

# Geomicrobiology and Microbial Geochemistry

Gregory K. Druschel<sup>1</sup> and Andreas Kappler<sup>2</sup>

1811-5209/15/0011-0389\$2.50 DOI: 10.2113/gselements.11.6.389



To understand the biogeochemical cycles of elements and the evolution of life on Earth, one needs to appreciate the interplay between biology, chemistry, and geology.

**G** eomicrobiology and microbial geochemistry (GMG) investigates the interaction between Earth, environmental systems, and microbial life. Microbes shape their geochemical surroundings through their metabolic and growth needs and thereby exert significant geochemical and mineralogical control on their local environments. In turn, local geochemical conditions dictate what metabolic processes are possible. These mutual influences mean that microbial evolution has occurred in concert with changing geosphere conditions and that microbes have driven major shifts in ocean, continent and atmospheric chemistry. If one wishes to understand element cycling in any system containing water, one must realize that microbes are critical to the story.

**KEYWORDS:** geomicrobiology, geochemistry, genetics, redox, biomineralization, evolution

## DEVELOPMENT OF GEOMICROBIOLOGY AND MICROBIAL GEOCHEMISTRY

The rapidly developing field of geomicrobiology and microbial geochemistry (GMG) is a subset of the broader disciplines of geobiology and biogeochemistry. GMG overlaps with biology (by studying microbes) but is specifically focused on combining chemical, biological, and geological perspectives together to characterize the role of microbes in environmental and geological processes. Geobiochemistry turns this perspective 180°, it establishes the role that geology plays in the development of organismal biochemical processes (Shock and Boyd 2015 this issue). Combined approaches that utilize methods to investigate microbial activity (physiology, genetics, culturing, microscopy) and geochemical processes (aqueous, mineral, isotope geochemistry) have been developed to address the important, and sometimes very complex, interactions between microbes and their (geological) surroundings.

The GMG field owes much to the early work of environmental microbiologists and geochemists. Environmental microbiology has a long history, arguably beginning with the invention and application of the microscope by Leeuwenhoek in the 17<sup>th</sup> century. However, the link between microorganisms and Earth processes was not fully recognized until Russian microbiologist Sergei Nicholaevitch Winogradsky (1856–1953) formulated the concepts of chemolithotrophy and autotrophy after investigating elemental sulfur

transformations by *Beggiatoa spp.* (1887; as reviewed by Dworkin 2012). Russian microbiologist Vladimir Vernadsky (1863–1945) illustrated the temporal dimension of the interaction between life and Earth by arguing that the biosphere has shaped Earth's surface environment throughout geological time (Vernadsky 1926). The Dutch biologist Lourens G. M. Baas Becking (1895–1963) came up with the notion that “everything is everywhere but the environment selects,” a novel concept in biology in which a community of organisms is determined by their physicochemical surroundings (see de Wit and Bouvier 2006).

Baas Becking also coined the term “geobiology” in an effort to describe the relationships between organisms and the Earth (Quispel 1998).

One of the first to bring together microbiology and geochemistry was Henry Ehrlich (now Professor Emeritus at Rensselaer Polytechnic Institute, New York, USA): his academic training as a microbiologist found a serendipitous union with geology when a colleague piqued his interest in pyrite oxidation caused by bacteria (Ehrlich 2012). His long career has furthered our understanding of the role of microorganisms in a number of element cycles. Other geochemists also blazed the trail towards linking key physical and chemical concepts to microbial processes. The work of American geologist Robert Berner (1935–2015) helped define fundamental concepts of carbon cycling through deep time and the associated formation of metal sulfides and carbonate minerals (both processes that involve microbial activity). Berner also focused discussion on how these small-scale processes might affect the global climate. Other geochemists who have contributed to understanding element cycling through microbial activity (using chemical speciation, energetics, isotope fractionation, kinetics) include Robert Garrels, Harold Helgeson, Samuel Epstein, and Stanley Miller.

Despite these deep historical roots, only in the last 15–20 years has GMG evolved into a robust discipline (Banfield and Nealson 1997). It is not a coincidence that the first generation of truly interdisciplinary scientists—trained at the intersection of microbiology, genetics, geochemistry, mineralogy, and computational approaches—have demonstrated the critical role that microbes play in processes ranging from the molecular to the global scale. From the history of the early Earth to the mobility of elements, new insights are shifting paradigms for how the community thinks about key problems in the field. For example,

1 Department of Earth Sciences, Indiana University Purdue University of Indianapolis  
723 W. Michigan St., Indianapolis, IN 46202, USA  
E-mail: gdrusche@iupui.edu

2 Center for Applied Geoscience (ZAG)  
Eberhard-Karls-University Tuebingen  
Sigwartstrasse 10, 72076 Tuebingen, Germany  
E-mail: andreas.kappler@uni-tuebingen.de

