

Evolution

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Introduction

It has become almost standard practice for philosophers of biology to bracket their writings with a pair of manifestoes. The first manifesto proclaims that the philosophy of science is not just about physics anymore. This is usually accompanied by an argument suggesting that a myopic focus on physics has led the philosophy of science to misrepresent the true nature of science. As we face a new millennium, the time has come to dispense with such proclamations. The philosophy of biology has come into its own and no longer needs to justify its existence. One look at the most recent Philosophy of Science Association conference (PSA 2000) should be enough to convince anyone of that fact: approximately one fourth of the presentations are in the philosophy of biology. The first manifesto has become manifest.

The second manifesto, on the other hand, often takes the form of a “call to arms” for philosophers to venture into fields of biology outside of evolutionary theory, such as ecology and molecular biology. That this call to arms has been at least partially successful is reflected in the inclusion of an essay in this volume on Developmental and Molecular Biology, distinct from the

present essay on Evolution. Thus, I need not apologize, as many have done before me, for focusing exclusively on evolutionary theory. Yet, since many of the debates in the philosophy of evolution overlap and intertwine with those in the philosophy of developmental and molecular biology, it is not entirely possible to separate the issues. In fact, philosophers seldom use the phrase “philosophy of evolution.” Philosophy of biology has often *meant* philosophy of evolution. However, perhaps it is time to be more explicit.

The philosophy of evolution considers issues that are both conceptual and empirical, and consequently it is practiced by philosophers and scientists alike. The following discussion will reflect that diversity. Some philosophy of evolution has looked to evolutionary theory to answer broader questions in the philosophy of science. For example, a recent volume explores epistemological issues through the lenses of evolution and other areas of biology (Creath and Maienschein 2000). While I applaud such work – in fact, I think there ought to be more of it – it does not make up the bulk of the philosophy of evolution, most of which focuses on issues specific to the discipline (although often with broader implications for issues such as causality and explanation). So, my focus will be on the specific rather than the general. Even so, philosophy of evolution at the dawn of the twenty-first century suffers from an embarrassment of riches, both in terms of the number of interesting topics and in terms of the number of insightful analyses exploring these topics. I cannot hope to do them all justice in an essay of this length. Thus, some topics will be touched on only briefly, some in more depth, and perhaps some not at all. My intention is to provide a guide to what I take to be the most important and interesting issues in the philosophy of evolution today, and to point the reader to classic as well as more recent sources.

Mechanisms of Evolution

Arguably, and perhaps uncontroversially, Charles Darwin's greatest contribution to biology was his theory of natural selection. Others had proposed theories of evolution, but it was Darwin's theory of natural selection that made evolution plausible by providing a mechanism through which evolution occurs.¹ According to this theory, if three conditions obtain: 1) organisms within a species vary from one another; 2) if some of those variations are heritable and advantageous to the organism; and 3) there are more organisms that can survive, leading to a "struggle for life," then organisms with advantageous variations will tend to survive better and reproduce more, leading to an increase in organisms with advantageous variations (and a decrease in organisms with harmful variations) over the course of generations.

According to Gould and Lewontin (1979), Darwin is often portrayed as having put forth natural selection as the sole mechanism of evolution in the first edition of the *Origin of Species*, only (misguidedly and under critical pressure) including other mechanisms in later editions. Against this view, Gould and Lewontin argue that Darwin was a pluralist concerning mechanisms of evolution (1979). Indeed, the last sentence of the Introduction to the first edition of the *Origin of Species* states: "I am convinced that Natural Selection has been the main but not exclusive means of modification" (Darwin 1964). Darwin endorsed such evolutionary mechanisms as Lamarckian use and disuse² and sexual selection (which Darwin considered a different mechanism from natural selection). Thus, even for Darwin, natural selection and evolution were not the same thing; natural selection was the primary, but not the only, mechanism of evolution. In contrast, Alfred Russel Wallace, who independently arrived at the theory of natural selection, is usually interpreted as being much more of a selectionist than

Darwin, at least for non-human animals.

The Neutralist/Selectionist Debate

During the twentieth century, there was much debate over mechanisms of evolution – is natural selection the sole or primary mechanism of evolution, or do other mechanisms play a greater role (Beatty 1984; Provine 1985)? One debate in particular (in its earlier versions, between Sewall Wright and R. A. Fisher) concerned the relative roles of natural selection and the phenomenon of *random drift*.³ Random drift occurs when physical differences between organisms are causally *irrelevant* to differences in their reproductive success, unlike natural selection, where physical differences between organisms *are* causally relevant to differences in their reproductive success (physical differences which confer an advantage tend to lead to greater reproductive success). For example, if a population of green and red moths is preyed on by a colorblind predator, any differences in reproductive success between the two types will not be due to the physical differences between the moths. As a result, particularly if the population is small, there may be a change in the distribution of types in the population over the course of generations. For example, the population of moths might become entirely red. This would be evolution, but not adaptive evolution. Thus, random drift is another possible mechanism of evolution, but it is a mechanism that tends to lead to an increase in nonadaptive (read: neutral) traits rather than adaptive ones. With the development of the neutral theory of molecular evolution (Kimura 1969, 1983), a theory that claims that the majority of evolutionary changes at the molecular level are the result of random drift acting on neutral mutations, the scientific debate (often called the neutralist/selectionist debate) over the relative roles of natural selection

and random drift intensified. Although some would proclaim the death of the neutralist/selectionist debate (Hey 1999), the debate continues today. In one recent version of the debate, disputants differ over whether a “nearly neutral” theory makes conceptual and empirical sense (Ohta and Kreitman 1996; Dover 1997b, 1997a; Ohta 1997). It is also interesting that even those who maintain the neutral model is not empirically adequate argue for its usefulness as a null model.

