

## Preface

This anthology brings together essays written by philosophers and scientists that address conceptual issues that arise in the theory and practice of evolutionary biology. This third edition differs substantially from the previous two, which were published in 1984 and 1994. Four new sections have been included (on women in the evolutionary process, evolutionary psychology, the existence of laws in biology, and race) and some additions and subtractions have been made in chapters present in previous editions.

Each part in this collection contains two or three chapters that develop opposing views of the problem at hand. Evolutionary biology is a living, growing discipline, and the same is true of the philosophy of evolutionary biology. One sign that a discipline is growing is that there are open questions, with multiple answers still in competition. I hope the clash of ideas presented here will be useful to evolutionary biologists and to philosophers of biology, both in their teaching and in their research.

In the remainder of this preface, I will briefly indicate what some of the major issues are that animate the chapters that follow.

### I Fitness

Darwin accorded a preeminent role to the process of natural selection in his account of how life has evolved. Central to the concept of natural selection is the idea of fitness: if the organisms in a population undergo a selection process, they must differ from each other in terms of their abilities to survive and reproduce. Herbert Spencer coined the slogan “survival of the fittest” to describe Darwin’s theory and Darwin adopted this description phrase, thinking that it might help readers avoid misunderstanding what he mean by his own term, “natural selection.” Had he realized the confusions that would ensue, maybe Darwin would have distanced himself from this slogan. For once the theory is summarized by the phrase “the survival of the fittest,” it invites the following line of criticism: Who survives? Those who are fit. And who are the fit? Those who survive. If the theory of natural selection comes to no more than this, then the “theory” is

no theory at all. It is a piece of circular reasoning, an empty truism, which masquerades as a substantive explanation of what we observe.

In the first chapter in part I, “The Propensity Interpretation of Fitness,” Susan Mills and John Beatty address this criticism by clarifying the probabilistic character of the concept of fitness. Their goal is to describe how the concept of fitness figures in contemporary biology and to show that the charge of circularity is entirely misguided. They formulate an interpretation of the fitness concept that draws on more general ideas concerning how the concept of probability might be understood; if fitnesses are probabilities, perhaps the propensity interpretation of probability (defended by Karl Popper in his influential book *The Logic of Scientific Discovery*) will help clarify what fitness is.

In the second chapter, I take up some of the questions that Susan Finsen (née Mills) and Beatty subsequently raised about their proposal. An organism has an expected number offspring, an expected number of grandoffspring, and a probability of having descendants that exist 1000 generations hence. Which of these probabilistic concepts is the organism’s fitness? And is it always true that an organism’s prospects for reproductive success can be represented as a probabilistic expectation? These questions must be addressed if the adequacy of the propensity interpretation of fitness is to be evaluated.

## II Units of Selection

Human beings are organisms, so it may strike us as entirely natural to think that the parts of organisms exist in order to benefit the organisms that contain them. We have hearts, so we naturally think that hearts exist in order to help organisms circulate their blood. And each of our cells contains genes, so we naturally think that genes exist in order to help organisms transmit traits from parents to offspring.

If we are prepared to think that hearts and genes have the functions of helping organisms to perform various tasks, why not frameshift this idea up a level and conclude that organisms have the function of helping the groups in which they live? If hearts help organisms survive, why not also say that organisms have hearts to help the species to which those organisms belong to avoid extinction? Conversely, if parts can have the function of helping the wholes in which they exist, why can’t the opposite relationship also obtain? Why not think of organisms as devices that have the function of guaranteeing the survival and reproduction of the genes they contain?

These questions are central to what is now called the problem of the units of selection. Let us assume that a trait—the opposable thumb, for example—evolved because it was good for the things that possessed it. But which objects should we regard as the relevant beneficiaries? Did the opposable thumb evolve because it helped the species to avoid extinction, or because it helped organisms survive and reproduce, or because

it helped genes coding for opposable thumbs to make their way into successive generations?

Darwin usually thought of natural selection as a process in which traits evolve because they benefit individual organisms. The two most famous exceptions to this pattern of thinking were his discussion in *The Origin of Species* of sterile castes in the social insects and his discussion in *The Descent of Man* of human morality. In both instances, Darwin argued that a trait sometimes evolves because it benefits the group and in spite of the fact that it is deleterious to the individuals possessing it. Later on, evolutionary biologists came to call such traits “altruistic.” The idea that some traits are group adaptations was a standard part of biological thinking during the heyday of the Modern Synthesis (1930–1960). For example, in his 1937 book *Genetics and the Origin of Species*, Theodosius Dobzhansky suggested that sexual reproduction may be a group adaptation, its function being to ensure that a species is genetically diverse, so that the species is less likely to go extinct if the environment suddenly changes.

