Non-silicate Minerals (Carbonates, Oxides, Phosphates, Sulfur-Containing, Oxalates, and Other Organic Crystals) Induced by Microorganisms

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Contents

Abstract Microorganisms inhabit almost every natural environment on Earth. Since the beginning of life, microorganisms have played a fundamental role in the geochemical cycling of elements and shaped our current environments. Microorganisms that form minerals, a process known as biomineralization, contribute substantially to these processes. Over half of the essential elements required by living organisms are incorporated into biominerals. More than 60 different biominerals are known in nature, including oxides and hydroxides, carbonates, phosphates, sulfates and sulfides, silicates, and organic crystals.

Biominerals are composite materials that often exhibit superior properties when compared to their abiotically formed counterparts. Their well-designed architectures and hierarchical structures offer structural support and protection, but also fulfill a wide variety of other functions. Biominerals often reflect the physicochemical properties of the environment the biomineral was formed in. Fossilized biominerals are therefore useful tools for paleoceanographic and paleoclimate reconstructions. Biomineralization not only fascinates biologists, it also provides sophisticated models for functional materials in materials science and affects the global aspects of the earth sciences.

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The chapter gives an overview over non-siliceous biominerals formed by microorganisms and lists them in tabular form ordered by taxonomic criteria. It features carbonates, oxides and hydroxides, phosphates, sulfur-containing biominerals, and organic crystals.

1 Introduction

Microorganisms inhabit almost every natural environment on Earth. They populate the deepest oceans (Kato and Bartlett 1997), driest deserts (Wierzchos et al. 2011; Chan et al. 2012), the coldest climates (Cockell et al. 2010), and even extreme acidic environments (Johnson and Hallberg 2003). Since the beginning of life, microorganisms have played a fundamental role in the geochemical cycling of elements and have shaped our current environments. Microorganisms that form minerals, a process known as biomineralization, contribute substantially to these geochemical processes.

Over half of the essential elements required by living organisms are incorporated into biomineral deposits. The earliest microbial biomineralization process, the production of magnetite by magnetotactic bacteria, dates as far back as 3.5 billion million years (Lin et al. 2017). More than 60 different biominerals are known in nature, including oxides and hydroxides, carbonates, phosphates, sulfates and sulfides, silicates, and organic crystals. Among non-siliceous biominerals, calcium-based minerals are widespread. This can be explained by the high availability of environmental calcium and the low solubility of calcium salts, making them thermodynamically stable within biological environments. Precipitation of calcium salts also provides effective means to maintain cellular calcium homeostasis (Mann 2001).

Two types of biomineralization pathways can be distinguished: **biologically induced mineralization** and **biologically controlled mineralization** (Lowenstam 1981; Lowenstam and Weiner 1989). In biologically induced mineralization, precipitation occurs due to a modification of the local microenvironment caused by the organism. This could be the result of metabolic activity, or simply of the presence of adsorption and nucleation sites provided by cellular components, such as cell walls or extracellular polymeric substances (EPS). The organism does not exert any active control over the mineralization process.

In **biologically controlled mineralization**, the organism exerts a high degree of control over all steps of mineral formation: the selective uptake and accumulation of elements from the local environment, as well as nucleation and growth of the mineral phase. All of these processes are genetically controlled. Typically, the formation of biominerals requires local areas with sufficient ion supersaturation. Such privileged environments have to be created within a biologically controlled system in order to isolate harmful elements (Weiner and Dove 2003). For this reason, controlled biomineralization processes often take place in specialized, membrane-delimited spaces, such as vesicles, where an organism can exert control over mineralization.

In addition, these confined spaces also influence mineral crystallization (Meldrum and O'Shaughnessy 2020).

Generally, mineral precipitation often reflects the physicochemical properties of the environment the biomineral was formed in, e.g., water or mineral chemistry, temperature, pH, pressure, and light intensity. Fossilized biominerals are therefore a useful tool for paleoceanographic and paleoclimate reconstructions (Weiner and Dove 2003; Li et al. 2013).

Furthermore, biominerals are composite materials that often exhibit superior properties, e.g., in mechanical testing, when compared to their abiotically formed counterparts. Typically, the inorganic mineral is intimately associated with organic matrix constituents that influence the material's properties. These "natural additives" are also believed to play an integral part in mineral formation.

The well-designed morphologies and hierarchical structures of biominerals offer structural support and protection, but also fulfill a wide variety of important biological functions such as motion, buoyancy, storage, and optical, magnetic, or gravity sensing (Mann 2001). The "eco-friendly" formation of complex three-dimensional architectures with exquisite structural control under ambient conditions is beyond the reach of current human technology.

These properties make biomineralization a highly interdisciplinary research area: The architectures emerging from biological self-organization not only fascinate biologists and medical scientists, they also provide sophisticated models for functional materials in materials science (Nudelman and Sommerdijk 2012) and affect the global aspects of the earth sciences.

The chapter gives an overview over non-siliceous biominerals formed by microorganisms and lists them in tabular form ordered by taxonomic criteria. It features carbonates, oxides and hydroxides, phosphates, sulfur-containing biominerals, and organic crystals. For this overview, organisms up to 1μm in size were considered to be microorganisms. Taxonomic description is given according to the Lifemap project (de Vienne 2016) available at http://lifemap-ncbi.univ-lyon1.fr/.

2 Carbonates

Calcium carbonate biominerals are the most abundant biogenic minerals found in nature occurring both in freshwater and marine organisms. Three anhydrous calcium carbonate polymorphs exist: the two thermodynamically stable forms aragonite and calcite and the metastable vaterite. All of these polymorphs can be found biogenically as **carbonate biominerals formed by microorganisms** (**Table 1**). Calcite is the thermodynamically most stable form under ambient conditions (Jamieson 1953). Sometimes marine biogenic calcites contain up to 30 mol% Mg^{2+} ions in their lattice, which is referred to as Mg-calcite. Calcium carbonate can also occur in hydrated form as amorphous calcium carbonate (ACC), monohydrocalcite (MHC), calcium carbonate hexahydrate, and the recently discovered calcium carbonate hemihydrate (CCHH) (Zou et al. 2019).

Table 1 Carbonates in microorganisms

	Biomineral	Species	References
BACTERIA			
Non-specified	Calcite ($CaCO_3$)	~50 marine bacterial isolates	Morita (1980)
	Mainly aragonite, Mg-calcite ($CaCO_3$), and monohydrocalcite ($CaCO_3 \cdot H_2O$)	Heterotrophic marine bacterial (and fungal) isolates	Krumbein (1974, 1979)
	Calcite ($CaCO_3$)	31 calcifying bacterial isolates (*Bacillus*, *Arthrobacter*, *Kingella*, and *Xanthomonas*)	Cacchio et al. (2003)
Proteobacteria			
Alphaproteobacteria			
Rhodospirillales	Siderite ($FeCO_3$)	*Acidiphilium* sp.	Sánchez-Román et al. (2014)
	ACC (and magnetite)	Several species, at least two genomic undescribed genera	Monteil et al. (2020)
Betaproteobacteria			
Burkholderiales	Calcium carbonate ($CaCO_3$)	*Alcaligenes*	Rivadeneyra et al. (1985)
	ACC and Mg-calcite spherulites	*Curvibacter lanceolatus*	Zhang et al. (2017a)
	Rhodochrosite ($MnCO_3$) and MnO_x	*Leptothrix discophora*	Zhang et al. (2002)
Gammaproteobacteria			
Oceanospirillales	Mg-calcite, aragonite ($CaCO_3$), and monohydrocalcite ($CaCO_3 \cdot H_2O$)	*Halomonas eurihalina*	Rivadeneyra et al. (1998)
Pseudomonadales	Aragonite ($CaCO_3$)	*MB-1* (marine *Pseudomonas*)	Greenfield (2006)
	Calcite ($CaCO_3$)	*Pseudomonas fluorescens*	Appanna et al. (1997)
	Calcite and vaterite ($CaCO_3$)	*Freshwater isolates of Pseudomonas and Acinetobacter*	Zamarreño et al. (2009)
Thiotrichales	First calcium oxalate	*Achromatium*	Schewiakoff (1893)
	Calcite ($CaCO_3$)		West and Griffiths (1913), Bersa (1920), La Rivière and Schmidt (1992), Head et al. (1996, 2000b), Gray (2006), Gray and Head (2014), Salman et al. (2015)

Xanthomonadales	ACC	*Stenotrophomonas maltophilia*	Enyedi et al. (2020)
Alteromonadales	Siderite ($FeCO_3$)	*Shewanella algae*	Parmar et al. (2000)
	Siderite ($FeCO_3$), vivianite [$Fe_3(PO_4)_2 \cdot 8H_2O$], magnetite (Fe_3O_4), green rust*	*Shewanella putrefaciens*	Fredrickson et al. (1998)
	Vivianite [$Fe_3(PO_4)_2 \cdot 8H_2O$] and siderite ($FeCO_3$)		Zachara et al. (1998)
	Magnetite (Fe_3O_4), ferrous hydroxy carbonate (FHC), carbonate, and ferric green rust*		O'Loughlin et al. (2013)
	Magnetite (Fe_3O_4), akaganeite (β-FeOOH), and siderite ($FeCO_3$)	*Shewanella algae*, *S. pealeana*	Roh et al. (2003)
Deltaproteobacteria			
Desulfovibrionales (SRB)	Ferroan dolomite [$CaMg(CO_3)_2$]	*Desulfovibrio*	Vasconcelos et al. (1995)
	Mg-calcite ($CaCO_3$) and Ca-dolomite [$CaMg(CO_3)_2$]	*Desulfonatronovibrio* sp., *D. hydrogenovorans*, *Desulfovibrio profundus*, and *SRB strains LVform1* and *LVform6*	Warthmann et al. (2000), Van Lith et al. (2003a, b)
	Greigite (Fe_3S_4), pyrite (FeS_2) and intermediates (FeS), sphalerite (ZnS), elemental sulfur, gypsum ($CaSO_4 \cdot 2H_2O$), struvite ($NH_4MgPO_4 \cdot 6H_2O$), magnesite ($MgCO_3$)	*Desulfovibrio desulfuricans*	Hallberg (1972)
	High Mg-calcite ($CaCO_3$), greigite (Fe_3S_4)	Bacteria (DSS-group) and archaea (ANME-1)	Reitner et al. (2005)
	Calcium carbonate ($CaCO_3$)	*Beggiatoa*	Boetius et al. (2000)
Myxococcales	Mg-calcite ($CaCO_3$)	*Myxococcus xanthus*	González-Muñoz et al. (2000),
	Vaterite ($CaCO_3$)		Rodriguez-Navarro et al. (2007)

(continued)

Table 1 (continued)

	Biomineral	Species	References
Terrabacteria			
Actinobacteria			
Propionibacteriales	Vivianite ($Fe_3(PO_4)_2.8H_2O$) [and siderite ($FeCO_3$)]	*Tessaracoccus lapidicaptus*	Sánchez-Román et al. (2014, 2015)
Micrococcales	Calcium carbonate ($CaCO_3$)	*Micrococcus*	Rivadeneyra et al. (1985)
	Calcite/vaterite ($CaCO_3$)	*Agromyces*, *Amycolatopsis*, *Brachybacterium*, *Nocardioides*, *Nocardiopsis*, *Paenibacillus polymyxa*, *Rhodococcus*, *Rothia*, *Streptomyces* sp., and *S. nitrosporeus*	Groth et al. (2001)
	Mg-calcite ($CaCO_3$)	*Brachybacterium*, *Paenibacillus polymyxa*, *Rhodococcus*, *Streptomyces*	
	Calcite, aragonite (CaCO3), and dolomite [$CaMg(CO_3)_2$]	*Nesterenkonia halobia*	Rivadeneyra et al. (2000)
	Calcite, vaterite ($CaCO_3$), and monohydrocalcite ($CaCO_3{\cdot}H_2O$)	*Arthrobacter sulfonivorans* and	Rusznyák et al. (2012)
Corynebacteriales		*Rhodococcus globerulus*	
	ACC ($CaCO_3$)	*Rhodococcus degradans*,	Enyedi et al. (2020)
Firmicutes Bacillales		and *Bacillus simplex*	
	ACC and vaterite ($CaCO_3$)	*Lysinibacillus* sp.	Lv et al. (2017)
	calcite ($CaCO_3$)	*Bacillus megaterium*	Lian et al. (2006)
	Calcium carbonate ($CaCO_3$)	*Staphylococcus*	Rivadeneyra et al. (1985)
Urease-producing bacteria (UPB)	Calcite ($CaCO_3$)	*Bacillus*, *Staphylococcus succinus*	Stabnikov et al. (2013)
		Sporosarcina pasteurii = *Bacillus pasteurii*	Gollapudi et al. (1995), Stocks-Fischer et al. (1999), Bang et al. (2001), Bachmeier et al. (2002)
Clostridia	Magnetite (Fe_3O_4), akaganeite (β-FeOOH), and siderite ($FeCO_3$)	*Thermoanaerobacter ethanolicus*	Roh et al. (2003)

Cyanobacteria	Amorphous Ca-rich carbonates (ACC)	68 phylogenetically diverse strains	Benzerara et al. (2014)
Gloeobacterales	Amorphous Ca/Mg/Sr/Ba-carbonate spherules [benstonite, $(Sr_1Ba_{2.7}Mg_{1.4}Ca_{0.9})Ca_6Mg(CO_3)_{13}$]	*Cand. Gloeomargarita lithophora*	Couradeau et al. (2012)
	ACC granules		Li et al. (2016a)
		Gloeomargarita lithophora	Blondeau et al. (2018)
	Sr/Ba-enriched, core-shell structured ACC granules		Cam et al. (2016)
Nostocales	Calcite ($CaCO_3$)	*Scytonema julianum*	Schönleber (1936)
		Geitleria	Friedmann (1979)
Oscillatoriophycideae	Dypingite [$Mg_5(CO_3)_4(OH)_2 \cdot 5H_2O$]	*Lyngbya* sp.	Power et al. (2007)
	Calcite and “nano-globules” ($CaCO_3$)	*Gloeocapsa* sp.	Bundeleva et al. (2014)
	ACC granules	*Cyanothece* sp.	Blondeau et al. (2018)
	Sr/Ba-enriched, core-shell structured ACC granules		Cam et al. (2016)
Spirulinales	Calcite ($CaCO_3$)	*Spirulina platensis*	Ramanan et al. (2010)
Synechococcales	Aragonite ($CaCO_3$) and ACC	*Rivularia*	Golubic and Campbell (1981)
	Calcite and aragonite ($CaCO_3$)	*Schizothrix calcicola*	Borowitzka et al. (1974)
	Calcite ($CaCO_3$)	*Synechococcus*	Dittrich et al. (2003)
	ACC, aragonite-like $CaCO_3$, calcite	*Synechococcus leopoliensis*	Obst et al. (2009)
	ACC granules	*Synechococcus calcipolaris*, *Synechococcus* sp., *Thermosynechococcus elongatus*	Li et al. (2016a), Blondeau et al. (2018)
	Gypsum ($CaSO_4 \cdot 2H_2O$), calcite ($CaCO_3$), and magnesite ($MgCO_3$)	*Synechococcus*	Thompson and Ferris (1990), Schultze-Lam et al. (1992)

(continued)

Table 1 (continued)