The debate over the relative roles of natural selection and random drift raises a number of philosophical issues. First, there are conceptual issues. Beatty (1984) argues that in some cases, random drift cannot be distinguished conceptually from natural selection, an argument that has been widely accepted. Beatty’s argument rests on the fact that natural selection and random drift are both probabilistic concepts, which creates a conceptual overlap. However, if Beatty is right, the very foundations of the neutralist/selectionist debate are called into question. Shanahan (1992) suggests that random drift and natural selection are on a continuum. Millstein (forthcoming) argues that when the two concepts are conceived as processes rather than outcomes, they can be distinguished from one another.

Second, if random drift plays even a small role in evolution, does that imply that evolution is indeterministic? Rosenberg (1988; 1994) claims that an omniscient account of evolution would have no need for the concept of random drift – that all instances of random drift can be explained in terms of natural selection. Rosenberg uses this claim to argue that although evolutionary *theory* is statistical, the evolutionary *process* is a deterministic one. According to Rosenberg, evolutionary theory is statistical purely for instrumental reasons; random drift serves merely as a useful fiction. A similar claim for the determinism of the evolutionary process is made by Horan (1994). Contra Rosenberg, Millstein (1996) argues that any evolutionary theory,

omniscient or otherwise, must take random drift into account – that random drift is not eliminable from evolutionary theory. Brandon and Carson (1996) further challenge Rosenberg's and Horan's claims; they maintain that it is more reasonable for a scientific realist to conclude that the evolutionary process is fundamentally indeterministic. Most recently, Horan and Rosenberg join with Graves in an attempt to counter the arguments of Brandon and Carson (Graves et al. 1999). Weber (forthcoming) and Millstein (1997) provide analyses of the positions of both camps.

However, without settling the debate between the determinist and the indeterminist, we can still ask whether the probabilities in evolutionary theory are in some sense objective, or whether they are purely epistemic, only appearing in the theory because we find probabilities useful and tractable in evolutionary contexts. If the evolutionary process is *indeterministic*, then the answer to this question is clear; evolutionary theory is probabilistic in an objective sense. On the other hand, if the evolutionary process is *deterministic*, there may still be a sense in which the probabilities employed by evolutionary theory are objective (Sober 1984; Brandon and Carson 1996; Millstein 1997). These issues bear further exploration.

The Adaptationist Programme and Its Challenges

In 1979, a debate related to, yet broader than the neutralist/selectionist debate was sparked by the publication of what would become a well-read and controversial essay entitled, "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme" (Gould and Lewontin 1979). As discussed above, natural selection leads to the accumulation of advantageous variations. According to Darwin, over long periods of time, the

accumulation of advantageous variations in a population would lead organisms to become adapted to their physical environments as well as to become adapted to one another. Thus, natural selection can provide explanations for adaptations that we observe in nature, such as the long, thick, chisel-like beaks of woodpeckers that are adapted for drilling wood and chipping away tree bark, enabling woodpeckers to feed on insects and tree sap. For Darwin, however, these adaptations were not necessarily perfect; for example, a bee sting will cause a bee's own death (1964: 472).

Gould and Lewontin charge that evolutionary biologists in England and the United States failed to heed Darwin's lessons – that so-called “adaptationists” not only focus almost exclusively on natural selection as the mechanism of evolution, but that they see the natural world as being as well adapted as it could possibly be (“Panglossian”). Furthermore, according to Gould and Lewontin, when adaptationists fail to explain the adaptive value of a particular trait, they either create another adaptationist story, simply assume there is another adaptationist story, or attribute the failure to an imperfect understanding of the circumstances of the organism. Instead of continuing to tell one adaptationist story after another, Gould and Lewontin maintain, evolutionists should consider other possible mechanisms, including, but not limited to, random drift. For example, the human chin may be a byproduct of developmental constraint, rather than a separate trait on which selection acts. Alternatively, a trait may have been selected for a specific function, but the trait (often in a modified form) is no longer serving that function. For example, it is believed that a bird's feathers evolved to assist in thermoregulation, but they are now used for a different function: flight. Much of evolution, Gould and Lewontin claim, may not be adaptive after all.

Gould and Lewontin's charges raise the question of what an *adaptation* is. On the standard

picture of adaptation (Brandon 1990 calls it the “received view”), adaptation is a *historical* concept; a trait is an adaptation if and only if it is the product of selection. This received view of adaptation rejects the *ahistorical* conception of adaptation, which would consider a trait an adaptation if it were of current benefit to its possessor, providing a good fit with the environment. Proponents of the received view would reserve the term “adaptation” for its historical meaning, using the term “adaptive” or “adaptedness” or “aptation” to refer to the ahistorical meaning. Sterelny and Griffiths (1999) provide useful examples of these two terms from the perspective of the received view. The human appendix, as a product of natural selection, would be considered to be an adaptation, but not adaptive, since it no longer benefits us in our present environment. However, the ability to read is adaptive (beneficial to us in our present environment) without being the direct result of natural selection (it is more likely a side effect of selection for other cognitive abilities). Some proponents of the historical view would restrict the term “adaptation” to traits that are currently serving the function for which they were selected, and many of these proponents have adopted the term *exaptation* (Gould and Vrba 1982) to refer to a trait that is serving a function other than the one for which it was selected. The example of a bird’s wings discussed above is an example of an exaptation.⁴

Recently, the received view of adaptation has come under some criticism. Elisabeth Lloyd (1992) argues that confusion between the historical and ahistorical senses of adaptation has contributed to some of the confusion in the units of selection debate. She further points out that the ahistorical conception of adaptation is at work in debates over the relationship between natural selection and sexual selection (should the product of sexual selection, for example, a peacock’s tail, be considered an adaptation?). Grene (1997) also questions the historical conception of adaptation, calling it “a move to the a priori that almost makes the theory of

natural selection a mere tautology.” In making this criticism, she quotes Sterelny, who states that “Natural selection is no explanation of adaptation, if adaptation is by definition whatever selection undisturbed produces” (Sterelny 1996: 197). This reexamination of the historical question is worthwhile, both for the reasons that Grene and Lloyd state, as well as to make sense of Gould and Lewontin’s claim that there can be selection without adaptation and adaptation without selection. It would seem that we are more tied to the pre-Darwinian, ahistorical notion of adaptation than we would like to think; perhaps another term should be used to refer to a product of selection (for further discussion of the concept of adaptation, see Burian 1983; Rose and Lauder 1996; Hull and Ruse 1998).

