continuous deformations of ecological relation. Second, characters must be *quasi-independent*. That is, there must exist a large number of possible phenotypic correlations between a given character change and other aspects of the phenotype. If character correlations are unbreakable, or nearly so, then no single aspect of the phenotype, like fins, could ever develop without totally altering the rest of the organism in generally nonadaptive ways. At the same time, despite the principle of continuity, there are points at which quantitative change becomes qualitative, and the principle of quasi-independence does not mean that every kind of restructuring of organisms is possible. These two principles are the beginning of a theory of the evolution of organisms. The theory still must be developed; at the moment we have only a kinematics of the evolution of abstract genotypes.

2 Adaptation

EVERY theory of the world that is at all powerful and covers a large domain of phenomena carries immanent within itself its own caricature. If it is to give a satisfactory explanation of a wide range of events in the world in a wide variety of circumstances, a theory necessarily must contain some logically very powerful element that is flexible enough to be applicable in so many situations. Yet the very logical power of such a system is also its greatest weakness, for a theory that can explain everything explains nothing. It ceases to be a theory of the contingent world and becomes instead a vacuous metaphysic that generates not only all possible worlds, but all conceivable ones. The narrow line that separates a genuinely fruitful and powerful theory from its sterile caricature is crossed over and over again by vulgarizers who seize upon the powerful explanatory element and, by using it indiscriminately, destroy its usefulness. In doing so, however, they reveal underlying weaknesses in the theories themselves, which can lead to their reformulation.

This element of immanent caricature is certainly present in three theoretical structures that have had immense effects on twentieth-century bourgeois thought: Marxism, Freudianism, and Darwinism. Marx's historical materialism has been caricatured by the vulgar economism that attempts to explain the smallest detail of human history as a direct consequence of economic forces. Freud's ideas of sublimation, transference, reversal, and repression have been interpreted to explain any form of overt behavior as a direct or transformed manifestation of any arbitrary psychological cause. In Darwinism the element that is

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both central to the evolutionary world view and yet so powerful that it can destroy Darwinism as a testable theory is adaptation.

The concept of adaptation not only characterizes explanations of the evolution of life forms but also appears in cultural theory as functionalism. According to the concept there exist certain "problems" to be "solved" by organisms and by societies; the actual forms of biological and social organizations in the world are seen as "solutions" to these "problems." Describing adaptation in these modern terms should not mask the fact that the concept has been inherited from a much older world view, one that was characteristic of the aristocratic and fixed world before the European bourgeois revolution. In that view the entire universe, including living organisms and especially the human species and its social organization, was perfectly fitted to serve a higher purpose. "The heavens declare the glory of God and the firmament showeth his handiwork" are the words of the Psalmist. The universe was the work of a divine creator, and its parts were made by him to fit together in a harmonious way, each part subserving the higher function. In the view of some, the primary object of this creation was man, whose nature was carefully fashioned to allow a new and more trustworthy race of angels to develop. The rest of the living world was designed to serve humankind. Cows were ideally designed to provide people with milk, and trees to give shade and shelter. The most important political consequence of this world view was the legitimation it provided for social organization. Lords and serfs, masters and slaves represented a division of power and labor that was necessary for the proper functioning of society and the working out of the divine plan.

The belief that organisms were marvelously fitted to their environments and that each part of an organism was exquisitely adjusted to serve a special function in the body, just as parts of the body politic were perfectly fitted to serve the needs of "society," was carried over into modern biological and anthropological thought. All that changed was the explanation. Having rejected the supreme designer as responsible for the world's perfection, Darwin needed to show that evolution by natural selection could lead to the same end. "In considering the origin of species, it is quite conceivable that a naturalist . . . might come to the conclusion that each species . . . had descended, like varieties, from other species. Nevertheless, such a conclusion, even if well founded, would be unsatisfactory until it could be shown how the innumerable species inhabiting this world have been modified, so as to acquire that perfection of structure and coadaptation which most justly excites