Earth's deep history is now understood to be completely interwoven with the evolution of microbes: the changes in iron and sulfur chemistry in ancient seas, the Great Oxidation Event of the Paleoproterozoic, and the cycling of carbon in surface and diagenetic processes (Canfield 2005; Johnston 2011; Lyons et al. 2014). In modern environments, the importance of microbes in the mobility of metals, radionuclides, and organic contaminants is now rigorously documented as a key component for predicting mobility and for mitigating contamination (Slater et al. 2008). Microbes are also critical for the many processes that affect water quality, agriculture, and climate. The importance of microbes in nitrogen cycling, for example, is key to understanding greenhouse gas levels; critical nutrients for crops; and contaminants that affect water quality, directly and indirectly, via harmful algal blooms in marine and freshwater systems (Falkowski et al. 2008; Taylor and Townsend 2010).

## HOW MANY MICROBES ARE THERE AND WHERE DO WE FIND THEM?

"Microbes" is the common term we apply to the bacterial and archaeal domains of life, and they possibly represent more than 50% of the biomass carbon on the planet. Microbes are almost always too small to be seen with the naked eye, commonly being about 1 micron in diameter, and usually shaped as spherical (cocci) or rod (bacilli) forms. As small entities in large numbers (densities of cells in marine settings are around  $10^6$  cells  $\text{mL}^{-1}$  on average but can reach  $10^{12}$  cells  $\text{mL}^{-1}$ ; Amaral-Zettler et al. 2010), microbes have a very large surface area. In total, there are  $\sim 10^{30}$  microbes on Earth, occupying almost every conceivable corner of the surface and subsurface where water, nutrients, and energy are found. This includes locations hostile to most other forms of life, such as deep within basalt fractures, within glaciers, in deep undersea thermal vents, in highly acidic (pH 0) waters with very high metal concentrations, and in the pores of rocks located in extremely dry deserts. In fact, it has proven difficult to find a place on Earth that contains even the smallest amount of liquid water and *no* microbial life.

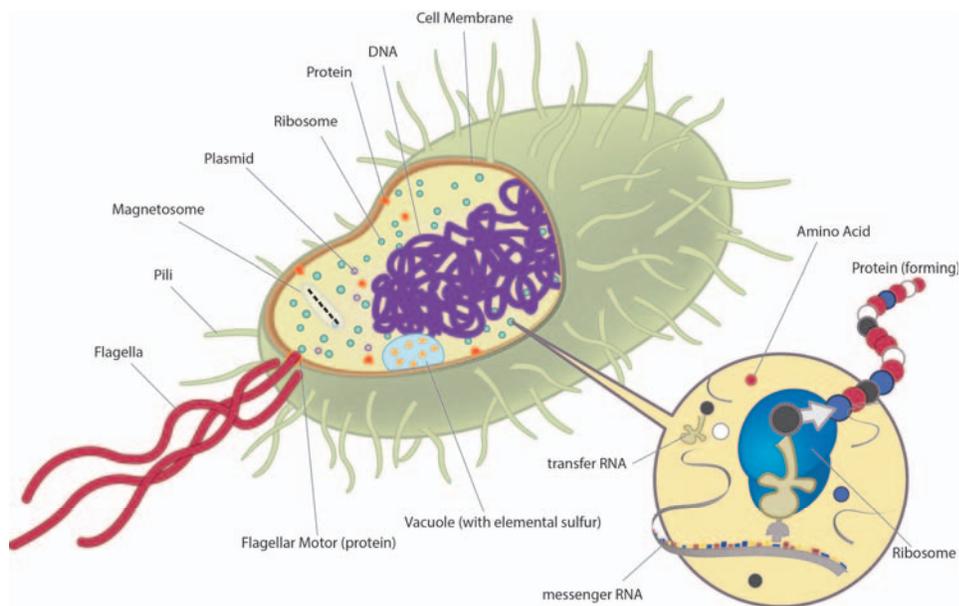
## WHAT ARE MICROBES MADE OF?

As with all living things, microbes have the ability to grow and replicate. Acquiring the elements necessary for this growth is an important part of how microbes interact with their geochemical surroundings. This includes harvesting the carbon, oxygen, nitrogen, phosphorus, and sulfur required for cellular materials and the metals (including iron, manganese, cobalt, nickel, zinc, and molybdenum) needed to form cofactors for specific enzymes and proteins. Microbial cells are mostly water (70–85%); the remaining biomass consists of a combination of four basic types of organic molecules (amino acids, nucleotides, fatty acids, and sugars), which combine to produce the key macromolecules in a microbe's cell (respectively: proteins, nucleic acids, lipids, and polysaccharides) (FIG. 1).

