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Geomycology: fungi in mineral substrata

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'Geomycology' can be defined as the impact of fungi on geological processes, including the alteration and weathering of rocks and minerals, the accumulation of metals and their role in nutrient cycling and influence on proliferation of microbial communities in mineral substrates. Although many studies on microbial interactions with minerals have been published in recent years, the main focus of geomicrobiology has been on prokaryotes. Recently, it has become apparent that epi- and endolithic fungi comprise a significant component of the microflora in a wide range of rocks including siliceous types (silica, silicates and aluminosilicates), sandstone, granite, limestone, marble and gypsum. However, to date little is known about their *in situ* growth patterns or biogeochemical roles in such an environment. The aim of this article is to highlight our recent work on the biogeochemical roles of fungi inhabiting limestone ($CaCO_3$) and dolomite ($CaMg(CO_3)_2$) rocks and to emphasise the importance of fungi as agents of geological change.

Keywords: epilithic, endolithic, limestone, dolomite, rocks, minerals, fungi

Between a rock and a hard place

The limitation of nutrients, moisture deficit and exposure to solar radiation makes rock substrates one of the most inhospitable habitats for microbial life. Nevertheless many fungi and lichens have evolved to survive and exploit microhabitats within and on the surface of rocks (Tables 1 & 2). Rock-inhabiting fungi have been reported in both igneous and sedimentary rocks including siliceous types (silica, silicates and aluminosilicates), sandstone, granite, limestone, marble and gypsum, and even from extreme environments like hot and cold deserts (Staley *et al*., 1982; Ehrlich, 1998; Sterflinger, 2000).

It is likely that fungi are ubiquitous components of the microflora of all rocks and along with cyanobacteria, chemolitho- and chemoorganotrophic bacteria and algae, constitute an important component of epilithic and endolithic microbial communities. Epilithic fungi colonise rock surfaces, where they often occur in symbiosis with algae or cyanobacteria as lichens. Fungi may also inhabit the rock sub-surface as endoliths in pre-existing cracks and fissures or as cryptoendoliths in mineral pores and cavities (Ehrlich, 1981; Staley *et al*., 1982; Johnstone & Vestal, 1992; Urzi *et al*., 1995; Panina *et al*., 1997; Sterflinger, 2000). Although sandstones, and to a lesser extent limestones, are the most common rock substrata colonised by microorganisms, little is known about their *in situ* growth patterns or biogeochemical roles in such an environment (Ehrlich, 1998).

Rocks can be defined as any naturally-formed, consolidated material composed of one or more minerals. Minerals are inorganic crystalline solids with a definite chemical composition (Plummer & McGeary, 1996). Free-living and symbiotic fungal forms are believed to be involved in the weathering of rocks by promoting mineral diagenesis (which can be generally defined as the transformation of a mineral into a different mineral) and dissolution. An important contribution to the weathering process can be the result of the excretion of metabolites, e.g. H^+, organic acids and other metal-binding ligands, which may result in dissolution of the host-rock through chemical attack on mineral surfaces (Johnstone & Vestal, 1992; Ehrlich, 1998; Gadd & Sayer, 2000). The weathering action of fungi may also occur as a result of oxidative or reductive attack of reactive mineral constituents, e.g. Mn and Fe (Grote & Krumbein, 1992; de la Torre &

Table 1. Known fungal genera in rock substrates
(adapted from Hirsch *et al*. 1994; Kumar & Kumar 1999; Sterflinger 2000; Verrecchia, 2000).

Fungal Genera	Limestone	Granite	Marble	Sandstone	Andesite	Basalt	Gneiss	Quartz
Absidia							*	*
Acremonium							*	*
Acremoniella			*					
Acrodyctis			*					
Alternaria		*	*	*			*	*
Alysidium			*					
Aphanocladium		*	*	*				
Aposphaeria			*					
Arthrinium							*	*
Aspergillus	*	*	*	*	*		*	*
Aureobasidium	*	*	*	*			*	*
Botrytis		*	*	*				
Camarosporium			*					
Candida				*		*		
Cephalosporium	*						*	*
Chaetocladium							*	*
Chaetomium				*				
Chloridium			*					
Ciliciopodium			*					
Cladosporium		*	*	*	*		*	*
Coniosporium		*	*					
Coniothyrium		*	*	*				
Cunninghamella					*			
Curvularia			*	*	*			
Drechslera			*					
Engydodontium		*	*	*				
Epicoccum		*	*	*				
Exophiala		*	*	*			*	*
Fusarium	*	*	*	*	*		*	*
Gilmaniella			*					
Gliocladium					*			
Gliomastix			*				*	*
Hormiscium			*					
Hormonema		*	*	*			*	*
Hortaea		*	*	*				
Humicola			*	*				
Lecythophora		*	*	*				
Lichenothelia		*	*	*				
Lipomyces				*				
Macrophoma			*	*				
Melanospora							*	*
Memnoniella			*					

