Science and Selection

Essays on Biological Evolution and the Philosophy of Science

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PART III TESTING OUR VIEWS ABOUT SCIENCE

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Interactors versus Vehicles

The distinction between organisms and species is as old as Western thought. Organisms are discrete, well-organized bodies that go through life cycles and die, while species are groups of similar organisms that mate and produce equally similar offspring. In 1859 Darwin added an evolutionary dimension to both concepts. According to Darwin, organisms are the things that possess the adaptations that allow some of them to cope better with their environments than do other organisms. Some organisms live long enough to reproduce; others do not. Through the culling action of selection, later generations can depart significantly in their characteristics from earlier generations. As a result, species evolve. In this century, genes joined organisms and species to form the basis for our common conceptions of biological phenomena. Genes are discrete bodies arranged linearly on chromosomes. They code for the structure of organisms and are passed on in reproduction. All that is needed to fit genes into an evolutionary framework is to note that on occasion they mutate.

As neat and intuitively appealing as the preceding characterization may be, biologists are challenging every part of it. Some biologists insist that the only entities that need to be referred to explicitly in evolutionary theory are genes. At bottom, evolution is a function of alternative alleles gradually replacing one another. Evolution is nothing but changes in gene frequencies. Other biologists insist that organisms are the primary focus of selection, and that individual genes cannot be selected in isolation from the effects of the entire genome in the production of organisms. Still others maintain that entities more inclusive than single organisms can be selected – possibly even species themselves. Others insist that selection is not as important to evolutionary change as advocates of the synthetic theory think, and that other factors are responsible for many if not most of the changes that occur.

Many of the issues that divide present-day evolutionary biologists are largely empirical, e.g., the prevalence of more gradualistic versus more saltative forms of evolution, the amount of genetic material that plays no role in the production of phenomes, and the extent of genetic disequilibrium. Others stem from the way in which biological phenomena are conceptualized. In this chapter I concentrate on conceptual issues, in particular the way that the traditional gene/organism/species hierarchy has influenced how evolutionary biologists conceive of the evolutionary process. Throughout the history of science, the ways in which scientists have conceived of natural phenomena have influenced the results of empirical research in ways that could not have been anticipated. The story of the tortoise and the hare is only one example. On some very commonsense notions of space and time, the hare should never be able to catch the tortoise; however, it does. Organisms and species are no less commonsense conceptions, conceptions that continue to bias how we all view biological evolution. These biases, in turn, bias how we view conceptual evolution when it is interpreted as an evolutionary process. Behavior evolved as surely as any other phenotypic characteristics of organisms and should be explicable in the same general terms – if they are general enough. Organisms can learn about their environments from interacting with them. What is more interesting, they can pass on this knowledge. They can learn from one another. Social learning has been developed to its greatest degree in science. Might not social learning in general and science in particular be explicable in these same terms? Might not biological evolution and conceptual change both be selection processes? If so, then we are aware of three different sorts of selection processes: biological evolution, the reaction of the immune system to antigens, and learning.

Although the source of a view is irrelevant to its ultimate validity, certain perspectives in the history of science have such bad track records that the presence of one of them in a conceptual system should at least raise doubts about the system. Anthropocentrism has long been recognized as an evil in science, a bias that supposedly was shed centuries ago. Yet it continues to influence the way we conceptualize the evolutionary process.

As organisms go, human beings are quite large, well organized, and discrete in space and time. We also reproduce sexually and give rise to our young in such a way that parents and offspring are easily distinguishable. Our reproduction and our growth are quite different processes. Similar observations hold for nearly all the organisms that immediately spring to mind when we think of organisms. The paradigm of an organism is an adult vertebrate, preferably a mammal. Unfortunately, these paradigmatic organisms are at the tail end of several important distributions. The vast majority of organisms that have ever lived have been small, unicellular, and asexual. According to recent estimates, systematists have described nearly 1.7 million species of organisms. Of these, about 751,000 are insects, 250,000 are flowering plants, and only 47,000 are vertebrates. But nearly all vertebrate species have been described, while most species of insects remain undescribed. According to one estimate, 30 million insect species are probably extant. But even that number shows a bias, because it includes only extant organisms when easily 99 percent of the species that have ever lived are extinct. Roughly 3.5 billion years ago, life evolved here on Earth. Not until 1.3 billion years ago did eukaryotes evolve. None of these were large, multicellular organisms, nor did they reproduce sexually. Multicellularity and sexuality evolved only 650 million years ago, during the Precambrian era. Hence, it seems strange to pick even insects as the paradigmatic organism, let alone vertebrates. The most common organisms that ever existed are blue-green algae.