Many philosophers and biologists think that Gould and Lewontin sounded the death knell for the adaptationist program (or at least exposed its weaknesses), but others have leapt to its defense, notably, Cronin (1991), Dawkins (1976), Dennett (1995), Futuyma (1988), and Mayr (1983). Some have argued that the Gould and Lewontin’s critique relies on Karl Popper’s falsificationism, and that since this view has been discredited, the charges against the adaptationist programme fall flat. Others have argued that falsifiability is an inappropriate criterion for a research programme. Still others point to the successes of the adaptationist programme, and defend its methodology. (Recent philosophical debate on adaptationism can be found in Dupré 1987; Brandon and Rausher 1996; Orzack and Sober 1996; Godfrey-Smith 1999)⁵

Far too much of the literature, in my view, mischaracterizes the adaptationist position (or its critique) as claiming that all traits are adaptive or mischaracterizes the anti-adaptationist position (or its critique) as claiming that all traits are nonadaptive. (Of course, it is generally one’s opponent who is mischaracterized.) Rather, the debate is over the *degree* to which

adaptation is found in nature, with both sides generally accepting that some traits are adaptive and some are nonadaptive. At least, that is the empirical, biological debate. But should philosophers of biology be taking sides on this empirical question? It certainly does seem that philosophers can clarify (and have clarified) these kinds of empirical debates, both in terms of the concepts and the arguments involved. However, in the end, the question is an empirical one, and philosophers should not take sides. Furthermore, as Beatty (1997) suggests, these kinds of “relative significance” debates may not even be resolvable. After all, if one is to argue that evolution has been significantly adaptive, what does that mean? Ninety percent? Greater than fifty percent? At least ten percent? The terms of the debate are vague, making resolution difficult. Furthermore, how would we even answer such questions? Certainly, we cannot examine all living populations and it is unclear what a representative sample would amount to in this situation. It seems more likely that there is a resolution to the *methodological* debate over whether it is better to pursue an adaptationist research programme or an anti-adaptationist research program. As Beatty (1987) argues, how we distribute the resources of the evolutionary community has to do with the questions we pose for ourselves. With regard to the question concerning the relative importance of selection versus drift, Beatty suggests that if this is a question we really want to answer, “then we really must give serious thought to distributing the resources of the evolutionary community between the pursuit of selection and drift hypotheses” (1987: 72). The same argument holds for adaptationist and nonadaptationist hypotheses in general.

Legacies of the Adaptationist Debate: Sociobiology, Contingency, and Laws of Biology

The adaptationist debate has given rise to several other philosophical debates. For example, one outgrowth of the adaptationist programme is sociobiology – the application of the theory of natural selection to animal behavior, and more controversially, human behavior in particular (the classic text is Wilson 1975). Thus, sociobiology maintains that much of human behavior (and not just human physical characteristics) can be explained as adaptations that enhanced our ancestors' ability to survive. E.O. Wilson (1975) identified *altruism* as the central problem of sociobiology; a theory proposing to explain behavior via natural selection must explain how it is that behaviors which seem to promote the fitness of others at the expense of one's own fitness could have evolved (see the section on Units of Selection for further discussion of altruism).

Some of the debate surrounding sociobiology echoes the general debate over adaptationism – critics argue that it engages in Panglossian, untestable story telling (e.g., Gould 1980), while defenders question the adequacy of the Popperian criterion in this context (e.g. Caplan 1982). Critics also accuse sociobiology of being committed to genetic determinism – the view that we are completely determined by our genes, with little or no role for environmental or cultural factors (Lewontin et al. 1984). Extreme versions of sociobiology bite this bullet, while defenses that are more reasonable acknowledge a considerable role for non-genetic as well as genetic factors. Of course, such a response still leaves open the difficult-to-answer question of the extent to which we are affected by each of these factors. Perhaps more damning are the accusations that sociobiology simply entrenches our existing stereotypes and prejudices by providing purportedly scientific explanations for behaviors such as male aggression and female “coyness.” There have been numerous feminist critiques of sociobiological explanations on grounds such as these (see, e.g., Harding 1986; Longino 1990); Hrdy argues that a reexamination of the evidence

overturns many of these sexist explanations (1999).

Further criticisms are offered by Kitcher (1985), but in a subsequent paper Kitcher points to a new sociobiology that might avoid many of the problems of the past (1990). This recent work (and philosophical controversy) in sociobiology focuses not on explaining specific behaviors, but on explaining broader human capacities as adaptations to an ancestral environment, a view known as “evolutionary psychology”.⁶ Other recent work attempts to draw ethical or epistemological implications from sociobiology (“evolutionary ethics” and “evolutionary epistemology,” respectively. See, e.g., Ruse 1998). Debate on these issues will likely continue into the future.

