



Filamentous fabrics in low-temperature mineral assemblages: are they fossil biomarkers? Implications for the search for a subsurface fossil record on the early Earth and Mars

B.A. Hofmann^{a,*}, J.D. Farmer^{b,1}

^aNatural History Museum, Bernstrasse 15, CH-3005 Bern, Switzerland

^bNASA Ames Research Center, MS-239-4, Moffett Field, CA 94035-1000, USA

Received 6 September 1999; accepted 15 November 1999

Abstract

The subsurface has been recognized as a possible habitat for microbial life on Mars. An analogous fossil record of subsurface life is nearly missing on Earth. Here we present evidence of the widespread occurrence of such a record: tubular filamentous structures with typical core diameters of 1–2 μm were found as inclusions in minerals deposited from low- T ($<100^\circ\text{C}$) aqueous fluids in subsurface environments at >140 localities worldwide. Filaments are frequently organized in composite structures with architectures similar to microbial mats. Filaments thickly encrusted by minerals exhibit gravity-oriented structures of macroscopic dimensions that are similar to stalactites. Environments of formation are sites of low- T water circulation in macroporous rocks such as volcanics, oxidized ores, limestone solution cavities and cavernous microfossils. The age of occurrence ranges from Precambrian to Subrecent. We interpret the filamentous structures as permineralized and encrusted microbial filaments based on the following arguments: tubular construction of filaments with constant core diameters typical of microbes (1.5–1.1 μm), coalescence of filaments to form mat-like structures, gravity draping of micron-thin filaments indicating an originally flexible consistency, and restriction to low- T mineral assemblages. These filamentous structures formed in subsurface environments are similar in size, morphology and construction to fossilized microbes observed in modern terrestrial and marine thermal springs. This newly recognized fossil record of subterranean microbial life opens up new perspectives in the study of the paleobiology of the terrestrial subsurface and in the exploration for fossil life on Mars. Potential host rocks on Mars include major nonsedimentary units such as volcanics and impactites.

© 2000 Elsevier Science Ltd. All rights reserved.

1. Introduction

Although a deep subterranean biosphere dominated by chemotrophic microbial life has been known for some time, it has only recently gained prominence (Delaney et al., 1998; Ghiorse, 1997; Gold, 1992, 1999; Parkes et al., 1994; Stevens, 1997; Walter, 1996a). The recognition of biological signatures in ancient subsurface hydrothermal environments has special relevance for studies of early biosphere evolution and in the exploration for past or present life on Mars (McKay et al., 1996; Walter, 1996a;

Farmer and Des Marais, 1999). Previous reports of filamentous fossil microbiotas or biofabrics from subsurface environments are restricted to a few single occurrences of well-preserved filaments at Warstein, Germany (Kretzschmar, 1982; Dexter-Dyer et al., 1984; Dahanayake and Krumbein, 1986), NE Scotland (Trewin and Knoll, 1999) and Belgium (Baele, 1999). Several occurrences of putative subsurface microbial fossils include salt dome cap rocks in the Texas Gull' (Sassen et al., 1988) and mineral veins in Germany (Hofmann, 1989; Walter and Reissmann, 1994) and Sweden (Pedersen et al., 1997). Evidence for former subsurface microbial activity has also been derived from corrosion patterns in marine basalts (Fisk et al., 1998; Furnes and Staudigel, 1999; Torsvik et al., 1998).

Our initial report of filamentous structures in subsurface minerals (Hofmann and Farmer, 1997) was followed

* Corresponding author. Tel.: +41-31-350-7240; fax: +41-31-350-7499.

E-mail address: beda.hofmann@unibe.unibe.ch (B.A. Hofmann).

¹ Present address: Department of Geology, Arizona State University, Box 871404, Tempe, AZ 85287, USA.

by a systematic search of museum collections and in the field. Two main types of samples emerged from this study: Firstly, minerals (dominantly chalcedony and zeolites) from low-temperature hydrothermally altered volcanics, dominantly chalcedony and zeolites, and, secondly, samples from oxidized ore deposits. In both cases, mineralized filaments formed a substrate for the nucleation and growth of paragenetically younger mineral phases. Small groups of samples are from solution cavities in limestones, serpentinized ultrabasic rocks and impactites. In total we have identified >140 occurrences in 65 geologically unrelated areas. Although tubular-shaped filamentous inclusions in chalcedony, of the type reviewed here, were previously described as fossil moss (Daubenton, 1782) and sponges (Bowerbank, 1842), inorganic interpretations have generally prevailed (Liesegang, 1915; Brown, 1957; Landmesser, 1984). However, since this early work, significant advances have been made in our understanding of the processes of microbial taphonomy and fossilization through studies of ancient microbiotas (Golubic and Hofmann, 1976; Knoll, 1984) and their modern analogs (Cady and Farmer, 1996; Farmer and Des Marais, 1994; Ferris et al., 1988; Schultze-Lam et al., 1996). This work also provides a basis for re-evaluating the origin of filamentous and “stalactitic” minerals previously considered as inorganic precipitates.

The fossilization of soft-bodied organisms occurs either through the alteration of original organic matter, or by its replacement with authigenic minerals (Allison and Briggs, 1991). Studies of microbial fossilization in rapidly mineralizing travertine and siliceous thermal spring systems indicate that this process more often involves the simple coating of external organic surfaces, with the rapid degradation of organic materials leaving behind external molds (Cady and Farmer, 1996). Often exterior organic surfaces, and the molds they produce, accumulate thin coatings of metalliferous precipitates which enhances their preservation during early diagenetic infilling and recrystallization. This process produces filamentous microfossils that have a tubular construction with an internal diameter similar to the size of the original bacterial filament (Fig. 1). Near deep sea vents, filamentous bacteria can become encrusted with silica, and the organic matter replaced by sulfides or Fe-hydroxides (Zierenberg and Schiffman, 1990; Duhig et al., 1992; Iizasa et al., 1998; Juniper and Fouquet, 1988; Little et al., 1999). In modern microbial mat organisms the diameter of filament molds produced by this process typically falls within the size range of 1–10 μm . Variations in the inner core diameters of filament molds reflect taxonomic or taphonomic differences. Continued accretion and overgrowth and the merging of adjacent filament coatings can produce composite filament molds with outside diameters exceeding 100 μm .



Fig. 1. Subrecent siliceous sinter from Excelsior Geyser crater, Midway Geyser Basin, Yellowstone National Park, Wyoming, USA. Light microscope view showing encrusted filaments of small heterotrophic organisms that resided within the framework of silicifying cyanobacterial (*Calothrix*) mats. In some examples, submicron molds are visible at the cores of opaline silica overgrowths where encrusted bacterial filaments were later removed by oxidation, leaving behind external molds. Scale: Encrusted filament (with central mold) is $\sim 2 \mu\text{m}$ in diameter.