None of this would matter to science if similar biases did not influence how evolutionary biologists think of biological evolution. When we think of evolution, we tend to think of fruit flies, flour beetles, deer, and humans. We do not think of slime molds, corals, dandelions, and blue-green algae, but if evolutionary theory is to be truly adequate it must apply to all sorts of organisms, not just to those organisms most like us. Multicellularity and sexuality are rare, peculiar, aberrant, deviant, yet nearly all the literature of evolutionary biology concerns large, multicellular organisms that reproduce sexually, and almost none of it deals with the vast majority of organisms. Critics complain of those biologists who want to generalize from the evolution of ordinary phenotypic traits to the evolution of behavior, but we have yet to generalize our understanding of the evolutionary process to the ordinary phenotypic traits of most of the organisms that have lived. If we are not sure whether our current understanding of biological evolution applies unproblematically to reproduction in blue-green algae, perhaps we should be a bit cautious about generalizing to the social organization of African hunting dogs or Yānomamö Indians. To put this cautionary note differently: one should not dismiss cultural or conceptual evolution as aberrant on the basis of such peculiar phenomena as the transmission of eye color in fruit flies. Perhaps a theory of evolution that would be adequate to handle the entire range of organisms that have functioned in this process might also be adequate to handle cultural and conceptual evolution.

Only a very few biologists have protested the biases so inherent in the literature of evolutionary biology (e.g., Bonner 1974; Thomas 1974; Janzen 1977; Dawkins 1982a,b; Jackson et al. 1986). They complain that many organisms lack *all* the characteristics usually attributed to organisms. Some organisms are not very well organized, at least not throughout their entire life cycle. For example, organisms that undergo considerable metamorphosis become dedifferentiated between stages, losing all their internal organization. In such circumstances, the parts of an organism can be rearranged quite extensively without doing much damage. Nor are the spatiotemporal boundaries of all organisms especially sharp. Some organisms go through stages during which they dissolve into separate cells. It becomes all but impossible in such circumstances to decide where one organism begins and another ends, whether one organism is present or hundreds. Zoocentrism notwithstanding, plants are organisms too. Furthermore, a strawberry patch may look like a series of separate plants until we notice the runners that connect those plants into a single network.

As foreign as these conceptions are to zoologists, botanists recognize tillers and tussocks, ramets and genets. For example, grasses frequently grow in tufts (tussocks) composed of numerous sprouts (tillers) all growing from the same root system. Which is the plant: each tiller, or the entire tussock? More generally, botanists term each physiological unit a ramet, and all the ramets resulting from a single zygote a genet. According to Harper (1977), natural selection acts on the genet, not on the ephemeral ramets. As Cook (1980, pp. 90–1) remarks: "Through the eyes of a higher vertebrate unaccustomed to asexual reproduction, the plant of significance is the single stem that lives and dies, the discrete, physiologically integrated organism that we harvest for food and fiber. From an evolutionary perspective, however, the entire clone is a single individual that, like you or me, had a unique time of conception and will have a final day of death when its last remaining stem succumbs to age or accident."

None of this would matter much if the organismic level of organization did not exercise such a disproportionately strong influence over the way in which evolutionary biologists tend to conceptualize the evolutionary process. If selection is a process of differential perpetuation of the units of selection, and if organisms are the primary focus of selection, then we had better know which entities we are to count – e.g., whether to count each little tuft of crabgrass in a field or the entire field. In cases of sexual reproduction, the distinction between reproduction and growth is usually quite clear and can be used to distinguish organisms. Offspring tend to be genetically quite different from their parents and siblings, and the genetic differences can aid in distinguishing separate organisms. But in cases of asexual "reproduction," our commonsense conceptions begin to break down once again. If the two cells that result from mitosis stay in physical contact with each other, we tend to think of them as parts of a single organism and to count the instance of mitotic division as growth. However, if the daughter cells float away from each other we treat them as separate organisms and count the instance of mitotic division as reproduction. Thus, the distinction between growth and reproduction that makes so much sense for "higher" organisms makes little sense in such cases. Why is continued physical contact so important? As long as runners continue to connect all the various strawberry plants in a patch into a single network, is it to count as a single organism? If one of these runners is severed, are there suddenly two organisms? As always, common sense is not good enough for the needs of science. (For one set of answers to the preceding questions, see Dawkins 1982a.)

Precisely the same sorts of problems arise at the genetic level. Early geneticists extrapolated from conceptions of macroscopic entities to genes. Genes, they thought, were like beads on a string. As genetics continued to develop and was eventually joined by molecular biology, we discovered that genes are not in the least like beads on a string. Only in very special circumstances can we treat single genes as if they controlled discrete characters. Epistatic effects are too common. Nor is the genome a crystalline lattice. Instead it seethes with activity: genes turning on and off, introns being snipped out, other segments moving from place to place in the genome, and so on. Even though all this turmoil at the genic level may have very little to do with adaptive phenotypic change (King 1984), it cannot be ignored in the individuation of genes. Although evolutionary biologists disagree about the sufficiency of genes for an adequate characterization of the evolutionary process, they all agree about their necessity. If changes in gene frequencies play an essential role in evolution, then we had better be able to count genes.