Controversies over adaptationism have also sparked a revival of the debate over whether there are laws in biology, a debate that has divorced itself from its previous context – the debate over whether biology is a legitimate science. The present debate takes the legitimacy of biology as a science for granted, and rightly so. Gould’s anti-adaptationist *Wonderful Life* suggests that the broad-scale of the history of life is contingent (Gould 1989). Beatty (1995) usefully distinguishes between a weak sense of contingency – evolutionary generalizations may hold for the present, although there are often exceptions, and those that do hold may change in the future course of evolution – and a strong sense of contingency that Gould seems to be endorsing – “replay the tape” of life from the same starting point, and we might get a different outcome (one without human beings, for example). Since all biological generalizations are contingent, evolutionary outcomes, Beatty argues, there are no laws in biology. Waters, on the other hand, argues that causal regularities (as distinguished from distributions) are ubiquitous in biology, and that these regularities exhibit the most important features traditionally attributed to scientific laws (1998). Beatty’s paper also led to a Philosophy of Science Association symposium

featuring several responses to Beatty (and to the argument against laws given in Rosenberg 1994), as well as an additional paper from Beatty himself (see *Philosophy of Science*, Supplement to Volume 64, Number 4). These papers provide a fruitful reexamination of the nature of scientific law and show that old philosophical problems can often yield new insights.

The Species Problems

Charles Darwin entitled his magnum opus *On the Origin of Species*. But what is a species? Ironically, Darwin denies the reality of species, leading one to wonder: Is it a book about nothing? Ghiselin (1969) and Beatty (1985) persuasively argue that the confusion is only apparent. In saying that species are “arbitrarily given for the sake of convenience” (Darwin 1964: 52), Darwin is referring to the species *category*, pointing out that it cannot be clearly distinguished from “sub-species,” which in turn blend into “varieties” and then “individual differences” (Darwin 1964: 51). However, Darwin does accept the reality of species *taxa* such as the cabbage, the radish, and the onion, and the evolution of these and other species taxa by natural selection form the primary subject matter of the *Origin*. Yet Darwin leaves “species” undefined. Species concepts are used in many different areas of biology, including taxonomy, macroevolutionary biology, and ecology, making the defining of “species” an important issue in biology.

Each of the ways of talking about species – as a category or as a taxon – generates a conceptual problem. The species category problem concerns the ontological nature of the species category itself – what sort of thing is the category *species*? Is it a natural kind, an individual, a set, or something else? The species taxon problem, on the other hand, has to do

with the criterion used to determine which organism are assigned to which species. Is it based on their morphological characteristics, their evolutionary history, whether they interbreed, or something else? We will examine each of these problems in turn.

Species Category Problem

For Carolus Linnaeus, originator of the modern system of biological classification, species were seen as natural kinds, a view that dates back to Aristotle (also called an “essentialist” or “typological” view of species). On this view, species have *essences*, in the Aristotelian sense. That is, one could specify the necessary and sufficient conditions for belonging to a kind – for example, the necessary and sufficient conditions for being a tiger. Furthermore, species were seen as static and unchanging.

Evolutionary theory presents a challenge to the view of species as unchanging essences.

As Hull states:

The only basis for a natural classification is evolutionary theory, but according to evolutionary theory, species developed gradually, changing one into another. If species evolved so gradually, they cannot be delimited by means of a single property or set of properties. If species can't be so delineated, then species names cannot be defined in the classic manner. If species names cannot be defined in the classic manner, then they can't be defined at all. If they can't be defined at all, then species can't be real. If species aren't real, then 'species' has no reference and classification is completely arbitrary (1965: 320).

In this way, evolutionary theory is sometimes seen as implying the unreality of species taxa, and thus the unreality of the species category. And yet organisms do, at least to some extent, sort into non-arbitrary groups. For example, both Bengal tigers and Siberian tigers are considered to be subspecies of the same species, tiger. On the other hand, Bengal tigers and Grant's zebras are not classified as the same species, although we could place them both into the category of "organisms that are striped." The latter category seems arbitrary, in a way that the category of tigers is not. So, perhaps the proper conclusion to draw is not that the species category is unreal, but that the essentialist view of species is false.

An alternative account that characterizes species as historical entities (often referred to as the Hull-Ghiselin view) has become prominent (see the classic papers Ghiselin 1974; Hull 1976, 1978; or the more recent Ghiselin 1997). On this view, species are not kinds (or classes of any sort); they are *individuals*. This means that they are integrated and cohesive entities with a restricted spatiotemporal location (as opposed to spatiotemporally unrestricted classes). It is argued that species must be considered to be individuals because they are the entities that evolve. Species come into existence, and go out of existence, similar to the way that organisms (also individuals) are born and die. Thus, for example, if a population of animals resembling tigers in every way were to evolve independently on another planet, they would not *be* tigers; they would be spatiotemporally separated from our own tigers and would therefore be of a different species. *Panthera tigris* is a proper noun, not the name of a class or a type. The Hull-Ghiselin view is often connected with Mayr's biological species concept (to be discussed below).

According to Sterelny (1995), there is a consensus forming in favor of the Hull-Ghiselin view. Nonetheless, there are (as Sterelny admits) dissenters to this consensus. Kitcher (1984;

1989), for example, argues that the species category can be construed as a set of organisms sharing a common property, and that (contra, e.g., Hull 1978) this view is *also* consistent with the evolutionary changes of a population over time. One could also be a pluralist concerning the question, viewing species categories “either individuals or sets, depending on the biological problem at issue” (Dupré 1992). Yet another alternative views the species category as being somewhere intermediate between an individual and a class; Mayr prefers the term “population” (Mayr 1987; Mishler and Brandon 1987)

Species Taxon Problem

There are an amazing number – perhaps as many as twenty or more – of different conceptions that spell out the way in which organisms are to be placed into species taxa (Mayden 1997). Here I will sketch the three primary alternatives.