our admiration" (Darwin 1859, p. 3). Indeed, in his chapter "Difficulties of the Theory," Darwin realized that "organs of extreme perfection and complication" were a critical test case for his theory. "To suppose that the eye, with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection seems, I freely confess, absurd in the highest degree" (p. 186). But such "organs of perfection" are only the extreme and obvious results of the process of natural selection, which lies at the center of Darwinian evolutionary theory. For Darwin, species originated through a continuing process of adaptation which, at the same that it produced new species, produced organisms whose parts were in harmony with each other so that the organism as a whole was in harmony with its environment.

BEING ADAPTED AND BECOMING ADAPTED

The concept of adaptation implies that there is a preexistent form, problem, or ideal to which organisms are fitted by a dynamical process. The process is adaptation and the end result is the state of being adapted. Thus a key may be adapted to fit a lock by cutting and filing it, or a part made for one model of a machine may be used in a different model by using an adaptor to alter its shape. There cannot be adaptation without the ideal model according to which the adaptation is taking place. Thus the very notion of adaptation inevitably carried over into modern biology the theological view of a preformed physical world to which organisms were fitted. When the world was explained as the product of a divine will, there was no difficulty with such a concept, since according to the creation myth the physical world was produced first and the organisms were then made to fit into that world. The Divine Artificer created both the physical world and the organisms that populated it, so the problems to be solved and the solutions were products of the same schema. God posed the problems and gave the answers. He made the oceans and gave fish fins to swim in them, he made the air and put wings on birds to fly in it. Having created the locks, *il Alto Fattore* made the keys to fit them.

With the advent of evolutionary explanations, however, serious problems arose for the concept of adaptation. Certainly the physical universe predated living organisms, but what are the physical schemata to which organisms are adapting and adapted? Are there really preexistent "problems" to which the evolution of organisms provides "solutions"? This led to the concept of ecological niche. The niche is a multidimensional description of all the relations entered into by an organism with the surrounding world. What kind of food, and in what quantities, does the organism eat? What is its pattern of spatial movement? Where does it reproduce? At what times of day and during what seasons is it active? To maintain that organisms adapt to the environment is to maintain that such ecological niches exist in the absence of organisms and that evolution consists in filling these empty and preexistent niches.

But the external world can be divided up in an uncountable infinity of ways, so there is an uncountable infinity of conceivable ecological niches. Unless there is a preferred or correct way in which to partition the world, the idea of an ecological niche without an organism filling it loses all meaning. The alternative is that ecological niches are defined only by the organisms living in them, but this raises serious difficulties for the concept of adaptation. Adaptation cannot be a process of gradual fitting of an organism to the environment if the specific environmental configuration, the ecological niche, does not already exist. If organisms define their own niches, then all species are already adapted, and evolution cannot be seen as the process of *becoming* adapted.

Indeed, even if we put aside ecological niches, there are difficulties in seeing evolution as a process of adaptation. All extant species, for a very large part of their evolutionary histories, have neither increased nor decreased in numbers and range. If a species increased on the average by even a small fraction of a percent per generation, it would soon fill the world and crowd out all other organisms. Conversely, if a species decreased on the average, it would soon go extinct. Thus for long periods of its evolutionary lifetime, a species is adapted in the sense that it makes a living and replaces itself. At the same time, the species is evolving, changing its morphology, physiology, and behavior. The problem is how a species can be at all times both adapting and adapted.

