Laminae development in opal-A precipitates associated with seasonal growth of the form-genus *Calothrix* (Cyanobacteria), Rehai geothermal area, Tengchong, Yunnan Province, China

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ABSTRACT

The western discharge apron at Meinuquan (Rehai geothermal area, Yunnan Province, China), which incorporates the upper terrace, terrace front, and lower terrace, is covered with laminated opal-A precipitates that have formed from the spring waters that flow across its surface. Laminae are formed of silicified *Calothrix* mats or featureless opal-A that contain no microbes, scattered spherical and rod-shaped microbes, and/or rare *Calothrix.* Rapid silicification of the *Calothrix* led to preservation of their basal heterocysts, vegetative cells, trichomes, tapering filaments, and laminated and splayed sheaths.

The *Calothrix* mats grew during the dry season when there was maximum sunlight because of low cloud cover. During this time, the mats grew under stable conditions because the water that flowed across the discharge apron was sourced from the springs, and temperature and water geochemistry was more or less constant. Growth of the *Calothrix* mats decreased during the wet season (April to late September) when sunlight is reduced due to the extensive cloud cover associated with the monsoonal rains. During the wet season, water flowing over the discharge apron is a mixture of rainwater, runoff from the surrounding hillsides, and spring water. Such variable flow conditions, water temperatures, and water geochemistry curtailed microbe growth and impacted silica precipitation.

The precipitates at Meinuquan are like those associated with some Icelandic hot springs. Although growth of *Calothrix* is controlled by sunlight in both settings, the periods of maximum sunlight in China (October-March) and Iceland (June-August) are at different times of the year because of their geographic locations.

Keywords: Opal-A, *Calothrix*, hot springs, microbe silicification, seasonal laminae.

1. Introduction

The form-genus *Calothrix,* first described and defined by Agardh (1824), is a common filamentous cyanobacterium found in modern spring systems throughout the world, including those in Yellowstone National Park (Weed, 1889; Tilden, 1897, 1898; Copeland, 1936; Norris and Castenholz, 2005), Iceland (Konhauser et al., 2001), New Zealand (Cassie, 1989), India (Roy et al., 2014), and Bulgaria (Lukavský et al., 2011). Although some species of *Calothrix* can survive in water temperatures up to 52-54°C (Castenholz, 1969, his Table 3; Colwell and Fuentes, 1975, their Fig. 2), most thrive where the water temperatures are in the 20-40°C range (Copeland, 1936; Nash, 1938; Walter, 1976; Cady and Farmer, 1996; Walter et al., 1996). Many other environmental factors also influence the growth and development of *Calothrix*, including UV radiation (Brenowitz and Castenholz, 1997; Dillon and Castenholz, 2003; Dillon et al., 2003; Norris and Castenholz, 2005). *Calothrix* has commonly been used to assess microbe silicification because naturally silicified specimens are abundant (Hugo et al., 2011) and this cyanobacterium is susceptible to silicification under controlled laboratory conditions (Phoenix et al., 2000, 2002; Yee et al., 2003; Benning et al., 2004, 2005).

This study focuses on laminated opal-A deposits that cover a hot-spring Meinuquan (Beauty Pond) discharge apron that is located in the Rehai geothermal area, which is situated ~13 km southwest of Tengchong in the Yunnan Province of China (Fig. 1). The stratigraphic architecture of these opal-A deposits is fundamentally control by the silicification of the *Calothrix* mats that thrived on this discharge apron. Using these samples, this paper focuses on (1) preservational aspects of *Calothrix* from different parts of the discharge apron, (2) the significance of the pigmentation that is evident in the silicified sheaths of some of the *Calothrix*, and (3) interpretation of the cyclic alternation between laminae formed of silicified *Calothrix* and laminae devoid of *Calothrix*. Through careful examination of the textures in the siliceous sinters, this research shows that the dry season, which is characterized by low rainfall and low cloud cover but many hours of sunshine, encouraged growth of the *Calothrix* mats whereas the onset of heavy rain and reduced hours of sunlight in the wet season led to the death of the *Calothrix* mats.

2. General setting

2.1. Geological setting

The Rehai Geothermal Field (Fig. 1B), characterized by numerous active springs with highly variable water temperatures, pH values, compositions (Table 1), and diverse arrays of microbes (Lin et al., 2002, 2005; Guo et al., 2003; He et al., 2004; Chen et al., 2008; Ding et al., 2008; Jiang et al., 2009; Lu et al., 2009; Song et al., 2009, 2010; Han et al., 2010; Hong et al., 2010; Hedlund et al., 2012; Briggs et al., 2014), is centered on the Ruidian-Tengchong Fault. The geothermal waters, which are probably of meteoric origin, are heated in the subsurface by magma (Zhao et al., 1996, their Fig. 3; Du et al., 2005; Shangguan et al., 2005) or the Yanshanian granite (Liao et al., 1991; Yan and Wan, 1998). The Tengchong volcanic field is located at the east end of the Xizang (Tibet) – Yunnan geothermal zone (Tong and Zhang, 1989; Kearey and Wei, 1993) near the border between China and Myanmar (Fig. 1A). Numerous volcanoes and extensive faulting characterize this area (Jiang, 1998; Jiang et al., 1998; Du et al., 2005; Wang et al., 2006), which formed when the Burmese Block was thrust under the Tengchong Microplate during the Cenozoic (Shangguan et al., 2005). Earthquakes are still common in the area today.

2.1. Climate

Detailed climate data are not available specifically for the Rehai geothermal area. Thus, the climate records for Tengchong county as provided by the China Meteorological Data Sharing System (http://cdc.cma.gov.cn) are used in this study.

