How does ‘liking’ relate to addiction or other ‘irrational wants’? Addictive drugs cause downregulation of dopamine D2 receptors, opioid receptors, and so on in the nucleus accumbens, striatum and other structures, which may contribute to negative withdrawal and distress feelings. Taking drugs as a form of hedonic self-medication to treat such dysphoric feelings is a common reason for relapse. But some presumably sensitized individuals remain persistently vulnerable to powerful urges to relapse even after withdrawal is gone, and even when not distressed. In such individuals, other neural changes underlying persistent drug-induced sensitization of mesolimbic dopamine-related circuitry may cause excessive ‘wanting’ to take drugs that lasts long after withdrawal, whether or not the ‘liking’ for drugs decreases, for instance with the development of tolerance. Such sensitized ‘wanting’ may distinguish users who might be legitimately viewed as compulsively addicted from other users who can more readily give up drugs.

Do hedonic reactions to higher pleasures such as art or music share brain mechanisms of ‘liking’? In humans, the same hedonic terms may be used to describe sophisticated cognitive and cultural pleasures, such as abstract art, as for simple sensory ones, such as chocolate ice-cream. It would have been plausible for higher human pleasures to be mediated by entirely different brain mechanisms, for example, cortical cognitive pleasures versus subcortical sensory pleasures. However, human neuroimaging studies have recently indicated that music, art, and even subjective reports of the overall well-being activate much of same ‘hedonic circuitry’ as does sweetness, including mesolimbic structures such as the nucleus accumbens, ventral tegmentum, and so on, as well as cortical circuitry. In other words, human cognitive and cultural pleasures, for example when listening to music, seem to have co-opted much of the same hedonic circuitry that evolved originally for basic sensory pleasures. There is evidence that some non-human primates can exhibit ‘wanting’ for simian erotica (in a famous pay-per-view experiment from Michael Platt and colleagues); and, in a case litigated by the best (human) legal minds (in an action against David Slater), that others can be enthusiastic photographers; however, we do not know whether any other animals experience ‘liking’ for non-primary sensory input.

What are some key puzzles concerning ‘liking’? Apart from the link between ‘liking’ and ‘wanting’, we need to know more about the network connectivity among the hedonic hotspots, to confirm the role of hedonic hotspots in enhancing ‘liking’ for diverse pleasures, beyond sweetness, and to understand how ‘liking’ is modulated by signals related to hunger, satiety, and other shorter and longer-term motivational states.

Don’t say: Dopamine is the ‘liking’ neurotransmitter.

Do say: ‘Liking’ is never simply inherent in a stimulus but rather must always be actively generated for it by hedonic brain systems.

Where can I find out more?

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Fungal biomineralization

Geoffrey Michael Gadd

Fungi are key organisms of the biosphere with major roles in organic-matter decomposition, element cycling, plant pathogenicity, and symbioses in aquatic and terrestrial habitats. The vast majority exhibit a filamentous, branching growth form and are aerobic chemoorganotrophs that derive carbon and energy from organic substances, and are particularly associated with soil, the plant-root zone, and rock surfaces. It is now known that some fungi are lithotrophs, deriving energy from the oxidation of inorganic materials, whereas others are photosynthetrotrophs, deriving additional energy from light for organic matter utilization when oxygen is limited. This means that fungi are of much wider environmental significance than previously thought and explains their ubiquity in locations previously thought to be iminical to fungal existence, such as the deep subsurface and other anaerobic locations. In addition to such free-living species, fungi associated with photosynthetic partners are also of profound biosphere importance. For example, lichens, which are composed of a symbiotic association between a fungus and a phototrophic alga and/or cyanobacterium, are pioneer colonizers and bioweathering agents of rocks and minerals. Mycorrhizas are symbiotic, plant-root-associated fungi found to colonize the majority of plant genera, where they improve plant nutrition through solubilization of essential metals and phosphate from soil minerals. Biomineralization in the soil can also immobilize toxic metals in the vicinity of plant roots, thereby benefiting plant colonization and facilitating revegetation of contaminated habitats. Wherever fungi are found, transformation of metals and minerals is a key aspect of their activity, with biomineralization an important feature. Fungal biomineralization is an important facet of geomycology — namely the roles of fungi in geochemical and geophysical processes. This article seeks to highlight the concept of biomineralization.
as applied to fungi, the occurrence and significance of important fungal biominerals in natural and synthetic environments, and the applied potential of fungal biomineralization in nanobiotechnology.

