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Taxonomic fidelity of silicified filamentous microbes from hot-spring systems in the Taupo Volcanic Zone, North Island, New Zealand

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ABSTRACT: Modern, silica-precipitating hot springs, like those found in the Taupo Volcanic Zone (TVZ) on the North Island of New Zealand, are natural laboratories for assessing microbial silicification. Many of the silicified microbes found in the siliceous sinters of these spring systems seem to be life-like replicas of the original microbes. Such preservation reflects the fact that many of the microbes are replaced and encrusted by opal-A before they are destroyed by desiccation and decay. The taxonomic fidelity of these silicified microbes depends on the preservation potential of those features which are needed to identify them. For example, identification of extant cyanobacteria, relies on as many as 37 different features, most of which are not preserved by silicification.

In the hot-spring systems of the TVZ, characterisation of cyanobacteria which have been replaced and encrusted by opal-A is typically restricted to colony morphology, the length, diameter and morphology of the filament, and the presence/absence of septa, branching or a sheath. In many cases, description is limited to a subset of these parameters. Such a limited set of morphological characteristics severely impedes identifications in terms of extant taxa. The physical changes which accompany the stepwise diagenetic progression from opal-A to opal-CT ± opal-C to microcrystalline quartz may lead to further degradation of the silicified microbes and the loss of more taxonomically important features. Clearly, considerable care must be taken when trying to name silicified microorganisms and make palaeoenvironmental inferences.

KEY WORDS: Cyanobacteria, hot springs, silicification, taphonomy.

The palaeoecological interpretation of siliceous sinters associated with subfossil or ancient hot-spring systems commonly relies on the comparison of mineralised microbes with extant taxa (e.g. Cady & Farmer 1996; Walter *et al*. 1996; Jones *et al*. 1997a). Such an approach is viable given that the distribution of microbes (e.g. bacteria, cyanobacteria and fungi) in these systems is fundamentally controlled by water temperature (T) and pH (e.g. Brock 1978). For example, Lynne & Campbell (2003), distinguished between low-T *Calothrix*-dominated facies and mid-T *Phormidium*-dominated facies for the purposes of recognising different depositional regimes in hot spring successions. Such an approach implicitly assumes that the mineralised microbes can be recognised and identified in terms of extant taxa. This, in turn, depends on the taxonomic fidelity of the mineralised microbe, and in particular, the preservation potential of those features which are critical for their identifications in terms of extant taxa.

The present paper focuses on the issue of taxonomic fidelity of silicified microbes found in the active and subfossil hot-spring systems in the Taupo Volcanic Zone (TVZ) (Fig. 1) on the North Island of New Zealand (Cassie 1989; Cassie & Cooper 1989; Jones *et al*. 1997a, b, 1998, 1999b, 2000, 2001b, 2002, 2003; Campbell *et al*. 2002; Lynne & Campbell 2003). This study focuses primarily on the filamentous cyanobacteria because they are common in these spring systems (Fig. 2) and there is a large database on their preservation styles. By using this database to examine the preservation potential of the criteria which have been used to identify extant cyanobacteria, a cautionary note is provided regarding the reliability of identifying silicified microbes in terms of extant taxa. Conversely, this approach also allows the recognition of those silicified microbes which can be identified with a reasonable

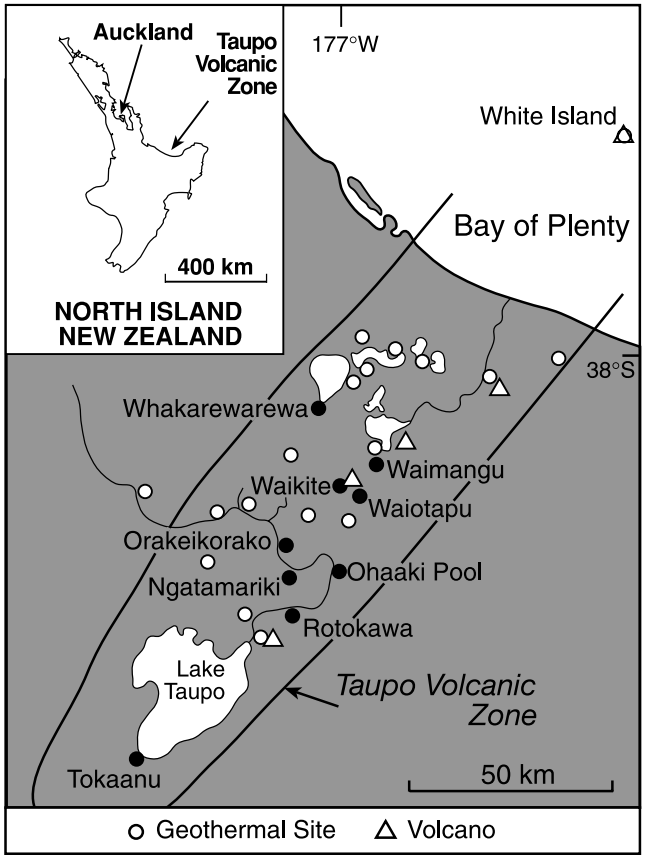

Figure 1 Map of North Island of New Zealand showing the location of the hot spring systems in the Taupo Volcanic Zone from which samples were collected for the present study.

