

Morphological Biosignatures from Subsurface Environments: Recognition on Planetary Missions

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Abstract The Earth is inhabited by life not just at its surface, but down to a depth of kms. Like surface life, this deep subsurface life produces a fossil record, traces of which may be found in the pore space of practically all rock types. The (palaeo)subsurface of other planetary bodies is therefore a promising target in the search for another example of life. Subsurface filamentous fabrics (SFFs), i.e. mineral encrustations of a filament-based textural framework, occur in many terrestrial rocks representing present or ancient subsurface settings. SFF are interpreted as mineral encrustations on masses of filaments/pseudofilaments of microbial origin. SFF are a common example of the fossil record of subsurface life. Macroscopic (pseudostalactites, U-shapes) and microscopic (filaments) characteristics make SFF's a biosignature that can be identified with relative ease. SFF in the subsurface are probably about as common and easily recognizable as are stromatolites in surface environments. Close-up imagers (~50 micron/pixel resolution) and microscopes (~3 micron/pixel resolution) on upcoming Mars lander missions are crucial instruments that will allow the recognition of biofabrics of surface- and subsurface origin. The resolution available however will not allow the recognition of small (~1 micron) individual mineralized microbial cells. The microscopy of unprepared rock surfaces would benefit from the use of polarizing filters to reduce surface reflectance and enhance internally reflected light. Tests demonstrate the potential to visualize mineralized filaments using this procedure.

Keywords Biosignatures · Subsurface biosphere · Mars

1 Introduction

The terrestrial subsurface is a now well-recognized habitat for heterotrophic and chemosynthetic microbial life forms (Amy and Haldeman 1997; Gold 1992; Stevens 1997; Stevens and McKinley 1995). Given the availability of a source of chemical energy, the limit for

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life essentially is given by the increasing temperature towards depth, roughly the 120°C isotherm (Kashevi and Lovley 2003). Voids in rocks that may range from microscopic pores to large caves (Boston et al. 2001a) provide space and facilitate access to energy sources for microbes. Present and past subsurface environments on other planetary bodies therefore are promising targets in the search for another example of life just like surface sediments. Subsurface conditions on different planetary bodies, including Earth, likely are less different and more stable than their surface counterparts. It is likely that pores and cavities in the Martian subsurface at depths corresponding to temperatures $>0^{\circ}\text{C}$ are filled with water (Burr et al. 2002; Clifford and Parker 2001). Such environments likely are quite similar to anaerobic deep subsurface environments on Earth where the presence of life is accepted (Aitken et al. 2004; McKinley et al. 2000; Moser et al. 2005; Parkes et al. 2005). While the presence of a subsurface biosphere is accepted, evidence of a fossil record of this subsurface life has been rather scarce (Furnes et al. 1999; Furnes and Staudigel 1999; Hofmann and Farmer 2000; Kretzschmar 1982; Reitner 2004; Schumann et al. 2004; Trewin and Knoll 1999; Westall et al. 2006a, 2006b).

2 Subsurface Filamentous Fabrics (SFF): A Fossil Record of Subsurface Biosphere(s)?

Based on large numbers of samples from ~ 200 localities, a so far largely ignored type of mineral fabric from subsurface environments has been recognized to be widespread (Hofmann and Farmer 2000). The structural building elements of SFF are filament threads, <1 to about 3 micron in diameter, showing multiple encrustations by a variety of minerals. Encrustations of filaments in various large-scale geometric arrangements result in characteristic macroscopic textures, such as layered internal sediments with matted fabrics, vertically arranged threads, streamers, U-loops (Boston et al. 2001b) indicating flexibility of filaments before mineral encrustation occurred, but also in irregular masses without macroscopic expression. Fabrics similar to SFF are known from caves where a microbial origin of “stalactitic snottites”, closely resembling mineralized SFF, is supported by gene sequence analysis (Hose et al. 2000), and from oxidizing shipwrecks where “rusticles”, similar again to SFF, form in a fully submersed environment (Cullimore and Johnston 2000). In these recent cave- and shipwreck environments sulfur- and iron oxidizing microorganisms appear to be the main organisms responsible for the formation of macroscopic fabrics. SFF may have formed in any subsurface environments colonized by microbial life, independent of the geological nature of the host rock.