This part of the Yunnan Province enjoys a highland subtropical climate with an average rainfall of 1480 mm/year and an average air temperature of 14.9°C (based on 1971-2000 period). The climate records between 2000 and 2013 are characterized by the following annual patterns.

- Annual variations in temperature that range from 1 to 17°C in December-January to 17-24°C in July, August, and September (Fig. 2A).
- Monthly rainfall that varies form 0 mm in January to as high as 375 mm in July (Fig. 2B).
- The maximum hours of sunshine is in the dry season (250-280 hours/month from October to April) when there is little cloud cover whereas the minimum hours of sunshine (less than 100 hours/month) is in the wet season (May to September) when there is maximum cloud cover because of the monsoonal rains (Fig. 2C).

Collectively, the temperature, rainfall, and hours of sunshine divided each year into the dry season (low T, low rainfall, high sunshine) and the wet season (high T, high rainfall, low sunshine). The wet season typically lasts from May to late September with the dry season extending from October to April.

3. Methods

Examination of the Meinuquan (Fig. 1C) complex took place in 2011 and 2013 when the discharge apron and nearby springs were examined, described, photographed, and water temperatures and pH measured. Samples of opal-A precipitates and water were collected in April, 2013. Water samples were passed through a syringe filter with a 0.22 μm filtration membrane before being stored in polypropylene bottles until analysis for major cations and anions at the Saskatchewan Research Council (Canada), about 4 weeks after they had been collected. The elements Ca, Mg, Na, K, Si and S were determined by Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES) and alkalinity (including p alkalinity) was determined by titration with sulphuric acid on an auto-titration system. The bicarbonate, carbonate and hydroxides were calculated from the pH and alkalinity results. The chloride was measured colorimetrically and fluoride was determined by ion selective electrode.

Samples of the precipitates were collected (with permission) where possible. Given that this is a major tourist attraction, sampling was done carefully so that little or no visible damage was done. In the Meinuquan complex, for example, sampling was restricted to the western discharge apron (Fig. 3) where short (up to 2 cm long) cores (1.5 cm and 3.0 cm diameter) were obtained from the upper terrace, the terrace front, and the lower terrace. Where possible, small hand samples were extracted.

Thermal images of the surfaces on the discharge apron were taken using a Fluke Ti 100 Thermal Imager, which measures temperatures from -20 to 250°C with a measurement accuracy of 2%.

Six large (3 x 2 cm) and two small (4.5 x 2 cm) thin sections, each impregnated with blue epoxy, were made from the available samples so that the fabrics of these precipitates could be established with particular emphasis being placed on the lamination styles.

Small fracture samples, broken from the cores and hand samples, were mounted on scanning electron microscope (SEM) stubs using conductive glue and then sputter coated with thin layer of carbon so that they could be examined on a JOEL 6400FE scanning electron microscope. Imaging was done with an accelerating voltage of 5 kV whereas energy-dispersive

X-ray (EDX) analyses and back scattered electron imaging (BSEI) were done with an accelerating voltage of 20 kV. The location and orientation of all samples was recorded so that the different fabrics could be related to each other. The 436 SEM photomicrographs formed an integral part of this study.

4. The Meinuquan complex

The Meinuquan (Beauty Pond) complex consists of a large, triangular shaped, varicoloured discharge apron that is bounded by a wall (up to 6 m high) on its north side and footpaths along its west and south margins (Fig. 1C). Most of the water that flows over this apron comes from Yanjiangquan (Figs. 1C, 3A), Zhenhuquan (Figs. 1C, 3A), and Gumingquan (Figs. 1C, 3B) springs, which are located on the north side of the footpath that is located on top of the wall that defines the northern boundary of the discharge apron (Figs. 1C, 3A). All of these springs have, to some extent, been anthropogenically modified.

The Meinuquan discharge apron is herein divided into the "eastern discharge apron" and the "western discharge apron" (Figs. 1C, 3A). The eastern discharge apron is formed of a raised, sloping bench that is bounded to the north by a vegetated area and the north wall and to the south by a narrow terrace (Fig. 3B). Along the south edge of the terrace, there is a steep drop-off to the pathway that is located below (Fig. 3B). Most of the water on this part of the system comes from Gumingquan (Drum Beating Spring), which discharges water with a T of 87°C, pH of 8.8, and a flow rate of 1.19 L/sec (Fig. 1C).

The "western discharge apron", which is ~ 14 m long (parallel to flow direction), ~ 12 m wide, and 5 m high, is divided into (1) the upper terrace that is centered around the top pool and has a low downslope gradient, (2) the terrace front where there is steep drop-off from the upper terrace, and (3) the lower terrace with a low downslope gradient that stretches from the base of the terrace front to the pathway (Fig. 3A). The water that flows across this discharge apron comes from Yanjiangquan and Zhenhuquan (Figs. 1C, 3A). Yanjiangquan (Sisters Spring) comprises the Young Sister that discharges water at ~86°C, pH of 9.0, and a flow rate of 0.3 L/sec and the Old Sister that discharges water at 91°C, pH of 8.9, with a flow rate of 0.2 L/sec. Zhenhuquan (Pearl Spring) discharges water with a T of 91°C, pH of 3.8, and a flow rate of 0.2 L/sec. The water from each of these springs discharges into small channels located on the north side of the footpath that is located at top of the wall that forms the northern margin of the Meinuquan complex. That water then flows through a pipe under the footpath and cascades down the wall into a shallow pool at the foot of the wall (Fig. 3A). The water in that pool has a temperature of 66° and pH of 9.1 (Fig. 1C). From there, the water disperses down the discharge apron. By the time it has reaches the channel at the bottom of the apron, the water has a T of 34°C and pH of 9.5 (Fig. 1C).