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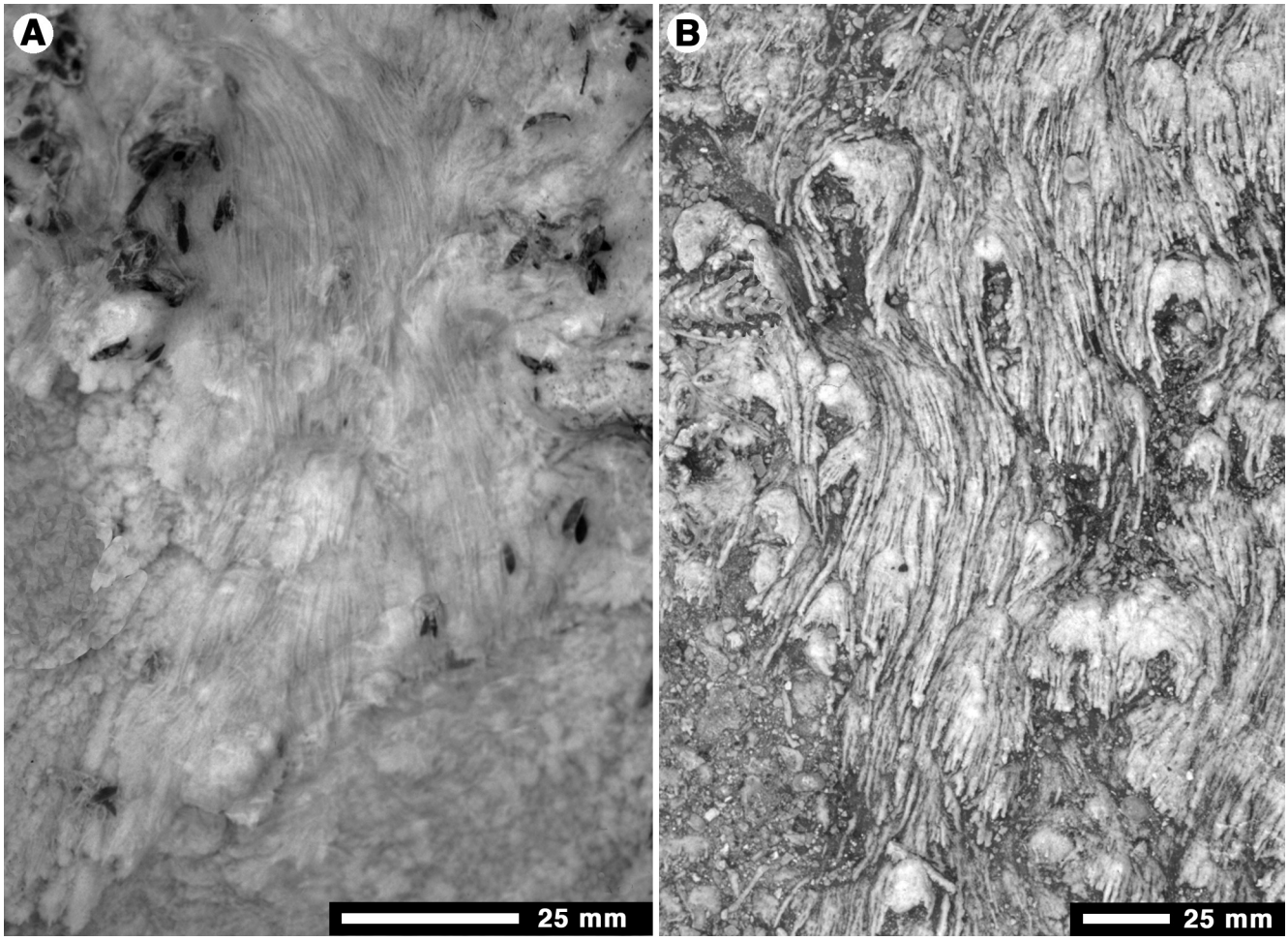

Figure 2 Field photograph of long filamentous microbes which are aligned parallel to current flow (from top to bottom of each photograph), which are commonly known as streamers. In each case, the morphology and habitat suggests that these are probably *Calothrix*: (A) Living filamentous microbes on the floor of the shallow (covered by <2 cm of water) stream location at the distal end of the discharge apron at Ohaaki Pool; (B) Well-preserved silicified filamentous streamers found on the discharge apron, approximately 50 m from Ohaaki Pool.

degree of certainty in terms of extant taxa. Therefore, such microbes have the potential of becoming invaluable tools for the palaeoecological interpretation of ancient sinters and other types of chert.

