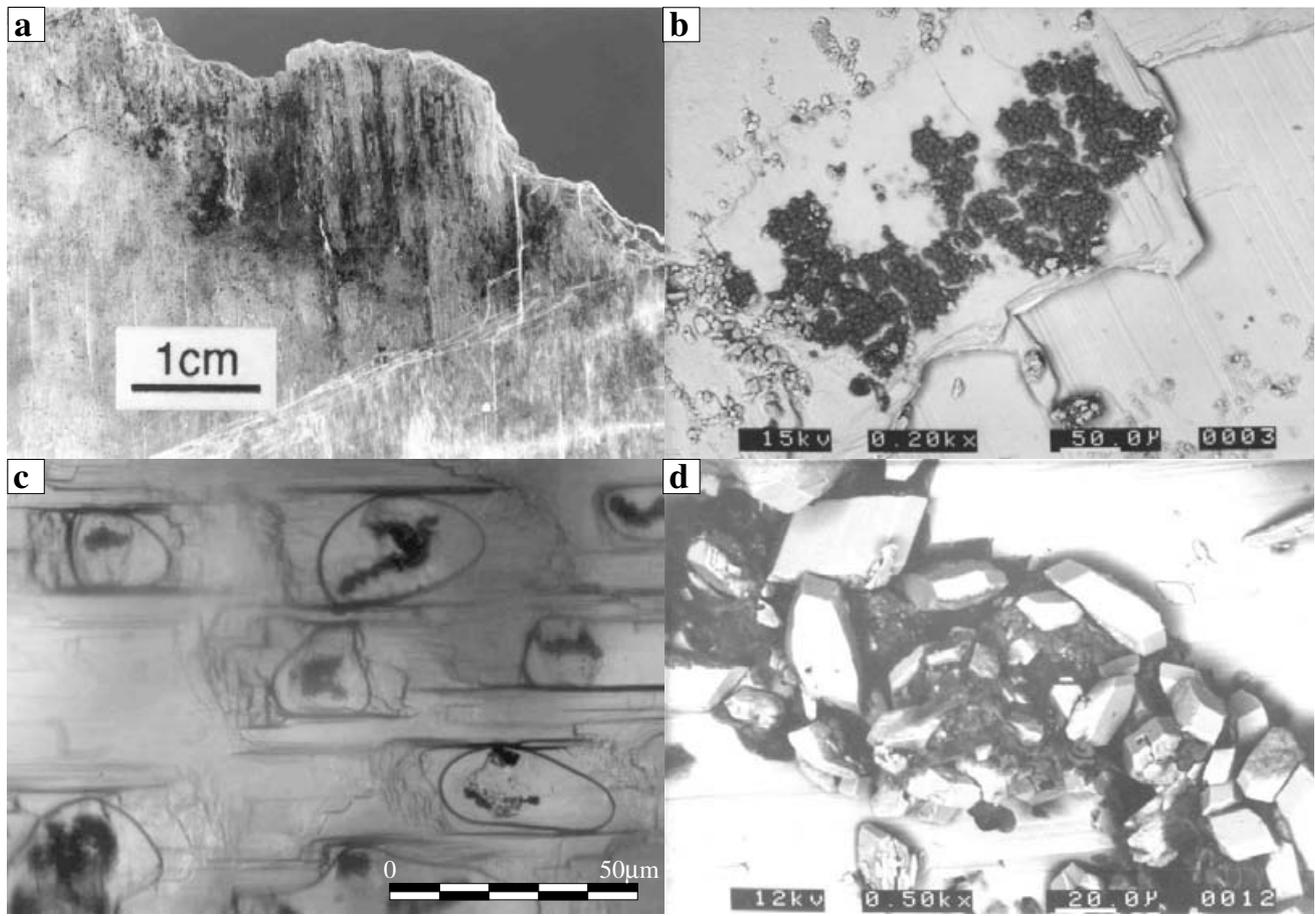


Fig. 4. Photomicrographs of microbe-bearing gypsum: (a) a sample of transparent gypsum showing black colouration along sub-surface cleavage planes, due to pigmented cyanobacteria; (b) a SEM backscattered image of cyanobacterial cells (black) on the gypsum cleavage surface (grey); (c) a transmitted light image of cyanobacterial masses enveloped in water within cavities in gypsum; (d) a SEM backscattered image showing new crystals of gypsum growing on the cleavage surface to bridge across dilated cleavage. Cyanobacterial cells (black) show close association with new crystals. Scale bars (a) 1 cm, (b),(c) 50 μm , (d) 20 μm .

