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New Horizons in Geomycology

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Geomycology can be simply defined as the roles and significance of fungi in processes of relevance to geology, and as such is part of the more general area of geomicrobiology (Gadd, 2010). Rock and mineral bioweathering, metal transformations, mineral formation, and cycling of the elements, all of which are involved in mineral soil formation, are the most obvious geomicrobial processes under this heading. In the case of fungi, their additional significance as major decomposers of organic material underlines their important role in the cycling of major elements such as C, H, N, O, P, S, as well all other elements that may be associated with organic matter. The majority of stable elements can be found in living organisms, including metal pollutants, and the release of these in decomposition can result in further interaction with environmental components resulting in mineral formation for example. There are therefore clear connections between organic and inorganic components of geomicrobial processes, and between the aerobic and anaerobic domains of life. This is not always appreciated in geomicrobiology where to some the “geo” prefix is equated with chemolithotrophy and anaerobiosis in certain prokaryotes.

While environmental microbiologists are generally aware of the global significance of fungi in organic matter decomposition, plant productivity, food spoilage and biodeterioration, there is rather less awareness of their significance in a geomycological context. The problem is exacerbated in geomicrobiology where the preponderant attention given to prokaryotes has lead to neglect of major eukaryotic groups such as fungi and algae. A recent example of such a narrow appreciation of microbial roles in major biosphere processes is found in a special edition of *Elements* dedicated to geomicrobiology where microbes were even defined as solely comprising bacteria and archaea (Druschel and Kappler, 2015), and with the entire perspective solely concentrating on these organisms. While some of this problem is undoubtedly due to the fragmentation and diversity of the different scientific communities that study prokaryotic and fungal processes, it is about time that geomycology received proper attention within geomicrobiology and Earth sciences as a vital and integral component. It is also clear that further integration is necessary between the different relevant disciplines. Geomicrobiology is by definition interdisciplinary requiring interaction between microbiologists, geologists, geochemists, mineralogists etc., yet there are still some obvious barriers that remain in some quarters. Witness the pejorative comments about Life Sciences in a section of the *Elements* editorial for example (“Microbiology (or biology) may not be your favourite subject. Or maybe you dreaded taking “life science” courses while at the university. Even if life science is not your preferred area of interest……”). Thankfully, there is a growing realisation in intelligent geological circles that microbes are important and this is bound to increase as knowledge and integration between disciplines develops. Another important point is that prokaryotes and eukaryotes are generally studied separately yet in the natural environment fungi rarely are found without bacteria, and *vice versa* in aerobic habitats. Even the obvious demarcation between aerobiosis and anaerobiosis is now rather blurred. It is abundantly clear that fungi are major geoactive agents in their own rite, but it is also clear that fungal-prokaryotic interactions are also of great significance. It is also evident that the extent of the biosphere influenced by fungi stretches into anaerobic domains and even to the deep subsurface where again interactions with prokaryotes appear highly significant.

Environmentally significant fungi are traditionally regarded as aerobic organisms (notwithstanding anaerobic alcoholic fermentation found in certain yeasts) and often dominant inhabitants of rock and mineral surfaces, and the soil. In such locations they are responsible for a plethora of processes of geological significance such as element cycling, formation and dissolution of minerals, and transformations of metals. Indeed, it appears that the mechanisms and scales of fungal weathering have been greatly underestimated which provides further impetus for more detailed studies. The existence of anaerobic fungi has been known for some time although little attention has been given to their geomicrobial significance until recent years. It is now clear that fungi can be found in, and can be major inhabitants of deep subsurface environments. The deep sea biosphere has hitherto been regarded as the sole domain of anaerobic prokaryotes but it is now known that fungi are significant components of the microbiota in deep-sea sediments, at hydrothermal vents, and at methane cold seeps. More recently, a comprehensive fossil record has shown that the igneous oceanic crust is a substantial microbial habitat with an abundance of diverse fungal species, leading to the hypothesis that this is the largest fungal habitat on the planet (Ivarsson *et al.*, 2016). Fossilized microbes have been found in veins and vesicles in ocean dredged or drilled basalts representing prior microbial communities with a majority of findings revealing fungi. These appear to exist in symbiosis with chemolithotrophic bacteria, and are proposed to be involved in organic matter decomposition, mineral dissolution and formation, and therefore element cycling. Further dissection of such communities using metagenomic approaches is a future challenge.

It therefore seems that future attention necessitates consideration of fungal-prokaryotic interactions, not only in the context of subsurface geochemistry, but also in rock and mineral substrates, aquatic habitats, soil and the plant root zone. The filamentous branching growth habit of filamentous fungi enables penetration, exploration and colonization of heterogeneous substrates, like the soil, as well as translocation of ions and nutrients enabling release of geoactive metabolites. Furthermore, the mycelium can act as a fungal highway upon which bacteria can be carried or migrate along enabling colonization of new locations, and passage over air gaps between soil particles (Warmink *et al.*, 2011). This phenomenon may determine the ecological success of certain soil bacteria, enhance organic pollutant degradation, and be involved in certain geomicrobial processes. Promotion of long-term carbon storage and soil fertility through fungal-bacterial interactions occurs in the oxalate–carbonate pathway for example (Martin *et al.*, 2012). Fungal symbioses with phototrophs (plants, cyanobacteria, algae) are of global geochemical significance with plant-root inhabiting mycorrhizal fungi responsible for major metal and mineral transformations and lichens being involved in rock bioweathering and soil formation. It is now known that these symbioses include other organisms of which their significance is now only just beginning to be understood. In mycorrhizas, helper bacteria colonize the hyphal surfaces while endobacteria occur inside arbuscular mycorrhizas (Bonfante, 2014). Diverse bacterial communities are associated with lichens and appear to exert physiological functions (Grube *et al*., 2014). It has also been shown recently that many common lichens also contain specific basidiomycetous yeasts embedded in the cortex and which correlate with phenotypic variations (Spribille *et al*., 2016). The simplistic view of a lichen solely being a phototroph-single fungal association seems now outdated. Multi-organism relationships in fungal symbioses appears to be an area ripe for future research not only to ascertain interactions between the component pro- and eukaryotes but also consequences for rock colonization and bioweathering phenomena.