Highly variable degrees of cementation of filamentous fabrics result in macroscopic aspects ranging from “hair-like tufts” to massive rocks without recognizable surface expression. Such mineral fabrics may be relatively easy to recognize at resolutions already implemented (Mars Exploration Rovers, Beagle 2) or foreseen for upcoming Mars landing missions (MSL, Phoenix, ExoMars-Pasteur). Terrestrial occurrences of SFF are found in a variety of rocks, mainly cavities in volcanics (57% of occurrences), in the oxidation zone of sulfide ore deposits (28%), and in sedimentary environments (10%). SFF, in particular the so-called moss-agates, have attracted the attention of researchers for a long time (Bowerbank 1842; Daubenton 1782; Razumovsky 1835). Descriptions of single occurrences during the past 25 years favor a biological explanation (Baele 1998; Feldmann et al. 1997; Hofmann 1989; Kretzschmar 1982; Reitner 2004; Schumann et al. 2004; Trewin and Knoll 1999). Morphologically similar filamentous fabrics also are known from numerous hydrothermal vent sites, and generally are biologically interpreted (Fortin et al. 1998;

Juniper and Sarrazin 1995). It is proposed here that SFF represent an expression of subsurface life that is as widespread in and characteristic of subsurface environments as are stromatolites in Precambrian sediments. SFF represent a type of biosignature with similar potential and limitations. The geological age of SFF ranges from sub-recent to Precambrian, with possible Archean examples (Hofmann et al. 2006).

Macroscopic characteristics of SFF: While some occurrences form massive blocks of chalcedony without distinctive macroscopic surface features, in many cases SFF exhibit characteristic morphologies resulting from the mineralization of filament bundles or filament streamers (Fig. 1a,b): Stromatolite-like matted fabrics resulting in layered, sometimes agate-like banding; pseudostalactites, vertically oriented tubular structures with a innermost core diameter of a few microns, much too small for stalactites which have mm-sized centers; association of numerous filaments to “ropes” or “stalks”, and U-loops: gravity-bent filaments attached at two ends, indicating a high initial flexibility (Fig. 1b). Minerals involved in the encrustation of filaments (Fig. 2) are all aqueous precipitates and include Fe-hydroxides, hematite, coronadite, Pb-phosphates, Fe-rich clays, pyrite, quartz, opal, calcite, zeolites, and others.

Fig. 1 a Example of subsurface filamentous fabric (SFF) from Jebel Irhoud, Morocco.

Goethite-encrusted filaments show only thin overgrowth of quartz and calcite, allowing recognition of fabric. Width of sample 18 cm. **b** Subsurface filamentous fabric from Sidi Rahal, Morocco. Sample is shown in original orientation showing gravity-oriented vertical encrusted filaments (single attachment) and U-loops formed from filaments/filament strands attached at 2 points. Field of view is 6 cm, diameter or encrusted filaments 0.15 to 0.5 mm. Photographs by Peter Vollenweider

