Essay Review

What Microbes Can Do: A Sensory Guide to Microbiology

March of the Microbes: Sighting the Unseen
John L. Ingraham
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John Ingraham's *March of the Microbes: Sighting the Unseen* is a sustained and richly illustrated argument for the biological importance of microbes. Taking biogeochemical, physiological, and evolutionary perspectives, Ingraham sets out to persuade us readers that each breath we take, every calorie we consume, and every beat of our hearts has microbial underpinnings. Rather than focusing on the science behind this intricate interweaving of our human lives and the microbial world we live in, Ingraham instead aims to show how microbial knowledge is available through ordinary perception. He takes a community-level perspective of microbial activity, in which he moves from an exploration of their roles as planetary metabolizers and the engines of evolution to a more traditional view of microbes as troublemakers in human health and agriculture. No reader could deny that he succeeds in making microbes fascinating and worthy of everyday attention. The only disappointment might be the modest way in which he does this, and his lack of pursuit of how knowledge of the significance of microbes has been generated.

Popular and other-disciplinary[1] books about microbes are undergoing a resurgence in the general scientific literature. Zimmer's *Microcosm: E. coli and the New Science of Life* (2008) is one of the foremost amongst this genre (see Spath et al. 2009, for three reviews and a response). Hird's book *The Origins of Sociable Life* (2009) is another example, where she sets out a "microontology" of the organization and evolution of microbial communities. Dyer's *Field Guide to Bacteria* (2003) is an excellent generalist introduction to the identification of prokaryotes (it includes archaea) and how to find out more about them. These volumes could be seen as recent exemplars of a much older trend to represent the scope and history of microbiology to a broader audience. Amongst these earlier works are de Kruif's *Microbe Hunters* (1953), first published in 1926; Postgate's *Microbes and Man* ([1969] 1975); or Margulis's many popular discussions of microbial evolution. Although this genre establishes a niche for books, such as Ingraham's, I suggest something else is currently creating the conditions for publications like this—something that has more to do with the nature of microbiology today.

Microbiology has always been viewed as a technology-driven science, due to its emergence in dependence on microscopy and pure-culture techniques. Recently, however, new technologies have partially liberated microbiological science from the laboratory and from culture-dependent approaches. The insights produced by modes of investigation, such as metagenomics (the culture-independent, sequence-based analyses of microbial communities), have radically expanded scientific knowledge of the microbial fundaments of planetary and organismal processes. This expansion of knowledge via microorganisms was also the case in the early years of molecular genetics, when microbial insights generated through model microbial organisms (e.g., *E. coli*, T4 phage, *Neurospora*, yeast) produced novel means of understanding genetics that could eventually be applied to multicellular organisms. However, in today's discoveries, rather than microbes being primarily tools, these new approaches have given priority to microbial involvement in making our world. Ingraham seizes upon this achievement but does something quite curious with it: He provides a guide to microbe watching with the "five unaided senses" (p. 22). After outlining some of the "sightings" that he shares with his readers, I will put Ingraham's perspective into

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a more conventional epistemological framework, and make a few suggestions for how philosophers and other scholars of science might follow through on what the book has to offer.

A Sensory Guide to Microbial Metabolism

The scientific "visibility" (i.e., detectability) of microbes is only the background to what Ingraham aspires to show his readers. His real aim is to bypass technicians and instruments, and begin to appreciate microbes in their own right. To do this, Ingraham shifts our focus from microscopic entities to macroscopic processes, all the while giving quiet credit to the more individualized approaches that have fed into this microbial-centric view of life. His trick for doing this is to encourage the cultivation of ordinary sense perceptions of microbial activity. He shows repeatedly how smells, tastes, and sights (and much more rarely and indirectly, sounds and tactile sensations) can become reliable guides to an expanded understanding of microbes. Ingraham's achievement is to make us realize how the apparently microscopic life world makes a perceptible difference to our lives from even the most ordinary and unspecialized point of view.