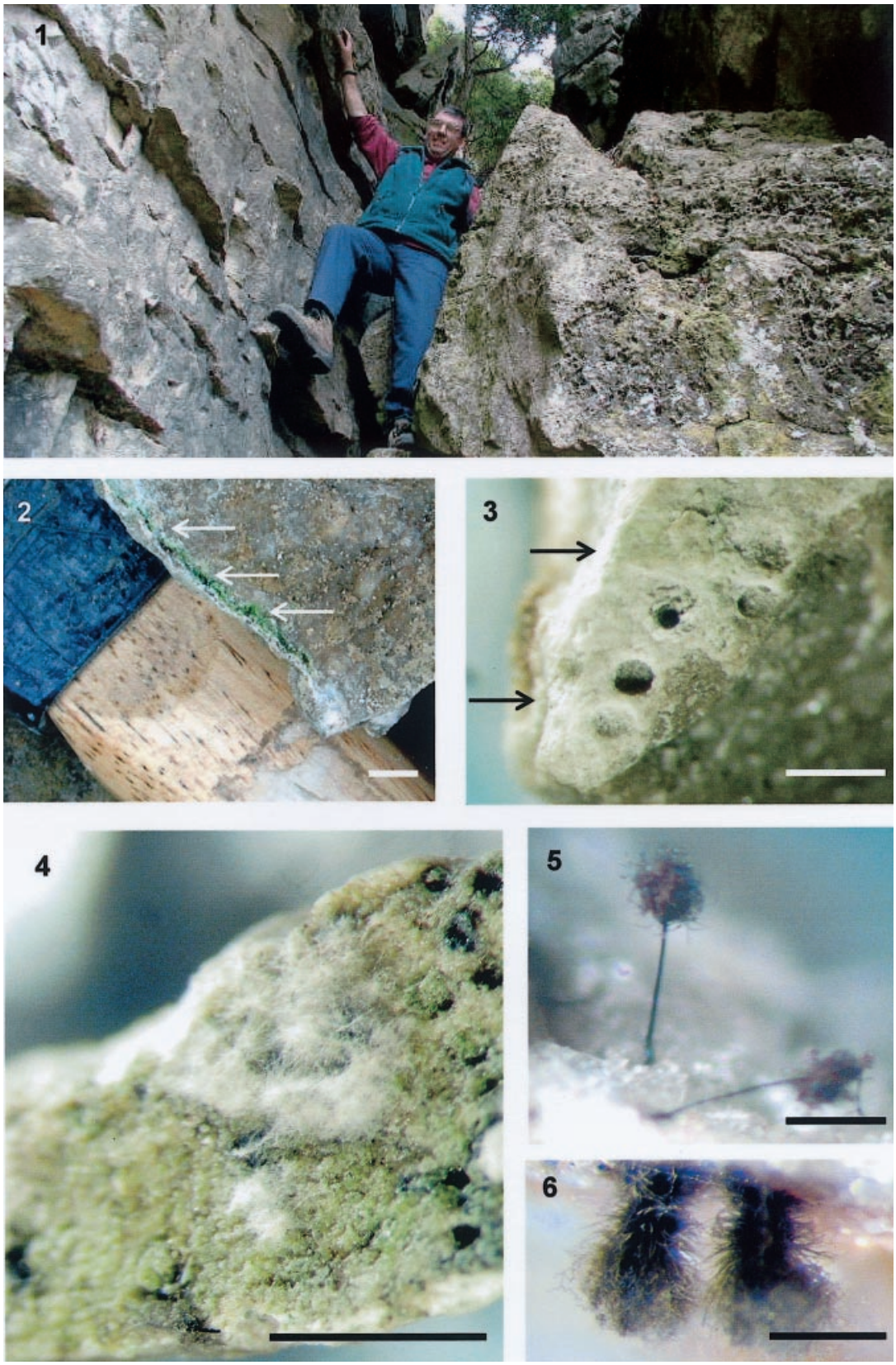
Fungal Genera	Limestone	Granite	Marble	Sandstone	Andesite	Basalt	Gneiss	Quartz
Moniliella							*	*
Monillia	*							
Monodictys			*					
Mucor			*				*	*
Paecilomyces		*	*	*				
Papulospora							*	*
Penicillium	*	*	*	*	*		*	*
Pestalotia			*					
Phaeococcomyces		*	*	*				
Phaeosclera			*					
Phaeotheca		*	*	*				
Phialophora			*				*	*
Phoma		*	*	*				
Phyllosticta			*					
Pithomyces			*					
Polyscytalum							*	*
Pseudobotrytis			*					
Pycnidiella							*	*
Rhinocladium			*					
Rhinocladiella			*					
Rhizoctonia							*	*
Rhizopus			*	*	*			*
Rhodotorula		*	*	*				
Sarcinomyces		*	*	*				
Sclerococcum			*					
Scopulariopsis			*				*	*
Scytalidium			*				*	*
Sordaria							*	*
Sporobolomyces				*				
Stachybotrys			*					
Staphylotrichum			*					
Stemphylium			*					
Taeniolella			*					
Tetracoccosporium			*					
Torula			*					
Trichocladium			*					
Trichoderma		*	*	*			*	*
Trichothecium							*	*
Trimmatostroma		*	*	*			*	*
Ulocladium		*	*	*			*	*
Verticillium		*	*	*				
Virgaria			*					

Gomez-Alarcon, 1994). Some fungi, e.g. *Lichenothelia* spp. can oxidize manganese and iron from metal-bearing minerals such as siderite ($FeCO_3$) and rhodochrosite ($MnCO_3$) to form desert varnish, an oxidized metal layer (patina) a few millimetres thick on rocks in arid and semi-arid regions (Grote & Krumbein, 1992). Dissolution of host-rock by fungi and lichens may clearly supply soluble nutrients critical to the survival and proliferation of microbial communities, e.g. trace metals, P, S, as well as organic metabolites and products arising from death and degradation (Gadd & Sayer, 2000).