This water coating gives the appearance of fluid inclusions (see e.g. Goldstein & Reynolds (1994)). They are fluid inclusions in the sense of being liquid water isolated within the mineral, but did not form in the conventional manner by entrapment of fluid during mineral growth. Normal fluid inclusions do occur in the gypsum: they are monophasic, up to 50 μm in size, and strongly controlled by the crystallographic structure (Fig. 5). They do not contain microbes, but it is quite possible that the microbe-bearing cavities evolved from the inclusions. The water is largely limited to the colonies and does not form continuous films. As calcium sulphate has a relatively high solubility, repeated cycles of water condensation and evaporation could cause localized redistribution of the mineral by dissolution and reprecipitation. This is confirmed by observations of clusters of micrometre-scale authigenic gypsum crystals which bridge across cleavage planes (see Fig. 4d). The authigenic gypsum shows a close spatial relationship with cyanobacteria (see Fig. 4d). Apart from the location of the microbes, there is no other reason for dissolution to be focused in cavities rather than along the cleavage planes. Therefore, available evidence suggests that the

cavities have developed around the colonies (see Fig. 6). Furthermore, the colonies have grown as the cavities have enlarged, such that the largest colonies occur in the largest cavities. As many of these colonies are free of significant amounts of admixed rock detritus (see Fig. 4c), they must have originated in sites where only one or two cells could penetrate, and subsequently reproduced and enlarged the cavity that they occupy. Thus the colonies have modified their mineral host to provide space in a protected environment, by accreting moisture which may have had the additional advantage of enhancing nutrient availability. The availability of nutrients should be more limited within gypsum crystals than in some other rock types which have a more complex chemistry, but the size of the colonies suggests that they have access to the required materials. Endoliths can also solubilize minerals directly (Bell 1993), and the close relationship between cyanobacteria and authigenic crystals (see Fig. 4d) further suggests that the colonies played a role in the redistribution of the gypsum.

Minor authigenic calcite occurs along some cleavage surfaces. The occurrence of calcite (a carbonate) within gypsum