The book starts with a very general account of the history of microbiology and its dependence on innovations in microscopy and staining, then molecular techniques. It is not through morphology, he insists, that microbes should be approached, but through metabolism. A metabolic understanding of the microbial world will illuminate its diversity, versatility, and world-shaping importance. Through an analysis of the metabolic capabilities of microbes, Ingraham can shift from the microbial bases of planetary biogeochemistry (the nitrogen, carbon, and sulfur cycles, as well as oxygen) to the microbial contributions to many human foodstuffs (cheese, champagne, sweeteners, thickeners). He outlines the highly collaborative nature of microbial life, whether between varieties of microbes or microbial–macrobial cooperatives. Lichens, ruminant guts, and crown galls on plants are just some of his examples. The versatile lifestyles enabled by such cooperation allow every environment imaginable to be colonized, including the most extreme and—from a human perspective—inhospitable.

Once this metabolism-centric view is established, with its emphasis on ecologically driven variability, Ingraham shifts back to what might be regarded as a more traditional perspective: that of microbes as pathogens and problems for health, agriculture, and industry. He includes fungi[2] in this survey (not just micro-fungi) and viruses, although any debate about the latter's aliveness is firmly quashed as "tiresome" (p. 17). Ingraham also gives insightful accounts of the therapies against the "felonious" nature of these microbes, and the microbial countermeasures against those therapies (e.g., antibiotic resistance). He touches on social aspects of microbiology with brief and rather limited discussions of anti-vaccination campaigns and genetic manipulation troubles (the latter interestingly discussed in relation not to agriculture but to snowmaking). Important debates in microbiology (for example, whether *Giardia* are amitochondriate eukaryotes and thus living fossils) are glossed over and summed up rather unsatisfactorily (e.g., pp. 273, 299). The book concludes with chapters that reflect on the environmental importance of microbes, with a focus on how the anthropogenic perturbation of many microbial communities (corals, marine phytoplankton) might affect human health. It is we who should be worried for our own sake, he advises: Microbes are far more likely to persist into the evolutionary future than we are. Their "health" is therefore our health, and a guide to our continued existence on the planet.

The ending of the book is a nice twist of the conventional medicalization of microbes. He turns the pathogenicity discussions back into a broader ecological discussion, thus showing how limited human interests with regard to microbes and large-organism conservation are embedded within and enriched by this larger perspective. In this strategy lies the book's success. But curiously, for a book that revels in the lesser known and the often overlooked details, the cover succumbs to what Ingraham is battling against. He rejects the assumption that to be interesting and attract attention certain visual elements of individual organisms are needed, notably shapes and colors. The cover, however, features diatoms exclusively. These eukaryotic microorganisms are an important protist group, and indisputably beautiful under the microscope, but are by no means the majority or even a good representative of the microbial communities that Ingraham is advocating we should recognize more in our daily lives. This slip between the cover and Ingraham's message exemplifies the uphill nature of the climb toward micro-awareness he and other ecologically oriented microbiologists are leading. The eco-microbiological surge may have begun, but it has a long way to go.

From Microbes as Tools to Microbes as Biological Forces

Such a surge might also be underway in philosophy of biology, where an increasing number of discussions have mentioned microbes and microbiology (e.g., Franklin 2007; Lyon 2007; O'Malley and Dupré 2007; Bouchard 2010; Ereshefsky 2010). One reason for the earlier philosophical neglect of microbiology may be because for much of biology, microbes are merely tools or resources for biological research. Although many molecular and genomic discoveries have been made on the basis of microbial cells and their components, the interest in these findings for non-microbiologists has often been in relation to what these findings said about genes, genomes, and biological processes in general. Tools themselves have rarely been a philosophical focus (this is different in history of biology, and there are good lessons to be learned from this difference), and this might be why microbes have not been either.

