

Iron in Earth Surface Systems: A Major Player in Chemical and Biological Processes

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As an essential nutrient and energy source for the growth of microbial organisms, iron is metabolically cycled between reduced and oxidized chemical forms. The resulting flow of electrons is invariably tied to reactions with other redox-sensitive elements, including oxygen, carbon, nitrogen, and sulfur. Therefore, iron is intimately involved in the geochemistry, mineralogy, and petrology of modern aquatic systems and their associated sediments, particulates, and porewaters. In the geological past, iron played an even greater role in marine geochemistry, as evidenced by the vast deposits of Precambrian iron-rich sediments, the “banded iron formations.” These deposits are now being used as proxies for understanding the chemical composition of the ancient oceans and atmosphere.

KEYWORDS: iron geochemistry, bacterial redox cycling, banded iron formations, iron isotopes

INTRODUCTION

Iron is the most abundant element in the Earth overall and the fourth most abundant element in the crust. During the early evolution and differentiation of the Earth, most iron, along with nickel and sulfur, was incorporated into the core, but significant amounts remained in the crust, such that iron comprises approximately 5% by mass of the present-day crust. Iron can possess variable valence states, and the energy involved in the transformation from one valence state to another has been utilized widely in biological systems. As a result of iron's abundance and its close association with biological systems, the chemical transformations and mineralogical phases of iron have played a key role in Earth surface systems. In this introductory article we highlight these critical processes.

GEOCHEMISTRY AND MINERALOGY OF IRON

Iron (Fe) can exist in a range of oxidation states, from -2 to +6, but the most common oxidation states are Fe(II) (ferrous iron) and Fe(III) (ferric iron). Elemental Fe (with an oxidation state of zero) is rare at the Earth's surface as it is readily oxidized to Fe(III) (oxyhydr)oxides (the components of “rust”). This variability in oxidation state produces a wide range of geologically, environmentally, and economically important iron minerals (SEE TABLE 1 AND FIGURE 1). The redox transformation of Fe(II) to Fe(III), and vice versa, is of major importance to a number of biological and element-cycling processes. The reduction of Fe(III) to Fe(II) at low temperatures, in the absence of free sulfide, is widely

mediated by *dissimilatory iron-reducing bacteria* (see Glossary for this and other terms). These microbes anaerobically reduce Fe(III) in order to gain energy, but they do not utilize the resulting Fe(II); rather they expel it into the surrounding environment. The electrons used to reduce Fe(III) come from the oxidation of either H₂ or simple organic molecules, although the oxidation of more complex organic molecules has been documented. A wide range of bacteria can participate in this process, including *Geobacter* sp., *Shewanella* sp., some sulfate-reducing bacteria, and some archaea.

TABLE 1 COMMON IRON MINERALS PRESENT AT, OR NEAR, THE EARTH'S SURFACE (MODIFIED FROM CUNDY ET AL. 2008)

Mineral Class	Name	Formula
Native or metal form	Native iron	Fe
Oxides/oxyhydroxides	Ferrihydrite	Fe ³⁺ ₄₋₅ (OH,O) ₁₂
	Goethite	FeO(OH)
	Lepidocrocite	Fe ³⁺ O(OH)
	Hematite	Fe ₂ O ₃
	Maghemite	Fe _{2.67} O ₄
	Magnetite	Fe ₃ O ₄
	Green rusts	Fe ⁽²⁺³⁺⁾ hydroxysalts general formula: [Fe ²⁺ _(1-x) Fe ³⁺ _x (OH) ₂] ^{x+} . [(x/n)A ⁿ⁻ ·(m/n)H ₂ O] ^{x-} , where x is the ratio Fe ³⁺ /Fe _{tot}
Carbonates	Siderite	FeCO ₃
	Ankerite	Ca(Fe,Mg,Mn)(CO ₃) ₂
Sulfides	Pyrite	FeS ₂
	Marcasite	FeS ₂
	Pyrrhotite	Fe _{1-x} S
	Mackinawite	FeS
	Greigite	Fe ₃ S ₄
Phosphates	Vivianite	Fe ₃ (PO ₄) ₂ ·8H ₂ O
	Strengite	FePO ₄ ·2H ₂ O
Silicates	Berthierine	(Fe ²⁺ ,Fe ³⁺ ,Al) ₃ (Si,Al) ₂ O ₅ (OH) ₄
	Chamosite	(Fe ²⁺ ,Mg,Al,Fe ³⁺) ₆ (Si,Al) ₄ O ₁₀ (OH,O) ₈
	“Glauconite”*	KMg(FeAl)(SiO ₃) ₆ ·3H ₂ O
	Greenalite	(Fe ²⁺ ,Fe ³⁺) ₂₋₃ Si ₂ O ₅ (OH) ₄
	Odinite	(Fe ³⁺ ,Mg,Al,Fe ²⁺) _{2.5} (Si,Al) ₂ O ₅ (OH) ₄