**Biomineralization**

Biomineralization can be loosely defined as the production of minerals by living organisms and occurs in all domains of life — Bacteria, Archaea and Eukarya. Examples ranging from the magnetosomes of certain prokaryotes to the teeth and skeletons of mammals involve complex systems under direct genetic control. However, most fungal (and prokaryotic) examples of biomineralization are not directly controlled, but rather result from metabolic activities that alter the external environment to favor mineral precipitation, such as changes in pH, O₂, and redox potential, redox transformations of metal species, and excretion of organic and inorganic metabolites such as CO₂, H⁺, or organic acids. In addition, the high metal-binding properties of cell walls and extracellular materials can result in nucleation and deposition of minerals. Such processes are often termed biologically induced biomineralization. Moreover, mineral formation can result from fungal activities in organic matter decomposition, as well as from bioweathering of rocks and minerals, where released metals or anionic species, such as phosphate, precipitate with metals and other ligands present in the environment, for example, carbonate. Biometalization — the microbial production of elemental forms of metals (including gold, silver, and mercury) and metalloids (such as selenium and tellurium) — is also increasingly discussed in a biomineralization context because it involves mechanisms analogous to those that occur in biomineralization.

**Fungal biominerals**

Fungal biomineralization is widespread in natural and human-influenced habitats. As with biominerals formed in other biological systems, the most common fungal biominerals are oxides, carbonates, phosphates, sulfates, and sulfides, with a particular association of oxalates with fungi, the best-known example being calcium oxalate.

**Oxalates**

Oxalic acid has a strong ability to complex with divalent metals, resulting in mineral dissolution, but can also act as a metal precipitant at appropriate concentrations (Figures 1 and 2). Many fungi found in soil, plant litter, and rotting wood, as well as fungal symbioses like mycorrhizas and lichens, produce copious amounts of oxalate. The deposition of mono- and dihydrated calcium oxalate (whewellite and weddellite, respectively) can be observed in both decomposing plant material and the built environment, where fungal degradation of plaster board, wood, and paper occurs (to name a few examples). Calcium oxalate biominerals are strong determinants of the formation of biomineralized lichen crusts on rock and mineral surfaces. Besides calcium oxalate, other metal oxalates may be formed, depending on the substrate. Fungal transformation of manganese oxides results in precipitation of manganese oxalate dihydrate (lindberghite). Hydrated copper oxalate (moolooite) can be found in lichens growing on copper-rich rocks, and magnesium oxalate dihydrate (glushinskite) in lichens on serpentinite and manganese ore. The formation of copper oxalate frequently occurs during growth of wood-rotting fungi on wood treated with copper-containing preservatives (such as copper-chrome arsenate) and is assumed to enhance copper tolerance. Copper oxalate also results from fungal biodeterioration of copper metal. Interestingly, the recalcitrance of copper oxalate can provide a protective crust on copper metal and this process has been explored for preservation of historical copper artefacts.

**Oxides**

Although oxide formation is most widely encountered in prokaryotes, several groups of fungi are able to oxidize soluble manganese(II) to insoluble manganese(III) and manganese(IV), resulting in the precipitation of black manganese oxide (Figure 1). These mycogenic manganese oxides are highly reactive and have high metal-sorption capacities with, for example, nickel, zinc, copper, cobalt, manganese, lead, and cadmium, and can also act as strong oxidants for certain elements such as arsenic and chromium. Manganese oxides also contain a significant proportion of organic carbon, which can act as a template for biomineralization. Fungal manganese oxides also play an important role in selenium biogeochemistry with aerobic fungal reduction of soluble selenium species occurring concomitantly with manganese(II) oxidation to manganese oxides.