Williams's (1966, p. 25) solution to the aforementioned complexities is to individuate genes in terms of selection. An evolutionary gene is "any hereditary information for which there is a favorable or unfavorable selection bias equal to several or many times its rate of endogenous change." Just as the limits of organisms are highly variable once one acknowledges the existence of such "nonstandard" organisms as dandelions and slime molds, the limits of evolutionary genes are also highly variable, depending on several contingent factors such as frequency of crossover. In organisms that reproduce sexually, the evolutionary gene tends to be quite small. In cases of asexual reproduction, it can be the entire genome. On the definition urged by Williams (1966) and adopted by Dawkins (1976), the genomes of some organisms consist in hundreds of thousands of genes; those of others in only one. Thus, from the perspective of either Mendelian or molecular genes, evolutionary genes are highly variable in size. Conversely, from the evolutionary perspective, Mendelian and molecular genes are no less artificial chimeras.

The most frequently voiced objection to Williams's evolutionary definition of *gene* is that it precludes neutral genes by definitional fiat. But this objection is no objection at all, because comparable implications follow from any definition in terms of activity. For example, Mendelian genes are defined in terms of patterns of phenotypic transmission. The only genes that count as Mendelian genes are those that exhibit phenotypic variation. If there are no alleles, there are no Mendelian genes. Of course, there are segments of the genetic material that do not have any differential effect on the phenotype. They are no less a part of the genetic material even though they do not function as Mendelian genes. Only if one thinks that a particular gene concept must subdivide all the genetic material into units of some sort or other do the preceding observations count as objections. If Williams's evolutionary gene concept must be rejected because it distinguishes only those genes that enter differentially into the evolutionary process, then the concept of the Mendelian gene must be rejected as well because it distinguishes only those genes that enter differentially into intergenerational character transmission.

Parallel problems arise at the third level of our commonsense biological conceptions, the species level. Given our relative size, duration, and perceptual acuity, organisms seem to be highly structured, discrete individuals; species do not. On the contrary, species appear to be little more than aggregates of organisms. Through the years biologists have chipped away at this bit of common sense as well (Dobzhansky [1937] 1951, pp. 576–80; Mayr 1963, p. 21; Hennig 1966, p. 6). However, it was Ghiselin (1966, 1974, 1981) who finally forced biologists to recognize that species as units of evolution are not "mere classes" or "just sets" but are more like individuals. Species certainly do not exhibit anything like the structure presented by the most highly organized organisms; however, they do possess spatiotemporal characteristics, and some even exhibit what is commonly termed "population structure." According to Michod (1982, p. 25), "population structure" refers traditionally to "any deviation from panmixia resulting in nonrandom association between genotypes during mating." But Michod sees no reason not to extend this term to include nonrandom associations during any part of a life cycle. I agree with Kitcher (1984) and Williams (1985) that removing or rearranging parts is likely to have a more serious effect on most organisms than on kinship groups, populations, or species, but the differences are in degree rather than in kind. The distinction that is commonly drawn between well-organized, discrete organisms and these more inclusive entities is not as absolute as one might think.

From these and other considerations, numerous authors have argued that species are the same sort of thing as genes and organisms – spatiotemporally localized individuals. Certainly species do not *seem* to be the same sort of thing as genes and organisms when one thinks of genes as beads on a string and vertebrates as typical organisms; however, once one surveys the wide variety of entities that count as genes and organisms, the suggestion begins to look more plausible. More important, this shift in our conception of species matters. It influences in fundamental ways the manner in which we understand the evolutionary process (Hull 1976, 1978a; Eldredge and Salthe 1984; Vrba and Eldredge 1984; Eldredge 1985). For instance, if species are conceived of as the same sort of things as genes and organisms, it is at least *possible* for them to perform the same functions in the evolutionary process. For instance, if species are conceptualized as individuals, it is at least possible for them to be selected. It does not follow, of course, that they are (Sober 1984). Ghiselin (1985, p. 141) presents this point as follows: "It would seem that species do very few things, and most of these are not particularly relevant to ecology. The speciate, they evolve, they provide their component organisms with genetical resources, and they become extinct. They compete, but probably competition between organisms of the same and different species is more important than competition between one species and another species. Otherwise, they do very little. Above the level of the species, genera and higher taxa never do anything. Clusters of related clones in this respect are the same as genera. They don't do anything either." Eldredge agrees and notes the irony in the fact that the very people who argued most forcefully for the real existence of species went on to deny them any significant role in the evolutionary process. Once species selection is properly understood, Eldredge (1985, p. 160) is forced to conclude that species result from the evolutionary process but do not function in it: "Species, then, do exist. They are real. They have beginnings, histories, and endings. They are not merely morphological abstractions, classes, or at best classlike entities. Species are profoundly real in a genealogical sense, arising as they do as a straightforward effect of sexual reproduction. Yet they play no direct, special role in the economy of nature."