Although the claim that prokaryotes could serve as model genetic systems had early roots in the late 19th century and early 20th century's "general microbiology" (which had a strong biochemical emphasis), it took the advent of molecular biology in the 1940s to irrevocably establish the practical importance of microbes for more general biological research. Ingraham mentions this, and the advent of metagenomics, in which the culture-independent sequencing of microbial communities in the wild as well as sometimes in the laboratory leads to analyses done on the basis of sequence indications. However, he largely avoids detailed discussions of how particular findings have been made, preferring to emphasize unaided sensory perceptions of microbes. This is in part because the default "invisibility" view is what he wants to avoid: microbes are indeed visible if not thought of as single cells. This strategy stops him, however, from reflecting on the fact that something has happened to microbiology in the last 15 years or so that gives microbes a rather different epistemic status than tools, and a rather different ontological status than invisible entities for specialists to examine. Ingraham mentions the "explosive growth phase" (p. 37) ecological approaches to microbiology are experiencing. However, he doesn't pursue these approaches themselves, and all mention of how the science was done is subordinated to the actual microbial activity, to the point of eclipsing the practices that revealed such activity. There are two particular implications of Ingraham's diminishment of a scientific perspective that I want to examine. The first is the shift from a morphocentric perspective and toward a metabolic focus; the second is to think a bit more about the intriguing axiom Ingraham mentions of "microbial infallibility," which is concerned with metabolic capacities.

While microbiology long ago abandoned morphocentrism in favor of biochemical, molecular, and cell-biological perspectives, everyday appreciation of Nature tends to be stuck in the aesthetics of shape and color. Ingraham's main message is that this is not enough: that any such viewer will be deprived of more diverse experiences of wonder and subsequent responsibility (e.g., in regard to climate change) if single-organism morphocentrism is maintained. He is perfectly happy to use shape and color at the community level, and much of his "sense-making" of microbes occurs through this strategy. I already mentioned the book cover as an example of the difficulties of pursuing such a tactic. There are other issues to think about too. Many philosophers of biology are anti-reductionists and prefer to take a "whole-organism" perspective. Seldom, however, does this mean that they take a whole-community perspective. It is worth thinking more about what these different levels of investigation mean for evolutionary theory, scientific practice (whole-organism approaches could be argued to be reductionist from a community-level perspective), and concepts of organism. It is for such reflections that many readers of this journal might be reading Ingraham. Indeed, the "everyman" who is the target of the book may have wanted to see such implications pursued as part of Ingraham's elucidation. Some reviewers have complained that the book is a bit wearing in its lists of microbial capacities and their effects (e.g., Turney 2010). Occasionally deeper discussions of what such sightings mean for the sciences of life and evolution could well have served as an antidote to any perception of the book being just one example after the other.

Microbial Infallibility in Light of Two Discoveries

A few times, particularly when discussing the non-biodegradability of plastics, Ingraham mentions "the fundamental dictum called microbial infallibility" (p. 157). This is the claim that every naturally occurring organic compound can be degraded by microbes, and it is often associated with the assertion that "no natural chemical reaction exists that cannot be exploited as a source of metabolic energy" (p. 22). For Ingraham the latter becomes an explanation of microbial diversity, which in a circular way is an explanation of planetary chemistry. Microbial infallibility was first outlined by Gale in his book *The Chemical Activities of Bacteria*, where he states (also somewhat circularly) the following: "Somewhere or other some organism exists which can, under suitable conditions, oxidise any substance which is theoretically capable of being oxidised" (1951: 5). This statement is sometimes referred to as a hypothesis or even a doctrine, but most frequently as "the principle of microbial infallibility" (e.g., Alexander 1964: 246). Its claims were extended to include chemicals introduced into microbial environments, such as pesticides and synthetic polymers (plastics). But in the 1960s and 1970s, a wave of publications sought to show that microbes were far from infallible; instead, they became "deficient," and many molecules, including some naturally existing ones, could be understood as "recalcitrant" to incorporation into biogenic processes (Alexander 1964; see Horvath 1972 for subsequent critiques of the fallibility argument). Ingraham agrees that this principle of infallibility is by no means secure, but thinks that in the fullness of evolutionary time it is possible that microbes will adapt to degrade the compounds that make up plastics (p. 157). The grounds for this belief are straightforward: evolution occurs, microbes are very adaptable, and plastics are new.