Hull and Ghiselin argue that their “species as individuals” thesis, discussed above, is the natural interpretation of Ernst Mayr’s influential *biological species concept*. According to Mayr, “*Species are groups of interbreeding natural populations that are reproductively isolated from other such groups*” (Mayr 1996: 264; italics in original). This view coincides with Mayr’s view of the speciation process, whereby the geographical isolation of populations leads to the evolutionary divergence of those populations, with the result that the populations are no longer able to interbreed (reproductive isolation). There are two common criticisms of this view. The first is that it is inapplicable to the classification of asexual organisms, a point that Mayr now acknowledges, suggesting that a different definition of species for asexual organisms should be developed (1996). This is a relaxation of his earlier position (Mayr 1987) that only sexually

reproducing organisms qualify as species. The second criticism comes primarily from botanists who point out that many plants are considered distinct species, yet they do sometimes interbreed. In response, Mayr now allows that organisms of different species may occasionally interbreed, so long as their biological properties prevent the “complete fusion” of the populations (Mayr 1996: 265). These changes seem to be a substantial weakening of the biological species concept, with the latter change making the concept much less precise.

Sokal and Crovello (1970) offer additional criticisms of the biological species concept. They contend that the concept is not operational, arguing that extensive field observations of interbreeding are “impractical,” leaving the biologist with “partial” or “circumstantial” evidence, and of course interbreeding cannot be observed in fossils at all. The biologist is forced to rely on the dissimilarities between organisms, which they maintain are “an imperfect reflection of infertility between organisms” (Sokal and Crovello 1970: 133). Furthermore, they charge that Mayr’s biological species concept ties the variation in nature to a biased, “abstract ideal” that prevents the discovery of new insights into the mechanisms of evolution (Sokal and Crovello 1970: 149). Their alternative, the *phenetic species concept*, places organisms into species on the basis of their overall similarities, thus allowing for a definition of species that remains constant with changes in evolutionary theory and which (purportedly) allows for an independent test of the theory. The idea of sorting organisms into species based on their similarities is not new; it pre-dates Darwin. Generally speaking, phenetic species concepts may categorize organisms into species based on their structural, behavioral, or genetic similarities.⁷ One version of the phenetic species concept is called numerical taxonomy (Sneath and Sokal 1973). This concept relies on computer analysis to determine the similarities between a large number of features. Phenetic species concepts have stirred up quite a bit of controversy, but currently are not all that popular,

due in part to the difficulty (if not impossibility) of objectively specifying the nature of “similarity.”

*Phylogenetic (evolutionary) species concepts*⁸ are an alternative to biological species concepts and phenetic species concepts. Whereas biological species concepts focus on a *process* of evolution (specifically, speciation), phylogenetic species concepts focus on the *pattern* of evolution (Sterelny and Griffiths 1999). That is, phylogenetic species concepts seek to reflect genealogical evolutionary history by characterizing species as lineages – “segments of the evolutionary tree” between two speciation events, or between a speciation event and an extinction event. Consider a branch of the evolutionary tree – a lineage. If that branch splits into two new branches, then two new species are formed, replacing the old species (the *stem species*). If the branch terminates, then the species has gone extinct. By focusing on the pattern of evolution, phylogenetic species concepts leave open the question of which particular process produced the pattern – the very issue that led the biological species concept into trouble. However, ultimately phylogenetic species concepts must face the same issue: when can we say that a lineage has divided into two new lineages? Additional criteria are needed, either reproductive isolation (which brings back all the problems of the biological species concept) or some other criteria. Sterelny and Griffiths (1999) suggest the ecological species concept (Van Valen 1976) or the cohesion species concept (Templeton 1989) as sources of possible criteria.

Recently, the plethora of species taxon concepts has led to various calls for pluralism (Kitcher 1984; Mishler and Brandon 1987; Ereshefsky 1998; Dupré 1999), as well as responses to these calls (Ghiselin 1997; Mayden 1997; Hull 1999). In 1969, Hull remarked that, “the biological literature on the species concept is overwhelmingly large” (1969: 180, n. 10). If it was overwhelmingly large in 1969, you could fairly well drown in the philosophical and biological

literature on species today. It is hard to predict how these issues will resolve themselves; the only certain prediction seems to be that we have not heard the last of the species taxa problem.

Tautology and the Nature of Fitness

No summary of the philosophy of evolution would be complete without a discussion of the “tautology problem,” given the amount of space that has been devoted to it. Yet given a proper understanding of tautology and evolutionary theory, there is neither a *prima facie* tautology, nor is there a problem. Nonetheless, much interesting philosophical discussion about the nature of fitness has arisen as a result of the misunderstanding.

The “problem” isn’t new, either. According to Hull (1969), evolutionists as far back as Darwin have been defending the theory of natural selection against the criticism that it is tautologous. Nonetheless, the criticism refuses to die, kept alive in large part by creationists who love to quote Popper’s claim that “Darwinism is not a testable scientific theory but a *metaphysical research programme*” (Popper 1974: 134; italics in original), but who ignore his subsequent recantation (Popper 1978).

The standard criticism goes as follows: the principle of natural selection is “the survival of the fittest,” but who are the “fittest”? Those that survive. The principle then becomes “the survival of those that survive.” Thus, the critics charge, the theory of natural selection is a tautology, and is therefore circular and empty; it says nothing about the way the world is, since it is true regardless of the empirical reality. This claim is often conjoined with the claim that the theory of natural selection is unfalsifiable – a tautology cannot be proven false.