A solution to the paradox has been that the environment is constantly decaying with respect to the existing organisms, so the organisms must evolve to maintain their state of adaptation. Evolutionary adaptation is then an infinitesimal process in which the organism tracks the ever-changing environment, always lagging slightly behind, always adapting to the most recent environment, but always at the mercy of further historical change. Both the occasional sudden increases in abundance and range of a species and the inevitable extinction of all

species can be explained in this way. If the environment should change in such a way that the present physiology and behavior of a species by chance makes it reproductively very successful, it may spread very rapidly. This is the situation of species that have colonized a new continent, as, for example, the rabbit in Australia, finding there by sheer chance environmental conditions (including the lack of competitors) to which it is better adapted than it had been to its native habitat. Eventually, of course, such a species either uses up some resource that had existed in great excess of its needs or otherwise alters the environment by its own activity so that it is no longer able to increase in numbers. The alternative, that the environment remains unchanged but that the species by chance acquires a character that enables it to utilize a previously untapped resource, is very much less likely. Such favorable mutations, or "hopeful monsters" may nevertheless have occurred as, for example, in the evolution of fungus gardening by ants.

The simple view that the external environment changes by some dynamic of its own and is tracked by the organisms takes no account of the effect organisms have on the environment. The activity of all living forms transforms the external world in ways that both promote and inhibit the life of organisms. Nest building, trail and boundary marking, the creation of entire habitats, as in the dam building of beavers, all increase the possibilities of life for their creators. On the other hand, the universal character of organisms is that their increase in numbers is self-limited, because they use up food and space resources. In this way the environment is a product of the organism, just as the organism is a product of the environment. The organism adapts the environment in the short term to its own needs, as, for example, by nest building, but in the long term the organism must adapt to an environment that is changing, partly through the organism's own activity, in ways that are distinctive to the species.

In human evolution the usual relationship between organism and environment has become virtually reversed in adaptation. Cultural invention has replaced genetic change as the effective source of variation. Consciousness allows people to analyze and make deliberate alterations, so adaptation of environment to organism has become the dominant mode. Beginning with the usual relation, in which slow genetic adaptation to an almost independently changing environment was dominant, the line leading to *Homo sapiens* passed to a stage where conscious activity made adaptation of the environment to the organism's needs an integral part of the biological evolution of the species. As Engels (1880) observed in "The Part Played by Labor in the Transition from Ape to Man," the human hand is as much a product of human labor as it is an instrument of that labor. Finally the human species passed to the stage where adaptation of the environment to the organism has come to be completely dominant, marking off *Homo sapiens* from all other life. It is this phenomenon, rather than any lucky change in the external world, that is responsible for the rapid expansion of the human species in historical time.

Extinction may be seen as the failure of adaptation in that genetic or plastic changes in an adapted species are unable to keep up with a change in the environment. A species' response to environmental alteration is limited by the morphological, physiological, and behavioral plasticity given by its present biology and by genetic changes that may occur by mutations and natural selection. Phenotypic and genetic plasticity is thus limited in kind but, more important, it is limited in rate of response, so the environment is sure eventually to alter in a way and at a rate that outdistances the species' adaptive response. More than 99.9 percent of all species that ever existed are extinct, and all are sure to be extinguished eventually.

The theory of environmental tracking does not solve the problem of evolution. It cannot explain, for example, the immense diversification of organisms that has occurred. If evolution is only the successive modification of species to keep up with a constantly changing environment, then it is difficult to see how the land came to be populated from the water and the air from the land, or why homoiotherms (warm-blooded organisms) evolved at the same time that poikilotherms (cold-blooded organisms) were abundant. This evolutionary diversification cannot be described in any consistent way as a process of adaptation unless we can describe preferred ways of dividing up the multidimensional niche space toward which species were evolving and, therefore, adapting. That is, the concept of adaptation is informative only if it has some predictive power. It must be possible to construct a priori ecological niches before organisms are known to occupy them and then to describe the evolution of organisms toward these niches as adaptation.

The exploration of other planets does provide the possibility of making such predictions, yet it also illustrates the epistemological difficulties involved. If there really are preexistent niches to which organisms adapt, then it ought to be possible to predict the kind of organisms (if any) that will be discovered on Mars or Venus, by examining the physical environments of those planets. In the building of devices to detect

life on these planets, predictions are in fact being made, since the detection depends upon the growth of hypothetical organisms in defined nutrient solutions. These solutions, however, are based on the physiology of *terrestrial* microorganisms, so the devices will detect only those extraterrestrial life forms that conform to the ecological niches already defined on earth. If life on other planets has partitioned the environment in ways that are radically different from those on earth, those living forms will remain unrecorded. There is no way to use adaptation as the central principle of evolution without recourse to a predetermination of the states of nature to which this adaptation occurs, yet there seems no way to choose these states of nature except by reference to already existing organisms.