Oxidation of iron(II) by fungi has received scant attention compared to prokaryotes, presumably because of the association of fungi with aerobic habitats where iron(III) predominates. However, mycorrhizal fungi can oxidize iron(II) in the context of iron(II)-rich silicates, where the expansive growth of iron(III) hydroxide causes microcracks, thereby promoting silicate bioweathering. Such a contribution to the iron cycle may be significant considering the ubiquity of mycorrhizal associations with plants and the presence of iron(II) in some of the Earth’s most common rocks and minerals. Another surprising fungal iron-biomineralization event was discovered in an extremely acidic environment with a high toxic metal and iron(III) content, where a fungus, *Purpureocillium lilacinum*, induced extensive formation of an iron sulfate mineral, hydroniumjarosite [(H₃O)Fe⁵⁺(SO₄)₂(OH)₆], which significantly influenced this habitat’s geochemistry. Formation of this mineral was previously ascribed to bacterial activity.

**Carbonates**

Carbonates are widely distributed biominerals, and numerous lines of evidence point to a fungal involvement in calcite formation. Calcium carbonate frequently occurs in fungal biofilms and crusts, including lichen thalli, especially on limestone and marble, whereas extracellular precipitation of calcite, vaterite and aragonite (all polymorphs of calcium carbonate) is readily observed in limestone microcosms or other calcareous media (Figure 2). A lead carbonate, hydrocerussite, has been detected in lichens growing on lead-containing smelter ores. Formation of needle-fiber calcite has long been attributed to fungal activity in calcareous environments, and the formation of
Figure 1. Examples of fungal biomineralization of calcium, manganese, copper, zinc, lanthanum, and lead.

(A) Aspergillus niger colonizing the surface of an ancient boar-tusk fragment and development of a white biomineralized surface crust of calcium oxalate monohydrate (whewellite) below the mycelial mat. Also seen are dark fungal sporing structures (conidiophores) (bar = 500 µm). (B) Manganese oxide production (dark spots) by oxidation of manganese(II) to manganese(IV) by Acremonium strictum (bar = 100 µm). (C) Deposition of copper oxalate hydrate (moolooite) crystals (green dots) around and encrusting hyphal cords of Beauveria caledonica growing on medium containing copper phosphate (bar = 1 mm). (D,E) Zinc biomineralization around hyphae of Rhizopogon rubescens growing in mycorrhizal symbiosis with Scots pine (Pinus sylvestris) in the presence of zinc phosphate. Crystals are deposited within the extracellular mucilaginous sheath enveloping the hyphae (bars = 20 µm in D and 5 µm in E). (F,G) Light microscopy images of crystals of lanthanum oxalate decahydrate (La₂(C₂O₄)₃·10H₂O) produced by A. niger grown on solid media containing (F) 5 mM and (G) 20 mM lanthanum chloride (bars = 100 µm). (H) Scanning electron microscopy image of a single crystal of copper oxalate (moolooite), as in (C), adjacent to a hyphal cord of B. caledonica (bar = 10 µm). (I) Hyphae of Serpula hirantioides and extensive manganese oxalate crystallization during growth with manganese chloride (bar = 20 µm). (J) Scanning electron microscopy image of a lead phosphate mineral produced by growth of Paecilomyces javanicus on an organophosphorus substrate in the presence of soluble lead (bar = 5 µm). (Images by Flavia Pinzari, Qianwei Li, Marina Fomina, Zhan Wei, Xia Kang, and Xinjin Liang.)

