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Fungi, Rocks and Minerals

Geoffrey Michael Gadd¹

ABSTRACT

Fungi are ubiquitous inhabitants of rock and mineral surfaces and are significant geoactive agents. Capable of numerous transformations of metals and minerals, fungi can prosper in the most adverse of environments, their activities underpinned by growth form and metabolism. Free-living filamentous species, microcolonial fungi and lichens can significantly change a rock's surficial structure and appearance, ranging from discolouration and staining to biodeterioration and the formation of new biogenic minerals and rock coatings. The presence and activity of fungi should be considered in any study of rock and mineral transformations that seeks to understand the biotic and abiotic processes that underpin geochemical change in the biosphere.

KEYWORDS critical zone, biomineralization, bioweathering, geomycology, rock coating

INTRODUCTION

Fungi are significant geoactive agents and are particularly important in the critical zone. Fungi are microorganisms capable of numerous transformations of metals and minerals and can, therefore, significantly alter the surface structure and chemistry of rocks and their constituent minerals. "Metal transformation" here refers to the direct and indirect roles of fungi in altering metal speciation and mobility. Rock and mineral alteration processes are important in rock bioweathering because they contribute to the formation and development of mineral soil and global biogeochemical cycles for constituent elements, including element availability for living organisms (Sterflinger 2000; Burford et al. 2003; Gadd 2007).

The study of the roles of fungi in geologically relevant processes is termed geomycology, which is an important part of the more general area of geomicrobiology (Gadd 2007, 2010). Because the vast majority of organisms and cellular structures are microscopic, fungi are studied using techniques commonly employed in microbiology. Bioweathering, soil formation, metal and mineral transformations, and element cycling are the most obvious phenomena mediated by fungi. The additional significance of fungi as major decomposers of organic material in the biosphere underlines their crucial role in the

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cycling of all elements associated with organic matter. The majority of the stable elements can occur in living organisms, and their release can result in further interaction with environmental components, including mineral precipitation. The characteristic utilization of organic substrates by fungi for growth and metabolism underpins their capacity for mediating geochemical change.

The kingdom Fungi is extraordinarily diverse with some estimates reaching several million species. While mushrooms, brackets, puff balls and lichens may be obvious macroscopic forms, most fungi are microscopic, ranging from unicellular yeasts to those with a branching filamentous lifestyle exhibited by the vast majority. Even mushrooms and toadstools arise from such a filamentous network (called the mycelium) that may occupy a large volume of the substrate. The filaments are called hyphae and these grow from the tip forward (apical growth).

Fungi are eukaryotic organisms, i.e. their cells contain membrane-bound organelles and clearly defined nuclei, making them distinct from bacteria and archaea (prokaryotes). Their lack of chlorophyll, as well as certain structural, growth and metabolic characteristics, separates them from plants and animals, though it is animals that are their closest evolutionary relatives. The most significant environmental roles of fungi are as decomposers of organic material and as animal and plant pathogens and symbionts. But there is a growing awareness among scientists that fungi are also significant geoactive agents. However, the demarcation between fungal and bacteriological research and the wider range of prokaryotic metabolic diversity has ensured that the geoactive significance of fungi has been largely unappreciated in consideration of biosphere processes. A recent collection of geomicrobiology reviews completely excluded fungi, even to the extent of defining “microbes” as being only bacteria and archaea (Druschel and Kappler 2015).

The ecological success and geoactive properties of fungi are underpinned by their growth habit and metabolism and their ability to form symbiotic relationships with other organisms, e.g. lichens and mycorrhizas. The vast majority exhibit a filamentous, branching mode of growth and have a range of sensory mechanisms that enables them to explore their environment, locate nutrients and avoid stress. Additional physiological and morphological responses can also be involved in survival, such as the production of black melanized cell forms that are resistant to thermal fluctuations, desiccation and ultraviolet irradiation (Gorbushina 2007).