SPECIFIC ADAPTATIONS

Evolutionists, having accepted that evolution is a process of adaptation, regard each aspect of an organism's morphology, physiology, and behavior as a specific adaptation, subserving the state of total adaptation of the entire organism. Thus fins are an adaptation for swimming, wings for flying, and legs for walking. Just as the notion of adaptation as an organism's state of being requires a predetermined ecological niche, so, even more clearly, assigning the adaptive significance of an organ or behavior pattern presumes that a problem exists to which the character is a solution. Fins, wings, and legs are the organism's solutions to the problem of locomotion in three different media. Such a view amounts to constructing a description of the external environment and a description of the organism in such a way that they can be mapped into each other by statements about function.

In practice the construction may begin with either environment or organism, and the functional statement then used to construct the corresponding structure in the other domain. That is, the problems may be enumerated and then the organism partitioned into solutions, or a particular trait of an organism may be assumed to be a solution and the problem reconstructed from it. For example, the correct mutual recognition of males and females of the same species is regarded as a problem, since the failure to make this identification would result in the wastage of gametes and energy in a fruitless attempt to produce viable offspring from an interspecific mating. A variety of characters of organisms, such as color markings, temporal patterns of activity, vocalizations (as in the "mating call" of frogs), courtship rituals, and odors, can then be explained as specific adaptations for solving this universal problem. Conversely, the large erect bony plates along the middorsal line of the dinosaur *Stegosaurus* constitute a character that demands adaptive explanation; they have been variously proposed as a solution to the problem of defense, either by actually interfering with a predator's attack or by making the animal appear larger in profile, as a solution to the problem of recognition in courtship, and as a solution to the problem of temperature regulation by acting as cooling fins.

Hidden in adaptive analyses are a number of assumptions that go back to theistic views of nature and to a naive Cartesianism. First it must be assumed that the partitioning of organisms into traits and the partitioning of environment into problems has a real basis and is not simply the reification of intuitive human categories. In what natural sense is a fin, leg, or wing an individual trait whose evolution can be understood in terms of the particular problem it solves? If the leg is a trait, is each part of the leg also a trait? At what level of subdivision do the boundaries no longer correspond to "natural" divisions? Perhaps the topology as a whole is incorrect. For example, the ordinary physical divisions of the brain correspond in a very rough way to the localization of some central nervous functions, but the memory of events appears to be diffusely stored, and particular memories are not found in particular microscopic regions.

As we move from anatomical features to descriptions of behavior, the danger of reification becomes greater. Animal behavior is described by categories such as aggression, altruism, parental investment, warfare, slave making, and cooperation, and each of these "organs of behavior" is provided with an adaptive explanation by finding the problem to which it is a solution (Wilson 1975). Alternatively, the problems to be solved in adaptation also may be arbitrary reifications. For example, by extension from human behavior in some societies, other animals are said to have to cope with "parent-offspring conflict," which arises because parents and offspring are not genetically identical but both are motivated by natural selection to spread their genes (Trivers 1974). A whole variety of manifest behaviors, such as the pattern of parental feeding of offspring, is explained in this way. Thus, the noise-making of immature birds or humans is a device to coerce the selfish parents into feeding their offspring, who otherwise would go untended.