* Glauconite is a series name rather than a mineral but is included here because of its common occurrence in many sedimentary rocks.

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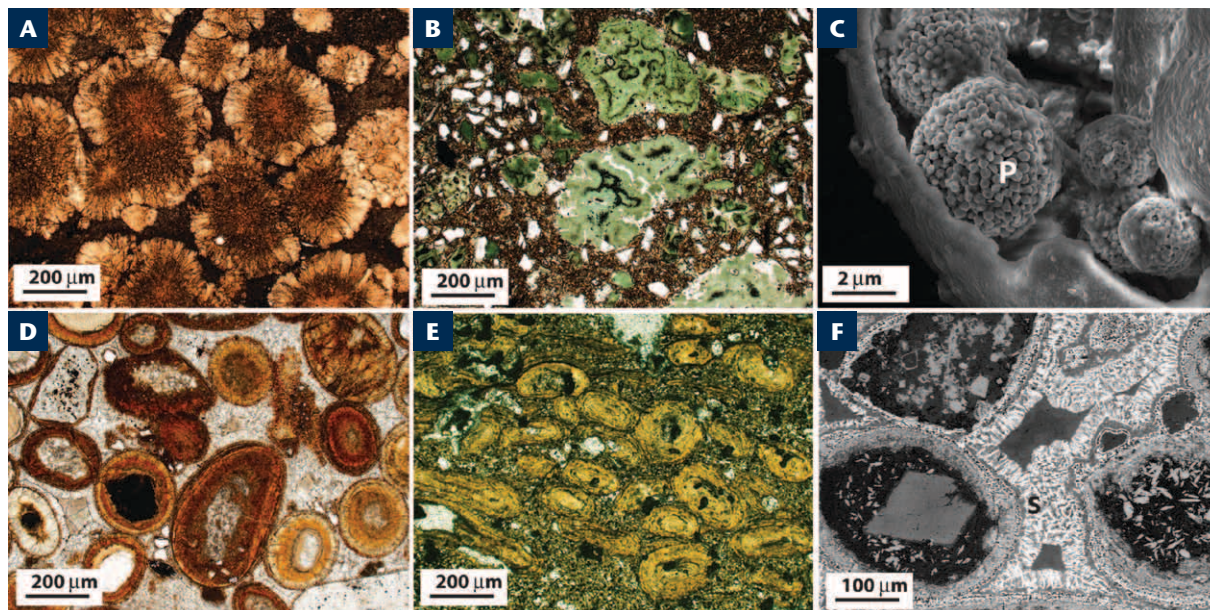


FIGURE 1 Images of iron minerals in sediments and sedimentary rocks. **(A)** Spherulitic siderite, showing microcrystalline cores and outer radiating crystals (non-marine Lower Cretaceous Wealden strata, southern England). **(B)** Glauconite pellets (green) in a glauconitic sandstone (Cretaceous Mardie Sandstone, Western Australia). **(C)** Pyrite framboids (P, spherical agglomerations of pyrite crystals) within a calcareous shell fragment (recent sediment, inner Great Barrier Shelf, eastern Australia). **(D)** Goethite ooids in an ooidal ironstone (Lower Jurassic, eastern England). **(E)** Berthierine ooids (yellow-green) set in a berthierine cement (green) in an ooidal ironstone (Lower Jurassic Frodingham Ironstone, eastern England). **(F)** Fringing siderite (S) of marine origin cementing ooids with hematite/goethite cortices (Upper Cretaceous, Book Cliffs, Utah, USA). The images in A, B, D, E are optical photomicrographs; C is a secondary electron image; and F is a backscattered electron image.