1. Methodology

The present study is based on siliceous sinter samples collected from the Ohaaki Pool, Waiotapu, Waimangu, and Whakarewarewa geothermal areas, which are located in the TVZ (Fig. 1). High magnification, high resolution scanning electron microscope (SEM) photomicrographs, which form the basis of this study, were obtained by mounting small, fractured samples of naturally air-dried sinter on SEM stubs, sputter coating them with a very thin layer of gold, and then examining them on a JEOL 6301F Field Emission SEM at an accelerating voltage of 2·5–5·0 kV. Samples were examined immediately after coating in order to minimise the development of artefacts in the gold coating.

2. Taxonomic framework

2.1. General comments

Cyanobacteria can be described according to their cell morphology, wall ultrastructure, colony/trichome morphology, genetic characters, physiology/biochemistry, culture conditions and habitat/ecology (Castenholz & Waterbury 1989; Castenholz *et al*. 2001, table B10. 1). Some of the confusion regarding the different taxonomic schemes can be attributed to the different approaches which have been taken to the classification of cyanobacteria. Some microbes have been 'botanically classified' with genera and species defined according to their morphological attributes and the habitat in which they were found (e.g. Copeland 1936; Cassie 1989). In his study of the cyanobacteria which inhabit the hot springs of Yellowstone National Park, Copeland (1936) named many different species on the basis of slight morphological variations and differences in habitat. Similarly, Cassie (1989) recognised and named taxa of cyanobacteria from New Zealand hot springs from a morphological basis. These classification schemes were developed without the benefit of cultures or genetic analyses. Other classification schemes, such as that employed by Castenholz (2001), are morphologically based, but with information derived from cultured material. This approach is used even though the cultured microbes do not always develop the same morphological features as the same taxa which grow in communities under natural conditions. The taxonomy of the cyanobacteria is in a state of flux, with generic descriptions being variable and generally reflecting how thoroughly a taxon has been studied (Castenholz 2001). As noted by Castenholz (2001), the generic framework of the cyanobacteria will have to undergo considerable revision in the future.

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Table 1 Features used to characterise Cyanobacteria (modified from Castenholz (2001, table B10.1) and their probability of detection in silicified cyanobacteria (based on qualitative assessment of silicified microbes from hot spring and geyser systems in the Taupo Volcanic Zone on the North Island of New Zealand)

Characteristic	Probability of detection in silicified Cyanobacteria			
	None	Low	Medium	High
Cell morphology				X
Cell shape			X	
Cell length			X	
Cell diameter				X
Number and regularity of planes of fission			X	
Colour of cells and cell suspension	X			
If present:				
sheath or glycocalyx				X
gas vacuoles with location			X	
motility (i.e. speed, rotation and smoothness)	X			
baeocyte ('endospore') description		X		
heterocyst and akinete description		X		
Ultrastructure		X		
Thylakoid arrangement	X			
Cell wall structural appearance	X			
Internal inclusions, storage granules	X			
Sheath structure				X
Colony/trichome morphology			X	
Colony or thallus shape, symmetry etc.			X	
Trichome type: tapered, straight, helical, setal constriction, shape of terminal cell				X
Presence and type of branching				X
Location and pattern of heterocysts and akinetes		X		
Morphological response to nutrient deficiencies	X			
Genetic characteristics	X			
DNA base composition	X			
Sequence analysis of 165 rDNA	X			
DNA-DNA hybridisation data	X			
Lipid profile	X			
Physiology/biochemistry	X			
Absorption spectrum (*in vivo*)	X			
Types of phycobilin pigments present	X			
Capacity for chomatic adaptation	X			
Temperature optimum and upper limit	X			
Capacity for dark chemoheterotrophy (aerobic versus anaerobic)	X			
Photoheterotrophy (with DCMU)	X			
Growth and/or acetylene reduction, aerobic and anaerobic, free of combined N	X			
Salinity tolerance	X			
pH range and tolerance		X*		
Vitamin requirement	X			
Sulphide sensitivity, sulphide-dependent anoxygenic photosynthetic capacity		X*		
$CaCO_3$-deposition, boring ability in $CaCO_3$				X
Culture conditions	X			
Specifics of isolation, growth medium, light intensity, conservation of cultures including type or reference strain, ability to grow on humid or dry agar	X			
Habitat/ecology		X*		
General and specific description of habitat: marine, freshwater, brackish, terrestrial; trophic level; flowing or static water, temperature, depth, light intensity regime, associated organisms of community, microenvironments, substrate etc.		X*		

*Conditions can, in some cases, be inferred from the rocks in which the microbes are preserved.

Fungi are commonly described using many of the same descriptors which are applied to the cyanobacteria (Table 1). Nevertheless, the classification of fungi is based largely on their life cycle, the morphology of the spores and sporocarps which they produce, and to a lesser extent, the morphology of the tissues (Moore-Landecker 1982; Madigan *et al.* 1997, table 18. 2; Tortora *et al.* 1998, p. 323). The chemistry of the fungal cell wall has also been used to

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classify fungi for research and industrial purposes (Madigan *et al*. 1997).