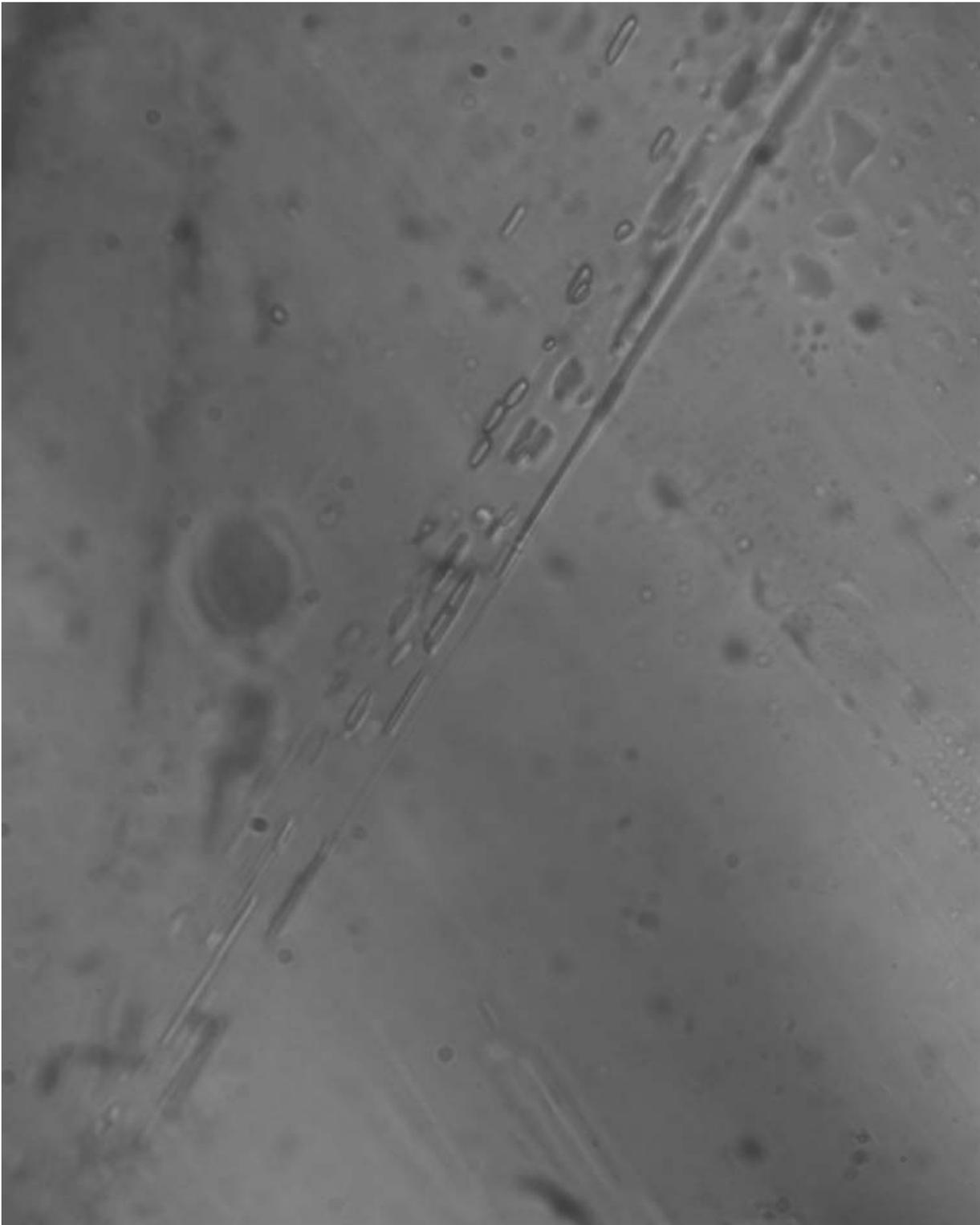


Fig. 5. A photomicrograph of selenite in transmitted light showing trails of monophasic fluid inclusions. Field width 1.0 mm.

(a sulphate) crystals shows that the moisture was able to introduce other components, favouring microbial growth. The precipitation of carbonate minerals requires bicarbonate-saturated waters, indicating that carbon dioxide may have been readily available, as bicarbonate, for photosynthesis.

Although the gypsum cannot supply a whole range of nutrients, the melt breccia host is a good source of ions as it is altered and fine-grained. An analogous scenario is the cyanobacterial colonization of the quartzose Beacon Sandstone in Antarctica (Friedmann 1982), where the required nutrients

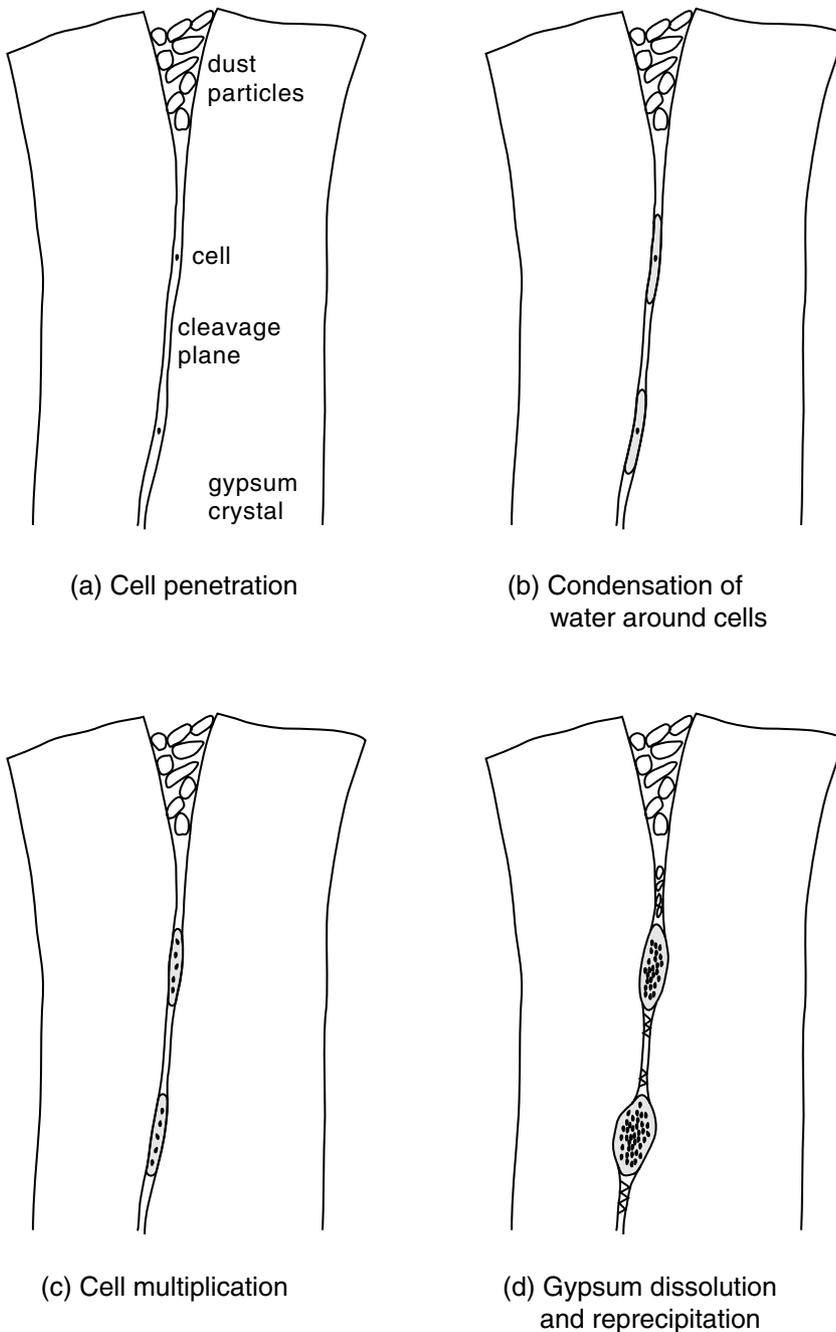


Fig. 6. Schematic stages for development of cyanobacterial communities within gypsum crystals, including (a) penetration of cleavage, (b) condensation of water, (c) cell multiplication and (d) gypsum dissolution and reprecipitation. Cell-bearing cavities in (d) are up to 1.5 mm in width; the cells and cleavage are enlarged for clarity.

