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Modern analogues and the early history of microbial life

Brendan P. Burns[a,b], Roberto Anitori[b,c,1], Philip Butterworth[b,c], Ruth Henneberger[b,c,3], Falicia Goh[a,2], Michelle A. Allen[a], Raquel Ibañez-Peral[c], Peter L. Bergquist[c,4], Malcolm R. Walter[a,b,*], Brett A. Neilan[a,b]

[a] School of Biotechnology and Biomolecular Sciences, University of New South Wales, Sydney, NSW 2052, Australia
[b] Australian Centre for Astrobiology, University of New South Wales, Sydney 2052, Australia
[c] Department of Chemistry and Biomolecular Sciences, Macquarie University, Sydney, NSW 2109, Australia

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ABSTRACT

Revealing the geological history of microbial life is very challenging. Microbes rarely are preserved with morphological fidelity, and even when they are, morphology is a poor guide to phylogeny and metabolism. Biological studies of environments considered analogous to those of paleobiological interest on the ancient Earth can inform interpretations and suggest new approaches. This paper reviews recent advances in our understanding of the biological diversity of two environments relevant to Archean paleobiology: those of extreme acidity and temperature (the Mt. Hood and White Island volcanoes), and high salinity (living stromatolites in Shark Bay). The combination of traditional microbial isolation with the use of modern molecular techniques has revealed that the microbial communities in these environments are much more diverse than originally thought. Through the extraction of whole microbial community DNA, enzymatic amplification of evolutionarily conserved genes, and cloning and sequencing of these genes, more specific and informed inferences concerning functional complexity in these extreme environments have now been made. Studies of the modern stromatolites have demonstrated that they have a very diverse range of micoorganisms, and contrary to previous interpretations, cyanobacteria are not the most abundant microbes present. In addition, many of the microorganisms are unique with no known close relatives, and these microorganisms may also possess novel physiologies vital to the integrity and persistence of stromatolites through space and time. Microbes in the volcanoes studied are present ubiquitously and include geochemically significant sulfur- and iron-cycling taxa. The findings from the studies reviewed here suggest that the Archean biota may have been functionally diverse and much more complex than has yet been revealed. The importance of studying modern analogues is stressed in that the biogeochemical processes occurring in these communities leave morphological, mineralogical, lipid and isotopic signals that could be sought in the rock record.

1. Introduction

Studies of modern analogues of ancient microbial environments play a vital role in the interpretation of the palaeobiological record. This has long been recognised, with, for example, the work of Mawson (1929) on the formation of oncoids (discoidal stromatolites) in a swamp associated with the Coorong Lagoon in South Australia and Black (1933) on cyanobacterial mats in the Bahamas, as analogues for ancient stromatolites. Verandsky (1926, republished in English translation 1998) and Baas Becking (1934) pioneered the field of biogeochemistry, turning to the study of microbial processes in the natural environment to elucidate low temperature geochemical processes such as sulfate reduction.

The discovery of Holocene stromatolites forming in Hamelin Pool, Shark Bay in Western Australia in the 1950s (Logan, 1961; Playford and Cockbain, 1976) greatly boosted research on the role of cyanobacteria in the formation of ancient stromatolites. Comparable studies proliferated in marine and lacustrine environments worldwide. Building on the work of Weed (1889), Walter et al. (1972) extended such studies to the thermal spring environment, concentrating on conically laminated cyanobacterial stromatolites comparable to the Proterozoic *Conophyton* spp. Research from this era is summarised in the book 'Stromatolites' (Walter, 1976).

* Corresponding author at: School of Biotechnology and Biomolecular Sciences, University of New South Wales, Sydney, NSW 2052, Australia. Tel.: +61 2 9385 3761; fax: +61 2 9385 1483.
E-mail address: malcolm.walter@unsw.edu.au (M.R. Walter).
[1] Present address: Ocular Immunology Laboratory, Casey Eye Institute, Oregon Health and Science University, Portland, USA.
[2] Present address: MerLion Pharmaceuticals Pty Ltd., 1 Science Park Road, Singapore 117528, Singapore.
[3] Present address: Environmental Research Institute, University College Cork, Cork, Ireland.
[4] Present address: Department of Molecular Medicine & Pathology, University of Auckland School of Medicine, Auckland, New Zealand.

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The development of microelectrode techniques led to detailed studies of metabolic processes in microbial mats at a millimetric scale, such as those on the mats in the salinas of Baja California (Jørgensen and Des Marais, 1986). This study also pioneered the use of fiberoptic light probes to characterise the photic microenvironment within cyanobacterial mats. These studies started to reveal the true complexity of such microbial ecosystems, a process that accelerated greatly with the development and application of the current techniques of genomics and proteomics, starting in the 1970s. At the same time, documentation of distinctive lipids (biomarkers) produced by microbes began (e.g., Palmisano et al., 1989), a field that has blossomed to become a major contributor to revealing the palaeobiology of the early Earth. Some results of the application of these modern techniques are described in the sections that follow, and we will focus our discussions on the significant biological diversity discovered in particular environments of high acidity and temperature (the Mt. Hood and White Island volcanoes), and elevated salinity (living stromatolites in Shark Bay).

Fig. 1. Intertidal stromatolites in Shark Bay, Western Australia. Scale bar (bottom right) approximately 1 m. Inset: example of surface stromatolite sample analysed by both culture and culture-independent techniques.

