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Preservation Style of Microbes in Siliceous Sinter Around Old Faithful Geyser, Yellowstone National Park, USA

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ABSTRACT

Siliceous sinters form at the surface as alkali chloride hot springs discharge and cool to temperatures below 100 °C. During this process, the silica carried in solution precipitates and accumulates to form sinters. The precipitating silica also silicifies everything in its flow path, including hot spring microbes. Fifteen siliceous sinter samples were examined under a Scanning Electron Microscope (SEM) to observe microbial preservation from sinter surrounding Old Faithful Geyser in Yellowstone National Park, USA. Our SEM images record pristine preservation styles of both low- and mid-temperature microbes. Low-temperature microbes thrive in <35 °C water and in our samples these filamentous microbes had total exterior diameters >8 µm. Mid-temperature microbes live in 35 to 59°C water and our mid-temperature sinter samples revealed filamentous microbes with total exterior diameters of <4 µm. Both low- and mid-temperature filamentous microbes consist of an inner trichome surrounded by an outer sheath. Our study shows permineralization, encrustation and a combination of both preservation styles occurring in our sinter samples. Preservation of low-temperature sized filaments in our samples consists of: (1) encrustation of filament sheaths with closely-packed opal-A spheres which occasionally form botryoidal clusters; (2) permineralization of filament sheaths resulting in complete replacement with smooth silica; (3) filaments with trichomes encrusted with opal-A spheres and sheaths replaced via permineralization with subsequent encrustation; (4) trichomes that are completely replaced by either encrustation or permineralization; and (5) filaments with no preserved trichome leaving hollow filament molds which are either partially or completely infilled with opal-A spheres. In our samples mid-temperature filaments were less commonly observed, but where present, preservation styles consist of: (1) permineralization followed by partial encrustation of the sheath; and (2) encrustation of the filament sheath. These multiple preservation styles indicate complex and variable processes are active around Old Faithful Geyser. The rarity of these sinter samples and their distinctive textures make them uniquely important in understanding life in hot springs, identifying biosignatures in siliceous sinters and understanding fluid flow at the surface in geothermal systems.

1. INTRODUCTION

Siliceous sinter is a terrestrial hot-spring deposit that forms where silica-rich, alkali chloride, hydrothermal fluids ascend quickly to the surface and discharge as hot springs. As the temperature of the discharging hot spring water decreases below 100 °C, the silica carried in solution precipitates (Fournier and Rowe, 1966; Weres and Apps, 1982, Fournier, 1985; Williams and Crerar, 1985). The silica deposits as opal-A on all surfaces over which hydrothermal water flows and where ponding occurs, entombing and silicifying everything in the hot spring channel including microbes that thrive in the hydrothermal fluid.

Modern, discharging alkali chloride hot spring vents and discharge channels can be divided broadly into: (1) near-vent high temperature zones (>60 °C); (2) mid apron-slope, mid-temperature areas (~35-59 °C); and (3) distal apron-slope, low-temperature zones (<35 °C; Walter, 1976a; Farmer and Des Marais, 1994; Cady and Farmer, 1996; Hinman and Lindstrom, 1996; Jones et al., 1997, 1998; Campbell et al., 2001; Lowe et al., 2001; Guidry and Chafetz, 2003; Lynne and Campbell, 2003; Handley and Campbell, 2011; Lynne, 2012). Measurements of filament exterior sheath and internal trichome diameters have been used as indicators of broad approximate temperature gradients for microbial communities and represent a range of spatial locations on the apron-slope (Walter, 1976a, b; Farmer and Des Marais, 1994; Cady and Farmer, 1996; Jones et al., 1998; Lowe et al., 2001; Guidry and Chafetz, 2003; Lynne and Campbell, 2003; Lynne 2012). Low-temperature (<35 °C) alkali chloride hot-springs commonly support coarsely filamentous, sheathed microbes. These microbes consist of an inner tubular filament mold or perhaps an interior trichome of porous cellular material, and thick outer sheaths, with a total exterior diameter of >8 µm. Mid-temperature waters (~35-60 °C), flowing over mid- to distal-apron slope settings, are inhabited by thin, sheathed filamentous microbes with <5 µm exterior diameters.

The study of thermophilic microbial biosignatures preserved in siliceous sinters is important, as hydrothermal systems and their associated hot springs may have been present during the formation of the Earth and other planets such as Mars. Therefore, silicified hot spring microbial biosignatures may represent the earliest signs of planetary life (Bock and Goode, 1996; Stetter, 1996; Farmer and Des Marais, 1994, 1999; Farmer, 2000; Westall et al., 2001, 2015; Konhauser et al., 2003; Maliva et al., 2005; Hofmann and Harris, 2008; Preston et al., 2008; Preston and Genge, 2010; Ruff et al., 2011; Djokic et al. 2017; Ruff and Farmer, 2016).