2. Morphology and structure

Filaments (Figs. 2 and 3) occur in high densities as inclusions in chalcedony, megaquartz, calcite, goethite, zeolites and some rarer minerals and are preserved due to encrustation by goethite, Fe-rich clay minerals or just by variations in grain size. Three filament morphotypes are tentatively recognized: (A) irregularly oriented filaments, forming “moss agate” where enclosed in chalcedony; (B) filaments showing gravity-induced vertical orientation, later overgrowths by minerals producing structures resembling stalactites; (C) strongly interconnected filaments producing mat- or stromatolite-like fabrics of planar or rope-like geometry. In all cases examined, filamentous microstructures pre-date the formation of their host minerals as is evidenced by the occurrence of filaments only thinly covered by minerals in open voids, and the orientation of mineral overgrowths showing radial growth of fibrous minerals nucleating on filaments. Also, the persistence of filaments across several nearby mineral grains, the restriction of filament inclusions to certain growth zones of host minerals and the presence of identical structures in different minerals like chalcedony and calcite from a single occurrence are evidence refuting the idea of a secondary emplacement (Feldmann et al., 1997).

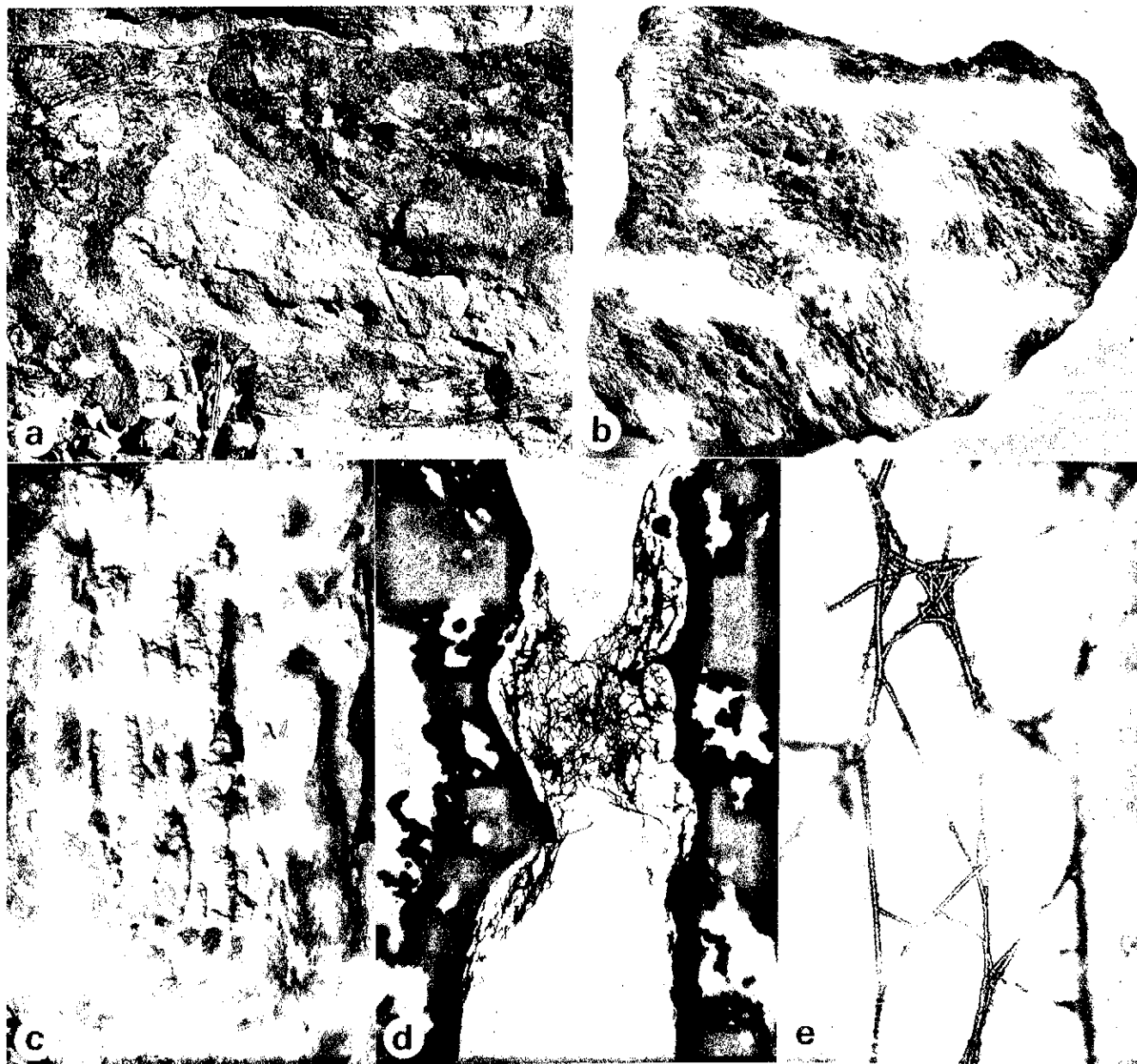


Fig. 2. Macroscopic and microscopic appearance of subsurface filamentous fabrics occurring in goethite chalcedony fracture infills in Tertiary volcanic rocks, Sleeping Beauty Ridge, Cady Mts., California: (a) irregular goethite chalcedony fracture with macroscopic filaments bundles. scale = 10 cm; (b) hand-specimen (13 × 15 cm) showing streamer-like surface texture resulting from parallel orientation of mineralized filaments; (c) bundles of filaments encrusted with goethite and quartz showing vertical orientation due to gravity draping (height 5 cm). Though similar to stalactites, the filamentous interior shows that the stalks result from the encrustation of filament strands; (d) thin section of fracture infill showing lightly mineralized filaments between heavily encrusted filament strands, embedded in fibrous quartz (chalcedony). height 2.0 mm; (e) thin section photomicrograph showing detail of mineralized filaments in chalcedony, height 190 μm .

The occurrence of vertically oriented structures resulting from filament encrustation (morphotype (B)) is widespread (Table 1). Such structures are commonly interpreted as stalactitic formations (e.g. Campbell and Barton, 1996). A non-stalactitic origin is indicated by the filamentous center close to 1 μm in diameter, deviations from vertical alignment, and, in some cases, known subaqueous formation. Vertically arranged “pseudostalactitic” minerals are the most easily rec-

ognized macroscopic expressions of mineralized filaments of subsurface origin (Fig. 2c).

