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Essay Review

Philosophy of biology in the twenty-first century

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The Oxford handbook of philosophy of biology, Ed. Michael Ruse; Oxford University Press, Oxford & New York, 2008, pp. xiv + 642, Price US$49.95 £30.00 paperback, ISBN 978-0-19-973726-0.

We have survived the first decade of what Craig Venter and others have called "the biological century" (p. 530). A complete draft of the human genome is now available to scientists and the general public (p. 451). But the human genome project seems like old news, and progress continues: over a hundred eukaryotic genomes have been sequenced since 2003; last year, a team led by Venter created the first bacterial cell controlled by a synthetic genome (Gibson et al., 2010). These developments in biology have brought with them a series of ontological, epistemological, and ethical questions. Small wonder that the philosophy of biology, which only emerged as a separate subfield in the 1970s (pp. 23–25), has become one of the most exciting areas of philosophy.

Assembling a philosophy of biology handbook is difficult, as the field encompasses several different types of research. Philip Kitcher (2005, p. 820) describes four standard approaches:

(1) Reassessing problems in general philosophy of science
(2) Developing new answers to classic philosophical questions
(3) Engaging with conceptual problems in biology
(4) Analyzing the ethical and social implications of biological discoveries

As might be expected given Michael Ruse's own research interests, roughly half of the book's chapters take the last approach. This breakdown is not necessarily representative of the field: for example, one recent survey does not even mention this fourth approach, and another highlights only the third (Griffiths, 2008; Haber, Hamilton, Okasha, & Odenbaugh, 2010). Nevertheless, the diverse chapters—all written specifically for this volume—do give the reader a feel for the many kinds of projects that interest philosophers of biology. In this review, I will discuss a subset of the chapters, extending key points and describing more recent developments in the area when possible.

After Ruse's introduction, which simply summarizes the twenty-five chapters, the book begins with David Hull's overview of "The history of the philosophy of biology." He restricts himself to the English-speaking world since the nineteenth century, plus a short section on Aristotle. It is a good summary, but inevitably there are sections where more detail would have been helpful: Herbert Spencer, for example, is mentioned only briefly, as the object of Chauncey Wright's attacks (p. 19). Though often ignored by modern philosophers of biology, Spencer—perhaps the most famous philosopher of his day—popularized the ideas of evolution and organism-environment interaction (Godfrey-Smith, 1996; Pearce, 2010b; Werth, 2009). He was also a foil for American philosophers like Charles Sanders Peirce, William James, and John Dewey, all of whom (as Hull indicates) closely followed developments in the life sciences (pp. 20–21). The precise ways in which biology shaped pragmatism are still being worked out. Dewey, for example, was influenced by philosophers combining Hegelian and biological ideas, as well as by debates in the 1890s about the causal factors of evolution. In the second half of the chapter, Hull provides an excellent sketch of how philosophy of biology developed into a separate subfield in the 1970s with the appearance of textbooks by Ruse and Hull along with seminal articles by Kenneth Schaffner, William Wimsatt, and others (pp. 23–25). He also emphasizes the importance of philosophically interested biologists: Richard Lewontin, for example, supervised and wrote papers with a series of young philosophers of biology (p. 27). This kind of collaboration continues today, with both biologists and philosophers contributing articles to journals such as *Biology & Philosophy* (p. 29).

André Ariew's chapter on "Population thinking" addresses the well-known contrast between the typologist (or essentialist) and the population thinker (pp. 64–65). Ernst Mayr famously placed Darwin in the latter category. Elliott Sober (1980) characterized the distinction in a new way, suggesting that essentialism and population thinking are two strategies for explaining variation: the former attempts to identify the 'natural state' of a type, while the latter focuses on statistical features of populations (pp. 65–68). The problem with Sober's account, according to Ariew, is that it

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rules out Darwin, whose own "nonstatistical theory of natural selection" differs from later versions (p. 69). Ariew provides a new account of population thinking, arguing that it is not a metaphysical but a methodological doctrine, according to which "regularities that occur in populations…emerge from the collective activities of individuals." The central question is how population-level order is possible despite individual-level variation (pp. 71–72). Thus even though Darwin was not a statistical thinker, he was a population thinker in Ariew's sense. More specifically he was a "force theorist," for he believed that regularities at the population level are the result of conditions faced by every individual—e.g., resource limits or 'checks' (p. 82). Statisticians like R.A. Fisher, in contrast, do not require such forces: all that matters is that life histories and reproductive schedules vary, and that certain histories and schedules are favored. There is a 'tendency' at the population level, and local causes at the individual level can be disregarded (p. 83). Although Ariew does not mention this in the chapter, the 'force theory' and 'statistical' approaches are related to two different ways of thinking about natural selection that are at the center of recent debates in the philosophy of biology (Matthen & Ariew, 2002; Stephens, 2004; Walsh, Lewens, & Ariew, 2002).

