




# FUNDAMENTALS OF GEOBIOLOGY

EDITED BY ANDREW H. KNOLL,  
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AND

KURT O. KONHAUSER

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# WHAT IS GEOBIOLOGY?

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## 1.1 Introduction

Geobiology is a scientific discipline in which the principles and tools of biology are applied to studies of the Earth. In concept, geobiology parallels geophysics and geochemistry, two longer established disciplines within the Earth sciences. Beginning in the 1940s, and accelerating through the remainder of the twentieth century, scientists brought the tools of physics and chemistry to bear on studies of the Earth, transforming geology from a descriptive science to a quantitative field grounded in analysis, experiment and modeling. The geophysical and geochemical revolutions both reflected and drove a strong disciplinary emphasis on plate tectonics and planetary differentiation, not least because, for the first time, they made the Earth's interior accessible to research.

While geochemistry and geophysics occupied centre stage in the Earth sciences, another multidisciplinary transformation was taking shape nearer to the field's periphery. Paleontology had long brought a measure of biological thought to geology, in no small part because fossils provide a basis for correlating sedimentary rocks. But while it was obvious that life had evolved on the Earth, it was less clear to most Earth scientists that life had actually shaped, and been shaped, by Earth's environmental history. For example, in *Tempo and Mode in Evolution*, paleontology's key contribution to the Neodarwinian synthesis in evolutionary biology, G.G. Simpson (1944) devoted less than a page to questions of environmental interactions. As early as 1926, however, the Russian scientist Vladimir Vernadsky had published *The Biosphere*, setting forth the argument that life has shaped our planet's surface environment throughout geologic time. Vernadsky also championed the idea of a noosphere, a planet transformed by activities of human beings. A few years later, the Dutch microbiologist Lourens Baas-Becking (1934) coined the term *geobiology* to describe the interactions between organisms and environment at the chemical level. Whereas most paleontologists stressed morphology and systematics, Vernadsky and Baas-Becking focused on metabolism – and in the long run that made all the difference.

Geobiological thinking moved to centre stage in the 1970s with articulation of the Gaia Hypothesis by James Lovelock (1979). Much like Vernadsky before him, Lovelock argued that life, air, water and rocks interact in complex ways within an integrated Earth system. More controversially, he posited that organisms regulate the Earth system for their own benefit. While this latter view, sometimes called 'strong Gaia,' has found little favor with biologists or Earth scientists, most now accept the more general view that

Earth surface environments cannot be understood without input from the life sciences. The seeds of these ideas may have been planted earlier, but it was Lovelock who really captured the attention of a broad scientific community.

As the twentieth century entered its final decade, interest in geobiology grew, driven by an increasing emphasis within the Earth sciences on understanding our planetary surface, and supported by accelerating research on the microbial control of elemental cycling, the ecological diversity of microbial life under even the most harsh environmental conditions (commonly referred to as *extremeophiles*), the use of microbes to ameliorate pollution (bioremediation) or recover valuable metals from mine waste (biorecovery), Earth's ancient microbial history, and efforts to understand human influences on the Earth surface system. And, in the twenty-first century, universities are increasingly supporting research and education in geobiology, international journals (e.g., *Geobiology*, *Biogeosciences*) have prospered, textbooks have been published (e.g., Schlesinger, 1997; Canfield *et al.*, 2005; Konhauser, 2007; Ehrlich and Newman, 2009), and conferences occur regularly. Without question, geobiology has come of age.

## 1.2 Life interacting with the Earth

Geobiology is predicated on the observation that biological processes interact with physical processes at and near the Earth's surface. Take, for example, carbon, the defining element of life. Within the *biosphere* – the sum of all environments that support life on Earth – carbon exists in a number of forms and in several key reservoirs. It is present as  $\text{CO}_2$  in the atmosphere; as  $\text{CO}_2$ ,  $\text{HCO}_3^-$  and  $\text{CO}_3^{2-}$

dissolved in fresh and marine waters; as carbonate minerals in soils, sediments and rocks; and as a huge variety of organic molecules in organisms, in sediments and soils, and dissolved in lakes and oceans. Physical processes move carbon from one reservoir to another; for example, volcanoes add CO<sub>2</sub> to the atmosphere and chemical weathering removes it. Biological processes do as well. In two notable examples, photosynthesis reduces CO<sub>2</sub> to sugar, and respiration oxidizes organic molecules to CO<sub>2</sub>. Since the industrial revolution, humans have oxidized sedimentary organic matter (by burning fossil fuels) at rates much higher than those characteristic of earlier epochs, making us important participants in the Earth's carbon cycle. Given the centrality of the carbon cycle to both ecology and climate, its biological and geological components are explored in two early chapters of this book (Chapters 2 and 3) and revisited in the context of human activities in Chapter 22.