In the subsurface examples documented here, filaments have a tubular construction with inner core diameters of 0.2–8.5 μm (average $1.5 \pm 1.1 \mu\text{m}$, $n = 486$). This overlaps with the range of diameters observed in the tubular-shaped molds formed by filamentous bacteria in both modern subaerial thermal springs and deep-sea vents. In our

Table 1
Selected occurrences of filamentous fabrics of subsurface origin and their main characteristics

Locality	Geological environment	Age	Filament mineralogy	Late stage minerals	Morphotype ^a	Filament diameter (μm)
Höwenegg, Hegau, Germany	V	Tertiary	pyrite, opal	zeo	C	1.6 ± 0.3 (n = 21)
lecland	V	Tertiary	goe,hem,cel	qtz,cha, zeo	A,B,C	1.6 ± 0.9 (n = 70)
Faeroer Islands	V	Tertiary	cha	zeo	A,B	1.2 ± 0.4 (n = 91)
Cady Mts., California, USA	V	Tertiary	goe	cha,qtz,cc	A,B,C	0.6 ± 0.2 (n = 29)
Priday Ranch, Oregon, USA	V	Tertiary	clay minerals	cht	A,B	1.9 ± 0.7 (n = 29)
Needles, Texas, USA	V	Tertiary	goe	cha	A	1.3 ± 0.3 (n = 7)
Sierra de Gallego, Chihuahua, Mexico	V	Tertiary	clay minerals	cha	A,B	3.3 ± 0.5 (n = 91)
Deccan Trapps, India	V	Cretaceous-Tertiary	cel,goe,hem,zeo	cha,qtz	A,B	1.1 ± 0.4 (n = 20)
Arz Rogd, Mongolia	V	U. Jurassic-L. Cretaceous	clay minerals	cha	A,C	1.1 ± 0.4 (n = 181)
Paraná basin, Brazil	V	U. Jurassic-L. Cretaceous	qtz	qtz	A,B	3.8 ± 1.9 (n = 251)
Campsie, Stirlingshire, Scotland	V	Devonian	hem	cha	A,B	1.4 ± 0.3 (n = 17)
Lake Superior area, USA	V	Precambrian (Proterozoic)	hem	cha	A,B	1.7 ± 0.5 (n = 11)
Lengenbach, Valais, Switzerland	OX	Quaternary to Recent	goe	void	C	0.3 ± 0.1 (n = 14)
Johanngeorgenstadt, Saxony, Germany	OX	Quaternary to Recent	goe	qtz	A,C	1.3 ± 0.5 (n = 22)
Bescheert Glück Mine, Saxony, Germany	OX	Quaternary to Recent	goe	cha	A	1.2 ± 0.3 (n = 23)
Herdorf near Siegen, Germany	OX	Quaternary to Recent	goe	goe	B	0.0 ± 0.5 (n = 7)
Huelgoat, Brittany, France	OX	Quaternary to Recent	goe	Ph-phosphate	C	3.4 ± 0.9 (n = 14)
Bleiberg, Carinthia, Austria	OX	Quaternary to Recent	goe	goe,cha	B	0.6 ± 0.2 (n = 101)
Matageme, Cerro de Pasco, Peru	OX	Quaternary to Recent	goe	goe	B	2.1 ± 0.7 (n = 13)
Tsumeb, Namibia	OX	Quaternary to Recent	goe	dufite	B	2.2 ± 0.6 (n = 23)
Broken Hill, New South Wales, Australia	OX	Quaternary to Recent	goe	goe	A,B	0.8 ± 0.2 (n = 6)
Hohenlimburg, Germany	SOL	Tertiary	goe	qtz	A,C	0.6 ± 0.3 (n = 27)
Warstein, Germany (Kretzschmar 1982)	SOL	Tertiary	goe	qtz,cc	A,C	1.1 ± 0.3 (n = 22)
Ries Impact Crater, southern Germany	I	Tertiary	? smectite	void	A	0.5 ± 0.3 (n = 41)

^a Types: V — volcanic host rocks; OX — oxidized orebodies; SOL — solution cavities in limestone; I — impact melt rock.

Mineral abbreviations: cc — calcite; cel — celadonite; cha = chalcedony; goe = goethite; hem = hematite; qtz = quartz; zeo — zeolites.

Filament morphotypes: A: irregular (“moss agate”); B: gravity-induced orientation (pseudostalactites); C: mat/stromatolite fabrics.

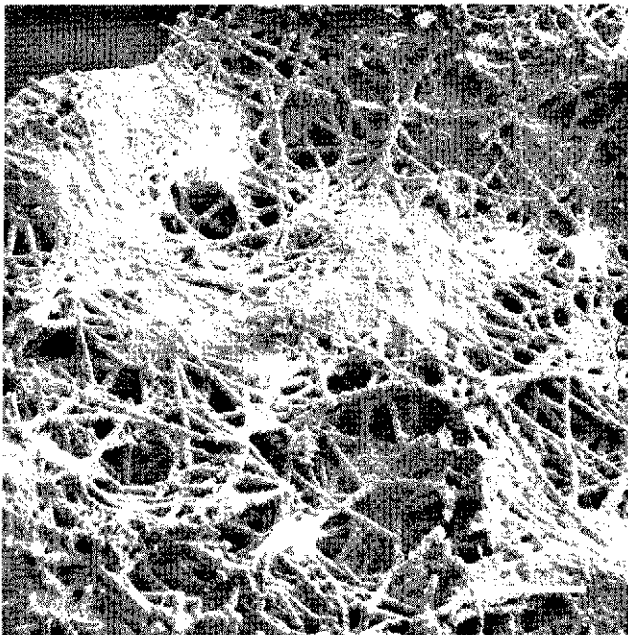


Fig. 3. SEM Micrograph showing goethite-encrusted filaments from oxidized pyrite ore, Lengenbach, Binn Valley, Switzerland. Sample is from contact of orebody with overlying glacial till, about 5 m below surface. Scale bar is 100 μm.

subsurface examples, inner core diameters are fairly constant within any particular occurrence, although there is a

certain size range between occurrences (Table 1). Compared with diameters of needle-shaped crystals with later mineral overgrowths that sometimes produce fabrics resembling mineralized filaments, the frequency distribution of filament diameters is quite narrow (Fig. 4). Filament molds tend to become infilled during later mineral precipitation and the outer diameter of filamentous structures increases with continued accretion, finally reaching macroscopic dimensions.

In modern microbial mats, the processes of growth, reproduction and taxis of filamentous species may lead to the formation of a variety of composite mat structures. In our subsurface examples, filaments often occur in bundles < 1–10 mm thick and up to 150 mm long. This lies within the size range of composite mat structures observed in living microbial mats. At the Cady Mts. (California) and Turnov (Czech Republic) sites, filaments are bundled into mat-like structures of up to 10 mm diameter and 15 cm length, that resemble the “streamer” mats seen in areas of flow in modern thermal springs. Variable orientation of filaments indicates that both gravity and water flow were factors controlling filament orientation. These composite structures are made up of tiny filaments that were apparently only a few μm in diameter and several cm long, indicating the former presence of flexible, nonbrittle materials of high strength such as biopolymers.

