Fossilization processes in siliceous thermal springs: trends in preservation along thermal gradients

S. L. Cady and J. D. Farmer

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

Abstract. To enhance our ability to extract palaeobiological and palaeoenvironmental information from ancient thermal spring deposits, we have studied the processes responsible for the development and preservation of stromatolites in modern subaerial thermal spring systems in Yellowstone National Park (USA). We investigated specimens collected from silica-depositing thermal springs along the thermal gradient using petrographic techniques and scanning electron microscopy. Although it is known that thermophilic cyanobacteria control the morphogenesis of thermal spring stromatolites below 73°C, we have found that biofilms which contain filamentous thermophiles contribute to the microstructural development of subaerial geyserites that occur along the inner rims of thermal spring pools and geyser effluents. Biofilms intermittently colonize the surfaces of subaerial geyserites and provide a favoured substrate for opaline silica precipitation. We have also found that the preservation of biotically produced microfabrics of thermal spring sinters reflects dynamic balances between rates of population growth, decomposition of organic matter, silica deposition and early diagenesis. Major trends in preservation of thermophilic organisms along the thermal gradient are defined by differences in the mode of fossilization, including replacement, encrustation and permineralization.

1996 Evolution of hydrothermal ecosystems on Earth (and Mars?). Wiley, Chichester (Ciba Foundation Symposium 202) p 150–173

Given the significance of hydrothermal systems in the early evolution of the biosphere (this volume: Barns et al 1996, Stetter 1996, Walter 1996), we look to the fossil record for evidence regarding the palaeobiology and palaeoenvironments of these ecosystems. Subaerial thermal springs are of interest because they contain many genera of thermophilic microorganisms that are likely to have existed early in Earth's history (Ward et al 1989). Recent studies have shown that fossiliferous analogues of modern subaerial siliceous thermal spring sinters (e.g. Drummond Basin, Australia [Walter et al 1996] and Rhynie Chert, Scotland [Trewin 1994, 1996 this volume, Rice et al 1995]) retain many of their primary macro-scale textural characteristics, even after diagenetic overprinting. However, the accurate reconstruction of ancient communities from

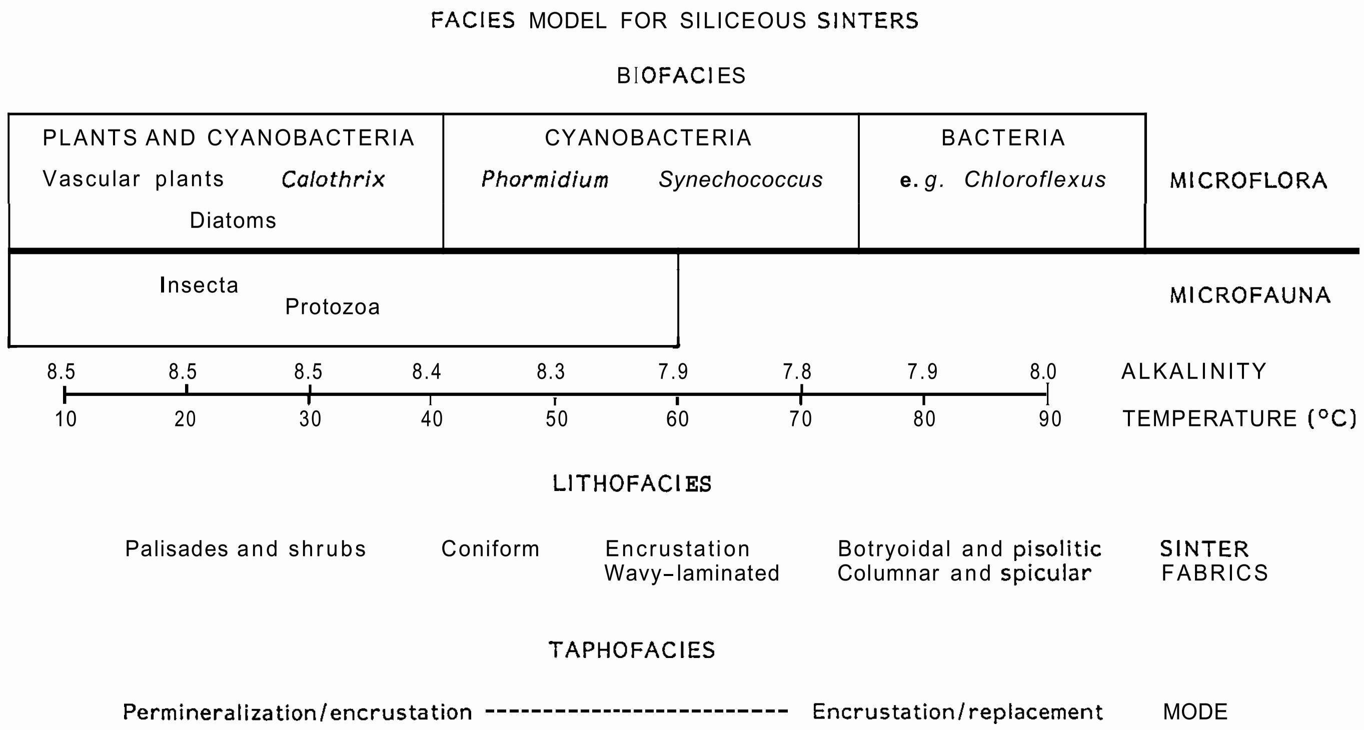
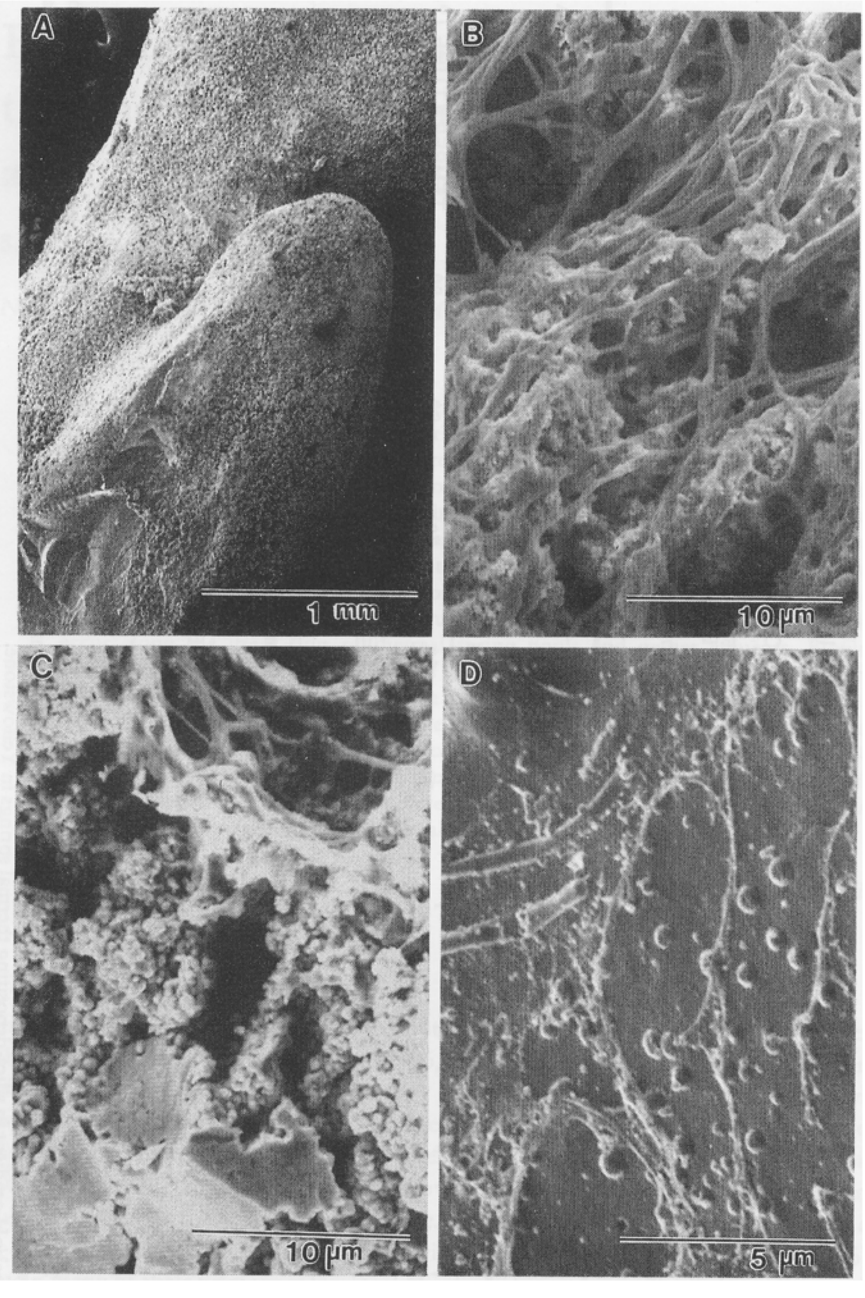


FIG. 1. Biofacies and lithofacies model for siliceous sinters developed by Walter (1976a) based on his studies of silica-depositing thermal springs in Yellowstone National Park **(USA).** Generalized taphofacies model summarizes observations of authors regarding preservational modes along thermal/pH gradient in silica-depositing thermal springs in Yellowstone.