are not derived from the host quartz but are blown in from volcanic rocks elsewhere in the region (Weed & Ackert 1986; Nienow & Friedmann 1993).

Adaptation to environment

The propensity for sulphates to form clear crystals makes them an advantageous habitat for photosynthesisers. Visible light penetrates the Haughton selenite crystals to a depth of at least 15 cm. The black colouration of the *Gloeocapsa* in the

selenite is caused by the synthesis of ultraviolet (UV) screening compounds, particularly the pigments scytonemin and gloeocapsin. This pigmentation is similarly observed in arctic epilithic cyanobacterial communities exposed to ambient solar radiation on the surface of rocks (Cockell *et al.* 2002, 2003b). Living within the selenite only provides limited protection from UV radiation. A 1 mm thickness of the Haughton selenite exposed to the environmentally relevant range 290–400 nm, covering the UVB and UVA regions, exhibited a mean absorbance of 0.12 (transmission of 0.88),

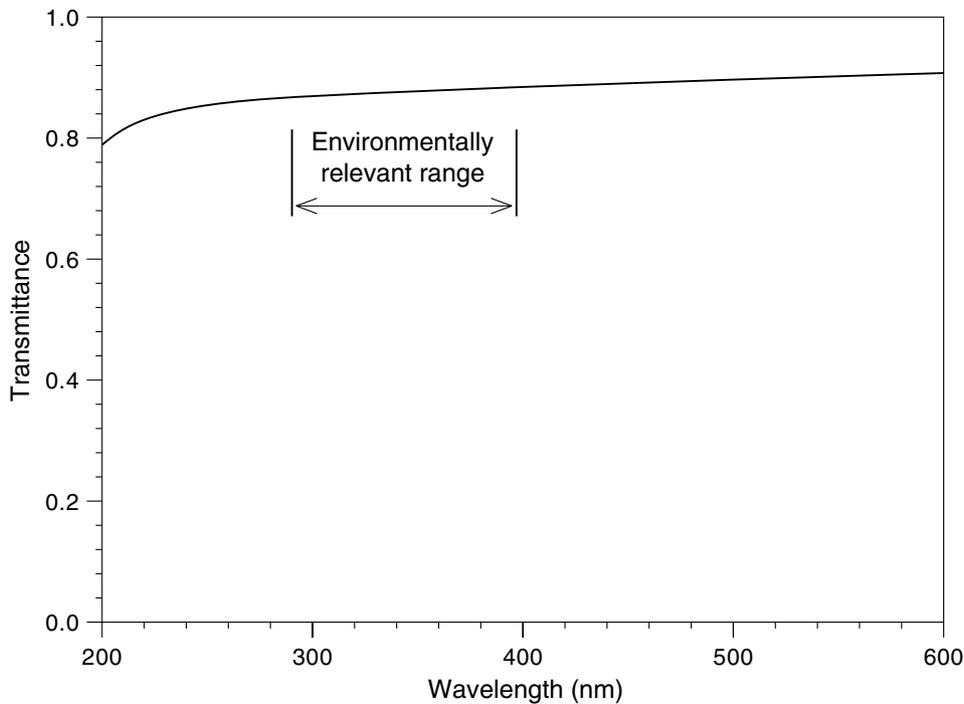


Fig. 7. The transmission spectrum for a 1 mm thickness of Haughton selenite, over the range 200–600 nm. The environmentally relevant range is 290–400 nm, covering the UVB and UVA regions.

representing just a 25% reduction in ambient UV exposure (Fig. 7). The development of photoprotective pigmentation was clearly essential in this circumstance.