Lichens are a fungal growth form, consisting of a symbiotic partnership between a fungus and a photosynthetic organism – either an alga or a cyanobacterium, but sometimes both. It is now known they can also contain a yeast as another fungal partner. Lichens are pioneer colonizers of rocks and are the initiators of bioweathering biofilms that are

involved in the early stages of mineral soil formation. Symbiotic root-associated mycorrhizal fungi (outside the scope of this article) are associated with the majority of plant species and are responsible for major mineral transformations and redistributions of essential metals and phosphate in the soil (Gadd 2007). Fungi are chemoorganotrophs, which means that they use carbon-containing organic compounds for growth and energy generation, and they excrete extracellular metabolites, such as organic acids, which are key to their interactions with rocks and minerals. Concrete, rock and mineral substrates used in buildings, monuments, statues, gravestones and other constructions of cultural heritage, are also subject to fungal colonization and transformation (Gadd 2017). In such locations, fungi are often the most visible and destructive of the colonizing microbiota.

FUNGI ON ROCK SURFACES

Free-living and symbiotic fungi are ubiquitous and are often the dominant inhabitants of rock and mineral surfaces and outer layers. Fungi may, in fact, be the most significant organisms in nature that can biodeteriorate rocks and minerals (Warscheid and Braams 2000).

A capacity for morphological and physiological adaptation ensures that fungi are found even in the most hostile of environments—such as deserts, polar regions, and polluted environments—where they may be subject to extremes of temperature, solar irradiation, and water availability, among other stresses. While most fungi are aerobic, it is now known that they have a significant presence in locations not usually regarded as prime fungal habitats, e.g. deep aquatic sediments, hydrothermal vents, and the igneous oceanic crust, where they may exist in symbiosis with prokaryotes (Iversson et al. 2016).

Although a variety of nutrients may be available on rock surfaces (e.g. airborne dust particles, industrial and domestic emissions and pollutants, and exudates from microbes, insects and animals), many fungi can grow in the presence of very limited amounts of nutrient. Diverse fungal communities are found, and there may even be some mineralogical control on the structure and diversity of rock-inhabiting populations. Colonization and metabolic activity can be affected by rock porosity and geochemical heterogeneities, which may provide specific nutrients and essential metals. For example, fungi that preferentially colonize a pegmatitic granite may have done so in response to the elemental constituents of the individual mineral components (Gleeson et al. 2005). This suggests that the organisms are selectively bioweathering minerals to release essential elements (e.g. potassium). Such effects of the rock substrate on fungal community composition may not be so obvious in rocks of lower heterogeneity (e.g. sandstone).

Lichens

Lichens are probably the most obvious fungal inhabitants of rock surfaces (FIG. 1). They are, therefore, intimately associated with elements that, besides O, account for over 99.9% of crustal rocks (i.e. Na, Mg, Al, Si, P, K, Ca, Ti, Mn, Fe). The nature of the rock can influence lichen communities, and this may be particularly evident on metalliferous substrates (Purvis and Pawlik-Skowronska 2008). Lichens exert physico-chemical changes on a rock substrate and interact with other rock-inhabiting microorganisms. The photosynthetic symbiotic partner of the lichen provides carbon for the fungus, while, if present, nitrogen-fixing cyanobacteria enrich the nitrogen status of the symbiosis and microenvironment, enhancing further biofilm development by free-living organisms.

The surface area of the terrestrial lithosphere colonized by lichens is colossal. Many lichens form an intimate association with outer rock layers, something that dramatically alters the rock's appearance and weathering rates. In contrast to bioweathering, the concept of "bioprotection" is the ability of lichens, and other biologically initiated rock crusts, to stabilize rock surfaces and protect against further erosion. Lichens also entrap airborne mineral particles and pollutants (de los Rios et al. 2002). Many thousands of lichen species are known as rock inhabitants, although relatively little is known about their geochemical activities, and they are quite unappreciated in geobiology. This is despite the lichen–rock system providing a fundamental paradigm model for microbial interactions with rock and mineral substrates (Banfield et al. 1999). As a result of lichen bioweathering, many rock-forming minerals exhibit extensive surface alteration, biodeterioration and chemical transformation (Chen et al. 2000).