2.2. Taxonomically significant characteristics

Taxonomically significant characteristics are those features of a microbe which are important for their identification to generic or species level. For many microbes, the importance of a particular characteristic also depends on the classification system being utilised. For example, morphological features are critical in some classification systems, whereas they are of little consequence if genetic (e.g. DNA sequencing) or physiological features underpin the classification system.

Silicification commonly limits taxonomic recognition of microbes because the silicification processes do not always preserve the characteristics which are used to describe extant cyanobacteria (e.g. Jones *et al*. 2001c). Herein, the probability of each characteristic being detected in silicified microbes is estimated (Table 1). These estimates apply only to those microbes which have been replaced and encrusted by opal-A. The stepwise phase transformation of opal-A to opal-CT, opal-C, moganite, and microcrystalline quartz will modify the preserved microbes which were originally replaced and encrusted by opal-A (Lynne & Campbell 2003; Rodgers *et al*. 2004). Such phase transformations will affect the morphology of the silicified microbes, and there is the possibility that all record of the microbes may be lost by the time that the opal-A has diagenetically transformed to microcrystalline quartz.

The qualitative estimates of the preservation probabilities of the taxonomically important criteria used to identify microbes are based on the SEM examination of several thousand silicified microbes from numerous siliceous sinters collected from the hot spring systems found on North Island, New Zealand (Jones *et al*. 1997a, 1998, 1999a, b, 2000, 2001a, b, c, 2003). It must be stressed that these represent general assessments because there are exceptions, as with all qualitative estimates.

In most samples, the morphology of individual cells, and the overall structure of the trichome or colony are well preserved, with details of branching and colony shape being readily apparent (Table 1). In some taxa (e.g. *Calothrix*), the sheath and its internal structure are preserved, and therefore, can be used to identify the microbe to genus level (Jones *et al*. 1997a, fig. 10A–J, 1998, fig. 14, 2001b, fig. 6E–H; Lynne & Campbell 2003). Such ultrastructures are rarely preserved in most silicified microbes.

DNA analyses can reveal the overall genetic composition of the microbial community that inhabits various parts of hot spring system (e.g. Fouke *et al*. 2000; Reysenbach *et al*. 2000; Blank *et al*. 2002; Fouke *et al*. 2003). Their feasibility in the study of silicified microbes has yet to be resolved, although Smith *et al*. (2003) have applied this technique to some silicified microbes from the hot-spring systems in New Zealand. As yet, however, the results of DNA analysis cannot be directly correlated with individual silicified microbes which are observed using the SEM.

In general, the physiology and biochemistry of cyanobacteria and fungi are impossible to determine from silicified microbes (Table 1). In some cases, however, it may be possible to make inferences about salinity, pH and sulphide levels from the sinters in which the silicified microbes were found, using mineralogical and geochemical evidence (e.g. Hampton *et al*. 2004).

Culture conditions, which are widely used in the characterisation of microbial taxa, are of little value to the study of silicified microbes (Table 1).

In some circumstances, the original habitat and/or ecology of microbes can be inferred from the siliceous sinters in which they are found (e.g. Cady & Farmer 1996; Walter *et al*. 1996; Lynne & Campbell 2003). However, such inferences, are general, and it is normally impossible to determine the exact temperature range, pH or water composition conditions under which the microbes grew. Even this approach must be applied with caution because conditions (e.g. T and pH) in micro-niches, rather than the large-scale environment, commonly control microbe distributions. For example, it is common to find microbes which prefer low-temperature conditions thriving in proximal areas around geyser vents which are under the direct influence of boiling water during eruptive phases of the geyser (e.g. Jones *et al*. 1997a, 2003).

3. Silicification of microbes in hot-spring systems

3.1. General comments

The silicification of microbes in hot-spring systems is commonly rapid (Fig. 2). If a microbe is to be preserved, silicification must take place before it is destroyed by desiccation and decay, a process that can take place in ten days or less (Bartley 1996). The silicification of some microbes begins while they are still alive (Walter 1976; Cassie & Cooper 1989; Schultze-Lam *et al*. 1995; Renaut *et al*. 1998; Jones *et al*. 2001c) and is commonly completed a few days after the microbes have died (Jones *et al*. 1997a). Indeed, the three-dimensional (3D) form displayed by many silicified microbes could only be achieved if silicification took place before their soft tissues began to collapse and decay following their demise (e.g. Jones & Kahle 1986). Rapid silicification has also been demonstrated experimentally (e.g. Oehler & Schopf 1971; Oehler 1976; Francis *et al*. 1978; Westall *et al*. 1995; Bartley 1996; Phoenix & Konhauser 1999; Phoenix *et al*. 2000). For example, Bartley's (1996) experiments showed that silicification had to be completed within days if the 3D form of the microbe was to be preserved.