A
1 mm
B
10 µm
C
10 µm
D
5 µm

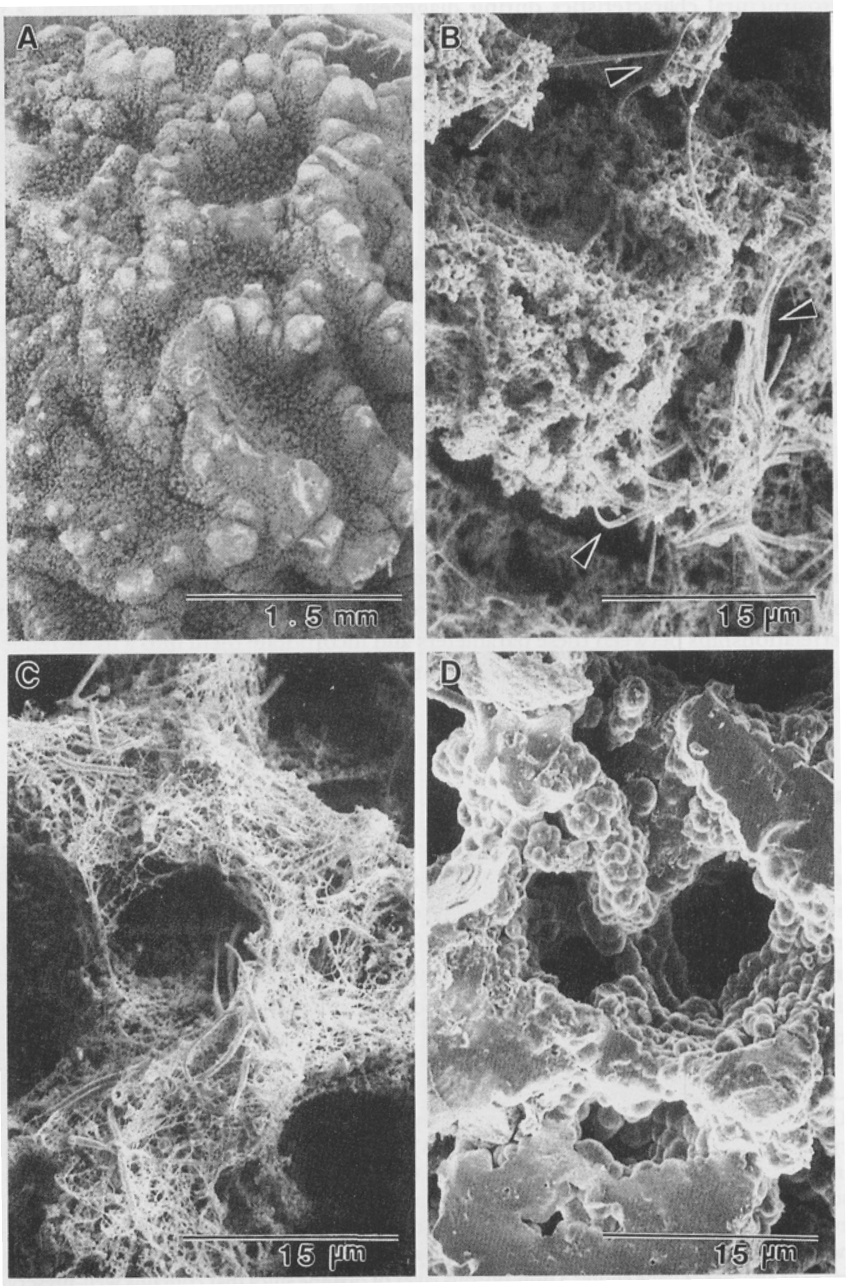
fossilized analogues is complicated by preservational biases and by the loss of fine-scale microstructural characteristics during diagenesis. A complementary approach is to study how modern hydrothermal ecosystems are converted to their fossil counterparts. Here we discuss examples from our studies of modern siliceous sinters in Yellowstone National Park (USA) to demonstrate how biotic and abiotic factors contribute to the morphogenesis and microstructural development of geyserites and thermal spring stromatolites. The apparent rarity of organically preserved microfossils in ancient siliceous sinters emphasizes the importance of understanding how microorganisms contribute to sinter morphogenesis.

Thermal spring stromatolites form in association with distinct microbial communities whose distribution along thermal spring outflows is controlled by steep thermal gradients and the composition of the hydrothermal fluids and dissolved gases (e.g. Brock 1978, Castenholtz 1984, Ward et al 1989). Walter (1976a), on the basis of studies in Yellowstone, developed a general framework for silica-depositing thermal springs that illustrates the association between the principle types of siliceous sinter and the dominant mat-forming bacteria in the overlying microbial mat community (Fig. 1). We include here a preliminary taphofacies model that summarizes major trends in early preservation we have observed in thermal spring geyserites and siliceous sinters from Yellowstone. Differences in modes of preservation are discussed in terms of dynamic balances between rates of population growth, organic matter decomposition, mineral deposition and early diagenesis. A main objective for future studies is to elucidate the interrelationships between these parameters and incorporate them into a more refined taphofacies model for understanding patterns of preservation in ancient sinter deposits.

Methods

To preserve microorganisms for laboratory investigation using low-voltage scanning electron microscopy (LVSEM), we fixed samples of sinter in the field using a 2.5% glutaraldehyde solution prepared from filtered spring water taken from sites where samples were collected. Samples were post-fixed in the laboratory using a 1M osmium tetroxide solution in cacodylate buffer, dehydrated in a graded ethanol series, critical point dried, and coated with a thin layer of amorphous carbon or gold to increase surface conductivity.

FIG. 2. LVSEM micrographs of spicular geyserite from an unnamed spring in Shoshone Geyser Basin, Yellowstone National Park (USA). **(A)** Spicules are characterized by an irregular porous surface texture that results from (B) the favoured deposition of opaline silica on discontinuous biofilms that contain filamentous thermophilic bacteria. (C) Cross-sectional view of fractured spicule showing the surface biofilm, a porous rind of opaline silica and an inner dense matrix of opaline silica that formed as a result of secondary infilling. (D) Fractured surface of another spicule shows a non-porous layer of opaline silica that contains wel-preserved morphological remains of filamentous and coccoidal(?) thermophiles.


A
1.5 mm
B
15 µm
C
15 µm
D
15 µm

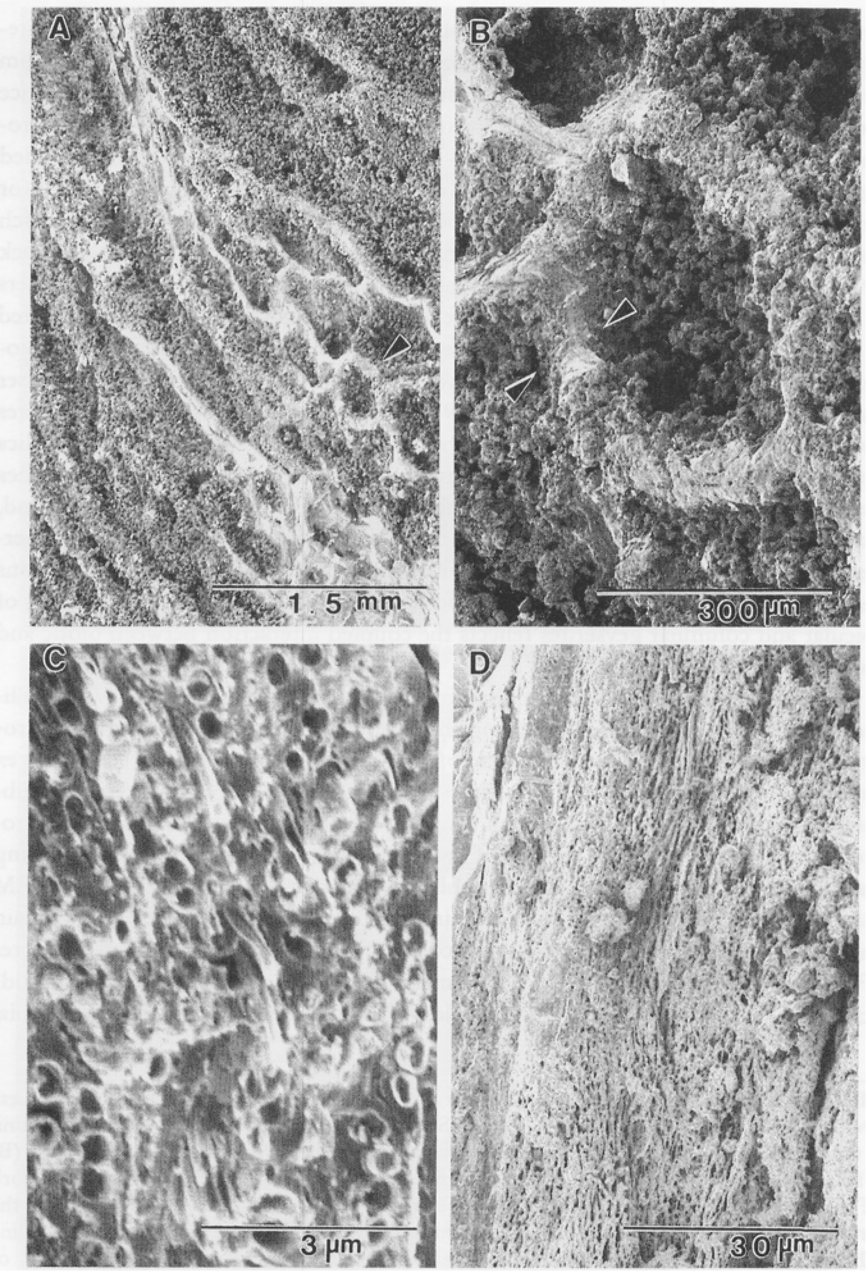
High temperature, near-vent environments