2. Living stromatolites

One of the best examples of modern analogues of early microbial life are living stromatolites. The most extensive modern stromatolites are those forming in a hypersaline marine environment at Shark Bay on the western coast of Australia (Logan, 1961) and in open marine waters in the Bahamas (Reid et al., 2000). Studies of the Bahaman stromatolites have shown that surface populations cycle between several community types and stromatolite construction is balanced between sedimentation and intermittent lithification by cyanobacteria (Reid et al., 2000). A filamentous cyanobacterium (*Schizothrix* sp.) initiated the first community, whereby carbonate sand grains were bound and trapped. A heterotrophic bacterial biofilm containing abundant extracellular polymeric substances (EPS) then followed, and in this cycle calcium carbonate precipitation was tightly regulated by sulfate reduction and EPS production (Kawaguchi and Decho, 2002; Decho et al., 2005; Visscher, 2000).

The endolithic cyanobacterium *Solentia* sp. dominates a final community, and the fusion of carbonate grains and microboring by this microorganism strengthens the lithified layer (Macintyre et al., 2000). The development of a laminated lithified stromatolite structure results from the cycling between these community types. A combination of cyanobacterial photosynthesis, sulfate reduction, and anaerobic sulfide oxidation was responsible for $CaCO_3$ precipitation (Visscher et al., 1998). The physical environment and the action of macroalgae and macrofauna influences final stromatolite macromorphology in the Bahamas (Andres and Reid, 2006). The following discussion will focus on recent advances in our understanding of the microbial diversity of the living stromatolite analogues in the intertidal regions of Shark Bay.

2.1. Shark Bay stromatolites

The living marine stromatolites of Hamelin Pool at Shark Bay are the most diverse, abundant, and widespread examples known (Fig. 1). Hamelin Pool is an 80 km long embayment located in the southeastern part of Shark Bay, a shallow hypersaline bay on the Western coast of Australia. Water flow into Hamelin Pool is restricted by a sandbank, and a combination of low rainfall, high evaporation rates, and the lack of freshwater input has resulted in salinities of up to twice that of normal seawater (Arp et al., 2001). The water is oligotrophic and also saturated in calcium carbonate, owing to the presence of shells from the bivalve *Fragum erugatum* (Berry and Playford, 1997). Water temperatures are 15–18 °C in winter and 26–30 °C in summer, though the temperature of exposed intertidal surfaces can reach 45–50 °C (Bauld, 1984). Hamelin Pool is thought to have become a hypersaline barred basin around 4200 years ago (Playford, 1990), and the increase in salinity in this area may result in a reduction in the level of grazing by higher eukaryotes, although this hypothesis is still under debate.

The extant stromatolites of Shark Bay are relatively young; the oldest were radiocarbon dated to be 1000–1250 years old, with a very slow growth rate of around 0.4 mm/year (Chivas et al., 1990). Early work often reported only taxonomic and physiological properties of one dominant type of cyanobacteria found in each stromatolite morphotype (Logan et al., 1974). However, these early studies of the microorganisms associated with stromatolites have suffered from a major problem: the current non-culturability of most environmental microorganisms. Thus the investigation of microbial ecology and diversity by traditional culture and microscope-based techniques has been severely limited by this problem, as the isolates obtained may not be representative of the total population.

Reports vary, but as little as 0.1% of microbial cells from a given environment may be culturable at present (Pace, 1997). However, modern molecular techniques have revolutionised microbial ecology and systematics by allowing the identification and phylogenetic analysis of these non-culturable microorganisms. These techniques involve extraction of whole microbial community DNA, enzymatic amplification of evolutionarily conserved genes, and cloning and sequencing of these genes. Recent reports using these culture-independent molecular techniques have thus begun to reveal the large microbial diversity (cyanobacteria, other bacteria, and archaea) of the Shark Bay intertidal stromatolites, allowing more specific and informed inferences concerning stromatolite functional complexity.

2.2. Cyanobacteria associated with Shark Bay intertidal stromatolites

The first studies referred to above involved the polyphasic examination of the microbial communities of Shark Bay intertidal columnar stromatolites, combining both culture-dependent and culture-independent nucleic acid based methods (Neilan et al., 2002; Burns et al., 2004; Burns et al., 2005). The community in these stromatolites was characterized by organisms of the cyanobacterial genera *Synechococcus*, *Xenococcus*, *Microcoleus*, *Leptolyngbya*, *Plectonema*, *Symploca*, *Cyanothece*, *Pleurocapsa*, *Prochloron* and *Nostoc*. *Microcoleus* has been shown to be associated with other intertidal stromatolites, including those of hypersaline waters (Castenholz et al., 2001; Moers and Larter, 1993). The nitrogen fixing activity of

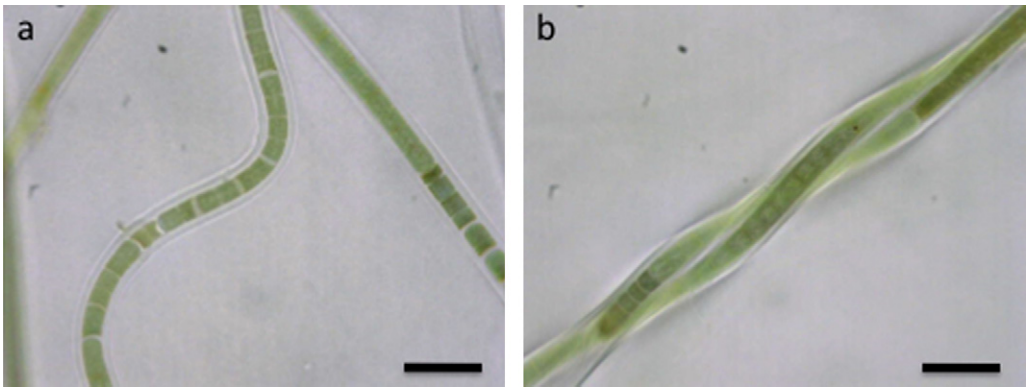

Fig. 2. Representative examples of filamentous cyanobacteria isolated from Shark Bay intertidal stromatolites (Burns et al., 2004). (A) *Euhalothece* sp.; (B) *Gleobacter* sp. Scale is 10 μm.

