

Starting Small:

Using Little Microbes to Tackle Big Philosophical Problems

(Essay Review of O'Malley's *Philosophy of Microbiology*)

Makmiller Pedroso
mpedroso@towson.edu
Philosophy & Religious Studies
Towson University, USA

At first glance, the field of microbiology might seem too specialized to have an impact on philosophy. Someone who has taken an introductory class in philosophy may imagine that philosophy only focuses on questions that deal with humans and other complex animals. Examples of such questions include ‘Is euthanasia morally permissible?’ ‘Do we have free will?’ ‘Is liberalism well-justified?’ For such a person, microbes might seem too simple to matter in philosophy. The book *Philosophy of Microbiology* by Maureen O'Malley offers an alternative picture. O'Malley convincingly argues that microbiology can be a “game changer” for philosophy of biology and other subdisciplines of philosophy—including philosophy of mind, environmental ethics, and philosophy of science. O'Malley makes her case by meticulously describing particular aspects of the microbial world and outlining how they can stimulate new avenues for research in philosophy.

In the first chapter of *Philosophy of Microbiology* the reader is greeted with a curious microbe, the magnetotactic bacteria, a single-celled bacterium that lives in aquatic habitats. These bacteria are equipped with tiny compasses that allow them to orient themselves in the Earth's geomagnetic field. Magnetotactic bacteria use these compasses to migrate downwards to their preferred habitat, regions with little or no oxygen. This behavior suggests that their compasses evolved to prevent them from being exposed to oxygen at the surface water. What is the relevance of magnetotactic bacteria to philosophy? A prominent research agenda in philosophy of mind involves providing an evolutionary account of our capacity to have mental states (e.g., thoughts) that represent external objects (e.g., a bicycle). The ability to make accurate mental representations could be viewed as an adaptation, gradually crafted by natural selection over an extended period of time. Magnetotactic bacteria provide a minimal model to test this hypothesis. In such a model, the compasses of

magnetotactic bacteria represent the type of information they were selected to discriminate, possibly “the direction of the oxygen-free water” (Millikan, 1989, p. 291). With such a minimal model at hand, we can use evolutionary accounts of magnetotaxis—the ability to navigate according to the Earth’s magnetic field—to study how representation devices could have evolved.

How did magnetotaxis evolve? A reasonable hypothesis is that magnetotaxis was directly favored by natural selection because magnetotactic bacteria were better at navigating away from well-oxygenated areas than their competitors. A major challenge for this hypothesis is that magnetotaxis does not seem to be the most efficient navigation system. Other microbes use more direct clues to navigate to their preferred habitats, such as light and oxygen concentrations (pp. 28-29). So, why did magnetotactic bacteria opt for such a baroque representation system? Maybe their compasses initially evolved for other purposes (e.g., some metabolic function) and were later co-opted to serve as a navigation system. The ability of such compasses to represent the direction of the oxygen-free water might have been a by-product of earlier rounds of selection. *Philosophy of Microbiology* discusses this and other hypotheses for the evolution of magnetotaxis in detail (p. 28ff.). Thus, although magnetotaxis is not as feature-rich as human mental states, it furnishes a valuable model to test different hypotheses of how representation devices could have evolved.

Philosophy of Microbiology does not advance a particular account of how magnetotaxis or mental representations evolved. This is not O’Malley’s aim. Her goal is to illustrate a particular strategy of how microbes can be used to construct models in philosophy. Here is O’Malley’s suggestion in a nutshell:

[P]ick an analogous microbial phenomenon to the human one you want to understand naturalistically, and see if this clarifies what the phenomenon is, and why the distinctiveness of the human version of this capacity is (p. 34)

Microbial examples serve as models for other phenomena of large organisms too, for example the ability of multicellular organisms to develop (p. 117ff.). In the 1990s, some philosophers turned their attention to developmental biology, partly because of the role of development at constraining the type of variation on which natural selection can operate (e.g., Amundson, 1994). Although development is typically associated with multicellular organisms, cells in microbial communities also differentiate in a genetically controlled manner. One example is the life-cycle of biofilms, a

type of microbial community, where cells display multiple phenotypes regulated by certain genes (Hall-Stoodley, Costerton, and Stoodley, 2004). Animal development and cell differentiation in microbial communities are certainly different processes, but comparative studies between microbes and metazoans could be illuminating. As O'Malley remarks, “[p]atterns similar to those of metazoans, such as network conservation, hierarchy and modularity, have been identified in the evolution of the regulation of prokaryote and even virus development” (p. 122). Once we recognize that microbial cells can also differentiate in a genetically controlled manner, it becomes artificial to limit the field of evo-devo to animal development.