Other biologically important elements also cycle through the biosphere. Sulfur, nitrogen, and iron (Chapters 4–6) all link the physical and biological Earth, interacting with each other and, importantly, with the carbon cycle. And oxygen, key to environments that support large animals, including humans, is regulated by a complex and incompletely understood set of processes that, again, have both biological and physical components (Chapter 7).

Unlike physical processes, life evolves, and so the array of biological processes in play within the biosphere has changed through time. The state of the environment supporting biological communities has changed as well. Indeed, given the close relationship between environment and population distributions on the present day Earth, it is reasonable to hypothesize that evolving life has significantly influenced the chemical environment through time and,

conversely, that environmental change has influenced the course of evolution.

While metabolism encompasses many of the biological cogs in the biosphere, other processes also play important roles. For example, many organisms precipitate minerals, either indirectly by altering local chemical environments (Chapter 8), or directly by building mineralized skeletons (Chapter 10). Today, skeletons dominate the deposition of carbonate and silica on the seafloor, although this was not true before the evolution of shells, spicules and tests. More subtly, organisms interact with clays and other minerals in a series of surface interactions that are only now beginning to be understood (Chapter 9). While much of geobiology focuses on chemical processes, organisms influence the Earth through physical activities as well – think of microbial communities that can stabilize sand beds (Chapter 16) or worms that irrigate sediments as they burrow (Chapter 11). The example of burrowing reminds us that while microorganisms garner much geobiological attention, plants and animals also act as geobiological agents, and have done so for more than 500 million years (Chapter 11).

In short, Earth surface processes once considered to be largely physical in nature – for example weathering and erosion – are now known to have key biological components (Chapter 12). Life plays a critical role in the Earth system.

## **1.3 Pattern and process in geobiology**

Geobiologists, then, study how organisms influence the physical Earth and vice versa, and how biological and physical processes have interacted through our planet's long history. Much of this research focuses on illuminating *process*: field and experimental studies of how organisms



participate in the Earth system, and what consequences these activities have for local to global environmental state. Geobiological research can be fundamental – that is, aimed at achieving a basic understanding of the Earth system and its evolution – or it can be applied. In the case of the latter, microbial populations have been deployed and even engineered to perform tasks that range from concentrating gold dispersed in the talus piles of mines, and removing arsenic from the water supply of Los Angeles, to respiring vast amounts of the petroleum that gushed into the Gulf of Mexico in 2010. Building on earlier chapters, Chapters 13–16 focus on techniques that are prominent in modern geobiological research.

Elucidating the changing role of life through Earth history, sometimes called *historical geobiology*, begins with a basic understanding of geobiological processes, but from there takes on a distinctly geological slant. We would like to interpret the geologic record in terms of active processes and chemical states, but rocks preserve only pattern. Thus, the geobiological interpretation of ancient sedimentary rocks requires that we understand how biological processes and aspects of the ambient environmental state are reflected in the geologically preservable patterns they create. For example, we can use the sulfur isotopic composition of minerals in billion-year-old shales to constrain the biological workings of the ancient sulfur cycle and sulfate abundance in ancient seawater, but can do so only in light of present day observations and experiments that show how biological and physical processes result in particular isotopic patterns.

Of course, there are at least two features that complicate this linkage of geobiological process to geologic pattern. For one, populations evolve, so biological processes observable today may not have been active during the deposition of ancient sedimentary rocks. For this reason, historical geobiology has

among its goals the establishment of evolutionary pattern in Earth history. The second complication is that many environmental states on the ancient Earth have no modern counterpart. Most obviously, modern surface environments are permeated with oxygen in ways unlikely to have existed during the first two billion years of our planet's development. Other differences exist, as well. Therefore, the present-day Earth system is far removed from the earliest systems where life evolved and then spread out across the planet; it represents a long accumulation of biological, physical and chemical changes through Earth history. Following a chapter on the origin of life (Chapter 17), perhaps the ultimate example of the intimate relationship between biological and physical processes, we present three chapters that outline Earth's geobiological history (Chapters 19-21). Oxygen, biological evolution and chemical change dominate these discussions, but there are other aspects to the story. For example, Chapter 18 discusses how the diversity of minerals found on Earth has expanded through time as the biosphere has changed, providing a twenty-first century account of an intriguing subject suggested long ago by Vernadsky.