As well as an important role in mineral dissolution, fungi can also play a role in secondary mineral formation through the precipitation of oxalates, e.g. whewellite ($CaC_2O_4.H_2O$) and weddellite ($CaC_2O_4.2H_2O$), and through metabolism-independent binding of metal ions onto fungal cell walls and other external surfaces (Arnott, 1995; Gadd, 1993; 1999). These kinds of interactions between fungi and rocks are of importance in stabilising mineral grains and may result in the formation of biogenic micro-fabrics (distinct micro-scale crystalline features attributable to biological activity that differ from the normal micro-scale crystalline

Table 2. Common lichen genera on rock (adapted from Prieto Lamas 1995; Easton 1997; Kumar & Kumar 1999; Matthes *et al*. 2000; Sterflinger 2000; Verrecchia, 2000).

Lichen Genera	Limestone	Granite	Feldspars	Serpentinite	Cupriferous rocks	Gabbro	Dolerite	Sandstone	Andesite	Basalt	Gneiss	Quartz
Acarospora					*							
Acrocordia	*											
Anaptychia	*											
Arthopyrenia	*											
Aspicila	*	*			*	*						
Bacidia	*								*			
Biatoria									*			
Blastenia	*											
Buellia	*											
Caloplaca	*			*				*				
Candelariella	*											
Catillaria	*							*				
Chiodecton	*											
Cladonia	*											
Coccocarpia	*											
Collema	*											
Dimelaena												*
Diploica	*											
Diploschistes								*				
Dirina	*											
Dirinaria	*							*				
Endocarpon	*								*			
Ephebe									*			
Heterodermia	*							*				
Laboria									*			
Lecanora	*			*								
Lechidella	*											
Lecidea	*	*			*							
Lepraria	*											
Leptogium	*											
Leptotrema	*											
Lichenella	*											
Ochrolechia				*								
Ochrolechia	*											
Opegrapha	*											
Parmelia	*	*	*			*	*	*	*		*	*
Parmeliella	*											
Parmelina	*											
Parmotrema	*											
Peltigera									*			
Peltula	*							*				
Pertusaria	*									*		
Phylliscum	*											
Phyllopsora	*											
Physcia	*											
Placynthium									*			
Porina									*			
Psorotrichia	*											
Pyxine								*				
Ramalina	*											
Rhizocarpon	*											
Roccella		*	*						*			
Sarcogyne	*											
Septrotrema									*			
Staurothele	*											
Stereocaulon										*		
Sticta	*											
Tephromela	*											
Thermucis									*			
Unsea	*										*	
Verrucaria	*								*			
Xanthoparmelia	*											
Xanthoria	*						*					



Figs 1-6 Fig1. Dolomitic limestone cliffs along the south-central portion of the Niagara Escarpment at the sample site at Mount Nemo, Ontario, Canada. Fig 2. Mount Nemo dolostone with the dark green band representing an endolith zone (marked by arrows) at depths of 0.5 to 1.0 mm inside freshly cleaved host-rock (bar marker = 5 mm). Fig 3. Highly weathered surface layer of Tunstead limestone (marked by arrows) (bar marker = 1 mm). Fig 4. Fungal hyphae growing on surface of re-hydrated Tunstead limestone (bar marker = 2 mm). Fig 5. Fungal reproductive structures growing out of pore in Kelso limestone (bar marker = 500 µm). Fig 6. Fungal reproductive structures growing out of pore in Mt. Nemo limestone (bar marker = 500 µm).

features exhibited by the host-rock) in mineral substrates (Goudie, 1996). However, fungal involvement in this aspect of geochemistry is largely unknown.

Recently, we have been investigating the role of epilithic and endolithic fungi in the transformation of carbonate minerals, particularly limestone ($CaCO_3$) and dolomite ($CaMg(CO_3)_2$). The work involved the use of light and environmental scanning electron microscopy to examine microbial communities *in situ* in Paleozoic dolomitic limestone samples from the Niagara Escarpment, Ontario, Canada and from Carboniferous limestone samples obtained from the Peak District, England, UK.

Limestone samples

The Canadian limestone samples (obtained from F.G. Ferris, Department of Geology, University of Toronto, Ontario, Canada, M5S 3B1) were collected along the south-central portion of the Niagara Escarpment at Mount Nemo and Kelso (Canada) (Fig 1). Rock samples were of dolomitic limestone ($CaMg(CO_3)_2$) and were Silurian to Late Devonian in age (438 to 360 Million Years BP). Limestone samples ($CaCO_3$) from Tunstead in the Peak District, England, UK (obtained from P. Burrows, Buxton Lime Industries Ltd, Tunstead House, Buxton, Derbyshire, UK, SK17 8TG) were collected from Tunstead quarry located in the Carboniferous limestone dome, Derbyshire (formed 325 Million Years BP). To minimise airborne contamination, samples were immediately placed in sterile plastic bags for storage and transport to the laboratory.

All freshly cleaved rock samples had a distinctive weathered layer extending between 1.0 and 5.0 mm into the limestone below the surface of the rock. The surface of the Tunstead limestone was covered by a lichen layer, below which was a dark grey band 1.0 to 4.0 mm thick of highly weathered material. In the Kelso and Mount Nemo limestones a thin dark green band, representing an endolith zone, approximately 1.0 to 2.0 mm thick at depths of 0.5 to 1.0 mm inside the host rock, was observed (Figs 2 & 3).