Despite their small size, microbes rule the animal world. As O'Malley shows, microbes are implicated in many phenomena philosophers are interested in. Consider development once again. The development of many multicellular organisms is primed to the colonization of microbial communities (p. 118ff). During the development of the bobtail squid, for instance, a specialized organ is formed that allows young squids to recruit the bioluminescent bacteria *Vibrio fischeri* from the environment. Leaving the microbes out of the picture would fail to explain the evolution of some of the developmental programs in the bobtail squid (Chapter 4; McFall-Ngai, 2014). Microbiology is also relevant for key issues in environmental ethics. Since most life is microbial and the health of ecosystems depends on microbes, a strong case can be made for the preservation of microbial ecosystems (p. 202ff). Despite this, little is being done to protect microbes endemic to particular environments, such as hot springs, from extinction (Cockell and Jones, 2009). As O'Malley points out, microbial examples are also helpful for studying what the units of conservation should be. The instrumental value of microbes to humans—e.g., the Earth's climate—is largely due to bacterial ecosystems rather than to individual species. This suggests that, in certain cases, the units of conservation should be the function of certain ecosystems rather than species (p. 205ff).

A recurrent theme in *Philosophy of Microbiology* is that microbiology is a fertile field for novel research in philosophy. Take the problem of defining biological species, such as *Homo sapiens* and *Salmonella enterica*. Although the species problem has attracted the attention of many philosophers, much of this work does not take microbiology into account (see Ereshefsky, 2010, for an exception). Yet, the biology of microbes makes defining microbial species particularly difficult (Chapter 3). A major reason for this stems from how prokaryotes exchange genes. In animals, genes are typically transmitted vertically, from parents to offspring via reproduction. In prokaryotes, on the other hand,

gene transfer can occur outside of reproduction via Horizontal Gene Transfer (HGT). The fact that prokaryotes can exchange genes horizontally makes it particularly challenging to define microbial species in terms of phylogenetic relations (p. 72ff.). The phylogeny of prokaryotes is inferred from the evolutionary history of a small portion of their genome, often the 16S rRNA gene localized in their ribosomes. But depending on the extent of genes horizontally transferred, a species definition based on a specific gene will generally fail to specify what conspecific organisms have in common (p. 74). Conspecific organisms could share a specific genetic marker while being very dissimilar in other regions of their genome. HGT casts doubt on how informative it is to define species in terms of particular genes, such as the 16S gene.¹

The evolutionary significance of HGT is not limited to the notion of species in microbiology. Darwin and others after him suggested that the evolution of life could be represented in terms of a single tree, where the lines represent species and the nodes represent speciation events. The fact that prokaryotes can exchange genes horizontally puts a strain on the assumption that there is a single (bifurcating) tree of life (p. 80ff.). A significant portion of the genome of prokaryote cells is prone to HGT. Moreover, unlike reproduction, HGT is not restricted to members of the same species. Accordingly, rather than providing cumulative evidence for the same tree of life, the phylogeny of horizontally transferred genes may support incongruent trees. If someone decides to focus on specific genetic markers, such as the 16S gene, the resulting tree of life will discard too much information. As Dagan and Martin (2006, p. 118.2) nicely phrase it, a tree based on specific genes—such as the 16S gene—will not be the tree of life but the “tree of one percent of life” at best. In this way, instead of a bifurcating tree, HGT suggests that a reticulate tree or a web might be a more accurate depiction of the evolution of life (Chapter 4; Doolittle, 1999).

Philosophy of Microbiology suggests a particular strategy for studying evolution:

[T]hat it may be most effective to construct any properly general account of evolution from the microbes up, rather than the macrobes down (p. 130).

For example, someone that takes a macrobes-first perspective might be tempted to think that there is a sharp line distinguishing unicellular organisms from multicellular organisms. Adopting a

¹ In addition to discussing the problem of defining species in microbiology (Chapter 3), O'Malley also discusses debates about the classification of microbes above the species level, such as kingdoms and the disputed prokaryote/eukaryote distinction (Chapter 2).

microbes-first perspective suggests otherwise:

Although most people—from both biologically trained and untrained perspectives—might think that multicellularity is an empirically obvious category, confidence in the notion of a clear line between unicellularity and multicellularity is likely to dissolve when an ecological perspective, particularly a microbial one, is brought to bear on life (pp. 156-157).

Let me to elaborate O'Malley's point by focusing on one of the examples she cites, biofilms.