The term geyserite is used (e.g. White et al 1964) to describe siliceous sinter that precipitates within or immediately adjacent to thermal springs and geyser effluents from hydrothermal fluids ejected at or above surface boiling temperatures—waters once thought to be 'sterile' (Allen 1934). Geyserites lack petrographically identifiable microfossils and commonly display micro cross-laminated fabrics characterized by banded laminae microns to submicrons thick (Walter 1976b). The lower temperature limit for geyserite precipitation was defined by Walter (1976b) as the 73 °C isotherm, which coincides with the upper temperature limit for photosynthetic bacteria (e.g. Brock 1978). Although non-photosynthetic bacteria were known to inhabit the spring waters at Yellowstone, Walter (1976b) was unable to prove that microorganisms contributed to geyserite morphogenesis and concluded, therefore, that geyserites formed abiogenically as a result of the rapid cooling and evaporation of thermal spring and geyser waters (e.g. White et al 1956). Walter (1976b) also noted that even at temperatures lower than 73 °C there was no clear evidence that microorganisms played a role in silica precipitation. We are not aware of any studies which have demonstrated that silica precipitation can be induced by the metabolic activity of bacteria. We have found, however, that organisms do contribute to the microstructural development of geyserites by providing a favoured substrate for opaline silica precipitation. Observations made using LVSEM on field-fixed specimens demonstrate that the morphogenesis of spicular and columnar geyserites reflects the coupled interaction between biotic and abiotic sedimentary processes.

Spicular geyserites, less than a millimetre or two in diameter and up to several millimetres in length (Fig. 2A), form along the innermost margins of pool rims. Petrographic examination shows that the microfabric of spicules consists of steeply convex to parabolic laminae that vary in thickness from tens to hundreds of microns. Submicron-thick laminae are visible with scanning electron microscopy, and submicroscopic laminae on the order of tens of nanometres thick have been identified using transmission electron microscopy (unpublished observation of S. L. Cady). LVSEM micrographs reveal that laterally discontinuous, micron-thick biofilms that contain submicron-size filaments intermittently colonize the surfaces of spicular geyserites (Fig. 2B). The divergence of adjacent filaments creates a ridged network that extends across the surfaces of the individual spicules. The highest concentrations of microbial

---

FIG. 3. LVSEM micrographs of columnar geyserite from unnamed spouter located near Octopus Pool, Yellowstone National Park **(USA). (A)** Top portion of knobby-shaped column is characterized by an irregular surface texture and protrusions of fine-grained opaline silica. (B) Viable filaments (arrows) occur along the outermost surface of substratum composed of network of silicified filment moulds. (B, C) Diverse microbial network that forms between the protrusions contains filament moulds that formed by the encrustation of filaments by opaline silica, and the apparent **loss** of microbial remains. (D) Silicified equivalent of (C) near base of knobby-shaped column demonstrates influence of microbial network in the development of abiotic fabric.


A
1.5 mm
B
300 μm
C
3 μm
D
30 μm

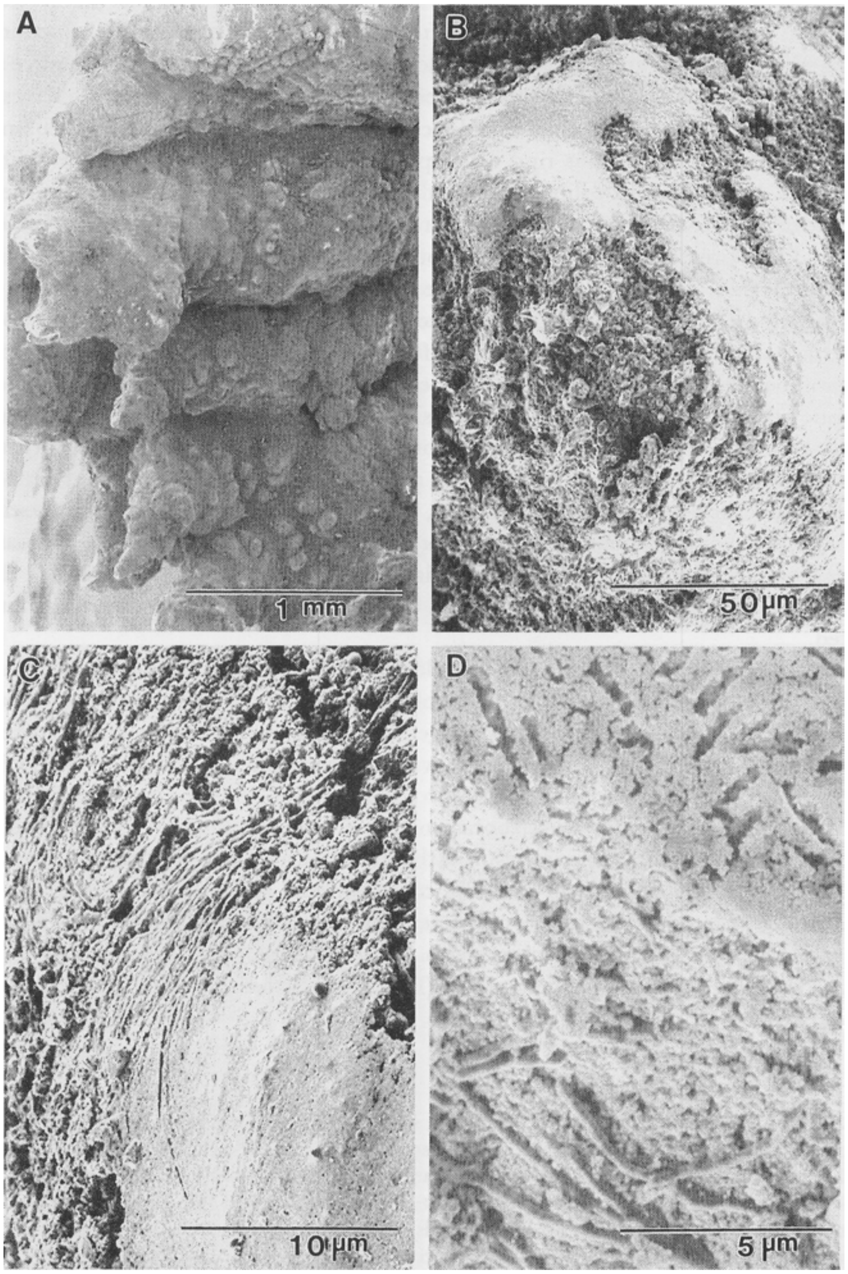
filaments were identified at the tips of spicules that formed along the inside rim of thermal springs at the air–water interface. These observations indicate that the directed accretion and growth of spicules results from the localized precipitation of opaline silica where filaments are concentrated. Additional evidence that the biofilms serve as loci for opaline silica deposition is seen in cross-sectional views of fractured spicules.

The internal microstructure of spicules consists of porous and non-porous submicroscopic laminae. A porous rind develops beneath the biofilms as a result of the favoured deposition of opaline silica on the surfaces of older biofilms and/or their degraded remains (Fig. 2C). The subsequent growth and coalescence of opaline silica grains on the organic substrate imparts a botryoidal texture on exposed surfaces within the porous rind. Porous laminae develop because the rate of opaline silica deposition at the outermost surface of the spicule outpaces the rate of secondary infilling of the porous rind. Dense, non-porous laminae may form as a result of the concomitant infiltration of the porous rind with opaline silica, or, in the absence of a biofilm, as a result of abiotic opaline silica deposition. The occasional presence of well-preserved morphological remains of microorganisms in the non-porous laminae (Fig. 2D) indicates that a considerable amount of secondary infilling may occur within a relatively short period. Such a condition could exist, for instance, if the inner pool rim became temporarily submerged due to fluctuations in the water level of the thermal spring. The mechanisms by which biofilms in the porous laminae and the morphological remains in the non-porous laminae become preserved in opaline silica are currently being investigated.

Microorganisms also influence the development of the microstructure of columnar geyserites. Prior to collection of the knobby-shaped column shown in Fig. 3A, we observed that it was periodically submerged by geyser eruptions (for approximately 3 min) every 15–18 min (92°C effluent water temperature). LVSEM micrographs reveal that between the knobby-shaped protrusions lies a diverse consortium of coccoids and filaments that form an elaborate microbial network (Fig. 3B). Silicification of the microbial network occurs as a result of the encrustation of microorganisms by opaline silica. Viable filaments (see arrows) occur primarily on the outer surfaces of the silicified substrate, which consists of filament moulds devoid of any morphologically identifiable ultrastructural organic remains. A comparison of the surface texture at the top of the periodically submerged column (Fig. 3C) with that at the base of the column,

---

FIG. **4**. LVSEM micrographs of cornices on side wall of columnar geyserite from unnamed spouter located near Octopus Pool, Yellowstone National Park **(USA)**. **(A)** Parallel and anastomosing **cornices** along side wall of columnar geyserite. (B) LVSEM investigation of fractured surface reveals that cornices consist of non-porous and **(C)** porous laminae that contain a high concentration of filament moulds with silicified extracellular and/or intracellular organic remains. (D) Laminae with high concentration of filament moulds also occur in the regions between the cornices. LVSEM micrographs shown in Figs **4C** and **4D** are rotated approximately 30° clockwise from images shown in Figs **4A** and 4B.