Even though group selection thinking was for many years a standard part of the evolutionary biologist’s toolkit, its fortunes plummeted after 1966; this was the year in which George C. Williams published his book *Adaptation and Natural Selection*. The most prominent message in Williams’s book was that group selectionism is a kind of sloppy thinking. Biologists had uncritically talked about traits existing “for the good of the species” even though more parsimonious explanations can be provided at lower levels. Although Darwin almost always favored individual selection over group selection, Williams’s critique of group selection thinking did not conclude that the classical Darwinian picture was the best way to think about adaptation. Rather, he suggested that we descend to a lower level still. The real unit of selection, Williams argued, is not the group, nor even the individual, but the gene. Thus was born the view of natural selection that Richard Dawkins later popularized in his book *The Selfish Gene*.

The first chapter in part 2 consists of excerpts from Williams’s *Adaptation and Natural Selection*. Williams emphasizes the importance of not assuming that a trait that benefits a group must be a group adaptation. The benefit to the group may be a side-effect, and not the reason the trait evolved. Williams also argues that hypotheses of group adaptation are less parsimonious than those that posit adaptations at lower levels. In defense of the genic point of view, Williams contends that genes have a longevity that gene combinations and whole organisms do not. Williams also argues, repeating an argument that R. A. Fisher made in his book *The Genetical Theory of Natural Selection*, that group selection must be a weak force, compared with individual selection, because groups usually go extinct and found colonies at a slower rate than the rate at which organisms die and reproduce.

In the second chapter in this section, “Levels of Selection: An Alternative to Individualism in Biology and the Human Sciences,” David Sloan Wilson argues that the selfish gene theory—the idea that the gene is the one and only unit of selection—rests on a

fallacy. Wilson does not urge a return to uncritical group selectionism; rather, he defends a pluralistic conception of selection, according to which adaptations can evolve for a variety of reasons. According to Wilson, the living world contains selfish genes, but it also contains well-adapted organisms and well-adapted groups; genic selection occurs, but so too do individual selection and group selection.

### III Adaptationism

Although Darwin accorded a central role to the process of natural selection, he allowed that other processes can influence the course of evolution. How important these other processes are, and how we should endeavor to understand the features of the living things that we observe, are the main issues in the controversy concerning adaptationism.

When a biologist studies a complex characteristic of morphology, physiology, or behavior, the first impulse is often to ask "What is this trait for?" The mind searches for the trait's adaptive significance. We observe the dorsal fins on a dinosaur and immediately set to work thinking about whether the fins were for self-defense, or for thermal regulation, or to attract mates. If one hypothesis of adaptive advantage does not pan out, we discard it and invent another.

In the first chapter in part III, "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme," Stephen Jay Gould and Richard C. Lewontin argue that this impulse toward adaptationist thinking has led biologists to neglect the possibility that many traits may be present for reasons that have nothing to do with their adaptive significance. Adaptationism, they suggest, is an assumption that is as pervasive as it is unproven. In the part's second chapter, "Optimization Theory in Evolution," John Maynard Smith replies to this criticism by outlining the elements that figure in adaptationist explanations; he defends the adaptationist approach by suggesting how particular adaptationist explanations can be tested.

Two questions float through the debate between adaptationists and anti-adaptationists. The first concerns what is true in the natural world: how important has natural selection been in evolution? Is it true that virtually all traits have evolved because of natural selection, or is this true only for some significantly smaller subset? The second question concerns how nature should be studied: is it sound methodology to formulate and test adaptive hypotheses? Should alternative, nonadaptive explanations, also be contemplated? That these are separate questions can be seen by considering the fact that one might be agnostic about what is true in nature, but still maintain that evolutionary inquiry requires the formulation and testing of hypotheses about natural selection. This distinction between biological and methodological questions is important to bear in mind in thinking about the adaptationism debate.

#### IV Women in the Evolutionary Process

Gould and Lewontin's critique of adaptationism was motivated in large measure by the rising popularity of sociobiology. Biologists had been interested in the evolution of behavior (human and nonhuman) for a long time, but Edward O. Wilson's publication in 1975 of his book *Sociobiology—The New Synthesis* was a rallying cry; it called on biologists to apply recent advances in evolutionary biology to the project of systematically understanding human mind and culture. For Gould and Lewontin, sociobiology was a symptom of a pervasive deficiency in evolutionary thinking. For adaptationists, sociobiology was a new opportunity.

Gould and Lewontin find it highly significant that adaptationists are happy to invent a new adaptive hypothesis to explain a trait if an old explanation is refuted by the evidence. Does this represent a flaw in adaptationism, or is it an unobjectionable consequence of the fact that adaptationism is a flexible research program? The two chapters in the present section embody opposing answers to this question in the context of discussing how evolutionary biology should address questions concerning female sexuality.