4.1. Water flow on western discharge apron

Water flow from the top pool is generally low because of the low combined volume (~ 42 L/min) of water that comes from Yanjiangquan and Zhenhuquan. This flow is focused largely into shallow, narrow channels that radiate downslope (Fig. 3A). Although the water in the channels may be up to 5 mm deep, it is typically no more than a thin film. Areas between these channels are dry or damp. The pattern of water dispersal across the discharge apron is highlighted by the colorful microbial mats that preferentially develop in the channels and along the margins of the channels (Fig. 3A).

The water in the top pool has a temperature of 66°C, whereas water in channels on the lower terrace has a temperature of 34°C. Thermal imaging shows that the laterally and vertically complex temperature gradients on the discharge apron are centered on the channels with flowing water (Fig. 4A-F). Thus, areas on the terrace front covered with black microbial mats are usually the "hot" areas with temperatures in the 40 to 50°C range, whereas areas devoid of microbial mats are typically "cold" with temperatures in the 20 to 25°C range (Fig. 4A-F). Areas between the "hot" and "cold" zones have transitional temperatures that are typically about 35°C (Fig. 4D). In many of the "warm" and "hot" areas there is no obvious running water and it is only with careful inspection that it becomes apparent that these areas are either damp or covered by a thin film of flowing water. In these areas it is impossible to measure the water temperature with a conventional thermometer.

On days when there is heavy rainfall, the entire surface of the discharge apron becomes soaked as the rainwater flows downslope, and runoff from the steep slopes around Meinuquan flows downslope. Mixing of the rainwater with the spring water leads to dilution of the spring water and reduction in its temperature and pH. During periods of heavy rainfall, the combined volume of rainwater and runoff may exceed the volume of spring water that is fed onto its surface. During the dry season, conditions on the Meinuquan discharge apron are relatively stable because virtually all of the water comes from the springs. During the wet season, however, conditions are highly variable with water temperature and geochemistry varying as rainwater and runoff mix with the spring discharge.

4.2. Surface deposits on the western discharge apron

The upper terrace is covered with white, laminated opal-A deposits that have a smooth surface (Fig. 5A). As the gradient becomes steeper, shallow rimstone pools develop. The terrace front is characterized by numerous microgours (Fig. 5B) that are morphologically akin to microgours found on the terrace fronts on Waikite Geyser in New Zealand (Jones et al., 2011, their Fig. 9E). These semi-circular microgours, with raised outer rims, are up to 3 cm long (parallel to terrace front) and up to 1 cm wide (90° to terrace front). Neighbouring microgours commonly merged to form larger structures (Fig. 3B). After heavy rain, water fills the small pools that commonly appear to have minor amounts of sediment on their floors.

The wet parts of the terrace front, located around the narrow streams of flowing water, are typically covered by green to black microbial mats that mask the underlying microgours (Fig. 5C-E). In areas with the highest water flow, filamentous microbes, up to 2 cm long, are highlighted by their coating of white opal-A that contrasts sharply with the green to black microbial mats in the background (Fig. 5D, E).

The surface of the discharge apron, especially in the marginal areas, is commonly covered with leaves, twigs, and pieces of grass that have come from the vegetation that grows around the spring. The opal-A encrusted leaves, twigs, and grass are commonly incorporated into the opal-A that has been precipitated on the surface of the terrace (Fig. 5F). Small lithoclasts formed largely of laminated silica, up to 10 cm long, 10 cm wide, and 5 cm thick, are scattered across the surface of the discharge apron (Fig. 5G). They are most common on the upper terrace and along the western margin of the lower terrace. Some are loose whereas other are cemented to the surface of the discharge apron (Fig. 5G).

5. Silicified biota

The opal-A precipitates on Meinuquan are characterized by laminae that are formed of *Calothrix* mats (Figs. 6-9) and laminae that contain various spherical, rod-shaped, and small, bicellular micorbes but few *Calothrix* (Figs. 10, 11).

5.1. Calothrix – *upper terrace*

On the upper terrace, *Calothrix* grow in tufts that are formed of numerous erect filaments (Figs. 6A, 7A, B). No pigmentation (Fig. 6A, 7A-C) is associated with these filaments that are (1) characterized by basal heterocysts that are 3.2 to 6.0 µm (average 4.3 µm) in diameter and 2.7 to 5.5 µm (average 3.8 µm) long, and separated by a septum from the first vase-shaped vegetative cell that is 3.7 to 6.6 µm (average 5.3 µm) in diameter and 5.2 to 7.0 µm (average 5.8 µm) long (Fig. 8C-E), (2) a septate trichome with vegetative cells that are 10-25 µm long and 4-6 µm in diameter (Fig. 8F), and (3) a sheath that has an external diameter up to 12 µm (Fig. 8G, H). The outer and inner surfaces of the trichomes are commonly covered with spherical particles of opal-A that are up to 1 µm in diameter (Fig. 8H). In contrast, the sheath is typically formed of polygonal opal-A particles that are up to 1 µm long (Fig. 8I).

The filaments in the tufts are heavily encrusted with opal-A (Fig. 6A). The thickness of the encrusted opal-A typically increases toward the distal ends of the filaments and commonly result in numerous filaments being encased by the same mass of opal-A (Figs. 6A, 7A-C). The amount of opal-A precipitated around and between the filaments varies along individual lamina and from lamina to lamina (Fig. 6).

