

An introduction to philosophy of microbiology

Philosophy of microbiology might seem like a highly specialized and even esoteric subfield of philosophy of biology. However, there are many good reasons to think that in fact microbes form the basis of all things biological and thus have major contributions to make to philosophy of biology. This chapter, and the book in general, will make that case.

The grounds for a philosophy of microbiology

Microbes are the most important, diverse and ancient life forms on our planet. The science of these organisms, microbiology, is the science of the most significant living entities and their influence on all the rest of life. Many philosophers will need to be persuaded of these claims, and this book will try to do that. Every scientific field has philosophical aspects, from how the objects of study are conceptualized to the ways in which those objects are known, but microbiology's philosophical issues have only just begun to attract sustained attention from philosophers of biology. These philosophical aspects have driven many debates in microbiological research itself. This book will set out some central philosophical issues in microbiology, along with suggestions for how microbiological insight contributes to and even transforms philosophy of biology. I will start by making a case for philosophy of microbiology based on a general appreciation of the microbial world and its significance for all life. If the world we inhabit is indeed a microbial world, then many of the standard philosophical ways in which we conceive biological phenomena and how they are investigated will have to be rethought. Each of the following chapters deals with a particular aspect of that rethinking.

This general project has a number of complications. One of them is that common terms for microscopic life forms are colloquial and contestable. 'Microbe', for instance, is a broad and convenient term that is used to cover a range of microscopic life (see Table I.1). It encompasses all

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Table I.1: *Terminology for microbes*

Microbe	A general term used to cover microscopic and usually unicellular life; equivalent in English to microorganism (in contrast to macrobe or macroorganism). It includes visible aggregations of unicellular life, such as biofilms and colonies. It may occasionally include viruses.
Prokaryote	Unicellular life with a flexibly organized intracellular structure that has limited or, more likely, poorly recognized compartmentalization.
Eukaryote	Unicellular and multicellular life forms with many well-known compartmentalized processes in each cell.
Bacteria	One of the two main groups of prokaryotes; also known as eubacteria.
Archaea	One of the two main groups of prokaryotes; also known as archaeobacteria.
Protist	Any unicellular eukaryote except for single-cell fungi, such as yeast (usually excluded but not always); multicellular algae are sometimes included.
Virus; bacteriophage	Non-cellular evolving entities able to use cells for reproduction. Viruses use eukaryotic cells; bacteriophage ('phage') use prokaryotic cells. The most inclusive term is still virus, however.

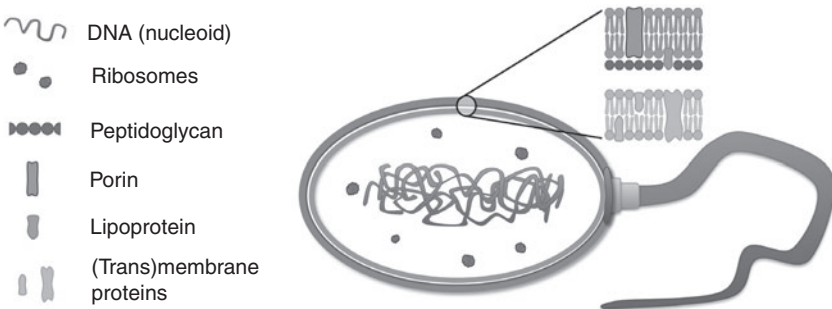


Figure I.1: A prokaryote cell. A schematic diagram of a prokaryote cell, in this case (because of cell wall differences) a Gram-negative bacterium such as *Escherichia coli*.

unicellular life forms (prokaryotes, protists, unicellular fungi and algae) and often includes viruses, even though these entities are not cellular and are rarely considered to be alive in the way that cellular life is. Several of the issues that revolve around formal and informal classification terminologies for microbial life will be discussed in Chapters 2 and 3. A further necessary clarification is that when I discuss the microbial world, I do not refer primarily to the laboratory world of microbiology. Although a vast amount of knowledge has been generated in over a century of laboratory studies, these approaches have obtained limited access to the far greater diversity of