Nostoc isolates in the nitrogen limited seawater of Shark Bay is likely to be significant in nutrient cycling of this system. Molecular analysis also revealed a number of sequences clustering with *Euhalothece*, and this group of cyanobacteria has also been identified in hypersaline microbial mats in other geographical locations (Garcia-Pichel et al., 1998; Nübel et al., 2000). Several isolates associated with the Shark Bay intertidal stromatolites (*Phormidium*, *Pleurocapsa*, *Nostoc*, and *Oscillatoriales*) were also observed to form a tough and sticky matrix of cells in culture (Burns et al., 2004). Extracellular polymeric substances, known to be produced by several of the cyanobacterial taxa identified provide an adhesive matrix to physically bind sediment, in addition to mediating carbonate precipitation (Arp et al., 2001).

Several cyanobacteria isolated from the extant analogues in Shark Bay were also filamentous (Fig. 2), a characteristic known to aid sediment trapping in stromatolites (Walter, 1976; Reid et al., 2000). Biofilms consisting of *Phormidium*, *Pleurocapsa*, *Nostoc*, and *Oscillatoriales* have also been shown to be involved in carbonate precipitation in hypersaline environments (Arp et al., 1999). Phylotypes related to *Synechococcus* were also observed in intertidal stromatolite DNA libraries (Burns et al., 2004), and the outermost cell surface of *Synechococcus* has been shown to have a role in fine-grained mineral formation (Schultze-Lam et al., 1992). This formation occurs with both live and dead cells, so such a process could be important in stromatolite lithification even after cell death. A Precambrian counterpart to *Synechococcus*, *Eosynechococcus*, has been described in ancient stromatolites (Hofmann, 1976), and owing to the characteristics of Shark Bay microbial mats, the preservation of cyanobacterial cells as microfossils could potentially occur (López-Cortés, 1999).

All the microorganisms isolated from Shark Bay stromatolites were cultivated on high salt media (Burns et al., 2004), and as described earlier these stromatolites forming in the intertidal zone are subjected to substantial salinity and desiccation stress. The primary productivity of intertidal mats in Shark Bay is considered to be quite low as a result of this pressure (Bauld et al., 1979). Particularly relevant to the hypersaline environment of Shark Bay is the necessity for many of the community members to have mechanisms of salt tolerance. Many prokaryotes isolated from microbial mats and other hypersaline environments adapt to salinity by accumulating compatible solutes to equalize the external and internal osmolarity (Roessler and Muller, 2001). Though the levels of compatible solutes in marine environments are often quite low (Cosquer et al., 1999), the close proximity of organisms and the microbially induced chemical cycling in stromatolites may concentrate these compounds to biologically significant levels. The microbial population of Shark Bay stromatolites is likely to possess similar adaptations to stress and preliminary data have indeed identified different mechanisms in both cyanobacteria and archaea (Goh, unpublished data).

As well as the significant salinity and desiccation stress stromatolites and their resident microorganisms are exposed to, high temperatures and the relatively thin atmospheric ozone layer contribute to a high ambient UV irradiance in Hamelin Pool (Palmisano et al., 1989). This relatively low ozone also contributes to the value of Shark Bay stromatolites as modern analogues. Many of the surface-dwelling cyanobacteria identified (Burns et al., 2004), are known to produce various sheath pigments that are also likely to play a photoprotective role in screening deeper members of the community from physiological damage. An interesting finding from these molecular analyses of the Shark Bay intertidal stromatolites was that a number of clones were most closely related to the genus *Prochloron* (Burns et al., 2004). This organism is previously only known to live in symbiosis with higher organisms (Kühl and Larkum, 2002). The discovery of potentially free-living *Prochloron* associated with stromatolites is of considerable evolutionary and ecological interest (Burns et al., 2004).

The importance of employing modern molecular techniques in the study of microbial communities associated with stromatolites is further illustrated by comparing the results obtained from recent studies on smooth and pustular mats in Shark Bay to early work on these mats by Golubic (1976). The excellent pioneering work of Golubic (1976) reported a small number of cyanobacterial taxa based on morphology (such as *Entophysalis*, *Microcoleus*, and *Lyngbya)*, however a combination of culturing and molecular techniques have revealed a much greater diversity of cyanobacteria associated with the intertidal smooth and pustular mats (Table 1). Although the populations of the different mat types have been revealed to be broadly similar, the various groups such as *Synechocystis* and *Pleurocapsa* unique to each mat type (Table 1) may contribute to differences in laminar architecture and macromorphology. The presence of certain cyanobacteria such as *Microcoleus* sp., *Euhalothece* sp., *Phormidium* sp., and *Leptolyngbya* sp. in each mat type suggests that a common cyanobacterial community may also exist in the Shark Bay intertidal environment.

2.3. Other bacteria associated with Shark Bay intertidal stromatolites

Microorganisms other than cyanobacteria are also prominent in these formations, and another study on the Shark Bay stromatolites revealed that novel proteobacteria were actually the dominant sequences (Papineau et al., 2005). It appears then that in contrast to the common perception, cyanobacteria do not seem to dominate in these stromatolites, though it is quite likely they still have major roles in primary production (Papineau et al.,

Table 1
Representative cyanobacteria identified from intertidal stratiform mats in Shark Bay.