Lichens that live on rocks are known as "saxicolous" lichens, and include all the distinct morphological forms that occur in lichens (crustose, foliose, and fruticose) (Chen et al. 2000; de los Rios et al. 2002). Crustose lichens form a crust on or beneath the rock and are tightly attached across their entire lower surface, becoming fully integrated within the stone substrate (FIG. 2). Foliose (leaf-like) and fruticose (bush-like) lichens attach to rock surfaces by only a proportion of their underside (de los Rios et al. 2002). The areas of attachment of lichens to rocks are where significant geochemical transformations occur, and where free-living cyanobacteria, bacteria, algae and fungi can also be involved altering a rock substrate (de los Rios et al. 2002; Gadd 2017). Some lichens (especially crustose species) are epilithic (surface dwellers) and/or endolithic (interior dwellers), with cryptoendoliths occupying structural cavities, chasmoendoliths inhabiting fissures and cracks, and euendolithic forms capable of active rock penetration (Wierzbos et al. 2012). These terms are also used for other rock-inhabiting microorganisms, although there are many overlaps, even for a given species. Colonization of the rock interior may provide protection from environmental extremes, an example being the lichen-dominated cryptoendolithic communities that are widespread in Antarctic deserts. Such

endolithic microhabitats may include lichenized and non-lichenized fungal hyphae (Wierzechos et al. 2012).

Microcolonial fungi

As well as free-living fungi, many of which may be of soil origin, there are a particular group of fungi that inhabit rocks known as the microcolonial fungi (FIG. 3). These do not exhibit the hyphal mode of growth but produce unicellular yeast-like and microcolonial growth, occurring as small black melanized colonies. This results in dark brown to black discolouration on colonized surfaces (Marvasi et al. 2012). This growth habit confers a high degree of resistance to environmental stresses and these organisms are considered the most persistent inhabitants of exposed rock surfaces. Filamentous hyphae may develop from these colonies and penetrate further (several mm to cm distances) into the rock through fissures and cracks, as well as by intracrystalline penetration. The interactions of microcolonial fungi with the rock substrate can lead to a variety of surface coatings or varnishes through the accumulation of metals and minerals in cell walls and extracellular materials (Gorbushina 2007).

Microcolonial fungi can cause “micropitting” in rocks, which leads to cavities that can contain the fungal colonies. The mechanism used by microcolonial fungi to produce these micropits appears to be by mechanical destruction through intracellular turgor (= hydrostatic) pressure and extracellular polysaccharide production rather than the acid dissolution mechanism used by many other types of fungi (Marvasi et al. 2012). Microcolonial fungi may also form casual mutualistic associations with algae in rock crevices, thereby obtaining carbon from their photosynthetic partner (Gorbushina 2007).

The biodiversity of microcolonial fungi is large and severely underestimated: only a relatively small number of species have been fully characterized. Nevertheless, several hundred strains have been documented, and numerous novel genera have been discovered.

MECHANISMS OF INTERACTION WITH ROCKS AND MINERALS

Fungal colonization can result in physical and biochemical effects on rocks, these effects being influenced by the rock’s chemistry and mineralogy. The presence of weatherable minerals, such as feldspars, may increase susceptibility to attack (Warscheid and Braams 2000). Transformation mechanisms involve physical and biochemical processes. These processes are not mutually exclusive, rather, they are generally interlinked.