The reverse redox reaction, whereby Fe(II) is oxidized to Fe(III), is also a common process and is undertaken by *iron-oxidizing bacteria*. Iron oxidizers use the energy gained from Fe(II) oxidation for growth. Many iron-oxidizing bacteria live under low-pH conditions (the so-called *acidophiles*) because at circumneutral pH the abiotic oxidation of Fe(II) is so rapid that microbes cannot compete with the abiotic reaction. These bacteria are abundant at mine-waste sites, where their activity produces characteristic orange-brown ochre deposits [a mixture of iron (oxyhydr)oxide minerals] and low-pH effluent, known as acid mine drainage (SEE FIGURE 2). Other iron oxidizers live in low-oxygen conditions at near-neutral pH (the so-called *neutrophiles*) for similar kinetic reasons and are common in iron-rich hot springs and mineral seeps.

As well as being a key energy source for microbes, the redox cycling of iron is intimately linked to other elemental cycles, on both local and global scales (FIG. 3). The reduction of Fe(III) is often tied to the oxidation of sulfur (from sulfide to sulfate), which is an important process in marine sediments. Also, this process can lead to the precipitation of Fe(II)-containing minerals (e.g. phosphates, carbonates, silicates, sulfides) or mixed-valence minerals (e.g. magnetite), which are an important part of the rock record (Taylor and Macquaker 2011 this issue) and can act as long-term sinks for contaminant metals (see Morse and Luther 1999; Taylor et al. 2008). Recent advances have also shown the key role that iron (oxyhydr)oxide mineral nanoparticles (defined as <100 nm in size and formed by the oxidation of ferrous iron) play in aqueous and soil systems. Because of their high surface-sorption capacity (Waychunas et al. 2005; Hassellöv and von der Kammer 2008), they play a

major role in trace element mobility in aquatic systems; they can also be used to remove trace metals and contaminants from polluted waters, leading to important applications in environmental technology.

STABLE ISOTOPES OF IRON: FINGERPRINTS OF BIOGENIC AND ABIOTIC PROCESSES

Iron occurs in nature as a mixture of four stable isotopes: ^{54}Fe , ^{56}Fe , ^{57}Fe , and ^{58}Fe . These have overall abundances in the Solar System of 5.85%, 91.75%, 2.12%, and 0.28%, respectively. In the last decade, the technology has been developed to measure subtle variations in these isotopic abundances with a high degree of accuracy, and this has provided new insights into the geochemical cycling of iron. The isotopic compositions of iron are usually expressed in terms of the ratio of ^{56}Fe to ^{54}Fe in comparison to that found within igneous rocks (Johnson et al. 2008). This ratio is given the symbol $\delta^{56}\text{Fe}$, and the value is in per mil (‰). Although measured isotopic variations (fractionation) resulting from natural processes are smaller than those recorded for some lighter elements, such as carbon or sulfur, significant fractionation of iron isotopes has been observed arising from the microbial reduction of Fe(III) (up to -3‰). The presence of significantly lower (or “light”) $\delta^{56}\text{Fe}$ values in some iron minerals has, therefore, been ascribed to the involvement of microbes in the reduction of Fe(III) to Fe(II), with subsequent transport and incorporation of the ferrous iron into the secondary mineral phase (Johnson et al. 2008).

Significant advances in our understanding of global processes involving iron have been made through the application of $\delta^{56}\text{Fe}$ isotope analysis. For example, $\delta^{56}\text{Fe}$ analyses of iron (oxyhydr)oxides in marine sediments have revealed that a process termed the *benthic iron shuttle* is a major pathway by which iron is supplied back to the ocean water column (Severmann et al. 2008; Homoky et al. 2009). In this process, Fe(II) in the porewaters of shallow-shelf sediments, formed by bacterial Fe(III) reduction, is reoxidized during sediment resuspension events, and the resulting fine-grained iron (oxyhydr)oxides, with negative $\delta^{56}\text{Fe}$, are transported into deeper water. Another example is in the recognition of a fingerprint for identifying redox-stratified ocean basins in the rock record. This has been achieved by integrating $\delta^{56}\text{Fe}$ analysis of rocks with chemical analysis (Fe_{total}/Al ratios) (Severmann and Anbar 2009). The $\delta^{56}\text{Fe}$ analysis of Fe(II) minerals, coupled with $\delta^{13}\text{C}$ and