In our study we examined the microbial preservation style of six modern siliceous sinter samples from the sinter surrounding Old Faithful Geyser, Yellowstone National Park, USA (Fig. 1). Our study site has an elevation of 2250 m which lowers the boiling point of the discharging hot springs to 92.5 °C. Therefore, at temperatures below 92.5 °C the silica precipitates from the thermal fluid and deposits opal-A which entombs, silicifies and preserves microbes that thrive in the discharging thermal water. Many previous studies on sinter samples from Yellowstone National Park are documented and have focused on microbial communities at various locations within the Park (e.g., Hinman, and Lindstrom 1996; Walter, 1976a, b; Inagaki et al., 2001; Lowe et al., 2001; Blank et al. 2002; Flot and Cady, 2002; Guidry and Chafetz, 2003; Kyle and Schroeder, 2007; Berelson et al. 2011; Inskeep et al. 2015). However, our study is unique as these are the first siliceous sinter samples to be examined from the Old Faithful mound and immediate vicinity in 22 years. Our results contribute to and widen our knowledge on microbial preservation within hot spring settings at Yellowstone National Park.

2. METHODS

Scanning Electron Microscopy (SEM) was used to examine the microbial preservation style of six siliceous sinter samples from the sinter apron surrounding Old Faithful Geyser. The samples were mounted on aluminium stubs with epoxy. These stubs were coated with platinum using a high-resolution Polaron SC7640 sputter coater. Samples were examined with a Phillips (FEI) XL30S field emission gun SEM, at an accelerating voltage of 20 keV, and a working distance of 10 mm.

3. RESULTS

Six samples (4-9, BP38, BPv, Ge, 6-24, HS1; Fig. 1) from the siliceous sinter terrace surrounding Old Faithful Geyser were examined under the SEM for their microbial preservation. Microbes indicative of both low- (<35 °C) and mid-temperature (35-59 °C) hot spring flow conditions were observed in our samples (Fig. 1A). A thermal infrared (TIR) image (Fig. 1B) captured in March 2012 shows the surface temperature at our sample sites and surrounding area. Temperature comparison of the discharging water based on microbial preservation (Fig. 1A) and the TIR data (Fig. 1B) demonstrates the temperature variability at our sample sites. Based on microbial preservation the locations of samples 4-9 and BP38 should be in areas with low-temperature water (<35 °C). This correlates well with the TIR image. Sinter samples HS1, Ge and 6-24 should be in zones where the water temperature is between 35 – 59 °C. The TIR data for the location of these three samples shows much cooler water on the surface. Sample BPv which contains both low- (<35 °C) and mid-sized (35-59 °C) microbial filaments is located in an area that the TIR data indicates 20 – 30 °C.

In our samples, low-temperature sized microbes ranged in size from 8 to 20 µm in total exterior diameter, while mid-temperature sized microbes ranged from 1.5 to 4 µm in total exterior diameter. Samples 4-9 and BP38 contained low-temperature sized microbial filaments. Sample BP38 also revealed etched and pitted filament surfaces typical of acidic steam condensate overprinting. Samples Ge, 6-24 and HS1 contained mid-temperature filaments. Sample BPv preserved both low- and mid-temperature filaments within the same sample. In most samples the interior trichome was not readily preserved and the trichome mold remained hollow, however, in a few samples the trichome molds were partially to completely infilled.

Two preservation styles are recorded within our sinter samples; encrustation and permineralization. Encrustation refers to deposition of opal-A precipitates on the exterior of the filament sheaths, while permineralization occurs when silica particles permeate into microbial cell walls and completely replace them. Where encrustation has occurred the filaments are preserved in a porous sinter. For permineralization, the filaments are embedded in a smooth silica matrix. This variation in preservation styles indicates multiple mechanisms control the preservation process. Our SEM observations for each sample are shown in Figures 2-4.