Physical mechanisms include penetration by the hyphae along points of weakness, or by direct tunnelling or boring, especially in a weakened or porous substrate (Jongmans et al. 1997; Hoppert et al. 2004). Weakening of a mineral lattice can also occur through wetting and drying cycles and subsequent expansion or contraction of the biomass. Lichens can

cause mechanical damage, such as disaggregation and exfoliation. This can occur by penetration of their anchoring structures, e.g. rhizines in foliose lichens, between grains and cleavage planes, and through expansion/contraction of the thallus (= vegetative body) on wetting/drying cycles (Chen et al. 2000). Separated rock and mineral grains or particles can be incorporated into the thallus, as well as secondary mineral products (de los Rios et al. 2002) (FIG. 4). These effects, in addition to removal of the lichen itself by animals and the weather, can lead to visible damage to a rock in just a few years (Gadd et al. 2014). Other physical effects are caused by a lichen's cell turgor pressure, its exopolysaccharide production, and lichen-induced secondary mineral formation. Secondary mineral formation through reaction of lichen-excreted organic acid anions with cations from the rock can result in "efflorescence", causing blistering, scaling, granular disintegration, and flaking (or "spalling") of the rock's outer layers. This is often considered to be a major mechanism of rock decay (Ranalli et al. 2009).

Biochemical weathering of rock and mineral substrates occurs through excretion of H^+ , CO_2 , organic acids, siderophores, and other metabolites, and this produces pitting, etching or dissolution (Banfield et al. 1999; Gadd 2010). Some organic metabolites effect dissolution by metal complexation and removal of these complexes from the mineral in a mobile form. Siderophores are Fe(III)-binding compounds excreted by organisms, but siderophores can also interact at lower affinity with other metals. Biogenic organic acids are very effective at mineral dissolution and are one of the most damaging agents of rock and mineral substrates, clearly underlining the importance of fungi in biochemical weathering (Gadd 2007). Of the suite of organic acids produced by fungi, oxalate is of major significance because of its ability to form metal complexes, resulting in mineral dissolution, and to cause physical damage by forming secondary metal oxalates that can expand in pores and fissures (Gadd et al. 2014). Citric and gluconic acid are other significant fungal metabolites. Oxalic acid is probably the most significant bioweathering agent produced by lichens, although lichens also produce a plethora of other compounds, termed 'lichen acids' (mainly polyphenolic compounds), which cause damage at the stone/lichen interface (Adamo and Violante 2000). In some extreme cases, and depending on the rock substrate, up to 50% of certain lichen thalli may comprise metal oxalates, which are the main secondary crystalline products of lichen bioweathering (Purvis and Pawlik-Skowronska 2008).

Biomineralization is the biologically mediated formation of minerals, and this process forms a core component of bioweathering of rocks and minerals. Fungal biomineralization can result from the oxidation or reduction of a metal species (which leads to altered solubility of that species) and to fungal metabolite excretion (e.g. oxalate). For example, soluble Mn(II) can be oxidized by many microbes, including fungi, and this results in formation of the black Mn oxides that are a common component of rock varnish.

Other metabolites include respiratory CO₂, which can lead to carbonate precipitation. The release of metals from rocks in mobile forms from abiotic weathering or biologically mediated mechanisms can, therefore, result in a variety of secondary mineral precipitates that include carbonates, phosphates, oxides and oxalates (Gadd 2010; Gadd et al. 2014). Such biomineral formations may contribute to physical disruption, staining and discolouration, and rock coating development (Gadd 2007, 2017; Gorbushina 2007; Fomina et al. 2010).

Fungal tunnels within soil minerals have been explained as a result of dissolution and “burrowing” within the soil mineral (Jongmans et al. 1997). Tunnels may also result after fungal exploration of pre-existing cracks, fissures, and pores in weatherable minerals and from the formation of a secondary mineral matrix of the same or different chemical composition as the substrate, e.g. secondary CaCO₃ or an oxalate (Fomina et al. 2010). The formation of a secondary mineral matrix can result in the fissures and cracks becoming cemented with mycogenic minerals. After the death and degradation of the original fungal hyphae, tunnels of similar dimensions to hyphae are left within the minerals.