5.2. Calothrix – *terrace front and lower terrace*

Like the *Calothrix* that form the mats on the upper terrace, the *Calothrix* (Fig. 6B, C) that form the mats on the terrace front and lower terrace (1) have a basal heterocyst (Fig. 8B, C), (2) taper distally (Fig. 9D), (3) have a sheath that in their distal parts, commonly splays outwards (Fig. 9E), and (4) are septate (Fig. 9F). These *Calothrix*, however, differ from those on the upper terrace by being larger in diameter (5 - 10 µm versus 3 - 5 µm), and having pigmented sheaths that appear yellow to dark brown when viewed in thin section under plane polarized light (Figs.

6B, C, 7D-G). BSEI and EDX analysis on the SEM did not reveal any detectable levels of elements other than Si in the silicified *Calothrix*. Thus, the colour is attributed to pigmentation that is inherent to the sheaths of the formative filaments. Patterns of silicification evident in the *Calothrix* from the terrace front and lower terrace include spherical beads of opal-A, ~ 1 µm in diameter, that commonly coat the inner and outer surfaces of the trichome wall (Fig. 9G, H), a sheath (Fig. 9I), with an external diameter of up to 16 µm that has been replaced by polygonal opal-A grains (Fig. 9J-K) that contrast sharply with the spherical opal-A spheres that coat the trichome (Fig. 9G, H).

5.3. Other microbes

Samples from all parts of the discharge apron include thin (< 0.5 mm) laminae formed largely of homogeneous opal-A (Fig. 10A, B) that have a glassy appearance in hand sample. Although *Calothrix* are typically absent from these laminae, there are examples where *Calothrix* filaments extent from the underlying mat, through the opal-A laminae, and into the overlying *Calothrix* mat. On the upper terrace, some of these opal-A laminae are characterized by micro-laminae that are defined by the presence of various types of microbes (Fig. 10C-H). The boundaries between the micro-laminae are poorly defined and commonly gradational (Fig. 10C). Microbes found in these laminae include spherical bodies up to 2 µm in diameter (Fig. 10D), and rod-shaped microbes up to 2 µm long and 0.5 µm in diameter (Fig. 10E). Homogeneous opal-A that commonly fills the gaps between the upper parts of the *Calothrix* filaments that extend from the underlying mats (Fig. 10F) can also contain various types of microbes (Fig. 10G, H).

On the terrace front and lower terrace, the laminae formed largely of homogeneous opal-A contain spherical microbes, rod-shaped microbes, and small-diameter, septate filaments (Fig. 11).

5.4. Taxonomic affinity of silicified biota

5.4.1. Calothrix

The silicified filamentous microbes that form the microbial mats on the upper terrace, the terrace front, and the lower terrace are morphologically consistent with form-genus *Calothrix* as described by Copeland (1936), Cassie (1989), Rippka et al. (2001), Uher (2007), Shalini et al. (2009), Berrendero et al. (2011), and Rinkel and Manoylov (2014). Diagnostic features include (1) large diameter, septate trichomes that taper distally (Fig. 9D), (2) the presence of a basal heterocyst (Figs. 8C-E, 9B, C), (3) a laminated sheath (Figs. 8G-I, 9I-K) that commonly splays in the more distal regions (Fig. 9E), and (4) the presence of a pigmented sheath for the filaments from the terrace front and lower terrace (Fig. 7D-G). These silicified filaments are morphologically akin to silicified specimens of *Calothrix* that have been described from various hot spring systems on the North Island of New Zealand, including those from Dragon's Mouth Geyser (Jones et al., 1997, their Fig. 10A-J), Ohaaki Pool (Jones et al., 1998, their Figs. 12, 14), and Tokaanu (Jones et al., 2003, their Figs. 7A-D, 8A, B).

From a morphological perspective, the *Calothrix* found on the upper terrace differ from those found on the terrace front and lower terrace by virtue of (1) their different growth styles, (2) the differences in the diameter of the filaments, and (3) the presence/absence of pigmentation in the sheaths. Although both have the fundamental characteristics of *Calothrix,* these differences are probably indicative of two different species. Although at least 80 freshwater and 14 marine morphotypes of *Calothrix* have been defined from temperate, subtropical, and tropical areas, many are difficult to identify (Rinkel and Manoylov, 2014). Thus, for the purposes of this study, the specimens from the upper terrace are referred to as *Calothrix* sp. A, whereas those from the terrace front and the lower terrace are referred to as *Calothrix* sp. B.

5.4.2. Other microbes

The microbes found in the opal-A precipitates from Meinuquan can only be characterized in terms of their shape, size, and for some specimens the presence of septa (Figs. 10, 11). The lack of diagnostic morphological features precludes identification.

6. Laminations

All of the opal-A precipitates on the Meinuquan discharge apron are laminated, with the laminae being highlighted by variations in colour, texture, and porosity (Figs. 6, 7D-G). The laminae found on the upper terrace are subtly different from those found on the terrace front and lower terrace.

Silicified *Calothrix* mats up to 4 mm thick dominate the precipitates that are found around the pool on the upper terrace (Figs. 6A, 10A). These silicified mats are either stacked one on top of the other or separated by laminae, typically < 1 mm thick, that are formed of dense, largely featureless opal-A (Fig. 6A). The variable appearance of the silicified *Calothrix* mats in hand sample and thin section is largely a function of the amount of opal-A that was precipitated around and between the filaments. Thus, areas with little opal-A encrustation are far more friable than those parts of the mats where opal-A encrustation around the filaments was extensive (Fig. 6A). Sharp, well-defined bases but diffuse, irregular upper boundaries characterize all of the laminae formed by the *Calothrix* mats (Fig. 9A).

