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The link between biomineralization and fossilization of bacteria: Insights from field and experimental studies

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ABSTRACT

Fossil biominerals and fossils of microorganisms in ancient rocks contain important biogeochemical signals. Decoding this record may reveal crucial information about the evolution of life on Earth and terrestrial paleoenvironments. However, the identification of traces of life especially in very old rocks is extremely challenging because the morphological and chemical signatures of biominerals and microfossils are subtle, of microscopic size and inevitably altered with aging. In this review, we stress on the fact that biomineralization is often the first step of fossilization and produces particular chemical, structural and morphological features that can be preserved in fossil biominerals or microfossils, with a special focus on Fe-biomineralization. The taphonomic processes affecting biominerals and microfossils and altering their morphology and/or chemical composition over time are then discussed in light of experimental fossilization simulations and field sample analyses. We suggest that taxonomic biases observed in the fossil record may be related to differential abilities of species to trigger biomineralization. This calls for studies of the effective biomineralizing activity and fossilization potential of each species present in highly diverse natural microbial communities. Finally, recent analytical developments leave little doubt that very substantial progress in the study of biomineralization processes and ancient biostructures will be achieved in the near future.

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1. Introduction

Minerals and microbes have coevolved throughout Earth's history. Minerals such as Fe-sulfides and clays may have played an important role in the origin and evolution of life by catalyzing the prebiotic synthesis of primordial life-forms on the early Earth (Wachtershauser, 1988; Ferris, 2005) and providing essential nutrients for microbial growth (Southam, 2012). Once microbes emerged on Earth, possibly more than 3.5 Ga ago (*e.g.*, Schopf et al., 2007; Staudigel et al., 2008), they have continuously and significantly affected Earth's surface mineralogy by participating in precipitation, dissolution and transformation of minerals (Banfield and Nealson, 1997; Konhauser, 2006).

Biomineralization is one of the most important mineral–microbe interactions. Biominerals can be carbonates, phosphates, silicates, sulfates, sulfides, oxides or hydroxides and involve very diverse cations such as iron, calcium, magnesium and/or manganese (Lowenstam, 1981; Weiner and Dove, 2003). Biomineralization can provide a benefit for microbes by supplying the cells with energy and nutrients needed to maintain cell structure and functions (*e.g.*, Phoenix and Konhauser, 2008). It moreover forms many kinds of minerals in large quantities and is thus pivotal in past and present biogeochemical cycles (Lowenstam, 1981; Weiner and Dove, 2003; Hazen et al., 2008; Benzerara et al., 2011; Konhauser and Riding, 2012).

Fossilization comprises all the processes leading to the preservation of traces of life in the geological record. When a microorganism dies, organic molecules and cellular structures are usually degraded very rapidly under the lytic action of enzymes, except in some particular cases of selective preservation of highly chemically resistant molecules such as those composing cell walls or extracellular polymeric substances (EPS) (Vandenbroucke and Largeau, 2007). The rare remaining organic molecules and cellular structures are then further altered during diagenesis and metamorphism over geological time scales. Alternatively, microbes can induce the formation of biominerals, which might be more resilient than organic bacterial structures and thus provide traces of life in the geological record (Schopf et al., 2007; Benzerara and Menguy, 2009; Jimenez-Lopez et al., 2010). Biominerals may also trap organic molecules (Kawaguchi and Decho, 2002; Chan et al., 2004; Dupraz et al., 2009; Miot et al., 2009a; Perez-Gonzalez et al., 2010; Chan et al., 2011) or entomb whole cells or cell structures and lead to the formation of microfossils (*e.g.*, Benzerara et al., 2004; Kappler et al., 2005; Goulhen et al., 2006; Benzerara et al., 2008; Miot et al., 2009a, 2011).

Modern hot spring environments, where *in situ* silicification of microbial communities sometimes occurs, provide examples of how biomineralization, either by encrusting bacteria or forming pseudomorphs of bacterial structures, facilitates the preservation of the morphology of bacteria and sometimes blocks or slows down the degradation of bacterial organic molecules (*e.g.*, Konhauser et al., 2003; Geptner et al., 2005; McCall, 2010). As a result, encrusted microbial cells better resist to the subsequent chemical degradation during diagenesis and metamorphism and can thus be preserved as microfossils in the geological record. Therefore, biomineralization can be seen as a first possible step of fossilization. This process takes place over timescales of a few hours, days or years and can therefore be studied in the laboratory.