	Biomineral	Species	References
ARCHAEA			
SRB	High Mg-calcite ($CaCO_3$) and greigite (Fe_3S_4)	Bacteria (DSS-group) and archaea (ANME-1)	Reitner et al. (2005)
EUKARYA			
Amoebozoa			
Evosea			
Eumycetozoa			
Myxogastria	Calcite ($CaCO_3$)	*Fuligo septica*	Mangenot (1932)
	Calcite ($CaCO_3$)	*Didymium*	Pobeguin (1954)
Tubulinea			
Elardia			
Arcellinida	Calcite ($CaCO_3$)	*Paraquadrula*	Deflandre (1953)
Haptista			
Haptophyta	Aragonite ($CaCO_3$)	*Polycrater galapagensis*	Manton and Oates (1980)
Prymnesiophyceae/ Coccolithophyceae	Calcite ($CaCO_3$)	*Pleurochrysis carterae*, *Emiliania huxleyi*, *Coccolithus pelagicus*, *Calcidiscus leptoporus*, *etc.*	Wilbur and Watabe (1963), Isenberg et al. (2006) **Reviews:** Young (2003), Brownlee et al. (2015), Monteiro et al. (2016), Taylor et al. (2017)
SAR			
Alveolata			
Ciliophora	Calcium carbonate inclusions	*Prorodon*, *Lacrymaria*, *Trachelocerca*, *Cardiostonza*, *Loxocephalus*, *Pleuronema*, *Vorticella*, *Amphisiella*, *etc.*	Fauré-Fremiet and Gauchery (1957)
	MgCaP-rich inclusions	*Euplotes vannus*	Hausmann and Walz (1979)
	Calcite ($CaCO_3$), Ca-P-rich inclusions	*Spirostomum ambiguum*	Pautard (1970)
	ACC	*Coleps hirtus*	Lemloh et al. (2013)

Dinophyceae	Calcite ($CaCO_3$)	*Thoracosphaeraceae* (e.g., *Thoracosphaera heimii*, *Scrippsiella*, *Leonella*, *Calciodinellum*)	Wall et al. (1970), Keupp (1981), Tangen et al. (1982), Zonneveld et al. (2005), Wendler and Bown (2013), Jantschke et al. (2020)
	MgCaP-rich inclusions	*Calciodinellum operosum aff.*, *Leonella granifera*	Jantschke et al. (2020)
Stramenopiles			
Ochrophyta			
Crysophyceaea	Calcite ($CaCO_3$)	*Pseudokephyrion*	Tappan (1980)
PX clade	Calcite and aragonite ($CaCO_3$)	*Padina pavonica*, *P. australis*	Borowitzka et al. (1974)
Rhizaria			
Retaria			
Foraminifera	Calcite and aragonite ($CaCO_3$)	Diverse benthic and planktonic species, such as *Orbulina universa*, *Globorotalia*, *Ammonia* sp., *Amphistegina lobifera*, *A. lessonii*, *etc.*	Blackmon and Todd (1959) **Reviews:** Goldstein (1999), Erez (2003), de Nooijer et al. (2014)
Rhodophyta			
Florideophyceae	Calcite and aragonite ($CaCO_3$)	*Liagora cenomyce*, *Lithophyllum moluccense*, *Corallina cuvierii*	Borowitzka et al. (1974)
Fungi			
Dikarya			
Basidiomycota			
Agaricomycotina			
Agaricomycetes			
Boletales	Mixture of calcite ($CaCO_3$) and whewellite ($CaC_2O_4{\cdot}H_2O$)	*Serpula himantioides* and *Cephalotrichum* sp.	Burford et al. (2006)
Ascomycota			
Saccharomyceta			
Pezizomycotina			
Ieotiomyceta			
Sordariomyceta			

(continued)

Table 1 (continued)

	Biomineral	Species	References
Lecanoromycetes	Hydrocerussite [$Pb_3(CO_3)_2(OH)_2$]	*Stereocaulon vesuvianum*	Jones et al. (1982)
Viridiplantae			
Chlorophyta			
Core chlorophytes			
Chlorodendrophyceae			
Chlorocendrales	ACC micropearls, Sr/Ba-rich	*Tetraselmis*	Martignier et al. (2017, 2018)
Chlorophyceae			
Chlamydomonadales	Calcite ($CaCO_3$)	*Phacotus lenticularis*	Kamptner (1950), Hepperle et al. (1996), Schlegel et al. (2000)
Trebouxiophyceae			
Chlorellales	Calcite ($CaCO_3$)	*Nannochloris atomus*	Yates and Robbins (1998)
	Calcite ($CaCO_3$)	*Chlorella* sp.	Ramanan et al. (2010)
Ulvophyceae			
TCBD clade			
Bryopsidales	Calcite and aragonite ($CaCO_3$)	*Neomeris annulata*	
Dasycladales		*Halimeda cylindracea*, *H. macroloba*, and *H. opuntia*	Borowitzka et al. (1974)
Streptophyta			
Streptophytina			
Charophyceae	Calcite and aragonite ($CaCO_3$)	*Chara corallina*	Borowitzka et al. (1974)
Zygnemophyceae			
Spirogyra	Aragonite ($CaCO_3$)	*Spirogyra*	Mann et al. (1987)
Zygnematales	Calcite ($CaCO_3$)	*Oocardium*	Wallner (1933), Rott et al. (2010)

Of these, **ACC** is a particularly important actor in biomineralization, because it is a frequent precursor phase of calcite or aragonite (Beniash et al. 1997; Addadi et al. 2003; Rodriguez-Blanco et al. 2017). Several microorganisms also produce stable amorphous calcium carbonate (ACC) as a biomineral (cf. Table 1). ACC—as a precursor phase or stabilized biomineral—has been widely recognized in many groups of organisms (Addadi et al. 2003). Interestingly, more than one amorphous state of calcium carbonate exists, a phenomenon termed polyamorphism (Cartwright et al. 2012). ACC is a poorly ordered material that varies in its water content and short-range structure. Biogenic ACCs can exhibit distinct short-range structural order characteristic of specific polymorphs (calcitic, aragonitic, or MHC-like ACC) (Levi-Kalisman et al. 2002; Addadi et al. 2003; Cartwright et al. 2012).

Foraminifera and coccolithophores are the major producers of calcium carbonate in the oceans (Baumann et al. 2003). Along with pteropods these groups dominate the global flux of calcium carbonate to the ocean floor (Schiebel 2002). Their high abundance and global distribution in modern oceans together with a high degree of fossilization make them attractive model organisms and climate proxies. Both groups are therefore studied extensively. Trace element and stable isotope composition of their shells is frequently used for paleoceanographic reconstructions, providing information about past seawater parameters, such as temperature, salinity, and pH (Spero and Williams 1988; Spivack et al. 1993; Hastings et al. 1998; Gussone et al. 2003; Baumann et al. 2005; Stevenson et al. 2014; Keul et al. 2017). One of the key questions is to understand how shell composition of a biologically controlled mineralization process can accurately reflect environmental parameters present at the time of formation. A fundamental understanding of the (intra)cellular calcification processes and mechanisms is essential to interpret proxy signals accurately.

Foraminifera are unicellular amoeboid protists that produce shells, the so-called tests. They are divided into four categories based on their test features: organic tests, agglutinated tests, imperforate calcitic tests, and, the most abundant today, perforate calcitic tests. Foraminifera occur ubiquitously in both planktonic and benthic marine environments. Their attractiveness as a source of climate proxies lies in their abundance and their ability to record seawater conditions. Different mechanisms for calcification from seawater have been proposed, including endocytosis of seawater (Bentov et al. 2009), transmembrane ion transporters, ion-specific organic templates (Bentov and Erez 2006), and mitochondrial activity (Erez 2003).

A general model for foraminiferal biomineralization is still lacking, but rotaliid foraminifera grow their tests in discrete steps of new chamber additions. Calcification takes place within a defined space [the delimited biomineralization space (DBS)], which is created actively by the rhizopodial network and preforms the shape of the new chamber (Erez 2003). In this defined zone, primary calcite nucleation occurs on the surface of an organic template, the primary organic sheet (POS) (Banner et al. 1973; Hemleben et al. 1977; Spero 1988). This newly formed chamber wall is then overlain by another layer of secondary calcite that extends over the entire test. For more details the reader is referred to the excellent reviews on foraminiferal biology (Goldstein 1999) and the complex and diverse nature of foraminiferal calcification (Erez 2003; de Nooijer et al. 2014).

Coccolithophores are a unicellular marine phytoplankton group characterized by a cell covering consisting of calcified scales called coccoliths. Coccoliths nucleate and grow within a specialized intracellular compartment, the Golgi-derived coccolith vesicle (for excellent reviews on coccolithophore calcification, see Young 2003; Brownlee et al. 2015; Monteiro et al. 2016; Taylor et al. 2017). This process starts with the nucleation of peripheral calcite crystals onto an organic baseplate (Walker et al. 2019; Marzec et al. 2019) inside the coccolith vesicle. Upon completion, the coccolith is subsequently extruded to the cell surface. Coccolith formation can be as fast as one per hour (Paasche 1962).

The biological mechanisms that control the intricate crystallization process are just starting to be understood. Recent studies using high-resolution cryoimaging revealed the presence of an intracellular compartment containing a calcium- and phosphorus-rich phase ([Ca] ~ 10 M) in the model organism *Emiliania huxleyi* (Sviben et al. 2016; Gal et al. 2017, 2018). By pulse-chase experiments using strontium instead of calcium ions, it was shown that the Ca-P-rich phase participates in coccolith formation and is used as calcium supply (Gal et al. 2017).

Recently, the structural similarity of this Ca-P-rich phase in coccolithophores and the Ca- and P-rich acidocalcisomes of the noncalcifying green alga *Chlamydomonas reinhardtii* was investigated (Gal et al. 2018). Acidocalcisomes are calcium-containing organelles that are considered the earliest form of an intracellular calcium pool (Ruiz et al. 2001; Docampo et al. 2005). Both Ca-P-rich compartments were shown to share many anatomical and chemical features, and based on these observations, a common dynamic calcium pool ancestor was suggested (Gal et al. 2018).

Interestingly, several other calcifying microorganisms possess similar intracellular, **membrane-bound granules** containing a disordered Ca-rich precursor phase that seem to be involved in mineral formation.

In members of **calcareous dinoflagellates**, dense **MgCaP-rich bodies** were identified by cryo-electron microscopy (Jantschke et al. 2020). These bodies seem to take part in calcium uptake, storage, and transport and are presumably secreted to the site of mineral growth, the outer matrix where the calcitic shell forms.

Similar **intracellular ACC inclusions** are known from cyanobacteria (cf. paragraph bacterial carbonate mineralization) and have been identified in the **green algae** *Tetraselmis cordiformis* (Martignier et al. 2017, 2018). Spherules of 0.4–1.2μm size were shown to consist of hydrated ACC. Because of the frequently observed internal zonation with alkaline-earth elements (Sr or Ba), these inclusions have been named “micropearls” (Martignier et al. 2017).

Intracellular “mineral concretions” have also been described in several **ciliate** species in the early twentieth century by Bernheimer (Bernheimer 1938) and Fauré-Fremiet (Fauré-Fremiet and Gauchery 1957). Even so, very little is known about biomineralization in ciliates. The first detailed description about the chemical nature of these inclusions was done by Pautard, who identified **intracellular spherules rich in calcium and phosphorus** in the ciliate *Spirostomum ambiguum* (Pautard 1970).

Furthermore, ciliates belonging to the genus *Coleps* form mineralized alveolar plates with a species-specific complex architecture. These alveolar plates are located within alveolar vesicles at the cell cortex. Recently, it has been shown that the alveolar plates are composed of an organic mesh-like structure that is mineralized with the **ACC** (Lemloh et al. 2013). Based on TEM observations, intracellular vesicles seem to be involved in calcium accumulation and transport.

A comprehensive study of the physiology and biochemistry of these precursor-rich spherules that extends over several phyla could shed light on the similarities and differences of these Ca-P-rich compartments and their ancestral origin.

Bacterial Carbonate Mineralization

Calcium carbonate deposits in **bacteria** are widespread and show a high degree of diversity. This is reflected by the variety of the calcium carbonate polymorphs found in bacterial cultures and in natural environments: Calcite, aragonite, vaterite, monohydrocalcite, and ACC have been identified in intra- and extracellular bacterial deposits (see **Table 1**).

Most of the bacteria precipitate calcium carbonate **extracellularly**, in close association with the bacterial cell wall (Beveridge and Murray 1976) and its extracellular polymeric substance (EPS) (Braissant et al. 2007; Dittrich and Sibler 2010; Flemming and Wingender 2010). Functional groups on the bacteria's surface, such as carboxyl, phosphate, hydroxyl, and sulfate, are able to complex and accumulate cations (such as Ca^{2+}). Calcium carbonate is subsequently formed as a result of alkalinization due to the bacterial metabolism, which is favoring precipitation.

During this process, **amorphous calcium carbonate (ACC)** has been observed to precipitate first and may transform into crystalline calcium carbonate polymorphs. ACC could be observed both in cultures, e.g., in vaterite-producing *Lysinibacillus* (Lv et al. 2017), Mg-calcite-producing *Curvibacter lanceolatus* (Zhang et al. 2017a) and aragonite-like calcium carbonate-producing *Synechococcus leopoliensis* (Obst et al. 2009), as well as in natural environments, such as cave sediments (speleothems) (Demény et al. 2016; Enyedi et al. 2020), marine ooids (Diaz et al. 2017), and hot springs (Jones and Peng 2012).

Recently, bacterial calcium carbonate mineralization has been applied in geotechnical engineering as a biocementation agent. Using urease-producing bacteria, the hydrolysis of urea into ammonium and carbonate is catalyzed. In the presence of Ca^{2+} ions, carbonate precipitation is initiated, a process called **microbially induced calcium carbonate precipitation (MICP)** (Seifan and Berenjian 2019). This novel and alternative type of construction material (De Muynck et al. 2010; Phillips et al. 2013; Chuo et al. 2020) is developing extensively and may be used for the strengthening of soil (Stabnikov et al. 2013), treatment of Ca-rich wastewaters (Hammes et al. 2003), oil recovery (Wu et al. 2017), or crack treatment (Gollapudi et al. 1995; Zhang et al. 2017b). In addition, the coprecipitation of other divalent cations such as Sr^{2+} and Ra^{2+} offers new possibilities for waste treatment (Kang et al. 2014).

Intracellular calcium carbonate inclusions are less common in bacteria. So far, intracellular calcite microspheres were only known from the large sulfur bacterium *Achromatium* (Head et al. 2000a; Gray 2006). These organisms accumulate microcrystalline calcium carbonate, in membrane-surrounded compartments filling most of the cell volume (Gray and Head 2014; Salman et al. 2015).

Recently intracellular amorphous calcium carbonate microspheres have been identified in several **cyanobacteria** species (for an overview see **Table 1**). Two phenotypes for ACC microsphere localization exist: They can be distributed randomly within the cell cytoplasm or lie at the cell poles (Benzerara et al. 2014; Li et al. 2016a). ACC biomineralization in cyanobacteria occurs within a microcompartment (Blondeau et al. 2018) and even in undersaturated extracellular solutions. Similar to other bacteria, *Gloeomargarita lithophora* has been shown to deposit other divalent cations with the ACC, even resulting in formation of core-shell globules (Cam et al. 2016). This accumulation of alkaline-earth elements is of particular interest for the remediation of radionuclides such as ^{90}Sr and Ra (Mehta et al. 2019).

In both cyanobacteria and *Achromatium*, the biochemical formation pathway and function of these intracellular, nonskeletal calcium carbonate inclusions are still not clear. Intracellular carbonates may act as inorganic carbon storage (Head et al. 2000b), control intracellular ion concentrations and buffer intracellular pH (La Rivière and Schmidt 1992; Salman et al. 2015), or regulate buoyancy (Couradeau et al. 2012).

3 Oxides and Hydroxides

Iron is the fourth most abundant element in the Earth’s crust. Iron is a redox-sensitive transition element with oxidation states between -II and +VI. Therefore, iron cycling is driven by chemical and microbial oxidation and reduction processes. Additionally, iron is an essential trace element for almost all known organisms. The availability of iron can structure entire microbial communities, and thereby influence the geochemistry of an area. A number of microorganisms are also able to biomineralize iron oxides and hydroxides and play a key role in the biogeochemical cycling of iron.

