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Benefits of bacterial biomineralization

V. R. PHOENIX[1] AND K. O. KONHAUSER[2]

[1]*Department of Geographical and Earth Sciences, University of Glasgow, Gregory Building, Glasgow G12 8QQ, UK*
[2]*Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E3*

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Corresponding author: V. R. Phoenix; e-mail: Vernon.Phoenix@ges.gla.ac.uk

INTRODUCTION

Terry Beveridge has been a tremendous influence on my work and career, right from the word go. In fact the very first time I was introduced to the concept of microbial biomineralization, it was by one of Terry's former postdocs (Kurt Konhauser) during a masters class at Leeds University, UK, back in 1996. Quickly hooked on the subject, a few months later I found myself beginning my PhD studies on biomineralization in hot-spring settings. Needless to say, it was the papers by Terry and his group which formed the bulk of my early readings on this subject. Whether it was Beveridge and Murray's pioneering early work on metal sequestration by the cell wall (Beveridge & Murray, 1976, 1980), the impact of proton motive force on metal binding (Urrutia *et al.*, 1992), the first report on hot-spring biomineralization (Ferris *et al.*, 1986), the role of metal binding in fossilization (Ferris *et al.*, 1988) or the role of S-layers in mineral nucleation (Schultze-Lam *et al.*, 1992), it was clear Terry and colleagues had discovered a veritable smorgasbord of bacteria–metal interactions. All of these Beveridge publications and more provided me with a fundamental understanding and solid foundation on which to build my own research. But this is true for anyone working in the field. Any publication that refers to bacterial metal adsorption and biomineralization (and there are many) will have numerous Beveridge references and all will be underpinned by Terry's theories. His influence is far reaching indeed. Terry has always had an incredible ability to cross-link disparate areas of science, to view problems from novel angles and thus shed a bright new light on many areas of microbiology. For example, his incredible understanding of the true complexity and dynamicity of cell wall composition and structure has led us to appreciate far more how this complex surface interacts with its surrounding metals and minerals. A particular highlight for me was his work illuminating how gram-negative lipopolysaccharide (LPS) and capsular material are dynamic, heterogeneous and environmentally sensitive materials which intimately control metal nucleation and mineral adhesion (e.g. Makin & Beveridge, 1996; Langley & Beveridge, 1999; Korenevsky *et al.*, 2002; Korenevsky & Beveridge, 2007).

Terry was instrumental in pioneering research into microbial biomineralization, a process that has itself existed since the very first single-celled organisms evolved on our planet. Whether inhabiting a deep-sea hydrothermal vent or shallow-water stromatolite, the solute-enriched nature of the primordial soup would have ensured that microbial biomineralization was commonplace. The slow deterioration of pristine microfossils over time can destroy evidence of their encrustation in mineral matrices. However, even rocks 1.9 Ga old contain clear evidence of microbial silicification with bacteria enclosed in a 'tough gelatinous mass that enveloped the organism layer upon convex layer' (Cloud, 1965). Indeed, such silicification processes are likely to have played an important role in the preservation of those microorganisms as microfossils (Westall *et al.*, 1995). Of course, if the environment is not conducive the mineral precipitation, some organisms can shift the saturation state of a given mineral phase through a variety of metabolically mediated processes (such as the oxidation and reduction of metals (Konhauser 2007), or processes that produce carbonate and/or consume H^+ (Ferris *et al.*, 2004)). Critical saturation state is reached and the mineral phase precipitates. These processes are helped by the fact that the cell surface is a highly reactive interface that provides ideal nucleation sites for mineral precipitation (Beveridge & Fyfe, 1985).

Whether the microbe is simply acting as a nucleation site or (inadvertently) metabolically shifting the saturation state of a mineral phase, the microbe has no real control over the process. They do not, for example, shape their biominerals into complex skeletal frameworks like the radiolarians nor do they form complex calcite shell structures like cocoliths (Anderson, 1981; Westbroek *et al.*, 1986). Yet this marriage

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of bacteria and biominerals has probably existed for nearly 4 billion years, since their evolution. One wonders, therefore, if this apparently uncontrolled process is actually advantageous to the organism. This tribute to Terry briefly summarizes some of the potential advantages of bacterial biomineralization currently reported and speculates on other possible beneficial side-effects that could be pertinent topics for future studies.