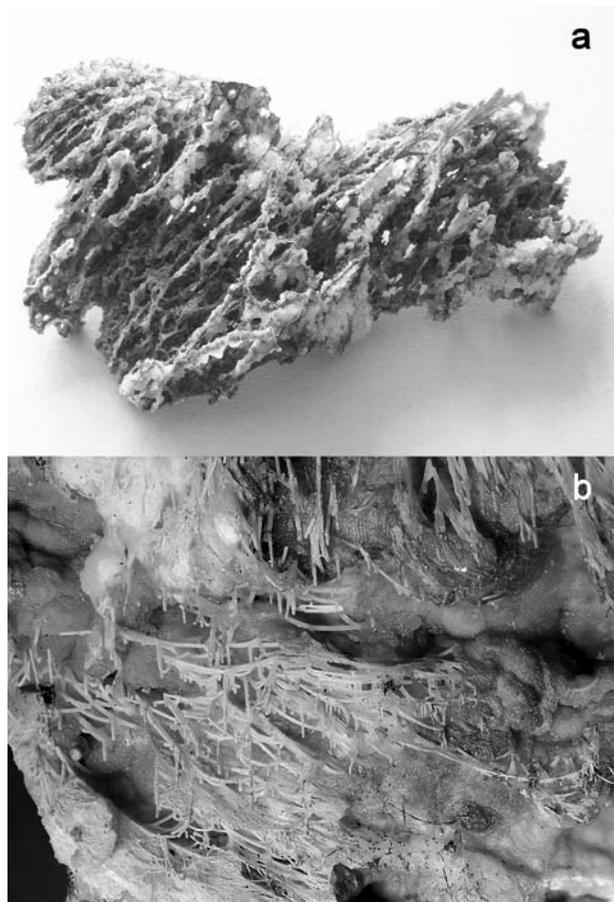
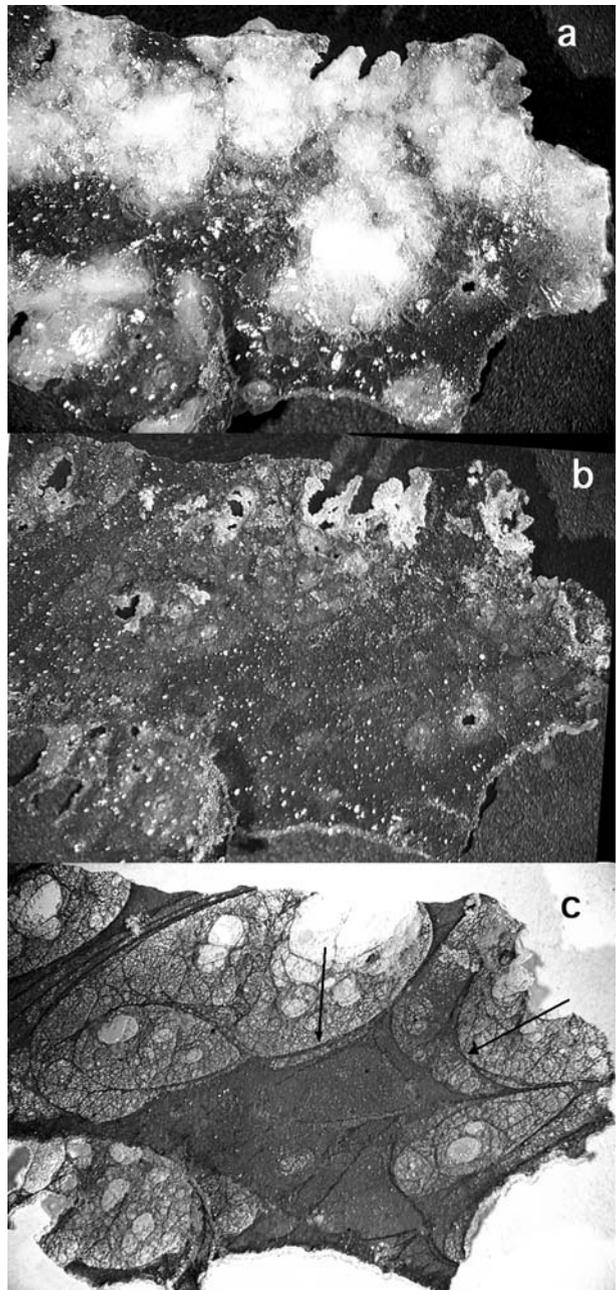


Fig. 2 Subsample of SFF from Jebel Irhoud, Morocco (Fig. 1a). **a** Untreated sample in air; **b** calcite encrustation dissolved with HCl, in air; **(c)** as **(b)** but in water immersion, strongly reducing surface scattering and showing filamentous texture. Many filament strand are strongly curved indicating initial flexibility (*arrows*). Field of view is 23 mm



Microscopic characteristics of SFF: Investigations of SFF by optical microscopy in thin sections and by SEM on natural and etched surfaces shows that filaments with characteristic diameters near 1 micron are the basis and textural oldest constituent of SFF. All other phases were formed later as encrustations on the filaments or as massive cavity fill. The shape

of filaments is irregular and highly bent, and differs from mineral fibers that show little bending and whose diameter is much more variable. Besides simple filaments, forms closely resembling the extracellular stalk of *Gallionella ferruginea* have been observed, mainly in one area in Iceland, in association with the more common filaments (Feucht et al. 2006; Hofmann and Farmer 2000).