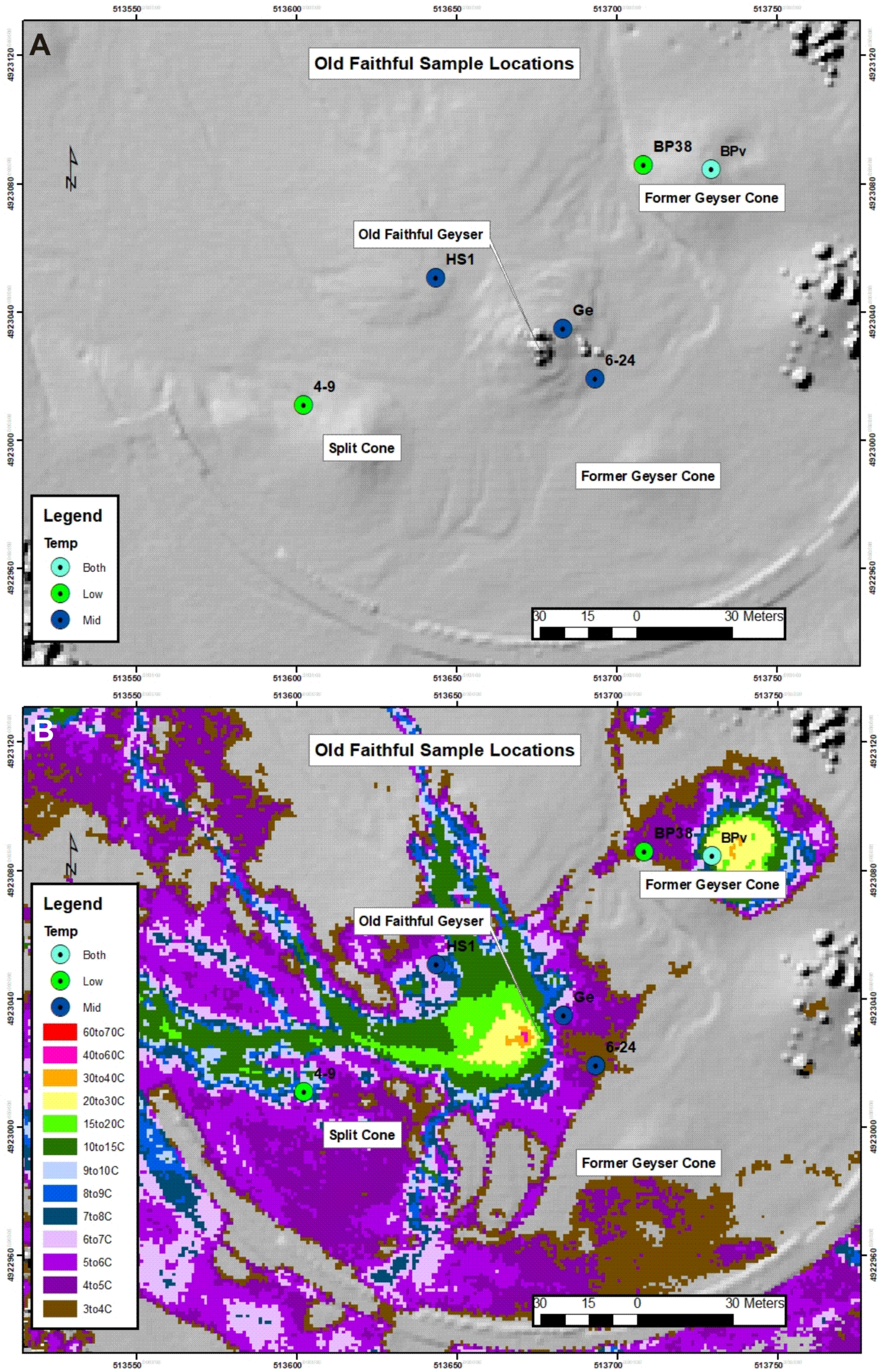

Figure 1: Sample locations on the sinter terrace surrounding Old Faithful Geyser. (A) Sample numbers, locations and discharging thermal fluid temperature indicated by microbial preservation within sinter sample. (B) Thermal Infrared image of area in (A) showing surface temperatures of discharging thermal fluid.