Aragonite needles within inactive fungal hyphae has added to current evidence. Chitin is a component of fungal cell walls, and it is notable that chitin-organo-templates for calcium biomineralization occur widely in molluscs, crustaceans, coralline algae, diatoms, and sponges, providing preferential sites for mineral nucleation. Fungal dissolution of calcareous minerals or rocks, such as limestone, can result in re-precipitation of calcium carbonate (CaCO₃), as well as formation of other secondary minerals such as dolomite [CaMg(CO₃)₂] and magnesium and calcium oxalates. In many arid and semi-arid regions, calcareous soils and near-surface limestones (calcretes) contain biomineralized fungal filaments entombed with calcite and calcium oxalate. The calcium oxalate can be degraded to calcium carbonate by oxalate-degrading (oxalotrophic) microorganisms, enhancing the cementation of such limestones. In fact, the oxalate–carbonate pathway describes the transformation of oxalate into carbonate, whereby plant or fungal-derived oxalate is degraded by oxalotrophic bacteria and fungi, leading to calcite precipitation. This is particularly evident in acidic tropical soils and oxalogenic plants like the iroko tree, Milicia excelsa. Oxalotrophy in many bacterial and fungal species presumably underlies the reason why calcium oxalate has not accumulated in the geological record.

The application of microbial carbonate precipitation has received considerable attention in environmental bioengineering as a means of soil stabilization, sand cementation, concrete repair and self-healing, and toxic-metal immobilization. Although a number of metabolic processes
can be involved, urea hydrolysis has received particular attention. Degradation of urea by urease-positive fungi leads to elevated external pH with the release of carbonate, which readily precipitates with available metals such as calcium, producing copious quantities of pure calcite. Should other metals be present, additional single and mixed-metal carbonates will form. In the natural environment, groups of ‘ammonia fungi’ — found in locations with high ammonium-containing nitrogenous substrates such as animal urine, feces, and decomposing carcasses — can mediate such biomineralization. An interesting aspect of fungal carbonate precipitation is that the products can exhibit nanoscale dimensions (Figure 3). Nanoscale fungal carbonates that have been produced include those of cadmium (otavite), copper, nickel, and cobalt.

**Phosphates**

Phosphate biomineralization may occur if phosphate, released from mineral substrates or decomposing organic matter, subsequently reacts with available metals. Some metal phosphates are extremely insoluble and effectively immobilize potentially toxic metals such as lead and uranium. Fungal-mediated formation of pyromorphite, a highly stable lead–phosphate mineral, has provided a biological explanation for the observed detoxification of lead-contaminated soil by addition of a phosphate source as well as the presence of pyromorphite in lead-contaminated soil. Similarly, fungal colonization of uranium oxides and metallic depleted uranium results in the formation of the stable

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**Figure 2. Examples of fungal biomineralization of uranium, calcium, and manganese.**

(A) Uranium phosphate biomineralization on the exterior surfaces of cord-like hyphal aggregates of *Beauveria caledonica* grown in proximity to metallic depleted uranium (bar = 1 µm). (B) Scanning electron microscopy image of a uranium phosphate mineral produced by growth of *Aspergillus niger* on an organophosphorous substrate in the presence of soluble uranium (bar = 5 µm). (C) Cluster of calcium oxalate crystals on a larger calcium oxalate crystal resulting after growth of *B. caledonica* in CaCO$_3$-containing medium (bar = 30 µm). (D,E) Scanning electron microscopy images of rhodochrosite (MnCO$_3$) precipitation on hyphae of *Neurospora crassa* grown in urea and MnCl$_2$-amended medium (bars = 30 µm in D and 5 µm in E). (F) Calcium carbonate deposition around filamentous hyphae of *N. crassa* grown with urea and CaCl$_2$ (bar = 100 µm). (G) Manganese oxalate (lindbergite) produced by *A. niger* growing on manganese oxide (bar = 200 µm). (H,I) Environmental scanning electron microscopy images of (H) biomineralized hyphae of a *Stemphylium* sp. (bar = 10 µm) and (I) hyphae of a *Doratomyces* sp. and associated crystals produced during growth on mortar amended with cobalt carbonate (bar = 5 µm). (Images by Marina Fomina, Qianwei Li, Zhan Wei, and Louise McGregor.)
Secondary uranium phosphate minerals uranophane and/or chernikovite. Other biomineralizations include phosphates of zinc, iron, and several rare earth elements (Figures 1 and 2).