On the terrace front and lower terrace, the opal-A precipitates are formed of alternating *Calothrix* mats and layers of homogeneous, glass-like opal-A. The deposits on these parts of the discharge apron are much harder than the precipitates found on the upper terrace. The silicified *Calothrix* mats on the terrace front and lower terrace differ from those on the upper terrace because (1) they are accentuated by the yellowish-brown pigmentation of the *Calothrix* sheaths

(Figs. 6B,C, 7D-G), (2) the growth patterns of the *Calothrix* are different, and (3) the patterns of opal-A precipitation around those filaments are also different (Fig. 6). In contrast, the laminae formed of homogeneous, glass-like opal-A with scattered non-filamentous microbes are the same over the entire extent of the discharge apron (Figs. 10, 11). On the lower terrace, the uppermost parts of these laminae, just beneath the base of the filamentous microbial mats, are commonly characterized by small (< 0.15 mm long), subangular to angular grains that are formed of opal-A, K-feldspar, and quartz (Fig. 6G).

7. Discussion

Laboratory experiments designed to examine the factors that control microbial silicification commonly use *Calothrix* because of its apparent susceptibility to silicification (e.g., Phoenix et al., 2000, 2002; Yee et al., 2003). Based on experiments involving *Calothrix* collected from Krusivik hot spring (Iceland), Phoenix et al. (2000) showed that (1) filaments became covered with a mineral crust, up to 5 μm thick, after only 12 days in a silica solution, (2) mineralization was restricted to extracellular material such as the sheath, and (3) the sheath allowed the microbes to survive because it provided sites for mineralization and acted as a filter against colloidal silica. Later experiments with the same strain of *Calothrix* led to the conclusion that this microbe was characterized by a highly reactive cell wall but a poorly reactive sheath (Phoenix et al., 2002). Further experiments with the same strain of *Calothrix* led Yee et al. (2003) to postulate that silica precipitation was largely abiogenic. Benning et al. (2005), however, argued that the single-step batch experiments used by Phoenix et al. (2000, 2002) and Yee et al. (2003) did not accurately reflect conditions in hot spring systems. They noted that other experiments that used organosilicon solvents or inorganic silica concentrations showed that microbial silicification depended on many different complex interactions (Ferris et al., 1988;

Westall et al., 1995; Konhauser et al., 2001; Toporski et al., 2002; Mountain et al., 2003). Hugo et al. (2011), based on samples collected from springs in Yellowstone National Park, suggested that early silicification of *Calothrix* was focused entirely in the sheath and argued that the microbes were more actively involved with silica precipitation than previously thought. Irrespective of the nuances involved, silicification must take place because the (1) microbes cannot prevent it, or (2) silica coating is, in some way, advantageous to the organism (Phoenix et al., 2000).

Silicified *Calothrix* have been reported from spring systems throughout the world, including those in Yellowstone National Park, U.S.A. (Cady and Farmer, 1996; Hugo et al., 2011), New Zealand (Jones et al., 1997, 1998, 2001a, b, 2003; Jones and Renaut, 2003), and Iceland (Konhauser et al., 2001). Rapid silicification seems to be the norm with *Calothrix* filaments commonly being partly silicified while they are still alive (Jones et al., 1998, their Fig. 15). Silicified *Calothrix* from New Zealand, for example, are typically well preserved with distally tapering septate filaments encased by laminated and splayed sheaths (e.g., Jones et al., 2001a, their Fig. 6G; 2003, their Fig. 7C). In addition to these features, silicified *Calothrix* from Meinuquan also display well-preserved basal heterocysts (Figs. 8C-E, 9B, C), vegetative cells (Figs. 8E, F, 9C, F), and trichomes (Figs. 8D, F, H, 9F, G, I). The fact that these soft-tissue components show little evidence of shrinkage or desiccation implies that silicification was rapid and took place before decay and distortion of the soft tissues started. Silicification of these elements involved opal-A spheres that are up to 1 μm but more commonly < 500 nm in diameter (Figs. 8E, H, 9G, H). The sheaths must have also undergone rapid silicification because laminae (Figs. 8H-I, 9I, K, L) and splaying (Fig. 9D, E) are apparent in the sheaths, and pigmentation of the sheath is still evident in *Calothrix* sp. B (Fig. 7D-G). Silicification of the sheaths, however, involved the development of polygonal-shaped opal-A particles, up to 1 μm long (Figs. 8I, 9L) that contrast sharply with the spherical opal-A particles evident in the silicified cells and trichome walls (compare Fig. 9L with 9H). Such polygonal-shaped opal-A particles are not unique to the Chinese specimens because they are also evident in silicified *Calothrix* from New Zealand (Jones et al., 1997, their Fig. 10G, J; Jones and Renaut, 2003, their Fig. 6G). The reason for this contrasting style of opal-A particles is not known. These inferences regarding the rapidity of silicification of *Calothrix* are consistent with conclusions that Bartley (1996) proposed based on the experimental silicification of various types of microbes.

The pigmentation of *Calothrix* sp. B on the Meinuquan discharge apron is similar to that associated with pigmented sheaths of extant *Calothrix*, which is generally attributed to the presence of scytonemin (Brenowitz and Castenholz, 1997; Dillon and Castenholz, 2003; Dillon et al., 2003; Norris and Castenholz, 2005). Variations in the pigmentation colour depends on the amount of scytonemin in the sheaths even among populations that are, according to their 16s rDNA, closely related (Dillon and Castenholz, 2003; Dillon et al., 2003). Although the exact cause of this variation is not known, it has generally been attributed to environmental factors (Dillon and Castenholz, 2003; Norris and Castenholz, 2005). Scytonemin, which is a stable molecule that is not actively degraded by cyanobacteria (Garcia-Pichel and Castenholz, 1991; Norris and Castenholz, 2005), is important because it acts as a barrier against UV radiation (Garcia-Pichel and Castenholz, 1991; Dillon and Castenholz, 1999, 2003; Dillon et al., 2003; Norris and Castenholz, 2005). The pigmentation in the sheaths of *Calothrix* sp. B from Meiuquan accentuates the laminae that are clearly evident in hand samples (Fig. 5H) and thin section (Fig. 6D-G). In contrast to *Calothrix* sp. B, no pigmentation is evident in the sheaths of *Calothrix* sp. A (Fig. 6A-C) from Meinuquan and there is less color differential between the constituent laminae (Fig. 5G). The lack of pigmentation in the sheaths of *Calothrix* sp. A may be due to scytonemin being absent or present only in very low concentrations.