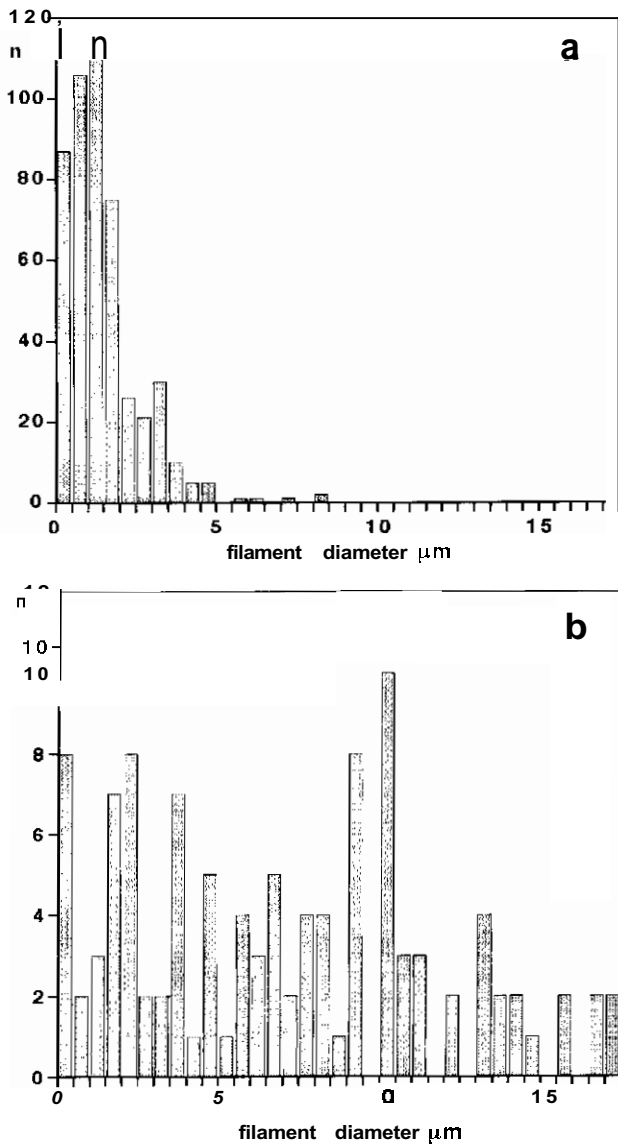


Fig. 4. Histograms showing the frequency distribution of diameters of (A) filamentous microstructures and (B) of associated fibrous minerals of nonbiogenic origin. The filaments from 21 different occurrences show a narrow peak close to 1 μm , while nonbiogenic minerals have no preferred diameter.

Filamentous structures from most investigated sites are branched (Figs. 2 and 3). In contrast to eucaryotes like the eumycota (fungi) and myxomyces (slime molds), individual bacterial filaments do not truly branch during growth. However, during the early stages of fossilization of bacterial filaments in modern mat systems, branched composite forms are often formed by coalescence of mineral overgrowths on adjacent filaments. Differentiating between true branching and coincidental joining of filaments is difficult. In some of our samples, filaments are morphologically differentiated, with attached globular structures 5–70 μm in diameter that resemble the sporangia of extant cellular slime molds (Madigan et al., 1997). Similar, complexly branched

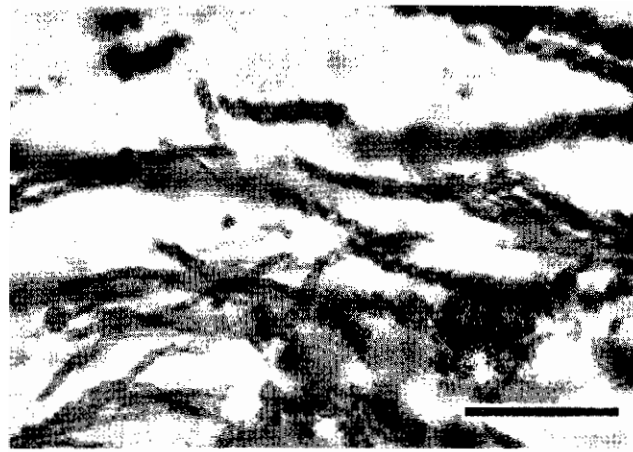


Fig. 5. Twisted threads of goethite closely resembling modern *Gallionella ferruginea* embedded in chalcedony from cavity in Tertiary basalt, Breiddalur, Eastern Iceland. Scale bar = 50 μm .

and differentiated forms interpreted to be fossil fungi or related groups have been reported previously from Warstein, Germany (Kretzschmar, 1982). At several sites in eastern Iceland we identified twisted stalks closely resembling the modern iron oxidizing bacterium *Gallionella ferruginea* (Fig. 5).

3. Environments of subsurface filament formation

Filamentous microstructures of probable microbial origin occur in numerous low-temperature subsurface environments that are typically characterized by fast mineral precipitation in large voids. The major types of geological environments are outlined briefly below.

3.1. Volcanic host rocks

Amygdules (vesicles) and lithophysae as well as open fractures and flow-top breccias are the dominant forms of macroporosity which is commonly filled in by secondary minerals such as celadonite, Fe-hydroxides, zeolites, and various varieties of silica minerals including agate, chalcedony, megaquartz and opal. Filaments described here were often formed during an early stage of void infill. Energy sources to support microbial life in such environments include various types of redox couples, and possibly gases produced by water–rock interaction (Stevens and McKinley, 1995). The conditions during filament formation can only be deduced indirectly from the replacing minerals. Fluid inclusion homogenization temperatures measured in quartz cementing filaments range from <70 to >200°C, indicating that late-stage mineral precipitation may have occurred at temperatures too high for life. The depth of formation can only be roughly estimated for most occurrences but is in the order of 10s to several 100 m. In the Cady Mts. (California) occurrence, 10–50 cm-thick

chalcedony veins containing goethite-encrusted filaments crop out over a distance of 2 km, demonstrating the presence of significant volumes of filament-rich rocks. Fig. 2 shows macroscopic mat-like fabrics, composed of filamentous forms, and microscopic filament architectures from this occurrence.

3.2. Oxidation zone of ore deposits

Oxidizable ores such as sulfides of Fe, Cu, Pb, Zn and Fe-rich carbonates are transformed into highly porous Fe-hydroxides minerals under near-surface conditions. Oxidation of sulfide- and ferrous iron can serve as a source of energy for a number of autotrophic microbes (Nordstrom and Southam, 1997; Schrenk et al., 1998). Filamentous structures, often showing gravity-induced parallel orientation or mat-like coalescence of filaments (Fig. 3) are very common in mineral samples from such environments and are commonly labeled as “stalactites” in collections. Formation temperatures were close to ambient, the depth of formation less than 10 to several 100 m (600–1000 m in the case of Tsumeb, Namibia).