Dry rock samples were mounted on double-sided carbon adhesive tape on 7 mm diameter aluminium stubs. The samples were coated with 10 nm C and 5 nm Au/Pd layers and then analysed using environmental scanning electron microscopy (ESEM) (Philips XL30 ESEM FEG). ESEM analysis of the rock samples revealed a diversity of microflora inhabiting the surface weathered layer of the limestone minerals including heterotrophic bacteria, cyanobacteria and fungi (Fig 7). Microbial filaments ranging between 1 – 3 µm in diameter and greater than 100 µm in length were found to be a common feature in all three limestone samples (Fig 7a-d). Although some resembled filamentous cyanobacteria (Fig 7d), yeast-like cells approximately 2 µm in length and hyphal structures perhaps indicative of polymorphic rock-inhabiting fungi were clearly identifiable (Fig 7a-c). Microbial colonies less than 100 µm in size consisting of spheroidal sub-units approximately 5 µm in diameter were also a common feature in the limestone samples (Fig 7e). Similar features in rocks from the Sonoran Desert were described by Staley *et al*. (1982) as microcolonial fungi. Other microbes observed in the dry mineral samples included oviform and rod-shaped heterotrophic bacteria often growing in biofilms on pore space walls (Fig 7f).

Isolation of fungi from limestone samples

For the purpose of isolating fungi from the minerals, freshly cleaved limestone samples approximately 1 cm^3 were surface sterilised for 20 min using UV radiation and then re-hydrated in 30 ml plastic universal containers. Cotton wool plugs soaked in double distilled H_2O were placed in each universal container to serve as a moisture reservoir. The moist-chambers were then incubated in the dark at 25°C over a period of 21 d. After incubation, fungal hyphae and associated reproductive structures were observed to be growing on the surface and out of the pores of re-hydrated limestone samples (Figs 4, 5, 6). These were aseptically isolated under the dissecting microscope using a sterile heated needle and cultured onto Petri dishes containing malt extract agar (MEA) comprising (l^{-1}double distilled H_2O) malt extract agar (Lab M) 15.0 g; chlortetracycline hydrochloride (Sigma, UK) 0.05 g; amended to pH 7.0 with 1.5 g sodium bicarbonate (Sigma, UK). The isolates were incubated at 25°C until visible fungal colonies were observed and then sub-cultured.

Cultured fungi

The predominant fungi isolated from all three limestone samples were black meristematic fungi, some resembling *Aureobasidium*-like spp. (Fig 8a-b). These organisms are common inhabitants of marble on Mediterranean monuments (Sterflinger, 2000). Many of these fungi exhibited polymorphic growth patterns with mycelial and yeast-like growth forms (Fig 8c-e). However, on stone surfaces, they often form micro-colonies comprising yeast-like cells and chlamydospores with thickened melanin-pigmented cell walls. Other isolates included *Penicillium*-like spp. A total of five strains were isolated from the three limestone samples. Ascomycetes are