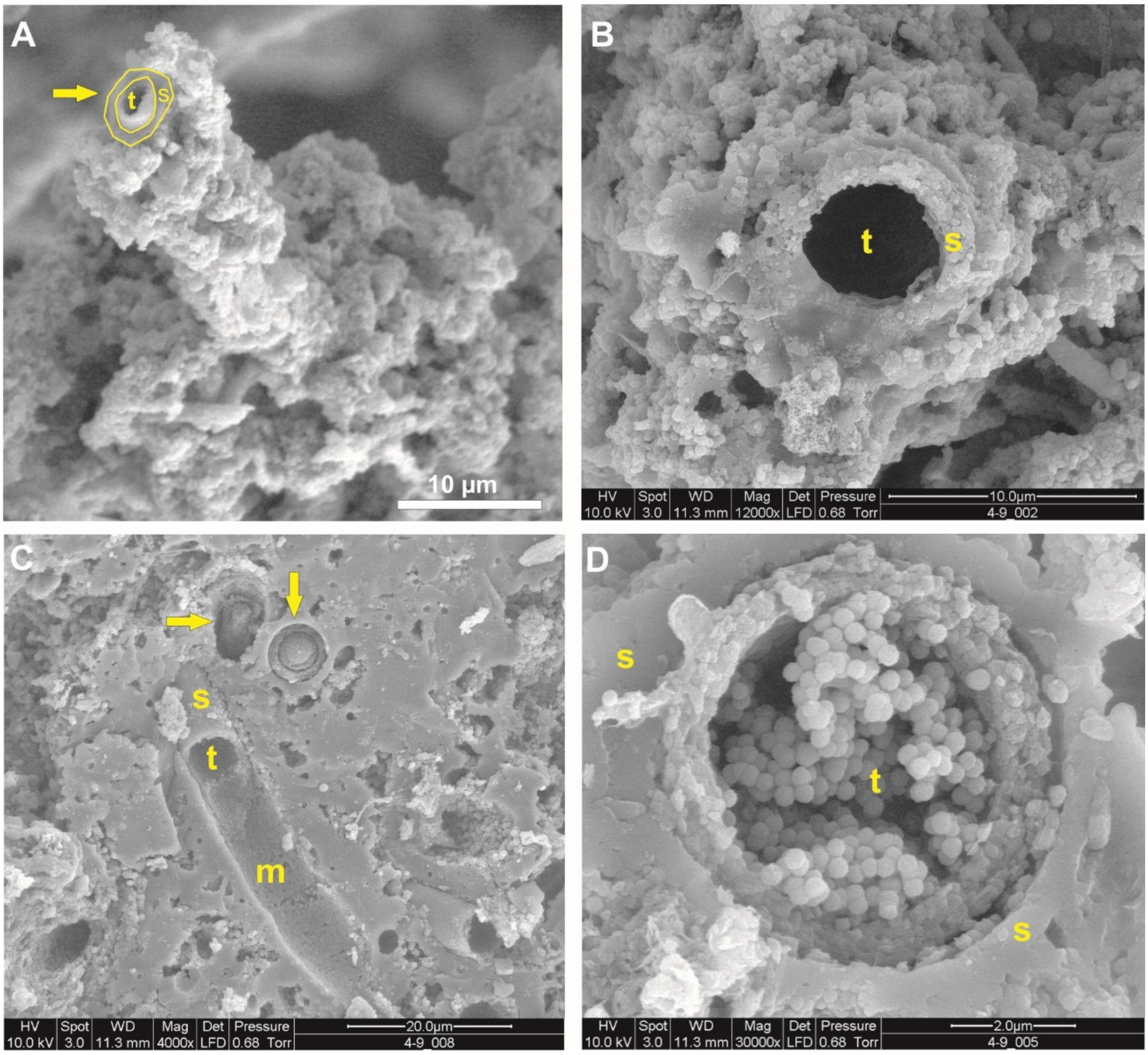

Figure 2: Preservation style of low-temperature sized filament sheaths and trichomes. Total exterior diameters of 6 to 8 µm. Sample 4-9. (A) Microbial filament (arrow) with hollow trichome (t) and outer sheath (s). Total microbial filament exterior diameter is 6 µm and is encrusted with opal-A spheres. Large voids within sample creating a porous sinter. (B) Outer sheath (s) silicified with opal-A spheres. No inner trichome preserved (t). (C) Filament mold (m), hollow outer sheath (s) preserved via permineralization and no trichome preservation (t). Arrows indicate other filamentous microbes within the sample. (D) Outer sheath (s) silicified with opal-A spheres. Opal-A spheres also infill void where trichome would have once occupied (t).