Biosignature potential of filaments and SFF: Morphological biosignatures (as chemical and isotopic signatures) alone will always have to be met with a level of caution (Garcia-Ruiz et al. 2002, 2003; Jones et al. 2004). The recognition of filaments is less ambiguous than that of coccoid microbes, and filaments tend to occur in large numbers in subparallel configuration, leading to macroscopic “streamers” (Hallberg et al. 2006). Biological and non-biological filamentous forms may be discriminated based on evidence of flexibility, characteristics of bending and diameter (absolute values and range) of single filaments. Filamentous microbes also tend to form macroscopically recognizable biofabrics. Filamentous shapes are found among primitive bacteria and archaea and it appears likely that the development of filamentous forms occurred early in the history of life, as filaments have been reported from Archean rocks (Rasmussen 2000; Walsh 1992, 2004; Westall et al. 2006a, 2006b). The presence of filamentous forms can thus be expected among the earliest life forms on Earth, and potentially, Mars. Filaments and filament-based biofabrics thus represent a very robust morphological biosignature. Filament-like structures may also form due to the mineralization of extracellular polymeric substances/microbial mucus (Jones et al. 2004; Westall et al. 2000b). While such filament-like forms are not fossils s.s., they nevertheless represent viable biosignatures.

Distinction between subsurface biological filaments and non-biological look-alikes: Biological filaments are thin (typically few microns diameter) threads that may reach a length of hundreds of microns. Non-biological threads also exist and may be mistaken for biological ones. How can they be distinguished? Among the possible non-biological threads fibrous minerals (e.g. asbestos, torodokite, palygorskite) and natural glass fibers (volcanic glass) appear the most similar forms, potentially giving rise to fabrics reminiscent of SFF, but of non-biological origin. A comparison between threads of certainly biological origin (recent filamentous microbes) and non-biological threads (Hofmann and Farmer, in prep.) indicates that biological filaments are less variable in thickness, and show more changes of direction, and a higher degree of bending, than non-biological ones. Also, flexibility indicated by the formation of U-loops and formation of mats is not expected in non-biological filaments. The presence of carbon in filaments and its isotopic composition may yield further hints of biogenicity, but such information may be obliterated due to oxidation or migration of organic matter.

3 Detection of morphofossils, including SFF, on planetary missions

Due to the ambiguity inherent to all morphological signatures of microbial life, such signatures will need confirmation using other characteristics such as isotopic or organic geochemistry. However, the potential of easy recognition renders non-microscopic morphological signatures an interesting target in planetary exploration (Brack et al. 1999; Westall et al. 2000a). Unsuccessful (Beagle 2), successful (Mars Exploration Rovers MER) and planned Mars landers (ESA's ExoMars, NASA's Mars Science Laboratory) all were/are equipped with imaging systems able to visualize biofabrics such as stromatolites and SFF.

Table 1 Resolutions of close-up and microscopic imaging instruments on Mars missions

Lander	Instrument	Resolution (micrometer/pixel)
Beagle 2	Close-up lens	50
Beagle 2	Microscope	4
Mars Exploration Rovers	Microscopic imager	30
Mars Science Laboratory	MAHLI	12.5–75
Phoenix	Robotic arm camera	23–122
Phoenix	MECA	4
ExoMars	Close-up imager (CLUPI)	15
ExoMars	Microscope	~3
For comparison		
Standard petrographic microscope ^a	40× obj.	0.31
Standard petrographic microscope ^a	100× obj.	0.12