The occurrences of microbes in sulphates in the Haughton crater are quite distinct from previous records in actively precipitating evaporite deposits. Occurrences in shallow water evaporites involved substantial amounts of ponding liquid water and have been engulfed by gypsum which precipitated in their habitat (Rothschild *et al.* 1994; Oren *et al.* 1995; Wei *et al.* 1998). By contrast, the Haughton microbes have colonized pre-existing selenite in an environment which involved relatively little liquid water and is not abnormally saline, so the microbes are not restricted to specialist halotolerant species. The Haughton gypsum is much more transparent to light than shallow water evaporitic gypsum, which is made translucent by other admixed mineral matter and a smaller crystal size. The Haughton gypsum also allows an order of magnitude greater light penetration than an Antarctic gypsum weathering crust (Hughes & Lawley 2003). These microbial communities are comparable with endoliths in sandstones and other porous rocks (Friedmann 1982; Nienow *et al.* 1988; Matthes *et al.* 2001). Endolithic microbial communities are also extensively documented in the rocks of the Arctic, particularly in the Haughton impact structure (Cockell *et al.* 2002). Previous records at Haughton include in the dolomite, and in a variety of clasts in the impact melt breccias including shocked gneisses (Cockell *et al.* 2002, 2003a). However, the gypsum is exceptional as an endolithic habitat in the depth of penetration from the rock surface, the high levels of light exposure for photosynthesis and the large size of colony that could develop along a cleavage surface.

The minor internal dissolution of gypsum has an important consequence for the immediate habitat. A calcium-rich brine may have a eutectic point (complete freezing of water) as low as $-50\text{ }^{\circ}\text{C}$, substantially increasing the proportion of the year that the enclosed water is liquid (Burt & Knauth 2003). At Haughton, this would confer little advantage as the gypsum is snow-covered for most of the year and the microbes would be dormant, but in environments where low temperature is combined with low precipitation (exemplified in the Antarctic, and potentially on other planets such as Mars) it could extend the period of annual activity. A further advantage applicable to low-temperature environments is that diurnal freeze–thaw cycles might be mitigated, reducing freeze–thaw stress to the microbes.

Significance on Mars

The occurrence of microbes in sulphates has implications for potential analogues on other planets. Surface precipitates on Earth are dominated by carbonates, particularly calcite (e.g. Riding 2000). However, sulphates are the predominant salts detected on the two main targets in the search for life elsewhere in the Solar System, Mars (Cooper & Mustard 2002) and Europa (Kargel *et al.* 2000; Carlson *et al.* 2002). As volcanic and/or hydrothermal activity, which introduces volatile sulphur compounds to the planetary surface (Kargel *et al.* 1999), appears to be a common feature of rocky planets, sulphur salts should dominate chemical precipitates. Evidence for photosynthetic activity within sulphate crystals is therefore interesting as a habitat that could be widespread on other planets. It is likely that photosynthesis is the

optimum mechanism for the harvesting of energy from stars by primitive life (Wald 1974), so habitats that support it are of universal importance.

The gypsum occurrence in the Haughton crater has particular significance for the exploration for life on Mars. The Viking missions provided the first indication that sulphate-bearing crusts might be widespread at the Martian surface by showing that sulphates dominate the soluble salt fraction at two widely separated sites (Banin *et al.* 1992). The global extent of the cemented layer is further suggested by observations of a duricrust at the Mars Pathfinder landing site (Moore *et al.* 1999) and by independent thermal inertia mapping with Mars Global Surveyor's Thermal Emission Spectrometer (Mellon *et al.* 2000), sulphates being a prime candidate as the main cementing agent (Cooper & Mustard 2002). Light-coloured sand dunes on Mars are possibly formed from the erosion, transport and redeposition of gypsum deposits (Thomas *et al.* 1999). Furthermore, meteorites from Mars contain sulphate phases which suggest evaporites at the Martian surface (Bridges & Grady 2000; Bridges *et al.* 2001). Finally, massive deposits of sulphates are suggested at the current Opportunity Mars Exploration Rover (MER) landing site (Moore 2004). The apparent abundance of sulphates, and the inherent involvement of water in their precipitation, makes them good candidates in the search for life on Mars (Rothschild 1990; Cid & Casanova 2001; Wentworth *et al.* 2002). The ready colonization of gypsum in the Haughton impact structure provides strong support that the Martian sulphates are indeed a potential habitat for life. Although the Haughton gypsum is a hydrothermal precipitate, it was deposited by the waning, cooling stage of activity (Osinski *et al.* 2001). It is therefore a low-temperature precipitate, which bears comparison with sulphates on Mars that appear to have been deposited from liquid water at the surface (Moore 2004). Transient hydrothermal activity may help to introduce the sulphates to the surface environment in the first instance (Newsom *et al.* 1999). Colonization within crystals on Mars could be particularly helpful, as this would provide shelter from the very strong winds that sweep the surface and transport large volumes of dust (Tanaka 2000). However, the same winds could help to disperse microbes within gypsum sand grains which accumulate in dune structures.