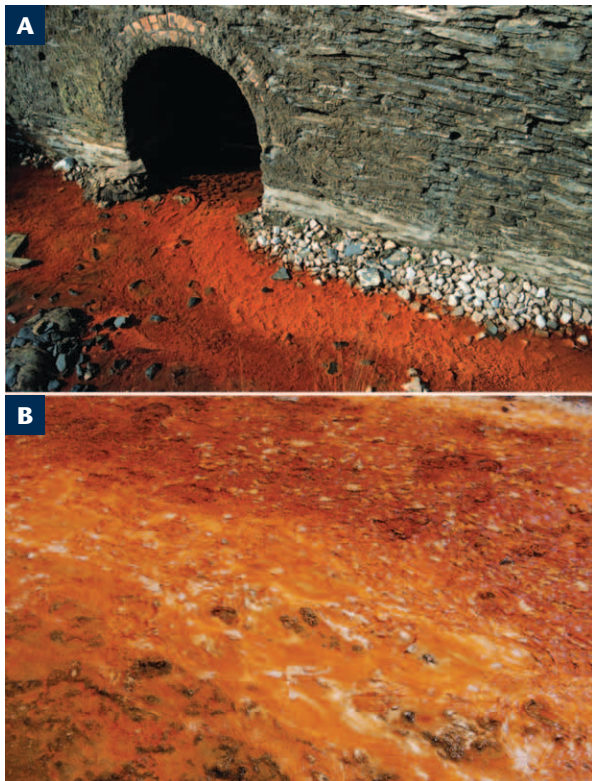


FIGURE 2 (A) Ochreous water draining from the disused Y Fan Pb-Zn mine near Llanidloes, Mid Wales. The water, with a pH of ~6, precipitates dominantly ferrihydrite with minor goethite. IMAGE COURTESY OF NICK PEARCE (B) Ochre precipitated from a stream impacted by acid mine drainage, northern England

$\delta^{18}\text{O}$ measurements, has also shed light on the origin of banded iron formations (BIFs) on the early Earth. The data indicate that ferrous iron minerals in BIF formed as a result of dissimilatory iron reduction of an initial ferric phase within the sediment during diagenesis (Heimann et al. 2010), although other interpretations, such as direct precipitation from seawater, have also been put forward (Rouxel et al. 2005).

IRON AS AN ESSENTIAL NUTRIENT: LINKS TO THE OCEAN-CLIMATE SYSTEM

The majority of iron enters the oceans via five processes: (1) deposition of wind-blown dust, (2) transport by rivers, (3) remobilization from shallow-shelf systems (the benthic shuttle), (4) hydrothermal emissions, and (5) glacial supply. Only hydrothermal emissions and solutes from rivers provide iron in dissolved form, and these sources are significantly less important than particulate forms of iron. For example, the global dissolved riverine load of iron is nearly three orders of magnitude less than the amount of particle-borne iron delivered from rivers, glaciers, and airborne dusts (Poulton and Raiswell 2002). Furthermore, some dissolved iron from rivers is lost to sediments, and so supply to the oceans from this source is even lower (Boyle et al. 1977). Particle-borne iron supplied to the oceans via rivers, glaciers, and dust is primarily in the form of clay minerals and iron (oxyhydr)oxides, and these are only sparingly soluble in seawater. This has led to questions about how the organisms that make use of iron in their metabolisms access the iron delivered to the oceans. Some iron is complexed by microbially produced organic compounds, termed *siderophores*, which preferentially bind Fe(III) and keep the iron in solution, thus preventing it from precipitating as a mineral phase. It has also been suggested that atmospheric processes can transform soil-derived iron (oxyhydr)oxides into more soluble species (Shi et al. 2009).

The relative contribution from rivers, dusts, and glacial inputs has been hard to quantify. Whilst river-derived iron may be the most significant source of supply to coastal waters, wind-driven inputs of land-derived particles are considered the most important source of iron to the open oceans (Moore and Braucher 2008) (Fig. 4). It has also been shown that glacially derived (Raiswell et al. 2006) and iceberg-borne (Raiswell et al. 2008) nanoparticulate iron (oxyhydr)oxides are more important than previously assumed. It is clear that we have a long way to go before we fully understand the budget of iron supply to the oceans.