3.3. Solution cavities in carbonate rocks

The first Fe-encrusted filaments of probable microbial origin were identified in low-temperature quartz deposited within solution cavities in massive Devonian limestone at Warstein, Germany (Kretzschmar, 1982). Similar occurrences are also known for several other sites within 50 km of Warstein. The age of these occurrences is poorly constrained, but is probably Tertiary. Filamentous microorganisms are enclosed in megaquartz and calcite. Quartz crystals are of the “Suttrop-Type” (Behr et al., 1979; Behr and Horn, 1984) and record a complex fluid history, with filaments being present only in the youngest growth zones. Fluid inclusion homogenization temperatures for the entombing quartz indicate crystallization at 100–160°C after filament formation (Kretzschmar, 1982; this study).

3.4. Open space in macrofossils

Pyritized ammonites from Jurassic black shales in England and Germany (Hudson, 1982) and from the Jurassic of Switzerland and the Cretaceous of southern France (own observations) contain geopetal features interpreted as stalactites (Hudson, 1982). Based on the similarity with pseudostalactitic features from volcanic and oxidation zone environments an interpretation as pyrite-encrusted, gravity-oriented microbial filaments appears more likely.

3.5. Other environments

A small number of samples showing structures resembling filamentous biofabrics are derived from hydro-

thermal veins in crystalline rocks (Campbell and Barton, 1996; Hofmann, 1989; Walter and Reissmann, 1994), Mississippi-Valley-type Pb–Zn-deposits (Peck, 1979), chalcedony veins in serpentinites (NMBE collection) and impact melt rocks (Ries, Germany, NMBE collection). Subaqueously formed carbonate speleothems (“pool fingers”) that appear to have formed by calcification of microbial filaments (Adolphe et al., 1991; Davis et al., 1990) are the closest recent analogue to filamentous subsurface biofabrics of pseudostalactitic habit.

4. Mineralogy and geochemistry

The filamentous structures studied here are systematically associated with iron minerals. Fe-rich clays and pyrite dominate in reduced mineral assemblages, while goethite and hematite dominate oxidized assemblages. The commonly observed replacement of goethite by Fe-rich clays indicates that goethite was a very common primary mineral on the filaments, perhaps even where it is now completely altered. The mineralogy of the filaments is relatively monotonous. Three phases of mineralization may be distinguished:

- (A) Initial precipitation forming filaments of approximately 1 μm diameter and composites of filaments. Minerals precipitated at this stage are fine grained and do not show preferential orientation. Fe hydroxides, celadonite and pyrite are the most common phases.
- (B) Deposition of later minerals on filaments, typically increasing the filament diameter to 20–40 μm . Minerals are radially oriented around tubular filaments and include chalcedony, goethite, hematite, clay minerals, zeolites and a wide variety of oxidation zone species.
- (C) Final cementation, leading to stalk-like forms up to several cm in diameter and several tens of cm long. The mineralogy is dominated by quartz varieties and/or calcite (hydrothermal) or a large variety of oxidation stage minerals (oxidation zones). Where stage (C) cementation is not complete, mineral-coated filaments are present in open pore space (Fig. 3).

An important observation is the fact that nearly identical filament geometries are present in samples of variable mineralogy, both in a single deposit and in distant occurrences. This indicates that the occurrence and morphology of mineralized filaments is independent of the host mineralogy, and is unlikely to be the product of specific mineral forming reactions.

The abundance of goethite as an early mineral in filament mineralization is consistent with formation temperatures $<100^\circ\text{C}$ (Diakonov et al., 1994). The

homogenization temperatures of fluid inclusions in quartz postdating filament formation ranges from <70 to 160°C for several occurrences, indicating a rise in temperature after filament formation.

Filaments do not contain microscopically visible remnant organic matter, which is consistent with the oxidation of organic materials shortly after entombment. This style of preservation was also noted in both modern (Cady and Farmer, 1996) and Devonian-aged siliceous sinters from Queensland (Walter et al., 1996b; Walter et al., 1998).

5. Estimating the abundance of subsurface biofabrics

The probability to find subsurface biofabrics in a randomly taken sample from volcanic rocks must be considered low because secondary minerals constitute only a very small fraction of such rocks. However, among samples of secondary mineral precipitates from volcanics and oxidized ores, subsurface biofabrics are quite common. A rough estimate can be made based on the abundance in mineral collections. Among 209 investigated specimens of quartz and zeolites from volcanic rocks and of oxidation zone minerals in the collections of the Bem Natural History Museum, 14% of samples from volcanic environments and 21% of samples from oxidized ore deposits contained filamentous structures of probable microbial origin (only samples collected prior to this study counted). This estimate may be biased for a number of reasons with possible under- and overrepresentation of filament-containing samples. Still, the common occurrence of subsurface biofabrics is demonstrated to such an extent that they can be regarded as an integral constituent of volcanic formations having undergone hydrous low-T alteration, and of oxidized ore deposits.

6. Discussion

6.1. Arguments supporting a biogenic origin of filamentous subsurface fabrics

The subsurface microstructures described here most likely were formed by fossilization of filamentous microorganisms. We infer a biological origin for the filamentous forms found in our subsurface examples, based on comparisons with the style of microbial preservation reported from modern mat systems found in rapidly mineralizing thermal spring environments (Fig. 1). Both fossil filamentous microbes from thermal springs and our subsurface filaments consist of curved, tubular and branching mineral filaments with constant core diameters, are largely devoid of organic matter and closely resemble known biological structures.

Probably the strongest argument for biogenicity is the tubular architecture of the filaments at a constant diameter, and the coalescence of these filaments into mat-like structures, often showing gravity draping. While various filamentous and spiral forms can be produced by growth in gels, we are not aware of any nonbiological process producing tubular filaments of this narrow size range (Figs. 2 and 4). Gravity draping (Fig. 2) is very common and suggests that the filaments initially consisted of flexible, nonrigid material such as an organic polymer. Other features supporting a biological interpretation are the branched morphology (Figs. 2 and 3) and the presence of differentiated structures, such as twisted stalks (Fig. 5) and globules associated with some filaments. Finally, filaments are typically present in mineral assemblages formed at temperatures below -100°C based on the abundance of primary goethite and geological context (Table 1). We find the similarity between these features and those observed in fossilized materials of modern terrestrial (Fig. 1; Cady and Farmer, 1996) and submarine (Pracjus and Halbach, 1996; Zierenberg and Schiffman, 1990) thermal spring environments to be especially compelling.