One of the most interesting and best-studied examples of microbial iron oxide biomineralization (**Table 2**) are the **magnetotactic bacteria (MTB**; for an extended overview, the reader is referred to the **other chapter of this book**). This group of microorganisms produces intracellular magnetic crystals composed of magnetite (Fe_3O_4) and/or greigite (Fe_3S_4) in a specialized, membrane-delineated compartment, the magnetosome (Schüler 2004). The nano-sized, magnetic crystals are usually arranged into chain-like structures which enable the organisms to navigate using the Earth’s magnetic field. This magnetotaxis allows MTB to position themselves in their preferred microaerobic oxygen concentration in vertically stratified environments (Frankel and Bazylinski 2009). Magnetotactic bacteria (MTB) are a paragon of biological controlled biomineralization, with their molecular machinery controlled at the gene level (Matsunaga et al. 1992; Schultheiss and Schüler 2003;

Table 2 Iron oxides in microorganisms

	Biomineral	Species	References
BACTERIA	Co- and Cr-containing magnetic inclusions	Different taxonomic groups (genera *Pseudomonas*, *Brevibacterium*, *Rhodopseudomonas*, and *Lactococcus*)	Ariskina (2003)
	Maghemite (γ-Fe_2O_3), magnetite (Fe_3O_4), and siderite ($FeCO_3$)	Thermophilic iron-reducing bacteria	Zhang et al. (1997)
	Magnetite (Fe_3O_4)		Zhang et al. (1998)
Incertae sedis	MnO_x (and FeO_x)	*Metallogenium*	Zavarzin (1961, 1981), Perfil’ev and Gabe (1965, 1969), Klaveness (1999)
Nitrospirae	Amorphous Fe-oxyhydroxide (FeOOH)	*Leptospirillum ferriphilum*	Yoshida et al. (2008)
	Magnetite (Fe_3O_4) or greigite (Fe_3S_4)	*Cand. Magnetobacterium bavaricum*	Spring et al. (1993), Jogler et al. (2010)
		Cand. Magnetobacterium bremense or strain MHB-1	Flies et al. (2005)
Proteobacteria			
Acidithiobacillia	Amorphous Fe-oxyhydroxide (FeOOH)	*Acidithiobacillus ferrooxidans*	Yoshida et al. (2008)
Alphaproteobacteria			
Caulobacterales	“Amorphous or noncrystalline magnet-sensitive inclusions” (Fe-rich)	*Caulobacter maris*	Vainshtein et al. (2002)
Rhizobiales	MnO_x and FeO_x	Two *Pedomicrobium*-like bacteria	Ghiorse and Hirsch (1979)
	“Amorphous or noncrystalline magnet-sensitive inclusions” (Fe-rich)	*Rhodopseudomonas* sp., *R. palustris*, *R. rutilis*	Vainshtein et al. (1997, 2002)
Rhodobacterales	Nano-goethite (α-FeOOH)	*Rhodobacter* sp.	Miot et al. (2009b)
Magnetotactic bacteria	Magnetite (Fe_3O_4)	α-PB: *Magnetospirillum gryphiswaldense*, *Magnetococcus*, *Magnetofaba*, *Magnetovibrio*, *Magnetospira*	Blakemore (1975), Frankel et al. (1979, 1983), Lovley et al. (1987), Bazylinski et al. (1993)
	Amorphous ferrihydrite, magnetite (Fe_3O_4)	*Aquaspirillum magnetotacticum* = *Magnetospirillum magnetotacticum*	Frankel et al. (1985)

(continued)

Table 2 (continued)

	Biomineral	Species	References
Also Delta- and Gammaproteobacteria	Magnetite (Fe_3O_4) or greigite (Fe_3S_4)	δ-PB: *Cand. Magnetoglobus multicellularis*, *Cand. Magnetomorum littorale*, *Cand. Magnetananas tsingtaoensis*, *Desulfovibrio magneticus* RS-1 γ-PB: strains BW-2, SS-5, GRS-1	**Reviews**: Bazylinski and Frankel (2003), Bazylinski et al. (2007), Faivre and Schüler (2008)
	Magnetite (Fe_3O_4)	Several species, ≥2 genomic undescribed genera	Monteil et al. (2020)
Betaproteobacteria			
Burkholderiales	MnO_x and FeO_x	*Leptothrix* OUMS1	Sawayama et al. (2011)
		Sphaerotilus discophorus	Rouf and Stokes (1964)
	Magnetite (Fe_3O_4)	*Burkholderia* sp.	Pan et al. (2015)
	Ferrihydrite	*Leptothrix ochracea*	Kennedy et al. (2004)
Nitrosomonadales		and *Gallionella ferruginea*	
	Hematite (Fe_2O_3), ferrihydrite, and goethite (α-FeOOH)		Hallberg and Ferris (2004)
	Fe-oxyhydroxide (FeOOH) and ferrihydrite	Stalk-forming Fe-oxidizing bacteria related to *Gallionella*	Chan et al. (2009)
Gammaproteobacteria			
Enterobacterales	Amorphous Fe(III)	*Escherichia coli*	Bauminger et al. (1980)
	"Amorphous or noncrystalline magnet-sensitive inclusions" (Fe-rich)		Vainshtein et al. (2002)
	Lepidocrocite [γ-FeO(OH)]	*Bacillus subtilis* and *E. coli*	Châtellier et al. (2001)
Pseudomonadales	Ferritin ("Fe(II) oxide-hydroxide-phosphate core")	*Azotobacter vinelandii*	Stiefel and Watt (1979)
	Ferritin (hydrated FeO_x) and amorphous iron phosphate	*Pseudomonas aeruginosa* *Azotobacter vinelandii*	Harrison et al. (1987)
	"Amorphous or noncrystalline magnet-sensitive inclusions" (Fe-rich)	*Pseudomonas aeruginosa*	Vainshtein et al. (2002)

Alteromonadales	Membrane-bound intracellular Fe granules and extracellular green rust, magnetite (Fe_3O_4), vivianite [$Fe_3(PO_4)_2 \cdot 8H_2O$], goethite (α-FeOOH)	*Shewanella putrefaciens*	Glasauer et al. (2002, 2003)
	Carbonate green rust [$GR^*(CO_3)^{2-}$], vivianite [$Fe_3(PO_4)_2 \cdot 8H_2O$], and magnetite (Fe_3O_4)		Kukkadapu et al. (2004), O'Loughlin (2008)
	Siderite ($FeCO_3$), vivianite [$Fe_3(PO_4)_2 \cdot 8H_2O$], magnetite (Fe_3O_4), green rust*		Fredrickson et al. (1998)
	Magnetite (Fe_3O_4), ferrous hydroxy carbonate (FHC), carbonate and ferric green rust*		O'Loughlin et al. (2013)
	Magnetite (Fe_3O_4), akaganeite (β-FeOOH), and siderite ($FeCO_3$)	*Shewanella algae*, *Shewanella pealeana*	Roh et al. (2003)
Chromatiales	"Amorphous or noncrystalline magnet-sensitive inclusions" (Fe-rich)	*Ectothiorhodospira shaposhnikovii*	Vainshtein et al. (1997, 2002)
Deltaproteobacteria			
	Greigite (Fe_3S_4), magnetite (Fe_3O_4)	Unknown group	Lefèvre et al. (2011)
Desulfovibrionales (SRB)	Carbonate green rust [$GR^*(CO_3)^{2-}$], vivianite [$Fe_3(PO_4)_2 \cdot 8H_2O$], and greigite (Fe_3S_4)	*Desulfovibrio alaskensis*	Zegeye et al. (2007)
	Magnetite (Fe_3O_4)	*Desulfovibrio magneticus*	Pósfai et al. (2006)
Desulfuromonadales	Magnetite (Fe_3O_4) and lepidocrocite [γ-FeO(OH)]	*Geobacter metallireducens*	Vali et al. (2004)
Terrabacteria			
Actinobacteria	Maghemite (γ-Fe_2O_3), and greigite (Fe_3S_4)	*Actinobacter* sp.	Bharde et al. (2008)
	Magnetite (Fe_3O_4)		Bharde et al. (2005)

(continued)

Table 2 (continued)

	Biomineral	Species	References
Firmicutes			
Bacilli	Lepidocrocite [γ-FeO(OH)]	*Bacillus subtilis* and *Escherichia coli*	Châtellier et al. (2001)
	"Amorphous or noncrystalline magnet-sensitive inclusions" (Fe-rich)	*Bacillus cereus*, *B. thuringiensis*, *Lactobacillus plantarum*, *Lactococcus lactis*, *Staphylococcus* sp.	Vainshtein et al. (2002)
Clostridia	Magnetite (Fe_3O_4), akaganeite (β-FeOOH), and siderite ($FeCO_3$)	*Thermoanaerobacter ethanolicus*	Roh et al. (2003)
EUKARYA			
Euryarchaeota			
Stenosarchaea			
Halobacteria	"Amorphous or noncrystalline magnet-sensitive inclusions" (Fe-rich)	*Haloarcula vallismortis*, *Halococcus* sp., *H. morrhuae*, *H. salifodinae*, *Haloferax mediterranei*, *H. volcanii*, *Halorubrum sodomense*	Vainshtein et al. (2002)
EUKARYA			
Cryptophyceae	Magnetite (Fe_3O_4)	2 unspecified species	Bazylinski et al. (2000)
Discoba			
Euglenozoa			
Euglenida	Magnetite (Fe_3O_4)	*Anisonema*	de Araujo et al. (1986)
SAR			
Alveolata			
Ciliophora	Magnetite (Fe_3O_4)	*Cyclidium* sp.	Bazylinski et al. (2000)
Dinophyceae	Magnetite (Fe_3O_4)	1 unspecified species	Bazylinski et al. (2000)
Stramenopiles			
Ochrophyta			
Chrysophyceae	FeO_x and MnO_x	Several species, e.g., *Anthophysa vegetans*, *Siderodendron manganiferum*, *Siphomonas fritschii*, and *Bikosoeca petiolata*	Pringsheim (1946)
Fungi			

Dikarya			
Basidiomycota			
Agaricomycotina			
Tremellomycetes	Magnetite (Fe_3O_4)	*Cryptococcus humicola*	Vainshtein et al. (2014)
Ascomycota			
Saccharomyceta			
Saccharomycotina			
Saccharomycetes			
Saccharomycetales	Magnetite (Fe_3O_4)	*Saccharomyces cerevisiae*	Vainshtein et al. (2014)
Pezizomycotina			
Ieotiomyceta			
Lecanoromycetes	Amorphous FeO_x	*Stereocaulon vulcani*	Jackson and Keller (1970)
	Goethite (α-FeOOH)	*Rhizocarpon geographicum* and 4 lichen species	Ascaso et al. (1976), Galván et al. (1981)
Fungi incertae sedis			
Mucoromycota			
Mucoromycotina	Ferritin (hydrated FeO_x)	*Phycomyces (blakesleeanus)*	Peat and Banbury (1968), David and Easterbrook (1971)
Viridiplantae			
Chlorophyta			
Core chlorophytes			
Chlorophyceae			
Chlamydomonadales	Magnetic mineral, most likely magnetite (Fe_3O_4) or pyrrhotite (Fe_7S_8)	*Chlamydomonas pleichloris "magnetotactica"*	de Barros et al. (1981)

* GR = green rust = $[Fe_{(6-x)}{}^{II}Fe^{III}{}_x(OH)_{12}]^{x+}\ [(A^{2-})_{x/2}\cdot yH_2O]^{x-}$

Komeili et al. 2004). The genes responsible for the biomineralization of magnetosomes are organized as clusters (Grünberg et al. 2001).

MTB are typically found within the *Alphaproteobacteria*, but have also been affiliated to *Delta-* and *Gammaproteobacteria*, as well as *Nitrospira*. MTB occur ubiquitously in diverse aquatic and sedimentary environments and are believed to contribute significantly to the biogeochemical cycling of iron with contributions reaching up to 10% (Faivre and Schüler 2008).

Many nonmagnetic oxyhydroxides, such as ferrihydrite and goethite, are sequestered by bacteria (cf. Table 2). Amorphous iron hydroxides and ferrihydrite are also considered precursor phases for magnetite formation.

Amorphous intracellular iron-rich inclusions of unclear function (Vainshtein et al. 1998) have been found in nonmagnetotactic *Gammaproteobacteria* (Glasauer et al. 2002; Vainshtein et al. 2002) and magnet-sensitive *Alphaproteobacteria* (Vainshtein et al. 1997).

Despite the fact that **manganese oxides (MnO_x)** are omnipresent, when compared to iron oxide biominerals, manganese biomineralization is way less studied. Manganese oxides occur in almost every terrestrial and marine environment, but they are also important adsorbents, battery materials, and catalysts in industry (Tebo et al. 2004). Manganese oxides are very porous minerals constructed from MnO_6 octahedra that show a high degree of structural variability. Due to their large surface areas, they belong to the most reactive minerals in natural systems. Commonly observed biogenic MnO_x mineral structures (see **Table 3**) are either layered [birnessite or vernadite (δ-MnO_2)] or tunnellike (todorokite) (Post 1999). Vernadite is considered a birnessite which is disordered along the layer stacking. It has to be mentioned that in a lot of cases, the exact structure of microbial MnO_x has not been determined.

A variety of microorganisms, mainly bacteria and fungi, are able to oxidize Mn (II) to the less soluble Mn(IV) through Mn(III) in aerobic environments (Tebo et al. 2004). The formation of Mn(III)/Mn(IV) in solution is a kinetically slow reaction (Morgan 2005), while the biological process is several orders of magnitude faster (Hastings and Emerson 1986; Bargar et al. 2005; Tebo et al. 2019). MnO_x readily precipitates onto microbial extracellular structures, such as EPS, and is commonly observed in association with biofilms and microbial mats. For this reason, natural manganese oxides in aquatic and soil environments are thought to be a result of microbially mediated oxidation (Nealson et al. 1988).

In most cases, **bacteriogenic MnO_x** closely resemble layered structured vernadite or birnessite (Villalobos et al. 2003; Jürgensen et al. 2004; Bargar et al. 2005; Webb et al. 2005; Saratovsky et al. 2006). Recent studies have revealed that bacterially mediated MnOx phases can also have todorokite structure (Kim et al. 2003; Kim and Stair 2004; Feng et al. 2010). Species of the freshwater bacterium *Leptothrix* seem to be able to produce both birnessite (Jürgensen et al. 2004; Saratovsky et al. 2006) and todorokite (Kim et al. 2003; Kim and Stair 2004).

Many **Ascomycete fungi** and some soil lichen (Pentecost et al. 2010) possess the capacity to oxidize Mn(II) and deposit MnO_x. The structure and function of these deposits as well as their role in environmental Mn cycling is currently not known.