Sarah Blaffer Hrdy, in her article "Empathy, Polyandry, and the Myth of the Coy Female," writes as a sociobiologist who found herself, starting in the 1970s, increasingly dissatisfied with the received wisdom on female sexual behavior. In his book *The Descent of Man, and Selection in Relation to Sex*, Darwin wrote that females tend to be "coy" and males tend to be "eager" in their mating behavior. By this he meant that females are more choosy in deciding with whom they will mate, and males are more promiscuous. A. J. Bateman defended this general thesis and attempted to give it an evolutionary explanation in a paper he published in 1948. In his laboratory work on fruitflies, Bateman observed that almost all the females reproduced, but about a fifth of the males did not. He argued that males increase their fitness by mating with multiple females, but that females do not increase their fitness by mating with multiple males. Males, unlike females, have something to gain from seeking new mating opportunities. This is why males are promiscuous and females are choosy. Hrdy's dissatisfaction with this paradigm grew out of a growing body of observational evidence that female primates often have multiple partners. These observations led her to seek out plausible adaptive explanations of this pervasive pattern. One of them, the "manipulation hypothesis," says that females gain protection and resources for their infants by having multiple partners. In addition to defending a new adaptationist explanation of female mating behavior, Hrdy also speculates about why biology largely ignored female sexual behavior until the 1970s. She conjectures that the growing representation of women in primatology, and the empathy that women brought to studying female primates, may have been contributing factors.

In some respects Elisabeth Lloyd is on the same wave length as Hrdy, but in other respects, she is not. In her chapter “Pre-theoretical Assumptions in Evolutionary Explanations of Female Sexuality,” Lloyd agrees with Hrdy that male bias has impeded the understanding of female sexuality. But whereas Hrdy is reacting against a conception of females as essentially different from males (the “coy” versus “eager” contrast), Lloyd takes issue with the assumption that female sexuality is to be understood if it were a carbon copy of male sexuality. Her particular subject is female orgasm. If male orgasm has a reproductive function, must the same be true of female orgasm? Lloyd argues against this assumption. Following a suggestion made by Donald Symons in his 1979 book *The Evolution of Human Sexuality*, Lloyd suggests that female orgasm may be what Gould and Lewontin call a spandrel. Females have orgasms for the same reason that males have nipples. Neither trait was selected for; rather, each evolved because of a developmental correlation. Males and females both have nipples because nipples are the outcome of developmental processes present in both sexes; this means that selection for nipples in females leads male nipples to evolve as well, even though nipples have no evolutionary function in males. Lloyd suggests that the same may be true of female orgasm; it has no evolutionary function, but evolved because there was selection for male orgasm. Lloyd concludes her chapter with a more general lesson—that philosophers of science need to pay closer attention to the social assumptions and prior commitments that influence the scientific process.

## V Evolutionary Psychology

Evolutionary psychology is a more recent adaptationist project than sociobiology. Whereas sociobiologists tend to focus on behaviors and try to explain them by ferreting out their adaptive significance, evolutionary psychologists tend to think of cognitive mechanisms, not behaviors, as the fundamental subject for evolutionary theorizing. Evolutionary psychologists also emphasize an idea that Maynard Smith mentions in his chapter in part III—that natural selection often occurs slowly, so that the traits we observe in a present population are not the ones that would be optimal for its present circumstance. Rather, the traits we observe now are often vestiges of traits that were adaptive in earlier, ancestral, environments. Evolutionary psychologists suggest that the way to understand the human mind as it presently is constituted is to understand the adaptive problems our ancestors faced; we are adapted to past conditions, not to present conditions.

This position is developed in the first chapter in this section, “Toward Mapping the Evolved Functional Organization of Mind and Brain,” by John Tooby and Leda Cosmides, who are two of the main founders of evolutionary psychology. Tooby and Cosmides argue that the human mind should be viewed as a collection of different adaptive mechanisms, each evolved to address a different adaptive problem. They op-

pose the idea that the mind guides behavior by deploying an all-purpose learning strategy; rather, it is a tool box filled with a large number of special-purpose cognitive tools. Tooby and Cosmides also argue that the complex adaptations that the human mind possesses tend to be species-typical universals. Whereas sociobiologists have often been open to the possibility that different individuals in the same species might have different adaptive features, evolutionary psychologists have been less friendly to the hypothesis of within-species adaptive variation; the only context in which they think this is plausible concerns differences between the sexes. In the second chapter in this section, "Evolutionary Psychology: A Critique," David Buller raises questions about the main tenets of evolutionary psychology. He agrees with Cosmides and Tooby that the mind has evolved, and that adaptive hypotheses about its features need to be considered; Buller's objections concern the details of evolutionary psychology, not its broad goals.