ADVANTAGES OF BIOMINERALIZATION

Terry and colleagues had clearly demonstrated that microbial biomineralization was a commonplace process. For me, as a PhD student back in 1997, this led to the question 'Can the bugs survive that process?' On first impression the initial reaction was 'not a chance'. Bacteria can be encrusted in mineral matrices several times the thickness of the cell. Surely that could not be a good thing. As previous studies had well documented the abundance of silicified microbes in hot-spring settings (e.g. Ferris *et al.*, 1986; Schultze-Lam *et al.*, 1995; Konhauser & Ferris, 1996), this became the first port of call in answering this question. The cyanobacteria *Calothrix* sp. (an isolate from the Krisuvik hot spring in Iceland) was then silicified in the laboratory. Despite being encrusted in a siliceous coating several microns thick, this phototroph was able to photosynthesize, and moreover, was doing so at the same rate as the nonsilicified control (Phoenix *et al.*, 2000). At that time, we noted that silicification was restricted to the outer surface of the sheath and that silicification resulted from the binding of preformed silica colloids. Interestingly, the importance of preformed silica colloids in silicification had been noted previously in natural settings by several of Terry's colleagues (Schultze-Lam *et al.*, 1995; Konhauser & Ferris, 1996) and these workers had also suggested that intracellular silicification must result in cell lysis. From this it was then hypothesized that the sheath behaved as a filter against colloidal silica, preventing mineralization of the cell wall (a surely more sensitive part of the cell envelope than the extracellular sheath) (Phoenix *et al.*, 2000). Something Terry had often shown was that cells alter their surface polymers in response to environmental stimuli (e.g. Korenevsky *et al.*, 2002). This seemed to be the case here. Both transmission electron microscopy (TEM) and synchrotron-based Fourier transform infrared analysis (SR-FTIR) demonstrated that this microbe thickened its sheath when placed in media supersaturated with respect to amorphous silica (Phoenix *et al.*, 2000; Benning *et al.*, 2004a,b), supporting the hypothesis that sheaths were instrumental in enabling the microbe to survive mineral encrustation. These findings were supported by other studies; *Sulfurihydrogenibium azorense* was also found to survive silicification and again the excretion of extracellular polymeric substances (EPS) was believed to be key (Lalonde *et al.*, 2005).

Of course, if some bacteria can survive biomineralization, then this leaves open the possibility that they can use it to their advantage. What then are the challenges that microbes face for which biominerals can be of use? For phototrophs, one clear example is the screening of detrimental solar radiation. Ultraviolet (UV)-B (280–320 nm) and UV-C (200–280 nm) are highly detrimental to life, especially between 240 and 270 nm due to significant adsorption by DNA (Tevini, 1993). This challenge is particularly applicable to the Earth's earliest phototrophs which, due to the lack of sufficient ozone, must have been bathed in highly detrimental fluxes of UV radiation (Pierson *et al.*, 1993). As silicification was likely commonplace in the silica-enriched shallow-water environments which early Precambrian phototrophs inhabited, we investigated its role as a UV screen. Significantly, silicified organisms displayed considerably higher resistance to UV radiation than nonsilificied microbes (Phoenix *et al.*, 2001). This worked because siliceous biominerals attenuated UV by an order of magnitude greater than the photosynthetic active radiation (PAR; 400–700 nm) required for photosynthesis.

To extend these results from the laboratory to a natural setting, an investigation was undertaken to examine this UV screening process at El Tatio, a high altitude geyser field in the North Chilean Andes (Phoenix *et al.*, 2006). Its location at high altitude and low latitude and the low levels of atmospheric moisture ensured high UV fluxes (UV-A and UV-B were ~35% greater than at sea level at this location (Piazena, 1996)). Phototrophic mats in the discharge channels were found to be heavily biomineralized in amorphous silica up to 5 μm thick (Fig. 1). Analysis of their radiation transmission properties demonstrated they attenuated the more harmful