Silicification of microbes in modern hot-spring systems reflects the balance between the rates of silica precipitation, secondary precipitation and decay of the organic matter (Cady & Farmer 1996; Walter *et al*. 1998). In areas where the water temperature is >20 °C, organic matter usually degrades before it can be replaced by silica (Walter *et al*. 1998). Cellular-level information will be preserved if organic matter is preserved (Walter *et al*. 1998), or if the sheaths were impregnated by minerals such as iron oxide which can survive early diagenesis (Ferris *et al*. 1988; Walter *et al*. 1998). Preservation also depends on there being sufficient silica to silicify the microbes before they are lost through collapse and decay. The highest probability for preserving microbes will be found in situations where the microbes are constantly immersed in waters which are strongly supersaturated with respect to amorphous silica, and in subaerial sites where aqueous silica supplied by spray, wave oscillation and capillary processes undergoes cooling and evaporation (Renaut *et al*. 1998).

3.2. Silicification of taxonomically important features

Potentially, silicified filamentous microbes can be described in terms of their filament length, filament diameter, filament morphology (e.g. tapering, straight or helical), the presence/absence of septa, the presence/absence of branching, the presence/absence of a sheath, and in some cases, the morphology of the colony (cf. Jones *et al*. 2001c). If a sheath is present, then information pertaining to its internal structure (e.g. laminae in *Calothrix*) may prove to be taxonomically important. Similarly, the style of branching, if present, can be of value. For fungi, locating, describing and identifying spores

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is critical to their recognition (e.g. Jones *et al*. 1999b, 2000). Such information will not be discernable in all silicified microbes. Even the best-preserved microbes will probably yield less than six morphological features which can be described with any degree of certainty (Jones *et al*. 2001c).

Filament length and filament diameter, readily apparent on SEM photomicrographs, are two fundamental attributes of any silicified microbe (Figs 3, 4). These dimensions are important because they are commonly used to characterise various microbes and are inherent to morphologically based classification schemes. Nevertheless, caution must be used in the determination of filament diameter because it can be significantly modified by the precipitation of opal-A cements around the filaments (Jones & Renaut 2003; Lynne & Campbell 2003). This issue is difficult to resolve because the opal-A cement may be impossible to recognise and separate from the opal-A that replaced the filament (or sheath). In the Waikite Geyser system, which is located in the Whakarewarewa geothermal area, acidic steam continues to permeate through microfractures which cut through many of the siliceous sinters. The acidity resulted from the condensation of H_2S in shallow groundwater and in steam following a falling in the local water table. That steam has caused differential etching of the opal-A, on a micron scale, that may be related to the variable water content (H_2O and OH) content of successive laminae (Jones & Renaut 2004). Such etching highlights the internal structure of the opal-A, which otherwise appears devoid of any structures (Fig. 3F). Etched cross-sections through silicified microbes commonly display numerous laminae, commonly <10 nm thick, which are concentrically arranged around the open lumen (Fig. 3B–E). Thus, the apparent diameter of the filament was progressively enlarged as additional laminae of opal-A were precipitated around the filament. In such circumstances, the external diameter of the silicified filament will be primarily a function of the rate and duration of cement precipitation, not the diameter of the original filament. It must also be remembered that filamentous microbes found in hot spring systems have a maximum diameter of 15–20 μm (e.g. *Calothrix*), and more typically, less than 2 μm (e.g. *Phormidium*). Thus, the precipitation of even the thinnest layer of cement will have a significant impact. For example, a 2-μm-thick layer of opal-A cement, will transform a filament with a diameter of 2 μm into a silicified filament that has a diameter of 6 μm. Many of the silicified filamentous microbes from Waikite Geyser, for example, are encased by layers of opal-A cement which increase the diameter of the original filament by up to 10 times. Accordingly, measurement of the external diameter of the silicified microbe will provide a diameter that bears no relationship to the diameter of the original microbe. This assessment is supported by those silicified filamentous microbes which vary in diameter along their length because of the pattern of opal-A precipitation (Fig. 4). In such specimens, the external diameter of the silicified filament will be of little value for identifying that microbe in terms of extant, non-silicified microbes.

An open lumen is still present in many of the silicified microbes found on the discharge aprons of the New Zealand spring systems (Fig. 3A, B, C, F). The diameter of the open lumen, which is commonly much smaller than the external diameter, is probably the most reliable estimate of the diameter of the original filament/trichome. However, the open lumen is usually only apparent on high-magnification SEM images of transverse sections across the filaments. However, measurement of this parameter must be treated with some caution because opal-A cements can be precipitated around the lumen wall in the same way that they can be precipitated around the sheath. Thus, the lumen may be significantly reduced in diameter. In many examples, the lumen is fully occluded by opal-A cement, creating a solid filament.

Taxonomically important morphological characteristics, other than filament length and diameter, are not apparent in all silicified microbes. Based on the present authors' experience with the silicified microbes from the New Zealand hot springs, these characteristics are, in order of decreasing frequency of detection: the presence or absence of a sheath, presence or absence of branching, trichome type (i.e. straight, tapered or helical), location of gas vacuoles, and spore types (Table 1). However, most silicified microbes lack these characteristics. If present, they may provide the critical information that is needed to identify the silicified microbe in terms of extant taxa.