Because iron is an essential and limiting nutrient for the growth of marine plankton (bacteria, algae) in surface ocean waters, it plays a major role in controlling the cycling of carbon. Such awareness has led to a reevaluation of the controls on marine plankton growth and the resulting uptake of CO_2 from the atmosphere, which has far-reaching implications for global climate. For example, increased Fe-containing dust deposition during glacial times increased productivity in the oceans and decreased atmospheric CO_2 concentrations—the so-called *iron hypothesis* (Martin 1990; Maher et al. 2010). It has been proposed that some biologically poor regions of the world's oceans could be “iron fertilized” and hence “geo-engineered” to increase carbon sequestration. Studies in the Southern Ocean (see Blain et al. 2007) have confirmed that long-term iron inputs into ocean water (in this case iron derived from deeper water rather than dust input) do indeed result in greater carbon sequestration. Recent assessments, however, suggest that such processes are unlikely to result in as large a sequestration of CO_2 as originally assumed (Lampitt et al. 2008).

IRON THROUGH EARTH HISTORY

Iron has played a pivotal role in the history of Earth's sedimentary rocks. For two billion years (3.8 to 1.8 billion years ago), vast quantities of iron-rich sediments were deposited on the seafloor in the form of banded iron formation (BIF). These rocks are comprised of iron-rich (~20–40% Fe) and silica-rich (~40–50% SiO_2) layers that are commonly banded on a wide range of scales, from layers meters in thickness to submillimeter-thick laminae that might represent seasonal events (Trendall and Blockley 1970). One of the interesting features of BIFs is that they precipitated

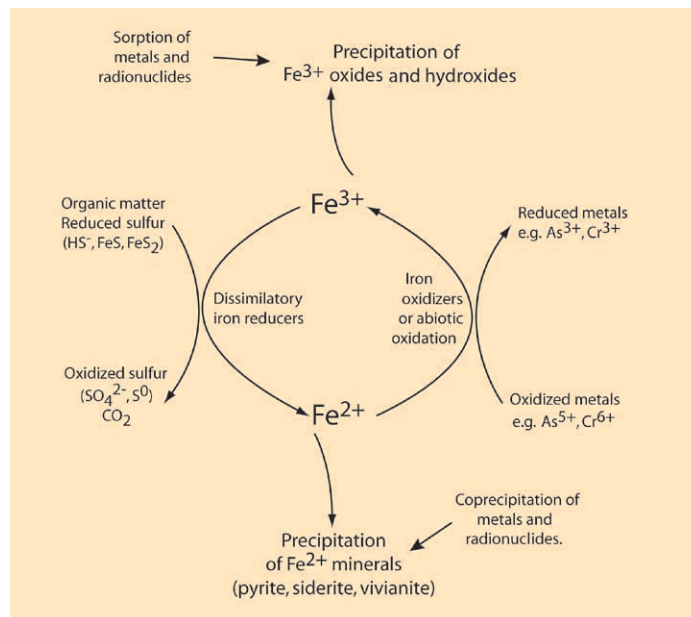


FIGURE 3 Interactions between the iron redox cycle and other elemental cycles

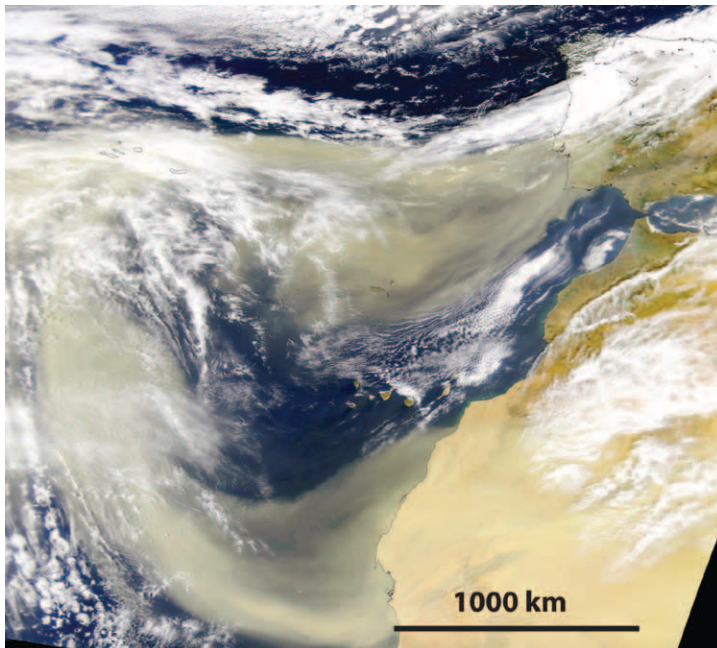


FIGURE 4 Wind-blown dust from the Sahara over the Atlantic Ocean. Such dust is believed to be an important supplier of iron to the North Atlantic Ocean and in turn is a major micronutrient for primary productivity. IMAGE COURTESY OF NASA