Ruse, writing on "Darwinian evolutionary theory," lists three methods of detecting adaptation: comparing related organisms, reverse engineering, and optimality modeling (pp. 48–51). Steven Orzack, in a later chapter, discusses the first and third methods in more detail. He begins with optimality models, arguing that a qualitative fit between model and data is not enough to establish the local optimality of a trait; after all, causes other than selection may explain the quantitative discrepancy (p. 95). He then moves on to the comparative method, where he introduces the problem of phylogenetic non-independence: i.e., different species may share a trait because they inherited it from a common ancestor (p. 98). Finally, he presents what he calls the "ensemble test of adaptationism," where an assemblage of individual tests of local optimality provides evidence for or against adaptationism, depending on how frequently a quantitative fit is found (pp. 105–107). Orzack points out that if we accept an "ensemble claim about nature" as the argument for the primacy of allopatric speciation, it should also work for adaptationism—and, I would add, for the relative importance of factors such as constraints on variation, ecosystem engineering, and the 'Baldwin effect' (Coyne & Orr, 2004; Pearce, 2011; Pearce, in press; Schwander & Leimar, 2011). Despite some obvious epistemological difficulties, it is at least possible to use a series of case studies "to make some progress in answering global questions piecemeal" (Maclaurin & Sterelny, 2008, p. 80).

In his chapter on "Teleology," Denis Walsh effectively counters a number of standard arguments against the compatibility of naturalism and teleology. He goes on to claim that goal-directedness can explain more than bare mechanism, as a goal-directed system often realizes its goal via different mechanical causes and in a variety of situations (pp. 123–124). In a brief sketch of function ascription in biology, Walsh makes a point that is often overlooked in philosophical discussions: Cummins' causal role account of functions "can underwrite the function/malfunction and function/accident distinctions by appeal to the pragmatics of explanation" (p. 127; see also Karen Neander's comment on proper functions, p. 386). In the final section of the chapter, Walsh suggests that phenotypic plasticity during development is evidence that organisms are teleological through-and-through: i.e., goal-directedness explains the regularity of organic development (pp. 129–132). Some questions remain. Does goal-directedness also explain variation caused by plasticity? Is plasticity really a necessary condition of adaptive evolution? Nevertheless, Walsh makes a good case for teleology naturalized.

Roger Sansom on "Evolvability" and Richard Richards on "Species and taxonomy" deal with ongoing debates among evolutionary biologists, in which new results and altered models appear constantly. Thus, I will focus on the relation of these chapters to more recent biological and philosophical work. There is a whole spectrum of meanings of evolvability (Pigliucci, 2008). It is often talked about in general terms, e.g., as "the genome's ability to produce adaptive variants" (Wagner & Altenberg, 1996). Sansom wisely narrows the definition to "the propensity to mutate adaptively in an environment" (p. 138). Unsurprisingly, making the idea experimentally tractable requires even further specification. A recent paper from Richard Lenski's group defines 'evolvability' as "the expected degree to which a lineage beginning from a particular genotype will increase in fitness after evolving for a certain time in a particular environment" (Woods et al., 2011). This narrowing allowed them to show that less fit genotypes can nevertheless eventually take over the population if they are more evolvable. In this case, those genotypes that were originally more fit contained alleles that interacted negatively with later mutations, cutting off the paths that led the originally less fit genotypes to success. Nevertheless, as Sansom rightly points out, we would also like to say that genotypes with a propensity to mutate adaptively across a wide range of environments are more evolvable than those with such a propensity only in certain environments (p. 152). Thus there may be room for both broader and narrower conceptions of evolvability.