But here, I think, is an example of where it seems too shallow to leave out the epistemological dimension of knowledge about such processes. Are there good grounds for thinking infallibility is a useful starting point for investigation? What discoveries have been made on the basis of predicting thermodynamic possibilities for metabolism? Ingraham briefly mentions the story of the discovery of anammox bacteria as he talks about the nitrogen cycle (p. 137). This is an important biogeochemical case that involved the detection of anaerobic ammonia-oxidizing bacteria (Strous et al. 1999; Kuenen 2008), thereby substantiating thermodynamic predictions made two decades earlier that such reactions could be produced biologically (Broda 1977). Subsequent supporting studies have overturned associated assumptions that ammonia oxidation, crucial to global nitrification, is entirely bacterial (Francis et al. 2005). Another recent discovery of organisms able to anaerobically oxidize methane solved the mystery of why vast methane reserves under the sea floor do not escape into the sea and atmosphere (DeLong 2000). Geochemists had hypothesized that anaerobic methane oxidization was occurring biologically, and that it had something to do with sulfate reduction (Martens and Berner 1977; Zehnder and Brock 1980). Until 2000, no organismal basis could be found. Then, in a flurry of micrographic and molecular studies, strong evidence for this hypothesized interaction was pieced together (Boetius et al. 2000; Valentine 2002; Hallam et al. 2004). In a reversed version of "normal" methanogenesis, anaerobic methane-oxidizing communities of archaea are believed to be thriving as they consume methane syntrophically in the company of sulfate-reducing bacteria.

These two stories have several commonalities of discovery and investigation. They involve predicted but thermodynamically constrained processes in previously undetected organisms; they are concerned with globally important nutrient cycles (and in fact cause major revisions in scientific understanding of them); they are undergoing modification in their biochemical details even as the initial findings are celebrated (Strous and Jetten 2004; Pernthaler et al. 2008). Such exciting developments are the backdrop against which Ingraham tells his stories of microbial activity. But the scientific dimension of what microbiologists are doing is so deeply subordinated to the accounts of what microbes can do that we gain little sense of why all this was not known before. This does not mean that microbes need to be seen as simple devices for a human-centric understanding of the world or that any account of microbiology should be a history of microbiologists (as it so often is). On these counts, Ingraham's eco-microbiological perspective is enriching and correcting, as it turns around standard perceptions of why anyone would study microbes and foregrounds microbial processes rather than great men and the occasional woman. But with the epistemological dimensions of these stories left out (as are all the references), what we have is something of a catechism (this is how it is, and here is how to respond) rather than an encouragement to inquire more critically into a discussion of how such knowledge is generated, what its relationship is to less ecological bodies of knowledge, whether such knowledge compels certain sorts of responses, and how to balance human interests against microbiologically generated awe.

Conclusion

Overall, when considered as a starting point for further investigation of the microbial world, *March of the Microbes* offers motivation and inspiration. These were Ingraham's goals, and on those grounds, the book achieves its purpose. Whether philosophers and historians of science can take his material further will depend on their willingness to mine the microbiological literature and examine, for example, contested claims, such as the principle of microbial infallibility or major shifts in biogeochemical assumptions.[3] For anyone in search of unexploited cases and rich veins of insight into biological processes at multiple levels, Ingraham will serve as an introduction to some major shifts in microbiological practice and theory. As an orienting device, and a broad framework for a process-oriented community-level biology, the book is well worth reading.

Notes

1. That is, from a point of view outside microbiology and its cognate disciplines.

2. I suspect this inclusion is because fungi fit into the broad category of "uncharismatic" organisms, as do microbes. Ingraham's agenda is explicitly one of affirmative action for microbes, and he sweeps up these other groups as he proceeds so that no organism is left behind.

3. A very nice example that would lend itself to an epistemological analysis is when Strous et al. (2002), veterans of the anammox story, outline a history of experiments that is "not the order in which they have been carried out—but rather how they should have been planned if we could start again" (694).

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