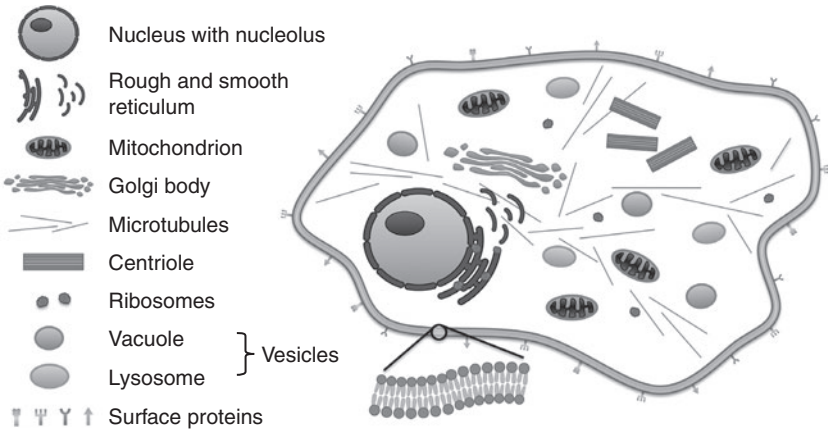


Figure I.2: A eukaryote cell. A schematic diagram of a generalized eukaryote cell (without a cell wall), depicting some specialized compartments and outer membrane structures. Structural features such as flagella, tubulin and actin are not shown, and the cell's size is not proportionate to the prokaryote in Figure I.1.

the uncultured microbial world. This largely unknown world interacts in complex ways with microscopic and macroscopic entities, including the Earth's geochemistry. The book's cover is meant to capture this perspective, and Chapter 5 will develop this theme in some detail. For now, I will simply make the case that the biological world *in general* is microbial. I will do this from the four perspectives of biodiversity, biogeochemistry, evolutionary history and symbiotic collaboration.

The case for a microbial world

The first task in presenting a philosophy of microbiology is to make a case that microbes are of special biological significance. To appreciate their importance, we will consider the quantity, biomass and variety of microorganisms (*biodiversity*). However, biodiversity on its own is not quite enough, even if it is impressive. The next step is to show that the extraordinary metabolic capacities of microorganisms have effects on the planetary processes that sustain all life forms (*biogeochemistry*). These biogeochemical cycles are themselves the products of evolution over the entire history of the Earth, in which microbes have not only themselves evolved but have had major evolutionary impacts on every other evolving life form (*evolutionary history*). This impact largely derives from the multiple capacities microbes have to work with other biological entities (*symbiotic*

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collaboration). The following chapters will explore each of these four perspectives in more detail. Here they are advanced in order to justify a focus on microbial life, and to support the claim that it needs to be prioritized in any general study of living things.

Biodiversity

Biodiversity is a property of the biological world that is important both ecologically and anthropocentrically. Most biodiversity on Earth is and always has been microbial, regardless of the greater visibility of animals and plants, and despite many differences in how biodiversity is calculated (see Chapter 5). Microbes outnumber all other life forms combined, even though no exhaustive enumeration of them has yet been made and probably will never be. It is unlikely that there is any environment on or around the Earth that is free of microbial life. Microbes can be found in the stratosphere (the atmospheric layer about 15–50 kms above the Earth's surface), in clouds and other condensed water in the troposphere (8–15 kms above the Earth), and as stowaways on materials sent into space by humans. Going in the other direction, there are microbes in the deepest darkest oceans, as well as several kilometres below the Earth's surface. This diversity of habitat is matched in some microbes by an ability to survive for millions of years in a dormant spore state (Lennon and Jones 2011). Even the most determined human efforts to render specific environments totally free of microbes invariably fail, due to individual and collective microbial strategies for endurance and dispersal (Kashefi and Lovley 2003).

There are an estimated $4\text{--}6 \times 10^{30}$ prokaryote cells on the planet and about an order of magnitude more of viruses (Whitman et al. 1998). Soil biodiversity is particularly rich, with 10^{16} prokaryotic cells in one tonne of soil – compared to 10^{11} stars in the Milky Way – from which a mere 10 grams may yield as many as 10^7 'species' groups (Curtis and Sloan 2005). To make those numbers more concrete, the number of cells in just one teaspoon of soil exceeds the number of humans currently inhabiting the whole continent of Africa (Editorial 2011). More than 50 per cent of the biomass on the planet is prokaryotic,¹ even though prokaryote cells are on average only one-tenth of the diameter of eukaryote cells and one-thousandth of the

¹ This estimate of relative biomass excludes the extracellular material of plants, such as cell walls and structural polymers, and has also been questioned by more recent and much lower estimates of sub-seafloor prokaryotic biomass (Kallmeyer et al. 2012). However, this new estimate assumes very small cell size and low carbon content in prokaryotes in restricted nutritional conditions. Those assumptions are likely to be incorrect and thus the revised estimate too low (Jørgensen 2012).

volume (Whitman et al. 1998). In oceans alone, microbes comprise more than 90 per cent of the total biomass (Sogin et al. 2006), and there are 100 million times more of them – 10^{28} – than there are stars in the entire universe (Editorial 2011). In whichever way the multivalent term of species is conceived, unless solely based on morphology, prokaryotes constitute by far the greatest number of lineages. Even if eukaryotes are considered separately, protists dominate the major groups constituting the eukaryotes (Adl et al. 2012; Chapter 2).