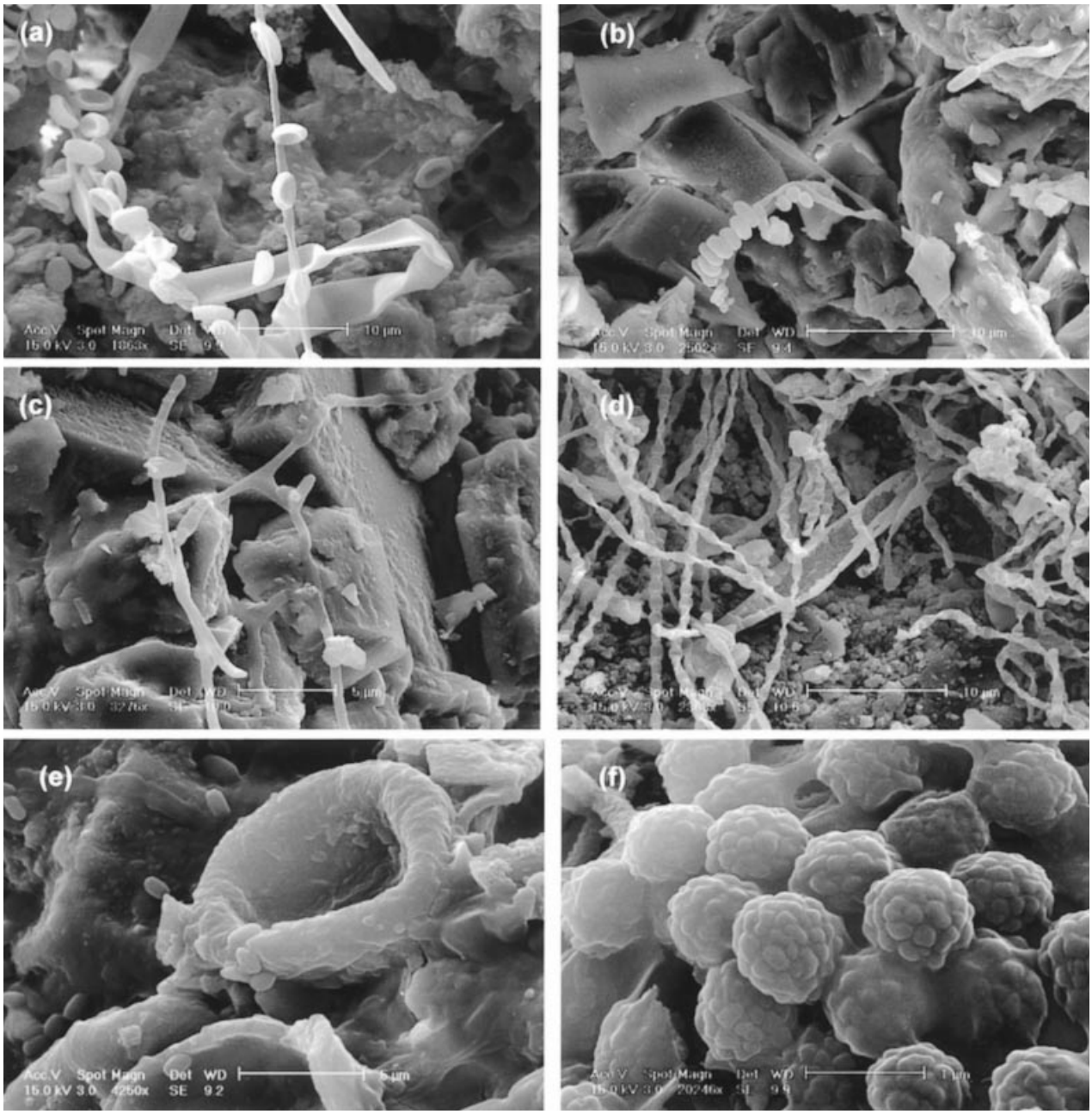


Fig 7 (a-c) Yeast-like cells approximately 2 µm in length and hyphal structures perhaps indicative of polymorphic rock-inhabiting fungi (bar marker = 10 µm, 10 µm and 5 µm respectively) (d) cyanobacterial filaments (bar marker = 10 µm) (e) micro-colonial fungi less than 100 µm in size consisting of spheroidal sub-units approximately 5 µm in diameter (bar marker = 5 µm) (f) oviform bacteria growing in biofilms on pore space walls (bar marker = 1 µm).

known to be common inhabitants of mineral substrates and building stone including sandstone, marble and granite, particularly in humid climates (Sterflinger, 2000). In addition, micromycetes with colony diameters between 500 – 800 µm were isolated from the three limestone samples (Fig 8f). These were slow growing and after four weeks growth on malt extract agar colonies remained less than 1 mm in diameter. Analysis of these micro-colonies using ESEM showed tightly-packed, intertwining hyphae less than 1 µm in diameter (Fig 8g).

Transformation of micro-fabrics in limestone by fungi

The re-hydrated mineral samples were analysed using Environmental Scanning Electron Microscopy (ESEM) and X-ray micro-analysis (EDXA) (Phoenix EDAX system) to evaluate *in situ* growth patterns and to provide evidence for biogeochemical roles of fungi in limestone rocks. Environmental Scanning Electron Microscopy (ESEM) was used to show the external