There is added significance for this mode of microbial habitat on Mars. In the terrestrial geological record, sulphates are liable to dissolution due to interaction with ground waters. Consequently, they are commonly only recognizable as crystal moulds or pseudomorphs (mineral replacements preserving the original crystal shape). On Mars, where surface water has been substantially less prevalent, there is a much higher likelihood that sulphates have survived unaltered through geologic time, as evidenced at the Opportunity MER landing site. Any primitive life taking advantage of this potential habitat could therefore have an unusually high preservation potential, and sulphate samples could record microbial activity from a period when there was more moisture at the Martian surface. If comparable

UV-screening pigments were developed on Mars, they should be detectable by non-destructive Raman spectroscopy, as has been suggested for Martian exploration (Wynn-Williams & Edwards 2000a; Ellery & Wynn-Williams 2003). Regardless of pigmentation, sulphate samples on Mars must be strong candidates for the analysis for biomarkers, using a range of high-resolution techniques during future exploration (e.g. Beegle *et al.* 2001; Warmflash *et al.* 2002; Skelley & Mathies 2003). Other endolithic habitats have been suggested as analogues for what could occur on Mars (Wynn-Williams & Edwards 2000b; Wierzchos & Ascaso 2002), but the known abundance of sulphates on Mars makes the gypsum particularly appropriate as an analogue. The Haughton gypsum also has a translucency and depth of endolithic penetration that exceeds other described analogues.

The significance of the impact setting is that it has hosted hydrothermal circulation which has mobilized pre-existing sulphate deposits and reprecipitated them as large crystals of exceptional clarity. Such remobilization of sedimentary gypsum deposits to form hydrothermal selenite is also observed elsewhere, for example in Nevada (Stewart 1980). This is a consistent difference between many sedimentary gypsum deposits and remobilized gypsum: the primary deposits are rich in mineral matter or have fine crystal size, giving them low translucency, while the secondary deposits consist of large translucent selenite crystals. Selenite does occur in other settings, such as in lacustrine deposits (Varol *et al.* 2002) and in caves (Foshag 1927), and microbial colonization must also be possible in these settings. However, the hydrothermal activity at the impact site has increased the likelihood that selenite occurs there. Where impact sites occur in sulphate-rich terrains elsewhere (prospectively on Mars), selenite could be a common feature.

We note, incidentally, that the abundant fluid inclusions in the Haughton gypsum represent a preserved record of the water from which the gypsum precipitated. In an analogous occurrence on Mars, this ancient water could be extracted and used to determine palaeo-water chemistry.

Summary

The impact-induced hydrothermal gypsum in the Haughton impact structure is a very favourable habitat for microbial colonization. The habitat combines a high energy input for photosynthesis with a high level of protection from wind and dehydration. Analogous cases in a remote setting could have a high detectability of microbial colonization if dark UV-screening pigments were evolved, and a high preservation potential on dry land surfaces, making them an important sampling medium in the search for evidence of life on other planets. Sulphates which occur on the Martian surface are an attractive objective for future analyses for biosignatures.

Acknowledgements

We are grateful to the sponsors of the NASA Haughton-Mars Project for support of fieldwork. Anonymous reviews

helped to improve the manuscript. Martin Baron is thanked for observations of fluid inclusions in the gypsum. Anne Wilkins supplied Fig. 4(d). Other essential technical support was provided by Barry Fulton and John Still. G.R.O. was funded through a NSERC grant to John Spray, University of New Brunswick.