## VI Laws in the Evolutionary Process

During the "bad old days," philosophy of science was dominated by logical empiricist ideas and physics was the science that dominated philosophical thinking about what science is. Both the influence of logical empiricism and the fixation on physics encouraged the idea that scientific inquiry is first and foremost the search for general laws. When philosophers of science took an occasional (and usually brief) look at biology, they often took away the impression that biology contains no laws, and just as often, they drew the conclusion that biology is deficient as a science. Echoing Kant, philosophers often concurred that there can be no "Newton of the blade of grass." Biology is not just different, it is inferior.

With the demise of logical empiricism and the growing realization that philosophy of science has to be more than philosophy of physics, the idea took hold that there are different kinds of science. One version of this idea holds that some sciences aim to find general laws while others seek to reconstruct the histories of particular events. Relativity theory and quantum mechanics are sciences of the first type, but evolutionary biology is a historical science. It is different, but not inferior.

John Beatty's chapter, "The Evolutionary Contingency Thesis," develops this view of evolutionary biology. His thesis is that there are no biological laws. When a biological generalization is true, it owes its truth to the fact that contingent evolutionary events turned out one way rather than another. Biological generalizations, since they depend on contingencies, are themselves contingent. And since they are contingently true, they are not laws. Beatty offers two further arguments in favor of this thesis. He argues that evolutionary biology is often given over to disputes about "relative significance." Two examples of what Beatty has in mind were the subjects of previous chapters of this anthology: the debate about adaptationism concerns how important natural selection has been and the units of selection debate concerns how important group selection has

been. Beatty contends that the centrality of such disputes to biology is evidence that there are no biological laws. Beatty also argues that evolutionary biology has forsaken the Newtonian ideal of seeking out parsimonious explanations and that this methodological difference between physics and evolutionary biology provides further evidence that there are no distinctively biological laws.

My chapter “Two Outbreaks of Lawlessness in Philosophy of Biology” replies to Beatty’s arguments and also to arguments for a similar conclusion advanced by Alexander Rosenberg in his 1994 book *Instrumental Biology or the Disunity of Science*. In reply to Beatty, I suggest that if a contingent evolutionary event  $E$  causes a biological generalization  $G$  to be true later on, then we should expect there to be a law linking  $E$  to  $G$ . This is consistent with Beatty’s claim that if  $G$  is contingent on  $E$  (where  $E$  is contingent), then  $G$  is not a law. I also argue that the prevalence of relative significance controversies in evolutionary biology is no evidence for biology’s lawlessness and that biology has not abandoned the principle of parsimony, when that principle is properly understood. Rosenberg’s brief for lawlessness is based on the fact that biological properties are multiply realizable. Take a biological property like “fitness” or “predator;” these predicates apply to organisms that differ vastly from each other in terms of their physical properties. Rosenberg thinks this fact of multiple realizability rules out there being any biological laws (aside from a generalization he calls the principle of natural selection). He also contends that the only objective probabilities discussed in science are the ones found in quantum mechanics. This means that the probabilities discussed in evolutionary biology are mere reflections of our ignorance; biologists use these probabilities to describe evolutionary processes because they don’t know enough about the physical details. Rosenberg takes this to show that the probabilistic generalizations used in evolutionary theory do not describe objective lawful relations.

## VII Reduction

Philosophers interested in how science changes have devoted a great deal of attention to the issue of theoretical reduction. When a new theory replaces an old one, is this because the later theory shows that the former theory is false or because the new theory captures and supplements the insights of the theory it supercedes? The relation of Mendelian genetics to molecular biology has been an important test case for this question. Does modern molecular theory show that Mendel’s ideas were false? Or does it show that Mendel was right? Advocates of the latter position tend to say that Mendelian genetics reduces to molecular biology.

In fact the problem of reduction—of understanding what it means for one theory to reduce to another—is more complicated than this. Sometimes a later theory shows that an earlier theory is true only in a limiting case. Einstein’s theory of special relativity is inconsistent with Newtonian mechanics, but the latter can be thought of as a special case of the former; Newtonian theory is a better and better approximation as

objects move more and more slowly. This leads some philosophers to maintain that Newtonian mechanics reduces to special relativity. A reducing theory (when supplemented with appropriate “bridge laws” that connect the vocabularies of the theories, as Ernest Nagel emphasized in his book *The Structure of Science*) may entail the reduced theory, or the reducing theory may (with bridge laws) entail that the reduced theory is false, though true as a special case. When a successor theory utterly discredits an earlier theory, showing not just that it is false but that it doesn’t even hold true in a special case, no reduction relation can be claimed to obtain. Here we have theory replacement, not reduction of any kind. This is arguably what happened when Lavoisier’s theory of combustion replaced the phlogiston theory.