SPECIFIC EXAMPLES OF FUNGAL ROCK AND MINERAL TRANSFORMATIONS

Fungi are involved in many environmental mineral transformations, and the roles of plant root symbiotic fungi in releasing phosphate and other nutrients from minerals is a major determinant of plant productivity. Many other transformations affect the structure and stability of rocks and minerals, leading to mineral dissolution and biodeterioration as well as the formation of new minerals, crusts and coatings. It is likely that many more novel and exciting mycogenic biominerals await discovery.

Carbonates

Carbonates can be broken down by fungi, usually as a result of acid formation (Adamo and Violante 2000). Fungal attack of carbonate substrates (e.g. limestone) can result in diagenesis of these substrates to secondary minerals that include dolomite [CaMg(CO₃)₂], glushinskite (MgC₂O₄·2H₂O), weddellite (CaC₂O₄·2H₂O), and whewellite (CaC₂O₄·H₂O) (Burford et al. 2003). Many lichens can dissolve calcite in limestone and dolomite through oxalate production, subsequent precipitation of calcium oxalate occurs at the lichen–rock interface.

In contrast to dissolution, many microbes (such as cyanobacteria, bacteria and algae) mediate carbonate formation, and a significant proportion of insoluble carbonate at the Earth’s surface is biotic in origin. Certain fungi can deposit calcium carbonate extracellularly (Burford et al. 2006; Li et al. 2015; Savkovic et al. 2016), although this is

more clearly demonstrated in the laboratory than in the environment (Bindschedler et al. 2016). For example, a mixture of calcite (CaCO_3) and calcium oxalate was precipitated on hyphae when selected species were grown in simulated limestone microcosms (Burford et al. 2006) (FIG. 5). In experiments by Li et al. (2015), fungi from calcareous soil precipitated calcite, strontianite (SrCO_3), vaterite in different forms [CaCO_3 , $(\text{Ca}_x\text{Sr}_{1-x})\text{CO}_3$] and olekminskite [$\text{Sr}(\text{Sr,Ca})(\text{CO}_3)_2$]. However, despite the frequent presence of CaCO_3 in fungal-containing biofilms and crusts (FIG. 5), in situ direct demonstration of the role of fungi in carbonate formation is scarce. The formation of needle-fibre calcite has long been attributed to fungal activity in calcareous environments, although physico-chemical processes are also plausible (Bindschedler et al. 2016).

Oxalates

Calcium oxalate is the most common environmental form of oxalate (Gadd et al. 2014). Calcium oxalate is produced by many free-living and symbiotic fungi, being formed by the precipitation of soluble calcium with fungal-excreted oxalate (Adamo and Violante 2000). Fungi can also produce many other metal oxalates when they interact with minerals that contain metals, including Ca, Cd, Co, Cu, Mg, Mn, Sr, Zn, Ni and Pb (Gadd 2007; Gadd et al. 2014). Some secondary crystalline metal oxalates that have been associated with lichens include glushinskite (hydrated magnesium oxalate) on serpentinite and manganese ore, and moolooite (hydrated copper oxalate) on copper-containing rocks (Chen et al. 2000; Purvis and Pawlik-Skowronska 2008). In many arid and semi-arid regions, calcareous soils and near-surface limestones (calcretes), biomineralized fungal filaments occur secondarily cemented with calcite and calcium oxalate. Calcium oxalate can also be degraded to calcium carbonate, which may cement pre-existing limestones (Bindschedler et al. 2016). Many limestone and marble monuments develop orange-brown patinas, called *scialbatura*, on their surfaces. These mainly consist of calcium oxalate and calcium carbonate, and their formation by free-living fungi and lichens may provide surface protection (Savkovic et al. 2016).