Metabolic function is centered on the production of specific proteins (enzymes), which are large molecules composed of amino acids that catalyze reactions and constitute more than 50% of the biomass per cell. Proteins are complexly structured chains of amino acids (peptides) that are constructed at ribosomes (FIG. 1 INSET). Enzymes are catalytic proteins that often have a metal (or metal-sulfide) center. They catalyze redox reactions in a "lock-and-key" manner, where the compounds that are part of the reaction are selectively brought to and from the reaction center, such that a specific enzyme only interacts with specific reactants. Deoxyribonucleic acid (DNA) contains the blueprint for protein construction and those instructions are carried to a ribosome (where proteins are produced) by a specific type of ribonucleic acid (RNA) called messenger RNA (mRNA). At the ribosome, amino acids are then assembled into proteins on another form of RNA called transcription RNA (tRNA) (FIG. 1 INSET). Microbial DNA, in general, contains the possible instructions for what a specific microbe is capable of (i.e. its metabolic potential), but the RNA or protein production are indicators of what the cell is actually doing at any one point (i.e. an indicator of its activity).

A specific microbe can be capable of multiple forms of metabolism and cellular function (as encoded on the DNA), but those forms may not necessarily be used, or expressed, at any one time. Specific sections of DNA (a gene) that encode for a specific cellular function can be turned on, or expressed, in response to environmental variables. In many cases, gene expression is correlated to the number of cells present and is regulated by cell-cell communication via the secretion of signaling molecules (called quorum sensing).

All microbial cells include an envelope of lipids called the cell membrane, which separates the inside from the outside of the cell (FIG. 1). Many microbial functions, including the generation of adenosine triphosphate (ATP, a key energy compound important for biosynthesis and growth) and many metabolic reactions, occur at proteins bound to the cell membrane. Intracellular fluid pH is maintained near-neutral in most organisms and at a higher pressure (called



**FIGURE 1** Generalized structure of a typical microbe. INSET: Details of how a basic protein is constructed at the ribosome. The information to construct a protein is transferred from DNA to mRNA. At the ribosome, tRNA and mRNA assemble chains of amino acids that become specific proteins in the cell.

the turgor pressure) than the cell's surroundings. A pH gradient, called the proton motive force, is kept across all cell membranes (lower pH outside the membrane), and it is this that drives ATP production.

Extracellular structures (outside the cell membrane) include peptidoglycan layers, additional lipid layers, and polysaccharide layers, all of which can form part of a rigid cell wall or capsule of material. Microbes can also possess appendages that grow out of the outer cell wall and that can facilitate cell movement. Shorter appendages, called pili, can cover the cell, whereas flagella are typically much longer and include a complex molecular motor that can turn the flagella like a propeller. Movement can also be facilitated by certain intracellular structures that some microbes possess, called vacuoles, which can be filled with gas to provide buoyancy.

The direction that a microbe travels is generally random (Brownian motion). Some microbes, however, can point themselves, either through sensing a chemical gradient (of a particular compound; this is called chemotaxis), or by using elongated structures containing magnetic minerals such as magnetite or greigite (called a magnetosome), which functions as a compass needle in the Earth's magnetic field.

## HOW HAVE MICROBES EVOLVED?

Microbial life is astounding in its diversity and is far from being completely defined. Some 99% of our knowledge of microbial diversity comes from applying molecular genetics techniques in a wide range of natural environments: glaciers to hot springs to deep-sea sediments (Pace et al. 2012). One gene that is present in all bacteria and archaea, but that has mutated enough over time to delineate different microbial species, is the gene that encodes for part of the ribosome: 16S rRNA. At present, there are over 4 million cataloged 16S rRNA gene sequences in databases (such as Genbank and SILVA), a number that is rapidly increasing.

In addition to what is likely a large number of undiscovered microbes on Earth, the DNA sequences of protein-encoding genes from known microbes are often of unknown function (i.e. the gene's sequence is known, but not its function). This suggests there is also much to discover in terms of new proteins, cofactors, and other molecular machinery associated with microbial function in many settings (popularly termed "microbial dark matter"). GMG researchers are continuing to expand the genetic database with specific genes and full genomes, in addition to RNA and proteins, and are continuing to link that information to microbial function in the natural environment (Dick and Lam 2015 this issue).