More important than entity counts, biomass and taxonomic diversity, however, is the extraordinary diversity of microbial abilities to generate energy, cope with environmental stresses, adapt quickly to new environments and take advantage of existing ones. Many of these capabilities depend on the metabolic versatility of microbes. Metabolism, the cell-based generation of energy, occurs via reduction-oxidation (redox) couplings that are based on the oxidation of electron donors and reduction of electron acceptors. Different redox pathways have combined in individual microorganisms or groups of them to produce the biogeochemical cycles that maintain life on the planet. Animals and fungi are heterotrophs, using carbon fixed by other organisms, whereas plants are almost all photoautotrophs, which use light energy to fix carbon. Microbes, however, can be heterotrophs, autotrophs or mixotrophs, the last involving the combination of very different metabolic strategies in relation to carbon sources (Madigan et al. 2008; Glossary). Two or more of the highly diverse metabolic strategies found in the microbial world may sometimes be found in the same organism. For example, a single organism may be both an oxygenic and an anoxygenic phototroph, or even a photoheterotroph (photosynthesizers that use organic carbon). Some microbes switch between chemoautotrophy (oxidation of inorganic chemical compounds, including carbon) and organic carbon use (chemoorganotrophy), or between aerobic and anaerobic respiration (Madigan et al. 2008; Glossary).

Numerous microorganisms are extremophiles, which means they can metabolize and reproduce in extreme conditions of heat, cold, acidity, salinity and other seemingly inhospitable environments (Harrison et al. 2013). Microbes in harsh environments, using low-energy reactions, may take thousands of years to generate biomass and divide but they nevertheless manage to survive and reproduce (Hoehler and Jørgensen 2013). Even more microbes enter into sustained metabolic mutualisms with other microorganisms, in which one group of organisms supplies as an end product the metabolic substrate for a differently metabolizing group (Morris et al. 2013). New discoveries of microbial metabolism are being

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made on a regular basis, because of environment-wide molecular detection strategies and the increasing scrutiny of previously unexplored environments and niches (see Chapter 5). Some of the most unusual metabolic discoveries made in the last two decades were predicted to exist primarily because of thermodynamic possibility and the assumption that microbes will always find a way to exploit potential energy gains (Kuenen 2008).

Although ecologists, policy makers and philosophers are not always in agreement about how to define and measure biodiversity (Faith 2007), they do agree that some level of diversity of life forms is important, and that efforts should be made to preserve known life and its habitats. Microorganisms are intrinsic to the maintenance of plant, animal and fungal biodiversity in ways that will be outlined below. The value we attach to macroorganismal diversity relies largely on microorganismal biodiversity, but despite this relationship it is very rare to hear much said about microbial conservation (see the concluding chapter).

Biogeochemistry

The functional diversity of microbes means that these organisms permeate all life. The global chemistry of life is based on and regulated by microbial metabolisms interacting with the Earth's geochemistry (Falkowski et al. 2008; Dietrich et al. 2006; see Chapter 5). Multitaxon groups of microbes deploying diverse and distinct metabolic pathways bring about most of the biogeochemical transformations necessary for life. The genetic bases of these pathways can be transferred horizontally between evolutionarily distant organisms. The interconnected carbon, oxygen and nitrogen cycles provide many of the major elements essential for life on earth, and microbes are deeply implicated in every phase of these cycles.

It is now a well-established fact that ancestral cyanobacteria were largely responsible for the Great Oxidation Event that occurred around 2.4 billion years ago (Canfield 2005). Chapter 1 will discuss this event and its importance for understanding major evolutionary transitions. Although today plants produce about 50 per cent of the oxygen in our atmosphere – in dependence on the cyanobacteria they captured as endosymbionts a billion years ago – this oxygen is all used up in terrestrial respiration and decay. The maintenance of our oxic (oxygenated) atmosphere is due to marine microbes contributing a net gain of oxygen, because of the way in which they decompose anaerobically in ocean sediments (Kasting and Siefert 2002). Photosynthesis by cyanobacteria in the oceans produces enormous amounts of organic carbon too, thus enabling a wide range of heterotrophic life in

marine environments. All secondary producers and consumers, including humans, are further dependent on microbes driving sulphur, iron, phosphorus and manganese cycles (Kolber 2007).