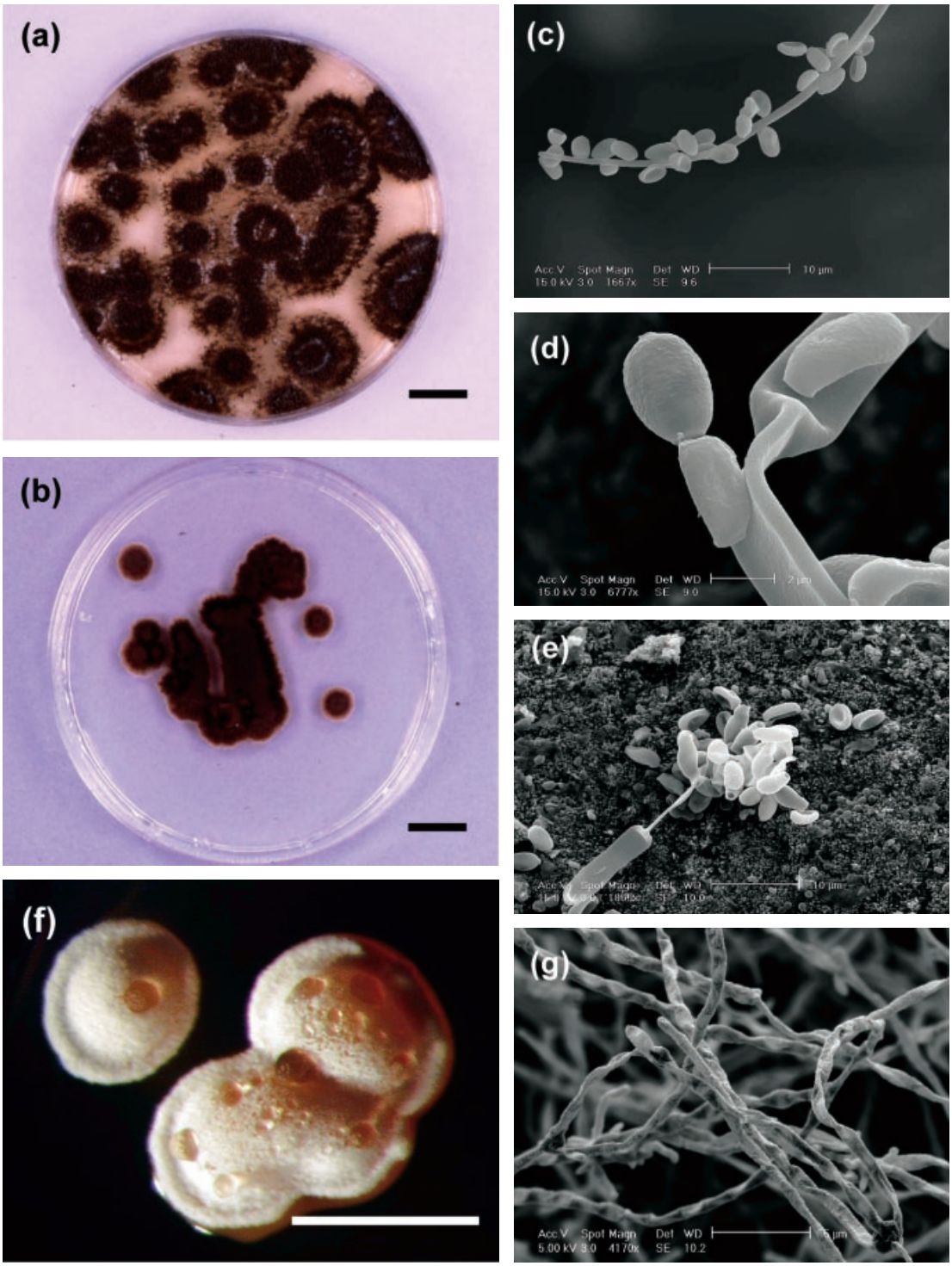


Fig 8 (a & b) Plate cultures of black meristematic fungi isolated from (a) Kelso limestone (bar marker = 1 cm) and (b) Tunstead limestone (bar marker = 1 cm) (c & d) ESEM micrographs showing growth patterns of the Kelso limestone isolate in plate cultures (bar marker = 10 µm and 2 µm respectively) and (e) ESEM micrograph of growth patterns of fungi *in situ* in Kelso limestone (bar marker = 10 µm) (f) plate cultures of micromycetes with colony diameters between 500 – 800 µm (bar marker = 1 mm) (g) ESEM micrograph showing growth patterns of micromycetes in plate cultures (bar marker = 5 µm).

physical structure of crystalline precipitates on fungal hyphae. X-ray micro-analysis (EDXA) was used to determine the elemental composition of crystalline precipitates on fungal hyphae. In both the Kelso and Tunstead limestone samples mineralized fungal hyphae (fungal hyphae with crystalline material adhering to external cell walls) was observed to be a common feature (Fig 9). In the Kelso limestone, plate-like crystals, with Na being the predominant metal component, and blocky crystals, with Ca the main

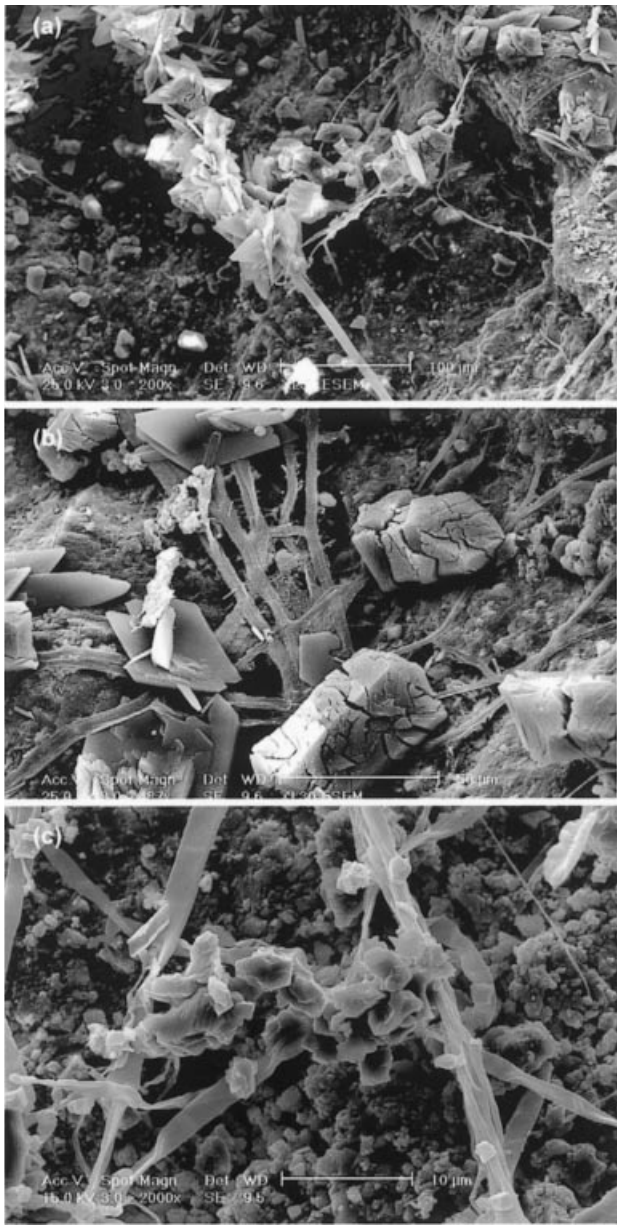


Fig 9 (a) ESEM micrograph of *in situ* fungal hyphae, mineralized with monoclinic crystals, in re-hydrated Kelso limestone (bar marker = 100 µm) (b) ESEM micrograph of in situ fungal hyphae, mineralized with orthorhombic crystals, in re-hydrated Kelso limestone (bar marker = 50 µm) (c) ESEM micrograph of *in situ* fungal hyphae, mineralized with poorly crystalline material, in re-hydrated Tunstead limestone (bar marker = 10 µm).

metal component, were precipitated on fungal hyphae (Fig 9a & b). The crystals exhibited different morphologies to crystalline micro-fabrics in the host rock, previously confirmed by powder X-ray diffraction (XRD) as dolomite ($CaMg(CO_3)_2$). In the Tunstead limestone, granular crystals, with Ca as the main metal component, were observed on fungal hyphae (Fig 9c). The crystals exhibited a similar morphology to crystalline micro-fabrics in the host rock, previously confirmed by XRD as limestone ($CaCO_3$). It was not possible to determine whether the crystals precipitated on fungal hyphae *in situ* in the limestone samples were formed directly as a result of fungal metabolic processes due to the diversity of the microflora within the rock samples. However, it is evident that the nucleation of crystalline material onto fungal hyphae plays an important role in the formation of what could be termed 'mycogenic' fabrics within rock substrates.