A
1 mm
B
50μm
C
10μm
D
5 μm

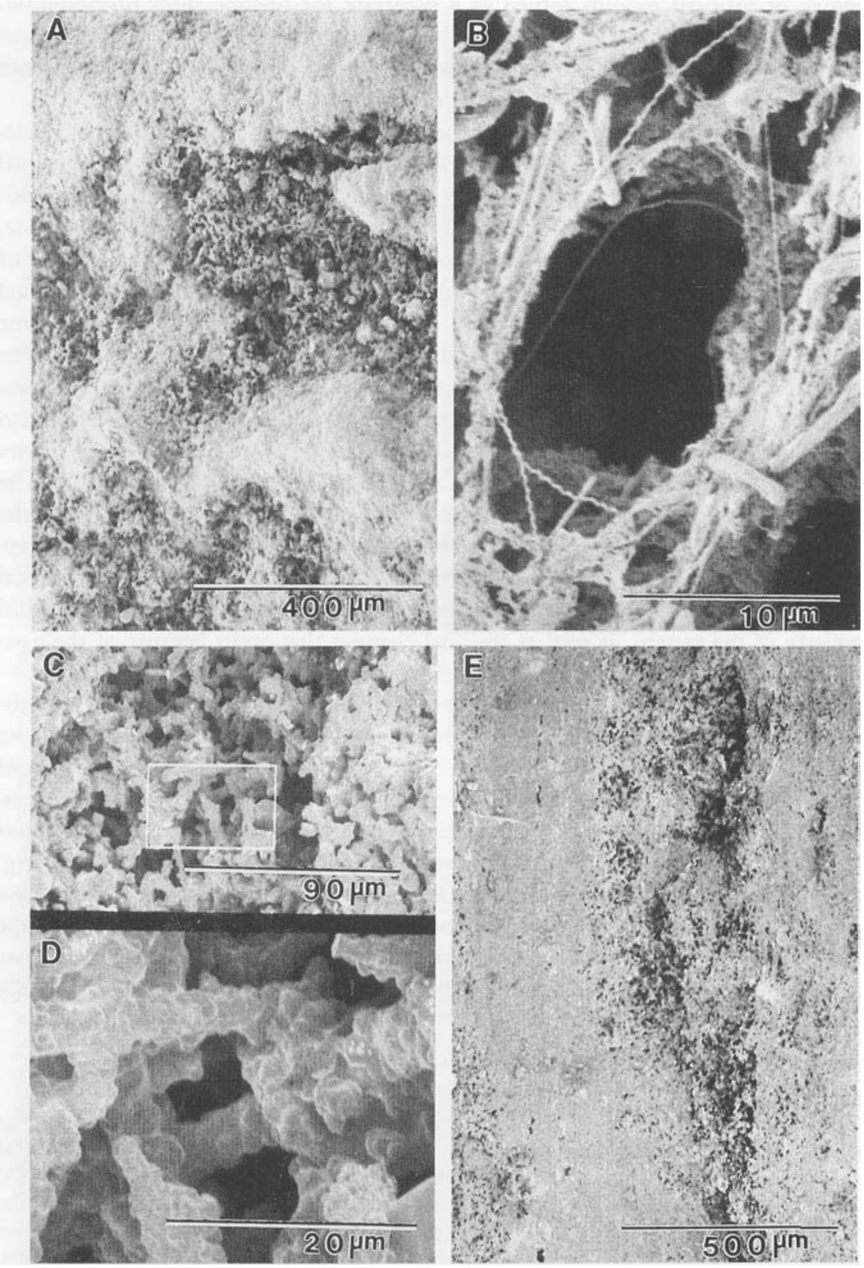
which is submerged most of the time (Fig. 3D), suggests that in the latter, a silicified network of filament moulds served as a substrate for opaline silica precipitation. Although preservation of this biotically directed fabric is unlikely without differences in the mineralogy of primary and secondary infilling phases, it is clear that the presence of the microbes controlled the localization of opaline silica deposition.

Regularly spaced cornices are one of the distinguishing microstructural characteristics of columnar geyserite (see Walter 1976b, Fig. 33). Walter (1976b) determined from field measurements that cornices, like the ones shown in Fig. 4A, form approximately once each year. An LVSEM micrograph of a fractured cornice surface (arrow, Fig. 4B) reveals the presence of porous laminae that contain high concentrations of filament moulds (Fig. 4C). Some of the filament moulds contain silicified microbial remains in various stages of degradation; intracellular remains protrude from some of the filament moulds whereas extracellular remains protrude from others. The approximately circular shape of many of the moulds indicates that the microorganisms must have been rapidly encased in opaline silica prior to degradation. LVSEM also reveals that laminae containing high concentrations of filament moulds (Fig. **4D)** are intercalated throughout the columnar geyserite with non-porous, abiotic laminae. The aperiodic intercalation of biotic and abiotic laminae suggest that local variations in the microenvironments ultimately control whether or not the microbes colonize the geyserites and, consequently, serve as a substratum for opaline silica deposition. Local variations in microenvironments include perturbations in the hydrodynamics or fluid chemistry of the system, as well as seasonal changes that occur because of the geographic location of the hydrothemmal system.

The preferred nucleation of silica on biofilms also produces discontinuous submicroscopic laminae on the surfaces of microspicules that can develop on spicules (Fig. 5A) and columns. As shown in Fig. 5B, the discontinuous laminae consist of dense patches of opaline silica that form on the sides (and top, not shown) of microspicules. The patches presumably accrete as a result of the evaporation and resultant precipitation of opaline silica from fluid droplets held in place by surface tension (e.g. Walter 1976b). These patches of extremely fine-grained opaline silica are almost always associated with relatively high concentrations of filaments. Filaments within the thicker parts of the laminae are completely entombed within the mineral matrix. Those filaments located around the edges of the opaline silica patches become partially

---

FIG. 5. LVSEM micrographs of microspicules on surface of spicular geyserite from an unnamed spring in Shoshone Geyser Basin, Yellowstone National Park **(USA).** LVSEM micrograph shown in Fig. **5A** rotated approximately 90° counterclockwise from vertical. **(A)** Microspicules that occur on the tops of actively accreting spicules are oriented toward the direction of the thermal spring pool. (B) Top view of microspicule shows discontinuous patches of opaline silica associated with (C) high concentration of silica-encrusted filaments. The patches form discontinuous submicroscopic laminae. (D) Comparison of viable filaments (bottom) and partial filament moulds (top) at the edge of a discontinuous lamina.


A
400 µm
B
10 µm
C
90 µm
D
20 µm
E
500 µm

encrusted in the dense matrix (Fig. 5C) and rapidly decompose to form filament moulds (Fig. 5D).