Richards provides a short overview of the history of taxonomic views from Linnaeus to Hennig (pp. 163–167). He then outlines the cladistic approach, which is now dominant (p. 168); thus, in newer museum exhibitions, visitors are constantly informed that dinosaurs are not extinct—for birds are dinosaurs. The reason for this claim is that cladists only recognize monophyletic groups, i.e., those consisting of an ancestral species, all of its descendants, and only its descendants (p. 167). Hence birds are dinosaurs, insects are crustaceans, and we are fish. As Richards says, the real debate now is *within* cladistics: what is the best way to construct a phylogenetic tree given character data? (p. 172) More recent work has made clear that questions about different methods of phylogenetic inference—parsimony, likelihood, Bayesian, distance—are essentially philosophical, rather than empirical (Haber, 2009). As Sober (2008, p. 333) describes, maximum likelihood methods try to find the tree that confers the highest probability on the character data, whereas maximum parsimony methods try to find the tree with the fewest character state changes. These methods often produce trees with completely different topologies (p. 171). Philosophers thus have much to contribute to the debate over phylogenetic inference, as demonstrated by a series of recent interventions (Kearney, 2007; Sober, 2008, pp. 232–252; Velasco, 2008; Autzen, 2011).

John Beatty's chapter on "Chance variation and evolutionary contingency" and David Sepkoski's chapter on "Macroevolution" both concern deep questions about evolutionary history. Beatty describes Darwin's analysis of changes in the position of orchid labellae. The labellum is usually the lowermost of an orchid's three petals, but reaches that position via a 180-degree twisting of the stem. In certain species, however, it is the topmost petal: in these cases, the stem is in some species twisted 360-degrees, and in others not twisted at all. According to Darwin, it is chance variation—or mutation order, as we might now say—that makes the difference (pp. 192–193). Beatty goes on to discuss more recent experimental work that highlights the importance of chance events, and not just the interplay of constraints and selection, in evolution (pp. 206–207; Lenski & Travisano, 1994; see also Desjardins, 2011). Sepkoski's chapter also emphasizes the importance of chance in evolution, but argues that on a hierarchical view, processes can be seen as random at one level but determinate at another. For example, although the asteroid responsible for the end-Cretaceous extinction had a causal history, and the extinction happened to favor certain groups, those groups could not in any sense 'prepare' for the event (pp. 228–230). The hierarchical account of evolution pioneered by Gould and others, which claims that selection operates on multiple interacting levels, brings with it a set of questions with which philosophers and biologists are still grappling (Grantham, 2007; Jablonski, 2008).

Kenneth Waters and James Griesemer both use their topics as springboards for discussions of philosophy of science methodology. Investigating classical and modern genetics, Waters argues against both Kitcher's ''layer-cake antireductionism'' and Schaffner's ''theoretical reductionism'' (pp. 244–250). According to Waters, the problem with both of these positions is that they are focused on theory instead of on investigative practice—on explanation rather than manipulation (pp. 251–252). He argues, citing experiments to determine the function of a protein in *C. elegans* neurons, that the molecular revolution was important not because it allowed reductionist theoretical explanations but because it provided a rich set of experimental tools. Basic theory, says Waters, is usually used only ''to help construct experiments and to explain experimental results''; for instance, genes and DNA play no role in explaining the function of the neuronal protein in the experiments he describes (pp. 256–258). The upshot of the chapter is that philosophers of science need to pay more attention to experimental practice within biology, and not just to general theories.

Griesemer gives the reader a good entry into the complicated world of ''Origins of life studies.'' He notes that the ''conceptual instability'' of the area presents a compelling set of questions, especially for those philosophers interested in ''the social organization of research, questions of disciplines and interdisciplines, collaboration and integration, [and] unity and disunity (pp. 264–265). At the origins of life, biology reaches its limit; thus, it can serve as ''a good test bed'' for ideas developed to explain life's evolution rather than its origin. Like engineers, philosophers can benefit from seeing how their concepts fracture when taken to extremes (p. 266, 285; Wimsatt, 2007). For example, the problem of the initial emergence of phylogenetic structure is likely of interest to philosophers of systematics (p. 284). Jason Robert's account of ''Evo-devo'' combines issues raised by Griesemer and Waters: evo-devo can be seen as *the* integrative project, and thus—like origins of life studies—involves many kinds of collaboration (p. 292); and it also boasts reductive and non-reductive ancestors in developmental genetics and comparative embryology, at least on one view of its origin (p. 302). Philosophers are just beginning to pay attention to developmental biology in its own right (and not only evo-devo), work that will likely require the focus on experimental practice that Waters endorses (Diteresi, 2010).