from an ocean water column that was dominantly anoxic; yet it is widely believed that the initial mineral phases were ferric (oxyhydr)oxides (Klein 2005). This implies that some oxidizing mechanism existed that transformed the ferrous iron-rich oceans into a ferric iron-rich sediment. At present, there are three hypotheses for the oxidation of Fe(II) to Fe(III): (1) ultraviolet photooxidation at the ocean surface, (2) reaction with oxygen produced by primitive cyanobacteria or their predecessors, and (3) anaerobic photosynthesis in which bacteria convert CO_2 into organic biomass using Fe(II) as their source of reducing power (Bekker et al. 2010).

The story of BIF is also a story in which the evolution of one geochemical cycle, that of oxygen, negatively impacted another, that of iron. As surface-ocean and atmospheric O_2 levels rose with time, ocean iron abundances fell, and eventually BIF disappeared from the rock record. However, it is not clear whether the demise of BIF was directly related to the reaction of seawater Fe(II) with O_2 (Holland 2006) or whether increased atmospheric oxygenation facilitated increased continental weathering of sulfide minerals, resulting in a greater supply of dissolved sulfate to the oceans. The newly available sulfate, in turn, allowed a group of bacteria known as the sulfate-reducing bacteria to generate dissolved sulfide in quantities sufficient to remove all the available iron from the oceans and eventually form pyrite, FeS_2 (Canfield 1998).

Interestingly, after an absence of nearly a billion years, BIFs reappeared around 750 Ma in association with global glaciations, the so-called *Snowball Earth* events. Hofmann and Schrag (2002) proposed that these BIFs were caused by a global freezing of the oceans, which led to water stagnation and a build-up of dissolved iron. Then, as the ice melted and ocean circulation became reestablished, the iron became oxidized and formed BIF in the oxic zone of upwelling areas. However, each of these iron formations is spatially and temporally linked with the extensive eruption of submarine mafic volcanic rocks, making it also possible that iron deposition was the result of iron inputs from these eruptions during that time (Bekker et al. 2010).

Throughout the Phanerozoic (from 545 million years ago to the present), the oceans have been predominantly oxygenated, and iron has been supplied to surface sediments in the ferric form. Under such conditions, the precipitation of ferrous iron minerals during sediment burial and diagenesis is driven either by bacterial reduction of ferric iron linked to organic matter oxidation or by reduction of ferric iron by free sulfide, itself a product of bacterial sulfate reduction. In rocks deposited throughout the Phanerozoic, diagenetic mineral assemblages involving iron are dominated by pyrite and iron-rich carbonates such as siderite (FeCO_3). The exceptions to these oxygenated ocean waters occur in localized basins where there was an absence of available oxygen (anoxic basins) or an absence of free oxygen coupled with the presence of free hydrogen sulfide (euxinic basins). Such basins may arise due to the input of high levels of organic matter derived from marine organisms. The decay of this organic matter consumes oxygen and leads to the formation of deep, stagnant waters. The Black Sea is a modern example of an euxinic basin. In addition, a number of periods of regional to possibly global oceanic anoxia have been postulated in the Phanerozoic (so-called *oceanic anoxic events*). These anoxic and euxinic conditions led to greater precipitation of pyrite. Certain mineralogical and geochemical techniques involving iron have been developed to recognize such conditions in the geological record (e.g. “degree of pyritization” and $\text{Fe}_{\text{total}}/\text{Al}$ ratios; see Lyons and Severmann 2006; Taylor and Macquaker 2011).