The point of the preceding is to jar those who are complacently satisfied with traditional, commonsense conceptions. Anyone who thinks that the preceding pages are excessive has never urged a nonstandard view on an intellectual community. The most common response is furious frustration. The world *must* be the way that it *seems*. The certainty with which such observations are proclaimed is historically quite contingent. No longer do ordinary people stamp their feet in frustration as they insist that the Earth must be in the middle of the universe or that space cannot possibly be curved. Many do continue to insist that species cannot possibly evolve. But such responses are not limited to ordinary people. Scientists (not to mention philosophers) are just as prone to such responses when their current commonsense perceptions are challenged. It is one thing to claim that over great stretches of space and time "straight" is "curved." Such expanses are not part of common sense, but organisms and species are. Hence, any attempt to alter how we view these entities is as threatening as any conceptual alteration can be.

As if treating genes, organisms, and species as the same sort of thing were not sufficiently counterintuitive, I have argued elsewhere that stratifying the organizational hierarchy in biology into genes, organisms, and species is "unnatural" (Hull 1980). I am not objecting to a hierarchical view of evolution (Arnold and Fristrup 1981; Eldredge 1985; Eldredge and Salthe 1984; Plotkin and Odling-Smee 1981). To the contrary, I think that evolution must be viewed hierarchically. Instead I am arguing that the traditional gene/organism/species hierarchy is seriously misleading. Common sense notwithstanding, it is "unnatural," and it is unnatural in just those respects that make the evolution of behavioral and conceptual evolution look so nonstandard. Objecting to *one* particular hierarchical ordering is not quite equivalent to objecting to all such orderings.

For me, a way of dividing the world is "natural" if it produces entities that function as such in general processes. If "genes" are a natural level of organization distinct from organisms and species, then there must be some function that genes and only genes perform in some natural process. As genes are commonly conceived, I think that there are no general processes in which genes and only genes function. The same can be said for organisms and species. There is nothing that all and only organisms do; nothing that all and only species do. To state the obvious: when I claim that there is no function performed by all and only genes, or organisms, or species, it does not follow that these entities perform no functions in any natural process; only that these are not natural subdivisions. Given a particular function, most genes and some organisms might perform it; given another function, most genes and organisms plus some species might perform it; and so on.

At one time, the division of plants into trees, bushes, and plants (herbs) seemed quite natural. Biologists now find it to be of no significance whatsoever. Currently, most people, including most biologists, find the distinction between genes, organisms, and species to be just as natural. It is not. One reason why evolutionary biologists have been unable to discover universal regularities in the evolutionary process is that they are not comparing like with like. They are dividing up the organizational hierarchy inappropriately. The appropriate levels are not genes, organisms, and species as they are traditionally conceived, but replicators, interactors, and lineages. Evolution needs to be viewed as a hierarchical process. The issue is the character of this hierarchy. My claim is that the regularities that elude characterization in terms of genes, organisms, and species can be captured if natural phenomena are subdivided differently: into replicators, interactors, and lineages. If not, this reworking of biological common sense serves no purpose whatsoever.

Previously I have set out the distinction between replicators, interactors, and lineages with respect to biological evolution (Hull 1980) and have shown how they might be extended to social learning and conceptual change (Hull 1982), but my emphasis in those papers is on replication. Here I expand on the notion of interaction with respect to both biological and conceptual evolution. Neither biological evolution nor social learning can be understood adequately entirely in terms of replication. The process that I term *interaction* plays too central a role to be omitted. The sort of social learning with which I am most concerned occurs in science. The account I set out is intended to apply to conceptual change in general, but the sort of conceptual change I emphasize is the sort that takes place in science.

REPLICATORS AND INTERACTORS

In his classic work, Williams (1966) redefined *gene* so that the extent of the genetic material that counts as a single gene depends upon the effects of selection. Dawkins (1976, p. 69) introduced the more general notion of a *replicator* to take the place of Williams's *gene*. Replicators include genetic replicators but "do not exclude any entity in the universe which qualifies under the criteria listed." According to Dawkins, replicators are those entities that pass on their structure intact through successive replications. Identity of structure is not good enough for selection processes. Identity by descent is required. However, identity seems a bit stringent for the individuation of replicators. Mutations with varying degrees of effect do occur. Allowing variations that have minimal effect on the functioning of a stretch of the genetic material to count as replicates of the "same" gene would not do excessive damage to the spirit of Williams and Dawkins's notion. Abandoning the requirement of descent would.

In his early writings, Dawkins (1976) emphasized replication so strongly that many of his readers interpreted him as arguing that replication is not just necessary for selection but also sufficient. In the interim Dawkins has "clarified" his position or, as his critics claim, "changed" it (Sober 1984). In any case, according to Dawkins's (1982a,b) current views, replication is necessary but not sufficient for selection. A second process, which I term *interaction*, is also necessary (Hull 1980). Interactors are those entities that interact as cohesive wholes with their environments in such a way as to make replication differential. Thus, selection can be characterized generally as any process in which differential extinction and proliferation of interactors causes the differential perpetuation of the replicators that produced them. Vrba (1984, p. 319) phrases this same definition of selection as follows: "Selection is that interaction between heritable, emergent character variation and the environment which causes differences in birth and/or death rates among variant individuals within a higher individual."