Stratiform mat type[a]	Microorganism identity	Identification method	Source
PM	*Entophyasalis major*	Microscopy	Golubic (1976)
SM	*Microcoleus* sp.	Microscopy	Golubic (1976)
SM	*Schizothrix* sp.	Microscopy	Golubic (1976)
TM	*Lyngbya aestuarii*	Microscopy	Golubic (1976)
TM	*Schizothrix* sp.	Microscopy	Golubic (1976)
PM	*Halomicronema* sp.	Molecular analyses	Allen et al. (2009)
PM	*Pleurocapsa* sp.	Molecular analyses	Allen et al. (2009)
PM	*Sprulina* sp.	Molecular analyses	Allen et al. (2009)
PM	*Chroococcidiopsis* sp.	Molecular analyses	Allen et al. (2009)
PM	*Cyanothece* sp.	Molecular analyses	Allen et al. (2009)
PM	*Oscillatoria* sp.	Molecular analyses	Allen et al. (2009)
SM	*Synechocystis* sp.	Molecular analyses	Allen et al. (2009)
SM	*Staniera* sp.	Molecular analyses	Allen et al. (2009)
SM	*Xenococcus* sp.	Molecular analyses	Allen et al. (2009)
SM	*Anabeana* sp.	Molecular analyses	Allen et al. (2009)
SM	*Thermosynehococcus* sp.	Molecular analyses	Allen et al. (2009)
SM	*Myxosarcina* sp.	Molecular analyses	Allen et al. (2009)
PM/SM	*Euhalothece* sp.	Molecular analyses	Allen et al. (2009)
PM/SM	*Microcoleus* sp.	Molecular analyses	Allen et al. (2009)
PM/SM	*Halothece* sp.	Molecular analyses	Allen et al. (2009)
PM/SM	*Arthrospira* sp.	Molecular analyses	Allen et al. (2009)
PM/SM	*Phormidium* sp.	Molecular analyses	Allen et al. (2009)
PM/SM	*Leptolyngybya* sp.	Molecular analyses	Allen et al. (2009)
PM/SM	Unknown cyanobacteria	Molecular analyses	Allen et al. (2009)

[a] PM, Pustular mat; SM, Smooth mat; TM, Tufted mat.

2005) and in generating the architecture of the mats. In terms of abundance, molecular data have revealed that the highest proportion of organism sequences in Shark Bay stromatolites are related to alpha proteobacteria (29%), candidate division WS1 (23%), actinobacteria (11%), and cyanobacteria (10%). Isolation of non-cyanobacterial microorganisms from the Shark Bay intertidal stromatolites revealed a dominance of *Bacillus* spp. within the Low G + C Gram-positive bacteria (Burns et al., 2004).

Bacillus spp. have not been previously reported from stromatolites, however some characteristics of *Bacillus* (e.g. antibiotic production, desiccation tolerance) may enhance their survival in the Shark Bay stromatolites. The surface of *B. subtilis* has also been found to bind fine-grained silicate minerals, as well as remove heavy metals from solution to form metallic silicates on their surface (Mera and Beveridge, 1993). Furthermore, the activity of urease has been shown in *Bacillus* spp. to promote and affect microbially induced $CaCO_3$ precipitation (Hammes et al., 2003). The presence and role of such metabolic activities in the Shark Bay stromatolites needs to be further studied to ascertain the exact roles of *Bacillus* spp. in stromatolite morphogenesis.

In addition to *Bacillus* sp. the presence of a range of other non-cyanobacterial microorganisms in Shark Bay intertidal stromatolites has been inferred by molecular analyses (Burns et al., 2004; Papineau et al., 2005), including *Thermoleophilum* spp. (green non-sulfur bacterium), *Rhodovibrio* spp., *Rhodobacter* spp., *Hyphomonas* spp. (phototrophic purple non-sulfur bacteria), *Desulfovibrio* (sulfate-reducing bacteria) and *Roseobacter* (aerobic purple bacteria). This concurs with other studies identifying phototrophic purple non-sulfur bacteria, green sulfur bacteria and sulfate-reducing bacteria in stromatolites (Bauld et al., 1979; Golubic, 1976; Visscher, 2000). These latter microorganisms have been implicated in stromatolite formation through the action of sulfur cycling (Visscher et al., 1999, 1998). *Hyphomonas* sp. have been suggested to be the primary colonizers on a submerged marine environment (Baier et al., 1983).

Other studies have demonstrated an involvement of *Hyphomonas* sp. in the formation of biofilms mediated by extracellular polymeric substances (Quintero and Weiner, 1995), though their roles in stromatolite morphogenesis are yet to be determined. *Roseobacter* have a functionally similar photosynthetic apparatus to that of the anoxygenic phototrophs (Candela et al., 2001), and thus this metabolism can be putatively inferred in Shark Bay stromatolites. It has also been shown that *Roseobacter* strains produce acylated homoserine lactones, which might be significant in the formation of biofilms, exoenzyme production, and antibiotic production (Gram et al., 2002). *Planctomycetales* have also been detected in Shark Bay stromatolites (Burns et al., 2004), and it has been suggested that their ability to attach to particles may have a significant role in the precipitation and dissolution of marine microaggregates (Fuerst, 1995).

2.4. Archaea associated with Shark Bay intertidal stromatolites

A group of microorganisms identified for the first time to be associated with stromatolites are the archaea (Burns et al., 2004; Papineau et al., 2005; Leuko et al., 2007). The majority of the archaea identified were closely related to archaea known to be abundant in hypersaline settings. As these archaea are known to possess various forms of phototrophic metabolism, these physiologies may be important in stromatolite communities in addition to cyanobacterial oxygenic photosynthesis (Burns et al., 2004). A number of organisms were related to the Crenarchaeota however their roles in stromatolite communities are currently unknown. The identification of sequences related to the methanogenic archaea is an interesting finding for this location, as it has been suggested that the high sulfate environment of Shark Bay could potentially restrict the presence of these organisms (Burns et al., 2004).