Although less spectacular than BIF formation, periods of iron-rich sediment deposition also took place during the Phanerozoic. These sedimentary units are generally in the form of oolitic ironstones, which were formed in shallow marine basins and are particularly common in Ordovician, Cretaceous, and Jurassic sequences. Their mineralogy is dominated by iron silicates (berthierine or chamosite; SEE TABLE 1 FOR MINERAL FORMULAE AND FIGURE 1) with distinctive oolitic textures. Their apparent lack of modern analogues led early researchers to postulate that they formed under unique conditions, linked either to climatic conditions that promoted intense tropical weathering on nearby landmasses or to large-scale volcanic exhalations. More recently, however, observations of mobile mudbelts in tropical settings associated with high levels of sediment transport and reworking (Aller and Blair 2006) have pointed to sedimentological and chemical conditions analogous to those that produced oolitic ironstones and resulted in similar mineralogical assemblages. It is likely, therefore, that conditions for widespread oolitic ironstone deposition during the Phanerozoic were linked to specific sea level conditions (either periods of lowest or highest sea level) and the presence of extensive, shallow-marine shelves rather than to climatic or volcanic episodes.

THIS ISSUE OF ELEMENTS

The articles that follow concern processes that intimately involve iron in aquatic systems and their associated sediments, particulates, and porewaters. They explore not only the modern expression of iron cycling but also the record left by past events in Earth’s history. Kurt Konhauser, Andreas Kappler and Eric Roden describe the role that iron plays in microbial metabolism and how iron redox cycling interacts with other element cycles (Konhauser et al. 2011). Alexis Templeton continues the theme of iron redox cycling by describing how these reactions underpin entire microbial communities in extreme environments that lack higher forms of life (Templeton 2011). Rob Raiswell highlights recent research that has shown the importance of nanoparticulate iron (oxyhydr)oxides for the transport of iron through the iron biogeochemical cycle (Raiswell 2011). Simon Poulton and Donald Canfield describe how

new analyses are revealing the important role of anoxic, iron-rich (ferruginous) oceans through Earth's history, and they highlight the need for research into the role such oceans played in the evolution of biogeochemical cycles (Poulton and Canfield 2011). Kevin Taylor and Joe Macquaker discuss the importance of iron in marine diagenesis and associated element cycling. In particular, they show how the relative amount and reactivity of iron in marine sediments lead to contrasting mineralogical records in rock successions (Taylor and Macquaker 2011). And last, Bruce Simonson reminds us of the importance of Precambrian iron formations as sources of iron (Simonson 2011).

CONCLUSIONS

It is clear that iron plays a key role in many processes, both biotic and abiotic, in Earth surface aquatic and sediment systems. The application of geochemical, mineralogical and isotopic analyses has shed significant light on both contemporary and ancient processes, providing important insights

into local and global element cycling, contaminant transfers and transformations, mineral–bacteria interactions and past oceanic conditions. The articles in this issue highlight the value, and necessity, of integrating these geochemical, mineralogical, petrographical and geomicrobiological techniques. Developments in both nanoscale analysis techniques and molecular geomicrobiology that are currently taking place will refine and extend our understanding of these processes. In particular, they may inform us on the extent to which micro- and nanoscale processes control iron and associated element cycling at the global scale, and they will help us retrieve from the rock record, using iron geochemistry and mineralogy as proxies, enhanced information on Earth's climate and evolution.

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GLOSSARY

Acidophiles – organisms that can withstand and often thrive in acidic environments (pH values ranging from 1 to 5). Acidophiles are found in a variety of acidic environments in surface systems, including sulfur and acid pools and geysers, and areas polluted by acid mine drainage.

Aerobic – pertaining to the presence of oxygen

Aerobic bacteria – bacteria that live and metabolize in the presence of free oxygen

Anaerobic – pertaining to the absence of oxygen

Anaerobic bacteria – bacteria that are able to live and metabolize in the absence of free oxygen

Archaea – a group of single-celled microorganisms (“prokaryotes”). They are distinct from bacteria in their evolutionary history. Archaea live in a wide array of environments, including many that are hostile to bacteria and eukaryotes.

Autotrophic bacteria – bacteria that can metabolize and produce carbohydrates, fats, and proteins from simple inorganic molecules (e.g. carbon dioxide) using energy from light (a process termed “photosynthesis”) or inorganic chemical reactions (a process termed “chemosynthesis”)

Bacterial sulfate reduction (BSR) – a process taking place during early diagenesis or within the water column in the absence of oxygen, by which bacteria (the so-called “sulfate-reducing bacteria”) reduce sulfate in seawater and liberate sulfide. This process is linked to the oxidation of organic carbon.

Banded iron (or ironstone) formation (BIF) – rock successions that contain thin layers of iron oxides (hematite or magnetite) alternating with layers of iron-poor chert (silica) and mudstone. These rocks are restricted to the Precambrian and are common throughout much of the rock record of the early Earth.