Finally, there is the question of us. Either directly or indirectly, humans appropriate nearly half of the total primary production on Earth's land surface. We fix as much nitrogen as bacteria do, and shuttle phosphate from rocks to the oceans at unprecedented rates. As Vernadsky predicted in his early discussion of the noosphere, humans have become extraordinarily important agents of geobiological change. In areas that range from climate change to eutrophication, from ocean acidification to Earth's declining supplies of fossil fuels and phosphate fertilizer, the human footprint on the biosphere is large and growing. Our societal future depends in part on understanding the geobiological influences of humans and in governing the technological

processes that have come to play such important roles in the modern Earth system (Chapter 22).

## **1.4 New horizons in geobiology**

It is difficult, if not impossible, to predict the future, and while it would be fun to attempt a forecast of the status of geobiology in say 20 years, we will avoid this. Rather, we highlight that under all circumstances, geobiology will increasingly look to the heavens. *Astrobiology* can be thought of as the application of geobiological principles to the study of planets and moons beyond the Earth. At the moment, claims about life in the universe largely constitute under-constrained statistical extrapolations from our terrestrial experience: some hold that life is abundant throughout the universe, but intelligent life is rare (Ward and Brownlee, 2000), while others suggest that life is rare, but intelligence more or less inevitable wherever life occurs (Conway Morris 2004). Clearly, the way forward lies in exploration. Both remote sensing and lander operations have made remarkable strides during the past decade (e.g., Squyres and Knoll, 2006), so we can be confident that on planets and moons within our solar system, direct observation of potentially geobiological patterns will sharply constrain arguments about life in our planetary neighborhood. And arguments about life in nearby solar systems will be framed in terms of geobiological models of planetary atmospheres glimpsed by Kepler and its technological descendents (Kasting, 2010).

This book, then, is a status report. It contains detailed but accessible summaries of key issues of geobiology, hopefully capturing the state and breadth of this emerging discipline. We have tried to be inclusive in our choice of topics covered

within this volume. We recognize, however, that the borders defining geobiology are fluid, and we have likely missed or underrepresented some relevant geobiological topics. We apologize in advance for this. We also hope and trust that in the future, geobiology will expand in both depth and breadth well beyond what is offered here. Our crystal ball is cloudy, but we can be certain that a similar book written twenty years from now will differ fundamentally from this one.

## References

- Baas-Becking LGM (1934) *Geobiologie of inleiding tot de milieukunde* *Diligentia Wetensch*, Serie 18/19. van Stockum's Gravenhage, The Hague.
- Canfield DE, Kristensen E, Thamdrup B (2005) *Aquatic Geomicrobiology*. Elsevier, Amsterdam.
- Conway Morris S (2004) *Life's Solution: Inevitable Humans in a Lonely Universe*. Cambridge University Press, Cambridge.
- Ehrlich HL, Newman DK (2009) *Geomicrobiology*, 5th edn. Marcel Dekker, New York.
- Kasting J (2010) *How to Find a Habitable Planet*. Princeton University Press, Princeton, NJ.
- Konhauser K (2007) *Introduction to Geomicrobiology*. Blackwell Publishing, Malden, MA.
- Lovelock J (1979) *Gaia: A New Look at Life on Earth*. Oxford University Press, Oxford.
- Schlesinger WH (1997) *Biogeochemistry: An Analysis of Global Change*. Academic Press, San Diego, CA.
- Simpson GG (1944) *Tempo and Mode in Evolution*. Columbia University Press, New York.
- Squyres S, Knoll AH, eds (2006) *Sedimentary Geology at Meridiani Planum, Mars*. Elsevier Science, Amsterdam. [Also published as *Earth and Planetary Science Letters* **240**(1).]

Vernadsky VL (1926) *The Biosphere*. English translation by D.B. Langmuir, Copernicus, New York, 1998.

Ward P, Brownlee D (2000) *Rare Earth: Why Complex Life Is Uncommon in the Universe*. Springer-Verlag, Berlin.

# THE GLOBAL CARBON CYCLE: BIOLOGICAL PROCESSES

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## 2.1 Introduction

Carbon is the fourth most abundant element in our solar system and its chemistry forms the basis of all life on Earth. It is used both as the fundamental building block for all structural biological molecules and as an energy carrier. However, the vast majority of carbon on the surface of this planet is covalently bound to oxygen or its hydrated equivalents, forming mineral carbonates in the lithosphere, soluble ions in the ocean, and gaseous carbon dioxide in the atmosphere. These oxidized (inorganic) forms of carbon are moved on time scales of centuries to millions of years between the lithosphere, ocean and atmosphere via tectonically driven acid-based reactions. Because these reservoirs are so vast ([Table 2.1](#)) they dominate the carbon cycle on geological time scales, but because the reactions are so slow, they are also difficult to measure directly within a human lifetime.