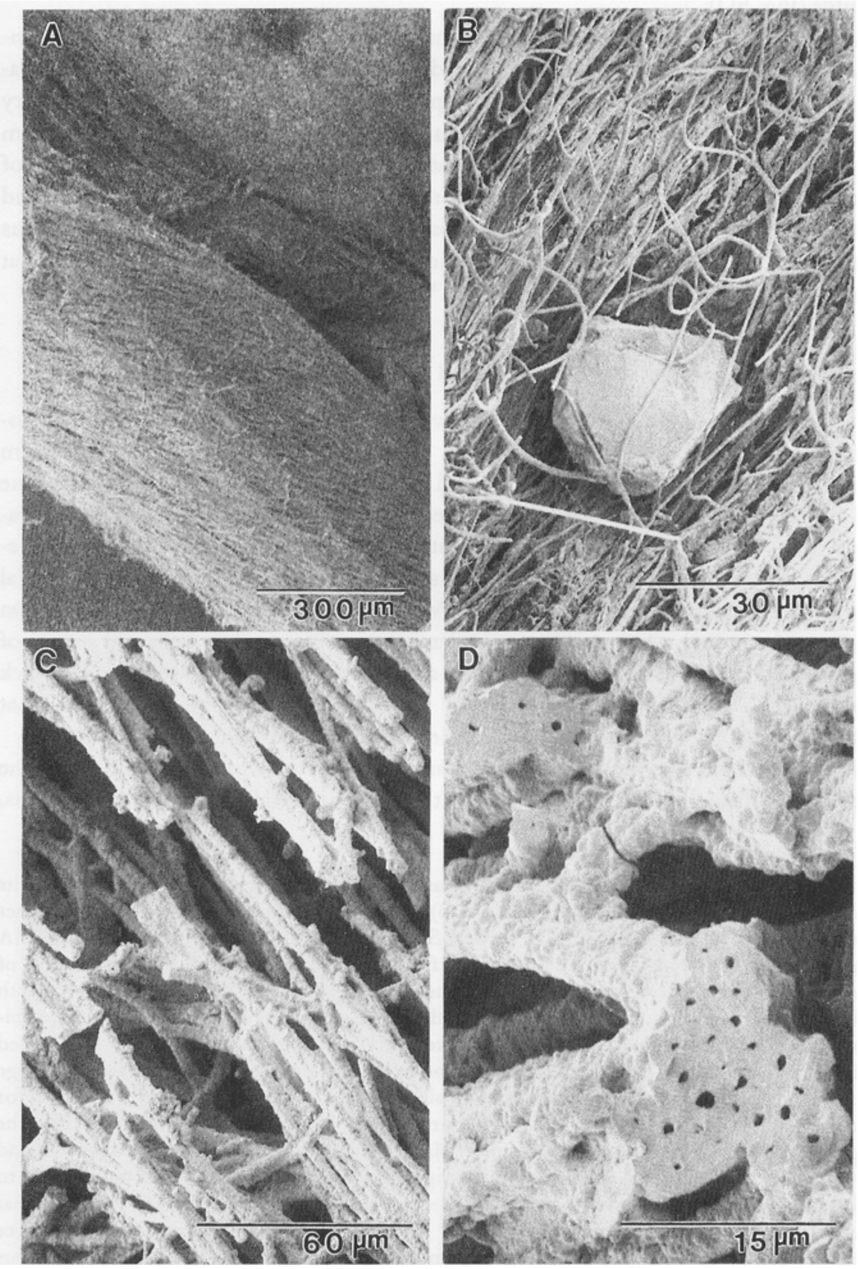
These examples illustrate how the potential to fossilize and preserve microorganisms within the subaerial geyserite regime depends upon the relative rates of population growth, microbial decomposition, primary silica deposition and secondary infilling. Petrographic observation by the authors of 2.5 Ma sub-Recent sinters from Steamboat Springs, Nevada (USA) indicate that the diagenetic recrystallization of opaline silica occurs earlier in porous rather than non-porous laminae of spicular and columnar geyserites. It appears that the loss of submicroscopic detail in the porous laminae during early diagenesis masks evidence of their biotic character. Sinters at Steamboat Springs have been described by White et al(1964).

Moderately high temperature pools and channels

At temperatures of ▬60–73 °C, thin yellow-to-orange mats dominated by the cyanobacterium *Synechococcus* and the gliding, filamentous, photosynthetic bacterium *Chloroflexus* cover the sinter surfaces of pond floors and outflows. At the transition zone (72–82 °C) between stratiform (flat-laminated) geyserite and moderately high temperature sinter, LVSEM micrographs reveal that microbial communities occur within irregular depressions bounded by ridges of dense, mat-free sinter (Fig. 6A). The microbial assemblage consists of rod-shaped *Synechococcus* and several species of long, thin filaments, including a *Spirulina*-like organism, that are attached to webs and strings of mucilage (Fig. 6B). The ridges appear to be areas of rapid accretion, although they lack any obvious morphological evidence of microorganisms or biofilms. Mats that develop within the depressions display little evidence of early mineralization.

A transition zone between the ridge tops and the valley depressions is indicated by the presence of silicified filament moulds along the outermost regions of the ridge margins.

FIG. 6. LVSEM micrographs of high temperature sinter comprising vent pool floor deposits at Octopus Spring, Lower Geyser Basin (A, B) and an unnamed spring in Shoshone Geyser Basin (C, D), Yellowstone National Park **(USA).** LVSEM micrograph shown in Fig. 6A rotated approximately 90° counterclockwise from vertical. **(A)** Sinter surface consists of elongate ridges of relatively non-porous opaline silica, separated by shallow depressions with active mat communities. Alternating spring flow and convective circulation generates bidirectional flow over surface with temperatures varying from about 72–82 "C. Unsilicified active mat community occurs in shallow depressions whereas mat organisms along ridge margins have undergone various degrees of silicification by encrustation. No evidence for microorganisms or biofilms were observed on ridges. (B) Mat community that exists near the upper temperature limit of *Synechococcus* mats. Mat assemblage consists of *Synechococcus* rods and several species of long thin filaments, including a coiled *Spirulina*-like organism, attached to webs and strings of dried mucilage. (D) Close-up view of porous area in (C) indicates that filamentous mat communities were eventually silicified by encrustation as the sinter surface accreted. (E) LVSEM of cross-section of laminated sinter showing alternation of porous patches that contain silicified filaments and finely laminated sinter with no apparent biotic component.


A
300 µm
B
30 µm
C
60 µm
D
15 µm

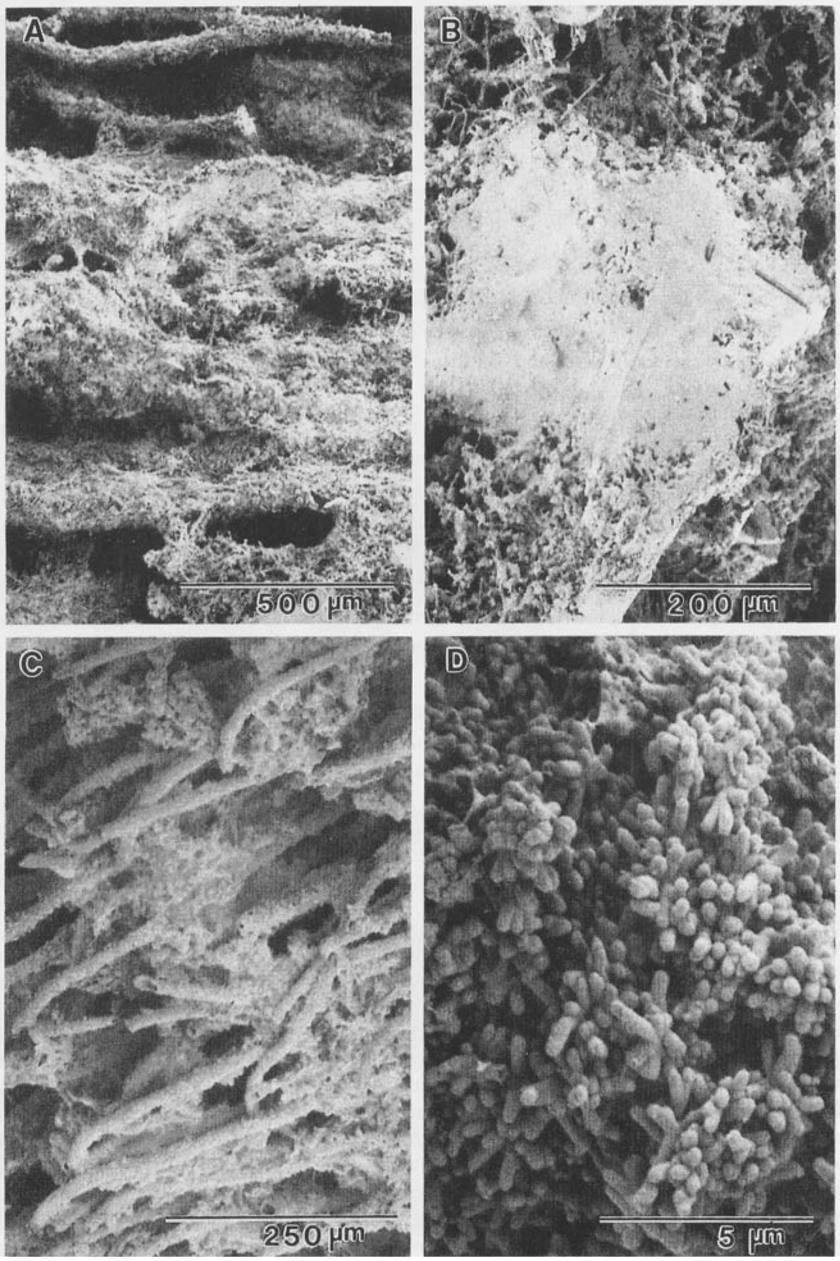
The vent pool floor at Octopus Spring from which the sample was collected is subjected to alternating spring flow and convective circulation that generates bi-directional flow over the sinter surface. Comparison with laminated sinters from an unnamed pool in Shoshone Geyser Basin (Fig. 6E) indicate that during accretion of the sinter surface, porous areas harboured filamentous mat communities that were eventually silicified by encrustation (Fig. 6C, D) and overstepped by fine laminae of opaline silica.

Mid-temperature pools and channels

At mid-temperatures (~35–59 °C), mat growth rates are high relative to rates of opaline silica deposition. Thick, gelatinous, green-to-orange-coloured mats dominated by the filamentous cyanobacterium *Phormidium*, are observed in outflow channels and terrace ponds (see Walter et al 1976). Within ponds, microbial phototaxis leads to clumping of cells and the development of preferred filament orientations. Such processes lead to the development of higher-order composite fabrics, including network, pinnacle and coniform morphotypes.