The lack of organic carbon in our structures is not surprising, considering that they originate on microbial filaments of approximately $1\ \mu\text{m}$ diameter that contained just a few weight percent organic carbon, and the rather oxidizing environment indicated by abundant goethite.

Among possible abiogenic origins of filaments (fibrous crystals, speleothems, fluid inclusion trails, vermiform crystal aggregates), none is compatible with gravity-draped tubular filaments of very restricted size range. Nonbiological explanations such as "biomorphs", noncrystallographic mineral precipitates experimentally formed in silica-rich environments (Garcia-Ruiz, 1981, 1994; Garcia-Ruiz and Amoros, 1998) cannot explain the very restricted size range in our samples, the independence of filament size and fabric architecture from the type of environment, and the gravity draping.

6.2. Involvement of microbes in mineral precipitation

The glycoproteins of bacterial cell walls have been shown to passively bind metal ions, and some metals (e.g. Fe, Mn, Ni, and V) are known to be important components of metalloenzymes and required co-factors for cell growth (Ehrlich, 1986). Thus, these elements are actively concentrated by many heterotrophic microorganisms, which enhances the opportunity for early diagenetic mineralization. The precipitation of Fe- and Mn-oxides may be directly mediated by physiological processes, with fine-grained metal oxides forming either intracellularly, e.g. as in some magnetotactic bacteria (Frankel et al., 1983), or accumulating on cell surfaces (Ferris

et al., 1988) or within exopolymer matrices (Geesy and Jang, 1989). The initial precipitation of Fe-hydroxides as an early phase could be due to active physiological mediation of Fe-precipitation by organisms. However, studies of modern thermal springs suggest that it is more likely that the bulk of the precipitation is driven by inorganic processes such as changes of temperature, pH and redox potential. Organisms, nevertheless, provide surfaces for the initial nucleation of minerals, in turn setting up morphological patterns that persist during subsequent growth and accretion. While this can result in a lack of preserved isotopic or other geochemical signatures for life, it may also lead to the formation of characteristic micro- and mesoscale biofabrics that are indicative of life (Farmer and Des Marais, 1994).

6.3. Types of involved micro-organisms

The types of micro-organisms potentially responsible for the formation of the subsurface filamentous structures discussed here is uncertain. The size range of the filaments and inferred preservational environments are consistent with a bacterial, archeal, or fungal origin. Energy requirements of micro organisms under such conditions could have been met by redox couples such as O_2 - H_2S , O_2 - Fe^{2+} or H_2 - CO_2 . However, the simple filamentous forms described here do not necessarily require biochemical simplicity. In fact, most heterotrophic communities contain many smaller filamentous and coccoidal species that are not easily preserved. Thus, taphonomic biases may mask the full range of metabolic complexity possible within microbial consortia (Jorgensen et al., 1992). Iron oxidizers are indicated as possible key candidates based on morphology (Fig. 5) and the predominance of ferric iron minerals as early precipitates on filaments.

6.4. Application in the search for fossil life on Mars

Based on the currently available information on the geology of Mars it appears very likely that formerly water-saturated macroporous subsurface environments (e.g. vesicular and brecciated volcanic and impact rocks) are very common and may even constitute major fractions of the upper Martian crust. Sulfide-rich rocks and iron carbonates, possible energy sources in presence of an oxidant, may also be present based on evidence from Martian meteorites. Rocks very similar to those hosting widespread terrestrial subsurface microbial fabrics are thus most likely present on Mars. It appears straightforward, therefore, to use terrestrial subsurface microbial fabrics as an analogue for potential remnants of similar Martian life forms. Potential target areas include all features indicative of possible water percolation (fractures, vesicles, secondary minerals). The macroscopic characteristics of filamentous fabrics (e.g. pseudostalactites) would provide means for relatively easy recognition. Unambiguous interpretation of

possible filamentous structures recognized on Mars will depend heavily on determining the modes of origin of terrestrial counterparts.

6.5. Further research on subsurface filaments

Further research will be needed to provide additional evidence for the proposed biogenicity of the subsurface filaments described in this study. Arguments to be tested include the presence of organic carbon in the center of filaments, enrichments of trace elements in filament cores, and fractionation of stable isotopes (e.g. Fe). A more detailed characterization of the environments of formation using petrography, stable isotopes and fluid inclusions is also planned. This will help to identify possible sites of active filament formation. Such sites will be needed to investigate the process of the actively ongoing filament mineralization in a way similar to studies in mineralizing hot spring environments (Farmer and Des Marais, 1994; Cady and Farmer, 1996).

7. Conclusions

Filamentous fabrics of possible microbial origin are common in terrestrial subsurface environments. Even though only a small fraction of subsurface biota may be fossilized in such a way, these micro- to macroscopic scale features are interpreted to be morphological evidence for the widespread occurrence of subsurface life in the geological past. Mineralization of microbes appears to be a common process in low-temperature subsurface environments. Unexplained morphological features such as certain "stalactites" with micron-sized cores (Campbell and Barton, 1996) and non-dendritic moss agates may have been formed by the encrustation and replacement of microbial filaments and associated composite mat features within environments previously considered to be devoid of microbial remains. Our results open perspectives for exploring new aspects of the fossil record of life on Earth and possibly on Mars and other planetary bodies. On Mars, subsurface environments consisting of porous volcanic rocks with water likely existed in the past and may even persist today as deep aquifers confined beneath a capping cryosphere of shallow crustal ground ice (Clifford, 1993). Modern and ancient groundwater environments have been identified as important targets for future exploration and sample return by the U.S. Mars Global Surveyor Program (McCleese, 1996). Our study suggests a potentially productive line of inquiry in the exploration for a Martian fossil record. Volcanic terranes are widespread on Mars and are likely to host a variety of low-temperature hydrothermal deposits and secondary minerals disseminated through volcanic host rocks as fracture (vein) and amygdaloid fills. Such secondary minerals are likely to be present in abundances too low to be detected by orbital remote sensing and may require the use of instrumented rovers for detection.

Acknowledgements

We thank all those who provided samples for the present study, particularly J. Arnoth, M. Helfer, A. Klee, P. and G. Penkert. We thank P. Vollenweider for photographic work and Ph. Hauselmann for fluid inclusion measurements. Work of BAH was partially funded by the Swiss National Science Foundation and Entwicklungsfonds Seltene Metalle (Pully, Switzerland). Work of JDF was funded by grants from NASA's Astrobiology Institute, the NASA Exobiology Program and the Director's Discretionary Fund, NASA Ames Research Center.