Table 3 Manganese oxides in microorganisms

	Biomineral	Species	References
BACTERIA			
Incertae sedis	MnO_x (and FeO_x)	*Metallogenium*	Zavarzin (1961, 1981), Perfil'ev and Gabe (1965, 1969), Klaveness (1999)
	MnO_x	Chemoorganotrophic bacteria	Grote and Krumbein (1992)
Proteobacteria			
Alphaproteobacteria			
Rhizobiales	MnO_x and FeO_x	2 *Pedomicrobium*-like bacteria	Ghiorse and Hirsch (1979)
Betaproteobacteria			
Burkholderiales	MnO_x	*Leptothrix echinata*	Beger (1935)
		Leptothrix discophora	Ghiorse and Chapnick (1983), Adams and Ghiorse (1986), Boogerd and de Vrind (1987), Emerson and Ghiorse (1992), Nelson et al. (1999, 2002), Robbins and Corley (2005)
	Nanocrystalline, todorokite-like MnO_x		Kim et al. (2003), Kim and Stair (2004)
	Single-layer microcrystals of Na-birnessite-like MnO_x		Jürgensen et al. (2004)
	Mixed-valent, layered MnO_x with the chemical formula $M^{n+}{}_yMn^{3+}{}_{0.12}[\square_{0.12}Mn^{4+}{}_{0.88}]O_2{\cdot}zH_2O$ similar to hexagonal birnessites, Zn-chalcophanite, and $Ca_2Mn_3O_8$		Saratovsky et al. (2006)
	MnO_x and FeO_x	*Leptothrix* OUMS1	Sawayama et al. (2011)
		Sphaerotilus discophorus	Rouf and Stokes (1964)
Gammaproteobacteria			
Methylococcales	MnO_x	*Clonothrix*	Perfil'ev and Gabe (1965)
Oceanospirillales	MnO_x	*Oceanospirillum*	Ennever and Summers (1975)

(continued)

Table 3 (continued)

	Biomineral	Species	References
Pseudomonadales	Todorokite [(Na,Ca,K,Ba,Sr)$_{1\text{-}x}$ (Mn,Mg,Al)$_6$O$_{12}$·(3-4)H$_2$O]	*Pseudomonas putida*	Feng et al. (2010)
	Vernadite (δ-MnO$_2$) and poorly crystalline hexagonal birnessite		Villalobos et al. (2003)
	MnO$_x$	2 *Pseudomonas species*	Zavarzin (1962)
Terrabacteria			
Actinobacteria			
Micrococcales	MnO$_x$	*Siderocapsa* = *Arthrobacter*	Ehrlich (1966)
Firmicutes			
Bacilli	MnO$_x$	*Bacillus*	Ehrlich (1966), Nealson and Ford (1980), Rosson and Nealson (1982)
	Layered phyllomanganate and amorphous MnO$_x$ similar to vernadite (δ-MnO$_2$)	*Bacillus*	Bargar et al. (2005), Webb et al. (2005)
Cyanobacteria/Melainabacteria			
Cyanobacteria			
Nostocales	MnO$_x$	*Anabaena*	Richardson et al. (1988), Richardson and Stolzenbach (1995)
Oscillatariophycideae	MnO$_x$	*Microcystis*	Richardson et al. (1988)
FCB group			
Bacteroidetes/Chlorobi group			
Bacteroidetes	MnO$_x$	*Flavobacterium*	Nealson (1978)
Chlorobi	MnO$_x$, CaMnO$_3$	*Chlorobium*, *Paludibacter*, *Acholeplasma*, *Geobacter*, *Desulfomicrobium*, *Clostridium*, *Acetobacterium*, and several other bacteria	Daye et al. (2019)

EUKARYA			
Amoebozoa			
Tubulinea	“Amorphous manganese compounds”	*Centropyxis*	Hedley et al. (1976)
SAR			
Stramenopiles			
Ochrophyta			
Chrysophyceae	FeO_x and MnO_x	Several species, e.g., *Anthophysa vegetans*, *Siderodendron manganiferum*, *Siphomonas fritschii*, and *Bikosoeca petiolata*	Pringsheim (1946)
PX clade			
Xanthophyceae	MnO_x	*Vaucheria*	Richardson and Stolzenbach (1995)
Fungi			
Dikarya			
Ascomycota			
Ascomycota incertae sedis	MnO_x, todorokite-like	*Acremonium*	Tani et al. (2004), Miyata et al. (2006), Saratovsky et al. (2009)
	MnO_x	Isolates of the phylum *Deuteromycota*, class *Agonomycetes*	Thompson et al. (2005)
		>10 fungal isolates	Schweisfurth (1971)
Saccharomyceta			
Pezizomycotina			
Ieotiomyceta	MnO_x	*Cladosporium cladosporioides*, *Alternaria alternata*, *Phoma glomerata*, *Penicillium frequentans*, and *P. steckii*	de la Torre and Gomez-Alarcon (1994)
Lecanoromycetes	MnO_x	*Catillaria chalybeia*	Pentecost et al. (2010)
Sordariomyceta	MnO_x	*“Monilicean fungus”= Monilia*	Robbins and Corley (2005)

(continued)

Table 3 (continued)

	Biomineral	Species	References
	MnO_x	*Plectosphaerella cucumerina* and *Acremonium strictum*	Santelli et al. (2011)
Dothideomyceta	MnO_x	*Pyrenochaeta* sp. and *Stagonospora* sp.	
	MnO_x	*Cladosporium sphaerospermum*, *Coniothyrium* sp., *Alternaria tenuis*	Grote and Krumbein (1992)
Eurotiomycetes		*Penicillium brevicompactum*, *P.* cf. *tenuissimum*, *P.* cf. *waksmannii*	
Basidiomycota	MnO_x	Non-specified " arthroconidial anamorph of a basidiomycete"	Emerson et al. (1989)
Viridiplantae			
Chlorophyta			
Core chlorophytes			
Trebouxiophyceae			
Chlorellales	MnO_x	*Chlorella* sp.	Richardson et al. (1988)
Chlorophyceae			
Chlamydomonadales	MnO_x	*Chlamydomonas*	Schulz-Baldes and Lewin (1975)
Sphaeropleales			
Scenedesmaceae	MnO_x	*Scenedesmus subspicatus*	Knauer et al. (1999)
		Scenedesmus	Richardson and Stolzenbach (1995)
Ulvophyceae			
OUU clade			
Ulotrichales	MnO_x	*Ulothrix* sp.	Robbins and Corley (2005)

Extracellular MnO_x precipitation has also been reported for different **algae**. Richardson et al. demonstrated that dense populations of large (>20 μm) photosynthesizing algae generate alkaline microenvironments that induce manganese oxidation (Richardson et al. 1988; Richardson and Stolzenbach 1995). Extracellular MnO_x covers the holdfasts of the green algae *Ulothrix* sp. (Robbins and Corley 2005) and is precipitated by the unicellular algae *Scenedesmus* but also stored intracellularly as Mn^{2+} (Knauer et al. 1999). The significance of phytoplankton on the manganese cycle, especially in freshwater, may be bigger than believed and should be further explored.

Manganese oxides have a large impact on the distribution and availability of other heavy metal cations in natural environments (Post 1999). Due to their porous structure, other divalent metal cations (e.g., Co, Ni, Cu, Pb, and Cd) can be efficiently adsorbed (O'Reilly and Hochella 2003)—an observation with obvious applications in the removal of Mn and other trace metals from contaminated water (Nelson et al. 1999, 2002; Tani et al. 2004; Hallberg and Johnson 2005). Manganese and iron oxides are powerful oxidants that participate in redox reactions of inorganic and organic compounds (Huang and Zhang 2020). Furthermore, mineralization of MnOx can lead to co-dissolution (Crowe et al. 2007) and/or coprecipitation of other elements. Overall, in a biogeochemical context, microbial manganese oxidation (Table 3) is highly significant (Tebo et al. 2004).

4 Phosphates

Microorganisms are key players in phosphorus cycling in nature. Using extracellular enzymes or the secretion of acids, microorganisms convert organic and inorganic phosphorous compounds into soluble and available forms (Tiessen 2008; Barea and Richardson 2015). Microorganisms take up phosphate (Pi) via specific transport systems (Torriani-Gorini et al. 1994) and have adapted to grow at both high and low Pi concentrations. By regulation of the Pi uptake and accumulation of phosphorus reserves, intracellular Pi levels in microorganisms are independent of extracellular concentration and remain rather constant. Phosphorus reserves in microorganisms occur typically in the form of inorganic polyphosphates (polyP) (Kulaev and Vagabov 1983; Kornberg et al. 1999; Kulaev and Kulakovskaya 2000; Kulaev et al. 2005; Schröder and Müller 2012), polymeric orthophosphates, or pyrophosphates (Torriani-Gorini et al. 1994). As part of their phosphorus metabolism, some microorganisms form **insoluble phosphate minerals** (**Table 4**) (Omelon et al. 2013). Their role in the formation of natural phosphate deposits (geological phosphorites) has been recognized since the early twentieth century (Blackwelder 1916; Cayeux 1936).

Understanding the mechanisms involved in the biogenic precipitation of calcium phosphates is particularly relevant to the search for traces of life (Mojzsis et al. 1996; Mojzsis and Arrhenius 1998; Blake et al. 2001) and in medical sciences, where pathological calcium phosphates are responsible for diseases, such as

Table 4 Phosphates in microorganisms

	Biomineral	Species	References
BACTERIA	$KNa_3(Fe_{1,5}Mg_{2,5})(PO_4)_3(OH)_3$	Unspecified SRB (bacteria and archaea)	Hallberg and Wadsten (1980)
	Hydroxyapatite $[Ca_5(PO_4)_3(OH)]$	Nanobacteria	Kajander and Ciftçioglu (1998)
Proteobacteria			
Alphaproteobacteria			
Rhizobiales	Struvite $(NH_4MgPO_4{\cdot}6H_2O)$	*Brucella abortus* and *B. melitensis*	Huddleson and Winter (1927)
Betaproteobacteria			
Burkholderiales	Amorphous iron phosphate	*Acidovorax* sp.	Miot et al. (2009a)
	Pyromorphite $[Pb_5(PO_4)_3(OH)]$	*Burkholderia cepacia*	Templeton et al. (2003)
	Nanocrystalline hydroxyapatite $[Ca_5(PO_4)_3(OH)]$	*Ramlibacter tataouinensis*	Benzerara et al. (2004)
Gammaproteobacteria			
Pseudomonadales	Struvite $(NH_4MgPO_4{\cdot}6H_2O)$	*"Bacterium putidum fluorescens"*= *Pseudomonas fluorescens/putida*	Robinson (1889)
		Pseudomonas calciprecipitans	Shinano and Sakai (1975)
	Chlorapatite $[Ca_5(PO_4)_3Cl]$	*Acinetobacter* sp.	Li et al. (2019)
Pseudomonadales/ Enterobacterales	Carbonate-rich fluorapatite [francolite, $(Ca,Mg,Sr,Na)_{10}\ (PO_4,SO_4,CO_3)_6\ F_{2-3}$]	"Gram-negative aerobic pseudomonads or facultatively anaerobic enterobacteria"	O'Brien et al. (1981)
	Struvite $(NH_4MgPO_4{\cdot}6H_2O)$ and monohydrocalcite $(CaCO_3{\cdot}H_2O)$	*Acinetobacter* sp., *Pseudomonas* sp.	Rivadeneyra et al. (1983, 1985)
Enterobacterales	Struvite $(NH_4MgPO_4{\cdot}6H_2O)$	*Proteus mirabilis*	Griffith (1978), McLean et al. (1988), Lerner et al. (1989), Sun et al. (2012)
	Hydroxyapatite $[Ca_5(PO_4)_3(OH)]$	*Providencia rettgeri and Escherichia coli*	Hirschler et al. (1990a, b)
	Hydroxyapatite $[Ca_5(PO_4)_3(OH)]$ and ACP	*Escherichia coli*	Cosmidis et al. (2015)

Alteromonadales	Membrane-bound intracellular Fe granules and extracellular green rust, magnetite (Fe_3O_4), vivianite [$Fe_3(PO_4)_2{\cdot}8H_2O$], goethite (α-FeOOH)	*Shewanella putrefaciens*	Glasauer et al. (2002, 2003)
	Magnetite (Fe_3O_4), carbonate green rust ($[Fe_{(6-x)}{}^{II}Fe^{III}{}_x(OH)_{12}]^{x}$ $^{+}(CO_3{}^{2-})_{0.5x}{\cdot}yH_2O$), and vivianite [$Fe_3(PO_4)_2\ {\cdot}8H_2O$]		Kukkadapu et al. (2004)
	Siderite ($FeCO_3$), vivianite [$Fe_3(PO_4)_2{\cdot}8H_2O$], magnetite (Fe_3O_4), green rust*		Fredrickson et al. (1998)
	Vivianite [$Fe_3(PO_4)_2{\cdot}8H_2O$] and siderite ($FeCO_3$)		Zachara et al. (1998)
Deltaproteobacteria			
Desulfobacterales	Fe-P-rich granules (similar to vivianite)	*Desulfosarcina/Desulfococcus*	Milucka et al. (2012)
Desulfovibrionales	Greigite (Fe_3S_4), pyrite (FeS_2) and intermediates (FeS), sphalerite (ZnS), elemental sulfur, gypsum ($CaSO_4{\cdot}2H_2O$), struvite ($NH_4MgPO_4{\cdot}6H_2O$), magnesite ($MgCO_3$)	*Desulfovibrio desulfuricans*	Hallberg (1972)
	Mackinawite (FeS), vivianite/metavivianite [$Fe_3(PO_4)_2{\cdot}8H_2O$]		Ivarson and Hallberg (1976)
	Mackinawite (FeS, tetragonal), pyrite (FeS_2), vivianite [$Fe_3(PO_4)_2\ {\cdot}8H_2O$], and greigite ($Fe_3S_4$)		Duverger et al. (2020)
	Hydroxysulfate green rust [$GR_2(SO_4{}^{2-})$] and vivianite [$Fe_3(PO_4)_2{\cdot}8H_2O$]	*Desulfovibrio alaskensis*	Zegeye et al. (2007)
	Vivianite ($Fe_3(PO_4)_2.8H_2O$), greigite (Fe_3S_4), pyrite (FeS_2)	*Desulfovibrio* and *Sulfurospirillum*	Berg et al. (2020)
	Mackinawite (FeS), greigite (Fe_3S_4), and vivianite [$Fe_3(PO_4)_2{\cdot}8H_2O$]	*Desulfovibrio vulgaris*	Zhou et al. (2014)

(continued)

Table 4 (continued)

	Biomineral	Species	References
Myxococcales	Struvite ($NH_4MgPO_4 \cdot 6H_2O$)	*Myxococcus xanthus*	Omar et al. (1994), Da Silva et al. (2000)
	Newberyite [$Mg(PO_3OH) \cdot 3H_2O$], schertelite [$(NH_4)_2MgH_2(PO_4)_2 \cdot 4H_2O$], and taylorite ($K_2SO_4$) in conjunction with struvite ($NH_4MgPO_4 \cdot 6H_2O$)	*Myxococcus coralloides*	González-Muñoz et al. (1994)
Terrabacteria			
Actinobacteria			
Micrococcales			
Brevibacteriaceae	Struvite ($NH_4MgPO_4 \cdot 6H_2O$)	*Brevibacterium antiquum*	Smirnov et al. (2005)
Micrococcaceae	Struvite ($NH_4MgPO_4 \cdot 6H_2O$) and monohydrocalcite ($CaCO_3 \cdot H_2O$)	*Brevibacterium* sp. *Arthrobacter* sp.	Rivadeneyra et al. (1983, 1985)
Propionibacteriales	Vivianite ($Fe_3(PO_4)_2.8H_2O$) [and siderite ($FeCO_3$)]	*Tessaracoccus lapidicaptus*	Sánchez-Román et al. (2014, 2015)
Streptomycetales	Ni-struvite ($NiNH_4PO_4 \cdot 6H_2O$)	*Streptomyces acidiscabies*	Haferburg et al. (2008)
Corynebacteriales	Hydroxyapatite [$Ca_5(PO_4)_3(OH)$]	*Bacterionema matruchotii* = *Corynebacterium matruchotii*	Takazoe and Nakamura (1965), Ennever et al. (1971, 1973), Moorer et al. (1993)
	Hydroxyapatite [$Ca_5(PO_4)_3(OH)$] and intracellular Ca-PL-P complexes		Boyan et al. (1984)
	Struvite ($NH_4MgPO_4 \cdot 6H_2O$) and monohydrocalcite ($CaCO_3 \cdot H_2O$)	*Corynebacterium* sp.	Rivadeneyra et al. (1983, 1985)
FCB group			
Firmicutes Bacilli		*Bacillus* sp. *Kurthia* sp. *Listeria* sp.	
	Struvite ($NH_4MgPO_4 \cdot 6H_2O$)	*Staphylococcus aureus*	Beavon and Heatley (1963)
		Bacillus pumilus	Nelson et al. (1991)