Fungal dissolution of phosphates can also result in formation of secondary minerals, including metal phosphates different from the parental phosphate mineral. Dissolution of rock phosphate (hydroxyapatite, fluorapatite), which is an essential process in determining phosphorus bioavailability when used as a fertilizer, results in calcium oxalate precipitation. Solubilization of struvite (MgNH₄PO₄·6H₂O), which can extensively crystallize in wastewater-treatment systems, results in formation of glushinskite (magnesium oxalate dihydrate). The production of phosphate- and carbonate-laden culture filtrates provides a means for biorecovery of valuable or critical metals from aqueous solution as insoluble phosphate or carbonate biominerals (Figure 3).

**Sulfides**
Sulfide is an intermediate in fungal sulfur metabolism but can also be involved in significant biomineralization events within and exterior to cells. Several yeasts (*Candida glabrata*, for example) produce intracellular nanoscale peptide-coated cadmium–sulfide crystallites, a process that essentially serves as a cadmium-detoxification mechanism and can be considered as an example of biologically controlled biomineralization. The crystallites, which are coated with γ-glutamyl peptides ('phytochelatins'), possess electronic, photochemical, and optical properties analogous to quantum semiconductor clusters and are therefore commonly referred to as ‘quantum dots’. Since their discovery, many other yeasts and filamentous fungi have been shown to be capable of their production, intracellularly and/or extracellularly; other mycogenic quantum dots include sulfides of lead and zinc, selenides of cadmium, zinc, and lead, and tellurides of cadmium and lead. Overproduction of sulfide in yeast can also result in extensive precipitation of nanoscale metal sulfides around cell walls.

**Fungal biomineralization and nanobiotechnology**
Fungal biomineralization can result in the production of nanoscale mineral and metallic products. This has engendered growing interest because of the wide-ranging potential of such substances across environmental, medical, and electronic contexts, and the desire to understand the importance of such materials to the organism. Nanoscale elemental particles of gold, silver, palladium, selenium, and tellurium can be produced by a wide range of fungal species (Figure 3). Nanominerals include oxides, carbonates, phosphates, selenides, tellurides, and sulfides that can incorporate a range of elements including copper, cadmium, zinc, manganese, nickel, barium, zirconium, iron, lead, strontium, selenium, tellurium, and titanium. It seems that the repertoire is almost limitless in view of the large numbers of nanoparticle-forming fungal species and susceptible elements, compounds, and minerals. Mineral and elemental nanoparticles can be formed inside or outside cells and deposited on cell walls, surface materials, and dead biomass (Figure 3).

For ease of harvest, extracellular nanoparticle production is clearly advantageous, although nanoparticle–biomass composite material may also exhibit interesting properties. Carbonized fungal mycelium produced through incineration at high temperature with nanoscale manganese oxide proved to be an effective electrochemical material in lithium-ion batteries and supercapacitors, and another carbonized fungal composite with zerovalent-iron nanoparticles could effect degradation of xenobiotic compounds.

Another area of nanobiotechnology investigates the application of fungi, particularly yeasts, as templates for synthesis of mesoporous nanomaterials; applications of these materials include their use as catalysts, chemical sensors, drug-, enzyme-, and cell-carriers, and in fuel cells and electronic devices. Mesoporous inorganic materials and organic composites synthesized using yeast-cell templates include oxides of titanium, silicon, and iron, as well as phosphates of zinc, magnesium, titanium, iron, silver, and zirconium, with metal phosphate/carbon mesoporous nanocomposites (the carbon arising from fungal biomass) showing enhanced electrochemical properties as battery materials.
Figure 4. Fungal biomineralization as a component of elemental cycles: potential applications, benefits to organisms, and environmental consequences.