Running the nitrogen cycle is a key biogeochemical role performed by large numbers of prokaryotes with diverse metabolisms. Only bacteria and archaea can accomplish nitrogen fixing, which is the metabolically expensive conversion of unreactive nitrogen gas into more reactive nitrogen compounds. Cyanobacteria fix the majority of marine nitrogen through a variety of methods (Kasting and Siefert 2002). On terra firma, legumes are well known for their bacterial symbioses, in which *Rhizobium* bacteria in root nodules supply plants with fixed nitrogen. The plants provide organic compounds to the bacteria and remove free oxygen, which damages the bacterial enzyme involved in nitrogen fixing. This symbiotic system will feature in Chapter 4. Other plants absorb the ammonia or nitrate produced by free-living prokaryotes. Nitrification is the oxidation of ammonia in soils and water. Mutualistic consortia of nitrifying bacteria work together in this process, with one group oxidizing ammonia (much of which is produced by the microbially assisted decay of organic matter to inorganic chemicals) to nitrite, and then another group converting nitrite to nitrate. In microbial denitrification processes, nitrate is usually converted anaerobically back to nitrogen gases, which can play a role in global warming. This step brings the nitrogen conversion process full cycle. New microbial contributions to previously unknown nitrification and denitrification processes have recently been discovered, leading to major revisions of nitrogen biogeochemistry (Francis et al. 2007).

Closely entwined with the nitrogen cycle and similarly affected by human activity is the carbon cycle. It too is essential to life on this planet and is microbially driven, albeit with considerable input from plants. Microbes decompose organic material, especially plant material, and mediate most of the carbon returned to the atmosphere. In addition, as the outline of photoautotrophy and the oxygen cycle showed, microbes and plants convert inorganic carbon to the organic carbon that is the basis of all non-autotrophic life. Prokaryotes store between 60–100 per cent of the amount of carbon stored in plants, and ten times more nitrogen and phosphorus (Whitman et al. 1998). Viruses, often neglected in biogeochemistry because of not being metabolizers themselves, are now thought to play major regulatory roles in nitrogen, carbon and other cycles due to viruses bursting open (lysing) prokaryote cells, which releases organic material (Danovaro et al. 2008).

From a biogeochemical point of view, therefore, whichever cycle is examined and whatever metabolism is involved, microbes form the basis

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of all necessary life processes. Even a reader determined to maintain a strictly anthropocentric perspective would need to acknowledge that we humans would not survive without the environmental conditions provided to us by microbes. Furthermore, we would not have evolved without them.

Evolutionary history

Microbes are the dominant life forms not only in today's world, but also in all past eras of the living Earth. The origins of life are exclusively microbial; life until recently was exclusively microbial; life in the future will most probably be exclusively microbial too. If there is indeed life on other planets in other galaxies, it is most likely to be exclusively microbial. Stephen Jay Gould (1941–2002), despite his palaeontological training, observed that the Earth always had been and always would be in the 'Age of Bacteria' (1994). However, the implications of this observation go beyond microbes themselves. The existence of microbial life has been the essential basis for the generation of all other life forms. Eukaryotic life began with unicellular eukaryotes; multicellular life began as a variety of organizations of communal microbes. None of the various scenarios for the origins of multicellularity and important subsequent transitions, such as those to metazoan body plans and flowering plants, happened in isolation from microbes.

Although the earliest dates for the emergence of microbial life are not fully agreed upon, almost all estimates, based on fossil and geochemical evidence, date prokaryote origins somewhere between 3.8 and 3.5 billion years ago. A second extraordinary event in the history of life on this planet was the emergence of oxygenic cyanobacteria 2.7 billion years ago (at the latest), and their gradual conversion of the Earth's atmosphere from anoxic to oxic. The first eukaryotic microorganisms probably appeared about 1.5 billion years ago but it took a further billion years (roughly 600 million years ago) for multicellular eukaryotes to make an appearance in the fossil record (Falkowski 2006; Knoll et al. 2006). Shortly afterwards, a mere 530 million years ago, the Cambrian explosion of modern multicellular metazoan body forms occurred.²

An appreciation of this timeline (see Figure I.3) and its utter domination by microbial evolution means that even if the evolution of life is thought of as a stepwise series of major transitions in complexity, and the most

² These are very rough dates and are much debated. Not only are there unresolved issues about fossils, but there is also considerable conflict between fossil and molecular evidence.