In the first chapter in this section, “1953 and All That: A Tale of Two Sciences,” Philip Kitcher defends the antireductionist position. He argues that the relationship of current molecular theory to Mendel’s “laws” is best viewed as one of theory replacement, not theoretical reduction. C. Kenneth Waters takes issue with Kitcher’s arguments in his chapter, “Why the Antireductionist Consensus Won’t Survive the Case of Classical Mendelian Genetics.”

The question of how Mendelian genetics is related to molecular biology is an instance of a larger question. Reductionism is often understood as a thesis about the whole of science. The idea is that the social sciences reduce to psychology, psychology to biology, biology to chemistry, and chemistry to physics. Like a nested set of Russian dolls, all sciences above the level of physics reduce to physics, directly or indirectly. Understood in this way, reductionism is a thesis about how the true theories that have been discovered (or will be discovered) in different sciences are related to each other. Truth cannot conflict with truth, so it is obvious that all these true theories are compatible with each other. But  $X$ ’s reducing to  $Y$  requires something more than just that  $X$  and  $Y$  be mutually consistent. One standard idea of what reduction requires is that  $Y$  must explain everything that  $X$  explains, and that  $Y$  must explain why  $X$  is true (to the extent that it is). Reductionism thus can be associated with the slogan “in principle, physics explains everything.”

Kitcher’s argument against reductionism in the case of Mendelian genetics draws on an influential argument against this general reductionistic thesis. Hilary Putnam and Jerry Fodor have both argued that macro-theories typically fail to reduce to micro-theories. An instance of their claim is the thesis that population biology does not reduce to particle physics. I describe and criticize this antireductionist argument in my chapter “The Multiple Realizability Argument Against Reductionism.”

## VIII Essentialism and Population Thinking

The phrase “discerning the essence of things” usually is interpreted to mean that one has identified what is most important. However, the phrase’s familiarity should not lead us to forget that the word “essence” is part of a substantive philosophical

doctrine, one that has exercised a considerable influence on metaphysics, both ancient and modern. Essentialism is a doctrine about natural kinds. Gold is a kind of thing; there are many samples of gold and they differ from each other in numerous respects. In the light of this diversity among gold things, how should science endeavor to understand what gold is?

The essentialist replies that science aims to discover properties that are separately necessary and jointly sufficient for being gold. If all and only the specimens of gold have a particular atomic number, then that atomic number may be the essence of gold. Discovery of essences is not an idle exercise but is fundamental to science's search for explanation. We understand what gold is by seeing what all gold things have in common. Understood in this way, the existence of variation within a kind is a distraction from what is important. Gold things vary from each other, but this variation needs to be set aside. Variation is a veil that we must see through if we are to see what is important.

In "Typological versus Population Thinking" Ernst Mayr argues that evolutionary biology has rejected essentialism in favor of an alternative philosophical framework, which he terms population thinking. I try to provide further clarification of Mayr's thesis in my chapter "Evolution, Population Thinking, and Essentialism." According to Mayr, essentialism may be a good research strategy when chemists try to understand gold, but it would be disastrous as a strategy for investigations in population biology. From a Darwinian point of view, the most important thing to understand about a species is how the individuals in it vary. This variation is what permits the species to evolve. A deep understanding of populational phenomena does not require that we brush aside the variation and discern what all members of a population have in common; rather, we have to characterize the variation and understand how it affects the ways in which the population will change.

## IX Species

When philosophers try to cite examples of natural kinds, they often mention chemical elements and biological species. I just exemplified half this pattern by describing gold as a natural kind whose essence is its atomic number. But is it correct to think of species in the same way? Is the house mouse (*Mus musculus*) a kind of creature in the same way that gold is a kind of stuff? And when we speak of "human nature," are we supposing that there is some property (an essence) that all and only the members of our species possess?

In "A Matter of Individuality," David Hull articulates a position that he and the biologist Michael Ghiselin have developed. Picking up on Mayr's anti-essentialism, they argue that species are individuals, not natural kinds. Species are born and die and have a significant degree of internal cohesiveness while they persist. Hull defends the idea

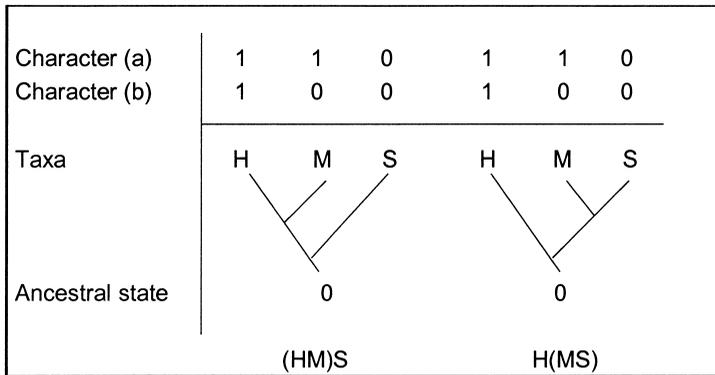
that a species is an integrated gene pool; organisms belong to the same species not because they are similar to each other, but because they reproduce with each other. Individualists such as Hull and Ghiselin have therefore endorsed Ernst Mayr's biological species concept, which defines a species as a group of populations that interbreed with each other but not with other populations.