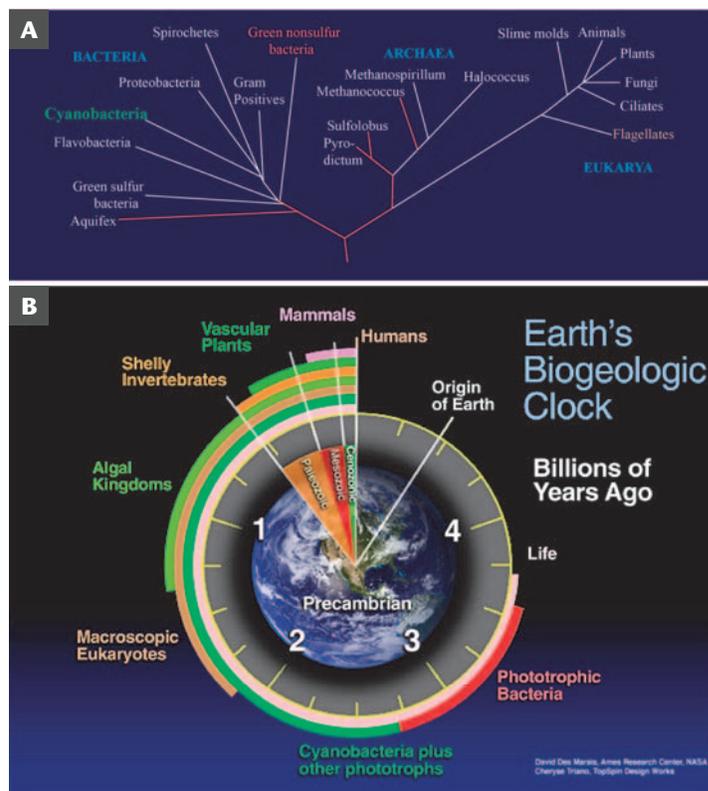
Evolutionary relationships between organisms can be defined by the degree of dissimilarity between the genes derived from a common ancestor, represented graphically in the form of a phylogenetic tree (FIG. 2A). Trees can be constructed from any common fragment of RNA or DNA (even the full genome) and similarities between any set of species can be compared. Life evolved from a last common ancestor (indicated by the first, or deepest, branching of the phylogenetic tree), which is closest to thermophilic microorganisms (FIG. 2A). The evolution of microbes occurred for about 2 billion years before even the simplest eukaryotes appeared (FIG. 2B), and the genetic variability in the microbial domains (bacteria and archaea) is extremely broad. Genetic variation occurs in two primary ways. First, random mutation of a specific DNA base pair. Second, the transfer of a genetic fragment from either a plasmid or a virus (termed "horizontal gene transfer"). On the tree

of life (FIG. 2A), random mutation occurs in small steps, resulting in a branching, dendritic pattern. Horizontal gene transfer, on the other hand, occurs by sharing a chunk of genetic material at one point in time and so tying together branches that may have, up until then, grown apart.

## WHAT DO MICROBES EAT?

Microbes harness energy from their geochemical surroundings by interacting with out-of-equilibrium redox compounds (the "edibles" and the "breathables"; see FIG. 3 caption), and they can also harvest the elements required for growth and reproduction (Nealson 2003). One consequence of these processes is that microbes often catalyze reactions that have a lot of energy but that are kinetically slow as abiotic reactions. One example is the exothermic reaction of H<sub>2</sub> with O<sub>2</sub> to make H<sub>2</sub>O, which is a microbial metabolism. Yet, if one were to put these molecules together in a sterile vessel they generally do not react because of the slow kinetics. If, however, you add a flame and ignite the hydrogen, the mixture explodes and releases the tremendous amount of potential energy stored in these molecules. Microbes tap into this stored energy in a more controlled fashion by using enzymes.

Microbes can gather energy using three general processes: chemotrophy, phototrophy, and disproportionation (FIG. 3A, C). Specific microbial metabolisms are remarkably varied, and organisms are known to bring together almost every thermodynamically viable combination of possible electron donor-acceptor pair that exists in water. Much like a battery, coupling of redox compounds harnesses a flow of electrons through the machinery of the microbe to



**FIGURE 2** (A) Representation of a simple phylogenetic tree based on DNA gene data. Distance is a quantitative measurement of genetic similarity; red lines are associated with thermophilic groups. MODIFIED FROM WOESE ET AL. (1990). (B) Representation of the timing of when key organisms appeared on Earth. Organisms are separated into major groups. MODIFIED FROM DES MARAIS (2000); COLOR-CODED GROUPS LINK SOME KEY GROUPS BETWEEN FIGURES 2A AND 2B.

drive all cellular processes; this energy is equivalent to the specific amount of free energy available from the reaction of the electron donor-acceptor pair (Fig. 3A, B).