The microfabric of coniform stromatolites formed by *Phormidium* are dominated by finely fibrous palisades of silicified filaments (Fig. 7A). Phototaxis produces a strong subvertical alignment of filaments (Fig. 7B). An LVSEM micrograph of a Recent Phormidium-type sinter reveals that the continued accretion of opaline silica onto the external surfaces of individual filaments eventually cemented them together to form palisades with cores of multiple filament moulds (Fig. 7C, D). The micron-size filament moulds are difficult to resolve with light microscopy, and the microfabric appears finely fibrous. Although higher-order tufted mat structures are preserved, organically preserved filaments have not yet been identified in sub-Recent *Phormidium*-type sinters (<0.07 Ma) from Artist Point in Yellowstone National Park (Nancy Hinman, personal communication).

FIG. 7. LVSEM micrograph of Phormidium filaments within a tuft that developed on the floor of a mid-temperature pond at Fountain Paint Pots, Lower Geyser Basin (**A,** B), and silicified equivalent of Recent siliceous sinter from Queen's Laundry Terrace, Sentinel Meadows (C, D), Yellowstone National Park (USA). LVSEM micrograph shown in Fig. 7A rotated approximately 60° counterclockwise from upward growth direction. **(A)** Strong alignment of Phormidium filaments reflects construction of tuft by phototaxis. (B) Close-up view of ***Phormidium*** tuft in Fig. 7A shows entrapment of sinter detritus by cyanobacterial filaments that are mostly vertically oriented in the growing mat. (C) Vertically aligned palisades of *Phormidium*-type silica-encrusted filaments. (D) Close up of sinter shown in Fig. 7C shows cross sections of palisades which have filament moulds in their cores, formed by the encrustation of a Phormidium-sized organism. Each palisade is a composite structure that formed by coalescence of adjacent encrusted filaments. The interior of filament moulds sometimes has a thin lining of botryoidal silica but cellular materials appear to have been removed by decay or autolysis following encrustation.


A
500 µm
B
200 µm
C
250 µm
D
5 µm

Low temperature terraces

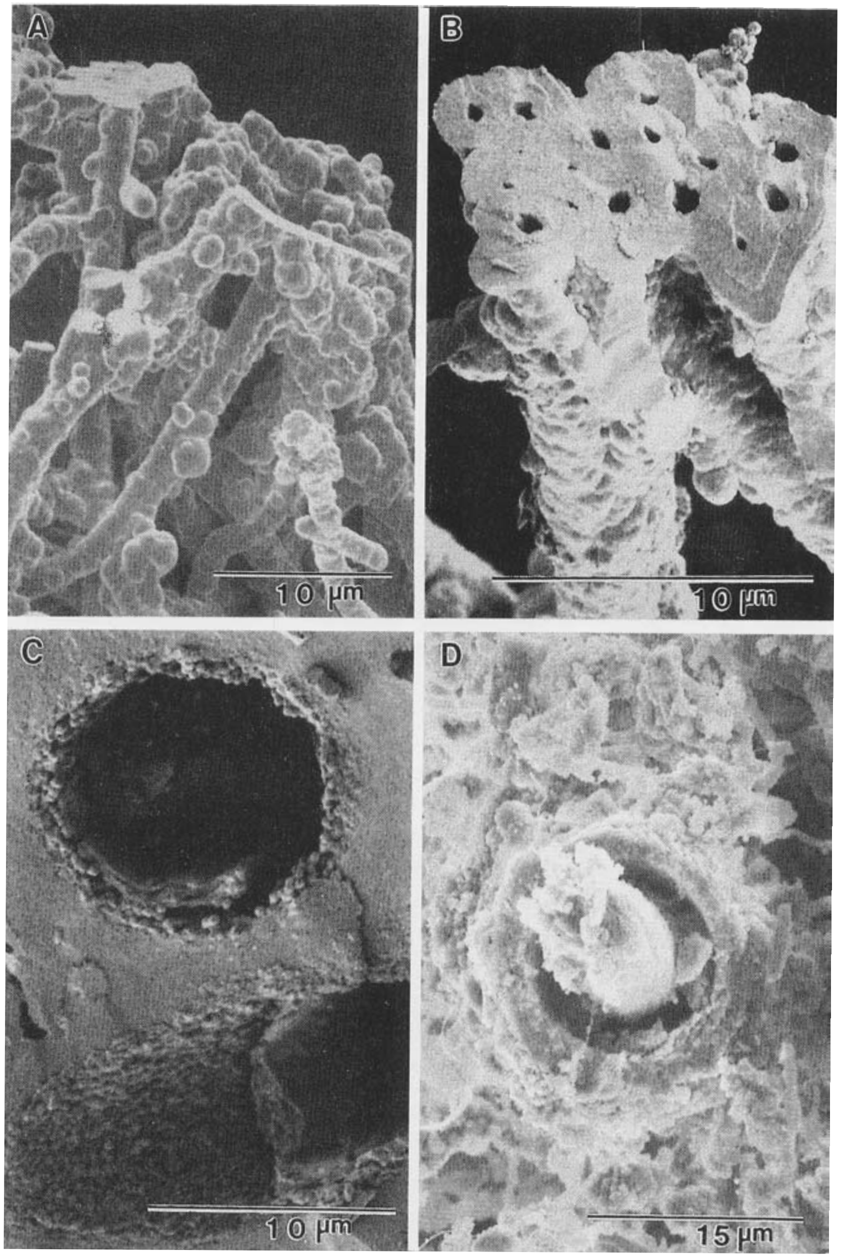
At low temperatures (<35°C), dark brownish–green Culothrix mats cover shallow terracette pools, forming flat carpets of vertically oriented filaments. Radially oriented Culothrix filaments also occur as overgrowths on mat-derived detritus and form small spherulites that are transported down broad terrace slopes and accumulate behind terracette dams. In deeper, low temperature ponds, Culothrix growth produces pustular mat surfaces. Shrub-like Calothrix mats form overgrowths on coniform *Phormidium*-type sinters in ponds where temperatures drop below 35°C (e.g. because of lateral channel shifting).

The microfabric of Culothrix mats consists of vertical palisades which anastomose and branch (Fig. 8A). Palisades are covered by a diverse community of epibionts that include small filamentous and coccoid forms, diatoms and even sessile protozoans. Each palisade typically has a core region that contains one or more filament moulds surrounded by porous patches of smaller, randomly oriented filaments and coccoids (Fig. 8B, 8C). As the various epibionts become encrusted with silica, they are incorporated into the palisade and form a porous rind around the palisade core. Cross-bridging of the palisades by growth of the epibiont community contributes to the complexity of the porous framework, which is eventually infilled by opaline silica. High concentrations of heterotrophic bacteria coat the surfaces of unsilicified Calothrix sheaths (Fig. 8D). Silicified equivalents of these bacteria probably account for the presence of a porous outer rim that surrounds some of the permineralized Culothrix-sized sheaths (e.g. Fig. 9C).

Petrographic study by the authors of Recent low temperature sinters from Excelsior Geyser Crater and Queen's Laundry Terrace (Yellowstone National Park) indicates that although organically preserved cyanobacterial sheaths are common, the *Calothrix*-type filaments display a range of degradational variants interpreted to reflect differences in the rates of organic decomposition and silica deposition. The recalcitrant nature of extracellular sheaths and capsules of cyanobacteria is well known (e.g. Golubic & Hofmann 1976). Taphonomic studies of cyanobacteria from siliceous

---

FIG. 8. LVSEM micrographs of Recent palisade sinter collected from the wall of Excelsior Geyser Crater, Midway Geyser Basin (A, B), and an active, unnamed spring in Shoshone Geyser Basin (C, D), Yellowstone National Park (USA). LVSEM micrographs shown in Figs 8A and C rotated approximately 90° counterclockwise from upward growth direction. **(A)** Palisade fabric formed by *Calothrix*-type filaments, a vertically growing cyanobacterium that dominates mat communities developed below 35°C. The ragged appearance of palisade surfaces results from the presence of a silicified community of small filamentous microbes that colonized palisade surfaces. (B) Cross section of palisade showing filament mould in core area formed by encrustation and overgrowth of *Calothrix*-sized filament, followed by accretion and encrustation of epibiont community. (C) *Calothrix* mat from floor of low temperature terrace pond consists of palisades formed by coalescence of silicified sheaths of a vertically growing cyanobacterium. (D) Close up of an individual ***Culothrix*** sheath showing a surface population of small, rod-shaped coccoids and associated mucilage.


A
10 µm
B
10 µm
C
10 µm
D
15 µm

subaerial thermal spring deposits in Kamchatka have shown that extracellular sheaths and capsules of cyanobacteria are selectively preserved during silicification (e.g. Gerasimenko & Krylov 1983). Organic preservation of cellular remains in the distal parts of the system, however, may also be enhanced by additional factors that include significant amounts of secondary infilling, changes in pH and microenvironments, and occurrence of these mats in a predominantly subaqueous environment. Although organically preserved sheath materials were not observed petrographically by the authors in sub-Recent *Calothrix*-type sinters from McGinness Hills (approximately 3.0 Ma, Nevada, USA), the palisade frameworks contain abundant filament moulds that have been infilled by secondary silica.