4. Discussion

Silicified microbes found in the sinters of the discharge aprons of modern hot-spring and geyser systems in the TVZ commonly appear to be exact replicas of the original microbe, even though most of their taxonomically important details have been disguised or destroyed by silicification. The loss of such information commonly takes place quickly (Smith *et al*. 2003) and before the opal-A starts to change to its thermodynamically more stable phases. Most of the silicified microbes found on these discharge aprons are probably less than 100 years old, and in the case of those found in the mound around one of the geysers at Tokaanu, they are known to be less than 50 years old (Jones *et al*. 2003). Mountain *et al*. (2003) and Handley *et al*. (2003) have shown that filaments in microstromatolites at Champagne Pool (Waiotapu geothermal area) are rapidly replaced and filled with opal-A. Recent experiments involving the placement of glass slides in Iodine Pool in the Waimangu Geothermal Valley has demonstrated that microbe silicification can take place in less than four days (Jones *et al*. in press). Despite the rapidity of this silicification, it is virtually impossible to identify the silicified taxa in terms of extant taxa because silicification has disguised or destroyed the taxonomically critical features.

To a large extent, the probability of being able to identify a silicified microbe in terms of extant taxa depends on the number of morphological features which are preserved, and if those features are, in some way, distinctive. For example, many *Calothrix* found in the siliceous sinters of the New Zealand spring systems are characterised by their large diameter, distally tapering, septate trichome that is encased by a laminated sheath that, in some specimens, is characterised by thin laminae which splay outward from the sheath exterior. The characterisation of this microbe by so many distinctive morphological characteristics means that its identification as *Calothrix* is relatively rigorous. Other silicified filamentous microbes are more difficult to identify with any degree of certainty because they can only be characterised by a few morphological features. For example, Jones *et al*. (2002) tentatively assigned silicified microbes in coniform stromatolites from the Tokaanu and Whakarewarewa geothermal areas to *Phormidium* based on their non-branching sheathed filaments, which have a diameter that is consistent with extant *Phormidium*. The paucity of morphological features, each of which could be indicative of a number of taxa, means that the identification must be regarded as tentative. Some taxa can be recognised on the basis of only one or two morphological characteristics. For example, *Spirulina* and *Arthrospira* are characterised by the distinctive helical coiling of their trichomes.

It is important to stress that it is commonly difficult to assign silicified microbes found on modern discharge aprons to

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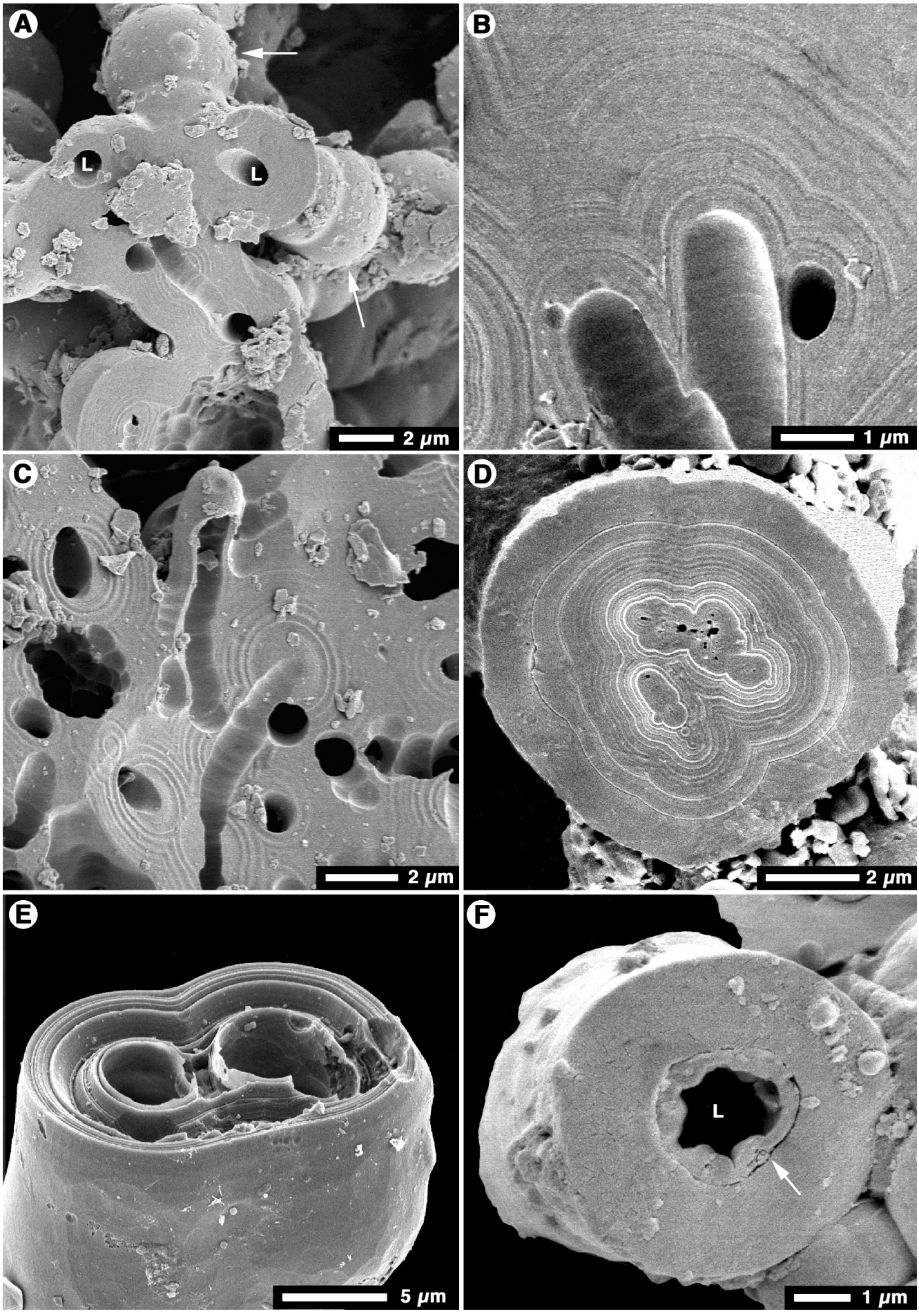