	Hydroxyapatite [$Ca_5(PO_4)_3(OH)$]	*Streptococcus mutans*, *S. sanguis*, *and S. sobrinus*	Streckfuss et al. (1974), Moorer et al. (1993)
Clostridia	Vivianite [$Fe_3(PO_4)_2{\cdot}8H_2O$]	*Alkaliphilus metalliredigens*	Roh et al. (2007)
Tenericutes	Struvite ($NH_4MgPO_4{\cdot}6H_2O$)	*Ureaplasma urealyticum*	Grenabo et al. (1984)
Bacteroidetes/Chlorobi			
Bacteroidetes	Struvite ($NH_4MgPO_4{\cdot}6H_2O$) and monohydrocalcite ($CaCO_3{\cdot}H_2O$)	*Flavobacterium* sp.	Rivadeneyra et al. (1983, 1985)
ARCHAEA			
TACK group			
Crenarchaeota			
Thermoprotei			
Sulfolobales	AFP and lipscombite [$Fe^{II}{}_xFe^{III}{}_{3-x}(PO_4)_2(OH)_{3-x}$]	*Sulfolobus acidocaldarius*	Miot et al. (2017)
	Fe- and P-rich globules, goethite (α-FeOOH), and AFP		Kish et al. (2016)
Euryarchaeota			
Stenosarchaea			
Halobacteria	$Mg_2(OH)PO_4{\cdot}4H_2O$	*Halorubrum distributum* and *Halobacterium salinarum*	Smirnov et al. (2005)
EUKARYA			
SAR			
Alveolata			
Ciliophora	Dahllite [carbonate-rich hydroxyapatite, $Ca_5(PO_4)_3(OH)$]	*Spirostomum ambiguum*	Pautard (1970)
	Hydroxyapatite [$Ca_5(PO_4)_3(OH)$]		Pautard (1958, 1959), Jones (1967)
	Calcian struvite [$(Mg,Ca)NH_4PO_4\ {\cdot}6H_2O$] guanine (Creutz et al. 2002)	*Paramecium tetraurelia*	Grover et al. (1997)

(continued)

Table 4 (continued)

	Biomineral	Species	References
Amoebozoa			
Tubulinea			
Elardia	ACP	*Cryptodifflugia oviformis*	Ogden and Hedley (1980)
Opisthokonta			
Metazoa			
Eumetazoa			
Bilateria			
Protosomia			
Ecdysozoa			
Nematoda	Hydroxypyromorphite [$Pb_5(PO_4)_3(OH)$]	*Caenorhabditis elegans*	Jackson et al. (2005)
Fungi			
Dikarya			
Ascomycota			
Saccharomyceta			
Saccharomycotina	Hydroxyapatite [$Ca_5(PO_4)_3(OH)$] and ACP	*Candida albicans*	Ennever and Summers (1975)
Pezizomycotina			
Ieotiomyceta			
Eurotiomycetes	**Uranyl phosphate species**, potassium uranyl phosphate hydrate ($KPUO_6 \cdot 3H_2O$), meta-ankoleite [$(K_{1.7}Ba_{0.2})(UO_2)_2(PO_4)_2 \cdot 6H_2O$], uranyl phosphate hydrate [$(UO_2)_3(PO_4)_2 \cdot 4H_2O$], meta-ankoleite [$K(UO_2)(PO_4) \cdot 3H_2O$], uramphite [$NH_4UO_2PO_4 \cdot 3H_2O$], and chernikovite [$(H_3O)_2(UO_2)_2(PO_4)_2 \cdot 6H_2O$]	*Aspergillus niger* and *Paecilomyces javanicus*	Liang et al. (2015)
Sordariomyceta	Chloropyromorphite [$Pb_5(PO_4)_3Cl$]	*Paecilomyces javanicus* and *Metarhizium anisopliae*	Rhee et al. (2012)

atherosclerosis, calcification of artificial heart valves, or the formation of urinary stones and dental calculus (Dorozhkin and Epple 2002).

In biological systems, calcium phosphates occur mainly in the form of nonstoichiometric sodium-, magnesium-, and carbonate-containing **hydroxyapatite [$Ca_5(PO_4)_3(OH)$]** (often called "biological apatite" or dahllite).

Recently, the formation of oceanic phosphorites has been recognized as occurring in close association with polyphosphate-accumulating bacteria (Omelon et al., 2013). In modern, actively forming phosphorite formations, marine bacteria such as *Pseudomonas* and *Acinetobacter* (Nathan et al. 1993) and the sulfide-oxidizing bacteria *Beggiatoa* (Brüchert et al. 2003; Goldhammer et al. 2010) and *Thiomargarita namibiensis* (Schulz et al. 1999; Schulz and Schulz 2005) have been identified. These bacteria accumulate phosphate as polyP in oxic conditions and release Pi under anoxic conditions, thus creating supersaturation with regard to apatite (Goldhammer et al. 2010; Brock and Schulz-Vogt 2011). Furthermore, it was suggested that polyphosphate granules from abundant diatoms act as mineral templates and contribute to the formation of calcium phosphate minerals in marine sediments (Diaz et al. 2008).

Similarly, many types of oral bacteria are known to contribute to the formation of dental calculus, although their specific role is not clear. Ennever et al. observed apatite mineralization caused by the actions of the dental bacteria *Bacterionema matruchotii* (Takazoe and Nakamura 1965; Ennever et al. 1971, 1973; Boyan et al. 1984). Interestingly, Takazoe and Nakamura noted intracellular polyP granules, which inhibit dental calculus mineralization (Takazoe and Nakamura 1965). Omelon et al. drew a parallel between phosphorite and calculus nucleation, proposing a similar pathway, bacterial Pi release from intracellular polyP storage, for both marine and oral bacteria (Omelon et al. 2013).

Apatite sequestration is mostly considered a biologically induced mineralization. Benzerara et al. demonstrated that the betaproteobacterium *Ramlibacter tataouinensis* crystallizes nanocrystalline hydroxyapatites with their *c* axes oriented perpendicular to the cell surface. This observation suggests one of the few examples of biologically controlled mineralization that results in well-orientated phosphates in bacteria (Benzerara et al. 2004).

Bacterial precipitation of **struvite ($NH_4MgPO_4 \cdot 6H_2O$)** was first described by Robinson in 1889 (Robinson 1889). According to Robinson, struvite was formed as a consequence of the combination of metabolically produced NH^{4+} ions with the magnesium and phosphate ions present in the medium, which could explain the presence of struvite in natural environments.

Since then, the production of struvite by bacteria has been widely documented for a variety of *Proteobacteria* (Robinson 1889; Huddleson and Winter 1927; Hallberg 1972; Shinano and Sakai 1975; Griffith 1978; Rivadeneyra et al. 1983, 1985; McLean et al. 1988; Lerner et al. 1989; Omar et al. 1994; González-Muñoz et al. 1994; Da Silva et al. 2000; Sun et al. 2012) and *Terrabacteria* (Beavon and Heatley 1963; Rivadeneyra et al. 1983, 1985; Grenabo et al. 1984; Nelson et al. 1991; Smirnov et al. 2005).

Struvite is also found in approximately every fifth **kidney stone** (Griffith 1978). To date, the production of this pathological biomineral in kidney stones has been attributed to bacterial action. Bacteria such as *Proteus*, *Pseudomonas*, *Klebsiella*, and *Staphylococcus* are commonly observed in the context of urinary infections. In experimental studies, struvite crystals were shown to form in vitro in the presence *Proteus mirabilis*, a Gammaproteobacterium commonly found in urinary stones of patients suffering from urolithiasis (Griffith 1978; McLean et al. 1988; Lerner et al. 1989; Sun et al. 2012). In this pathological biomineralization process, urea-splitting bacteria such as *Proteus* and some *Staphylococci* convert urea to ammonia, which leads to an increase of pH and the precipitation of struvite.

The production of struvite and other magnesium phosphates by **myxobacteria** is of special interest (Omar et al. 1994; González-Muñoz et al. 1994; Da Silva et al. 2000). Myxobacteria are interesting and common prokaryotic organisms of high ecological importance. These bacteria inhabit various types of soil and play an active role in the degradation of organic materials (Shimkets et al. 2006). According to the experimental studies, they contribute significantly to the formation of struvite in nature. Under certain conditions, magnesium can be replaced by nickel forming the biomineral "nickel struvite" ($NiNH_4PO_4 \cdot 6H_2O$) which has been identified in the nickel-resistant *Actinobacterium Streptomyces acidiscabies* (Haferburg et al. 2008).

Another insoluble magnesium phosphate, $Mg_2(OH)PO_4 \cdot 4H_2O$, was shown to be produced by the halophilic archaeon *Halobacterium salinarum*. It is currently the only repot of this unusual form of phosphorus reserve (Smirnov et al. 2005).

Vivianite [$Fe_3(PO_4)_2 \cdot 8H_2O$] is commonly observed in reductive environments and occurs in anoxic freshwater sediments where it is often associated with organic matter (Rothe et al. 2016). Under these conditions, with a sufficiently high ortho-phosphate and Fe^{2+} concentration and in the absence of S^{2-} ions, vivianite is stable (Nriagu 1972). Iron (III) oxides are considered an important precursor phase for vivianite formation. The formation of vivianite has been linked to **dissimilatory iron-reducing bacteria** such as *Shewanella putrefaciens* in culture experiments (Fredrickson et al. 1998; Zachara et al. 1998; Glasauer et al. 2002, 2003; Kukkadapu et al. 2004). In dissimilatory iron-reducing bacteria, the oxidation of organic matter is coupled to the reduction of iron oxides (Fredrickson et al. 1998; Zachara et al. 1998; Glasauer et al. 2003; O'Loughlin et al. 2013). The nature of the minerals formed from the reduction of synthetic and natural iron oxides depends on the ions present in culture medium. If enough HCO^{3-} and $HPO_4{}^{2-}$ ions are available, first vivianite and then siderite are formed (Zachara et al. 1998). In the absence of counterions, magnetite or "green rust" is formed as a product of a solid-state conversion (Fredrickson et al. 1998). Green rust is a layered iron hydroxide that acts as a reactive intermediate and slowly converts into vivianite in the presence of phosphate (Hansen and Poulsen 1999).

Extracellular vivianite and siderite nanoglobules have been shown to form on the cell surface of the *Actinobacterium Tessaracoccus lapidicaptus* isolated from sediments in Rio Tinto, Spain. The Fe-rich carbonates and phosphates are found within the bacterial EPS matrix, which provides nucleation sites for crystal growth. The works of Sánchez-Román link microbial P, C, and Fe cycles and could explain the formation of vivianite and siderite in natural environments (Sánchez-Román et al. 2014, 2015).

There are also indications for **intracellular Fe- and P-rich granules** in microorganisms involved in the anaerobic oxidation of methane coupled to sulfate reduction (AOM). A consortium of methanotrophic archaea and sulfate-reducing *Deltaproteobacteria* mediates this process. Milucka et al. presented evidence for intracellular precipitates rich in iron and phosphorus in the involved *Deltaproteobacteria* species *Desulfosarcina* and *Desulfococcus* (Milucka et al. 2012).

In the hyperthermophilic archaeon *Sulfolobus acidocaldarius*, a passive process of iron phosphate nucleation has been described (Kish et al. 2016). Iron phosphate compounds [Fe- and P-rich globules, goethite (α-FeOOH), and AFP] have been shown to grow within the cell envelope's S-layer independently of metabolic activity. In an artificial maturation experiment, these iron phosphates transformed into **lipscombite** $[Fe^{II}{}_{x}Fe^{III}{}_{3-x}(PO_4)_2(OH)_{3-x}]$ under hydrothermal conditions (Miot et al. 2017). With their shape depending on the initial mineral/organics ratio, lipscombite minerals are suggested as proxies for the presence of biogenic matter in iron deposits.

Some microorganisms detoxify Pb through pyromorphite precipitation. Micro X-ray diffraction on intracellular Pb hotspots inside the nematode *Caenorhabditis elegans* showed that crystalline **hydroxypyromorphite** $\mathbf{[Pb_5(PO_4)_3(OH)]}$ can be formed internally by an organism (Jackson et al. 2005). Nematodes are indigenous soil organisms, and given their high density in soil, biogenic pyromorphite formation may be relevant to Pb cycling in soils.

Rhee et al. observed the formation of **chloropyromorphite** $\mathbf{[Pb_5(PO_4)_3(Cl)]}$, the most stable lead mineral that exists, under the influence of the fungal strains *Paecilomyces javanicus* and *Metarhizium anisopliae* (Rhee et al. 2012). The mycogenic chloropyromorphite formation from metallic lead probably demonstrates a microbial survival strategy in lead-contaminated environments.

In a similar manner, fungi have also been shown to precipitate a variety of different **uranium-containing phosphate biominerals** when grown with an organic phosphorus source (Liang et al. 2015). The uranium minerals were located extracellularly, in association with the fungal hyphal matrix. Sequestration of uranium and lead phosphate minerals by fungi demonstrates their role in U, Pb, and P biogeochemistry and their potential application in element recovery or bioremediation.

5 Sulfur-Containing (Sulfates, Sulfides, and Elemental Sulfur)

Sulfates [Gypsum ($CaSO_4 \cdot 2H_2O$), Jarosite [$KFe^{3+}{}_3(SO_4)_2(OH)_6$], Barite ($BaSO_4$), and Celestite ($SrSO_4$)]
Compared to carbonate and silicate, phosphate, or oxide biominerals, detailed information about **sulfate biominerals (Table 5)** is limited (Bosselmann and Epple 2008) on macroscopic observations. Biological formation pathways and molecular control await further elucidation.

Biogenic sulfate crystals were already described by Fischer in the late nineteenth century, when he identified **calcium sulfate crystals** (gypsum) located at the poles of the desmid algae *Closterium* by dissolution experiments (Fischer 1884). This finding was later confirmed by Ondracek in 1936 (Ondracek 1936) and Kopetzky-Rechtperg in 1949 (Kopetzky-Rechtperg 1949). Almost 100 years after their first description, these crystals were shown to consist of barite ($BaSO_4$) with traces of celestite ($SrSO_4$) by means of EDX spectroscopy (Brook et al. 1980). However, some crystalline vacuolar inclusions in the desmid algae *Bambusina* and *Gonatozygon* have been shown to consist of calcium sulfate (Brook 1981).

Gypsum ($CaSO_4 \cdot 2H_2O$) biominerals have also been found to be associated with the surface of bacterial cells in environmental and cultivated samples [for an extended review, see Van Driessche et al. (2019)].

Microbial gypsum deposits have been identified in several nonmarine environments: Extracellular biomineralization of gypsum, calcite, and magnesite was observed in the bacteria *Synechococcus* growing in natural alkaline lake water (Thompson and Ferris 1990). Gypsum was nucleated close to the bacterial cell envelope, whereas calcite was formed secondarily due to the photosynthetic metabolism of *Synechococcus*. Further research suggested the bacterial S-layer as a mineral nucleation site (Schultze-Lam et al. 1992).

Bacteria of the genus *Arthrobacter* isolated from marine evaporite beds have been shown to mineralize gypsum in polar environments (Cockell et al. 2010). Sulfide-oxidizing bacteria have been suggested to take part in gypsum formation in limestone caves (Galdenzi and Maruoka 2003; Mansor et al. 2018). This is supported by gypsum precipitation and Ca isotopic fractionation experiments in the presence of the sulfur-oxidizing bacterium *Acidithiobacillus thiooxidans* (Harouaka et al. 2016). Ca and S isotopic compositions were evaluated as biosignatures that can be utilized to detect subsurface life.

Jarosite [$KFe^{3+}{}_3(SO_4)_2(OH)_6$] is only formed under strong acidic conditions ($pH<4$) (Bigham et al. 1996b), even in the presence of microorganisms (Bigham et al. 1996a). Therefore, microbial biomineralization of jarosite has been mainly observed in natural acidic environments, such as mines, drainage waters, or acidic rivers. Bacterial formation of jarosite related to their metabolic activity has been demonstrated in culture experiments and natural environments (Ivarson 1973; Lazaroff et al. 1982; Ziegler et al. 2009).