Geochemical activity in the majority of fungi is underpinned by their chemoorganotrophic metabolism, filamentous explorative lifestyle and/or symbiotic relationships (mycorrhizas, lichens) with phototrophs. Physical and biochemical activities contribute to element mobilization from rocks, minerals, metal-bearing substrates, and organic matter. Released components can be accumulated by biota, contribute to environmental pools, or biomineralize with available ligands and metal species. Biomineral deposition may be enhanced by metabolite excretion, sorption mechanisms, and redox reactions. Biominerals may be recycled or transformed into new mineral phases through bioweathering.

Benefits of nanomaterial production
The most obvious benefit that may accrue to fungi from nanomineral or nanometal formation is the immobilization of toxic metals. This effect may be largely incidental, in most cases being a side-effect of metabolism, structure, and environmental chemistry. There is one clear mechanism linked with metal resistance, which is the intracellular synthesis of cadmium sulfide crystalites, referred to previously. Although intracellular nanoparticle production by fungi has been observed for several elements, possibly to prevent cytotoxicity, there is little evidence to date of any cellular expulsion mechanism as has been observed in some bacteria. Extracellular nanomaterials may influence metal toxicity, although it is unclear whether encrustation will adversely affect the producing organism. Although biomineralization can serve a protective function by reducing metal toxicity, it is possible that encrustation may affect nutrient uptake and viability. However, many biomineralizing fungal systems do remain viable — even yeast cells encapsulated in synthetic mineral sheaths. For filamentous fungi, differential distribution of biominerals on growing mycelium, resulting from spatial differences in cell wall composition and biochemical activity, may ensure continued growth and survival through non-biomineralized growing hyphae.

More recently, it was realized that fungal nanoparticles may have wider benefits to the producing organisms because of their catalytic properties. Nanozymes are inorganic nanoparticles that exhibit enzyme-like properties in redox reactions, and have applications in medical, engineering, agricultural, and environmental technologies. Nanozymes include metals and metal oxides, and most of their catalytic reactions mimic those of oxidase, peroxidase, catalase, and superoxide dismutase. Because fungi can mediate the formation of reactive nanoparticles, including metal oxides, these biomaterials are receiving some well-deserved attention. Fungal manganese oxide nanoparticles possess oxidase activity and can oxidize several elemental species, revealing an unappreciated role for these nanoparticles in the biogeochemical cycles of rare earth elements, metals, and metalloids.

Of the minerals that can potentially act as nanozymes, ferrihydrite ($\text{Fe}_2\text{O}_3\cdot\text{(OH)}_3$) is of particular interest because of its ubiquity in the Earth’s surface and its known catalytic properties, which imitate natural peroxidase, an antioxidant enzyme pivotal for the removal of reactive oxygen species to combat oxidative stress. It was discovered that ferrihydrite nanoparticles produced by fungal biotransformation of hematite indeed possess peroxidase activity, acting as nanozymes to scavenge cytotoxic hydrogen peroxide. Fungal produced magnetite nanoparticles also exhibit peroxidase-like activity. Since teragram-level quantities of mineral nanoparticles occur in the Earth system, it is likely that some of them, particularly those of biotic origin, will exhibit catalytic properties. This raises intriguing questions about the significance of biogenic nanomaterials in the evolution of the lithosphere and the biosphere.