^aBased on a 1024 pixel frame analogous to MER/Beagle 2

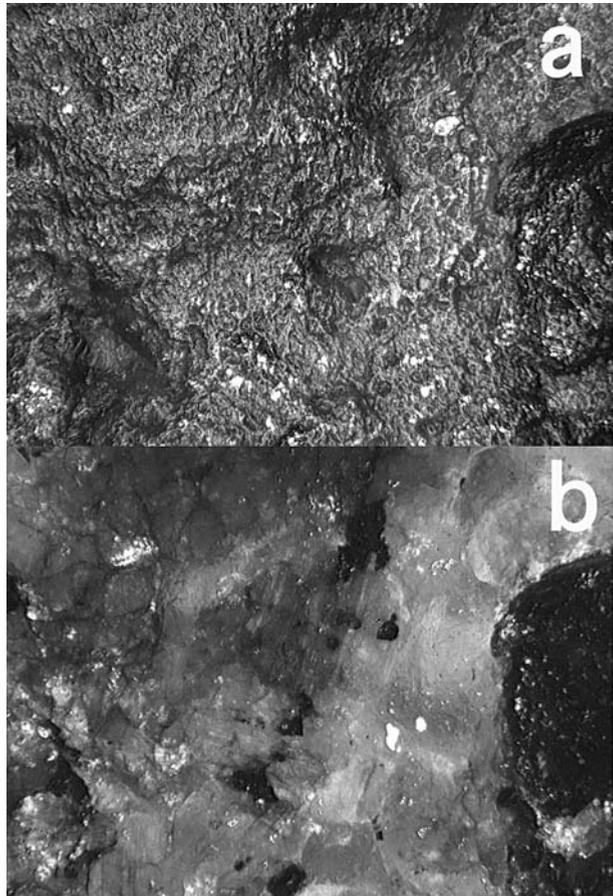
While the panoramic camera systems typically have resolutions in the millimeter range, close-up imagers such as the close-up lens on Beagle 2, the Microscopic imagers on the MER Rovers, the Close-up imager (CLUPI) on ExoMars and the Mars hand lens imager (MAHLI) on MSL are able to visualize biofabrics with sufficient resolution to allow a detailed comparison with terrestrial counterparts. Typical resolutions for imaging systems on Mars missions are given in Table 1. The main purpose of intermediate resolution imaging (in the order of 50 microns/pixel) is the interpretation of rock and soil textures, but the potential of recognizing biofabrics is an important feature as well. Even higher resolutions can be achieved by using microscopes such as on Beagle 2 (Thomas et al. 2004) and foreseen for the Phoenix lander (MECA) and ESA's ExoMars mission (Table 1).

When using high magnifications in optical microscopy in laboratory situations, thin sections for transmitted light, typically 20 micrometers thick, or highly polished samples for reflected light are used. In the next generation of planetary missions such sample preparation will not be available. When unprepared samples have to be used for microscopy, as foreseen in the ExoMars mission, tricks may be needed to overcome some of the disadvantages brought about by the irregular nature of sample surfaces. Field geologist typically wet the surface of rock samples exactly for this purpose. Sample wetting or immersion in a liquid appears impractical on planetary missions. However, a similar effect can be obtained by using doubly polarized light in a manner identical to the observation of internal reflections in reflected light microscopy (Figs. 2, 3, 4). For the imaging of 3D surfaces of rocks, sample preparation is not needed. Test conducted with unprepared rock surfaces and resolutions amenable to microscopes foreseen for upcoming Mars missions demonstrate that SFF filaments can be made visible under such non-ideal conditions (Fig. 4).

Several cases of fossilization of microbial fabrics in open-space infills, in terms of accessibility to close-up and microscopic imaging, are known from Earth and could similarly exist on other planetary bodies, e.g. Mars:

3D textures in open space: Slightly mineralized filaments in cavities (Figs. 1, 2). Textures of this type can be investigated with close-up and microscopic imagers without sample

Fig. 3 Surface of Mars meteorite Sayh al Uhaymir 094, natural surface. **a** Automontage of image stack taken in plane polarized light, mainly light scattered from the surface. **b** Automontage of image stack taken in crossed polarized light, showing mainly light reflected from below the surface of the sample. Field of view is 770 micrometer



preparation, relying 100% on surface scattered light. Due to significant relief, stacking of images and recombination into a single image is needed.