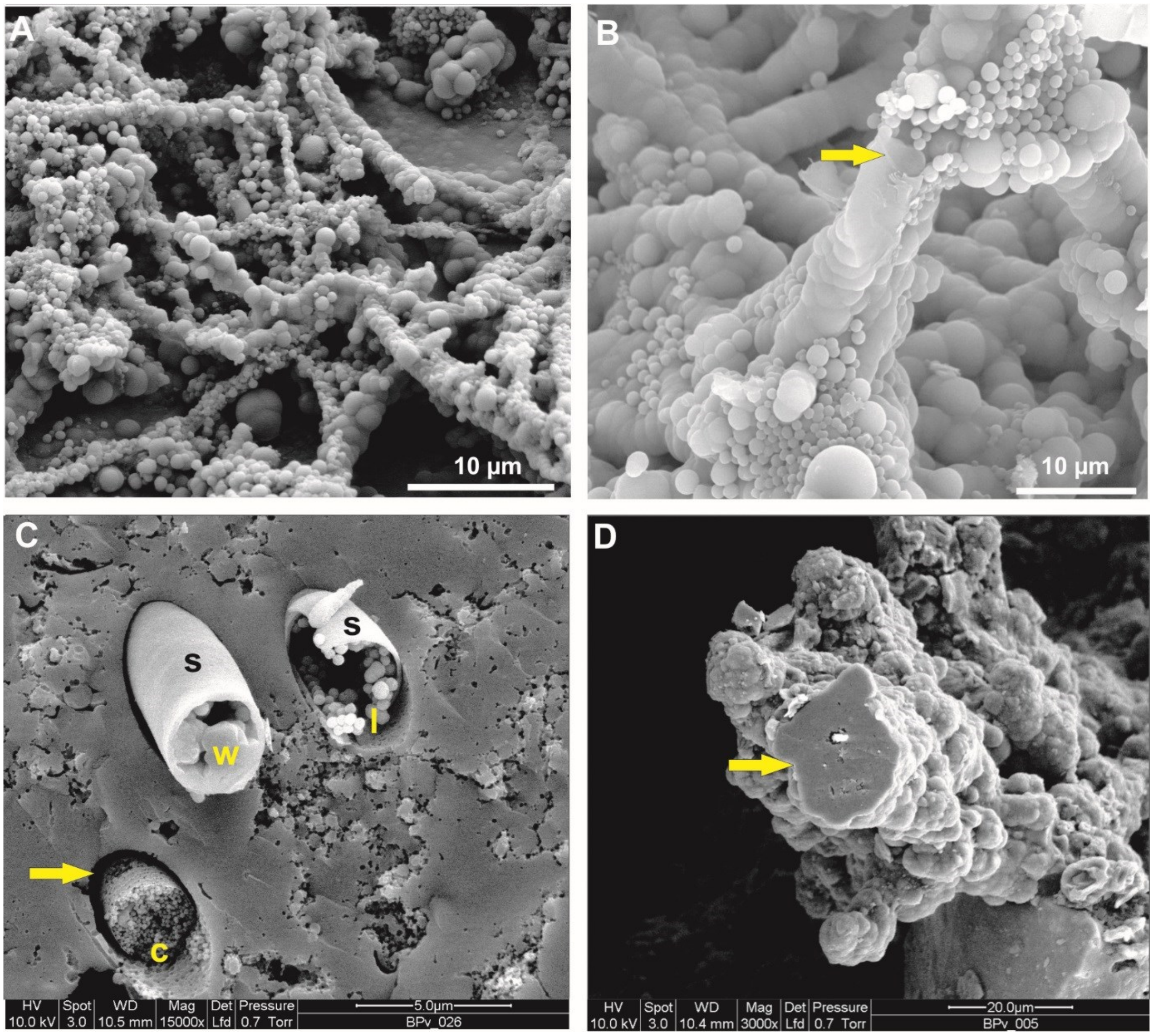

Figure 3: Preservation style of low- and mid-temperature sized filaments. (A-B) Sample Ge. Mid-temperature filaments with total exterior diameters of <4 µm. (A) Encrustation of filaments with opal-A spheres within a porous sinter. (B) Filament showing no distinction between sheath and trichome due to vitreous silica infill (arrow). (C-D) Sample BPv. (C) Filaments ~3 µm in total exterior diameter are preserved in a variety of styles from permineralization of outer filament sheaths (s) to no outer sheath preservation (arrow). Hollow sheaths partially infilled with loosely-compacted, opal-A spheres (l), opal-A spheres welded together (w), or closely-packed opal-A spheres (c) completely replacing filament leaving no evidence of outer sheath or trichome. Pitted smooth silica surface suggests minor dissolution via acidic steam condensate. (D) Outer filament sheath encrusted with opal-A spheres. 2 µm diameter trichome protrudes from sheath that is infilled with vitreous silica (arrow). Low-temperature sized filament with a total exterior diameter of 20 µm.