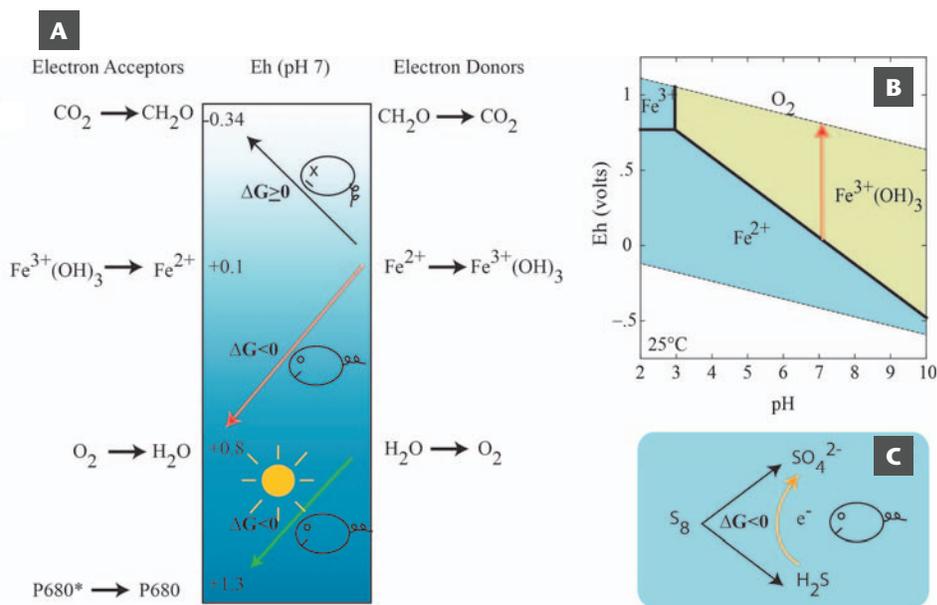
In order for a microbe to utilize these redox compounds for energy generation, the compounds must be brought inside the cell membrane (Fig. 1). But, many redox compounds cannot diffuse across the lipid membrane. They require additional molecular transporters that facilitate movement of specific molecules across the membrane. Once inside the membrane, redox compounds interact with the specific proteins that catalyze the metabolic reaction and act to harness the energy from the flow of electrons. This energy drives biosynthesis reactions that construct organic molecules and so form macromolecules for cell growth and replication. Microbes can build these molecules from the most basic carbon building block, carbon dioxide (termed “autotrophy”), or from more complex molecules that the organism sources from the external environment (termed “heterotrophy”).

Microbial metabolic processes can significantly control the dissolution and precipitation of certain minerals (Gadd 2010). Microbes are able to utilize minerals as electron donors or acceptors. These minerals can be many orders of magnitude larger than a cell. The problem of utilizing minerals as electron donors or acceptors is solved by the microbes producing molecules that either solubilize minerals (chelators) or that can themselves transport the electrons out of the cells (electron shuttles).

Thus, microbes are capable of dissolving minerals as part of their metabolism. However, they also produce minerals as a direct or indirect consequence of their metabolism. This occurs by the microbe producing a chemical species (e.g. sulfide or poorly soluble metal ion) that will lead to direct precipitation or that changes the surrounding conditions in ways that favor mineral precipitation (e.g. pH). This “induced biomineralization” is a critical process in the formation of many mineral groups, including carbonates, metal oxides, metal sulfides, phosphates, elemental forms, and silica. These biominerals can differ from identical/similar minerals produced abiotically (e.g. in size, crystallinity, and the incorporation of organics) in that they are often dispersed or occur as complex aggregates of nanoparticles with very high surface areas.

Microbes metabolizing and growing are not the only way microbes interact with their surroundings. Coupled with the presence of key reactive sites as part of their extracellular material, microbes exhibit a huge surface area and have the potential to play a large role in the mobility of metals, ions, and organics through sorption processes (e.g. Fein et al. 1997). These same reactive sites at the microbe surfaces can additionally influence the spatial positioning of specific ions coming together to make minerals, effectively templating specific minerals via interaction with extracellular microbial materials such as polysaccharides.

Microbial metabolic processes that drive redox transformations can have a significant impact on the cycling of many environmentally and geologically significant materials, including carbon, oxygen, iron, nitrogen, sulfur, selenium, manganese, arsenic, and uranium. Falkowski et al. (2008) developed a model for global geochemical cycling that



**FIGURE 3** (A) Relative positions, expressed as electropotential (Eh), of electron acceptors (“breathables”; LEFT) and electron donors (“edibles”; RIGHT) at pH 7. The energy for cellular function comes from the energy separation of these redox couples, much like connecting opposite terminals of a battery ( $\Delta G_R < 0$  is energetically possible, where  $\Delta G_R$  is the Gibbs Free energy of the reaction). (B) Eh–pH diagram showing how geochemists view the same information, but with pH as a variable. Note in both 3A and 3B panels that the red arrow couples Fe<sup>2+</sup> oxidation with oxygen reduction in the thermodynamically favorable direction. Three types of general metabolism are associated with redox reactions: chemotrophy (red arrows), coupling energetically favorable redox donor/acceptor pairs; phototrophy (green arrow), coupling an energetically favorable e<sup>-</sup> donor with an e<sup>-</sup> acceptor at a photoactive enzyme site in a high energy state (due to interaction with photons); and (C) disproportionation (yellow arrow), the splitting of a single source molecule into a more reduced and a more oxidized form. This is fermentation, the same type of reaction that creates alcohol from sugar.

illustrated the importance of biologic element cycling tied to abiotic atmospheric and deep geological element fluxes associated with tectonics, mountain building, erosion, geothermal activity, and sediment diagenesis. If one wishes to interpret element cycling on the surface of the Earth, or potentially any other planet, then the microbial transformations that are based on protein-catalyzed metabolic reactions must be a key part of the task.