A second hidden assumption is that characters can be isolated in an adaptive analysis; any interactions among characters are considered to be secondary and to represent constraints on the adaptation of each character separately. Similarly, each environmental problem to be solved is isolated and its solution regarded as independent of other interactions with the environment, which are at most constraints on the solution. Obviously, a *ceteris paribus* argument is necessary for adaptive reconstructions; otherwise all traits would have to be considered in the solution to all problems and vice versa, leading to a kind of complex systems analysis of the whole organism in its total environment. The entire trend of adaptive evolutionary arguments is toward a Cartesian analysis into separate parts, each with its separate function.

The third hidden assumption is that all aspects of an organism are adaptive. The methodological program of adaptive explanation demands an a priori commitment to such explanations for all traits that can be described. This commitment establishes the problematic of the science as one of *finding* the adaptation, not of asking whether it exists at all. The problematic is an inheritance from the concept of the world as having been designed by a rational creator so that all aspects of it have a function and can be rationalized. The problem of explanation is to reveal the workings of this rational system.

The weakness of evolutionary theory is manifest in the assumption that all traits, arbitrarily described, are adaptive. If the assumption is allowed to stand, then adaptive explanations simply become a test of the ingenuity of theorists and of the tolerance of intellectuals for tortured and absurd stories. Again, it is in behavioral traits that the greatest scope for rationalization appears, for example, explanations of the supposed mass suicide of lemmings by drowning as being a population regulation device that is adaptive for the species as a whole. If, on the other hand, the assumption is dropped, traits that are difficult to rationalize can be declared nonadaptive, allowing evolutionists to explain just those traits that seem most obviously to fit their mode of explanation, relegating the others to the category of "non-Darwinian" (King and Jukes 1969). Some evolutionists (Kimura and Ohta 1971) now regard a large part of the variation in protein structure among species as random, irrational, and non-Darwinian, but this is bitterly contested by conventional Darwinians who accept that adaptationist methodological program without reserve (Ford 1975).

Given the assumptions of the adaptationist program, there are great difficulties and ambiguities in determining the adaptation of a given organ. Every trait is involved in a variety of functions, yet it cannot be claimed to be adaptation for all. Thus a whale's flipper can destroy a small whaling boat, but no one would argue that the flipper is an adaptation for destroying surface predators rather than for swimming. Nor does the habitual and "natural" use of an organ necessarily imply that it is an adaptation for that purpose. The green turtle, *Chelonia mylas*, uses its front flippers to propel itself over dry sand to an egg-laying site above high-water mark, then digs a deep hole for the eggs in a slow and clumsy way, using its hind flippers as a trowel. But the turtles use these swimming paddles in this way for lack of anything better; flippers cannot be regarded as adaptations either to land locomotion or to hole digging. If sufficiency of an organ is not a sufficient condition of its being an adaptation, neither is necessity of an organ a necessary condition. Every terrestrial animal above the size of an insect must have lungs, because the passive transpiration of gases across the skin or by a tracheal system would not suffice for respiration in a large volume. Lungs can properly be considered an adaptation for breathing because without them the animal would suffocate, but most adaptations are not so essential. The striping of zebras may be an adaptation to protective camouflage in tall grass, but it is by no means certain that a species of unstriped zebras would go extinct from predation, or even that they would be less numerous.

The problem of judging the adaptive importance of a trait from its use becomes more difficult when the use itself must be reconstructed. The bony plates of *Stegosaurus* may have been a device for temperature regulation, predator protection, and species recognition simultaneously. Nor is this doubt restricted to extinct forms. Some modern lizards have erectile "sails" along their dorsal lines and or brightly colored, inflatable gular pouches. These may serve as both aggressive display and sexual recognition signals, and the dorsal spines may also be heat regulators. In principle, experiments can be done on living lizards to determine the effect of removing or altering these characters, but in practice the interpretation of such alterations is dangerous, since it is not clear whether the alteration has introduced an extraneous variable. Even if it could be shown that an organ functions in a variety of ways, the question of its adaptation is not settled because of the implied historical causation in the theory of adaptation. The judgment of whether the lizard's gular pouch is an adaptation for species recognition depends upon whether natural selection is supposed to have operated through the more frequent correct matings of individuals with the pouch. If, when the pouch reached a certain size, it also incidentally frightened predators, it would be a *preadaptation* for this latter purpose. The distinction between those uses for which an organ or trait is an adaptation and those for which it is a preadaptation could be made only on historical grounds by a reconstruction of the actual forces of natural selection. Even for extant organisms, this is impossible.