Recently, several novel archaea have been isolated and characterized for the first time from the Shark Bay stromatolites: *Halococcus hamelinensis* (Goh et al., 2006), and *Haloferax elongans* sp. nov. and *Haloferax mucosum* sp. nov. (Allen et al., 2008). These organisms had several unique metabolisms for this group of archaea, and characterisation of other novel microorganisms identified from extant stromatolites may reveal further unique metabolisms or pathways. Although the exact role of archaea in stromatolite biology is still unknown, they are likely to be important community members involved in nutrient cycling. Although some Halobacterial species have been shown to be capable of fixing CO_2 (Javor, 1988), it remains to be determined whether halobacterial

species in stromatolites are involved in the calcification process, in addition to cyanobacteria and other bacteria.

2.5. Summary of Shark Bay stromatolite microbial diversity

Recent results using molecular analyses have demonstrated a very diverse range of micoorganisms present in modern stromatolites. Hypersalinity appears to be the factor of prime importance in the development of the stromatolites in Shark Bay, and this is reflected in the types of microorganisms identified. Studies have also shown that many of the stromatolite microorganisms are unique with no close known relatives (Burns et al., 2004; Papineau et al., 2005), and these microorganisms may also possess novel physiologies vital to the integrity and persistence of stromatolites. Combined with our knowledge on the prevailing environmental conditions, this immense diversity of prokaryotic life associated with modern stromatolites suggests an intimate association between biotic and non-biotic factors in stromatolite formation. Most studies on both the Shark Bay and Bahaman stromatolites also revealed that eukaroytes were scarce in these extant formations (Reid et al., 2000; Burns et al., 2004; Papineau et al., 2005), though one study has documented various flagellates in Shark Bay (Al-Qassab et al., 2002), and a wide range of animals are also present (Walter, 1994). The exact role or impact of higher eukaryotes on the intertidal stromatolites of Shark Bay remains to be determined. Furthermore, the differences observed between microbial community compositions of living stromatolites in different locations, such as that between the Bahamas and Shark Bay (Reid et al., 2000; Burns et al., 2004; Papineau et al., 2005), suggests that different stromatolite morphologies depend on the community present. For example different stromatolite structures may result if specific microorganisms trap sediments differently (Papineau et al., 2005). The numerous novel or unknown microbes identified also may play pivotal roles in stromatolite systems that we do not yet understand.

3. Mt. Hood and White Island

Another example of modern analogues of ancient microbial systems are those found in moderate to high temperature acidic hydrothermal environments, such as the composite stratovolcanoes of Mt. Hood and White Island. Located in OR, USA, Mt. Hood (Fig. 3) has been dominated by recurrent volcanic activity for the past 1.5 million years (Scott et al., 1997; Williams et al., 1982).

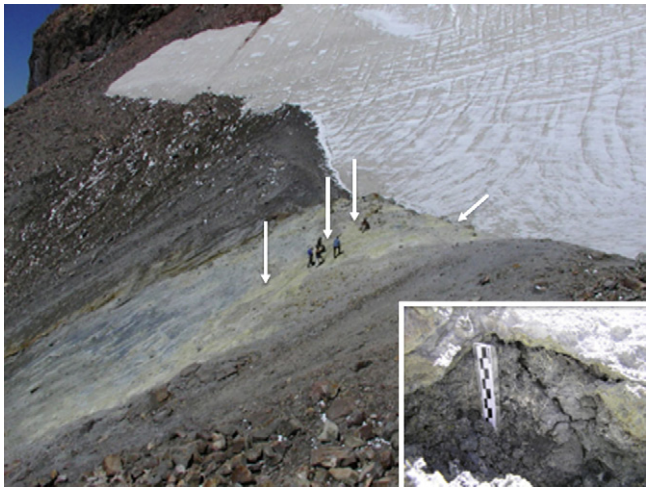

Fig. 3. Devil's Kitchen, Mt. Hood. Arrows indicate areas sampled. Inset: close-up of one of the areas sampled, scale bar 8 cm.

Fig. 4. South-western side of the Eastern subcrater, White Island. Arrow indicates area sampled. Inset: close-up of one of the areas sampled, scale bar approximately 6 cm.

Lava flows, domes and volcanic deposits are mainly composed of andesite, with other volcanic rock types also present (basalt, andesitic basalt and dacite). Today, volcanic activity is limited to the Hot Rocks and Devil's Kitchen hydrothermal fields close to the summit region. These two fumarolic areas are permanently ice-free environments with local microclimates within the Mt. Hood glacial region. The ground of these hydrothermally heated areas consists of soft material of highly altered and degraded andesite with visible sulfur accumulations. The other major components are the opaline precipitates cristobalite and tridymite, with clay minerals also present. White Island, located at the north-eastern end of the Taupo Volcanic Zone (Fig. 4), one of the most volcanically active regions on Earth (Wilson et al., 1995), is the subaerial aspect of a large marine volcano in the Bay of Plenty (North Island, NZ) (Cole et al., 2000). The volcano is the product of a succession of andesite–dacite lava flows and pyroclastic deposits (Cole et al., 2000). The modern day surface expression of the hydrothermal system is principally contained within the crater area (Clark and Cole, 1986). Numerous high temperature fumaroles and hot acid springs discharge onto the crater floor of loose unconsolidated sand, silt and gypsum-veined rocks. This floor is highly altered due to the low pH of the hydrothermal waters and condensates (Baumgart, 1959; Hedenquist et al., 1993). White Island also contains submerged, shallow (~10–30 m) hydrothermal vents near its shoreline (Sarano et al., 1989; Tait and Tait, 2001). The hydrothermal regions of Mt. Hood are situated within a glacial environment at a much higher altitude (~3150 m above sea level) than those of White Island that are in a temperate climate at, and below, sea level. In contrast to the comparatively dry degraded andesites of Mt. Hood the terrestrial hydrothermal regions of White Island are saturated with magmatic condensates and meteoric surface waters.