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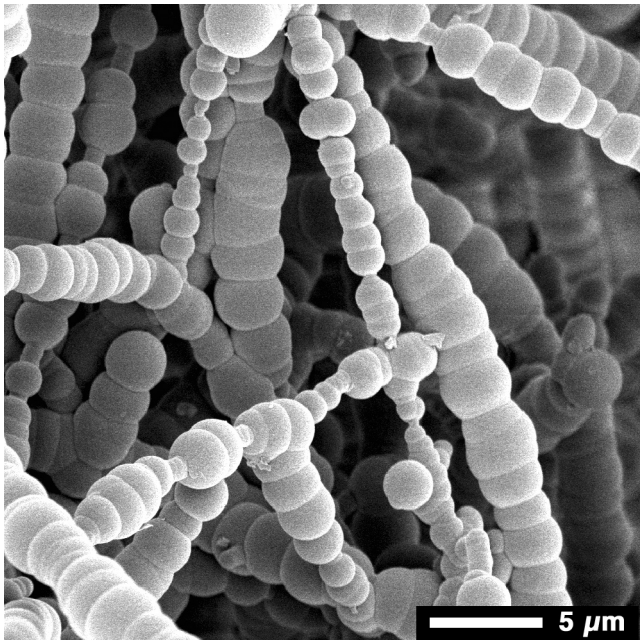

Figure 4 Scanning electron microscope photomicrograph showing silicified filamentous microbes from a sinter on the discharge apron of Waikite Geyser in the Whakarewarewa geothermal area. Note the significant variations in the diameters of filaments both between filaments and along the length of individual filaments.

a particular group of microbes. Thus, in many cases it can be virtually impossible to determine if a silicified filamentous microbe is a cyanobacterium, a bacterium or a fungus (cf. Schultze-Lam *et al.* 1995). For example, without terminal spores, ascii and their associated ascospores (Jones *et al.* 1999b, fig. 11), it might be impossible to distinguish fungal hyphae from a cyanobacterial filament.

The silicified microbes found on the discharge aprons of hot-springs and geyser systems in the TVZ develop through the replacement of their tissues by opal-A, and in many cases, encasement by subsequent opal-A cement precipitation. As shown by Jones & Renaut (2004, table 2), the opal-A associated with the New Zealand hot springs contains up to 15 wt.% water. During diagenesis, opal-A, which is the least stable form of SiO_2 (Krauskopf 1956), will change to opal-CT ± opal C, and eventually, to microcrystalline quartz (Fournier 1985a; Rodgers & Cressey 2001). Such changes are primarily caused by dehydration (e.g. Scurfield & Segnit 1984; Herdianita *et al.* 2000; Campbell *et al.* 2001) which takes place during burial or exposure to high temperatures (Fournier 1985b). Lynne & Campbell (2003) suggested that the phase change is accompanied by a change from microspheres (opal-A) to bladed lepispheres (opal-CT ± opal-C) to equant microcrystalline grains (quartz), similar to the sequence long established in marine cherts. Such changes can also lead to the physical degradation of the silicified microbes, and hence, further loss of features which are critical to the identification of microbes in terms of extant taxa. For example, Lynne & Campbell (2003) argued that the open lumens could only be expected in microbes which are replaced and encrusted by opal-A, and/or a mixture of opal-A and opal-CT. The above authors suggested that further phase changes are invariably accompanied by complete filling of the open lumens. However, the lumens of many filamentous microbes are filled with opal-A even before any phase transformations have taken place (e.g. Jones *et al.* 2001c, fig. 4A). Thus, it might be expected that virtually all trace of silicified microbes will be lost by the time that the opal-A has undergone the full spectrum of stepwise diagenetic changes to microcrystalline quartz (cf. Lynne & Campbell 2003). However, this is not inevitable because silicified microbes can still be recognised in the sinters of many ancient hot spring systems, including those found in the Devonian strata of the Drummond Basin of Australia (White *et al.* 1989; Walter *et al.* 1996, 1998), the Rhynie chert of Scotland (Trewin 1994; Rice *et al.* 1995, 2002), and Pleistocene strata of New Zealand (Campbell *et al.* 2001). Therefore, it appears that the longevity of silicified microbes may also depend on factors other than the simple phase transformations which transpire as opal-A changes to microcrystalline quartz.