References

- Banin, A., Clark, B.C. & Waenke, H. (1992). Surface chemistry and mineralogy. In *Mars*, pp. 594–625. University of Arizona Press, Tucson.
- Beegle, L.W., Kanik, I., Matz, L. & Hill, H.H. (2001). Electro-spray ionization high-resolution ion mobility spectrometry for the detection of organic compounds. 1. Amino acids. *Anal. Chem.* **73**, 3028–3031.
- Bell, R.A. (1993). Cryptoendolithic algae of hot semiarid lands and deserts. *J. Phycology* **29**, 133–139.
- Bridges, J.C., Catling, D.C., Saxton, J.M., Swindle, T.D., Lyon, I.C. & Grady, M.M. (2001). Alteration assemblages in Martian meteorites: implications for near-surface processes. *Space Sci. Rev.* **96**, 365–392.
- Bridges, J.C. & Grady, M.M. (2000). Evaporite mineral assemblages in the nakhlite (martian) meteorites. *Earth Planet. Sci. Lett.* **176**, 267–279.
- Burt, D.M. & Knauth, L.P. (2003). Electrically conducting, Ca-rich brines, rather than water, expected in the Martian subsurface. *J. Geophys. Res.* **108**, doi: 10.1029/2002JE001862.
- Cabrol, N.A., Grin, E.A., Newsom, H.E., Landheim, R. & McKay, C.P. (1999). Hydrogeologic evolution of Gale Crater and its relevance to the exobiological exploration of Mars. *Icarus* **139**, 235–245.
- Carlson, R.W., Anderson, M.S., Johnson, R.E., Schulman, M.B. & Yavrouian, A.H. (2002). Sulfuric acid production on Europa: the radiolysis of sulfur in water ice. *Icarus* **157**, 456–463.
- Cid, A. & Casanova, I. (2001). Sulphates in Martian soils: a clear exobiological target. In *Proc. First Eur. Workshop on Exo-/Astrobiology (European Space Agency Special Publication, 496)*, pp. 201–202. European Space Agency, Noordwijk.
- Cockell, C.S., Lee, P., Osinski, G., Horneck, G. & Broady, P. (2002). Impact-induced microbial endolithic habitats. *Meteor. Planet. Sci.* **37**, 1287–1298.
- Cockell, C.S., Osinski, G.R. & Lee, P. (2003a). The impact crater as a habitat: effects of impact processing of target materials. *Astrobiology* **3**, 181–191.
- Cockell, C.S., Rettberg, P., Horneck, G., Scherer, K. & Stokes, M.D. (2003b). Measurements of microbial protection from ultraviolet radiation in polar terrestrial microhabitats. *Polar Biol.* **26**, 62–69.
- Cooper, C.D. & Mustard, J.F. (2002). Spectroscopy of loose and cemented sulphate-bearing soils: implications for duricrust on Mars. *Icarus* **158**, 42–55.
- Dickson, L.G. (2000). Constraints to nitrogen fixation by cryptogamic crusts in a polar desert ecosystem, Devon Island, N.W.T., Canada. *Arctic, Antarctic Alpine Res.* **32**, 40–45.
- Ellery, A. & Wynn-Williams, D. (2003). Why Raman spectroscopy on Mars? – a case of the right tool for the right job. *Astrobiology* **3**, 565–579.
- Farmer, J.D. (2000). Hydrothermal systems: doorways to early biosphere evolution. *GSA Today* **10**(7), 1–9.
- Farmer, J.D. & Des Marais, D. (1999). Exploring for a record of ancient Martian life. *J. Geophys. Res.* **104**, 26977–26995.
- Foshag, W.F. (1927). The selenite caves of Naica, Mexico. *Amer. Mineral.* **12**, 252–256.
- Friedmann, E.I. (1982). Endolithic microorganisms in the Antarctic cold desert. *Science* **215**, 1045–1053.
- Frisch, T. & Thorsteinsson, R. (1978). Haughton astrobleme: a Mid-Cenozoic impact crater, Devon Island, Canadian Arctic Archipelago. *Arctic* **31**, 108–124.
- Goldstein, R.H. & Reynolds, T.J. (1994). *Systematics of Fluid Inclusions in Diagenetic Minerals (SEPM Short Course, 31)*. SEPM, Tulsa.
- Hughes, K.A. & Lawley, B. (2003). A novel Antarctic microbial endolithic community within gypsum crusts. *Environ. Microbiol.* **5**, 555–565.
- Kargel, J.S., Delmelle, P. & Nash, D.B. (1999). Volcanogenic sulfur on Earth and Io: composition and spectroscopy. *Icarus* **142**, 249–280.
- Kargel, J.S., Kaye, J.Z., Head, J.W., Marion, G.M., Sassen, R., Crowley, J.K., Ballesteros, O.P., Grant, S.A. & Hogenboom, D.L. (2000). Europa's crust and ocean: origin, composition, and the prospects for life. *Icarus* **148**, 226–265.
- Matthes, U., Turner, S.J. & Larson, D.W. (2001). Light attenuation by limestone rock and its constraint on the depth distribution of endolithic algae and cyanobacteria. *Int. J. Plant Sci.* **162**, 263–270.
- Mellon, M.T., Jakosky, B.M., Kieffer, H.H. & Christensen, P.R. (2000). High-resolution thermal inertia mapping from the Mars Global Surveyor Thermal Emission Spectrometer. *Icarus* **148**, 437–455.
- Moore, H.J., Bickler, D.B., Crisp, J.A., Eisen, H.J., Gensler, J.A., Haldemann, A.F.C., Matijevic, J.R., Reid, L.K. & Pavlics, F. (1999). Soil-like deposits observed by Sojourner, the Pathfinder rover. *J. Geophys. Res.* **104**, 8729–8746.
- Moore, J.M. (2004). Blueberry fields for ever. *Nature* **428**, 711–712.
- Newsom, H.E., Hagerty, J.J. & Goff, F. (1999). Mixed hydrothermal fluids and the origin of the Martian soil. *J. Geophys. Res.* **104**, 8717–8728.
- Newsom, H.E., Hagerty, J.J. & Thorsos, I.E. (2001). Location and sampling of aqueous and hydrothermal deposits in Martian impact craters. *Astrobiology* **1**, 71–88.
- Nienow, J.A. & Friedmann, E.I. (1993). Terrestrial lithotypic (rock) communities. In *Antarctic Microbiology*, ed. Friedmann, E.I., pp. 343–412. Wiley-Liss Inc., New York.
- Nienow, J.A., McKay, C.P. & Friedmann, E.I. (1988). The cryptoendolithic microbial environment in the Ross Desert of Antarctica: light in the photosynthetically active region. *Microbial Ecology* **16**, 271–289.
- Oren, A., Kuhl, M. & Karsten, U. (1995). An endoevaporitic microbial mat within a gypsum crust: zonation of phototrophs, photopigments, and light penetration. *Marine Ecology Progress Series* **128**, 151–159.
- Osinski, G.R. & Spray, J.G. (2003). Evidence for the shock melting of sulfates from the Haughton impact crater, Arctic Canada. *Earth Planet. Sci. Lett.* **215**, 357–370.
- Osinski, G.R., Spray, J.G. & Lee, P. (2001). Impact-induced hydrothermal activity within the Haughton impact structure, arctic Canada: generation of a transient, warm, wet oasis. *Meteor. Planet. Sci.* **36**, 731–745.
- Rathbun, J.A. & Squyres, S.W. (2002). Hydrothermal systems associated with Martian impact craters. *Icarus* **157**, 362–372.
- Riding, R. (2000). Microbial carbonates: the geological record of calcified bacterial-algal mats and biofilms. *Sedimentology* **47** (supplement 1), 179–214.
- Robertson, P.B. & Sweeney, J.F. (1983). Haughton impact structure: structural and morphological aspects. *Can. J. Earth Sci.* **20**, 1134–1151.
- Rothschild, L.J. (1990). Earth analogs for Martian life. Microbes in evaporites, a new model system for life on Mars. *Icarus* **88**, 246–260.
- Rothschild, L.J., Giver, L.J., White, M.R. & Mancinelli, R.L. (1994). Metabolic activity of microorganisms in evaporites. *J. Phycology* **30**, 431–438.
- Skelley, A.M. & Mathies, R.A. (2003). Chiral separation of fluorescamine-labelled amino acids using microfabricated capillary electrophoresis devices for extraterrestrial exploration. *J. Chromat. A* **1021**, 191–199.
- Stewart, J.H. (1980). Geology of Nevada. *Nevada Bureau of Mines and Geology Special Publication* **4**.
- Tanaka, K.L. (2000). Dust and ice deposition in the Martian geologic record. *Icarus* **144**, 254–266.
- Thomas, P.C., Malin, M.C., Carr, M.H., Danielson, G.E., Davies, M.E., Hartmann, W.K., Ingersoll, A.P., James, P.B., McEwen, A.S., Soderblom, L.A. & Veveřka, J. (1999). Bright dunes on Mars. *Nature* **397**, 592–594.
- Varol, B., Araz, H., Karadenizli, L., Kazanci, N., Seyitoglu, G. & Sen, S. (2002). Sedimentology of the Miocene evaporitic succession in the north of Çankiri-Çorum Basin, central Anatolia, Turkey. *Carbonates Evaporites* **17**, 197–209.
- Wald, G. (1974). Fitness in the Universe: choices and necessities. *Origins Life Evol. Biosphere* **5**, 7–27.
- Warmflash, D., Larios-Sanz, M., Fox, G.E. & McKay, D.S. (2002). Progress in the use of rapid molecular techniques to detect life forms in