Baum and Donoghue, in their chapter "Choosing Among Alternative 'Phylogenetic' Species Concepts," oppose the biological species concept and other species concepts that are, in their terminology, "character-based." This is not because they embrace the idea that species are natural kinds. Rather, they favor a "history-based" species concept that groups individuals into species according to their genealogical relationships. Consider four contemporaneous organisms *a*, *b*, *c*, and *d*. The fact that *a* and *b* breed with each other, but cannot interbreed with *c* and *d*, does not show that *a* and *b* belong to a species that does not include *c* and *d*. Perhaps *a* and *c* are more closely related to each other than either is to *b* and *d*. If so, it won't be true that *a* and *b* belong to a species that fails to include *c*.

As noted above, Hull argues for the thesis that species are individuals by emphasizing certain similarities between species and individual organisms. Organisms are born and die, and their cells interact in ways that affect their mutual survival; they have a common fate. In similar fashion, species originate in speciation events and go extinct, and their member organisms affect each other's chances for long-term reproductive success by virtue of belonging to a common gene pool. The disagreement between Mayr's species concept and various phylogenetic species concepts arises from a difference between species and many organisms. The cells of an organism interact with each other, thus affecting their future, and those same cells also trace back to an embryo. The cells have a special history unique to them and their current interactions means that their futures are bound together by a common fate. However, not all individuals are like this. Consider a fleet of ships. Their forming a single armada means that their futures are bound together, but the ships may have very different genealogies. Ships *a* and *b* may belong to one fleet while ships *c* and *d* belong to another, even though *a* and *c* were built in one shipyard while *b* and *d* were built in another. Grouping by current interactions can cross-cut grouping by genealogy. Are organisms to be grouped into species by their current reproductive interactions, or by their genealogies?

## X Phylogenetic Inference

We do not directly observe that human beings are more closely related to mice than either is to snakes. Rather, we observe various characteristics that the three groups display; what we observe are patterns of similarity and difference. Human beings and mice are warm-blooded, but snakes are not. Mice and snakes do not have opposable



**Figure P.1**

Two kinds of similarity. (a) When H and M share a derived character (1) that S lacks, (HM)S is more parsimonious than H(MS); (b) when M and S share an ancestral character (0) that H lacks, (HM)S and H(MS) are equally parsimonious.

thumbs, but human beings do. How are we to use observations such as these to infer phylogenetic relationships?

In “The Logical Basis of Phylogenetic Analysis,” James Farris argues for a hypothetico-deductive approach. We should choose genealogical hypotheses on the basis of their explanatory power, where the most explanatory hypothesis is the one that is most parsimonious. Farris endorses the cladistic idea that the parsimony of a phylogenetic hypothesis should be measured by counting the number of independent originations of features that the hypothesis requires to explain the data. The fact that human beings and mice are warm-blooded, while snakes are not, favors the (HM)S hypothesis over the H(MS) hypothesis. (HM)S means that humans and mice have a common ancestor that is not an ancestor of snakes. However, the fact that mice and snakes lack opposable thumbs, while human beings have them, is not evidence favoring H(MS) over (HM)S. The reason can be understood by considering figure P.1.

The two characters depicted in the figure are each dichotomous, with “0” in each case representing the state of the ancestor that humans, mice, and snakes share, and “1” representing the derived (= non-ancestral) character state. The distribution of character (a) across the three taxa has humans and mice sharing a derived character state (a “synapomorphy”). If a tree begins in state 0, how many changes must occur in the tree’s interior to produce the distribution of character (a) found at the tips? The answer is that (HM)S requires that there be at least one change, while H(MS) requires at least two. Thus (HM)S is the more parsimonious explanation of character (a). Character (b) is different. Here the similarity that unites mice and snakes is ancestral (a “symplesiomorphy”). Notice that (HM)S and H(MS) can each explain the distribution of character

(b) by postulating that a single change has occurred; the two trees are equally parsimonious. This explains why cladistic parsimony involves a rejection of the idea that overall similarity is to be taken as evidence of phylogenetic relatedness; some similarities provide such evidence, but others do not. If you are inclined to think that the warm-bloodedness of humans and mice indicates that they are more closely related to each other than either is to snakes, you are agreeing with the dictates of cladistic parsimony. And if you also think that the absence of an opposable thumb in mice and snakes is not evidence that they are more closely related to each other than either is to humans, you are here agreeing with cladistic parsimony as well.