Fungal biomineralization in ‘extreme’ environments
Although fungi are primarily associated with aerobic environments, it is now realized that they are widely found in habitats previously thought to be hostile towards fungal development. The existence of anaerobic fungi has been known for some time, particularly those inhabiting the digestive systems of herbivores; however, more recently the deep subsurface was also found to host significant fungal populations. Fungi have been detected in sedimentary rock matrices in the terrestrial subsurface, deep-sea sediments, hydrothermal vents, methane cold seeps, and the
igneous oceanic crust, where they exist in association with prokaryotic communities. In fact, the igneous oceanic crust has been described as the Earth’s largest fungal habitat. Biomineralized and fossilized hyphae are commonly found in deep subsurface locations, as well as evidence of fungal penetration of carbonates and zeolites. Fungal survival and influence on mineral transformations is undoubtedly complemented by redox reactions and sulfate reduction mediated by prokaryotic partners. Fungi are also ubiquitous in metal-rich environments, whether arising from natural rocks and minerals, ore deposits, mine wastes, or pollution, where they are likewise involved in metal and mineral transformations. It seems that polluted or other ‘extreme’ environments may provide a source of new fungal species capable of biomineralization. Some acidophilic fungi from acid-mine drainage have been shown to biomineralize rare earth elements and uranium. Other previously uncharacterized fungi have been isolated from uranium, iron, gold, and gemstone mine sites, copper and lead mine tailings, and metal-contaminated waters and soil.

**Fungal biomineralization and cultural heritage**

Fungi are the most significant biodeteriorative organisms in the built environment and of cultural heritage, with biomineralization a striking feature of the many effects caused by free-living and lichenized fungi. Apart from staining and discoloration, the development of biomineralized coatings and substrate penetration can lead to disruption and exfoliation of outer layers. Such coatings or patinas often contain oxalates, their composition depending on the metals present within the substrate. Oxalates occur widely on surfaces of marble and limestone buildings and monuments, and on sandstone, granite, plasters, cave and wall paintings, murals, frescoes, and sculptures: strikingly, lichen thalli may comprise up to 50% metal oxalates. Mortar, cement, and concrete may also be biodeteriorated through mineral dissolution and biomineralization. Conversely, the formation of biomineralized crusts on rock, stone, or other mineral-based structural components can provide a resistant protective coating.

**Fungal biomineralization as a key process of environmental and applied significance**

It is clear that fungal biomineralization is a key environmental process influencing metal and nutrient bioavailability and is an important component of the biogeochemical cycles for probably all elements found in the environment and associated with organic matter (Figure 4). Key phenomena occur in the aerobic environment, where they influence plant productivity, bioweathering of rocks and minerals, the formation and development of soil structure, and biodeterioration in the built environment and of cultural heritage. Fungal biomineralization also occurs in the deep subsurface, and other extreme environments, where, until relatively recently, fungal importance was overlooked.

It is interesting that fungi are capable of the production of all of the main classes of minerals traditionally regarded as ‘biominerals’ in controlled biomineralization. Although many examples of fungal biomineralization might be gratuitous events resulting from ‘normal’ metabolism or be related to fungal macromolecular structure, some appear to be under specific control, relying in some cases on specific redox or enzymatic transformations. A mixed repertoire is likely to be possible in many organisms. Thus, the boundaries between biologically controlled and biologically induced biomineralization in fungi are increasingly blurred. Although biomineralization can result in toxic-metal detoxification, further benefits to the organism may arise from the catalytic activities of nanoscale biomineral products. Fungal biomineralization at the nanoscale is also of applied significance (Figure 4). Fungal-derived nanoparticles and nanocomposite biomaterials show physical, chemical, and biological properties relevant to environmental and biomedical biotechnology, bioengineering, and electronics, and are particularly relevant to bioremediation and element biorecovery. It is desirable that future work in the field of fungal biomineralization should push ahead with practical developments and real exploitation, rather than just remaining a topic for theoretical or proof-of-principle laboratory studies. Fungal biomineralization is a fascinating topic of wide significance, providing clues about evolution of the biosphere and offering insights directly relevant to environmental health and human existence.

**FURTHER READING**


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