Precipitates found on the discharge aprons of hot springs, irrespective of their composition, are commonly characterized by layering that is highlighted by variations in colour, composition, and/or fabric (e.g., Walter et al., 1972; Jones et al., 1997; Kano et al., 2003; Okumura et al., 2011, 2013). Many of these successions are characterized of recurring “couplets” (paired laminae with different fabrics) that have typically been linked to cyclic variations in the local climate that operate on diurnal, seasonal, and/or annual time scales (Symoens, 1957; Monty, 1967; Walter et al., 1972; Doemel and Brock, 1974, 1977; Monty, 1976; Park, 1976; Golubic and Focke, 1978; Chafetz and Folk, 1984; Chafetz et al., 1991; Casanova, 1994; Freytet and Plet, 1996; Renaut et al., 1996; Jones et al., 1998, 1999; Konhauser et al., 2001; Kano et al., 2003; Berelson et al., 2011; Petryshyn et al., 2012) and/or seasonal variations in the composition of the microbial communities that inhabit these systems (Norris et al., 2002; Lacap et al., 2007; MacKenzie et al., 2013; Briggs et al., 2014). In such complicated systems it is perhaps not surprising that the linkage between laminae cyclicity and specific aspects of the depositional environments is difficult to identify, even when careful monitoring is employed in modern, active environments. Berelson et al. (2011), for example, showed that siliceous stromatolites from Obsidian Pool in Yellowstone National Park included 80 couplets (light lamina formed of erect filaments alternating with dark lamina formed of reclining silicified bacteria) that formed over a period of 141 days for an average of 1.75 couplets per day. They argued that this average number probably reflects the fact that there might have been days when the diurnal contrasts in factors, such as temperature, were insufficient to trigger a change in the fabrics of the precipitates.

Laminated precipitates found on the western discharge apron of the Meinuquan complex primarily reflect the growth cycles of the *Calothrix* microbial mats, whereby conditions favourable for their growth were periodically interrupted by periods when their growth ceased. *Calothrix* is a common inhabitant of those parts of hot spring systems where the water temperatures are in the 20-40°C range (Copeland, 1936; Nash, 1938; Walter, 1976; Cady and Farmer, 1996; Walter et al., 1996). Sinters from Krisuvik hot spring in Iceland are characterized by layers formed mainly of intact, vertically aligned silicified cyanobacteria (mostly *Calothrix*) that have a sharp base and gradational top that alternate with layers of opal-A that are devoid of microbes (Konhauser et al., 2001). Konhauser et al. (2001) argued that the alternating laminae must reflect the growth and activity of the microbes because the spring waters that flow across the discharge apron have a more or less constant temperature throughout the year. Thus, it was suggested that maximum growth of the *Calothrix* took place during the spring and summer when there is almost continuous daylight (~ 20 hours per day in June) given that Iceland lies close to the Arctic Circle. In contrast, during the winter month, growth of the microbial mats ceased because the number of hours of daylight is severely reduced (4 to 7 hours in January). Thus, development of the *Calothrix* mats was linked directly to the hours of sunlight that varied between different seasons.

The Meinuquan discharge apron, like Krisuvik, experiences seasonal variations in climate. In the Tengchong area, low air temperatures characterize the dry winter months even though the number of hours of sunlight is high because cloud cover is minimal (Fig. 2). During the wet season, the air temperatures are higher but the number of hours of sunlight is low because of the increased cloud cover associated with the monsoonal rains (Fig. 2). Under similar climate conditions, Lacap et al. (2007) found that floating microbial mats in tropical geothermal spring pools in the Philippines became established and grew thicker during the dry season between January to April. With the onset of heavy rains in July those mats were physically damaged and the biomass decreased. For the high temperature springs in the Rehai geothermal area, Briggs et al. (2014) found that the spring waters had higher concentrations of K, Ca, ammonia, Na, N, DOC, and $\delta^{18}O$ in June than they did in January. They argued that these changes were related to differences in the run-off from the surrounding area and/or the shallow recharge of the area, both of which are related to rainfall. Analyses of the high temperature springs (excluding Meinuquan) showed that the microbial biotas sampled in June contained more non-thermophilic microbes that samples collected in January (Briggs et al., 2014).