Fungi are capable of numerous metal and mineral transformations, as are prokaryotes, and the significance of these is receiving growing interest not only in a geomycological context, but also for a variety of potential applications in bioremediation, element biorecovery and the production of useful biomineral and biometal(loid) products. Immobilization of toxic metal and radionuclide species provides avenues for bioremediation but also for metal biorecovery from aqueous solutions, wastes and leachates. In recent years, a variety of mycogenic minerals have been discovered, some previously only thought to arise by abiotic reactions such as various lead and uranium phosphates. In view of global concerns over the security of supply of metals and minerals, this area is worthy of serious investigation as we need to conserve existing Earth resources, recycle and reclaim, and negate geopolitical uncertainties. In this context, the vast and largely unexplored fungal biodiversity is a valuable resource and it seems that further searches in so-called extreme environments may reveal organisms with so far unknown but useful properties. Extremophily is again an attribute that is overwhelmingly presented as being the preserve of prokaryotes but fungi show remarkable abilities in relation to environmental stress such as extremes of pH and temperature, nutrient limitation, solar irradiation, and toxic pollutant-contaminated environments, probably more so than many run-of-the-mill aerobic chemoorganotrophic bacteria. For example, a new fungal isolate, *Penidiella* sp., from acidic metal-containing mining environments was able to accumulate the rare earth element dysprosium in acidic conditions by reaction with phosphate at the cell surface (Horike and Yamashita, 2015). A novel fungal species, *Coniochaeta fodinicola*, isolated from acidic waters from a uranium mine, was able to accumulate substantial amount of U under acidic conditions (Vazquez-Campos *et al*., 2015). Fungi isolated from calcareous soil were able to mediate carbonate precipitation of metals including strontium as strontianite ($SrCO_3$), and novel Sr-substituted vaterite [$(CaxSr_{1-x})CO_3$] and olekminskite [$Sr(Sr,Ca)(CO_3)_2$] (Li *et al*. 2015). Carbonates have many industrial uses and a combined carbonized biomass-Mn oxide composite, derived from heat treatment of Mn carbonate encrusted fungal biomass, was shown to have excellent electrochemical properties in supercapacitors and lithium-ion batteries (Li *et al*. 2016). Could future developments in this area contribute a sustainable biotic solution for energy storage systems? In many cases, fungal mediation of biomineral precipitation results in nanoscale biomineral or metalloid products and this has been observed for a variety of metal(loid) elements including Pb, Cd, Se and Te. Nanoscale biomineral and biometal(loid) products clearly offer further biotechnological potential because of their high surface area to volume ratio and chemical reactivity. Future efforts should seek to understand the physical and chemical parameters that optimise the production and size of mycomineral particles, perhaps even enabling tailoring for specific industrial needs.

Another obvious area of geomycology for future endeavour relates to the built environment. The geomicrobial mechanisms employed by microbes to attack rock and mineral based substrates can readily be translated into the built environment, with the fungal properties of lignocellulose degradation also contributing to structural biodeterioration and decay. Such processes have consequences for cultural heritage, historic monuments and buildings as well as modern built structures. While the built environment offers additional strictures and benefits for microbial colonization and attack, fungi are responsible for some of the most obvious manifestations of biodeterioration and decay. Despite this, knowledge is still limited or fragmentary regarding the organisms involved, and the significance of bioweathering in relation to abiotic weathering. Application of modern molecular and genomic analyses of population diversity coupled with advanced microscopic techniques and modelling will undoubtedly throw further light on this important problem, although the significance of unculturable microbes may still remain a speculative area. It is also evident that cultural studies are still essential to elucidate properties and mechanisms. As an example, a specific group of rock-inhabiting fungi that form black microcolonies on rock and mineral substrates are ubiquitous in nature and in the built environment yet many species are novel and remain uncharacterised (Isola *et al.*, 2016) and, compared to other fungi, little is known of their physiology and biochemistry although there are indications that this is unusual and specialised (Nai *et al.*, 2013).

The ubiquity and importance of fungi in the biosphere underlines the importance of geomycology as a conceptual framework encompassing the environmental activities of fungi, their impact, and their applied significance. Future endeavour using modern metagenomic and molecular analyses complemented by laboratory investigations on tractable organisms should characterize biodiversity and reveal links between phylogeny and function, including novel geoactive properties and new metabolic insights. Due consideration of fungal-prokaryotic relationships will extend our geomicrobiological knowledge through aerobic and anaerobic domains of the biosphere, as well as the significance of phototrophic symbioses in plant productivity, bioweathering and soil formation. Translation of geomicrobial knowledge to the built environment will provide detailed knowledge of biodeterioration mechanisms and the organisms involved, and may even contribute to means of control or prevention, and structural composition and design. Examination of the metal and mineral-transforming properties of fungi, including those isolated from extreme environments, will enable the formation of novel biomineral and biometal(loid) products of potential use in biotechnology. Interdisciplinarity and integrated approaches are essential and these may also serve to reduce some of the demarcation boundaries that exist within microbiology, and between microbiology and other scientific disciplines.

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