Our studies are the first describing the microbial community of the Mt. Hood hydrothermal areas and the most comprehensive survey to date of the White Island microbial ecosystem (Henneberger et al., 2006; Butterworth, 2004; Ibañez-Peral et al., 2006). Only few bacterial species and one alga (*Cyanidium caldarium*) have previously been cultured from White Island and a culture-independent 16S ribosomal RNA (16S rRNA)-based report, limited to the analysis of a single environmental sample, identified microbes related to green sulfur Bacteria, purple non-sulfur Bacteria, *Ralstonia solanacearum* and an uncultured Firmicutes (Kaplan, 1956; Hamilton and Baumgart, 1959; Donachie et al., 2002; Lee et al., 2007). For our studies numerous samples from the hydrothermal regions of Mt. Hood (degraded andesites; Fig. 3 inset) and

White Island (sediment, gravel, water and macroscopically visible microbial biota; Fig. 4 inset) were analysed comprehensively for microbial community composition using both culturing and 16S rRNA-based methodologies. The communities were also investigated by light microscopy and fluorescence *in situ* hybridisation (FISH), and screened for the presence of genes involved in sulfur and iron metabolism.

3.1. Physical and geochemical environment

Degraded andesite samples from the Devil's Kitchen hydrothermal field were highly acidic, with pH values ranging from 0.95 to 4 (the majority were between 1.4 and 3). Surface temperatures varied from 33 to 47 °C, whilst temperatures from just 0.5 to 1 cm below the surface and around fumaroles reached between 80 and 89 °C, the latter representing the approximate boiling temperature of water at the Devil's Kitchen elevation. Superheated fumaroles were also present in the Hot Rocks hydrothermal field; however, the ground temperature at 1 cm depth at selected sites within this area was lower (55–60 °C) than in the Devil's Kitchen area. Mt. Hood samples were very low in organic carbon and nitrogen (<1200 and 11 mg/kg wet weight, respectively), whilst iron, sulfate and sulfur contents were high (e.g. SO_4^{2-} and Fe up to 25.4 and 19 g/kg wet weight, respectively). The high sulfate and sulfur content was specifically associated with the hydrothermally altered andesites, as levels were much lower in unaltered control gravel near Devil's Kitchen.

The temperature and pH of White Island terrestrial crater samples ranged from 36 to 104 °C and 0.0 to 4.5, respectively; the shallow ocean vent samples varied between 25 and 52 °C, and pH 6.0–7.5. High concentrations of iron and sulfate were present in terrestrial water samples: total iron ranged from 12.5 to 249 mg/l and total sulfate from 2320 to 13,900 mg/l. These concentrations are comparable to those found in acid mine drainage and hot acid spring environments worldwide (Chiodini et al., 1996; Xu et al., 1998; Johnson and Hallberg, 2003; Rzonca and Schulze-Makuch, 2003). Numerous trace elements such as chloride, phosphate, calcium and magnesium were also present. Total organic carbon levels were very low (<2.0 mg/l), consistent with the low concentrations of dissolved organic matter found in low pH environments (Johnson and Hallberg, 2003).

3.2. Microbial ecology

The Mt. Hood samples did not contain macroscopically visible microbial communities, and microscopic analysis indicated an overall paucity of organisms. Mainly coccoid cells, with irregular or well-defined morphologies and of different sizes (0.5–2.0 μm in diameter) were present. Cell abundances were higher at the soil surface, where temperatures were relatively lower, than in the deeper (up to 10 cm), higher temperature layers. Cells were unevenly distributed throughout the samples, mainly occurring in small clusters or groups seemingly associated with mineral structures, though the identity of these structures was not determined. Some puta-

