

Plausible mechanisms for the boring on carbonates by microbial phototrophs

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Abstract

Photosynthetic microbes, particularly cyanobacteria, that bore into carbonates are ancient biological players in various geologic phenomena such as the destruction of biogenic carbonates and coastal limestones, the reworking of carbonate sands and the cementation of microbialites. Their signatures are important tools for paleoenvironmental reconstruction, and they play a significant role in marine aquaculture. In spite of their geologic, environmental and economic importance, the mechanism by which they are able to excavate calcareous and calcophosphatic mineral substrates remains unknown. Excavation by acidulation, commonly thought to be a possible mechanism, constitutes nothing less than an apparent paradox, in that the geochemical consequence of oxygenic photosynthesis should be carbonate precipitation, not dissolution. Three alternative mechanistic models are presented here that may allow cyanobacterial boring to proceed and be still consistent with available evidence, as well as microbiological and geologic/geochemical principles. They are based on either temporal or spatial separation of photosynthesis and respiration, and on the active extrusion of calcium ions through an active cellular uptake and transport process. From the three models, the latter is shown to be most appropriate in describing and explaining the boring phenomenon. Several experimental approaches are discussed that would be appropriate to elucidate the paradox.

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1. Introduction

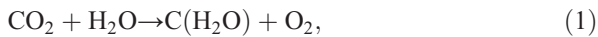
There can be little doubt that the relationship between living beings and carbonates is one of the most conspicuous interactions between the animate and the inanimate realms on the planet. Biological mediation of carbonate precipitation pervades our environment through many spatial scales and drives an important component of the geological carbon and metal cycles. We find it at the microscale in the form of subtle micritization in microbialites or as highly organized intracellular formation of beautifully sculpted coccoliths

in open ocean plankters. Mollusks and gastropods cast their shells, and corals relentlessly build massive reefs. A very diverse, evolutionarily divergent set of organisms is engaged in active carbonate precipitation, from bacteria, to algae and to animals. A record of fossil evidence, from Precambrian stromatolites to Holocene marine deposits, attests both to the continuity and to the antiquity of this relationship. It was indeed this very fossil evidence that brought about the birth of Sedimentology as a science in nineteenth century England.

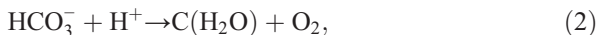
The sedimentary side of the formation/dissolution equation has received most attention by geobiologists, and much progress has been made in understanding the various environmental and cellular mechanisms

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involved in the process. Examples are known for microbially mediated precipitation of a variety of metal carbonates from carbonate and metal ions in solution. The simplest form of biotic carbonate precipitation involves the formation of microenvironments around small cells or organisms due to their metabolic activity. In these microenvironments, the concentrations of chemical species depart from those in the bulk phase in such a way that they can promote the local precipitation of carbonate. Calcification by photosynthetic cyanobacterial communities constitutes an archetypical example of this kind of indirect mechanism (Golubic et al., 2000; Merz-Preiß, 2000; Pentecost and Whitton, 2000; Arp et al., 2001). Oxygenic photosynthesis, which can be chemically abstracted for geochemical purposes as,



or, at neutral or slightly alkaline pH, as,



effectively consumes protons. This can in turn drive the thermodynamic equilibrium for metal carbonate dissolution–precipitation,



towards the solid phase. The free energy of dissolution is given by

$$\Delta G = RT \ln(\text{IAP}/K_{s0}),$$

where IAP is the ion activity product (Stumm and Morgan, 1996). If $\text{IAP} > K_{s0}$, the solution is said to be super-saturated with respect to the appropriate mineral phase and precipitation will be thermodynamically favored. Dissolution will be favorable when $\text{IAP} < K_{s0}$. Photosynthetic organisms may actually derive physiological benefits from concurrent photosynthesis and calcification (McConnaughey and Whelan, 1997). In fact, any other biological metabolism that consumes protons will have similar consequences, as is the case in sulfate reduction (Visscher et al., 2000; van Lith et al., 2003). More biologically controlled carbonate precipitation is attained by some cyanobacteria, where precise amounts of calcite crystals are used as ballast to counteract upwelling currents (Garcia-Pichel et al., 2002). The mechanism of coccolith formation in eukaryotic plankters, is biologically directed (i.e. genetically controlled) and very refined. It involves ionic transport into specific intracellular organelles, the generation of high intra-organelle supersaturation levels, and a regulation of the process through kinetic inhibition

and promotion of nucleation by polymeric templates (de Vrind-de Jong and de Vrind, 1997).

But organisms are also active at the erosional side of the cycle. Grazing on surface biofilms by hard-toothed higher animals and invertebrates (Shachak et al., 1987), as well as by the growth of chasmolithic and cryptoendolithic (Friedmann and Weed, 1987) microbes can result in significant physical erosion of limestones. Some organisms will tend to dissolve carbonates chemically (Ehrlich, 1996) by virtue of their metabolic activity. Aerobic heterotrophic bacteria, fermenting, sulfide-oxidizing and nitrifying bacteria, can dissolve acid-labile minerals due to the production of acid as by-product of metabolism (carbonic, organic, sulfuric and nitric acids, respectively). In the case of aerobic heterotrophs, it is possible to switch their naturally acidulant metabolism by supplying preferentially organic sources that yield alkali upon catabolic processing, such as amino acid rich protein hydrolysates; they will then tend to precipitate carbonates. In a more directed mode of dissolution, higher organisms, such as sponges (Hatch, 1980) and polychaetes (Haigler, 1969) are also known to actively bore into carbonate substrates, in a process of directed excavation. But by far the most common, widespread and environmentally significant of carbonate borers are microorganisms: fungi (Burford et al., 2003), microalgae and cyanobacteria (Golubic, 1969) that actively dissolve carbonate substrates, excavating microscopic galleries as they grow within them (Fig. 1). While the boring mechanism of any of these organisms remains unknown, the production of acid equivalents has often been suggested (Haigler, 1969; Golubic et al., 1984).

Thus, it should be evident that a synthetic understanding of the mechanisms that underlie the interactions between carbonates and living organisms has the potential to benefit interpretive models in a range of biological, environmental and geological disciplines. But to achieve such mechanistic understanding requires necessarily an interdisciplinary approach that draws from, and is consistent with, basic mineralogical, geochemical, and biological principles. It requires the experimental testing of such models under controlled, simplified conditions in the laboratory. It also requires that the models can be scaled up to explain a wealth of geological and biological observations in nature.

2. Diversity and relevance of carbonate-boring microorganisms

Carbonate microborers are found among filamentous or pseudofilamentous forms of both eukaryotes (fungi,

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