A few technical points regarding the standard criticism – if there is anything wrong with

the phrase “the survival of the fittest,” it is that it is an analytic statement, not that it is a tautology, as Sober (1984) points out. A tautology is a statement that is true by virtue of its logical form alone, such as “Either it is raining or it is not raining.” An analytic statement, on the other hand, is a statement that is true by virtue of the meaning of its constituent words (i.e., true by definition), with the classic example being “a bachelor is an unmarried man.” If the phrase “the survival of the fittest” were to be worded as a statement that could be true or false – it isn’t a statement in its current form – then it would be characterized as an analytic statement rather than a tautology. Still, even as an analytic statement, the critics’ charge that the phrase is circular, empty, and/or unfalsifiable lingers.

One possible line of response to the standard criticism involves a reexamination of the concept of “fittest”. If the only thing that makes one group of organisms fitter than another is that the first group in fact survived when the second did not, then this seems to be the source of the circularity. In response to this concern, Mills and Beatty (1979) and Brandon (1978) independently developed the propensity interpretation of fitness (although Brandon prefers the term “adaptedness”). On this view, fitness is not defined in terms of an organism’s *actual* survival or reproductive success. Instead, fitness is an organism’s *propensity*, or ability, to survive and reproduce in a particular environment. (Fitness is never defined absolutely, but always relative to a given environment; what enhances survival or reproductive success in one environment may not do so in a different environment.) Thus, “the survival of the fittest” is not “the survival of the survivors,” but rather “the survival of those who have the greatest propensity to survive.” The organisms that have the greatest propensity to survive may not in fact survive; consider, for example, two identical twins, one of which is struck by lightning and dies, the other which survives and leaves offspring. Both are equally fit (have the same propensity to

survive and reproduce), yet one has greater actual reproductive success. In this manner, the propensity interpretation of fitness attempts to break the purported circularity of the theory of natural selection.

The propensity interpretation of fitness is not without its critics (see, for example Rosenberg 1982; Rosenberg and Williams 1986). Even Beatty and Finsen (née Mills) return to point out some technical difficulties with their own position (Beatty and Finsen 1989). Nonetheless, the view enjoys widespread acceptance among philosophers of biology (see, for example, Burian 1983; Brandon and Beatty 1984; Sober 1984; Richardson and Burian 1992). Sober responds to Beatty and Finsen's self-criticisms and points out that whereas the criticisms apply to the particular mathematical implementation of the propensity interpretation, they do not challenge the nonmathematical heart of the propensity interpretation (Sober 2000).

In spite of the popularity of the propensity interpretation as an account of the concept of fitness, some philosophers – including Beatty (1992), who has changed his position on this issue – have argued that it does not actually solve the tautology problem. Rather, Waters suggests, if we spell out the principle of the survival of the fittest as “Organisms with greater higher fitnesses in (environment) E will probably have greater reproductive success in E than (conspecific) organisms with lower fitnesses” (1986: 211), there are two basic ways of interpreting the term “probably”: the propensity interpretation and the frequentist interpretation. Waters argues that if one chooses the propensity interpretation, the principle is true by definition; if one chooses the frequentist interpretation, the principle is not analytic, but it is untestable.

If this argument is correct, does that mean that the theory of evolution is circular and unfalsifiable? It might, if the phrase “the survival of the fittest” actually described the theory – but it does not. The real problem with the standard criticism is that it misrepresents evolutionary

theory, as Hull (1969) and Waters (1986) note. As discussed above, the present-day theory of evolution includes not only natural selection as a possible mechanism leading to the differential survival and reproduction of types; random drift is a possible mechanism, as are migration and mutation. In other words, in any particular case survival may not be “the survival of the fittest.”

Even Darwin’s theory of natural selection alone is not captured by this phrase;⁹ as previously mentioned, Darwin described natural selection as a process requiring 1) a struggle for existence where not all organisms that are born can survive, 2) heritable variations between organisms in the population, and 3) variations that confer a differential ability to survive and reproduce. Whether any or all of these conditions obtain in a particular population is an empirical question, not a matter of definition, and thus we can test the population for the presence or absence of the three conditions. The theory of natural selection is neither circular nor vacuous.

The tautology problem ought to be a dead issue, even if there are those who refuse to let it go. However, its offspring, the proper conception of fitness, remains a fruitful area of research (Recent discussions of the concept of fitness in evolutionary theory appear in *Biology and Philosophy*, volume 6, as well as Weber 1996; Stout 1998; Abrams 1999).

Units of Selection

Life can be viewed as a hierarchy of levels, from genes, to cells, organs, and organisms, to populations and species, to yet higher levels. This raises the following questions: which of these levels (or units) does natural selection act upon? Or does it act on one level in some case, but act at different levels in other cases? Is there one level that it *usually* acts on? These questions form

the core of what is known as the “units of selection”¹⁰ problem (Lloyd 1992 identifies four units of selection problems). The answers to these questions might seem to be arbitrary, if one assumes, for example, that what benefits the group also benefits the individual organism. Consider, however (as Darwin did), the case of sterile worker ants. Clearly it is not advantageous to the individual ants to be sterile (an organism that cannot reproduce has zero fitness), so how could such ants be the product of natural selection? Darwin’s answer is that sterile worker ants could have been selected because they were “profitable to the community” (Darwin 1964: 236). If this analysis is correct, sterile worker ants are an example of group selection, but not individual selection; sterility benefits the group, but not the individual. Nonetheless, most of Darwin’s examples of natural selection are of individual rather than group selection, and many consider individual, organismic selection to be the “received view” of natural selection.¹¹ However, there is a great deal of controversy surrounding the received view (see, e.g., Brandon and Burian 1984).