The most important feature of the preceding definitions of selection is that selection involves more than just correlations. As Sober (1981, 1984) and Brandon (1982) emphasize, selection is a *causal* process. In my terminology, replicators are causally related to interactors, and the survival of these interactors is causally responsible for the differential perpetuation of replicators.[1] Brandon and Burian (1984) and G. C. Williams (personal correspondence) have complained that my definition of selection mistakenly includes drift as a form of selection. However, when the notion of *interactor* included in this characterization of selection is unpacked, drift is excluded. An entity counts as an interactor only if it is functioning as one in the process in question. It is not enough that in past interactions it functioned as an interactor. Thus, if changes in replicator frequencies are not being caused by the interactions between the relevant interactors and their environments, then these changes are not the result of selection. In instances of drift, there may be genes and organisms, but there are no interactors, only replicators.

Like Dawkins's notion of replicator, *interactor* is defined with sufficient generality that it is not necessarily limited to one commonsense level of organization. Certainly organisms are paradigm interactors, but entities at other levels of the traditional organizational hierarchy can also function as interactors. Genes, chromosomes, and gametes interact with their environments just as surely as do organisms, and these interactions can influence replication frequencies. Entities more inclusive than organisms can also function as interactors – e.g., colonies, hives, and other forms of kinship groups. If the traditional organizational hierarchy is retained, then both replication and interaction wander from level to level. The obvious solution to this state of affairs is to replace the traditional organizational hierarchy with a hierarchy whose levels are delimited in terms of the evolutionary process itself.

The distinction between replication and interaction is important because it helps to disambiguate the phrase "unit of selection." When gene selectionists say that genes are the primary units of selection, they mean that genes are the primary units of replication. They do not mean to assert that they are the only or even primary units of interaction. For example, Williams (1966) emphasizes the role of genes in replication without proposing that evolution is nothing but changes in gene frequencies. Organisms play as large a role in his discussion as in the writings of his critics, in some cases more so. Conversely, when organism selectionists insist that organisms are the primary units of selection, they mean that organisms are the primary focus of interaction, not of replication. Similar remarks hold with respect to group selection. When Wilson (1975) insists that colonies can function as units of selection, he does not mean that they are replicators; he means that they form higher-level interactors. Some species selectionists seem to maintain that species can sometimes function as replicators, others that they might well function as interactors (Dawkins 1982a; Eldredge 1985; Williams 1985).

Although distinguishing replicators from interactors helps to clarify the disagreements between advocates of various sorts of selection, it does not eliminate them completely. Proponents of group selection insist that close kin form groups and that these groups function as interactors in the evolutionary process. Organism selectionists counter that everything that needs to be said about kin selection can be said in terms of the inclusive fitness of individual organisms. The difference is between kin-group selection and kin selection. Gene selectionists dismiss inclusive fitness as a sop that Hamilton (1964a,b) threw to organism selectionists. Gene selectionists acknowledge that both replication and interaction function in the evolutionary process, but they maintain that evolutionary theory can, at bottom, be couched entirely in terms of replication, and that any causal processes that do not eventuate in changes in replicator frequencies (usually gene frequencies) simply do not matter. Opponents of genic selectionism, including Wimsatt (1980) and Sober and Lewontin (1982), admit that reference to changes in gene frequencies is adequate for the "bookkeeping" aspect of selection but insist that the bookkeeping aspect by itself leaves out too much of the causal story. They want to expand the axioms of evolutionary theory to include reference to the causal relations responsible for evolution's taking place the way that it does. Williams (1985, p. 2) is content with evolutionary theories limited to the bookkeeping aspect and finds the criticisms of such theories by Wimsatt (1980) and Sober and Lewontin (1982) to be based on "unrealistic expectation." Genic selectionists also seem to fear that including explicit reference to the causal interface between interactors and their environments will complicate evolutionary theory prohibitively, possibly even challenging the Weismann barrier.

Strangely enough, the most vocal defenders of the necessary role of organisms (or, more generally, interactors) in the evolutionary process – in opposition to what they see as an overemphasis on genes (or, more generally, replicators) – are also among those who are most skeptical about evolutionary "just so stories" (e.g., Gould and Lewontin 1979), while several of the strongest advocates of genic selectionism see nothing wrong with evolutionary scenarios (Dawkins 1982b; Ridley 1983; Williams 1985). Defenders of the role of organisms in evolution warn that many of the characteristics that evolutionary biologists claim are adaptations might well be nothing but effects. In addition, the ease with which adaptationist scenarios can be constructed to explain particular adaptations casts considerable doubt on the entire program. Hence, they conclude that we cannot leave organisms and their adaptations out of the evolutionary story, but we must include reference to them only with great care. Defenders of the adequacy of genes in setting out the basic axioms of evolutionary theory do not think that discerning organismic adaptations is all that problematic. Although organisms and their adaptations do not play a central role in the fundamental axioms of evolutionary theory, secondary reference to them is nevertheless scientifically reputable. At the risk of putting too fine a point on the dispute, Williams (1985, pp. 2, 15) thinks that his critics are too optimistic about the potentialities of evolutionary theory and too pessimistic about the legitimacy of adaptive scenarios.