Oxides

Several fungi can promote Mn(II) oxidation to black Mn(IV) O_2 . In many cases, fungal oxidation is effected through production of hydroxycarboxylic acid metabolites such as citrate, lactate, malate, or gluconate. Fungal MnO_x material has a todorokite-like tunnel structure, which contrasts with other reported microbial MnO_x materials which have layered birnessite-type structures. Some fungi can oxidize Mn(II) and Fe(II) in metal-bearing minerals such as siderite (FeCO_3) and rhodochrosite (MnCO_3) and precipitate them as oxides. Manganese and iron oxides are major components (20–30%) along with clay (~60%) and various trace elements in the brown-to-black veneers known as desert varnish or rock varnish (Gorbushina 2007). Conversely, manganese-reducing microbes

may mobilize oxidized or fixed manganese. Most fungi that reduce Mn(IV) oxides do so through the production of metabolites that can act as reductants such as oxalate which results in the formation of lindbergite (Mn oxalate dihydrate) (Wei et al. 2012).

Phosphates

Fungi can liberate orthophosphate from insoluble inorganic phosphates in rocks and minerals by producing acids or chelators (e.g. gluconate, citrate, oxalate, and lactate) which complex the metal and result in dissociation. Liberated phosphate can then be used as a nutrient by the fungi, or another organism, or can reprecipitate with other mobile metal species and so form metal phosphates. Fungal solubilization of rock phosphate results in reprecipitation of calcium oxalate, while fungal dissolution of pyromorphite $[\text{Pb}_5(\text{PO}_4)_3\text{Cl}]$ results in lead oxalate formation (Sayer et al. 1999). Many fungi are also capable of uranium oxide solubilization and can form secondary uranium phosphate minerals of the meta-autunite group, uramphite and/or chernikovite (Fomina et al. 2007). Fungi may also liberate orthophosphate from sources of organic phosphate in organic matter by means of phosphatase enzymes, the liberated phosphate then reprecipitates with other reactive metals. Several common soil fungi and yeasts can induce lead bioprecipitation as highly insoluble pyromorphite during growth on organic phosphates (Liang et al. 2016).

Silicates

Many lichens and free-living fungi play a role in silicate dissolution and therefore contribute to the genesis of clay minerals and to soil and sediment formation (Banfield et al. 1999; Adamo and Violante 2000). Etching may be observed on silicate surfaces after fungal colonization. In Antarctic sandstone, cryptoendolithic lichens caused a reduction in cohesion between individual sandstone grains, which resulted in surface flaking (Chen et al. 2000). Silicate dissolution may release important nutrients that otherwise would remain bound (e.g. P, K and Fe). In lichen weathering of silicates, fungal extracellular polysaccharides can become mixed with calcium, potassium, iron, clay minerals and nanocrystalline aluminous iron oxyhydroxides. Biotite-group minerals $[\text{K}(\text{Mg},\text{Fe}(\text{II}))_3\text{AlSi}_3\text{O}_{10}(\text{OH},\text{F})_2]$ can be penetrated along cleavage planes by fungal hyphae, partially converting biotite to vermiculite $[(\text{Mg},\text{Fe}(\text{II}),\text{Al})_3(\text{Al},\text{Si})_4\text{O}_{10}(\text{OH})_2 \cdot 4\text{H}_2\text{O}]$. Depending on the species and the mineral substrate, clay minerals associated with lichen weathering also include kaolinite, halloysite, goethite $[\text{FeO}(\text{OH})]$, illite, allophane and imogolite,, with halloysite, kaolinite and vermiculite being the most common (Chen et al. 2000).