Partially cemented 3D textures: Textures formed in open space but showing strong cementation, e.g. microbial mats of filaments with thick overgrowths of minerals. Surface textures may indicate the presence of microbial textures, even though a detailed imaging based on the surface is not possible. Cross sections are then needed, potentially provided by fractures or drillcores. Surface scattered light only provides preliminary information, while details depend on light from below the mineral surface.

Completely cemented 3D textures: Textures formed in open space, but later on completely cemented by minerals (Fig. 4). The surface of such materials may not indicate any biological textures at all, while these may be perfectly preserved as inclusions in the minerals. Surface scattered light only provides information about the enclosing mineral(s), while light from below the surface must be analyzed for detailed information.

In order to get optical access to both the surface morphology and textural evidence inside rocks, two types of imaging situations are therefore required:

Fig. 4 Surface chert (fine-grained low-T quartz) containing inclusions of goethite-encrusted filaments. SFF from basaltic host rocks, Breiddalur, eastern Iceland, natural surface. **a** Automontage of image stack taken in plane polarized light, mainly light scattered from the surface. **b** Automontage of image stack taken in crossed polarized light, showing mainly light reflected from below the surface of the sample. Filaments are not visible in (a), but clearly discernible in (b). Field of view is 770 micrometer



(1) Imaging of the surface scattered light, comparable to standard visual observations of solid rock surfaces with the naked eye, a hand-lens or binocular lenses (Figs. 2a,b, 3a, 4a).

(2) Imaging of light from below the rock/mineral surface, comparable to macroscopic observations of a wet or polished rock surface (avoiding directly reflected light), or microscopic observation of a thin section, or of a polished surface using doubly crossed polarized light in a standard reflected light microscope. This can be achieved without sample preparation or surface wetting by using doubly crossed polarized light (Figs. 3b, 4b). The incident beam is linearly polarized and passes a second polarizing filter after the sample, allowing only the transit of light whose direction of polarization has been changed due to passing through minerals, this effectively eliminated all surface scattered light. This method of observation reduces the intensity of the observed light by a factor of $\sim 3\text{--}20$ in a standard petrographic microscope, leading to correspondingly increased exposure times.

The importance of colour: Mineral constituents of Martian rocks display strongly different colours: Iron oxides and hydroxides are brown to red-brown, bluish in case of wind-polished hematite surfaces, pyroxenes and olivines are greenish brown, feldspars and many salt minerals are colourless. While in an image of a Mars rock (Fig. 3b) the different minerals are hard to identify, in a colour image the difference between feldspars and mafic minerals

is strongly accentuated. Also, color enhances the contrast between iron-stained filaments in Fig. 4b and the grey matrix.

Apart of biosignatures characteristic of surface-bound life (e.g. stromatolites, wrinkle structures) subsurface biosignatures such as SFF have a good potential to be discovered, if present at landing sites, with the close-up and microscopic imagers foreseen on upcoming Mars missions. Zones containing significant amounts of aqueous minerals, as recognizable from orbit (Bibring et al. 2006) would be preferred areas for prospection for SFF. Colour information is important for the understanding of the areal distribution of minerals in close-up or microscopic images.

4 Conclusions

Apart from life in sedimentary surface environments, dominantly relying on photosynthesis, a subsurface biosphere exists on Earth and possibly also exist(ed) on Mars and other planetary bodies. Subsurface filamentous fabrics (SFF), common in low-T subsurface palaeoenvironments from the sub-recent to the Archean, are interpreted as the fossil record of this subsurface biosphere, being a type of fabric formed by the mineralization of filament-like structures of microbial origin (filaments or mucoid pseudofilament). SFF, as well as biofabrics from sedimentary environments (e.g. stromatolites) are amenable to imaging at intermediate resolutions (~50 micron/pixel). Details of microbial textures in SFF, stromatolites or other biofabrics may be visualized using microscopic imagers, even though the resolution of instruments foreseen for upcoming missions, and the lack of sample preparation, will not allow the detection of single fossilized cells. Microscopic imaging may be greatly enhanced by automatic combination of image stacks (partially focused) to a single in-focus image, and the use of polarizing filters to enhance the proportion of light reflected from below the surface of a sample.