I find myself in partial agreement with both sides of this dispute. I think that any adequate theory of evolution must include reference to the interactor-environment interface (Odling-Smee and Plotkin 1984), but that the inclusion of such reference need not complicate evolutionary theory any more than including reference to replication does. It is certainly true that interactions are as varied as the myriad causal situations that give rise to the incredible array of adaptations that makes the study of biology so endlessly fascinating, but the information contained in the genetic makeup of organisms for these adaptations is just as multifarious. The introduction of either sort of complexity into the general characterization of the evolutionary process would be lethal, but no such introduction is necessary. In both cases, all that must actually be included in formal statements of evolutionary theory are the general characteristics of replicators and interactors and how they are interrelated. Only when this general theory is applied to particular cases is the actual informational content of the replicators and the causal situations that produced the particular adaptations relevant. Scientific theories are general. Their applications are contingent and often idiosyncratic.[2]

With respect to applications, I see no reason to shy away from claiming that a particular characteristic arose as an adaptation to a putative past environment, even though such claims may often be false. In most cases, little rides on the correctness of particular adaptationist scenarios. Showing that processes other than replication and interaction are actually responsible for biological evolution would be of prime importance. It would bring into question our basic conception of the evolutionary process. Detailing difficulties in applying evolutionary theory is of secondary importance. All scientific theories are difficult to apply. Inferences to particular cases must be possible if evolutionary theory is to be testable, but such testing need not be easy or automatic. Critics of evolutionary theory are not content with its being falsifiable. They insist that it must be easily falsifiable, when no scientific theory is easily falsifiable.

However, adaptationist scenarios are so fascinating that they often seduce biologists into ignoring even more fundamental aspects of the evolutionary process. Also, there is a tendency to think that adaptationist scenarios have greater warrant than they actually have. For most species, such misplaced confidence is unlikely to do much harm. However, similar mistakes in the context of the human species can do considerable damage. We may be innately territorial or sexually dimorphic in socially relevant ways. We *may* be, but the substantiation available for such claims is not all that impressive. Social policies based on such shaky ground are likely to be misconceived and the results deleterious. But to repeat my general point: The general notion of adaptation is central to a selectionist view of evolution. Questions about which particular structures arose as adaptations to which particular environmental changes are relevant only to the testing of selectionist versions of evolutionary theory.

Although Dawkins has come to accept the distinction between replicators and interactors, he prefers a somewhat different terminology: "My main concern has been to emphasize that, whatever the outcome of the debate about organism versus group as *vehicle*, neither the organism nor the group is a *replicator*. Controversy may exist about rival candidates for replicators and about rival candidates for vehicles, but there should be no controversy over replicators *versus* vehicles.

Replicator survival and vehicle selection are two aspects of the same process" (Dawkins 1982a, p. 60).

Once the distinction between replicators (on the one hand) and vehicles or interactors (on the other hand) is made, the issues that divide present-day evolutionary biologists can be stated more clearly. Of course, this distinction does not decide these issues. Slight differences in how the distinction is drawn can influence the resulting resolutions. As Kawata (1987) points out, Dawkins's vehicles and my interactors are not precisely equivalent concepts. According to Dawkins, genes are replicators, not vehicles. They ride around in vehicles, directing their behavior. On my account, genes are both replicators and interactors. If genes are anything, they are entities that interact with their environments in such a way as to bias their own replication. In one place, Dawkins (1982a, p. 45) notes that the wings of birds are for flying and then asks, "What are DNA molecules for?" He answers that "DNA is not 'for' anything. If we wish to speak teleologically, all adaptations are for the preservation of DNA; DNA itself just *is*." Yes and no. Organisms are characterized by adaptations. So are molecules of DNA. They are extremely well adapted to replicate. The major effect of this replication is, as Dawkins insists, the preservation of the structure of DNA. Once it is recognized that one and the same entity can function both as a replicator and as an interactor, the image of genes riding around in vehicles becomes less persuasive.

Sober (1984, pp. 253–5) also complains that Dawkins defines his terms in ways to guarantee that organisms cannot possible function as replicators. One reason that Dawkins has for rejecting organisms as replicators is meiosis. At meiosis, parental genomes are dismembered; then new genomes are reassembled at fertilization. If retention of structure largely (or totally) intact is necessary for replicators, then only small sections of the genome can function as replicators in cases of sexual reproduction in genetically heterogeneous populations. Both restrictions should be noted. Dawkins's central argument for genes being the only replicators applies only to organisms when they reproduce sexually. If genes are the only replicators in cases of asexual reproduction, he needs an additional argument. His central argument also does not apply to sexual reproduction in genetically homogeneous populations. Although crossover can occur in such populations, it makes no difference to the structure of the resulting genomes. However, as Williams (1985, p. 5) notes, even in such cases, phenotypes "can play no role in bookkeeping because, even in a clone, the successive generations of phenotypes may be markedly different because of environmental variables that affect development."