Combining biotic and abiotic reactions is another consideration when characterizing the role of microbes in element cycling. This is because the products of specific metabolic processes may interact with other compounds abiotically in key ways. Such reactions are often very fast and not easily detected through chemical analyses. Nonetheless, these reactions (sometimes called cryptic reactions) often govern reaction pathways, isotope fractionation, and the availability of other compounds necessary for metabolism (Hansel et al. 2015 this issue).

## HOW DO WE CHARACTERIZE MICROBES AND THEIR LINK TO GEOCHEMISTRY?

While the discovery of microbes came with the invention of the microscope, our characterization of microbes and their metabolism has greatly advanced by using new genetic and chemical techniques. Prior to the availability of genetic information, microbe characterization was based on pure cultures, the isolation of individual microbial species being accomplished through specific electron donor-acceptor combinations under controlled

physicochemical settings. Culturing continues to be a critical part of identifying and characterizing microbial function. But the modern analysis of a microbe's genetic and protein materials have revolutionized this practice over the last 30 years. Today, we utilize techniques to quantify the DNA (genetics), RNA (transcriptomics), and proteins (proteomics) from microbes to identify and characterize microbes and gain new insights into their functions in the environment. Collectively, these molecular techniques are termed "omics" (Dick and Lam 2015 this issue). Scientists are now integrating both microscopy and omics information. By attaching tags to genetic fragments that bind to specific RNA sequences, we can "illuminate" specific microbes under the microscope (including optical and electron microscopes). Another part of the microbe that is used for identification are the lipids that comprise the cell membrane. These lipids are important indicators of microbial presence (they are "biomarkers") because the long-chain carbon "skeleton" of the lipid is very resistant to change; the specific structure of lipid can be unique to specific groups of organisms. Thus, these compounds may serve as molecular fossils long after the organism dies.

Microbial metabolism often plays a vital role in controlling the details of geochemical cycling of specific elements. Therefore, choosing the appropriate spatial or temporal scale over which to sample is critical. This is a challenge: sampling at too coarse a scale may group together microbes with geochemical processes that are not necessarily related to each other. Investigating these processes, therefore, requires appropriate tools for the appropriate timescale. The application of in situ tools for the analysis of redox species in aquatic systems has been a key advancement for understanding the role of microbes in element cycling, as has the development of techniques that can stabilize the chemical components that minimize changes between the sampling and analysis steps. Nanoscale and molecular characterization of microbe-geochemical interactions have also proven critical to the advancement of the GMG field, with synchrotron-based extended X-ray absorption fine structure/ X-ray absorption near-edge structure (EXAFS/ XANES), scanning transmission X-ray microscopy (STXM), (nano-) secondary ion mass spectrometry ((nano-)SIMS), with various types of instrumentation (electron microscopes, diffractometers, spectroscopes, and electrochemical, and chromatographic machines) being important. As with other geochemical lines of inquiry, isotopes, especially of elements involved in metabolic reactions, are a critical tool for investigating microbial processes. Especially powerful in this context is the ability to quantify isotopic fractionation associated with the interaction of inorganic electron acceptor-donor compounds with specific enzymes.

Observation of particular chemical components in specific settings can indicate control by microbial processes when abiotic processes that are known to drive the same chemistry are too slow. For example, the abiotic reduction of sulfate to sulfide at low temperatures is a very slow chemical process; thus, the observation of significant fluxes of sulfide at lower temperatures is strong evidence that microbial sulfate-reduction metabolism is responsible. Sulfur isotopes are also strongly fractionated by sulfur-reducing bacteria (Johnston et al. 2007; Fike and Grotzinger 2008), providing yet another line of chemical evidence for the role of microbes in a specific geochemical process.

The idea that certain chemical or mineralogical phenomena can be a biomarker for life is a significant driver of research, especially because any proof of life requires that an observed chemical signature would be impossible without life. While this may sound like a simple task, it has proven not to be

so easy, especially when we are looking for proof of life in ancient rocks or meteorite fragments and utilizing robotic spacecraft on, or orbiting above, other planetary bodies.