The case of the worker ant appears to be an extreme case of altruism, which Rosenberg usefully characterizes as behavior that “increases the reproductive fitness of another at the expense of one’s own reproductive fitness” (Rosenberg 1992) – an evolutionary sense of altruism which does not require conscious intention on the part of the altruist. Less extreme examples of group selection explanations for apparent altruism are offered by Wynne-Edwards (1962), who claims that organisms will limit their reproduction to preserve their food supply and prevent extinction of the population. Many consider the idea of group selection to have been dealt a deathblow in 1966 by G. C. Williams’s classic *Adaptation and Natural Selection*. G. C. Williams argues that group selection, although not impossible, is unlikely, and that most purported cases of group selection can be explained more simply. However, the alternative

explanations that he provides are not individual (organismic) selection explanations; they are explanations citing selection at the level of the gene, a view that is endorsed and popularized by Dawkins in *The Selfish Gene*.

What exactly is genic selection? To help clarify his position, Dawkins introduces the terms “replicator” (for which the gene is the primary, but not exclusive example) and “vehicle” (for which the organism is the primary, but not exclusive example). Hull modifies these terms and renames them to “replicator” and “interactor.” Hull defines a replicator as “an entity that passes on its structure directly in replication” (1980: 318). A gene replicates itself (relatively) directly, whereas the traits of an organism are not passed directly to its offspring (genes are transmitted, and development must occur). An interactor, on the other hand, is defined as “an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential” (Hull 1980: 318). Selection is then defined as “a process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them” (Hull 1980: 318).¹² These definitions leave us with *two* levels of selection questions – we can ask, “at which levels does replication occur?” and “at which levels does interaction occur?”

So, in one sense, Dawkins’s (and G.C. Williams’s) genic selectionism does not go against the received view – Dawkins accepts organisms as interactors in the selection process, acknowledging that genes are “[o]bviously...selected by virtue of their phenotypic effects (Dawkins 1982: 117). This might lead one to conclude, as Reeve and L. Keller do, that “the debate is resolved” since “the unit of replication is the gene (or, more precisely, the information contained in a gene), and the organism is one kind of vehicle for such genes, a vehicle being the entity on which selection acts directly”; participants on different sides of the debate simply have

chosen to focus on one aspect rather than the other (1999: 5).

However, this conclusion is too hasty, and misses the larger units of selection debate over whether replicators or interactors are “the” causal agents in the selection process. As Sober explains Dawkins’s position: “Those who argue that the single gene is the unit of selection often seem to think of genes as the deeper cause of evolution by natural selection...genes cause phenotypes, and phenotypes then determine survival and reproductive success” (Sober 1984: 228; see also Lloyd 1988 for a thorough analysis of Dawkins’s views). Furthermore, it is the replicators, not the interactors, which actually survive or fail to survive in the process of natural selection. On the other side of the debate are those who attribute the causal agency to the interactor (e.g., Sober 1984; Lloyd 1988; Brandon 1990). Defenders of the interactor view often trace their views to Mayr’s assertion that “natural selection favors (or discriminates against) phenotypes, not genes or genotypes” (1963: 184) or to Hull’s definition of natural selection (quoted above), both of which attribute causal agency to the interactor. Proponents of the interactor view often acknowledges that replicator views are good for “bookkeeping” – that is, they are empirically adequate – but argue that they fail to capture the true causal picture. Since the primary interactor is usually taken to be the organism, whereas the primary replicator is usually taken to be the gene, Dawkins’s focus on replicators *is* (in this sense) a challenge to the received view.

Thus, the question of which unit is “the” unit of selection has focused on two sub-questions: are groups only rarely units of selection, if at all? Are genes or organisms best seen as the true (causal) units of selection? Concerning the former question, Sober and D.S. Wilson argue that, properly defined, group selection is more prevalent than is usually supposed (Wilson and Sober 1994; Sober and Wilson 1998). Sober and D. S. Wilson also argue that attempts to

explain apparent altruism as organismic selection – either by claiming that organisms that help their offspring are favored by selection (kin selection) or that organisms that help each other are favored by selection (reciprocal altruism) – can be better understood through the lens of group selection.

With regard to the latter question, some have argued against Dawkins’s genic selectionism on the grounds it is reductionistic and that genes are context-sensitive; the same gene can enhance fitness in one context and reduce it in another (see, e.g., Wimsatt 1980; Sober and Lewontin 1982). Sterelny and Kitcher, on the other hand, maintain that this argument does not weaken the case for gene selection, since the fitness of any unit of selection is necessarily relative to context (1988). An alternative account is provided by Brandon (1990), who argues that conceptually, we can describe a dual hierarchy of interactors and replicators, but that it is an empirical question as to whether selection actually occurs at any of the interactor levels (e.g., chromosome, gene, organism, group, species). Brandon maintains that we have ample evidences for selection at level of the organism; the existence of selection at the other levels is suggestive, but not conclusive. Brandon’s account relies on Wesley Salmon’s “screening off” account of causation; Sober (1984) uses an alternative conception of causation (causes increase the chances of their effects in all causally relevant background contexts). There has been much recent debate between these two accounts (Brandon et al. 1994; Sober and Wilson 1994; van der Steen 1996; Brandon 1997; Hitchcock 1997).

Waters (1991) points out that proponents of gene selection and proponents of individual selection share a common assumption of realism concerning the level of selection. (Presumably, the same can be said about proponents of group selection.) That is, they assume that “there is a uniquely correct identification of the operative selective forces and the level at which each

impinges” (Waters 1991: 554). Waters argues that our realism about the levels of selection must be *tempered*; we must acknowledge “that the causes of one and the same selection process can be correctly described by accounts which model selection at different levels” (Waters 1991: 572). Sober and D. S. Wilson defend the realist position; they argue that different hypotheses about the units of selection will produce different predictions (1994). Others claim neutrality on this realism issue (Lloyd 1989) or make instrumentalist claims (Sterelny and Kitcher 1988).