Table 5 Sulfate biominerals in microorganisms

	Biomineral	Species	References
BACTERIA			
Proteobacteria			
Acidithiobacillia	Tooeleite [$Fe_6(AsO_3)_4SO_4(OH)_4 \cdot 4H_2O$], schwertmannite [$Fe_8O_8(OH)_6SO_4$], and jarosite [$KFe^{3+}{}_3(SO_4)_2(OH)_6$]	*Acidithiobacillus ferrooxidans* =*Thiobacillus ferrooxidans* Review: (Yang et al. 2020)	Morin et al. (2003), Egal et al. (2009)
	Jarosite [$KFe^{3+}{}_3(SO_4)_2(OH)_6$]		Ivarson (1973), Lazaroff et al. (1982), Daoud and Karamanev (2006)
	Gypsum ($CaSO_4 \cdot 2H_2O$)	*Acidithiobacillus thiooxidans*	Harouaka et al. (2016)
Betaproteobacteria			
Ferrovales	Jarosite [$KFe^{3+}{}_3(SO_4)_2(OH)_6$]	*Ferrovum*	Ziegler et al. (2009)
Deltaproteobacteria			
Desulfovibrionales	Greigite (Fe_3S_4), pyrite (FeS_2) and intermediates (FeS), sphalerite (ZnS), elemental Sulfur, gypsum ($CaSO_4 \cdot 2H_2O$), struvite ($NH_4MgPO_4 \cdot 6H_2O$), magnesite ($MgCO_3$)	*Desulfovibrio desulfuricans*	Hallberg (1972)
	Schwertmannite [$Fe_8O_8(OH)_6SO_4$], jarosite [$KFe^{3+}{}_3(SO_4)_2(OH)_6$], and greigite ($Fe_3S_4$)	*Non-specified SRB*	Gramp et al. (2009)
Myxococcales	Barite ($BaSO_4$)	*Myxococcus xanthus*	González-Muñoz et al. (2003)
Nitrospirae	Jarosite [$KFe^{3+}{}_3(SO_4)_2(OH)_6$]	*Leptospirillum*	Ziegler et al. (2009)
Terrabacteria			
Actinobacteria			
Micrococcales	Gypsum ($CaSO_4 \cdot 2H_2O$)	2 *Arthrobacter* isolates	Cockell et al. (2010)
Cyanobacteria			
Synechococcales	Gypsum ($CaSO_4 \cdot 2H_2O$), Calcite ($CaCO_3$), and magnesite ($MgCO_3$)	*Synechococcus*	Thompson and Ferris (1990), Schultze-Lam et al. (1992)

(continued)

Table 5 (continued)

	Biomineral	Species	References
Firmicutes			
Clostridia	Jarosite [$KFe^{3+}{}_3(SO_4)_2(OH)_6$]	*Sulfobacillus thermosulfidooxidans*	Ding et al. (2007)
EUKARYA			
Haptista			
Haptophyta			
Pavlovales	Barite ($BaSO_4$)	*Exanthemachrysis gayraliae* *Pavlova* sp.	Fresnel et al. (1979), Gayral and Fresnel (1979)
SAR			
Alveolata			
Dinophyceae	Celestite ($SrSO_4$) with traces of barite ($BaSO_4$)	*Achradina pulchra*	Gómez et al. (2017)
Ciliophora	Barite ($BaSO_4$)	*Loxodes*	Hubert et al. (1975), Neugebauer and Machemer (1997)
		Loxodes and *Remanella*	Rieder et al. (1982)
Rhizaria			
Retaria			
Foraminifera	Barite ($BaSO_4$)	*Stannophyllum zonarium*	Tendal (1972)
Acantharia		*Aschemonella ramuliformis* *Galatheammina* sp.	Gooday and Nott (1982)
		Psammetta erythrocytomorpha	Schulze and Thierfelder (1905), Schulze (1907)
		Agglutinating Foraminifera, two-chambered (Hyperammina-like)	Bertram and Cowen (1998)
	Celestite ($SrSO_4$)	*Podactinelius sessilis* [uncertain taxonomic affinity (Levine et al. 1980)]	Bütschli (1906)
		Acanthometra pellucidum sp.	Odum (1951)
		Phyllostaurus siculus	Wilcock et al. (1988)

Polycystinea			
Collodaria	Celestite ($SrSO_4$)	*Collosphaera huxleyi*	Müller (1858)
		Sphaerozoum neapolitanum (swarmer cells)	Hollande and Martoja (1974)
		Sphaerozoum punctatum	Anderson (1981), Hughes et al. (1989)
		Collozoum and *Collosphaera*	Anderson et al. (1990)
Fungi			
Dikarya			
Ascomycota			
Saccharomyceta	Jarosite [$KFe^{3+}{}_3(SO_4)_2(OH)_6$]	*Purpureocillium lilacinum*	Oggerin et al. (2013)
Viridiplantae			
Streptophyta			
Streptophytina			
Charophyceae	Barite ($BaSO_4$)	*Chara fragilis*	Schröter et al. (1975)
	Barite ($BaSO_4$)	*Chara*	Sievers and Schmitz (1982)
Zygnemophyceae			
Zygnematales	Barite ($BaSO_4$)	*Spirogyra*	Kreger (1957), Kreger and Boeré (1969)
Desmidiales			
Desmidiaceae	Barite ($BaSO_4$)	*Micrasterias denticulata*	Meindl (1984), Niedermeier et al. (2018)
	Barite ($BaSO_4$)	*Pleurotaenium* and *Micrasterias*	Brook et al. (1980)
	Barite ($BaSO_4$)	*Micrasterias thomasiana*	Wilcock et al. (1989)
	Gypsum ($CaSO_4{\cdot}2H_2O$)	*Pleurotaenium* and *Tetmemorus*	Fischer (1884), Ondracek (1936), Kopetzky-Rechtperg (1949)
Closteriaceae	Gypsum ($CaSO_4{\cdot}2H_2O$) later identified as. . . (see below)	*Closterium*	

(continued)

Table 5 (continued)

	Biomineral	Species	References
	Barite ($BaSO_4$)	Six *Closterium* species	Brook et al. (1980)
	Barite ($BaSO_4$) [and celestite ($SrSO_4$)]	*Closterium littorale*	
	Barite ($BaSO_4$)	*Closterium lunula*	Wilcock et al. 1989)
	Barite ($BaSO_4$) or celestite ($SrSO_4$)	*Closterium moniliferum*	Brook et al. (1988), Krejci et al. (2011a, b)
Gonatozygaceae	Calcium sulfate ($CaSO_4$)	*Bambusina brebissonii* and *Gonatozygon brebissonii*	Brook (1981)
	Barite ($BaSO_4$)	*Gonatozygon kinahani*	
Peniaceae	Gypsum ($CaSO_4{\cdot}2H_2O$)	*Penium*	Fischer (1884)

The formation of jarosite is enhanced by the metabolic activity of iron-oxidizing bacteria such as *Acidithiobacillus ferrooxidans* (Ivarson 1973; Lazaroff et al. 1982; Daoud and Karamanev 2006). In acidic mine drainages with high arsenic content, *A. ferrooxidans* was shown to promote the formation of tooeleite, an As(III)-Fe(III) sulfate mineral [$Fe_6(AsO_3)_4SO_4$ $(OH)_4 \cdot 4H_2O$] (Morin et al. 2003; Egal et al. 2009). This offers new possibilities for the removal of As(III) from high-arsenic acid wastewaters.

Biomineralization of jarosite by a fungal isolate, *Purpureocillium lilacinum*, has been shown in the extreme acidic, highly metal-containing environments of Rio Tinto (Oggerin et al. 2013). Nucleation starts on the fungal cell wall, suggesting that extracellular polymeric substances (EPS) act as biomineral nucleation sites.

Sequestration of iron-containing sulfates is suggested to be a strategy for microbial survival and growth, thereby enabling metal resistance and tolerance.

Barite/Celestite

Biomineralization of **barite and celestite** is of special interest, since these organisms have evolved strategies to selectively accumulate Sr and Ba in the presence of up to five orders of magnitude excess calcium. This level of biological control is highly remarkable, taking into account the chemical similarity of Ca^{2+}, Mg^{2+}, Sr^{2+}, and Ba^{2+} ions. Nevertheless, the biological strategies for ion discrimination, uptake, transport, and accumulation are still an enigma to date. The main challenges for these studies remain the high biomineral solubility and the selective quantification of subcellular ion distributions (Krejci et al. 2011b). Answering these questions could be extremely useful for remediation of ^{90}Sr from the environment and nuclear waste.

Furthermore, barite and celestite biominerals quickly dissolve after cell death, because seawater is undersaturated with respect to Ba/Sr. Hence, although Ba/Sr-sequestering organisms belong to the most abundant plankton members, they are very rarely encountered as fossils. Nevertheless, celestite and barite biomineralizations are creating vertical and horizontal concentration gradients, and thereby strongly affect the oceanic cycling of strontium and barium. Barium and strontium depletion in seawater might affect calcification in many marine organisms and restrain the use of Sr/Ca or Ba/Ca ratios as proxies for paleoenvironmental reconstructions (Decelle et al. 2013).

Barite ($BaSO_4$) biominerals are commonly found in desmid and stonewort green algae.

Desmids are unicellular, ubiquitous freshwater green algae that can be easily cultivated and are therefore considered a model system to study Sr/Ba biomineralization. Most intracellular crystalline deposits in desmids are already visible using a light microscope (Brook et al. 1980, 1988; Meindl 1984; Wilcock et al. 1989). $BaSO_4$ crystals are either located in small terminal vacuoles at the tips of the cells, as in *Closterium moniliferum* (Wilcock et al. 1989), or distributed randomly in the cytosol, as in *Micrasterias denticulata* (Meindl 1984).

Barite and celestite have high densities, much higher than the densities of cell constituents or other common biominerals. This is why the specific gravities of barite and celestite facilitate gravitaxis. Surprisingly, in desmids, the $BaSO_4$ crystals appear not to be involved in a gravity-sensing mechanism, and their function remains unclear. But in a variety of other organisms, barite crystals are supposed to have a function in graviperception as so-called statoliths.

In the rhizoids (a kind of roots used for mechanical stabilization) of green algae of the order **Charales** (or "stoneworts") barite accumulations consisting of 7 nm-sized barite spheres were identified (Schröter et al. 1975; Sievers and Schmitz 1982). These particles seem to act as statolith in graviperception, guiding motion of the algae and growth of the rhizoids (Braun 2002).

The **ciliates** *Loxodes* and *Remanella* possess Müller vesicles located at its anterior dorsal margin. These vesicles contain a spherical inclusion, the so-called Müller body, which contains nanometer-sized barite (Hubert et al. 1975) and enables the organism with graviperception (Hemmersbach et al. 1998).

Barite has also been identified in different **microalgae**. Intracellular barite microcrystals occur in at least two planktonic flagellated species of the order Pavlovales (Fresnel et al. 1979; Gayral and Fresnel 1979) and the in the algae *Spirogyra* (Kreger 1957; Kreger and Boeré 1969). The function of these deposits is uncertain.

Bertram and Cowen report barite in the shell of some agglutinated **foraminifera** besides calcium carbonate (Bertram and Cowen 1998). Due to the undersaturation of seawater with respect to barite, the authors conclude a great biological control of barite chamber wall formation. Gooday and Nott describe micrometer-sized barite crystals in the two foraminifera species *Aschemonella ramuliformis* and *Galatheammina* sp. that are found in great depth (Gooday and Nott 1982). Whether these observations describe associated sedimentary barite or controlled barium biomineralization in foraminifera is not clear.

Recently, the marine bacterium *Myxococcus xanthus* has been shown to produce extracellular barite in vitro (González-Muñoz et al. 2003). The authors suggest that **bacterial barite precipitation** occurs on extracellular nucleation sites. Bacterially induced barite precipitation and its role in the oceanic barium cycle have remained largely unexplored.

The most prominent examples of **celestite** ($SrSO_4$) biomineralization can be found in the Rhizaria: The skeleton of Acantharia as well as the central capsules (vegetative stage) (Müller 1858) and membrane-bound vesicles (swarmer cells) of polycystine radiolarians (O. R. Anderson et al. 1990) are known to be built from celestite with a small fraction of barite ($Ba/Sr \sim 0.003$).

The crystalline inclusions in the polycystine radiolarian *Collosphaera huxleyi* were first described in 1858 by Müller (Müller 1858). Based on the crystal symmetry, he concluded that they were made of celestite. Later on, this observation was supported by Anderson and Hughes (Anderson 1981; Hughes et al. 1989) as well as Hallande and Martoja (Hollande and Martoja 1974). The function of the celestite crystals in polycystine radiolarians is still a matter of debate; they are discussed to help sinking and settling in greater depth during their reproductive cycle.

Acantharia are cosmopolitan, marine unicellular protists that are sister to the silica-secreting polycystine radiolarians. They are well known for their intricately shaped mineral endoskeletons comprised of celestite ($SrSO_4$). Despite their exceptional features, Acantharia biomineralization remains largely unexplored, cultivated isolates are missing, and at the moment, genomic information is unattainable.

Surprisingly, acantharians and polycystine radiolarians are not the only organisms that form this highly unusual biomineral. The endoskeleton of the dinoflagellate *Achradina pulchra* is also composed of celestite with traces of barite as revealed by X-ray microanalysis (Gómez et al. 2017). As in many other cases, the function of this biomineral is unclear.

Sulfides and Elemental Sulfur (Table 6)

Sedimentary sulfides are mainly produced by sulfate-reducing bacteria (SRB). Therefore, microorganisms are assumed to drive the formation of iron sulfides, in particular, **pyrite (FeS_2)**, one of the most common sulfide minerals in the geological record.

Unfortunately, the mechanisms of biogenic pyrite formation by **sulfate-reducing bacteria (SRB)** remain largely unexplored. One of the main reasons for that is probably the difficulty to achieve pyrite formation in microbial cultures. However, there are some indications for its microbial origin: Sedimentary sulfides are generally enriched in light sulfur isotopes (Thode et al. 1953) and have a characteristic morphology, the so-called framboidal pyrite (Rust 1935; Folk 2005). Pyrite “framboids” are raspberry-shaped aggregates (Ø 2–50 μm) composed of microcrystals (typically 0.5–2 μm) commonly found in reducing sediments (Folk 2005). Since the early observations, they seemed to be closely associated with organic matter, which has been demonstrated by means of scanning transmission X-ray microscopy (Maclean et al. 2008) and nano-SIMS (Wacey et al. 2015).

Several in vitro experiments were conducted trying to understand the role of SRB in pyrite formation. Formation of mackinawite (FeS) and greigite (Fe_3S_4), which are both believed to be potential pyrite precursor phases (Wilkin and Barnes 1997; Hunger and Benning 2007), is commonly observed in SRB cultures (Table 6). Pyrite formation in culture was reported only in a few instances (Hallberg 1965, 1972; Rickard 1969; Duverger et al. 2020; Berg et al. 2020). In a recent study, pyrite was shown to form very rapidly in cultures of a consortium of sulfur- and sulfate-reducing bacteria using Fe(III)-phosphate as substrate most likely enhanced polysulfides (Berg et al. 2020). Duverger et al. followed the formation of iron sulfides in *Desulfovibrio desulfuricans* using electron microscopy, X-ray diffraction, and synchrotron-based spectroscopy. The authors demonstrate a strong dependence of the biogenic sulfide composition on the iron source. These studies shed new light on understanding the mechanisms of biogenic pyrite formation, which are essential for the use of biogenic pyrite as paleoenvironmental proxy or as biosignature of early life.