Biofilms are densely packed microbial communities that stage a myriad of social interactions. Cells within biofilms communicate via signalling molecules, aggregate with each other, and engage in chemical warfare. HGT mediates many of these social interactions within biofilms. Consider one specific type of HGT called 'conjugation.' In conjugation, Mobile Genetic Elements (MGEs) are transmitted through cell-cell bridges from one cell to another. MGEs are analogous to infectious agents: they are self-interested DNA segments that can benefit or harm their hosts. Sometimes MGEs encode selectively advantageous traits, such as antibiotic resistance (Davies and Davies, 2010). Additionally, biofilms provide a favorable setting for conjugation—probably because of the increased cell density and stability of biofilms (Sørensen et al., 2005). In this way, genes within a biofilm can be thought of as a communal good that different cells can tap into via HGT (p. 105; Ehrlich et al., 2010).

As O'Malley remarks, the role of HGT in microbial communities such as biofilms suggests that they are 'superorganisms,' collectives akin to multicellular organisms (pp. 105-6). If so, biofilms are superorganisms of a curious sort. Multicellular organisms such as ourselves undergo 'reproductive bottlenecks': we start very small, from a single-celled zygote, and we then blow up to the size of a person. Multicellular organisms begin and end with single-celled bottlenecks. However, as O'Malley notes, microbial communities such as biofilms do not undergo reproductive bottlenecks (p. 158). For this reason, O'Malley considers definitions of organisms that do not require reproductive bottlenecks (p. 158ff.). Let me suggest an alternative route. Specifically, consider the following question instead: can biofilms perform some of the functions of reproductive bottlenecks by alternative means? Two functions are typically associated with reproductive bottlenecks. One of them is that reproductive bottlenecks foster evolutionary change in organisms. Because an embryo starts anew every genera-

tion, new mutations in early development can exert a multitude of downstream effects on the mature organism (Dawkins, 1982; Godfrey-Smith, 2009). However, HGT can produce evolutionary innovations by creating new combination of genes within a biofilm (Ereshefsky and Pedroso, 2013, *forth*). For instance, Ehrlich et al. (2010) advance the hypothesis that the resilience of biofilms associated with chronic infections is in part due to HGT constantly producing novel strains with improved survival conditions in the host. The other key function of reproductive bottlenecks is to decrease the chance of conflict between the cells within an organism by increasing the genetic relatedness among the organism’s cells. HGT performs this function in biofilms. In particular, horizontally transferred MGEs can infect non-cooperative bacteria and turn them into cooperators—if the MGEs in question encode the cooperative gene (Nogueira et al., 2009). This is not to say that there are no important differences between reproductive bottlenecks and HGT in biofilms. Reproductive bottlenecks foster evolutionary change because mutations in early development are transmitted to the cells in the adult organism; HGT promotes evolutionary novelty in biofilms by shuffling genes around (Ehrlich et al., 2010). Reproductive bottlenecks increase genetic relatedness by causing cells in the adult organism to share the same genome, the zygote’s genome; HGT, in contrast, increases genetic relatedness with respect to a restricted portion of a cell’s genome (Birch, 2014). Yet, HGT in biofilms can achieve some of the effects of reproductive bottlenecks, production of evolutionary novelties and reduction of conflict.² Although biofilms (and other microbial communities) do not satisfy standard definitions of organisms, my overall suggestion is that multicellular organisms and microbial communities may achieve similar effects (e.g., increased genetic relatedness) via alternative evolutionary mechanisms (e.g., reproductive bottlenecks versus HGT in biofilms).³

Philosophy of Microbiology is part of a growing literature that brings to the fore the significance of microbiology to philosophy (e.g., Dupré, 2012; O’Malley, 2013). O’Malley’s book provides a superb overview of this literature and suggests different ways microbiology can be incorporated into philosophical research. Microbial examples can serve as suitable model systems; microbes are key players in many phenomena in the animal world that philosophers are interested in; and microbiology is a fertile field for novel research avenues in philosophy. Furthermore, O’Malley’s book is accessible to newcomers. Key concepts from microbiology, such as HGT, are explained

² In addition, biofilms can undergo ‘ecological’ bottlenecks, such as cases in which biofilm infections are initiated by a few cells or when biofilms are subject to antimicrobial treatment (Brockhurst et al., 2010).

³ Cf. Clarke (2013), Doolittle and Zhaxybayeva (2010), and Ereshefsky and Pedroso (*forth*).

in detail as she uses them (she also provides a glossary at the end of her book of some technical terms). In sum, *Philosophy of Microbiology* is a lucid, accessible, and well-argued book. The reader will not only be introduced to intriguing facts about the microbial world, but she will also gain an appreciation of how connected the fields of microbiology and philosophy are.

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