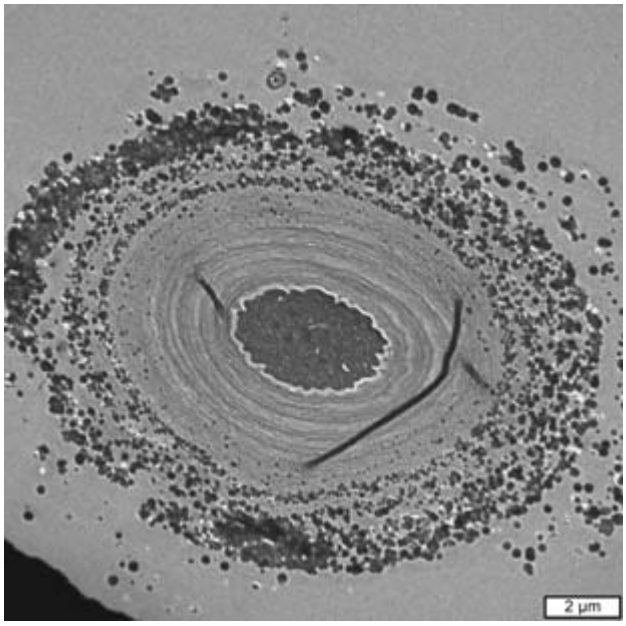

Fig. 1 Transmission electron micrograph showing a cyanobacterial filament encrusted in amorphous silica colloids. Sample taken from El Tatio geyser field, Northern Chile (as described in Phoenix *et al.*, 2006). Scale bar: 2 μm.

wavebands of UV radiation significantly greater than PAR, and would have thus added increased UV screening protection to each filament in addition to those provided by pigmentation (Phoenix *et al.*, 2006). Silica biominerals coalesce and grow, and further precipitation leads to large sinter matrices with cyanobacteria entrapped within, often in stromatolitic form. Cryptoendolithic communities were also found within the sinter (i.e. microbes that had actively migrated into void spaces in the sinter). Significantly, both stromatolites and cryptoendoliths exhibited viable cyanobacteria living 1–10 mm below the sinter surface. Current UV-B intensities (today no UV-C reaches the Earth's surface) were reduced to tolerable intensities within ~1 mm of the sinter surface, yet sufficient PAR for photosynthesis was able to penetrate 5–10 mm into the sinter, depending on sinter type. This favorable niche between 1 and 5–10 mm corresponded to the depth at which viable cyanobacteria were found. Remodeling these data for early Precambrian solar intensities again revealed almost identical PAR penetration with UV-B and -C attenuated sufficiently between 1 and 2.5 mm of the surface, generating a highly protective niche 4–7 mm thick were the correct balance between PAR and UV was struck (Phoenix *et al.*, 2006).

However, even PAR can reach intensities that are too great for the organism, resulting in photobleaching and photooxidative death. It is curious that many cyanobacteria become light saturated at a few to few tens of percentage of the typical midday incident PAR. Consequently it is also possible that biomineralization and subsequent burial under thin layers of silica sinter may be a mechanism by which phototropic bacteria help reduce PAR to manageable intensities (Konhauser *et al.*, 2001; Phoenix *et al.*, 2006). There is clearly a balance here between too much and too little.

It has also been suggested that some biominerals may act as a source of essential nutrients. Konhauser *et al.* (1994) suggested that iron phosphate precipitates encrusting microbes in epilithic biofilms on Ellesmere Island (Canadian Arctic) provided a viable source of phosphate under nutrient-limited conditions. The phosphate itself may have come from a variety of sources (cellular degradation, rock substratum, or windblown clays), but once reprecipitated in the biomineral phase, this process prevented the essential nutrient from being flushed from the system (Konhauser *et al.*, 1994). The idea of biominerals behaving as sources of nutrients can also be extended to clays; the clays providing a source of exchangeable nutrients (Stotzky & Rem, 1966). Certainly, it has been shown that clay biomineralization can be a common process (Konhauser & Urrutia, 1999). Iron (hydr)oxides are also common biominerals and have considerable capacity to absorb ions on their surfaces, thus again providing a potential source of exchangeable nutrients. Alternatively, biominerals may not just adsorb nutrients, but may also absorb toxins. Indeed, clays have been shown to provide bacteria protection against toxins by immobilizing the toxin onto the clay's reactive surface (Habte & Barrion, 1984). It follows that clay biominerals, or indeed any biomineral with significant adsorption capacity, might achieve a similar outcome. Interestingly, the biomineralization process itself can generate toxic by-products that require remediation by the microbe. For example, the reduction of oxygen during Fe(II) oxidation can generate toxic oxygen radicals which can damage cellular components. Such toxins are a problem for the iron oxidizer *Gallionella ferruginea*. This organism, however, overcomes this by growing a stalk that nucleates iron oxidation (and oxygen radical production) away from the sensitive cell (Hallbeck & Pedersen, 1995). Similar processes may also explain why some bacteria facilitate the oxidation of Mn(II) to form manganese oxides (MnO_2). For example, some aerobic respiring bacteria, such as *Arthrobacter siderocapsulatus*, use Mn^{2+} oxidation to remove excess intracellular levels of hydrogen peroxide when their catalases cannot break it down fast enough (Ehrlich, 2002).