It should be noted that **greigite (Fe_3S_4)**, the ferrimagnetic sulfur equivalent of magnetite, is not only formed as an intermediate in sulfate-reducing bacteria (SRB; see paragraph before) but also formed anaerobically by magnetotactic bacteria (MTB; see paragraph on oxides/hydroxide or other chapter of this book) (Pósfai

Table 6 Sulfide and sulfur biominerals in microorganisms

	Biomineral	Species	References
BACTERIA	Elemental sulfur (S^0)	Sulfur-oxidizing bacteria	Reviews: Kleinjan et al. (2003), Dahl and Prange (2006)
	Framboidal pyrite (FeS_2)	*Non-specified nanobacteria* and bacteria	Schopf et al. (1965), Wilkin and Barnes (1997), Schieber (2002a, b), Folk (2005)
Unclassified bacteria	Elemental sulfur (S^0)	*Thermothrix azorensis* sp.	Odintsova et al. (1996)
Proteobacteria			
Acidithiobacillia			
Acidithiobacillales	Elemental sulfur (S^0), polythionates	*Acidithiobacillus ferrooxidans* = *Thiobacillus ferrooxidans*	Steudel et al. (1987), Prange et al. (2002)
Alphaproteobacteria			
Rhodospirillales	Elemental sulfur (S^0)	*Magnetospirillum*	Kawaguchi et al. (1992), Spring and Bazylinski (2006)
Betaproteobacteria			
Burkholderiales	Elemental sulfur (S^0)	*Spirillum serpens* *Sphaerotilus natans*	Maier and Murray (1965)
		Macromonas	La Rivière and Schmidt (1992)
Deltaproteobacteria			
Desulfovibrionales (SRB = Bacteria and Archaea)	Pyrite and marcasite (FeS_2), greigite (Fe_3S_4), FeS (mackinawite, tetragonal), pyrrhotite ($Fe_{1-x}S$)	*Desulfovibrio desulfuricans*	Rickard (1969)
	Greigite (Fe_3S_4), pyrite (FeS_2) and intermediates (FeS), sphalerite (ZnS), elemental sulfur, gypsum ($CaSO_4 \cdot 2H_2O$), struvite ($NH_4MgPO_4 \cdot 6H_2O$), magnesite ($MgCO_3$)		Hallberg (1972)

	Mackinawite (FeS), vivianite/metavivianite ($Fe_3(PO_4)_2·8H_2O$)		Ivarson and Hallberg (1976)
	Mackinawite (FeS), pyrite (FeS_2), vivianite ($Fe_3(PO_4)_2·8H_2O$), and greigite (Fe_3S_4)		Duverger et al. (2020)
	Pyrrhotite ($Fe_{1-x}S$)		Neal et al. (2001)
	Galena (PbS)		Leleu and Goni (1974)
	Mackinawite (FeS)		Stanley and Southam (2018)
	Vivianite ($Fe_3(PO_4)_2.8H_2O$), greigite (Fe_3S_4), pyrite (FeS_2)	*Desulfovibrio* and *Sulfurospirillum*	Berg et al. (2020)
	Pyrite (FeS_2) and gel-like phase [supposably hydrotroilite ($FeS·nH_2O$)]	*Desulfovibrio*	Hallberg (1965)
	Wurtzite (ZnS)	*Desulfovibrio*	Leleu et al. (1975)
	Mixture of sphalerite (ZnS) and mackinawite (FeS)	*Desulfovibrio vulgaris*	Williams et al. (2005)
	Mackinawite (FeS), greigite (Fe_3S_4), and vivianite [$Fe_3(PO_4)_2·8H_2O$]		Zhou et al. (2014)
	Mackinawite (FeS) and greigite (Fe_3S_4)	*Desulfovibrio hydrothermalis*	Picard et al. (2018)
	Mackinawite (FeS)	*Desulfovibrio capillatus*	Ikogou et al. (2017)
	Sphalerite (ZnS) and heazlewoodite (Ni_3S_2) or vaesite (NiS)	*Non-specified SRB*	Gramp et al. (2007)
	Covellite (CuS)		Gramp et al. (2006)
	Schwertmannite [$Fe_8O_8\ (OH)_6SO_4$], jarosite [$KFe^{3+}{}_3\ (SO_4)_2(OH)_6$], and greigite ($Fe_3S_4$)		Gramp et al. (2009)
	Mackinawite (FeS) and greigite (Fe_3S_4)		Gramp et al. (2010)
	Mackinawite (FeS)		Herbert et al. (1998)
	Pyrite (FeS_2)	Mainly *Desulfotomaculum*	Donald and Southam (1999)
	Greigite (Fe_3S_4)	Group *Desulfosarcina/Desulfococcus*	Reitner et al. (2005)
Magnetotactic bacteria	Sphalerite-like FeS, mackinawite (FeS), and greigite (Fe_3S_4)	*Non-specified MTB*	Pósfai et al. (1998)

(continued)

Table 6 (continued)

	Biomineral	Species	References
	Pyrrhotite ($Fe_{1\text{-}x}S$)		Farina et al. (1990)
	Pyrite (FeS_2) and greigite (Fe_3S_4)		Mann et al. (1990)
	Greigite (Fe_3S_4)		Heywood et al. (1990)
	Magnetite (Fe_3O_4), pyrite (FeS_2), and greigite (Fe_3S_4)		Bazylinski (1996)
Epsilonproteobacteria			
Campylobacterales			
Helicobacteraceae	Elemental sulfur (S^0)	*Thiovulum*	La Rivière and Schmidt (1992); Lane et al. (1992), Gros (2017)
Gammaproteobacteria	Greigite (Fe_3S_4)	High similarity to *Thiomicrospira* sp. and *Stenotrophomonas maltophilia*	Simmons et al. (2004)
Thiotrichales	Elemental sulfur (S^0)	*Achromatium*	La Rivière and Schmidt (1992), Head et al. (1996, 2000a), Gray et al. (1999, 2004), Gray and Head (2014), Salman et al. (2015)
		Beggiatoa alba	Strohl et al. (1981)
	Elemental sulfur (S^0), cyclooctasulfur	*Beggiatoa alba* and *Thiomargarita namibiensis*	Pasteris et al. (2001), Prange et al. (2002)
	Elemental sulfur (S^0)	*Beggiatoa*	Winogradsky (1887), Teske and Nelson (2006)
		Thiobacterium and Thiospira	La Rivière and Schmidt (1992)
		Thiomargarita	Schulz et al. (1999), Prange et al. (2002)
		Thiomicrospira crunogena	Javor et al. (1990)
		Thioploca	Teske et al. (1995), Otte et al. (1999)
		Thioploca and *Beggiatoa*	Maier and Murray (1965), Larkin and Strohl (1983), Pasteris et al. (2001)
		Thiothrix	Larkin and Strohl (1983), Howarth et al. (1999)

Chromatiales	Elemental sulfur (S^0)	*Chromatium vinosum*	Pattaragulwanit et al. (1998)
		Chromatium vinosum, *Thiocapsa roseopersicina*	Brune (1995)
		Thioalkalivibrio	Sorokin et al. (2001)
Chromatiaceae (purple sulfur bacteria)		*Chromatium*, *Amoebobacter*, *Lamprobacter*, *Lamprocystis*, *Thiocapsa*, *Thiocystis*, *Thiodictyon*, *Thiopedia*, *Thiospirillum*	Pfennig and Trüper (1992)
Chromatiaceae and Ectothiorhodospiraceae	Elemental sulfur (S^0), sulfur chains	*Thiocapsa roseopersicina*, *Chromatium vinosum*, *Marichromatium purpuratum*, *Allochromatium vinosum*, *Halorhodospira halophila*, *H. abdelmalekii*	Prange et al. (2002)
Enterobacterales	Elemental sulfur (S^0)	*Escherichia coli*, *Aerobacter*	Maier and Murray (1965)
Terrabacteria			
Actinobacteria	Maghemite (γ-Fe_2O_3) and greigite (Fe_3S_4)	*Actinobacter* sp.	Bharde et al. (2008)
Firmicutes			
Clostridia			
Clostridiales	FeS unspecified, with NiS	*Desulfotomaculum* sp.	Fortin et al. (1994)
	Mackinawite (FeS)	*Desulfosporosinus orientis*	Stanley and Southam (2018)
FCB group			
Bacteroidetes/Chlorobi			
Chlorobi (green sulfur bacteria)	Elemental sulfur (S^0), sulfur chains	*Chorobium vibrioforme*	Prange et al. (2002)
	Elemental sulfur (S^0)	*Chlorobaculum tepidum*	Marnocha et al. (2016, 2019)

(continued)

Table 6 (continued)

	Biomineral	Species	References
ARCHAEA			
TACK group			
Crenarchaeota			
Thermoprotei			
Sulfolobales			
Desulfurococcales	Elemental sulfur (S^0)	*Acidianus*, *Sulfolobus*, *Pyrodictium*, *Pyrococcus*, and *Thermococcus*	Kletzin et al. (2004)
Euryarchaeota			
Stenosarchaea			
Methanomicrobia	Elemental sulfur (S^0)	Methanotrophic archaea (ANME-2)	Milucka et al. (2012)
EUKARYA			
Viridiplantae			
Chlorophyta			
Core chlorophytes			
Chlorophyceae			
Sphaeropleales	Elemental sulfur (S^0)	*Chlorella fusca* = *Scenedesmus fusca*	Krauss et al. (1984)

et al. 1998), several types of rod-shaped *Gammaproteobacteria* living in sulfidic environments (Simmons et al. 2004), and *Actinobacteria* (Bharde et al. 2008).

Sulfur globules are formed as a metabolic oxidation product of reduced sulfur compounds, such as sulfide, polysulfides, thiosulfate, or polythionates, in diverse groups of prokaryotes.

Sulfur globules are stored within two large groups of **sulfur bacteria**, autotrophic and chemotrophic (“colorless”) sulfur-oxidizing bacteria, and some thermophilic *Archaea* (Kletzin et al. 2004). Groundbreaking work on the description of chemotrophic sulfur bacteria *Beggiatoa* and their sulfur globules was published by Winogradsky in the late nineteeth century (Winogradsky 1887). Most chemotrophic sulfur oxidizers, such as *Achromatium* and *Beggiatoa*, belong to the order *Thiotrichales* (see **Table 6**), Gram-negative sulfur bacteria. Autotrophic sulfur oxidizers are mainly found within the purple (*Chromatiaceae* and *Ectothiorhodospiraceae*) (Pfennig and Trüper 1992; Brune 1995; Pattaragulwanit et al. 1998; Sorokin et al. 2001; Prange et al. 2002) and green (*Chlorobi)* sulfur bacteria (Prange et al. 2002; Marnocha et al. 2016, 2019), heliobacteria (*Helicobacteraceae*), and some species of cyanobacteria (Brune 1995). Chemotrophic bacteria use the energy derived from the oxidation of sulfur compounds to fix carbon dioxide, whereas autotrophic bacteria use reduced sulfur compounds as electron donors for photosynthesis (Kleinjan et al. 2003). Some other bacteria, including *Escherichia coli* (Maier and Murray 1965), produce sulfur as part of detoxification from sulfide.

The site of sulfur deposition varies in both groups, i.e., sulfur globules are deposited either intracellularly or extracellularly. Sulfur globule formation is still not fully understood, and a general mechanism for the formation and degradation of sulfur deposits is lacking. In most cases, the chemical nature of the deposited sulfur has also not been resolved yet. Typically, polymeric, water-insoluble sulfur is accumulated as a transient or final metabolic product depending on the organism, the culture conditions, and the sulfur substrate. Transient sulfur deposits have been suggested to act as energy reservoirs (Vetter 1985).

Recently, the speciation of sulfur in the sulfur globules of different groups of sulfur-oxidizing bacteria could be resolved using in situ XANES. The following sulfur species could be identified: In anaerobically grown, phototrophic sulfur bacteria, cyclooctasulfur was present, whereas in aerobically grown bacteria cultures, organic polysulfanes and polythionates dominate (Prange et al. 2002).

Most of today’s sulfur deposits are considered biogenic, emphasizing the fundamental role of sulfur bacteria in the biogeochemical sulfur cycle (Dahl 2020).

6 Oxalates and Other Organic Crystals

Probably the most common organic crystals found in nature are oxalate biominerals. Among living organisms, they are widely distributed throughout the three kingdoms of fungi, plantae, and animalia. Out of these, plants and fungi (and lichens) are the major generators of both natural oxalic acid and oxalate biominerals.

Calcium oxalate is by far the most abundant oxalate biomineral, and is commonly found in rocks and soil. Among microorganisms, fungi are the main oxalate biomineral contributors (**Table 7**). Calcium oxalates are widely distributed among fungal classes and appear mostly extracellularly, in close association with the surface of the fungal hyphae. In fungi, the possibility of intracellular oxalate formation is still a matter of debate (Arnott 1995). Fungal calcium oxalate is commonly found in its monohydrate form **whewellite** ($CaC_2O_4 \cdot H_2O$) and its dihydrate form **weddellite** ($CaC_2O_4 \cdot 2H_2O$). Similar to plants, oxalate crystal morphologies in fungi are highly diverse, ranging from needlelike to rhombohedral.

Calcium oxalates have also been found in a great number of **lichens** (Wadsten and Moberg 1985), a complex symbiotic association of a fungal mycobiont (usually an ascomycete) with one or more photosynthetic partners, the photobiont (e.g., green algae or cyanobacteria). These organisms combine to a heterogeneous structure forming the main body of the lichen, the thallus. Oxalate biominerals are commonly found in association with the lichen thallus outside of the protoplasm (Arnott 1995; Burford et al. 2003). In foliose lichens, weddellite crystals are located in proximity to the photobiont layer. It could be possible that the crystal water entrapped in the calcium oxalate crystals is used to maintain photosynthetic photobiont activity during dry periods (Clark et al. 2001).

Calcium oxalates are commonly associated with fungi and lichens in their natural environments, e.g., on mineral substrates and in the rock-lichen interface (Baran and Monje 2010), on plant leaves (Clark et al. 2001), and in soils and leaf litter (Graustein et al. 1977; Dutton and Evans 1996). Fungi and lichens are essential constituents of epi- and endolithic microbial communities and often play an important part in the **rock weathering process**. They contribute to the dissolution of rocks through the excretion of H+ and other organic acids, or through participation in redox reactions with mineral constituents (e.g., Mn or Fe) (Burford et al. 2003; Fomina et al. 2006). Oxalic acid is produced in large quantities by all classes of fungi. In solution, oxalate ions rapidly form complexes with cations. Many of the resulting oxalate salts, especially those of divalent cations, have a very low solubility and precipitate (Baran and Monje 2010). The incorporation of heavy metal ions into oxalates in fungi and lichen is considered a detoxification process and probably contributes to fungal metal tolerance (Gadd 1993).

As a strong leaching agent, oxalic acid contributes significantly to the many metal and mineral transformations mediated by fungi, including the formation of oxalate minerals. For example, the oxalic acid-producing *Aspergillus niger* is able to precipitate calcium oxalate when cultured on calcium carbonate (Sayer and Gadd 1997) or gypsum (Gharieb et al. 1998) by dissolution of the substrate. In ectomycorrhiza, a symbiotic association of fungi with the feeder roots of higher plants, essential plant nutrients are mobilized directly from insoluble mineral sources through excretion of oxalic acid. For instance, apatite dissolution by oxalic acid is linked to phosphorus acquisition and calcium oxalate sequestration (Wallander 2000; Smits et al. 2012; Schmalenberger et al. 2015).