Studies of microbial roles in specific element cycles and the use of biomarker evidence in modern systems provide context to decipher the record of microbial processes recorded in ancient rocks. Conversely, the ancient rock record provides us with an opportunity to see how microbial processes affect large-scale element cycling over time as other conditions (for example climate) have changed. Lyons et al. (2015 this issue) reviews how chemical indicators of microbial processes may be preserved in rocks (rocks that have gone through diagenesis, if not metamorphism), and what that rock record may tell us about how Earth and life have changed through time. Our picture now of early Earth, including the conditions of the atmosphere and oceans, the weathering of ancient craton material, and the preservation of ancient sediments, is interwoven with the evolution of microbial life. Chemical and isotopic evidence for biotic and abiotic processes are linked to the evolutionary patterns observed in the genetic tree of life. In particular, early Earth was a place devoid of appreciable oxygen, and the earliest microbial metabolisms that evolved were almost certainly anaerobic and probably involved hydrogen, iron, and sulfur. At the base of the genetic tree of life, ancient microbes are most similar to microbes found in anoxic environments today. However, it is also thought that microbes capable of oxygenic photosynthesis (generating O<sub>2</sub>), especially cyanobacterial species, evolved relatively quickly thereafter. This shift helped to shape the chemical changes on early Earth, leading to the Great Oxidation Event when O<sub>2</sub> became a major component of the atmosphere for the first time (Lyons et al. 2014). Earth processes, in turn, have almost certainly influenced microbial evolution: the role of metal availability, the intensity of ultraviolet radiation at Earth's surface, and element fluxes from mineral weathering have probably affected the evolution of microbes and their specific, protein-based, functionalities.

## EMERGING TOPICS IN GEOMICROBIOLOGY AND MICROBIAL GEOCHEMISTRY

This issue of *Elements* aims to illuminate the importance of microbes in natural systems. We will show the rapid growth in our understanding that has come from characterizing links between microbes and their geochemical surroundings through time, and highlight emerging opportunities with the advent of new tools and paradigms. The following key areas in the field of GMG will be discussed:

- The principles and origins of geobiochemistry – defining the interplay of Earth processes and its effects on the evolution of microbial metabolisms.
- The application of omics to Earth processes – new capabilities for sequencing the macromolecules that comprise microbial cells and whole microbial communities will offer insights into GMG.
- The identification of reactive intermediates – these are a key to understanding microbial roles in element cycling.
- The emerging geochemical views of Earth's ancient microbial world – forming a basis for a new picture of Earth's coupled geochemical and microbial evolution.
- The emerging frontiers – examples of how GMG is forging ahead with other allied fields to advance scientific understanding.

From a practical standpoint, GMG tackles fundamental science with significant societal relevance: the recovery and use of oil, coal, and natural gas; the responsible utilization of Earth materials used for electronics, batteries, food production, and building materials of all kinds; the supply of clean, fresh water; and how climate change will impact all manner of Earth systems supporting civilization. Considering deep time, GMG processes can also help us understand how the biogeosphere adapts to global changes: the past can be the key to the future.

To reach these goals, GMG scientists are embracing opportunities for future advances. Integrating omics and geochemical data will require advanced computational approaches to uncover new details of the interactions between microbes and their surroundings. Merging the ancient rock record and the record of evolutionary changes contained in the DNA of microbes may yield key information on how Earth systems respond to changes on a global scale and how we may look for evidence of life on other planets. Considering the key spatial and temporal scales across which linked microbial and geochemical parameters change may help us unravel the role that microbes play in processes ranging from local to global scales.

As more is learned about links between microbes and their surroundings, the fundamental scientific advances of GMG can also be applied in concert with other fields and modes of inquiry. Details about the function of microbes can yield key insights on human health. This might come about by investigating our own microbial flora and understanding

how specific protein-catalyzed reactions function, how they are triggered, and how they may be utilized or inhibited towards better human health. Microbes play key roles in formation of many natural and synthetic biomaterials (that may have fundamentally different properties) and in the development of biogeobatteries as an alternative energy source. Additionally, microbes could play a very important role in recycling of materials critical to modern society. Lastly, GMG applications are closely linked to the main goal of astrobiology: the search for life on other planets (Templeton and Benzerara 2015 this issue).

## ACKNOWLEDGMENTS

Our thanks go especially to executive editor Jodi Rosso and principal editor Patricia Dove for their assistance with preparing this issue. GKD acknowledges support from the National Science Foundation (EAR 1304352) and from all participants in an NSF-supported workshop (EAR 1346732) held October 2013 on the current state and future opportunities for the field of geomicrobiology and microbial geochemistry where the idea for this issue was born. AK was supported by the European Research Council under the European Union's Seventh Framework Programme (FP/2007–2013)/ERC Grant, Agreement n. 307320 – MICROFOX. Thanks to Greg Dick, Alexis Templeton, Joe Pachut, and Gabe Filippelli for providing early reviews on this article. Thanks to several anonymous reviewers and Greg Dick for editing this manuscript and providing valuable suggestions for improvement and clarity. ■