CONCLUSIONS

Fungi are critically important biotic agents of geochemical change, especially in the critical zone at the interface between the atmosphere, hydrosphere, biosphere, and

lithosphere, and fungi can exist as rock coatings. They effect many metal and mineral transformations in rock substrates through their branching, filamentous mode of growth, their ability to morphologically adapt to adverse environments, their organic carbon-based metabolism that excretes a range of geoactive metabolites, and their symbiotic relationships with other organisms (e.g. lichens and mycorrhizas). Such biotic processes can occur faster than purely abiotic changes. The full range of their activities and their proper significance in the environment as well as their relationships with other geoactive microorganisms that inhabit rocks and minerals, requires further detailed study. Geomycology has an important role to play at the interface between biology and geology. There is a need for both biologists and geologists to broaden their intellectual scope and to initiate more interdisciplinary research and collaboration to achieve a fuller understanding of the roles that the remarkable organisms play in shaping our planet.

In brief, fungi rock!

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FIGURE CAPTIONS

FIGURE 1 Rock surface completely covered with multiple lichen species in Wester Ross, Scotland. Scale bar ~ 3 cm. IMAGE BY G.M. GADD.

FIGURE 2 Crustose lichens on calcareous rock showing dissolution and integration with the rock. (A) *Caloplaca erodens* Hafelinier can dissolve a rock surface, turning it mealy and depressed. The grey particles belong to the lichen structure. The yellow colony in the top-right is a different species. (B) *Verrucaria maura* Obermayer 11298 becomes tightly integrated with the rock surface, forming a lithocortex. The black spots are apical parts of perithecia (reproductive structures containing fungal spores). When perithecia decay, they leave distinct pits in the rock surface. (C) The lithocortex formed by *V. maura* which develops from bioweathered rock material. The small dark dots are the algal symbiont occurring as single cells or clusters of cells. Scale bars all 1.0 mm. IMAGES COURTESY OF MARTIN GRUBE (KARL-FRANZENS-UNIVERSITÄT, GRAZ, AUSTRIA).

FIGURE 3 Colony appearance, structure and cell form in microcolonial fungi (MCF). (A) Pinhead-size MCF colonies on rocks from the central Namib desert (southwest Africa). Scale bar 150 µm. (B) Scanning electron microscope image of a typical fungal microcolony consisting of yeast-like melanized cells. Scale bar 30 µm. (C) Light microscope image of typical MCF cell form in culture. Scale bar 50 µm. IMAGES COURTESY OF ANNA GORBUSHINA (FREIE UNIVERSITÄT BERLIN, BERLIN, GERMANY).

FIGURE 4 Transverse sections of lichen interacting with a granitic rock and a mica. (A) Artificially coloured scanning electron microscope (in back-scattered electron mode)

image of the lichen thallus and granite interface. The blue is the lichen thallus, the fragments in red and pink are feldspar, and white is quartz. Scale bar 0.5 mm. **(B)** Superimposition of two images: one from the contact zone between the lichen fungal partner (mycobiont) and the mica obtained using scanning electron microscopy in back-scattered electron mode, the other being the same sample observed with confocal laser scanning microscopy. Red indicates the mica and oxalates; green (and yellow) corresponds to the mycobiont. Scale bar 40 μm . IMAGES COURTESY OF CARMEN ASCASO AND JACEK WIERZCHOS (MNCN, CSIC, MADRID, SPAIN).

FIGURE 5 Fungal growth and biomineralization in limestone and dolomite. **(A)** Fluorescence microscope image of fungal hyphae (blue) growing between mineral grains in dolomite from Mount Nemo (Ontario, Canada). Scale bar 50 μm . **(B)** Fluorescence microscope image of hyphae (blue) growing in dolomite from Kelso (Ontario, Canada). Scale bar 50 μm . **(C)** Scanning electron microscope (SEM) image of in situ mineral precipitation (calcite and/or calcium oxalate) on fungal hyphae in Kelso limestone. **(D)** SEM image of calcite and calcium oxalate on hyphae of a *Serpula* species after growth in a limestone-amended microcosm. Scale bar 20 μm . IMAGES EUAN BURFORD AND G.M. GADD, UNPUBLISHED AND ADAPTED FROM BURFORD ET AL. (2003, 2006).