

The art of biomineralization

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Microorganisms are Earth's tiniest geochemists and architects, creating biominerals using biochemical machinery that has evolved over time. The results encompass a vast array of mineralogy and morphology, many in beautiful forms that spark our curiosity about their genesis and composition. A common attribute is the intimate association of organics and minerals, so to understand the formation process and products, we need to unravel the mechanisms of how these organic-mineral precipitates form. We focus on iron minerals because iron plays a central role in biogeochemical cycling. We are also compelled by the elegant iron oxyhydroxide biomineral shapes that certain iron-oxidizing microbes make. These twisted stalks, sheaths, and branching tubes are easy to recognize and are therefore useful targets for (spectro)microscopic approaches such as STXM and TEM. These have shown that iron oxidizer biominerals are iron oxyhydroxides that form either on an organic polysaccharide template or as an iron-polysaccharide co-precipitate. This strategy is not confined to just one clade of iron-oxidizers, as it has been adopted by both Gallionellaceae like *Ferriphaselus spp.* and Zetaproteobacteria like *Mariprofundus ferrooxydans*. This fact allows us to explore the genetic basis for iron biomineralization using comparative genomics, which can be further validated via biochemistry, genetics, and transcriptomics. Our observations to date suggest that biomineralization is a process that involves coordinated metabolism and behavior, including iron oxidation, polysaccharide formation, chemotaxis/motility, and cell-cell communication. Because mineral formation starts with iron oxidation, we have focused on probing the function of iron oxidation genes/proteins and reconstructing the iron oxidation pathways in Gallionellaceae and Zetaproteobacteria. Having identified and validated iron oxidation genes, we are then able to recognize the potential for iron biomineralization in uncultured organisms, as we have demonstrated in marine iron microbial mats. Our work thus far suggests that the ability to make iron oxyhydroxide biominerals is widespread across taxa and likely a common environmental phenomenon.