To some extent, the reliability of identifications attached to silicified microbes depends on the morphological complexity of the microbe. The cyanobacteria *Calothrix* and *Phormidium* have been reported from many modern, subfossil and fossil spring systems (e.g. Cady & Farmer 1996; Jones *et al.* 1998, 2002). Importance has been attached to these genera because they thrive under different temperature regimes and hence, on different parts of the discharge apron (e.g. Cady & Farmer 1996, fig. 1; Lynne & Campbell 2003, table 2). However, the ease and reliability of identifying silicified specimens of these genera is quite different. *Calothrix* can usually be identified with a high degree of confidence because it is characterised by a large diameter distally tapering filament, the laminated nature of its sheath and the laminae which commonly splay outward from the exterior of the sheath. These features are so distinctive that it is difficult to confuse *Calothrix* with any other microbe. In contrast, *Phormidium* is an architecturally simple microbe with few really distinctive features. It is characterised by a small diameter, non-branching trichome (typically <2 μm) that is housed in a thin, gelatinous sheath (Cassie 1989). This simple architecture means that it is commonly difficult to separate this genus from other genera, especially after it has been silicified (e.g. Jones *et al.* 2002). Nonetheless, this comparison between *Calothrix* and *Phormidium* highlights the issue of taxonomic fidelity by showing that some silicified microbes (e.g. *Calothrix*) can be identified with a high degree of confidence.

Part of this problem associated with the identification of silicified microbes can be attributed to the general paucity of detailed descriptions which are accompanied by high-quality SEM photomicrographs which document silicified microbes from modern hot spring and geyser systems. Silicified microbes have commonly been identified in terms of extant taxa without a full evaluation of their preserved features and taxonomic fidelity. Some of the problems outlined in the present study

Figure 3 Internal structures of silicified microbes, as revealed by natural etching in an acidic steam. All samples are from the Waikite Geyser complex in the Whakarewarewa geothermal area: (A) Silicified filamentous microbes with open lumens. Note the bulbous morphology of the opal-A that has formed around the filaments (arrows) and the internal laminations evident in fractured surfaces; (B) Etched fractured surface through opal-A encasing an open lumen. The very thin laminae evident provide evidence of the gradual accretion of opal-A cement around the filaments; (C) Etched fractured surface through a group of silicified filamentous microbes. Profiles of internal laminae show that the filaments were encased by bulbous masses of opal-A which grew through the gradual accretion of isopachous cement layers; (D) Etched, transverse cross-section through a filamentous microbe showing numerous, thin layers of opal-A which are concentrically arranged around the lumen that has also been filled with opal-A cement; (E) Deeply etched transverse cross-section through two filamentous microbes showing laminae which are concentrically arranged around the open lumens; (F) Transverse cross-section through a filamentous microbe showing an open lumen (L), and a discontinuity (arrow) between the silicified sheath and the opal-A cement that encases the sheath.

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might be resolved if there was a better understanding of how known microbial taxa were silicified and if there were more detailed descriptions of silicified microbes from geothermal systems throughout the world. Such information might provide the basis for more confident identifications of the microbes, and thereby, increase their usefulness as proxies for ancient environmental conditions.

5. Conclusions

Analysis of silicified microbes from siliceous sinters found on the discharge aprons of hot-spring and geyser systems in the TVZ shows that many of them are difficult to identify in terms of extant taxa, despite the fact that they seem to be so well preserved. The concept of taxonomic fidelity, which focuses on the preservation potential of taxonomically important characters, is central to this issue. The probability of accurately identifying a silicified microbe in terms of extant taxa hinges on the relationship between the features which are preserved in the silicified microbes relative to the features which have been used to classify them. Unfortunately, the taxonomic identification of many microbes, such as the cyanobacteria, relies on features such as cell ultrastructure, genetic characters and various physiological/biochemical characters which have a low probability of being preserved in silicified microbes. Physical changes which accompany the transformation of the unstable opal-A to the more stable forms of SiO_2 will modify the physical appearance of the silicified microbes, and thereby, further reduce the probability of accurate identification.

The problems emanating from the concept of taxonomic fidelity may be overcome if: (1) attention is focused on the silicification of known microbes so that an understanding of the probability of preserving various characteristics can be firmly established; and (2) detailed descriptions and illustrations of silicified microbes from siliceous sinters throughout the world become available. Collectively, such information might allow some of the problems associated with taxonomic fidelity to be resolved.

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