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### Modern analogues and the early history of microbial life

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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

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).

## **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



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

Stratiform mat type <sup>a</sup>	Microorganism identity	Identification method	Source
PM	<i>Entophysalis major</i>	Microscopy	Golubic (1976)
SM	<i>Microcoleus</i> sp.	Microscopy	Golubic (1976)
SM	<i>Schizothrix</i> sp.	Microscopy	Golubic (1976)
TM	<i>Lyngbya aestuarii</i>	Microscopy	Golubic (1976)
TM	<i>Schizothrix</i> sp.	Microscopy	Golubic (1976)
PM	<i>Halomicronema</i> sp.	Molecular analyses	Allen et al. (2009)
PM	<i>Pleurocapsa</i> sp.	Molecular analyses	Allen et al. (2009)
PM	<i>Sprulina</i> sp.	Molecular analyses	Allen et al. (2009)
PM	<i>Chroococidiopsis</i> sp.	Molecular analyses	Allen et al. (2009)
PM	<i>Cyanothece</i> sp.	Molecular analyses	Allen et al. (2009)
PM	<i>Oscillatoria</i> sp.	Molecular analyses	Allen et al. (2009)
SM	<i>Synechocystis</i> sp.	Molecular analyses	Allen et al. (2009)
SM	<i>Staniera</i> sp.	Molecular analyses	Allen et al. (2009)
SM	<i>Xenococcus</i> sp.	Molecular analyses	Allen et al. (2009)
SM	<i>Anabeana</i> sp.	Molecular analyses	Allen et al. (2009)
SM	<i>Thermosynechococcus</i> sp.	Molecular analyses	Allen et al. (2009)
SM	<i>Myxosarcina</i> sp.	Molecular analyses	Allen et al. (2009)
PM/SM	<i>Euhalothece</i> sp.	Molecular analyses	Allen et al. (2009)
PM/SM	<i>Microcoleus</i> sp.	Molecular analyses	Allen et al. (2009)
PM/SM	<i>Halothece</i> sp.	Molecular analyses	Allen et al. (2009)
PM/SM	<i>Arthrospira</i> sp.	Molecular analyses	Allen et al. (2009)
PM/SM	<i>Phormidium</i> sp.	Molecular analyses	Allen et al. (2009)
PM/SM	<i>Leptolyngbya</i> sp.	Molecular analyses	Allen et al. (2009)
PM/SM	Unknown cyanobacteria	Molecular analyses	Allen et al. (2009)

<sup>a</sup> 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



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

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 result-





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