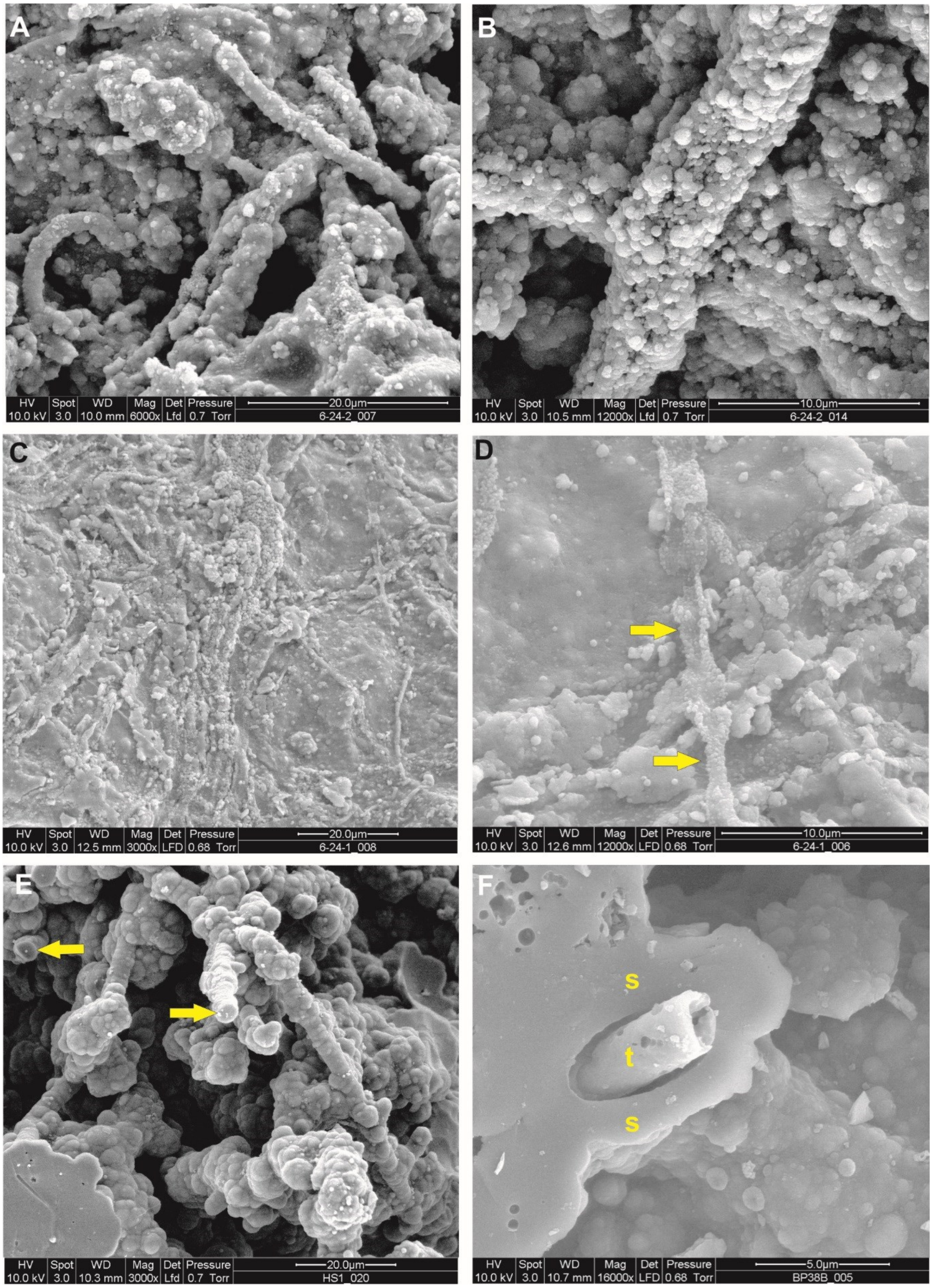

Figure 4: Low- and mid-temperature sized filaments with a range of preservation styles. (A-B) Sample 6-24. Mid-temperature sized filaments, 4 µm in total exterior diameter. Filament sheaths encrusted with opal-A spheres in a porous sinter matrix. Zones within the sample also display smooth silica with minimal opal-A spheres. (C-D) Sample 6-24. Mid-temperature sized filaments, 1.5 µm in total exterior diameter. (C) Overview of filaments in smooth vitreous silica matrix. (D) Partially decayed filament outer sheath with opal-A spheres clustering and infilling empty sheath (arrows). (E) Sample HS1. 4 µm total exterior diameter, mid-temperature filaments (arrows) infilled with vitreous silica with trichome extruding from centre. Exterior of sheaths encrusted with botryoidal opal-A spheres. (F) Sample BP38. 8 µm total exterior diameter of low-temperature filament showing sheath (s) and trichome (t). Minor pitting on smooth surfaces indicate post-depositional dissolution via acidic steam condensate.