Whereas Farris thinks of phylogenetic inference from a hypothetico-deductive point of view, Joseph Felsenstein's approach is statistical. In his article "Cases in which Parsimony and Compatibility Methods Will Be Positively Misleading," Felsenstein addresses a question about the property of statistical consistency. A method of inference is statistically consistent if it is bound to converge on the true hypothesis as the data set is made large without limit. Felsenstein assumes that an acceptable method of phylogenetic inference must be consistent and then constructs a simple example in which parsimony fails to converge on the truth. In his own article, Farris discusses Felsenstein's argument and points out that the assumptions Felsenstein makes about the evolutionary process are unrealistic; Farris concludes from this that Felsenstein's argument does not demonstrate any defect in the parsimony criterion. For himself, Felsenstein agrees that the assumptions he makes that allow him to derive the result about statistical inconsistency are unrealistic, however, he takes this to show that parsimony must make substantive assumptions about the evolutionary process. Parsimony is not a "purely methodological" inference criterion, but makes sense only to the extent that its implicit assumptions about the evolutionary process are correct.

One of the principal issues that divides Farris and Felsenstein concerns how much one must know about the evolutionary process before one can make inferences concerning genealogical relationships. Farris maintains that relatively modest assumptions suffice to justify the method of cladistic parsimony; Felsenstein holds that the assumptions required for one to use cladistic parsimony, or any other method, are far more substantive.

## **XI Race—Social Construction or Biological Reality?**

Does group selection occur? Is adaptationism true? These questions, addressed in previous chapters, can be answered only after one clarifies what group selection is and what adaptationism asserts. The question "do races exist?" conforms to the same pattern.

How should the concept of race be defined? One possibility, discussed by Kwame Anthony Appiah in his chapter "Why There Are no Human Races," is provided by the thesis of racialism, which is a version of essentialism (the subject of part VIII). This is

the idea that we can “divide human beings into a small number of groups, called ‘races,’ in such a way that the members of these groups shared certain fundamental, heritable, physical, moral, intellectual, and cultural characteristics with each other that they did not share with members of any other race.” Appiah argues that if this is what races are, then races do not exist. They are like phlogiston and witches—things thought at one time to exist, but which later scientific inquiry has discredited. When people talk of races, they are imposing on reality a set of categories of their own devising, rather than describing nature as it really is.

Racial essentialism is not the only way to answer the question of what a race is. Perhaps races can be conceptualized as biological subspecies. If so, the doubts that biologists have had about the reality of subspecies in general will be relevant to assessing the reality of human races in particular. And conversely, if subspecies are legitimate taxonomic categories, human races may be so as well. One way to approach this question is via the taxonomic philosophy of pheneticism. Pheneticists define taxa by forming similarity clusters. The members of a taxon need not all possess a set of characteristics that is unique to them (as the essentialist demands). Rather, they must be more similar to each other than they are to other individuals not in the taxon. If we cluster human beings in this way, will the resulting taxonomy approximate what human beings call races? If clustering yielded this result, phenetic races would exist, even if essentialist races do not. But what if the clusters are miles away from what people in a country (the United States, for example) call “races?”

Here we must attend to a distinction that Appiah discusses, and which also figures prominently in Robin Andreasen’s chapter “A New Perspective on the Race Debate.” If similarity groupings of human beings don’t correspond much to what people ordinarily call races, then the pheneticist will conclude that common sense races do not exist. But this leaves open the possibility that phenetic races exist. It’s just that people have often misconceived what races are. Here’s an analogy: at one time people thought that whales are fish. Scientific taxonomy eventually rejected this idea, but did not conclude that fish is not a proper taxon. Rather, the conclusion was drawn that fish comprise a taxon whose membership differs from what people had thought. Even if common sense races do not exist, it is an open question whether scientific races exist.

Andreasen introduces a third way of clarifying the question of whether races exist, one that she thinks is superior to both essentialism and pheneticism. This is provided by cladistics. Cladism is a taxonomic philosophy according to which a scientifically legitimate taxon is a monophyletic group. A monophyletic group is comprised of an ancestor and all its descendants. Birds constitute a real taxon, not because they are similar to each other, but because Aves is monophyletic. If a bird gave birth to an organism that lacked wings, that wingless organism would still be a bird. According to the cladistic point of view, if the human species contains distinct lineages that rarely if ever interbreed, those lineages comprise cladistic races. Andreasen argues that human races

were at one time a biological reality, but more recently the reproductive separation of lineages started to break down. For Andreassen, races once existed but now they are on the way out.