The best example of an organism functioning as a replicator is the direct transmission of a phenotypic change to successive generations through fission. For example, if a portion of the cortex of a paramecium is surgically removed and reinserted with the cilia facing the opposite direction, this phenotypic changes is transmitted to subsequent generations. In light of this example, Dawkins (1982b, p. 177) responds as follows:

> If, on the other hand, we look at underlying replicators, in this case perhaps the basal bodies of cilia, the phenomenon falls under the general heading of replicator propagation. Given that macromolecular structures in the cortex are true replicators, surgically rotating a portion of cortex is analogous to cutting out a portion of chromosome, inverting it, and putting it back. Naturally the inversion is inherited, because it is part of the germ-line. It appears that elements of the cortex of *Paramecium* have a germ-line of their own, although a particularly remarkable one in that the information transmitted does not seem to be encoded in nucleic acid.

When Dawkins (1976) introduced the term *replicator*, he intended it to be more general than *gene*. Although genes, as they are currently understood, may not be limited to the nucleus, they are limited to nucleic acids – DNA and RNA. The basal bodies of cilia do not count as genes, but they might well count as replicators and form a "germ-line" of their own. Even so, in the paramecium example, the inverted cortex is not being transmitted indirectly via the basal bodies but directly. Obviously something must be going on at lower levels of analysis when a paramecium splits down the middle to form two new organisms, but I fail to see why this fact counts against treating organisms in this situation as replicators. After all, even though entities less inclusive than genes are involved in genetic replication, it does not follow that genes are not replicators. Standards should not be invoked for organisms more stringent than those applied to genes. Organisms behave in ways that make them candidates for replicators seldom enough without ruling them out by definition. As it turns out, in the most common situation in which one might want to view organisms as replicators – asexual reproduction via fission – it makes no difference. In asexual reproduction, usually the entire genome functions as a single replicator, and there is a one-to-one correlation between genomes and phenomes. Hence, the numbers will always turn out to be the same.

A second reason that organisms are not very good candidates for replicators concerns the different senses in which genes and organisms can be said to "contain information" in their structure. Genes do not code in a one-to-one fashion for phenotypic traits. Given a particular genome, numerous alternative phenomes are possible depending on differences in the environment. Given any one gene, numerous different alternative traits are possible depending on differences in the environment as well as elsewhere in the genome. The net effect is that both individual genes and entire genomes code for reaction norms, not for specific traits or phenomes. In this sense, the information in a genome is largely "potential." In any one instance of translation, these reaction norms are narrowed to one eventuality, to a single phenome. All other possibilities, equally "programmed" into the genetic material, are not realized. To use Wimsatt's felicitous terminology, each genotoken gets to produce a single phenotoken. The net effect is the loss of nearly all the potential information in the genome. The only information that an organism as a replicator can pass on is the information realized in its structure. (For an exhaustive treatment of the role of "information" in evolution, see Brooks and Wiley 1986.)

Both Dawkins (1982b) and I (Hull 1976, 1978a) have been concerned to break the hold that a fairly narrow conception of organisms has on the minds of many evolutionary biologists, but toward different ends. According to Dawkins, nests and mating calls are as much a part of a bird's phenotype as are its beak and webbed feet. In response to Gould's (1977) claim that selection cannot see genes and pick among them directly but must use bodies as an intermediary, Dawkins (1982a, p. 58) retorts: "Well, it must use *phenotypic effects* as intermediaries, but do they have to be bodies? Do they have to be discrete vehicles at all?" In answering no to both questions, Dawkins plays down the role in evolution of organisms as discrete bodies or even as vehicles. I have argued at some length that organisms are not as discrete, unitary, and well organized as we tend to assume in order to urge a role for entities more inclusive than single organisms as interactors, not in order to question the role of organisms as paradigmatic interactors. Dawkins (1982b) and Williams (1985) argue that organisms can never function as replicators in the evolutionary process. Although I am not willing to go this far, I agree that when organisms do function as replicators, the effects of organismal replication are likely not to be extensive.

The point of the preceding discussion has been to show why traditional conceptions are not adequate for biological evolution strictly construed. If simplistic notions of genes, organisms, and species are not adequate for ordinary biological evolution, then they are surely not adequate for construing social learning as a selection process. But before turning to this topic, I need to present at least one particular example of the improved understanding that my revised conceptual apparatus brings to biological phenomena. One of the major topics in recent literature in population biology has been explanations of the prevalence of sexual reproduction. The problem can be stated quite simply. If the name of the game in biological evolution is to pass on one's genes, then sexual reproduction is a very inefficient way of accomplishing this end, because sexual reproduction has a 50 percent cost. At any locus where the male and the female differ, each has only a 50-50 chance of passing on its alleles rather than those of its mate. Conversion from sexual reproduction to parthenogenesis would double the contribution of a female to future generations. So, though in theory sexual reproduction should be quite rare, in fact it is "almost universal" (Maynard Smith 1971, p. 165).