In summary, encrustation and permineralization preservation processes act on the filamentous microbes within our samples from the sinter terrace surrounding Old Faithful Geyser. Low-temperatures filaments have undergone preservation via both encrustation and permineralization, as have mid-temperature filaments. Encrustation and permineralization preservation processes can be further sub-divided into six preservation styles to create a wide array of microbial preservation sinter architecture within our samples (Fig. 5; Table 1).

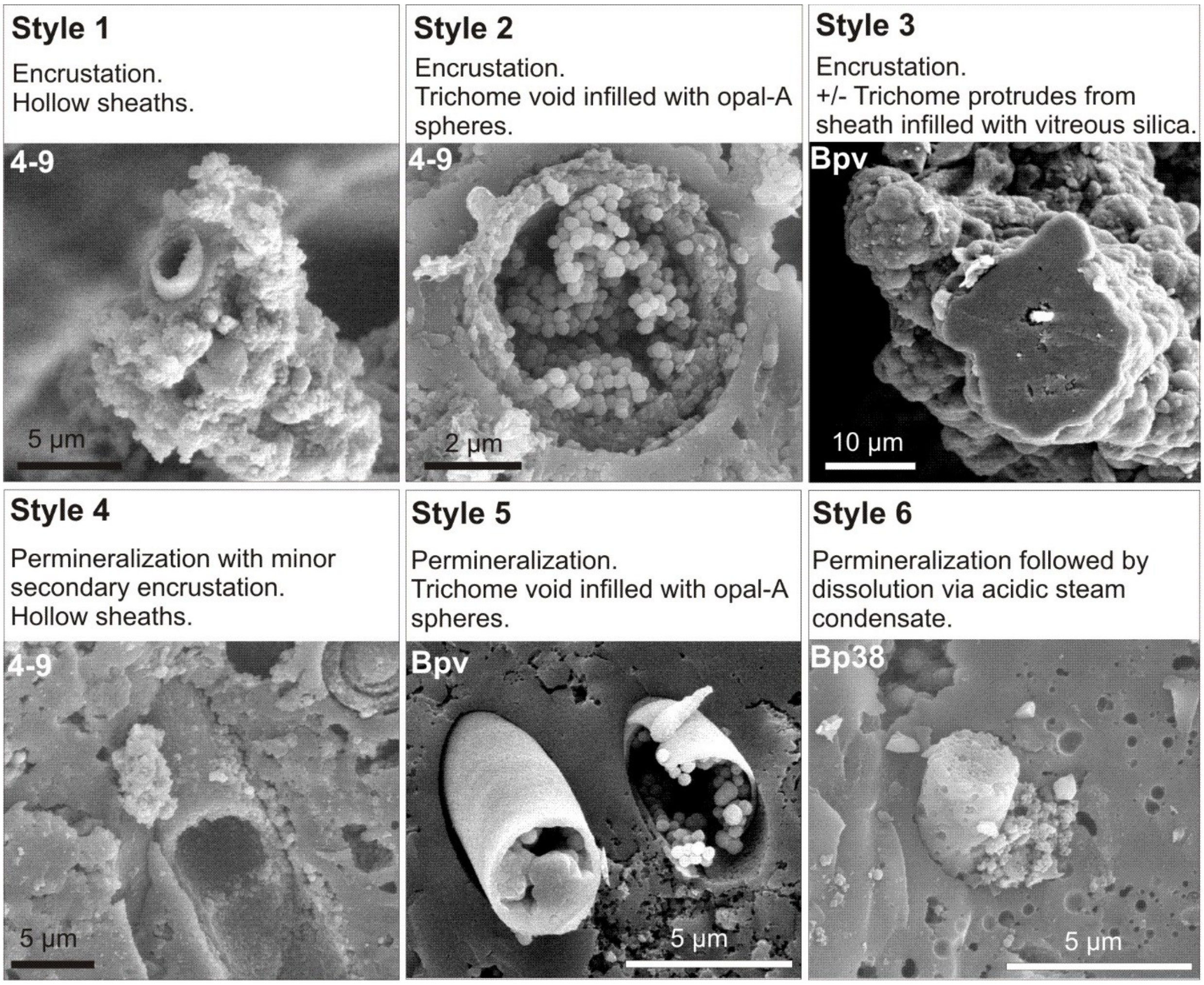

Figure 5: Six styles of microbial preservation observed in sinter from the surrounding apron of Old Faithful Geyser. Sample number of image given in upper left corner.

Table 1: Microbial preservation style observed in sinter samples from the Old Faithful Geyser sinter apron.