OTHER POSSIBLE BENEFITS?

So what other benefits may biominerals afford bacteria?

(1) One which is particularly easy to visualize is its role as a suite of armor, protecting the microbe from grazing protozoan. I have watched, with great fascination, as amoebae graze through a lawn of cyanobacteria. The amoebae consume food particles via phagocytosis; they simply envelop their food. How then, would this process be made more difficult if the cyanobacterium was encrusted in a thick mineral matrix? The phagocytosis process utilized by amoeba is quite capable of consuming mineral particulates, and thus the mineral coating *per se* may not prevent consumption. However, as biominerals grow they significantly increase the size of the organism, especially as the mineralization process often glues several or indeed many organisms together. At some stage the microbe–mineral composite will simply become too large to be enveloped. At this stage, phagocytosis becomes impossible. This biomineral armor is analogous to that described by Heijnen *et al.* (1992), whereby clays provide bacteria with protective microenvironments against grazing protazoa. This role for biominerals has yet to be demonstrated, but it would take relatively simple experiments to investigate this hypothesis.

(2) Biominerals may also play a role in protecting the organism against dehydration. Like the 'protection from predation' theory, this has yet to be proven, and is thus again one for future study. The key here lies in the observation that a number of biominerals are hydrated when they precipitate. These minerals (e.g. amorphous silicates and iron hydroxides) can dehydrate over time to form more crystalline phases, but in the first instance they can more closely resemble hydrated gels. It is also probable that their highly porous structure can facilitate water retention. As shown in Fig. 1, the biomineral displays considerable pore volume between silicate colloids. These pore spaces would behave as nano-reservoirs for water; the colloidal framework behaving as a sponge. Thin

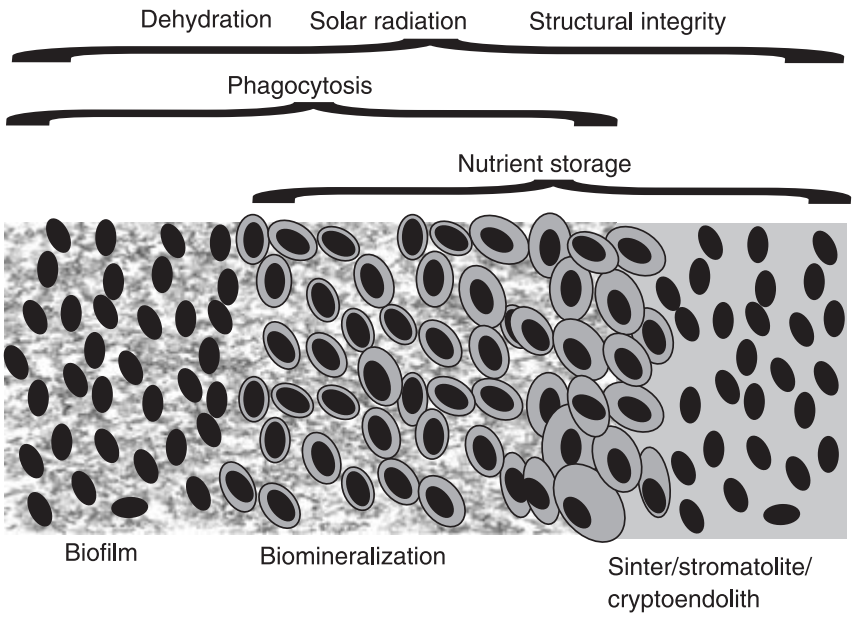

Fig. 2 Schematic summarizing the similarity in advantages afforded by both extracellular polymers and biomineralization. This is illustrated in a progressive continuum of increasing mineral association, from unmineralized biofilm (i.e. cells encased in EPS), through biomineralized cells to, ultimately, fully entrapped cells in sinter.

biomineral layers may not help much over long-term dehydration, but are likely to be more important during intermittent dehydration events. For example, silicification of shallow-water phototrophic communities was believed prevalent in the early Precambrian (Konhauser *et al.*, 2001; Phoenix *et al.*, 2001; Phoenix *et al.*, 2006). Tidal and wave action would have resulted in their intermittent submergence and exposure. During exposure, hydrated amorphous silica biominerals may have been instrumental in preventing catastrophic dehydration of the microbe. Preliminary data from hot-spring siliceous sinters from the El Tatio geyser field suggested that sinters may in fact be important in keeping water activity above that required for microbial survival (Phoenix *et al.*, 2003). Further work is required to determine the effectiveness of this mechanism in thin biomineral matrices. Interestingly, the entrapment of moisture and thus promotion of growth conditions has been recorded in cryptoendolithic communities (e.g. Omelon *et al.*, 2006), which could be considered to be similar to a biofilm encased in a thick biomineral matrix.