Growth of the *Calothrix*-dominated mats on the Meinuquan discharge apron is controlled by the interaction between the spring waters that flow over its surface and seasonal variations in the hours of sunshine and rainfall. During the dry season (October to April), rainfall is minimal (Fig. 2) and water flow over the discharge apron is sourced mainly from the springs. During those times, growth of the microbial mats and silica precipitation is controlled largely by water temperature and the geochemistry of the spring waters. Given the low volumes of spring waters that disperse across the discharge apron, growth of the *Calothrix*-dominated mats is patchy, being limited to those areas where suitable temperature regimes exist in and around the channels that funnel the spring water downslope (Fig. 4). These shallow channels are prone to frequent temporal changes in direction as opal-A precipitation commonly leads to the formation of dams across the channels that impeded downslope flow. During the wet season, two important changes take place, namely: (1) the composition of the water flowing over the discharge apron becomes more variable, ranging from just spring water on rain-free days to waters that are a mixture of rain, run-off, and spring water on wet days, and (2) on wet days water will flow over the entire surface of the discharge apron and will not be confined to the shallow channels that funnel the spring water downslope on dry days. Given that Meinuquan is located on a steep valley side, run-off can be high. Heavy rain and run-off leads to (1) the entire discharge apron being kept wet, (2) considerable volumes of non-spring water flowing over the discharge apron, and (3) cooling and dilution of the spring waters as they mix with the rainwater and runoff. Such fluctuating conditions would probably be detrimental to growth of the *Calothrix* mats and severely curtail precipitation of opal-A.

On Meinuquan, the cyclic alternation between silicified *Calothrix* mats and layers of opal-A with only a sparse microbially biota can be attributed to seasonal contrasts in the weather that have a significant impact on the volume and geochemistry of the water that flows across the discharge apron. Maximum growth of the *Calothrix* mats on the Meinuquan complex probably takes place during the dry season when the number of hours of sunlight was at its maximum and growth was associated with water that was sourced largely from the springs. Although this conclusion is similar to that reached by Konhauser et al. (2001) for Krisuvik hot spring in Iceland, it is important to note that the periods when sunlight is at a maximum is different in the two areas. For Meinuquan, growth of the *Calothrix* mats took place during the dry season from October to April when sunlight is at a maximum because of low cloud cover. In contrast, growth of the *Calothrix* mats at Krisuvik takes place during the summer months (May to August) when Iceland experiences almost continuous sunlight because of its proximity to the Arctic Circle. Although sunlight is the environmental factor that promotes the growth of *Calothrix* in both areas, the sunlight maxima in Tengchong and Krusivik occur at different times of the year because they are related to different controlling factors.

8. Conclusions

Detailed examination of recent opal-A precipitates on the Meinuquan discharge apron has led to the following important conclusions.

- The precipitates are formed of alternating silicified *Calothrix* mats and thin layers of opal-A that are generally devoid of *Calothrix.*
- *Calothrix* sp. A and sp. B are exceptionally well-preserved with basal heterocysts, distally tapering filaments, laminated and splayed sheaths, silicified vegetative cells, and trichomes being readily apparent. Such preservation indicates that rapid silicification took place before the microbes underwent desiccation and decay.
- Pigmentation of the sheath, related to the presence of scytonemin, is evident in *Calothrix* sp. B. This pigmentation, which provided *Calothrix* with UV protection, accentuates the laminated appearance of the deposits.
- The laminae reflect seasonal climate controls with the total number of hours of sunlight being the key factor. Sunlight irradiance is at a maximum during the dry season when cloud cover is minimal. In contrast, during the wet season from April to September, sunlight is reduced because cloud cover is extensive due to the monsoonal rains.
- During the dry season, the water that flows over the discharge apron is sourced largely from the springs. During the wet season, water that flows over the discharge apron is more variable because it is formed of rainwater, runoff, and spring waters.
- The alternating laminae in the opal-A deposits at Meinuquan are similar to those reported from Krusivik hot spring in Iceland. Although the hours of sunlight seem to be responsible in both settings, the actual timing differs for the two areas. On Iceland, maximum sunlight occurs during the summer, whereas on Meinuquan, maximum sunlight occurs during the winter dry season.

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FIGURE CAPTIONS

Fig. 1. (A) Location of Tengchong in western China. (B) Map of Rehai geothermal area, located about 13 km SW of Tengchong, showing locations of main springs. (C) Map of Meinuquin area (see panel B) showing location of Gumingquan, Yanjingquan, and Zhenzhuquan springs along the north margin that discharge water onto the main discharge area. The discharge apron is topographically divided into the east and west segments (see Fig. 2). Small black arrows indicate water flow directions based on observations in the field. Water temperatures (T) and pH shown for each spring were measured on April 28, 2013. Flow rates (F) provided by Rehai Geothermal area.

Fig. 2. Monthly variations in (A) temperature, (B) rainfall, and (C) hours of sunshine between January, 2000 and December 2013 for the Tengchong area based on weather records provided by the China Ground International Exchange Station. The total yearly rainfall is shown in lower right corner of each annual graph.

Fig. 3. Meinuquan complex. Black arrows indicate main water flow directions. White letter X indicates point common to panels A and B. (A) West side of complex showing discharge apron that has formed below outflow pipe that funnels water from Yanjingquan (Y) and Zhenzhuquan (Z) into the area. (B) View to northeast, taken from same spot as image shown in panel A, showing variacoloured discharge apron. Note position of Gumingquan (G) and the artificial pool that was built below Gumingquan (Fig. 3C).

Fig. 4. Paired views (A and B, C and D, E and F) of terrace front showing multicolored surfaces and corresponding thermal image of approximately the same area. For each pair of images the white arrow indicates set of keys (cold) that remained in the same place for both

images. Note lateral variations in surface temperatures and correlation between high temperature areas and coloured areas of terrace front that are covered with microbial mats.

Fig. 5. Surface features of west discharge apron at Meinuquan. (A) Upper terrace of discharge apron showing location of “top pool” beneath outflow pipe that is located near the top of the wall. (B) Microgours on surface of steep, terrace front. (C) Steep terrace front showing colour variations due to different microbial consortiums. (D) Close-up view from central part of panel C showing white, silica encrusted filamentous microbes between surfaces covered with brown microbial mats. (E) Terrace front discharge covered with white, silica-encrusted filamentous microbes. (F) Lower part of west margin of discharge apron showing silica-encrusted twigs and pieces of grass (arrows) and small lithoclast (LC) formed of silica spring deposits enmeshed in the opal-A precipitates that cover the surface of the discharge apron. (G) Laminae in cut and polished sample from the upper terrace. (H) Laminae in cut and polished sample from the lower terrace. White substrate at base is part of a quartz pebble.