Fungi and lichen also play an important role in mineral formation through the precipitation of various **secondary minerals**, such as calcite (Verrecchia 2000). In

Table 7 Oxalate crystals in microorganisms

	Biomineral	Species	References
EUKARYA			
Fungi			**Reviews:** (Arnott (1995), Khan (1995), Dutton and Evans (1996), Gadd (1999), Verrecchia (2000), Baran and Monje (2010), Gadd et al. (2014)
Dikarya			
Ascomycota			
Saccharomyceta			
Pezizomycotina			
Ieotiomyceta			
Dothideomyceta	Weddellite ($CaC_2O_4{\cdot}2H_2O$)	*Dirina massiliensis*	Edwards et al. (1997)
	Whewellite ($CaC_2O_4{\cdot}H_2O$) and weddellite ($CaC_2O_4{\cdot}2H_2O$)		Edwards et al. (1992)
	Whewellite ($CaC_2O_4{\cdot}H_2O$)		Edwards et al. (1991)
Eurotiomycetes	Unspecified Ca-oxalate	*Penicillium oxalicum*	Jarvis et al. (1990)
	Lead oxalate [$Pb(C_2O_4)$] and Ca-oxalate (unspecified)	*Aspergillus niger*	Sayer et al. (1999;), Li et al. (2016b)
	Metal oxalates (Zn, Co, Mn, Cu Cd)		Sayer and Gadd (1997)
	Unspecified Ca-oxalate		Gharieb et al. (1998); Li et al. (2019)
Sordariomyceta	Mix of calcite ($CaCO_3$) and whewellite ($CaC_2O_4{\cdot}H_2O$)	*Cephalotrichum* sp.	Burford et al. (2006)
	Unspecified Ca-oxalate similar to trihydrate ($CaC_2O_4{\cdot}3H_2O$)	*Cryphonectria parasitica*	Englander and Corden (1971)
	Unspecified Ca-oxalate	*Leucostoma cincta*, *L. persoonii*	Traquair (1987)
	Weddellite ($CaC_2O_4{\cdot}2H_2O$)	*Dasyscyphus capitate/Incrucipulum capitatum*	Horner et al. (1983)
Lecanoromycetes	Glushinskite [$Mg(C_2O_4){\cdot}2H_2O$]	*Lecanora atra*	Wilson et al. (1980)
	Moolooite (hydrated copper oxalate, $CuC_20_4.nH_20$, n ~ 0.1)	*Acarospora rugulosa* and *Lecidea theiodes*	Purvis (1984)

(continued)

Table 7 (continued)

	Biomineral	Species	References
	Moolooite (hydrated copper oxalate, $CuC_20_4.nH_20$, n ~ 0.4–0.7)	4 different lichen species	Chisholm et al. (1987)
	Whewellite ($CaC_2O_4{\cdot}H_2O$) and Weddellite ($CaC_2O_4{\cdot}2H_2O$)	*Pertusaria coralline*	Jones et al. (1980)
	Lindbergite ($MnC_2O_4.2H_2O$)		Wilson and Jones (1984)
	Weddellite ($CaC_2O_4{\cdot}2H_2O$) and whewellite ($CaC_2O_4{\cdot}H_2O$)	15 different lichen species	Wadsten and Moberg (1985)
	Whewellite ($CaC_2O_4{\cdot}H_2O$)	*Parmelia chlorochroa*	Erdman et al. (1977)
		Calenia triseptata, *Tricaria carnea*, *Echinoplaca strigulacea*	de Oliveira et al. (2002)
		Circinaria gyrosa	Böttger et al. (2014)
	Weddellite ($CaC_2O_4{\cdot}2H_2O$)	*Xanthoparmelia chlorochroa*, *X. cumberlandia*, *Rhizoplaca melanophthalma*, *R. chrysoleuca*, *R. haydenii*, and *R. marginalis*	Clark et al. (2001)
	Whewellite ($CaC_2O_4{\cdot}H_2O$) and anhydrous iron (III) oxalate [$Fe_2(C_2O_4)_3$]	*Caloplaca callopsima* and *Diploschistes ocellatus*	Ascaso et al. (1982)
	Weddellite ($CaC_2O_4{\cdot}2H_2O$), whewellite ($CaC_2O_4{\cdot}H_2O$), $ZnC_2O_4{\cdot}2H_2O$, anhydrous lead oxalate (PbC_2O_4)	*Diploschistes muscorum*	Sarret et al. (1998)
	Whewellite ($CaC_2O_4{\cdot}H_2O$)	*Xanthoria parietina*	
Basidiomycota			
Agaricomycotina			
Agaricomycetes			
Phallomycetidae	Whewellite ($CaC_2O_4{\cdot}H_2O$) and weddellite ($CaC_2O_4{\cdot}2H_2O$)	*Hysterangium crissum*	Graustein et al. (1977)

Agaricomycetidae			
Atheliales	Whewellite ($CaC_2O_4 \cdot H_2O$)	*Piloderma fallax*	Tuason and Arocena (2009)
Boletales	Mix of calcite ($CaCO_3$) and whewellite ($CaC_2O_4 \cdot H_2O$)	*Serpula himantioides*	Burford et al. (2006)
	Unspecified Ca-oxalate	*Serpula himantioides*	Gharieb et al. (1998)
	Whewellite ($CaC_2O_4 \cdot H_2O$)	*Paxillus involutus*	Schmalenberger et al. (2015)
Agaricomycetes inc. sedis			
Polyporales	Ca-oxalate and Cu-oxalate	*Poria placenta* and *Poria vaillantii*	Sutter et al. (1983, 1984)
Fungi incertae sedis			
Mucoromycota			
Mucoromycotina	Weddellite ($CaC_2O_4 \cdot 2H_2O$)	*Mucor mucedo*	Urbanus et al. (1978)
		Mucor plumbens, *Cunninghamella echinulata*	Jones et al. (1976)
	Unspecified Ca-oxalate	*Mucor heimalis*, *Rhizopus oryzae*	Powell and Arnott (1985)
		Gilbertella persicaria	Whitney and Arnott (1986)
	Weddellite ($CaC_2O_4 \cdot 2H_2O$), whewellite ($CaC_2O_4 \cdot H_2O$), and glushinskite [$Mg(C_2O_4) \cdot 2H_2O$]	Unspecified *Mucorales*	Kolo and Claeys (2005)

semiarid regions, fungi biomineralized with both calcite and calcium oxalates have been observed by Verrechia et al. (Verrecchia et al. 1990). It has been proposed that in these climates, calcium oxalate can decompose resulting in calcium carbonate deposits (Verrecchia 2000).

The interaction of oxalic acid secreted by the fungi and lichens with different substrates is believed to be their principal oxalate biomineralization route. For this reason, a variety of other **metal oxalate biominerals** has been identified **in association with rock weathering** by fungi and lichens.

The alkaline-earth oxalate **glushinskite** (magnesium oxalate dihydrate, Mg $(C_2O_4){\cdot}2H_2O$) has been found in the lichen thallus and at the lichen-rock interface of *Lecanora atra* (Wilson et al. 1980). It could be shown in vitro that glushinskite forms together with weddellite and whewellite oxalate biominerals when fungi of the order *Mucorales* interact with carbonate substrates and seawater (Kolo and Claeys 2005).

Early studies of the oxalic-, citric-, and formic acid-producing fungus *Aspergillus niger* showed the transformation of different insoluble inorganic metal compounds into insoluble metal (Cu, Cd, Co, Zn, and Mn) oxalates (Sayer and Gadd 1997). In a similar manner, biogenic **lead oxalate dihydrate** $[Pb(C_2O_4){\cdot}2H_2O]$ was formed by *Aspergillus niger* growing on insoluble lead minerals, such as pyromorphite $[Pb_5(PO_4)_3Cl]$ (Sayer et al. 1999) or fluorapatite $[Ca_5(PO_4)_3F]$ (Li et al. 2016b). These inorganic substrates were solubilized by the lichen's metabolic action, releasing Pb^{2+} ions that were immobilized as lead oxalate. The lichen hyperaccumulator *Diploschistes muscorum* forms extracellular **zinc oxalate dihydrate** $(ZnC_2O_4{\cdot}2H_2O)$ and **anhydrous lead oxalate** (PbC_2O_4) in Zn^{2+}- and Pb^{2+}-containing solutions (Sarret et al. 1998).

Lindbergite $(MnC_2O_4{\cdot}2H_2O)$ could be identified in the lichen *Pertusaria corallina* on manganese-rich ores (Wilson and Jones 1984).

Inclusions of **moolooite** (hydrated copper oxalate, $CuC_20_4{\cdot}nH_20$), a naturally occurring copper oxalate of vivid blue color, were recognized in different whewellite- or weddellite-sequestering lichens growing in extremely rich copper environments (Chisholm et al. 1987).

So far, **non-hydrated Fe(III) oxalate** has only been reported in the lichen *Caloplaca callopsima* in association with an iron-rich dolomite (Ascaso et al. 1982). So far, there is no evidence for Fe(II) oxalate dihydrate biominerals, known as humboldtine $(FeC_2O_4{\cdot}\ 2H_2O)$.

The accumulation and immobilization of metal ions from the environment through oxalate biomineralization by fungi and lichens offers a variety of potential applications in environmental biotechnology: in detoxification, metal and radionuclide leaching, biorecovery, and bioremediation, or as catalyst. Furthermore, metal oxalates have been suggested as biomarkers for the existence of primitive life forms in extreme or extraterrestrial environments (Frost et al. 2003; Böttger et al. 2014; Cheng et al. 2016).

Besides oxalate biominerals the only organic crystals found in microorganisms are microcrystals of the **purine bases guanine** and **uric acid** (see **Table 8**). Recently, they have been identified in various phytoplankton, such as

Table 8 Organic crystals in microorganisms

	Biomineral	Species	References
EUKARYA			
SAR			
Alveolata			
Colpodellida		*Chromera velia*	Mojzeš et al. (2020)
Dinophyceae	Anhydrous β-guanine	*Gonyaulax polyedra*	DeSa et al. (1963, 1968), Schmitter (1971)
		Gonyaulax, *Prorocentrum*, *Gymnodinium*, *Nocticula*, *Crypthecodinium*, *Gyrodinium*, *Ceratium*, *Glenodinium*	Pokorny and Gold (1973)
		C. operosum aff., *Leonella granifera*	Jantschke et al. (2020)
		Amphidinium carterae *Symbiodiniaceae*	Mojzeš et al. (2020)
		At least three other species including *Symbiodinium voratum*	(Jantschke, unpublished)
	Calcium oxalate	*Symbiodinium*	Doyle and Doyle (1940), Taylor (1968)
	Uric acid		Clode et al. (2009), Kopp et al. (2013)
Ciliophora	Guanine with hypoxanthine and traces of xanthine	*Paramecium tetraurelia*	Creutz et al. (2002)
	Hypoxanthine and guanine	*Parauronema acutum*	Soldo et al. (1978)
Stramenopiles			
Ochrophy			
Eustigmatophyceae			
Goniochloridales	Anhydrous guanine	*Trachydiscus minutus*	Moudříková et al. (2017)
Eustigmatales		*Microchloropsis gaditana*, *Vischeria* sp.	Mojzeš et al. (2020)
Vacuoliviride		*Vacuoliviride crystalliferum*	
Synurophyceae		*Synura petersenii*	

(continued)

Table 8 (continued)

	Biomineral	Species	References
Fungi			
Dikarya			
Ascomycota			
Saccharomyceta			
Saccharomycotina			
Saccharomycetales	Uric acid	*Candida utilis* and *Saccharomyces cerevisiae*	Svihla et al. (1963)
Viridiplantae			
Chlorophyta			
Core chlorophytes			
Chlorophyceae			
Chlamydomonadales	Anhydrous guanine	*Chlamydomonas reinhardtii* *Dunaliella acidophila* *Haematococcus pluvialis*	Mojzeš et al. (2020)
Sphaeropleales			
Scenedesmaceae		*Desmodesmus quadricauda*	(Moudříková et al. 2017)
Trebouxiophyceae			
Trebouxiales		*Lobosphaera incisa*	Mojzeš et al. (2020)
Streptophyta			
Klebsormidiophyceae	Uric acid	*Klebsormidium flaccidum*	Mojzeš et al. (2020)

dinoflagellates, green algae, and eustigmatophytes, as well as ciliates (Creutz et al. 2002; Moudříková et al. 2017; Jantschke et al. 2019; Mojzeš et al. 2020).

Crystalline deposits in **dinoflagellates** are very abundant and are well known from ultrastructural studies, where they are usually referred to as “crystal-like bodies” or “crystal-like particles.” Interestingly, these crystalline deposits were first believed to be composed of calcium oxalate (Doyle and Doyle 1940; Taylor 1968). Later on, they were reidentified as **uric acid** crystals using nano-SIMS, EELS, and GC-MS in *Symbiodinium* (Clode et al. 2009; Kopp et al. 2013). DeSa et al. were the first to identify the crystalline material in the dinoflagellate species *Gonyaulax polyedra* (DeSa et al. 1963, 1968) as **guanine**. Recently, deposits of intracellular anhydrous β-guanine were also found in the calcifying species *Leonella granifera* and *Calciodinellum operosum aff.* by means of in situ Raman microscopy and electron diffraction (Jantschke et al. 2019, 2020).

Interestingly, similar Raman data has been obtained from various other dinoflagellate species, including *Symbiodinium* (Mojzeš et al. 2020 and Jantschke, unpublished). Species of the genus *Symbiodinium* are of high ecological importance due to their endosymbiotic relationship with corals. At the moment, contradicting observations about the chemical nature of the crystals in *Symbiodinium* exist. The morphology of the uric acid crystals observed by Clode and Kopp (Clode et al. 2009; Kopp et al. 2013) shows a high resemblance to the guanine crystals observed (Jantschke et al. 2019, 2020). However, uric acid has a distinctively different Raman signature and could not be detected in *Symbiodinium* cells, only in the green freshwater algae *Klebsormidium flaccidum* (Mojzeš et al. 2020). Uric acid and guanine are both part of the cell’s purine metabolism, with uric acid being the end product of a series of enzymatic degradation reactions. Whether the organic crystals in *Symbiodinium* are indeed uric acid or guanine, or whether these nitrogen compounds are an expression of different nitrogen accumulation pathways, the status of the symbiotic relationship, and/or environmental conditions, needs to be reexamined.

It is important to note that intracellular guanine crystals were also identified in **other microalgae**, including the chlorophyte *Desmodesmus quadricauda* and the eustigmatophyte *Trachydiscus minutus* (Moudříková et al. 2017), and the ciliate *Paramecium tetraurelia* (Creutz et al. 2002). Therefore, the appearance of intracellular guanine crystals seems to be a trait not unique to dinoflagellates only. Very recently, Mojzes et al. demonstrated the widespread occurrence of guanine reserves among taxonomically distant microalgal species inhabiting different environments. The authors suggest an early evolutionary origin of guanine microcrystals as nitrogen storage and attribute them an important yet unattended role in nitrogen cycling that needs to be further elucidated (Mojzeš et al. 2020).

The **function** of organic crystals (uric acid/guanine) is a matter of discussion. The uric acid deposits in *Symbiodinium* are suggested to be a nitrogen assimilation and exchange product between cnidarian hosts and their dinoflagellate symbionts (Clode et al., 2009; Kopp et al., 2013). Alternatively, they could function as an eyespot and be responsible for the photoreceptive behavior of the cell (Yamashita et al. 2009). DeSa et al. suggested a functional role of guanine in bioluminescence (DeSa et al.

1963, 1968). However, the presence of guanine crystals in nonluminescent dinoflagellate species could not be explained by this idea (Pokorny and Gold, 1973; Schmitter, 1971). Since then, guanine deposits in dinoflagellates are believed to be a nitrogen accumulation product (Schmitter, 1971). Crystalline anhydrous guanine is very interesting because of its extremely high refractive index of 1.83 (W. J. Schmidt 1949). This is the reason why these crystals are very good reflectors and are known to be used by fish and other animals for light manipulation, to produce structural colors, and in vision to build mirrors that reflect light (Gur et al. 2017). It could well be that intracellular guanine crystals also influence light exploitation and photosynthetic performance as suggested by Jantschke et al. (Jantschke et al. 2019).

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