Symbiotic collaboration

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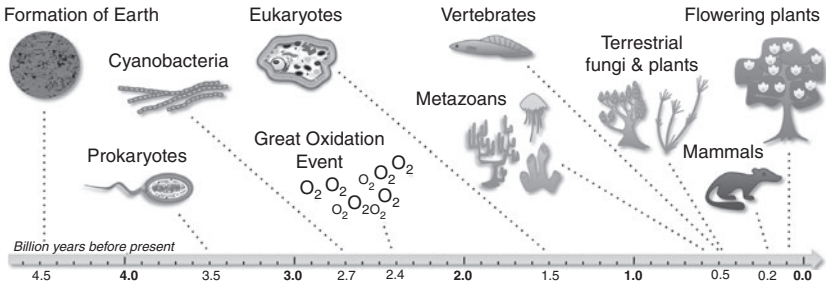


Figure I.3: The evolutionary importance of microbes, with approximate dates.

impressive biological achievements restricted to those that occurred in the last 500 million years, microbial evolution has to be considered in order to contextualize more recent evolutionary developments. Microbes, including viruses, are usefully understood as the engines of evolutionary change, and the several senses in which this is meant will be explored in the following chapters. Evolutionary biologist Theodosius Dobzhansky (1900–1975) is well known for his truism about biology only making sense in the light of evolution (1973). This claim may need microbiological qualification: *all biology and its evolution should be considered in light of microbial evolution.*

Symbiotic collaboration

Multicellular dependence on unicellularity goes beyond a linear relationship in time, and into the present-day constitution of all organisms. A multiplicity of symbioses with microorganisms operates at every level of life. Symbiotic relationships include endosymbioses (within cells), ecto- or episymbioses (on the outside of cells), obligate and facultative dependencies, and mutualist, commensalist and parasitic interactions (Moya et al. 2008). Every symbiosis probably involves microbes, even when the focal symbionts are macrobial. Many mutualistic symbioses are closely integrated and result in the coevolution of the biological entities involved (Herre et al. 1999). I will use the term *collaboration* to describe the flexible symbiotic relationships that have both opt-in and opt-out possibilities, and which involve fluid functional rather than fixed taxonomic relationships (Dupré and O'Malley 2009; see Chapters 4 and 5). These interactions may be reciprocally beneficial in certain conditions; they can endure for millions of years. In others, there may be neutral or negative outcomes for one or more of the participants, but the arrangement nevertheless persists over evolutionary

time. More generally, collaboration of various sorts is inescapable amongst living entities and it occurs dynamically at every level of life.

Eukaryotes, although often perceived as instances of autonomous complexity, are defined by their endosymbiont organelles: mitochondria and – in the case of plants, algae and some protists – plastids (see Glossary). The most common of the latter are chloroplasts, the photosynthesizing unit in eukaryotic cells. There are no eukaryotes without mitochondria, and (within eukaryotes) no plants without chloroplasts. Some of these organelles may have reduced or altered functions, such as the divergent mitochondria called mitosomes and hydrogenosomes (Embley and Martin 2006). Some parasitic plants may have greatly reduced chloroplast genomes and no photosynthetic function. However, despite large evolutionary modifications to the ancestral mitochondrion and chloroplast, the designation of ‘eukaryote’ is based upon microbial collaboration of a fundamental kind. Later chapters will consider a variety of evolutionarily persistent symbioses involving viruses, prokaryotes and other organisms. These relationships exhibit complex balances of cooperation and exploitation, and are maintained by diverse inheritance mechanisms. In many cases, although there are theoretical advantages to non-cooperation, collaborative arrangements between microorganisms and multicellular organisms have given the collective the status of an evolutionary unit.

The diversity and persistence of such arrangements do not mean that microbial collaboration is free of competition, or that competitive interactions are not biologically important. They do imply that we need a better understanding of collaborative processes between organisms, and that microbes will always be involved in such partnerships, whatever realm of life is the focus. A microbiological perspective therefore will lead to a better understanding of evolution, ecology and biology in general. All these areas of research have philosophical aspects, and in addition, microbiology directly informs many standard philosophical questions about biological and evolutionary individuality, evolutionary transitions, and the nature of life. The following chapters will elaborate on these themes in some detail.

To sum up this section about the importance of microbes, all four of these perspectives – biodiversity, biogeochemistry, evolution, symbiosis – point toward the conclusion that from the biosphere to the single organism, and from early life until now, this world is microbial through and through. Microbes may be invisible individually, but collectively they constitute the greatest biological forces on the planet. These four perspectives separately and combined make a case for philosophers of biology to think more inclusively about microorganisms.