Style	Style description	Low-temperature microbes sample number	Mid-temperature microbes sample number
1	**Encrustation** of outer sheath by opal-A spheres and no trichome preservation leaving hollow sheaths.	4-9	
2	**Encrustation** of outer sheath by opal-A spheres and no trichome preservation but trichome void infilled with opal-A spheres.	4-9	6-24
3	**Encrustation** of outer sheath with opal-A spheres +/- trichome protruding from sheath that is infilled with smooth vitreous silica.	BPv	Ge HS1
4	**Permineralization** resulting in smooth silica outer sheath and no trichome preservation leaving hollow sheaths. Minor, secondary opal-A encrustation on outer sheath.	4-9	
5	**Permineralization** with smooth silica and no trichome preserved but trichome void partially infilled with opal-A spheres.		BPv
6	**Permineralization** followed by dissolution.	BP38	

DISCUSSION

In our samples, preservation via encrustation is favoured over permineralization. Microbial filaments within samples 4-9, BPv 6-24, Ge and HS1 all revealed encrustation of their sheaths with opal-A spheres. Samples 4-9, BP38 and BPv also contained microbial filaments that were preserved via permineralization resulting in smooth silicified surfaces. These two differing preservation processes indicate a variety of mechanisms control microbial preservation.

Permineralization and encrustation are the result of two different depositional processes. Permineralization requires the opal-A precipitate to penetrate microbial cells and completely replace them. For encrustation processes, the opal-A precipitate deposits on microbial sheath exteriors. To allow cell penetration for permineralization processes, the opal-A must be small enough to penetrate cell membranes and significantly smaller than the opal-A precipitates required for encrustation.

The size of the opal-A spheres can be explained by: (1) The level of oversaturation of silica in solution, which influences the degree of silica polymerization and nucleation. When the degree of oversaturation of silica is high, silica polymerization results in the formation of colloids and opal-A spheres deposit (Iler, 1979). If oversaturation of silica in solution remains low, polymerization does not occur so readily and monomeric silica deposits to form vitreous silica (Iler, 1979); (2) Flow rates: At low flow rates, silica colloids have time to grow and flocculate producing precipitates of opal-A spheres which subsequently deposit on any available substrate such as filamentous microbes. In fast-flow conditions the silica colloids do not have time to grow and flocculate so the colloids remain small (Iler, 1979).

Two samples (4-9, BPv) that showed preservation via encrustation (Styles 1-3) also revealed low-temperature microbes. The hot spring setting that favours low-temperature microbes is typically a shallow, slow-flow setting, where ponding often occurs and the water temperature is <35 °C. This setting would provide ideal conditions for silica colloids to flocculate with ample time to grow prior to deposition. Three samples (6-24, Ge, HS1) also showed filamentous preservation via encrustation (Styles 2 and 3) but with mid-temperature sized filaments. Encrustation suggests slow-flow water but as it is mid-temperature filaments that are preserved, their presence suggests ponded water in the temperature range of 35-59 °C.

Three of our samples fall into Style 3 category (HS1, BPv, Ge) which show encrustation of microbial exterior sheaths and vitreous silica infill. The combination of both encrustation and vitreous silica infill suggests variations in the level of silica oversaturation and/or flow rate. Sample BPv was located adjacent to a vent and sample Ge was located adjacent to Old Faithful Geyser vent. Their close proximity to vents may have influenced their microbial preservation style. In these near-vent settings, the force behind eruptive events results in rapidly ejected water with subsequent fast-flow rates over existing sinter terraces. Between eruptive cycles, the water ponds until either evaporated or another eruption occurs. During the ponding time, silica polymerization, nucleation and flocculation could take place. The combination of fast- and slow-flow rates at the same site could explain the combination of encrustation and vitreous silica preservation style (Style 3). Furthermore, sample BPv contained both low- and mid-temperature microbes. This indicates changes in the discharging water temperature between <35 °C and 35-59 °C. Dual preservation styles and the preservation of both low- and mid-temperature microbes suggest variable flow rates and water temperatures discharged from the vent adjacent to sample site BPv. These findings suggest microbial preservation of sinters in vent locations is complex and involves several preservation mechanisms.

Sample 4-9 further demonstrates the complexity of preservation with three microbial preservation styles observed within the same sample. In all three preservation styles, the trichome was not preserved. Two of the preservation styles consist of encrustation (Styles 1 and 2) while the third style is permineralization (Style 4). The degree of oversaturation of silica with respect to opal-A and localised flow rates can account for the variety of preservation styles.

These rare samples provided an opportunity to examine microbial preservation in samples from the sinter terrace surrounding Old Faithful Geyser. Our study has shown that filamentous microbes are well-preserved but their preservation is dependent on complex interactions between depositional conditions, flow rates, hot spring setting and silica oversaturation levels of the discharging fluid.

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