Calcium oxalates, e.g. whewellite ($CaC_2O_4.H_2O$) and weddellite ($CaC_2O_4.2H_2O$), commonly occur in association with fungal hyphae in soils and leaf litter, as well as in lichen thalli, and are formed as a result of fungal and lichen excretion of oxalic acid (Arnott, 1995; Gadd, 1999). However, oxalate salts are not the only metals and minerals associated with fungal hyphae and lichen thalli in rock substrates (Table 3). Fungi are known to be highly effective biosorbents for a variety of cations including Fe, Ni, Zn, Ag, Cu, Cd, and Pb (Gadd, 1990). Metal binding by fungi can occur through metabolism-independent binding of ions onto cell walls and other external surfaces and can be an important passive process of both living and dead fungal biomass, often eventually leading to nucleation and deposition of mineral phases (Gadd, 1990; Sterflinger, 2000). The metal-binding capacity can be influenced by environmental pH, with the binding capacity of biomass decreasing at low pH for metals such as Cu, Zn and Cd (de Rome & Gadd, 1987). Cell density also effects binding capacity, with lower cell densities allowing a higher yield per unit of biomass (Gadd, 1993). The presence of melanin and chitin in fungal cell walls may also strongly influence the ability of fungi to act as biosorbents (Gadd & Mowll, 1995; Manoli *et al*., 1997).

Conclusions

While the techniques used for isolating epi- and endolithic fungi from the mineral samples may have been to some extent selective and provide no accurate information on fungal community composition, it seems clear that fungi comprise a significant component of the microflora in limestones. Our work suggests that fungi play an important role in the transformation of limestone minerals through the formation of distinct 'mycogenic' fabrics in rock substrates. Although the precise mechanisms involved in the formation of 'mycogenic' fabrics is unclear it seems likely that both metabolism-dependent and metabolism-independent processes play integral roles.

Table 3. Summary of previous studies showing evidence of mineralization of fungal hyphae and lichen thalli with different minerals (*denotes common biogenic minerals) (adapted from Grote & Krumbein 1992; de la Torre & Gomez-Alarcon 1994; Easton 1997; Verrecchia 2000).

Mineral	(i) Fungal Hyphae	(ii) Lichen Thalli	Example of Organism
Birnessite ($(Na,Ca,K)\ Mn_7O_{14}.\ 3H_2O$))	Fungi on siderite boulder and Natraqualf soil		*Alternaria spp.* *Cladosporium spp.*
*Calcite ($CaCO_3$)	Fungi on stalactites, Quaternary eolianites and calcretes	Lichens on roofing tiles, andesite, volcaniclastite and exposed caliche plates in weathered basaltic and rhyolitic rocks	*Caloplaca aurantia* *Verrucaria spp.*
*Desert Varnish (MnO and FeO)	Fungal action on siderite and rhodochrosite in desert regions and sandstone limestone and granite monuments		*Alternaria alternata* *Cladosporium cladosporoides* *Lichenothelia spp.* *Penicillium frequentans* *Penicillium steckii* *Phoma glomerata*
Ferrihydrite ($Fe_2HO_8.H_2O$ or $5Fe_2O_3.9H_2O$)	Lichen on recent lava flow, on olovine of basalt, gabbro and augite		*Pertusaria corallina* *Stereocaulon vulcani*
*Glushinskite ($MgC_2O_4.2H_2O$)	Lichen/rock interface on serpentinite		*Lecanora atra*
Goethite (FeO(OH))	Lichen on metamorphic rocks, feldspars, granite and gneiss	*Parmelia conspersa*	*Parmelia tiliacea*
Halloysite ($Al_2Si_2O_5(OH)_4.2\ H_2O$)		Action of lichens on cave deposits and waters	*Lasallia spp.* *Mucor spp.* *Parmelia spp.* *Penicillium spp.* *Rhizocarpon spp.* *Rhizopus spp.*
*Humboldtine ($FeC_2O_4.2H_2O$)		Lichens on Fe rich crystalline limestone and cupriferous rocks	*Acarospora smargdula* *Aspicila alpina* *Lecidea lactea*
Hydrocerussite ($Pb_3(CO_3)_2(OH)_2$)		Mycobiont of lichen in ruins of a lead smelting mill	*Sterocaulon vesuvianum*
*Mn-oxalate ($MnC_2O_4.2H_2O$)		Lichen on Mn ore	*Pertusaria corallina*
Montmorillonite ($X_{0.33}Al_2Si_2O_{10}(OH)_2.nH_2O$) [$X=Na^+,K^+,Ca^{2+},Mg^{2+}$]		Action of lichens on cave deposits and waters	*Lasallia spp.* *Mucor spp.* *Parmelia spp.* *Penicillium spp.* *Rhizocarpon spp.* *Rhizopus spp.*
*Moolooite ($CuC_2O_4.0.44H_2O$)		Lichens on cupriferous rocks	*Acarospora rugulosa* *Lecidea inops* *Lecidea lactea*
Todorokite ($(Mn,Ca,Mg)Mn_3O_7.\ H_2O$)	Fungi in cave deposits and waters		*Mucor spp.* *Penicillium spp.* *Rhizopus spp.*
*Weddellite ($CaC_2O_4.2H_2O$)	In leaf litter and soils	On serpentinite, cupriferous rocks, andesite and volcaniclastite	*Acarospora rugulosa* *Aphyllophorales spp.* *Aspicilia calcarea* *Caloplaca aurantia* *Caloplaca flavescens* *Geastrum spp.* *Hypogymnia physodes* *Hysterangium crassum* *Lecanora atra* *Lecanora rupicola* *Lecidea inops* *Lecidea lactea* *Ochrolechia parella*
*Whewellite ($CaC_2O_4.H_2O$)	In Nari Limecrusts, Quaternary calcretes, forest leaf litter and soils	On basalt, serpentinite, cupriferous rocks, gabbro, dolerite, andesite and volcaniclastite	*Acarospora rugulosa* *Acarospora smargdula* *Aspicila alpina* *Aspicilia calcarea* *Aspicilia radiosa* *Caloplaca flavescens* *Hypogymnia physodes* *Lecanora atra* *Lecanora rupicola* *Lecidea inops* *Lecidea lactea* *Ochrolechia parella* *Parmelia conspersa* *Parmelia subrudecta* *Pertusaria corallina* *Xanthoria ectaneoides*