The problem is so acute that evolutionary biologists who are strongly inclined to dismiss group selection in other contexts are forced back on this mechanism for the evolution of sex. For example, Williams (1971, p. 161) concludes: "Sexual reproduction must stand as a powerful argument in favor of group selection, unless someone can come up with a plausible theory as to how it could be favored in individual selection. And if group selection can produce the machinery of sexual reproduction, it ought to be able to do many other things as well."

Among the many things that group selection has been introduced to explain is the evolution of sociality and, with it, the rise in importance of social learning. Hence, sex and society are intimately connected in theorizing about the evolutionary process. But in the preceding discussion, the most important premise gets slipped in when no one is noticing, i.e., that sexual forms of reproduction are prevalent. As my earlier discussion indicates, sexual reproduction is a relatively recent innovation. For three-quarters of the existence of life on Earth, the sole form of reproduction was asexual. If one looks at every measure save one, it is still extremely common. If one looks at number of organisms, amount of energy transduced, biomass, etc., asexual reproduction remains extremely prevalent. Only if one compares numbers of species do sexual forms of reproduction turn out to be "nearly universal." But asexual organisms do not form species of the sort that exist among sexual organisms. To be sure, systematists group all organisms in species (taxospecies); however, as far as real groupings in nature are concerned, asexual organisms do not form *genealogical* units of the sort formed by sexual organisms.

The difference between asexual and sexual reproduction is fundamental. As Maynard Smith (1971, p. 163) notes, "At the cellular level, sex is the opposite of reproduction; in reproduction one cell divides into two whereas it is the essence of the sexual process that two cells should fuse to form one." In fact, the differences are so fundamental that many authors argue that the same term should not be applied to both. Either sexual or asexual reproduction is not really "reproduction." Hence, one solution to the problem of the prevalence of sex when meiosis exacts a 50 percent cost is that it is not prevalent. It is as rare as it should be given its cost. The reason why it took so long for sex to evolve is that it is advantageous in only very special circumstances. In fact, it took only a little over a billion years for the first living creatures to evolve. It took almost 3 billion years more for sexuality to make an appearance. If the time it takes for something to evolve is any measure of its evolutionary advantage, sexual reproduction may not be all that advantageous. Hence, from this perspective, Williams's (1985, p. 103) explanation of sexuality in vertebrates begins to sound more plausible. According to Williams, sexual reproduction in derived low-fecundity organisms such as vertebrates is "a maladaptive feature, dating from a piscine or even protochordate ancestor, for which they lack the preadaptations for ridding themselves."

The usual response to the preceding observations is that something has gone wrong. Sexual reproduction evolved quite early and has been widespread throughout the history of life on Earth. After all, forms of parasexual reproduction exist among extant blue-green algae. There is no reason to assume that such forms of gene exchange were any less prevalent in the past. In the first place, mere gene exchange does not pose the same problem as meiosis. The issue is the cost of meiosis. And by all indications gene exchange among prokaryotes is extremely rare, ranging from one cell in 240,000 replications to one in 20 million. If such rare occurrences of gene exchange are sufficient to label an entire higher taxon "sexual," then Jackson et al. (1986) are just as warranted in labeling an entire group "clonal" just because a few forms exhibit clonality. One need not argue that sexual reproduction evolved quite early and is nearly universal in order to recognize it as an important innovation in biological evolution. Even though it is a relatively recent innovation and still quite rare, it served as an "evolutionary trigger" to give rise to species and, through them, to much of the diversity of life that we see all around us.

On the view that I am urging, replicators should be compared with replicators, interactors with interactors, and lineages with lineages. When one makes such comparisons, the results are quite different than when one compares genes with genes, organisms with organisms, or species with species. For one thing, sexual reproduction becomes "rare." Although their terminology is different, those authors who have looked at clonal organisms have been forced to make very similar distinctions. When the authors in Jackson et al. (1986) look at evolution in clonal organisms, they are forced to distinguish between ramets and genets. They compare ramets with ramets and genets with genets in estimating such things as fitness and the speed of evolutionary change. The effects of this change in perspective are dramatic in biological evolution. They should be no less pervasive when one turns one's attention to social learning as a selection process.

CONCEPTUAL EVOLUTION: REPLICATION

Dawkins introduced the notions of replicator and vehicle because of their generality and because of the common associations of such terms as *gene* and *organism*. However, *replicator* and *vehicle* also have their connotations. As far as I can see, the connotations of the term *replicator* are entirely appropriate whereas those of *vehicle* are not. Vehicles are the sort of thing that agents ride around in. More than this, the agents are in control. The agents steer and the vehicles follow dumbly. The picture that Dawkins's terminology elicits is that of genes controlling helpless and hapless organisms. Although Dawkins explicitly assigns an evolutionary role to both replicators and vehicles, his terminology is likely to mislead one into treating vehicles as passive tools in the hands of all-powerful replicators. As Sober (1984, p. 255) repeatedly emphasizes, "The units of selection controversy began as a question about causation." For this reason, I prefer *interactor* to *vehicle* (see also Williams 1985).

Dawkins intends *replicator* to apply to any entity that happens to possess the appropriate characteristics. In biological evolution, he insists that only genes function as replicators (the paramecium example