References

- Adolphe, J.-P., Choppy, B., Loubiere, J.-F., Paradis, J., Loleilhavou, F., 1991. Biologie et concrétionnement: un exemple, les baguettes de gours. *Karstologia* 18, 49–55.
- Allison, P.A., Briggs, D.E.G., 1991. Taphonomy of soft-bodied animals. In: Donovan, S.K. (Ed.), *The Processes of Fossilization*. Columbia University Press, New York, pp. 120–140.
- Baele, J.-M., 1999. Karst and silification in continental and margino-littoral environment: two examples in the Meso-Cenozoic of Southern Belgium. In: Audra, P. (Ed.), *Karst 99*, Grand Causses, Vercors, France. Université de Provence, pp. 49–54.
- Behr, H., Hess, H., Oehlschlegel, G., Lindenberg, H.G., 1979. Die Quarzmineralisation vom Typ Suttrop am N-Rand des rechtsrheinischen Schiefergebirges. In: Meiburg, P. (Ed.), *Geologie und Mineralogie des Warsteiner Raumes*. Der Aufschluss, Sonderband 29, Heidelberg, pp. 205–231.
- Behr, H.J., Horn, E.-E., 1984. Quarzbildung und Verkieselungsprozesse in den Karbonatkomplexen des Rheinischen Schiefergebirges. In: Walter, H.W. (Ed.), *Postvariszische Gangmineralisationen in Mitteleuropa*. Verlag Chemie, Weinheim, pp. 27–45.
- Bowerbank, J.S., 1842. On the spongy origin of moss agates, other siliceous bodies. *AMNH* 10, 9–18, 84–91.
- Brown, R.W., 1957. Plantlike features in thunder eggs and geodes. *Annual Report of the Board of Regents of the Smithsonian Institution*, pp. 329–339.
- Cady, S.L., Farmer, J.D., 1996. Fossilization processes in siliceous thermal springs: trends in preservation along the thermal gradient. In: Bockand, G.R., Goode, J.A. (Eds.), *Evolution of Hydrothermal Ecosystems on Earth (and Mars?)*. Wiley, Chichester, pp. 150–173.
- Campbell, W.R., Barton, P.B., 1996. Occurrence and significance of stalactites within the epithermal deposits at Creede, Colorado. *Can. Mineral.* 34, 905–930.
- Clifford, S.M., 1993. A model for the hydrologic and climatic behavior of water on Mars. *J. Geophys. Res.* 88, 2456–2474.
- Dahanayake, K., Krumbein, W.E., 1986. Microbial structures in oolitic iron formations. *Miner. Deposita* 21, 85–94.
- Daubenton, L.J.M., 1782. Sur les causes qui produisent trois sortes d'herborisations dans les pierres. *Mem. Acad. Roy.* 667–673.
- Davis, D.G., Palmer, M.V., Palmer, A.N., 1990. Extraordinary Subaqueous speleothems in Lechuguilla Cave, New Mexico. *NSS Bull.* 52, 70–86.
- Delaney, J.R., Kelley, D.S., Lilley, M.D., Butterfield, D.A., Baross, J.A., Wilcock, W.S.D., Embley, R.W., Summit, M., 1998. The quantum event of oceanic crustal accretion: impacts of diking at mid-ocean ridges. *Science* 281, 222–230.
- Dexter-Dyer, B., Kretzschmar, M., Krumbein, W.E., 1984. Possible microbial pathways in the formation of Precambrian ore deposits. *J. Geol. Soc. (London)* 141, 251–262.
- Diakonov, I., Khodakovskiy, I., Schott, J., Sergeeva, E., 1994. Thermodynamic properties of iron oxides and hydroxides. I. Surface and bulk thermodynamic properties of goethite (α-FeOOH) up to 500 K. *Eur. J. Mineral.* 6, 967–983.
- Duhig, N.C., Davidson, G.J., Stolz, J., 1992. Microbial involvement in the formation of Cambrian sea-floor silica-iron oxide deposits, Australia. *Geology* 20, 511–514.
- Ehrlich, H.L., 1986. *Geomicrobiology*. Marcel Dekker, New York.
- Farmer, J.D., Des Marais, D.J., 1994. Biological versus inorganic processes in stromatolite morphogenesis: observations from mineralizing sedimentary systems. In: Stal, L.J., Caumette, P. (Eds.), *Microbial Mats: structure development and environmental significance*. NATO ASI series, G35, Springer, Berlin, pp. 61–68.
- Farmer, J.D., Des Marais, D.J., 1999. Exploring for a record of ancient Martian life. *J. Geophys. Res.* 104 (E-11), 26977–26995.
- Feldmann, M., Neher, J., Jung, W., Graf, F., 1997. Fungal quartz weathering and iron crystallite formation in an Alpine environment, Piz Alv, Switzerland. *Eclogae Geol. Helv.* 90, 541–556.
- Ferris, F.G., Fyfe, W.S., Beveridge, T.J., 1988. Metallic ion binding by *Bacillus subtilis*: implication for the fossilization of microorganisms. *Geology* 16, 149–152.
- Fisk, M.R., Giovannoni, S.J., Thorset, I.H., 1998. Alteration of oceanic volcanic glass: textural evidence of microbial activity. *Science* 281, 978–980.
- Frankel, R.B., Papaefthymiou, G.C., Blakemore, R.P., O'Brien, W., 1983. Fe₃O₄ precipitation in magnetotactic bacteria. *Biochim. Biophys. Acta.* 763, 147–159.
- Fumes, H., Staudigel, H., 1999. Biological mediation in ocean crust alteration: how deep is the deep biosphere?. *EPSL* 166, 97–103.
- Garcia-Ruiz, J.M., 1981. Crystal aggregates with induced morphologies grown by silica gel technique. *Bull. Mineral.* 104, 107–113.
- Garcia-Ruiz, J.M., 1994. Inorganic self-organization in Precambrian cherts. *Origins Life Evol. Biosphere* 24, 451–467.
- Garcia-Ruiz, J.M., Amoros, J.L., 1998. Carbonate precipitation into alkaline silica-rich environments. *Geology* 26, 843–846.
- Geesy, G.G., Jang, L., 1989. Interactions between metal ions and capsular polymers. In: Beveridge, T.J., Doyle, R.J. (Eds.), *Metal Ions and Bacteria*. Wiley, New York, pp. 325–357.
- Ghiorse, W.C., 1997. Subterranean life. *Science* 275, 789–790.
- Gold, T., 1992. The deep, hot biosphere. *Proc. Natl. Acad. Sci. USA* 89, 6045–6049.
- Gold, T., 1999. *The Deep Hot Biosphere*. Copernicus, New York, 235pp.
- Golubic, S., Hofmann, H.J., 1976. Comparison of Holocene and mid-Precambrian Entophyalidacea (Cyanophyta) in stromatolitic algal mats: cell division and degradation. *J. Paleontol.* 50, 1074–1082.
- Hofmann, B., 1989. *Genese, Alteration und rezentes Fliess-System der Uranlagerstätte Krunkelbach (Menzenschwand, Südschwarzwald)*, Nagra Technical Report, Baden, Switzerland.
- Hofmann, B.A., Farmer, J.D., 1997. Microbial fossils from terrestrial subsurface hydrothermal environments: Examples and implications for Mars. In: Clifford, S.M., Treiman, A.H., Newsom, H.E., Farmer, J.D. (Eds.), *Conference on Early Mars: Geologic and Hydrologic Evolution, Physical and Chemical Environments, and the Implications for Life*. Lunar and Planetary Science Institute, Houston, pp. 40–41.
- Hudson, J.D., 1982. Pyrite in ammonite-bearing shales from the Jurassic of England and Germany. *Sedimentology* 29, 639–667.
- Iizasa, K., Kawasaki, K., Maeda, K., Matsumoto, T., Saito, N., Hirai, K., 1998. Hydrothermal sulfide-bearing Fe-Si oxyhydroxide deposits from the Coriolis Troughs, Vanuatu backarc, southwestern Pacific. *Mar. Geol.* 145, 1–21.
- Jorgensen, B.B., Nelson, D.C., Ward, D.M., 1992. Chemotrophy and decomposition in modern microbial mats. In: Schopf, J.W., Klein, C.C. (Eds.), *The Proterozoic Biosphere: A Multidisciplinary Study*. Cambridge University Press, Cambridge, pp. 287–293.
- Juniper, S.K., Fouquet, Y., 1988. Filamentous iron-silica deposits from modern and ancient hydrothermal sites. *Can. Mineral.* 26, 859–869.
- Knoll, A.H., 1984. Exceptional preservation of photosynthetic organisms in silicified carbonates and silicified peats. *Philos. Trans. Roy. Soc. (London)* 311B, 111–122.