Three of the chapters analyze epistemological and ethical problems arising from developments in genetics and genomics. Zachary Ernst argues that genomics should not lead us to abandon the concept of a gene; we simply need to ''learn a more nuanced lesson about what genes are, how they function, and how they are to be found'' (p. 316). He closes with a call for a philosophy of computer science: computers are handling greater and greater volumes of data, overcoming many of our epistemic limitations and changing what is possible in biology (pp. 324–325). Lisa Gannett discusses ''Genes and society,'' and in particular the human genome project. She employs a distinction between 'upstream' and 'downstream' inquiry, corresponding to scientific research and its application, respectively. Bioethicists normally reside downstream and philosophers of science upstream, but some paddling or drifting may be in order (pp. 453–454). I agree that Dewey's work suggests a better approach, one which incorporates ''evaluative as well as descriptive dimensions of science'' (p. 468), though a discussion of his views on the interdependence of means and ends would have clarified his position (Dewey, 1938). Robin Andreasen examines genetics and race in medicine, distinguishing between those who would eliminate race as a variable in medical research; those who would keep it but believe it to be socially constructed; and those who would keep it and allow that it is at least partly explained by genetics and thus geographic ancestry (p. 479). Andreasen defends the last of these because it leaves open the relevant empirical questions (p. 500). She also points to an important debate about how to understand genetic differences: a locus-by-locus analysis gives different results from one that includes gene correlations (p. 499; Edwards, 2003). Philosophers have begun to address this issue, but more work is needed (Hacking, 2006).

Anya Plutynski's chapter on ''Ecology and the environment'' begins with a history of the balance of nature idea, still often discussed by philosophers (Walter, 2008; Pearce, 2010a). She points out that the idea has survived despite changes of vocabulary from ''harmonious integration'' to ''feedback mechanisms'' (p. 511). However, the so-called diversity-stability hypothesis—that diverse ecosystems are more stable—is difficult to pin down experimentally, and she concludes the section by urging environmentalists to be more cautious in using terms like 'fragility' and 'balance' (p. 513). In examining ecological methodology, Plutynski surveys philosophical discussion of models as tools and of tradeoffs in model building (pp. 514–517). This conversation has continued more recently in a special issue of *Biology & Philosophy* (vol. 21, no. 5) devoted to the work of Richard Levins (see also Weisberg, 2007). She ends with a short section on environmental decision-making, but does not provide an argument for the precautionary principle beyond the claim that we should by now be used to uncertainty and underdetermination in science (pp. 517–520). (Unfortunately the bibliography of this particular chapter is full of mistakes and missing references.)

Environmental issues bring together economists and biologists, two groups that also share an interest in evolutionary game theory. William Harms and Brian Skyrms review the game theory literature on the ''Evolution of moral norms.'' They describe three kinds of projects in this area, corresponding to three evolutionary stages (p. 434–435):

(1) Evolution of ''behavior in consonance with ... norms''
(2) Evolution of various enforcement behaviors
(3) Evolution of moral language and its meaning

Philosophers have primarily analyzed the first of these stages, and shown that (at least in prisoner's dilemma scenarios) ''positive correlation of types'' leads to cooperation (pp. 438–440). Harms and Skyrms then describe several experiments in which the possibility of punishment alters the results dramatically before moving on to the final stage, moral language. This last section draws on work by both authors, and is likely to be controversial—at least as an account of morality. Skryms suggests that animal warning cries are ambiguous in the same sense as moral intuitions: an alarm call can be interpreted either ''as indicating the nature of the predator or as prescribing the correct evasive behavior'' (pp. 445). Such signals, however, do not carry moral force; it is not immoral to ignore an alarm call. Harms proposes that moral normativity arises when enforcement signals are internalized. An internalized signal would be 'true' when the relevant convention is violated, but could also command directly (p. 445–446). Ethicists will likely not be convinced, but recent work has continued to show that evolutionary considerations can illuminate at least some aspects of our ethical life (Joyce, 2006; Kitcher, 2011).

I have not been able to discuss every chapter of the book; my choices were based on my own interests and expertise, rather than on quality. The Oxford handbook is a good introduction to the varied concerns of philosophers of biology. Several classic topics—for instance, the units and levels of selection—are missing, but these have been thoroughly treated elsewhere. Those wanting more detail on focused conceptual issues such as adaptation, genes, information, mechanisms, and reductionism will likely prefer the Cambridge companion (Hull & Ruse, 2007). On the other hand, the handbook boasts many more chapters on topics of wider interest: agriculture, rhetoric, feminism, race, etc. There is never room to include everything in such collections: I especially missed chapters on modeling, experimentation, evolutionary transitions, and adaptive feedback (on the latter, see Barker, 2008). I have described the handbook as a good introduction to the field, and it is; but more importantly—and this was its role for me—it serves as a guide to the different subspecialties of the philosophy of biology, allowing researchers to move out of their existing niches and discover new adaptive possibilities.

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