If there is anything like consensus on these contentious issues, it would probably be surrounding the idea of a hierarchical view of selection (the origins of which are in Lewontin 1970). That is, most philosophers and biologists accept the idea that it is possible for selection to occur at more than one level – even G. C. Williams and Dawkins now accept the *possibility* of group selection. Accepting a hierarchical level of selection, however, leaves open the question of which level of selection predominates in nature – again, is it primarily the organism or the gene? Does group selection occur often, or very rarely if at all? Others argue for the prevalence of species selection (e.g., Eldredge and Gould 1972; Stanley 1979; Lloyd and Gould 1993).¹³ Gould and Lloyd declare “emerging consensus in favor of the interactor approach” (1999: 11904), but consensus on that point seems less clear.

Evolving Out of the Past and Into the Future

Many of the issues discussed above are longstanding issues in the philosophy of evolution. And yet, that doesn’t mean the field is standing still – far from it. As I hope I have shown, progress has been made in many of these areas. It’s just that, as tends to happen with philosophical analyses, the settling of some issues only raises further questions. I have tried to

indicate the direction in which each of the debates seems to be heading, or ought to be heading. Here I will consider broader issues for the future.

In 1969, David Hull chastised the fledgling field of the philosophy of biology for being misinformed about biology and the issues and distinctions that biologists find important. Some three decades later, philosophers have taken Hull's admonition to heart, and yet there is still always more to do. For example, philosophers have explored issues surrounding macroevolution (large-scale evolutionary changes at or above the species level) such as the theory of punctuated equilibria (which challenges the Darwinian thesis of gradual evolution) and the related idea of species selection (discussed briefly above). They have examined the question of progress – does evolutionary theory overturn the idea that the history of life is progressive, or is there still some sense in which there is progress? If so, what is it (see, e.g., Nitecki 1988; McShea 1991; Ruse 1993)? And yet, philosophers of evolution have only begun to scratch the surface on macroevolutionary issues such as contingency (discussed briefly above), the mass extinction debates (Grantham 1999b calls for a philosophical examination of these debates) and stochastic macroevolutionary models (see Grantham 1999a; Millstein 2000). What does it mean to say that there are “autonomous” theories of macroevolution, distinct from microevolutionary theories? Philosophy of evolution should continue to be vigilant about exploring topical issues in biology such as these.

Perhaps more controversially, I think that philosophers of evolution ought to pay more attention to philosophical issues that arise outside of academia. For example, the action that the Kansas Board of Education took in July 1999 that had the effect of minimizing the teaching of evolution highlights the importance of philosophers being involved in the creationist/evolutionist debates. Of course, there are some notable explorations in this area (Kitcher 1982; Ruse 1996;

Pennock 1999), but in general philosophers of evolution seem to shy away from such engagements, perhaps because of philosophical worries concerning general debates about the nature of science, or perhaps because of a general distaste for taking a stand on controversial issues of the day. Whatever the reason, I think we neglect our duties when we shy away from such controversies.

Notes

¹ Plausible, that is, to present-day biologists and some of Darwin's contemporaries. Not everyone was initially persuaded by Darwin's arguments.

² Lamarckian evolution, long considered to be a refuted theory, has recently experienced a resurgence with the publication of Cairns, Overbaugh, and Miller's controversial essay claiming to have demonstrated the occurrence of directed mutation in bacteria (Cairns et al. 1988). This in turn has led to a philosophical reexamination of Lamarckism in general and the concepts of directed and random mutation in particular (see e.g., Sarkar 1991; Keller 1992; Jablonka and Lamb 1995; Millstein 1997).

³ Migration and mutation are also considered mechanisms of evolution, when evolution is construed as a change in gene frequencies (not an uncontroversial definition in itself).

⁴ Similar issues arise in discussions of the related notions of function and teleology, both of which are longstanding issues in the philosophy of biology. The classic works are by Cummins (1975) and Wright (1973). For an excellent collection containing these and other germinal works as well as more recent work, see Allen, Bekoff, and Lauder, eds. (1998). Here, as in other areas of the philosophy of evolution, there have been calls for pluralism.

⁵ Other recent debates center on the connections between development and adaptationism. See Amundson (1994), Kaufman (1993) Griffiths (1996), and this volume. Why not cite this volume?

⁶ The interface between philosophy of biology and philosophy of psychology in general is a recent and burgeoning area (see, e.g., Hardcastle 1999).

⁷ Sokal and Crovello's version of the phenetic species concept construes "similarity" very liberally, including morphological, physiological, biochemical, behavioral, genetic, protein, and ecological similarities (1970, 150)

⁸ Here I speak of phylogenetic species concepts in general, rather than the particular phylogenetic species concept defended by Mishler and Donoghue (1982), , and Mishler and Brandon (1987), or the (different) phylogenetic species concept defended by Cracraft (1983)

⁹ In fact, the phrase "survival of the fittest" was coined by Herbert Spencer in 1864, not Darwin, and was not included in the *Origin of Species* until the fifth edition, at the urging of Alfred Russel Wallace. Philosophers and biologists have been sorry ever since.

¹⁰ In what follows, I will use "units of selection" and "levels of selection" interchangeably, although there are those who would distinguish them (e.g., Brandon 1982).

¹¹ In what follows, I will use "individual selection" and "organismic selection" interchangeably, even though, for example, some would argue that species are individual as well (see Species section above).

¹² See Darden and Cain (1988) for an analysis of Hull's model of natural selection and an alternative characterization.

¹³ These debates appear to be examples of "relative significance" debates, *sensu* Beatty (see above discussion).

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