Chemolithoautotroph (or lithotroph) – an organism that uses an inorganic substrate (usually of mineral origin) to gain energy via aerobic or anaerobic respiration. All chemolithoautotrophs are microbes; no known macrofauna possess this ability.

Chemosynthesis – the biological conversion of simple carbon molecules (usually carbon dioxide or methane) and nutrients into organic matter using the oxidation of inorganic molecules (e.g. hydrogen gas, hydrogen sulfide) as a source of energy (in contrast with “photosynthesis,” where sunlight is used)

Diagenesis – a term describing chemical reactions and physical conditions that act upon a sediment following its deposition. As a general rule, the term “early diagenesis” is used to describe the changes that take place within a sediment during the uppermost few tens of meters of burial.

Dissimilatory iron reduction (DIR) – the process by which bacteria reduce Fe(III) to Fe(II). In this process, which is linked to the oxidation of organic carbon, the Fe(II) is not utilized by the bacteria but is expelled into the surrounding environment.

Eukarya – one of the three domains of cellular life (the other two being Archaea and Bacteria). The cells of eukaryotes contain a nucleus and other complex structures within a cell membrane. All plants, fungi, and higher animals are eukaryotes.

Euxinic – water column conditions in which dissolved oxygen is absent and dissolved sulfide is present

Extremophiles – organisms that can live under conditions of extreme heat (“thermophiles”), cold (“cryophiles”), acid (“acidophiles”), and salinity (“halophiles”)

Heterotrophic bacteria – bacteria that use preexisting organic carbon (e.g. dead plants and animals) for growth and the formation of carbohydrates, fats, and proteins

Hyperthermophile – an organism that thrives in extremely hot environments (above 60 °C). Hyperthermophiles are commonly archaea, although some bacteria are able to tolerate temperatures of around 100 °C.

Iron (oxyhydr)oxides – a general term that is used to cover the range, and often mixture, of iron oxide and hydroxide minerals present in natural systems

Microaerophiles – microaerophilic bacteria are bacteria that need oxygen to survive, but require environments containing lower levels of oxygen than are present in the atmosphere.

Nanoparticle – any mineral (or other) particle that is less than 100 nanometers in size. Due to their small size, nanoparticles have very high surface area to volume ratios, in comparison with much larger particles; therefore, they have a high capacity to adsorb trace elements and contaminants. Additionally, due to their large surface area and small size, they are often believed to display increased toxicity. Many iron minerals, especially iron (oxyhydr)oxides, can be present as nanoparticles.

Neutrophiles – organisms that thrive in low-oxygen, neutral-pH conditions

Oolitic (or ooidal) ironstone – a rock enriched in iron (greater than 15% by weight) containing ooids (concentric coated grains up to 2 mm in size) composed of the iron minerals berthierine, goethite, or hematite. Ooids composed of pyrite may also occur but are rare. This rock type is most common in the Phanerozoic.

Photoferrotrophs – organisms that can gain energy, and thereby metabolize, through the oxidation of Fe(II) to Fe(III). Such organisms may have been important in the formation of banded iron formations during the Precambrian by allowing the precipitation of Fe(III) minerals from oceans dominated by Fe(II).

Photosynthesis – a process that converts carbon dioxide into organic compounds using the energy from sunlight. Photosynthesis can occur in plants, algae, and many species of bacteria.

Phototrophs – organisms that carry out photosynthesis to acquire energy. They use the energy from sunlight to convert carbon dioxide and water into organic materials. Most phototrophs are autotrophs, also known as photoautotrophs.

Redox reaction – a chemical reaction in which one chemical element, or compound, is reduced and one is oxidized. Such reactions are commonly mediated by bacteria or archaea, which gain energy from the reactions.

Siderophores – compounds secreted by microorganisms, including bacteria and fungi, that bind to Fe(III). This keeps the Fe(III) in solution and is believed to be one mechanism by which Fe(III) can be utilized by plankton in seawater.

Thermophile – an organism that thrives at moderately high temperatures, between 45 and 60 °C. Many thermophiles are archaea, and it is believed that thermophiles represent some of the earliest life on Earth. Thermophiles are found in geothermally heated regions of the Earth, such as hot springs and deep-sea hydrothermal vents.