Implications for preservation in ancient deposits

As the LVSEM micrographs shown in Fig. 9 illustrate, thermophiles in subaerial silica-depositing thermal springs are preserved by several modes of fossilization, which include replacement, encrustation and permineralization. We are currently investigating how the different mechanisms of microbial preservation in hydrothermal environments affect the morphological and ultrastructural fidelity of microbes in progressively older sinters. Knoll (1985) suggested that the model proposed by Leo & Barghoom (1976) for the silicification of wood may be applicable to silica permineralization of microbial remains. Leo & Barghoorn (1976) proposed that the vascular tissues of plants, as well as their degradational products, provide a template for silica deposition via hydrogen bonding of exposed hydroxyl and functional groups with monosilicic and polysilicic acid. As discussed by Knoll (1985), a limited amount of microbial cellular decomposition under anaerobic conditions, accompanied by early mineralization, may also enhance the expectancy for preservation of cellular material. Recent studies indicate that silica deposition may be promoted by mechanisms in addition to partial cellular degradation. Schultze-Lam et al (1993) reported that silicification of thermophilic cyanobacteria in Icelandic hot springs is predominantly a surface-mediated process in which sheaths concentrate silica and initiate the mineralization process. Fossilization experiments (Westall 1994) indicate that silicification

---

FIG. 9. LVSEM micrographs illustrating the different modes of fossilization of thermophilic bacteria identified in **(A)** subaerial geyserites and (ED) thermal spring stromatolites from Yellowstone National Park **(USA). (A)** Encrusted/replaced filamentous microorganisms preserved in a horizontal fenestral cavity in modem subaerial geyserite, unnamed spring, Sentinel Meadows. (B) *Phormidium*-type Recent sinter from Queen's Laundry Terrace, Sentinel Meadow, showing fossilization by filament encrustation and the subsequent removal of cellular materials to form a filament mould. **(C)** *Calothrix*-type sinter from Recent Excelsior Geyser Crater, Midway Geyser Basin, showing preservation of sheath by permineralization. Filament moulds contain an outer porous rind and adjacent dense lamellar material interpreted to be the silica infused sheaths of *Calothrix*-type filaments. (D) *Calothrix*-dominated sinter from active unnamed spring in Sentinel Meadows showing silicified extracellular sheath and intracellular remains.

mechanisms are species-specific; the character of the cell wall and external layers influences the type of mechanism and rate of fossilization. It has also been shown that the chemical composition of the solute influences the fidelity of microbial preservation. Ferris et al (1988) demonstrated experimentally that a delay in the rate of cellular degradation of iron-laden thermophilic bacteria allowed the silicification of intact cellular structures, presumably because of the inhibitory effect of iron on wall-degrading autolysins.

Our study of geyserites from active systems has allowed us to recognize that both biotic and abiotic processes contribute to geyserite morphogenesis. Filamentous biofilms, when present, contribute to the formation of subaerial geyserites by providing a favoured substrate for the localized precipitation of opaline silica. It will be important for future studies to determine whether geyserites can be produced abiotically and whether the biotic and abiotic microstructural characteristics of geyserites can be distinguished after diagenetic overprinting.

We have also observed general trends in preservation along the thermal gradient. Permineralization of cyanobacterial sheaths in Recent and sub-Recent materials has been petrographically identified by the authors only in low temperature (<35 °C) microfacies. We have observed that filament moulds, rather than permineralized remains, are preserved in the mid-temperature to moderately high temperature pools and channels. Although microorganisms cannot be resolved petrographically in high temperature geyserites, the occurrence of high concentrations of filament moulds identified using LVSEM indicates that encrustation and degradation of microorganisms is the dominant mode of fossilization at the high temperature end of the system. To summarize, the potential to preserve organic remains increases with decreasing temperature along the thermal gradient of subaerial silica-depositing thermal springs. These materials, however, must be investigated at the ultrastructural level, where distinctions between preservational modes can be more exact. Exceptions to the general trend in preservation result from variations in the local microenvironment.

We have also found that the persistence of macro-scale biofabrics in sub-Recent and ancient siliceous sinters can be related to diagenetic effects, which tend to accentuate differences between primary and secondary textures in sinter stromatolites. The rate and pathway of the diagenetic recrystallization of opaline silica to quartz may be influenced by differences in the trace composition, crystallinity, microstructure, grain size and habit of primary and secondary phases, as well as by differences in the porosity of laminae in geyserites and thermal spring stromatolites.

Acknowledgements

This research was supported by a National Research Council research associateship to Sherry Cady and by a grant from NASA's Exobiology Program to Jack Farmer. We thank the staff of the National Park Service at Yellowstone National Park for their logistical assistance in the field, especially Robert Lindstrom and Roderick Hutchinson. Laboratory and microscope facilities were kindly provided to the authors by David Blake at NASA Ames Research Center, and to Sherry Cady at the National Center for Electron Microscopy, Lawrence Berkeley National

Laboratory (United States Department of Energy Contract #DE-AC03-76SF00098). Improvements to the manuscript were made by Malcolm Walter and David Des Marais.

References

Allen ET 1934 The agency of algae in the deposition of travertine and silica from thermal waters. Am J Sci 28:373–389

Barns SM, Delwiche CF, Palmer JD, Dawson SC, Hershberger KL, Pace NR 1996 Phylogenetic perspectives on microbial life in hydrothermal ecosystems, past and present. In: Evolution of hydrothermal ecosystems on Earth (and Mars?). Wiley, Chichester (Ciba Found Symp 202) p 24–39

Brock TD 1978 Thermophilic microorganisms and life at high temperatures. Springer-Verlag, New York

Castenholtz RW 1984 Composition of hot spring microbial mats: a summary. In: Cohen Y, Castenholtz RW, Halvorson HO (eds) Microbial mats: stromatolites. Alan R. Liss, New York, p 107–119

Ferris FG, Fyfe WS, Beveridge TJ 1988 Metallic ion binding by *Bacillus subtilis*: implications for the fossilization of microorganisms. Geology 16:149–152

Gerasimenko LM, Krylov IN 1983 Postmortem alterations of cyanobacteria in the algal–bacterial films in the hot springs of Kamchatka. Dokl Akad Nauk 272:215–218

Golubic S, Hofmann HJ 1976 Comparison of modern and mid-Precambrian Entophysalidaceae (Cyanophyta) in stromatolitic algal mats: cell division and degradation. J Paleontol 50:1074–1082

Knoll AH 1985 Exceptional preservation of photosynthetic organisms in silicified carbonates and silicified peats. Philos Trans R Soc Lond Ser B Biol Sci 311:111–122

Leo RF, Barghoorn ES 1976 Silicification of wood. Botanical Museum Leaflets, 25-1. Botanical Museum, Harvard University, Cambridge, MA

Rice CM, Ashcroft WA, Batten DJ et al 1995 A Devonian auriferous hot spring system, Rhynie, Scotland. J Geol Soc 152:229–250

Schultze-Lam S, Ferris G, Wiese R 1993 Silicification of cyanobacteria in an Icelandic hotspring microbial mat. Geological Society of America, Abstracts with Programs, 26:192A

Stetter KO 1996 Hyperthermophiles in the history of life. In: Evolution of hydrothermal ecosystems on Earth (and Mars?). Wiley, Chichester (Ciba Found Symp 202) p 1–18

Trewin NH 1994 Depositional environment and preservation of biota on the Lower Devonian hot-springs of Rhynie, Aberdeenshire, Scotland. Trans R Soc Edinb 84:433–442

Trewin NH 1996 The Rhynie cherts: an early Devonian ecosystem preserved by hydrothermal activity. In: Evolution of hydrothermal ecosystems on Earth (and Mars?). Wiley, Chichester (Ciba Found Symp 202) p 131–149

Walter MR 1976a Hot-spring sediments in Yellowstone National Park. In: Walter MR (ed) Stromatolites. Elsevier, Amsterdam, p 489–498

Walter MR 1976b Geyserites of Yellowstone National Park: an example of abiogenic stromatolites. In: Walter MR (ed) Stromatolites. Elsevier, Amsterdam, p 87–112

Walter MR 1996 Ancient hydrothermal ecosystems on Earth: a new palaeobiological frontier. In: Evolution of hydrothermal ecosystems on Earth (and Mars?). Wiley, Chichester (Ciba Found Symp 202) p 112–130

Walter MR, Bauld J, Brock TD 1976 Microbiology and morphogenesis of columnar stromatolites (*Conophyton, Vacerrilla*) from hot springs in Yellowstone National Park. In: Walter MR (ed) Stromatolites. Elsevier, Amsterdam, p 273–310

Walter MR, Des Marais DJ, Farmer JD, Hinman N 1996 Palaeobiology of mid-Palaeozoic thermal spring deposits in the Drummond Basin, Queensland, Australia. Palaios, in press

Ward DM, Weller R, Shiea J, Castenholtz RW, Cohen Y 1989 Hot spring microbial mats: anoxygenic and oxygenic mats of possible evolutionary significance. In: Cohen Y, Rosenberg E (eds) Microbial mats, physiological ecology of benthic microbial communities. American Society for Microbiology, Washington DC

Westall F 1994 How bacteria fossilize: experimental observations and some theoretical considerations. In: Awramik SM (ed) Death Valley International Stromatolite Symposium (Abstracts), Laughlin, Nevada, October 15-17, 1994, p 88–89

White DE, Brannock WW, Murata KJ 1956 Silica in hot-spring waters. Geochim Cosmochim Acta 10:27–59

White DE, Thompson GA, Sandberg GH 1964 Rocks, structure, and geologic history of Steamboat Springs thermal area, Washoe County, Nevada. Geol Surv Prof Paper 458B

DISCUSSION

Walter: Have you made a positive identification of any of these filamentous organisms as archaea?