- Kretzschmar, M., 1982. Fossile Pilze in Eisen-Stromatolithen von Warstein (Rheinisches Schiefergebirge). *Facies* 7, 237–260.
- Landmesser, M., 1984. Das Problem der Achatgenese. *Pollichia* 72, 5–137.
- Liesegang, R.E., 1915. Die Achate. Theodor Steinkopff, Dresden und Leipzig.
- Little, C.T.S., Herrington, R.J., Haymon, R.M., Danelian, T., 1999. Early Jurassic hydrothermal vent community from the Franciscan Complex, San Rafael Mountains, California. *Geology* 27, 167–170.
- Madigan, M.T., Martinko, J.M., Parker, J., 1997. *Biology of Microorganisms*. Prentice-Hall, London, 986pp.
- McCleese, 1996. The Search for Evidence of Life on Mars. NASA (www.hq.nasa.gov/office/oss/mccleese.htm).
- McKay, D.S., Gibson, E.K., Thomas-Keptra, K.L., Vali, H., Romanek, C.S., Clemett, S.J., Chillier, X.D.F., Maechling, C.R., Zare, R.N., 1996. Search for past life on Mars: possible relic biogenic activity in Martian meteorite ALH84001. *Science* 273, 924–930.
- Nordstrom, D.K., Southam, G., 1997. Geomicrobiology of sulfide mineral oxidation. In: Banfield, J.F., Nealson, K.H. (Eds.), *Geomicrobiology, Reviews in mineralogy* 35. Mineralogical Society of America, Washington, D.C. pp. 361–390.
- Parkes, R.J., Cragg, B.A., Bale, S.J., Getliff, J.M., Goodman, K., Rochelle, P.A., Fry, J.C., Weightman, A.J., Harvey, S.M., 1994. Deep bacterial biosphere in Pacific Ocean sediments. *Nature* 371, 410–413.
- Peck, S.B., 1979. Stalactites and helictites of marcasite, galena, and Sphalerite in Illinois and Wisconsin. *NSS Bull.* 41, 27–30.
- Pedersen, K., Ekendahl, S., Tullborg, E., Fumes, H., Thorset, I., Tummyr, O., 1997. Evidence of ancient life at 207 m depth in a granitic aquifer. *Geology* 10, 827–830.
- Pracejus, B., Halbach, P., 1996. Do marine moulds influence Hg and Si precipitation in the hydrothermal JASDE field (Okinawa Trough). *Chem. Geol.* 130, 87–99.
- Sassen, R., McCabe, C., Kyle, R., Chinn, E.W., 1988. Deposition of magnetic pyrrhotite during alteration of crude oil and reduction of sulfate. *Org. Geochem.* 14, 381–392.
- Schrenk, M.O., Edwards, K.J., Goodman, R.M., Hamers, R.J., Banfield, J.F., 1998. Distribution of *Thiobacillus ferrooxidans* and *Leptospirillum ferrooxidans*: implications for generation of acid mine drainage. *Science* 279, 1519–1522.
- Schultze-Lam, S., Fortin, D., Davis, B.S., Beveridge, T.J., 1996. Mineralisation of bacterial surfaces. *Chem. Geol.* 132, 171–181.
- Stevens, T.O., 1997. Subsurface microbiology and the evolution of the biosphere. In: Penny, A., Haldeman, D. (Eds.), *The Microbiology of the Terrestrial Deep Subsurface*. Lewis Publishers, Boca Raton, NY, pp. 205–223.
- Stevens, T.O., McKinley, J.P., 1995. Lithoautotrophic microbial ecosystems in deep basalt aquifers. *Science* 270, 450–454.
- Torsvik, T., Fumes, H., Muehlenbachs, K., Thorseth, I.H., Tummyr, O., 1998. Evidence for microbial activity at the glass-alteration interface in oceanic basalts. *EPSL* 162, 165–176.
- Trewin, N.H., Knoll, A.H., 1999. Preservation of Devonian chemotrophic filamentous bacteria in calcite veins. *Palaios* 14, 288–294.
- Walter, H., Reissmann, R., 1994. Organische(?) Strukturen in Achatgangen des Osterzgebirges. *Palaont. Z.* 68, 5–16.
- Walter, M.R., 1996a. Ancient hydrothermal ecosystems on earth: a new palaeobiological frontier. In: Bock, G.R., Goode, J.A. (Eds.), *Evolution of Hydrothermal Ecosystems on Earth (and Mars?)*. Wiley, Chichester, pp. 112–127.
- Walter, M.R., Des Marais, D.J., Farmer, J.D., Hinman, N.W., 1996b. Paleobiology of mid-Paleozoic thermal spring deposits in the Drummond Basin, Queensland, Australia. *Palaios* 11, 497–518.
- Walter, M.R., McLoughlin, S., Drinnan, A.N., Fanner, J.D., 1998. Paleontology of Devonian thermal spring deposits, Drummond Basin, Australia. *Alcheringa* 22, 285–314.
- Zierenberg, R.A., Schiffman, P., 1990. Microbial control of silver mineralization at a sea-floor hydrothermal site on the northern Gorda Ridge. *Nature* 348, 155–157.