References

- C.M. Aitken, D.M. Jones, S.R. Larter, *Nature* **431**, 291–294 (2004)
- P.S. Amy, D.L. Haldeman, *The Microbiology of the Terrestrial Deep Subsurface* (Lewis, Boca Raton, 1997), 356 pp
- J.M. Baele, *Ann. Soc. Géol. Nord* **6**(2), 127–133 (1998)
- J.-P. Bibring, Y. Langevin, J.F. Mustard, F. Poulet, R. Arvidson, A. Gendrin, B. Gondet, N. Mangold, P. Pinet, F. Forget, T.O. Team, *Science* **312**, 400–404 (2006)
- P.J. Boston, M.N. Spilde, D.E. Northup, L.A. Melim, Lunar planetary Science Conference XXXII. Paper 2015, 2001a
- P.J. Boston, M.N. Spilde, D.E. Northup, L.A. Melim, D.S. Soroka, L.G. Kleina, K.H. Lavoie, L.D. Hose, L.M. Mallory, C.N. Dahm, L.J. Crossey, R.T. Schelble, *Astrobiology* **1**(1), 25–55 (2001b)
- J.S. Bowerbank, *Ann. Mag. Nat. Hist.* **10**(1842), 9–18, 84–91 (1842)
- A. Brack, B. Fitton, F. Raulin, ESA SP-1231, 1999, p. 188
- D.M. Burr, J.A. Grier, A.S. Mcewen, L.P. Keszthelyi, *Icarus* **159**, 53–73 (2002)
- S.M. Clifford, T.J. Parker, *Icarus* **154**, 40–79 (2001)
- D.R. Cullimore, L. Johnston, *Can. Chem. News Nov/Dec*, 14–15 (2000)
- L.J.M. Daubenton, *Mémoires de l'Académie Royale des Sciences*, 1782, pp. 667–673
- M. Feldmann, J. Neher, W. Jung, F. Graf, *Ecologiae Geologicae Helveticae* **90**, 541–556 (1997)
- C. Feucht, B. Hüsser, B.A. Hofmann, 5th European workshop on Astrobiology, Budapest, Oct. 2005. *Int. J. Astrobiol.* **5**(86) (2006)
- D. Fortin, F.G. Ferris, S.D. Scott, *Am. Mineral.* **83**, 1399–1408 (1998)
- H. Furnes, K. Muehlenbachs, O. Tumyr, T. Torsvik, I.H. Thorseth, *Terra Nova* **11**(5), 228–233 (1999)
- H. Furnes, H. Staudigel, *Earth Planet. Sci. Lett.* **166**, 97–103 (1999)