Fig. 6. Thin section photomicrographs (all plane polarized light) showing contrasts between laminated opal-A precipitates from the upper terrace (A) terrace front (B), and lower terrace (C). All images in correct orientations. Samples impregnated with blue epoxy so that porosity is highlighted. Images show alternation of porous filamentous laminae with laminae characterized by low porosity. Note pigmentation colours associated with *Calothrix* sp. B in panels B and C.

Fig. 7. Thin section photomicrographs (all plane polarized light) of laminated opal-A precipitates from the upper terrace (A-C) terrace front (D, E), and lower terrace (F, G). (A) Tufts of *Calothrix* sp. A growing from common level. Note increase in thickness of encrusting opal-

A towards top of each filament. (B) Tuft of *Calothrix* sp. A with upper parts of filaments encrusted by thick layers of opal-A. (C) Upper part of tuft showing intertwined filaments of *Calothrix* sp. A (arrows) encrusted with thick layer of opal-A. (D, E) Sample from terrace front showing open, porous (blue) laminae alternating with white, dense, opal-A laminae. Yellowish-brown hue due to pigmentation associated with *Calothrix* sp. B. Note variations in proportions of porous laminae and white, dense laminae evident in panels D and E. (F, G) Sample from lower terrace showing recurring cycles formed of porous laminae (blue) alternating with laminated formed of dense, opal-A with yellowish-brown pigmentation associated with *Calothrix* sp. B. In panel G, note small opal-A lithoclasts evident in upper part of dense, opal-A laminae (arrows).

Fig. 8. SEM photomicrographs of *Calothrix* sp. A from sample collected from upper terrace near pool (same sample that is shown in Fig. 7A-C). (A) Vertical cross-section showing basal areas of filamentous microbial tufts growing from common level. Note numerous filaments in each tuft and porous areas between the tufts. White letter B indicates tuft shown in panel B. (B) Enlarged view of tuft showing numerous filaments encased in opal-A. (C, D) *Calothrix* sp. B with well-preserved basal heterocysts (H). (E) Basal heterocyst (H) succeeded by vase-shaped vegetative cell. (F) Distal part of filamentous microbe showing filament wall (W), septa (S), and silicified vegetative cells (SC). (G) Oblique cross-sections through silicified *Calothrix* sp. B filament showing sheath (SH) around open lumens (L). (H) Oblique longitudinal section showing trichome (T) encased by sheath (SH). (I) Vaguely laminated sheath formed of polygonal opal-A grains.

Fig. 9. SEM photomicrographs of *Calothrix* sp. B forming mats on terrace front (Fig. 7D, E) and lower terrace (Fig. 7F, G). (A) Mats formed of *Calothrix* sp. B, from terrace front. (B)

Basal heterocyst (H). (C) Basal part of filament showing basal heterocyst (H), vase-shaped vegetative cell, and collapsed trichome encased by sheath. (D) Longitudinal section through filament, with sheath, showing distal tapering. (E) Distal part of filament showing splaying of sheath (arrows). (F) Silicified vegetative cell, septa, and trichome wall (W) in middle part of *Calothrix* sp. B filament. (G) Outer surface of trichome covered with small opal-A spheres. White letter H indicates position of panel H. (H) Enlarged view of opal-A spheres with strands of mucus on outside of trichome. (I) Oblique transverse section through *Calothrix* sp. B showing sheath around silicified trichome. (J) Longitudinal cross-section through silicified filaments of *Calothrix* sp. B showing open trichome (T), wall of trichome (W), and sheath (Sh). (K) Enlarged view from panel J showing trichome wall (W) and sheath (SH). Note polygonal shape of opal-A grains that form the sheath. (L) Outer surface of sheath covered with polygonal opal-A grains.

Fig. 10. SEM photomicrographs of sample from upper terrace (same sample as shown in Figs. 7A-C, 8) showing non-filamentous laminae. (A) General view showing contrast between filamentous mats (FM) and non-filamentous (NF) laminae. Contrast in appearance between different mats reflects the amount of opal-A that was precipitated around and between the filamentous microbes. Box labeled B indicates position of panel B. (B) Laminae formed of opal-A sandwiched between two laminae that are formed of silicified *Calothrix* sp. A. C indicates position of panel C. (C) Opal-A laminae divided into parts I (mainly spherical microbes), II (mainly rod-shaped microbes), and III (rare to no microbes). Boundaries indicated by white dashed lines. D and E indicate positions of panels D and E, respectively. (D) Group of spherical microbes embedded in featureless opal-A. (E) Group of small rod-shaped microbes held in featureless opal-A. (F) Upper part of filamentous microbial mat

showing areas between distal ends of *Calothrix* sp. A. (C) filled with featureless opal-A and spherical and bicellular microbes. (G, H) Examples of microbes found in featureless opal-A that fills areas between distal parts of the *Calothrix* sp. A like those shown in panel F.

Fig. 11. SEM photomicrographs showing microbes found in opal-A laminae that occur between the *Calothrix* sp. B mats in sample from lower terrace. (A) Featureless opal-A matrix between distal ends of the *Calothrix* sp. B, with scattered spherical and rod-shaped microbes. (B) Rod-shaped microbes. (C) Group of spherical, multicellular, and rod-shaped microbes. (D, E) Spherical and rod-shaped microbes. (F) Bicellular microbe.