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References

Arnott, H. J. (1995). Calcium oxalate in fungi. *In*: Khan.S.R. ed. *Calcium Oxalate in Biological Systems*, pp 73-111. CRC Press, Boca Raton.

de la Torre, M. A. & Gomez-Alarcon, G. (1994). Manganese and iron oxidation by fungi isolated from building stone. *Microbial Ecology* **27**: 177-188.

de Rome, L. & Gadd, G.M. (1987). Copper adsorption by *Rhizopus arrhizus*, *Cladosporium resinae*, and *Penicillium italicum*. *Applied Microbiology and Biotechnology* **26**: 84-90.

Easton, R. M. (1997). Lichen-rock-mineral interactions: an overview. *In*: McIntosh, J. M. & Groat, L. A. ed. *Biological-mineralogical Interactions* **21**: pp. 209-239. Mineralogical Association of Canada Short Course Series, Ottawa, Ontario, Canada.

Ehrlich, H. L. (1981). Microbial formation and decomposition of carbonates. *In*: Ehrlich, H. L. ed. *Geomicrobiology*, pp. 101-123. Marcel Dekker, Inc, New York, Basel.

Ehrlich, H. L. (1998). Geomicrobiology: its significance for geology. *Earth-Science Reviews* **45**: 45-60.

Gadd, G. M. (1990). Fungi and yeasts for metal accumulation. *In*: Ehrlich, H. L. & Brierley, C. L. ed. *Microbial Mineral Recovery*. pp 249-275. McGraw-Hill, New York.

Gadd, G. M. (1993). Interactions of fungi with toxic metals. *New Phytologist* **124**: 25-60.

Gadd, G. M. (1999). Fungal production of citric and oxalic acid: importance in metal speciation, physiology and biogeochemical processes. *Advances in Microbial Physiology* **41**: 47-92.

Gadd, G. M. & Mowll, J. L. (1995). Copper uptake by yeast-like cells, hyphae and chlamydospores of *Aureobasidium pullulans*. *Experimental Mycology* **9**: 230-240.

Gadd, G. M. & Sayer, G. M. (2000). Fungal transformations of metals and metalloids. pp237-256. *In*: Lovley, D.R. ed. *Environmental Microbe-Metal Interactions*, American Society for Microbiology, Washington.

Goudie, A. S. (1996). Organic agency in calcrete development. *Journal of Arid Environments* **32**: 103-110.

Grote, G. & Krumbein, W. E. (1992). Microbial precipitation of manganese by bacteria and fungi from desert rock and rock varnish. *Geomicrobiology Journal* **10**: 49-57.

Hirsch, P., Eckhardt, F. E. W. & Palmer, Jr., R. J. (1994). Fungi active in weathering of rock and stone monuments. *Canadian Journal of Botany* **73**: 1384-1390.

Johnstone, C. G. & Vestal, J. R. (1993). Biogeochemistry of oxalate in the antarctic cryptoendolithic lichen-dominated community. *Microbial Ecology* **25**: 305-319.

Kumar, R. & Kumar, A.V. (1999). *Biodeterioration of stone in tropical environments: an overview*. The John Paul Getty Trust, USA.

Manoli, F., Koutsopoulos, E. & Dalas, E. 1997. Crystallization of calcite on chitin. *Journal of Crystal Growth* **182**: 116-124.

Matthes, U., Ryan, B. D. & Larson, D. W. (2000). Community structure of epilithic lichens on the cliffs of the Niagara Escarpment, Ontario, Canada. *Plant Ecology* **148**: 233-244.

Panina, L. K., Badalyan, A. G., Bogomolova, E., Wollenzien, U., Gorbushina, A. A., Krumbein, W. E., Soukharzhevsky, S.M. (1997). EPR-spectra of dark-coloured micromycetes isolated from marble. *Mikologiya i Fitopatologiya* **31**: 46-51.

Plummer, C. C. & McGeary, D. (1996). *Physical Geology*. Wm. C. Brown Publishers, Dubuque,USA.

Prieto Lamas, B., Rivas Brea, M. T. & Silva Hermo, B. M. (1995). Colonization by lichens of granite churches in Galicia (northwest Spain). *The Science of the Total Environment* **167**: 343-351.

Sterflinger, K. (2000). Fungi as geologic agents. *Geomicrobiology Journal* **17**: 97-124.

Staley, J. T., Palmer, F. & Adams, J. B. (1982). Microcolonial fungi: common inhabitants on desert rocks. *Science* **215**: 1093-1095.

Urzi, C., Wollenzien, U., Crizeo, G., Krumbein, W. E. (1995). Biodiversity of the rock inhabiting microbiota with special reference to black fungi and yeasts. *In*: Allsopp, D, Cowell, R. R. & Hawksworth, D. L. ed. *Microbial diversity and ecosystem function*, pp 289-302. CAB International: Wallingford.

Verrecchia, E. P. (2000). Fungi and Sediments. *In*: Riding, R. E. & Awramik, S. M. ed. *Microbial Sediments*, pp 69-75. Springer-Verlag, Berlin.