## REFERENCES

- Amaral-Zettler L and 15 coauthors (2010). A global consensus of marine microbes. In: McIntrye AD (ed) *Life in the World's Oceans: Diversity, Distribution, and Abundance*. Wiley-Blackwell, Oxford, pp 223-246
- Banfield JF, Nealson KH (eds) (1997) *Geomicrobiology: Interactions Between Microbes and Minerals*. Reviews in Mineralogy Volume 35. Mineralogical Society of America, Chantilly, 448 pp
- Canfield DE (2005) The early history of atmospheric oxygen: homage to Robert M. Garrels. *Annual Review of Earth and Planetary Sciences* 33: 1-36
- de Wit R, Bouvier T (2006) 'Everything is everywhere, but, the environment selects'; what did Baas Becking and Beijerinck really say?" *Environmental Microbiology* 8: 755-758
- Des Marais DJ (2000) When did photosynthesis emerge on Earth? *Science* 289: 1703-1705
- Dick GJ, Lam P (2015) Omic approaches to microbial geochemistry. *Elements* 11: 403-408
- Dworkin M (2012) Sergei Winogradsky: a founder of modern microbiology and the first microbial ecologist. *FEMS Microbiology Reviews* 36: 364-379
- Ehrlich HL (2012) Reminiscences from a career in Geomicrobiology. *Annuals Reviews Earth and Planetary Sciences* 40: 1-21
- Falkowski PG, Fenchel T, Delong EF (2008) The microbial engines that drive earth's biogeochemical cycles. *Science* 320: 1034-1039
- Fein JB, Daughney CJ, Yee N, Davis TA (1997) A chemical equilibrium model for metal adsorption onto bacterial surfaces. *Geochimica et Cosmochimica Acta* 61: 3319-3328
- Fike DA, Grotzinger JP (2008) A paired sulfate-pyrite  $\delta^{34}\text{S}$  approach to understanding the evolution of the Ediacaran-Cambrian sulfur cycle. *Geochimica et Cosmochimica Acta* 72: 2636-2648
- Gadd GM (2010) Metals, minerals and microbes: geomicrobiology and bioremediation. *Microbiology* 156: 609-643
- Hansel CM, Ferdelman TG, Tebo BM (2015) Cryptic cross-linkages among geochemical cycles: novel insights from reactive intermediates. *Elements* 11: 409-414
- Johnston DT (2011) Multiple sulfur isotopes and the evolution of Earth's surface sulfur cycle. *Earth-Science Reviews* 106: 161-183
- Johnston DT, Farquhar J, Canfield DE (2007) Sulfur isotope insights into microbial sulfate reduction: When microbes meet models. *Geochimica et Cosmochimica Acta* 71: 3929-3947
- Lyons TW, Reinhard CT, Planavsky NJ (2014) The rise of oxygen in Earth's early ocean and atmosphere. *Nature* 506: 307-315
- Lyons TW, Fike DA, Zerkle A (2015) Emerging biogeochemical views of Earth's ancient microbial worlds. *Elements* 11: 415-421
- Nealson KH (2003) Harnessing microbial appetites for remediation. *Nature Biotechnology* 21: 243-244, doi: 10.1038/nbt0303-243
- Pace NR, Sapp J, Goldenfield N (2012) Phylogeny and beyond: Scientific, historical, and conceptual significance of the first tree of life. *Proceedings of the National Academy of Sciences of the United States of America* 109: 1011-1018
- Quispel A (1998) Lourens G. M. Baas Becking (1895-1963), Inspirator for many (micro)biologists. *International Microbiology* 1: 69-72
- Shock EL, Boyd ES (2015) The principles of geobiochemistry. *Elements* 11: 395-401
- Slater GF, Cowie BR, Harper N, Droppo IG (2008) Variation in PAH inputs and microbial community in surface sediments of Hamilton Harbour: implications to remediation and monitoring. *Environmental Pollution* 153: 60-70
- Taylor PG, Townsend AR (2010) Stoichiometric control of organic carbon-nitrate relationships from soils to the sea. *Nature* 464: 1178-1181
- Templeton A, Benzerara K (2015) Emerging frontiers in geomicrobiology. *Elements* 11: 423-429
- Vernadsky VL (1926) *The Biosphere*. English translation edition by DB Langmuir (1998) Copernicus, New York, 192 pp
- Woese CR, Kandler O, Wheelis ML (1990) Towards a natural system of organisms: Proposal for the domains Archaea, Bacteria, and Eucarya. *Proceedings of the National Academy of Sciences of the United States of America* 87: 4576-4579.
- Winogradsky S (1887) Ueber Schwefelbakterien. *Botanische Zeitung* 45: 489-610 ■