## XII Cultural Evolution

Do cultures evolve in a way that is structurally similar to the way that biological populations evolve? In the biological process of natural selection, organisms participate in a struggle for existence; evolution occurs because fitter organisms tend to outsurvive their less fit competitors. In a process of cultural selection, the ideas in a culture compete with each other in a marketplace, where fitter ideas are the ones that tend to attract more adherents. By this process, the mix of ideas in a culture changes. One difference between these cases concerns the mode of transmission. Biological traits are transmitted from parents to offspring by the passing along of genes, while ideas are transmitted from teachers to students by learning. But this point aside, the analogy seems clear-cut.

In their chapter “Does Culture Evolve?” Joseph Fracchia and Richard C. Lewontin pose a number of challenges for the project of modeling cultural change as an evolutionary process. At the most general level, they doubt that a single “transhistorical law or generality” can explain the dynamics of all cultural change and they also doubt that the evolutionary approach will be able to capture “the particularity, the uniqueness of all historical phenomena.” They also have more specific objections. Fracchia and Lewontin note that recent evolutionary models of cultural change (as opposed to nineteenth-century progressivist theories of cultural development) depict culture in terms of the traits (ideas) of individuals. The state of a culture is given by the frequencies of different ideas in it. Fracchia and Lewontin object to this reductionist approach—a country’s military power and its gross domestic product cannot be represented at the level of individuals, so the evolutionary approach will fail to capture how these social facts are causes and effects in social change. The problem of methodological individualism is a standard part of the philosophy of the social sciences, and here we see it making itself felt in the philosophy of biology.

In my chapter “Models of Cultural Evolution,” I try to explain how selectional models of cultural evolution and selectional models of biological evolution are related to each other by focusing on how each understands the concepts of fitness and heredity. I discern three types of model, not just two, and then discuss the distinction between source laws and consequence laws that I developed in my book *The Nature of Selection*. Given a set of heritable traits that differ in fitness, a selectional model will be able to compute the consequences of those initial conditions by describing how the population is apt to change. However, such models are often silent on why the traits have the fitness values they do. It is one thing to describe the consequences of fitness

differences, another thing to describe their sources. Models of cultural evolution have mainly focused on describing the consequences of fitness differences, while saying little about the sources. For example, the decline in birth rate that occurred in nineteenth-century Italy can be described as a process of cultural selection in which the trait of having fewer children had higher cultural (not biological) fitness than the trait of having more. There is nothing false about this description, but it does leave unanswered the question of why preferences about family size suddenly changed, or why women suddenly had the power to control their own reproduction in ways that were not possible before.

One important distinction to bear in mind in thinking about cultural evolution is the difference between the following two questions: Do cultural traits ever evolve by a process of cultural selection? How useful is this way of thinking about cultural change for answering the questions that historians and social scientists wish to address? The intelligibility of an approach and its fruitfulness are separate matters.

### **XIII Evolutionary Ethics**

In *Sociobiology: The New Synthesis*, Edward O. Wilson suggests that “the time has come for ethics to be removed temporarily from the hands of the philosophers and biologized.” In “Moral Philosophy as Applied Science,” Wilson and Michael Ruse set forth their reasons for thinking that evolutionary biology has a great deal to contribute to our understanding of morality. Philip Kitcher responds skeptically in his chapter “Four Ways of ‘Biologizing’ Ethics.”

A central distinction that is relevant to understanding this dispute is that between descriptive and normative statements. A descriptive statement describes what is the case without commenting on whether the facts that obtain are good or bad, just or unjust, and so on. A normative statement makes judgments about whether something is good or bad, right or wrong, etc. These two sets of statements are sometimes called is-statements and ought-statements, but it would be a mistake to think that descriptive statements never contain the word “ought” and that normative statements never use the word “is.” The statement “many people think that capital punishment ought to be abolished” is descriptive, not normative, while the statement “slavery is wrong” is normative, not descriptive.

When we ask whether evolutionary biology has anything useful to say about ethics, we need to divide this question in two. Does evolutionary biology help us understand why this or that normative statement is true or false? Does evolutionary biology help us understand why this or that descriptive statement about ethics is true or false? It is perfectly possible that evolutionary biology throws light on why human beings have the ethical beliefs and feelings they do, and yet says nothing about which of those ethical beliefs (if any) are true. Wilson and Ruse maintain that evolutionary considerations

are relevant to both types of inquiry; it is important to bear in mind that separate arguments are required to establish that both types of relevance exist.

**Acknowledgments**

I am grateful to Mavis Biss, Holly Kantin, Greg Novack, Eric Saidel, Larry Shapiro, and Karen Strier for their help.