(3) These rock-bound cryptoendolithic communities have also been shown to benefit from solar warming of the rock surface, which creates a more favorable growth environment (e.g. Omelon *et al.*, 2006). Could the thermal capacity of biominerals in anyway help to warm the community? The lower thermal capacity of minerals compared to water ensures that this geological material heats up more quickly. Biofilms are predominantly water, but those that are very heavily cemented in biomineral might, possibly, be expected to warm quicker. Although pure speculation could very heavily mineralized phototrophic biofilms gain an advantage from solar warming?

(4) Another area that merits further research is the impact of biominerals on biofilm rheology. One would envisage that the incorporation of biominerals will likely increase their structural integrity, but this requires quantification. The impact on biofilm 'stiffness' and strength will not only depend on the type and density of the biomineral, and its state of dehydration, but also on the nature of the organism being encased. For example, in examining biomineralized filaments under the light microscope I have observed that they often appear to form straight and apparently relatively inflexible rods. This can cause them to snap into shorter lengths. One would speculate that a biofilm crosscut by inflexible rods would display significantly greater rigidity and strength compared to, for example, a biofilm containing biomineralized single cells. The impact of biomineralization on biofilm strength and structural integrity may have consequences for mass transport within the biofilm. Increases in strength and structural stability can require an increase in biofilm density (Beyenal & Lewandowski, 2002). Problematically this is accompanied by a decrease in diffusivity which can inhibit mass transport of essential nutrient and gasses through a biofilm. The incorporation of biominerals, however, into the biofilm matrix could aid in maintaining the strength and shape of a biofilm while reducing the need to increase significant biofilm density. Complex biofilm morphologies increase biofilm surface area, enhancing mass transport of essential nutrients across the biofilm/water interface. Could then biominerals help to maintain the structure of these complex morphologies?

Discussion of nutrient mass transport brings this article full circle to the problem of nutrient transport across the biomineral itself. Cells can be fully enclosed within a biomineral matrix which can be several times the thickness of the microorganism. One might expect this to inhibit the transport of essential nutrients, and terminal electron acceptors and donors to the bacterium. Or, indeed, the transport of waste away from the organism. Quantifying diffusion coefficients of these vital

components across the biomineral matrix will be essential to unraveling the extent to which biominerals may impart a negative influence over the microorganism. Any benefit the biomineral can provide is only valid if this significantly outweighs its detrimental side-effects. As stated previously, examination of rates of photosynthesis in silicified and nonsilicified cyanobacteria revealed biomineralized organisms exhibited the same metabolic rates as those which were unsilicified (Phoenix *et al.*, 2000, 2001). Clearly in this example the mass transport of CO_2 (probably in the form of bicarbonate) across the siliceous crust was not inhibited enough to slow photosynthesis. Although silicification of organisms initiated as colloids, these eventually coalesced in that particular study to form apparently continuous crusts. Despite this, photosynthesis was not inhibited. It is probable that the amorphous silica was precipitated as a highly hydrated amorphous gel which enabled relatively uninhibited diffusion of bicarbonate (and ultimately oxygen) through the biomineral. Other biominerals, however, may exhibit far lower diffusivities and may significantly reduce mass transfer of essential nutrients to, and waste products away from, the microbe. Under these conditions, interconnected pore spaces and channels, such as fractures, across the biomineral would be essential.

When one steps back and examines the potential benefits and detrimental side-effects of biominerals, they conspicuously appear to parallel those afforded by extracellular polymers. EPS has been shown to protect against solar radiation (Garcia-Pichel & Castenholz, 1991; Ehling-Schulz *et al.*, 1997), dehydration (Scott *et al.*, 1996), and phagocytosis (Schwarzmann & Boring, 1971) and is a key component of biofilms, helping maintain their structural integrity. One might describe this similarity as exopolymer reciprocation. Both extracellular substances (EPS and biominerals) affording bacteria a curiously similar set of advantages (Fig. 2), but are energetically less expensive. Certainly, this synergy has potential to be explored further.

As one might expect, there are many questions remaining in the field of microbial biomineralization. Terry, who did so much to pioneer this area, would be pleased to know this. His highly inquisitive mind would have relished the challenges that lay ahead.

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