In the absence of actual historical data on natural selection, the argument that a trait is an adaptation rests on an analysis of the organism as a machine for solving postulated problems. Using principles of engineering, the investigator performs a design analysis and compares the characteristics of the postulated design with those of the organ in question. Thus the postulate that the dorsal plates of *Stegosaurus* are adaptations for heat exchange rests on the porous nature of the bone, suggesting a large amount of blood circulation; on the larger size of the plates over the most massive part of the body, where heat production is greatest; on the alternating unpaired arrangement of the plates to the left and right of the midline, suggesting the proper placement of cooling fins; and on the constriction of the plates at their base, nearest the heat source, where they would be inefficient radiators. A more quantitative engineering analysis is sometimes made, proposing that the organ or character is actually optimal for its postulated purpose. Thus Leigh (1971), using hydrodynamic principles, showed that the shape of a sponge is the optimal shape for that creature, on the supposition that the problem for the sponge is to process the maximum amount of food-containing water per unit time.

The fit is not always perfect, however. Orians (1976) has calculated the optimal distribution of food sizes for a bird that must search for and catch prey, then return with it to a nest (central-place foraging). A comparison of the prey caught with the distribution of available prey sizes did indeed show that birds do not take food items at random, that they are biased toward larger items; however, they do not behave according to the calculated optimum. The explanation offered for the failure of a close fit is that because of the competing demand to visit the nest often enough to discourage predators, the birds spend less time searching for optimal prey than they would if the behavior were a pure adaptation to feeding efficiency. This is a paradigm for adaptive reconstruction. The problem is originally posed as efficiency of food gathering. A deviation of the behavior from random in the direction predicted is regarded as strong support for the adaptive explanation, and the discrepancy from the predicted optimum is accounted for by an ad hoc secondary problem that acts as a constraint on the solution to the first. There is no methodological rule that instructs the theorist in how far the observation must deviate from the prediction before the original adaptive explanation is abandoned altogether. By allowing the theorist to postulate various combinations of problems to which manifest traits are optimal solutions, the adaptationist program makes of adaptation a metaphysical postulate that not only cannot be refuted but is necessarily confirmed by every observation. This is the caricature that was immanent in Darwin's insight that evolution is the product of natural selection.

NATURAL SELECTION AND ADAPTATION

A sufficient mechanism for evolution by natural selection is contained in three propositions:

1. There is variation in morphological, physiological, and behavioral traits among members of a species (the principle of variation).
2. The variation is in part heritable, so that individuals resemble their relations more than they resemble unrelated individuals and, in particular, offspring resemble their parents (the principle of heredity).
3. Different variants leave different numbers of offspring either in immediate or remote generations (the principle of differential fitness).

It is important to note that all three conditions are necessary as well as sufficient conditions for evolution by natural selection. If the variants do not differ in their reproductive success, then of course there is no natural selection. The existence of *heritable variation* is especially crucial. If variation exists but is not passed from parent to offspring, then the differential reproductive success of different forms is irrelevant, since all forms will produce the same distribution of types in the next generation. Any trait for which the three principles apply may be expected to evolve. That is, the frequency of different variant forms in the species will change, although it does not follow in all cases that one form of the trait will displace all others. There may be stable intermediate equilibria at which two or more variant forms coexist at a characteristic stationary frequency.