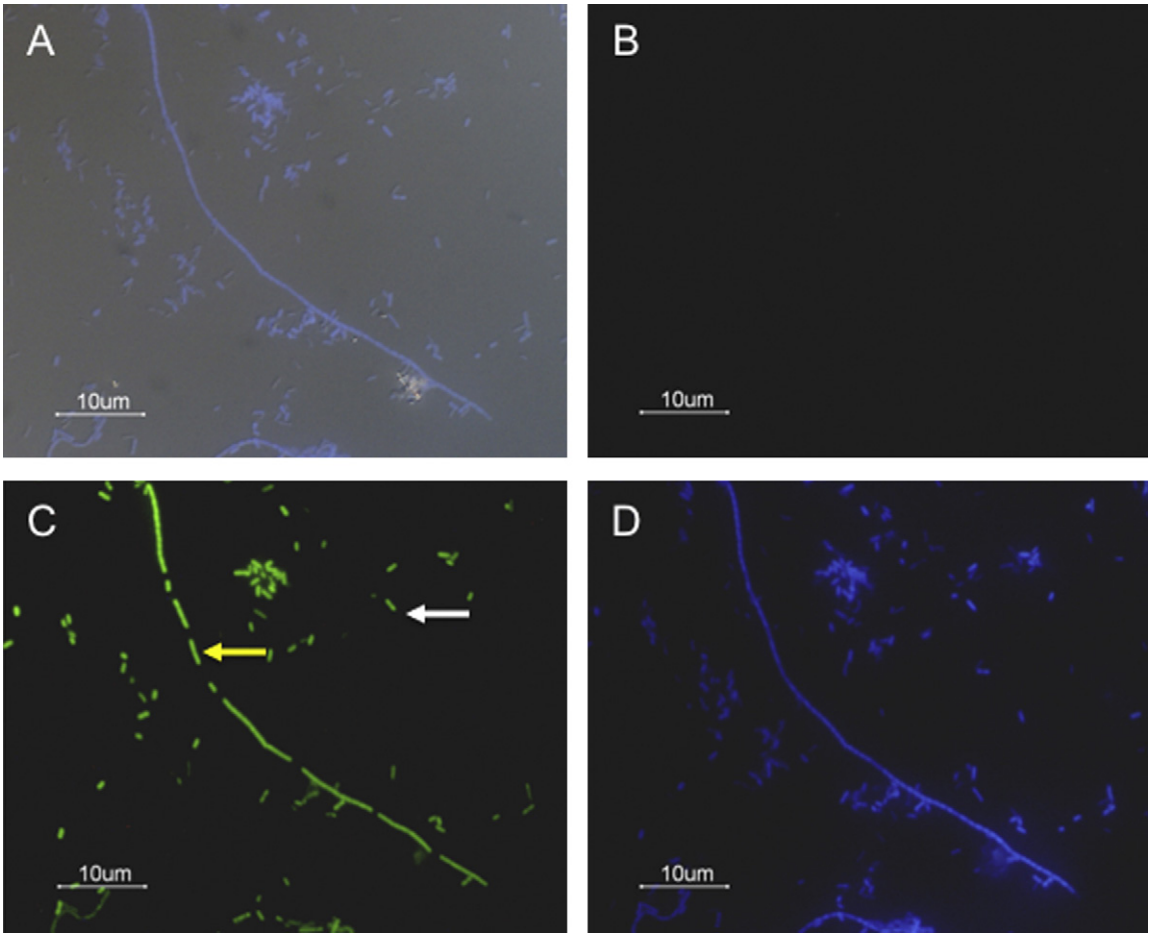

Fig. 5. An example of the White Island bacterial morphotypes identified by FISH. Same field of view shown in each panel. (A) Differential interference contrast microscopy overlaid with DAPI stained image (DAPI specifically stains nucleic acids; blue fluorescence); (B) FISH with DNA probes targeting Archaea (none were visualised in this sample); (C) FISH with DNA probes targeting bacteria – bacterial cocci (white arrow) and filamentous rods (yellow arrow) are observed by green fluorescence. D: DAPI stain, blue fluorescence.

tive Archaea were identified by FISH, supporting the culture-based enrichment and isolation of members of this domain. Bacteria were not detected, despite the liquid culture enrichment of rod-shaped bacterial cells from several samples. The overall utility of FISH was limited by the strong, non-specific background fluorescence resulting from the presence of clay and other minerals in the Mt. Hood samples.

Macroscopically visible microbial communities, including streamers, were present in some areas of White Island (Fig. 4). A range of prokaryotic-sized bacilli, cocci and filamentous forms were microscopically identified in a third of the samples from the main crater region and in all shallow ocean vents. One marine sample contained large (~10 μm × 2–3 μm) bacterial filamentous forms, as have been reported in other sulfur-rich hydrothermal and/or acidic sites (Fenchel and Bernarde, 1995; Johnson and Hallberg, 2003). The majority of cells were visualised in samples at ≤54 °C, and none were seen above 71 °C; cell abundances were higher in areas of relatively lower temperature (30–36 °C) and higher pH (4.5–6.5). Microbes were not detected in the majority of samples where the pH was 4 or lower, except for two samples (T = 50 and 54 °C). The distribution and abundance of White Island microbes mostly displayed a temperature and pH dependence, supporting long established observations that organisms can thrive in environments of high temperature or low pH, but that life is rare where a combination of both extremes exists (Brock and Darland, 1970). Conclusive FISH identification of Bacteria was achieved in those areas with macroscopically visible microbial communities, as the presence of relatively large numbers of cells overcame the generally strong non-specific background fluorescence present (Fig. 5). As with the Mt. Hood soils, this background noise resulted from minerals, and was particularly problematic when examining the putative Archaea-specific fluorescence seen in certain samples.

Culture and culture-independent methodologies demonstrated that the Mt. Hood and White Island hydrothermal environments were both dominated by thermoacidophilic bacterial and archaeal communities of moderate diversity, as noted in other similarly acidic, high temperature environments (Burton and Norris, 2000; Ng et al., 2005). The majority of the White Island taxa, dominant or otherwise, were most closely related to uncultured organisms, whilst those from Mt. Hood included a higher proportion of previously cultured species. Eukaryotes (diatoms and the red alga/rhodophyte *C. caldarium*) were detected in a small number of White Island samples at temperatures (54–89 °C) that are mostly higher than the known upper limit of approximately 60 °C for this domain (Rothschild and Mancinelli, 2001). Further sampling and analyses would be required to determine if these eukaryotes are truly associated with these sites, or whether they originated (e.g. via water run-off) from an adjacent, lower temperature area (Brown and Wolfe, 2006; Castenholz, 1969; Ciniglia et al., 2004).