The geological record of microfossils and fossil biominerals contains an important geochemical/mineralogical legacy which provides information about the evolution of early life on our planet, or other planets such as Mars (*e.g.*, Schopf et al., 2007; Benzerara and Menguy, 2009; Javaux and Benzerara, 2009; Brasier and Wacey, 2012). However, these signals are often difficult to interpret. Indeed, fossil biominerals or microfossils exhibit a huge variety of morphologies and chemical compositions, which result partly from the biological processes that formed them (*i.e.*, the biomineralization processes) and partly from the diagenetic and metamorphic processes that they have experienced (*i.e.*, their taphonomic history) (*e.g.*, Gourier et al., 2004; Kopp and Kirschvink, 2008; Papineau et al., 2010; Zabini et al., 2012). Moreover, there are abiotic pathways that lead to the formation of minerals with geochemical, morphological, and/or mineralogical characteristics similar to some biominerals or microfossils, resulting in potentially misleading interpretations (*e.g.*, Golden et al., 2001; Brasier et al., 2002; García-Ruiz et al., 2003; Golden et al., 2004; Van Zuilen et al., 2007; García-Ruiz et al., 2009). It is thus essential to understand how diverse microbes form diverse minerals with diverse chemical (including isotopic signatures), morphological and structural properties; how specific of life these properties are; and how such features, *e.g.*, morphology, chemistry and structure are altered during aging.

Although an integrative link between biomineralogy and taphonomy is required, these scientific fields have usually been developed by different communities. Here we will show that crucial information can be retrieved from field and experimental studies on (1) the origin of particular chemical, structural and morphological features observed in fossil biominerals with a stress on biomagnetites; (2) the mechanisms of microfossil formation and the fineness of what can be preserved in them; (3) the extent and the conditions under which traces of life (microfossils or biominerals) are erased by taphonomic processes (in particular under increasing P and T conditions); and (4) the extent of the microbial diversity that may actually be preserved in the fossil record owing to biomineralization processes. This review will also provide details about the recent analytical tools that allow studying both modern systems in which biomineralization occurs and ancient samples where traces of biological structures and processes need to be identified.

2. Basics of biomineralization

Three general steps in the formation of minerals can be impacted by microbes (Mann, 2001; Bäuerlein, 2003; De Yoreo and Vekilov, 2003; Weiner and Dove, 2003). The first step consists in the achievement of a sufficient supersaturation of a solution with mineral phases, possibly within a localized zone around or inside the microbes. The raise of supersaturation favors precipitation kinetically and sometimes leads to the formation of minerals that would otherwise not be observed. Achievement or increase of supersaturation is induced by the metabolic activity of microbes. It is sometimes achieved in compartments such as the periplasm of Gram-negative bacteria or intracellular or extracellular vesicles (Benzerara and Miot, 2011). The very broad metabolic diversity encountered in prokaryotes explains the large diversity of biominerals they can form. If some bacterial groups/species are more efficient than others in triggering biomineralization, then they might be more prone to fossilization and this may induce taxonomic biases in the fossil record. The second and third steps that microbes can impact are the nucleation and the growth of biominerals by production of polymers that lower surface tension and/or poison mineral growth such as those composing sheaths (Banfield et al., 2000), capsules (Mullen et al., 1989), S-layers (Schultze-Lam and Beveridge, 1994), filaments (Chan et al., 2004) or fibers (Miot et al., 2009b). Numerous studies have demonstrated that carboxyl groups and phosphate groups in particular present on bacterial cell surfaces can bind metal ions and result in mineral growth when a sufficient concentration of appropriate counterions such as CO_2^{3-}, HPO_4^{3-}, or HS^- is available (*e.g.*, Beveridge and Murray, 1980; Fein et al., 1997; Fein, 2004).

Overall, three different types of microbial biomineralization have been summarized in the literature (Dupraz et al., 2009): (1) first, biologically controlled mineralization (BCM) referring to cases in which a microorganism exerts a strict control on the nucleation, growth, morphology, composition and final location of the biomineral. Such biominerals can thus be considered as fossils (*i.e.*, traces of past life) when preserved in the geological record (*e.g.*, Benzerara and Menguy, 2009). BCM minerals are generally structurally well-ordered with a narrow size distribution and may show species- or strain-specific crystal habits (Bazylinski and Frankel, 2003). (2) Biologically induced mineralization (BIM) describes the process in which mineral precipitation results from interactions between microbial activity and the environment