- J.M. Garcia-Ruiz, A. Carnerup, A.G. Christy, N.J. Welham, S.T. Hyde, *Astrobiology* **2**(3), 335–351 (2002)
- J.M. Garcia-Ruiz, S.T. Hyde, A.M. Carnerup, A.G. Christy, M.J. Van Kranendonk, N.J. Welham, *Science* **302**, 1194–1197 (2003)
- T. Gold, *Proc. Natl. Acad. Sci. USA* **89**, 6045–6049 (1992)
- K.B. Hallberg, K. Coupland, S. Kimura, D.B. Johnson, *Appl. Environ. Microbiol.* **72**(3), 2022–2030 (2006)
- B. Hofmann, *Nagra Technical Report 88-30*, Baden, Switzerland, 195 pp., 1989
- B.A. Hofmann, J.D. Farmer, *Planet. Space Sci.* **48**, 1077–1086 (2000)
- B.A. Hofmann, Y. Krüger, A.E. Fallick, M. Eggimann, M.J. Van Kranendonk, 6th European Workshop on Astrobiology, Lyon, 16–18 October 2006. *Int. J. Astrobiol.* 2006 (in press).
- L.D. Hose, A.N. Palmer, M.V. Palmer, D.E. Northup, P.J. Boston, H.R. Duchene, *Chem. Geol.* **169**, 399–423 (2000)
- B. Jones, K.O. Konhauer, R.W. Renaut, R.S. Wheeler, *J. Geol. Soc. Lond.* **161**, 983–993 (2004)
- S.K. Juniper, J. Sarrazin, in *Seafloor Hydrothermal Systems*, ed. by S.E. Humphris, R.A. Zierenberg, L.S. Mullineaux, R.E. Thomson (American Geophysical Union, Washington, 1995), pp. 178–193
- K. Kashevi, D.R. Lovley, *Science* **301**, 934 (2003)
- M. Kretzschmar, *Facies* **7**, 237–260 (1982)
- J.P. McKinley, T.O. Stevens, F. Westall, *Geomicrobiol. J.* **17**, 43–54 (2000)
- D.P. Moser, T.M. Gihring, F.J. Brockman, J.K. Fredrickson, D.L. Balkwill, M.E. Dollhopf, B.S. Lollar, L.M. Pratt, E. Boice, G. Southam, G. Wanger, B.J. Baker, S.M. Pfiffner, L.-H. Lin, T.C. Onstott, *App. Environ. Microbiol.* **71**(12), 8773–8783 (2005)
- R.J. Parkes, G. Webster, B.A. Cragg, A.J. Weightman, C.J. Newberry, T.G. Ferdelman, J. Kallmeyer, B.B. Jørgensen, I.W. Aiello, J. Fry, *Nature* **436**, 390–394 (2005)
- B. Rasmussen, *Nature* **405**, 676–679 (2000)
- G. Razumovsky, *Bull. Géol. Soc. Fr.* **6**, 165–168 (1835)
- J. Reitner, in *Geobiologie. 74. Jahrestagung der Paläontologischen Gesellschaft, Göttingen, 02. bis 08. Oktober 2004. Kurzfassungen der Vorträge und Poster*, ed. by J. Reitner, M. Reich, G. Schmidt (Universitätsdrucke Göttingen, Göttingen, 2004)
- G. Schumann, W. Manz, J. Reitner, M. Lustrino, *Geomicrobiol. J.* **21**, 241–246 (2004)
- T.O. Stevens, in *The Microbiology of the Terrestrial Deep Subsurface*, ed. by A. Penny, D. Haldeman (Lewis, Boca Raton, New York, 1997), pp. 205–223
- T.O. Stevens, J.P. McKinley, *Science* **270**, 450–454 (1995)
- N. Thomas, B.S. Lüthi, S.F. Hviid, H.U. Keller, W.J. Markiewicz, T. Blümchen, A.T. Basilevsky, P.H. Smith, R. Tanner, C. Oquist, R. Reynolds, J.-L. Josset, S. Beauvivre, B. Hofmann, P. Rüffer, C.T. Pillinger, *Planet. Space Sci.* **52**, 853–866 (2004)
- N.H. Trewin, A.H. Knoll, *Palaios* **14**, 288–294 (1999)
- J.N. Walsh, *Precamb. Res.* **54**, 271–293 (1992)
- M.M. Walsh, *Astrobiology* **4**(4), 429–437 (2004)
- F. Westall, A. Brack, B. Hofmann, G. Horneck, G. Kurat, J. Maxwell, G.G. Ori, C. Pillinger, F. Raulin, N. Thomas, B. Fitton, P. Clancy, D. Prieur, D. Vassaux, *Planet. Space Sci.* **48**, 181–202 (2000a)
- F. Westall, C.E.J. De Ronde, G. Southam, N. Grassineau, M. Colas, C. Cockell, H. Lammer, *Philos. Trans. Roy. Soc. B* **361**, 1857–1875 (2006a)
- F. Westall, S.T. De Vries, W. Nijman, V. Rouchon, B. Orberger, V.K. Pearson, J. Watson, A. Verchovsky, I. Wright, J.-N. Rouzaud, D. Marchesini, A. Severine, *Geol. Soc. Am. Spec. Pap.* **405**, 105–131 (2006b)
- F. Westall, A. Steele, J. Toporski, M. Walsh, C. Allen, S. Guidry, D. McKay, E. Gibson, H. Chafetz, *J. Geophys. Res.* **105**(E10), 24511–24527 (2000b)