- soil: implications for interplanetary astrobiology missions. *Lunar Planet. Sci.* **XXXIII**, abstract 1963.
- Weed, R. & Ackert, R.P. (1986). Chemical weathering of Beacon Supergroup sandstones and implications for Antarctic glacial chronology. *South African J. Sci.* **82**, 513–516.
- Wei, D., Liu, Z., Deng, X. & Xu, S. (1998). Biomineralization of mirabilite deposits of Barkol Lake, China. *Carbonates Evaporites* **13**, 86–89.
- Wentworth, S.J., Thomas-Keprta, K.L. & McKay, D.S. (2002). Water on Mars: petrographic evidence. *Lunar Planet. Sci.* **XXXIII**, abstract 1932.
- Wierzchos, J. & Ascaso, C. (2002). Microbial fossil record of rocks from the Ross Desert, Antarctica: implications in the search for past life on Mars. *Int. J. Astrobiol.* **1**, 51–59.
- Wynn-Williams, D.D. & Edwards, H.G.M. (2000a). Proximal analysis of regolith habitats and protective biomolecules in situ by laser Raman spectroscopy: overview of terrestrial Antarctic habitats and Mars analogs. *Icarus* **144**, 486–503.
- Wynn-Williams, D.D. & Edwards, H.G.M. (2000b). Antarctic ecosystems as models for extraterrestrial surface habitats. *Planet. Space Sci.* **48**, 1065–1075.