The predominant prokaryotic taxa identified by culture-independent 16S rDNA sequence analysis of hydrothermal samples are listed in Table 2. Archaea dominated both the Mt. Hood and White Island hydrothermal areas. The identification of Archaea is a first for White Island. Crenarchaeal Sulfolobales (*Sulfolobus* spp. and *Acidianus* spp.) represented the major taxa detected in the Mt. Hood samples, with Euryarchaeota (class Thermoplasmata) also being present, and even dominant, in some areas. Various Euryarchaeota (class Thermoplasmata, class Thermococci and unknown classes) dominated the White Island microbiota, whilst Crenarchaeota were detected in only 30% of the terrestrial sites and in none of the shallow ocean vents. The majority of bacterial taxa identified at Mt. Hood differed from those present on White Island, with the exception of *Acidithiobacillus* spp. Members of the order Acidimicrobiales and *Sulfobacillus* spp. were amongst the other major taxa detected on Mt. Hood, whilst 16S rDNA sequences obtained from White Island mainly represented *Acidithiobacillus* spp., *Thiomonas* spp. and uncultured or unidentified members of various phyla (e.g. Firmicutes and α-proteobacteria). Thermoacidophilic bacteria and Archaea were also identified in enrichment and pure cultures, for example, *Sulfobacillus* spp., *Sulfolobus* spp. and *Ferroplasma* sp. from Mt. Hood; and Firmicutes (e.g. *Alicyclobacillus* spp.), α-proteobacteria, uncultured Bacteria (e.g., Bacteroidetes) and various Crenarchaeota and Euryarchaeota (e.g. *Thermoplasma* spp.) from White Island.

Table 2
Dominant taxa identified using 16S rDNA sequencing from Mt. Hood and White Island.

Mt. Hood	White Island
Bacteria	
Cultured and uncultured members of:	*Acidithiobacillus* spp.
Sulfobacillus spp.	*Thiomonas* spp.
Acidithiobacillus spp.	Various uncultured bacteria
Order Acidimicrobiales	
Archaea	
Acidianus spp.	Various uncultured crenarchaeota
Sulfolobus spp.	Various uncultured euryarchaeota
Class Thermoplasmata	

The majority of the Mt. Hood and White Island prokaryotes are closely related to known (or suspected) sulfur- and iron-metabolising organisms, such as those detected in acidic sulfur-rich hydrothermal areas and acid mine drainage sites, environments that are often dominated by chemoautotrophic iron and sulfur oxidisers (Hallberg and Johnson, 2001). These chemoautotrophs possess metabolic pathways that allow them to perform such oxidative reactions; the screening of samples for the relevant genes therefore provides indirect evidence that specific reactions are occurring in a particular environment. Three metabolic genes were detected in samples from White Island – Sulfur Oxygenase Reductase (*sor*) and *soxB*, both of which code for enzymes involved in sulfur oxidation, and *rus*, a gene encoding an enzyme involved in iron oxidation (He et al., 2000; Petri et al., 2001; Yarzabal et al., 2003). *Sor* genes were also identified in Mt. Hood samples and in a cultured archaeal isolate that displayed autotrophic growth by oxidising sulfur, mineral sulfides, and ferrous iron (Henneberger, 2008).

3.3. Summary of White Island and Mt. Hood microbial diversity

Microbial metabolic pathways based on sulfur and iron are believed to be amongst the earliest to have evolved (Vargas et al., 1998; Wagner et al., 1998). In modern environments, microorganisms are still intimately involved in the cycling of sulfur and iron, and these processes represent important aspects of microbial life in volcanic environments (Reysenbach and Cady, 2001). Nonetheless, many details of these cycles, their impact on biogeochemical processes and their distribution remain unclear (Macalady and Banfield, 2003; Madsen, 2005). Culture-independent and culture-based analyses of the microbiota inhabiting these hydrothermal environments strongly suggests that microbial involvement in sulfur and iron cycles, via oxidation of elemental sulfur, sulfides and iron, is occurring in these acidic settings. The evidence for this proposition includes: (i) the predominance of microorganisms closely related to known sulfur- and iron-metabolising species and bioleaching microorganisms; (ii) the identification of genes encoding key metabolic enzymes in both sulfur and iron oxidation pathways; (iii) the enrichment and isolation of sulfur- and iron-oxidising species; and (iv) the prevalence of sulfur and iron compounds in the hydrothermal areas analysed.

4. Concluding remarks

These studies of modern analogues to ancient microbial communities have shown that they are much more diverse than originally thought. The advent of modern molecular techniques have revolutionised these types of analyses and vastly improved our understanding of the total diversity present. Although culture-independent molecular studies alone do not allow us to absolutely determine whether sequences represent active organisms, we can take advantage of phylogenetic affinity with well-studied species to make rational predictions about the metabolic contributions of organisms identified. In particular, as described here both for living stromatolites and hydrothermal/acidic environments, organisms from the domain Archaea are both prominent and likely to play important roles in these communities. In general, eukaryotes are also scarce in these modern analogues in comparison to prokaryotes, likely a result of the harsh or 'extreme' conditions in which they are found. The environment selects for the prevailing organisms (e.g., temperature, acid, salt-tolerant), and it is likely that under similar conditions on the early Earth organisms possessing similar adaptive traits may have thrived. For example the Mt. Hood and White Island volcanoes can be compared to early Archaean examples in the Pilbara region of Western Australia (Van Kranendonk, 2006) that may have hosted a similar microbiota.

These studies have also revealed dynamic interactions between the biotic and non-biotic environment, with geobiological processes occurring as a function of both organism metabolism and the surrounding geochemical environment. These processes may also result in structures that can be detected in the fossil record, thus the study of modern analogues (from community structure, biomineralisation, to mechanisms of adaptation under extreme conditions) is critical to afford rational interpretation of the rock record and assist in our overall understanding of early life on Earth.

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