Cady: No, but we are currently using transmission electron microscopy to investigate how they become silicified. This work necessitates collaboration with microbiologists familiar with the identity and ultrastructural characteristics of the organisms; we hope to have that information in the near future.

Stetter: Did you say that silicate begins to crystallize at the tips of these filamentous organisms?

Cady: No, silica is preferentially deposited at the tips of the spicules, which are a particular morphotype of geyserite that forms along the inner rim of thermal spring pools and around the mouths of some geyser effluents. We have observed the highest concentrations of viable filaments at the tips of the spicules that form near the air–water interface. The preferred deposition of opaline silica on the organisms at the tips of the spicules is presumably what causes the geyserite to accrete with the elongated spicular form.

Stetter: Sometimes we encounter problems in our attempts to clone hyperthermophiles in glass capillaries under the laser microscope, since they rapidly attach onto the glass surface. Filaments, especially, appear to be very sticky, mainly at their ends. In their natural environments, these organisms are faced with a dilemma: on the one hand they have to attach to the surface or they will be washed away to colder areas, and on the other, according to your results, there is silica precipitation, which also kills them. They have a difficult life.

Cowan: With respect to the filamentous organisms that you see in the geyserites, I would expect there to be a substantial population of the bacterial genus *Thermus*. This genus is a significant colonizer of boiling terrestrial hydrothermal environments, even though it will only grow up to about 80°C in the laboratory. It is very well known that if you dip a slide into a boiling hydrothermal pool, you get massive colonization of the glass surfaces, and *Thermus* is one of the predominant colonizers.

Walter: The temperature point is interesting: you don't really know the temperature of the water that is actually hitting the tip of those spicules.

Cady: That is true, but we have observed that the highest concentration of filaments occur on spicules that form at the air–water interface, where they are not only splashed with spring water, but often become temporarily submerged due to fluctuations in the water level of the pool.

Walter: At the elevation of Yellowstone, water boils at about 96 °C, and you are somewhat below this because you're right at the air–water interface. It would be interesting to know what the temperature actually is.

Farmer: We've measured the temperature of the vents: the problem is that the erupted hot water travels through the air before it splashes onto sinter surfaces, and we don't know its temperature by the time it reaches the surface. The change could be significant, so vent temperature is probably not an accurate parameter.

Cady: It is worth emphasizing that although Brock (1978) demonstrated that extreme thermophiles live in boiling pools by submerging glass slides which became colonized, we have shown for the first time that biofilms influence the microstructural development of geyserite. The preferential deposition of silica at the tips, where filaments are concentrated, indicates that the biofilms also have a significant influence on the morphological development of spicular geyserite.

Cowan: I agree entirely. In hydrothermal systems the total cell populations are orders of magnitude higher in the sediment fractions than in the aqueous phase. The consensus is that cells are strongly adhered to sediment particles and I would expect the same to apply in these deposition areas.

Walter: Sherry is being polite in not pointing out that what she's doing is completely revising work I did 25 years ago when I concluded that these structures were entirely abiogenic.

Pentecost: The cyanobacteria found in travertines appear to be much the same as those you have found. They are motile and phototactic, and often they will creep under the travertine, if it is porous enough, to form endolithic communities. Do you have any evidence for endolithic communities in your sinters?

Cady: We have observed what appear to be stratified endolithic communities on columnar geyserite located several centimetres away from the edges of the pools. Jack Farmer may have something more to say about the presence of endoliths in the mid-to-low temperature sinters.

Farmer: We do find endoliths in dried areas around inactive vents. Even in columnar geyserites near vents, you can take small geyserite columns, break them in half, and see the bands of colour a millimetre or so below the surface. Whether these are endoliths or entombed thermophilic cyanobacteria is unclear, and we don't know yet whether they are still viable. Certainly the pigments are still there!

Cowan: There are some interesting issues relating to the local conditions required to preserve the biological material. The mechanisms causing biological structures to dissipate before silica deposition certainly include enzymic and chemical lysis. Anything that inhibits these processes is likely to promote the preservation of the biological structure, irrespective of what happens later. Such effects may be critical within the first 12h of the deposition process. Silica may play a key role, possibly by 'immobilizing' the cells. You suggested that metal ion inactivation may also play a role: we might speculate that inactivation of degradative enzymes is also important.

Knoll: **A** lot of the beautiful textures that you see with the scanning electron microscope are really present in part because there's a lot of pore space that allows you to see the way the silica has been deposited. Have you done any vertical studies going down into the sinters to see what happens to these textures as diagenesis occludes that pore space' In other words, once you have something that instead of 50% porosity is 100% silica, are the textures still as apparent as they are at the surface?

Cady: Yes, the relatively rapid encrustation of the microorganisms enhances preservation of the microbial mat architecture, Even if organic remains degrade prior to permineralization, differences in the mechanism, timing and temperature of formation of primary and diagenetic silica phases accentuate textural differences between the primary biofabric and the authigenic matrix.

Trewin: Many of the textures Sherry Cady has illustrated are identical to those in the Rhynie chert, both on a macro (e.g. plant stem) or micro (cyanobacterial filament) scale. In the Rhynie chert all opaline silica has been converted to microquartz. However, the biogenic structures are present, so it does seem that the textures of value for identification of biota can remain even after the whole deposit has been converted into a mosaic of chert.

Cady: The presence of degraded remains in the biotic laminae increases the number of potential nudeation sites for opaline silica deposition. These laminae are characterized by an extremely he-grained matrix of opaline silica that can be recognized petrographically, even after the opaline silica transforms *to* quartz.

Knoll: In the Gunflint Chert, which might be one of the best Precambrian analogues of this system, differences in crystal size between the organic-rich and organic-free areas are still seen. This can be preserved for a long time.

Farmer: We have also been looking at these systems in places other than Yellowstone. In most cases, organic preservation is poor, consistent with what we have seen in Yellowstone. Tracking deposits back in the rock record a few million years, and into the 350 Ma old Drummond Basin material that Malcolm Walter showed in his paper (Walter 1996, this volume), there isn't much organic matter preserved there either. Most biological information consists of biofabrics. Dave Des Marais has completed total organic carbon analyses on the sinters from the Drummond Basin. **I** wonder if he could share some of those results?

Des Marais: They are consistent with what was said earlier about poor preservation at higher temperatures and better preservation as you approach ambient conditions. The most organic-rich material is found at the low-temperature end of the system, and it contains as much as a few tenths of a percent of organic carbon. In sinter formed above 70 °C, the organic carbon content is below the detection limit. We've made isotope measurements of this, and even at the high temperature end we see values identical to the isotopic values we see at the low temperature end, which is dominated by plant fragment material. It seems likely that small plant fragments are being incorporated in high temperature sinters, and even those small bits are dominating the organic carbon present. This implies that bacterial preservation is pretty poor relative to plant preservation. We're still working out the proper way of analysing more recent sinters, keeping in mind that that the organic matter is quite sensitive to the procedures that we would use, for example, to remove carbonates from the travertines.

Stetter: Could the reduced preservation at high temperatures also be due to differences in cellular structure? Hyperthermophiles seldom have the rigid peptidoglycan wall found in most bacteria; instead, they usually have a rather loose surface layer made up of glycoproteins which may be destroyed more easily.

Cady: Yes, it is likely that differences in cellular structure would result in the preferential preservation of some species over others. Don't the archaea have quite a diverse range of cell envelopes and extracellular structures?

Stetter: There are only a few examples I know of. Rod-shaped methanogens such as *Methanobacterium*, *Methanothermus* and *Methanopyrus* have a pseudomurein cell wall and grow at temperatures between 60 and 110"C depending on the genus (Zeikus & Wolfe 1972, Lauerer et al 1986, Huber et al 1989). *Methanobacterium thermoautotrophicum* and *Methanothermus* sp. occur in terrestrial hot springs while *Methanopyrus* sp. thrives within submarine black-smoker walls.

Cady: Another point worth making is that petrographic and morphological descriptions of these materials should be supplemented by biomarker and isotopic studies similar to those of our colleagues Roger Summons and David Des Marais. To correctly interpret the preservational biases in the fossil record, it is important for us to include all of these techniques when evaluating the biogenicity of ancient hydrothermal materials.

References

Brock TD 1978 Thermophilic organisms and life at high temperatures. Springer-Verlag, New York

Huber R, Kurr M, Jannasch HW, Stetter KO 1989 A novel group of abyssal methanogenic archaebacteria (*Methanopyrus*) growing at 110°C. Nature 342:833–834

Lauerer G, Kristjansson JK, Langworthy TA, Konig H, Stetter KO 1986 *Methanothermus sociabilis* sp. nov., a second species within the *Methanothermaceae* growing at 97 °C. Syst Appl Microbiol 8:100–105

Walter MR 1996 Ancient hydrothermal ecosystems on Earth: a new palaeobiological frontier. In: Evolution of hydrothermal ecosystems on Earth (and Mars?). Wiley, Chichester (Ciba Found Symp 202) p 112–130

Zeikus JG, Wolfe RS 1972 *Methanobacterium thermoautotrophicus* sp. n., an anaerobic, autotrophic, extreme thermophile. J Bacteriol 109:707–713