These necessary and sufficient principles for evolution by natural selection contain no reference to adaptation. Darwin added the postulate

of adaptation to explain the mechanical cause of the phenomenon of differential reproduction and survival. The "struggle for existence," according to Darwin, was the result of the tendency of species to reproduce in excess of the resources available to them, an idea he got from reading Malthus's (1798) *Essay on the Principle of Population.* The struggle would be won by those individuals whose morphology, physiology, and behavior allowed them to appropriate a greater share of the resources in short supply, or those who could survive and reproduce on a lower resource level, or those who could utilize a resource that was unsuitable for their competitors. In these latter two forms the struggle for existence was freed from the idea of actual struggle between individuals. "I should premise that I use the term Struggle for Existence in a large and metaphorical sense . . . Two canine animals in a time of dearth may be truly said to struggle with each other which shall get food and live. But a plant at the edge of the desert is said to struggle for life against the drought" (Darwin 1859, p. 62).

Given this struggle in its "large and metaphorical sense," an engineering analysis should be able to predict which of two individuals will better survive and reproduce. By studying the bones and muscles of the legs of two zebras and by applying simple mechanical principles, one should be able to say which of the two can run faster and therefore better escape predators. Further, it is in principle possible to predict the direction of evolution of leg muscles and bones by a local differential analysis, since the superior of any two slightly different shapes can be discerned.

The struggle for existence also redirects the idea of adaptation from an absolute to a relative criterion. So long as organisms are considered only in relation to their ecological niche, they are either adapted, in which case they will persist, or they are unadapted and are on their way to extinction. But if individuals of the same species are considered in relation to each other, they are competing for the same set of resources or struggling to reproduce in the same unfavorable environment (the plants at the edge of the desert), and their relative adaptation becomes the focus. Two forms of a species might both be absolutely adapted in the sense that the species would persist if it were made up entirely of either form, yet when placed in competition the greater adaptation of one would lead to the extinction of the other. By the same consideration, the relative adaptation of two distinct species cannot in general be compared because species are never competing with each other in the same exclusionary way as are forms of the same species. If two species overlapped so much in their ecological niches that their abundances were critically determined by the same limiting resource, one species would become extinct in the competition. Occasionally, of course, an introduced species does extinguish another species, as in the case of the Mediterranean fruit fly, which was extinguished in eastern Australia by the sudden southward spread of the Queensland fruit fly, a very close relative that lays its eggs in the same cultivated fruit. At first sight, the engineering approach to differential fitness seems to remove the apparent tautology in the theory of natural selection. Without this design analysis Darwinian theory would simply state that the more fit individuals leave more offspring in future generations and would then determine relative fitness from the number of offspring left by different individuals. Since, in a finite world of contingent events, some individuals will, even by chance, leave more offspring than others, there will be a posteriori tautological differences in fitness among individuals. From that, one can only say that evolution occurs because evolution occurs. The design analysis, however, makes it possible to determine fitness a priori, and therefore one can judge the relative adaptation of two forms in the absence of any prior knowledge of their reproductive performances.

Or can one? The conditions for predicting from relative adaptation analysis are the same as for judging absolute adaptation. A change in length of the long bones of zebras' legs, allowing them to run faster, will be favored in evolution provided (1) that running speed is really the problem to be solved by the zebra, (2) that the change in speed does not have countervailing adverse effects on the animal's adaptation to solving other problems set by the environment, and (3) that lengthening the bone does not produce countervailing direct developmental or physiological effects on other organs or on its own function. Even though lions prey on zebras, it is not necessarily true that faster zebras will escape more easily, since it is by no means certain that lions are limited by speed in their ability to catch prey. Moreover, greater speed may be at the expense of metabolic efficiency, so if zebras are food limited, the problem of feeding may be made worse by solving the problem of escaping from predators. Finally, longer shank bones may be more easily broken, cost more developmental energy to produce, and create a whole series of problems of integrated morphology. Relative adaptation, like the judgment of absolute adaptation, must be a *ceteris paribus* argument and, since all other things are never equal, the final judgment as to whether a particular change in a trait will produce relatively greater adaptation depends upon the net effect on the entire organism. The alternative would be to maintain that the engineering analysis of a predetermined problem is to be taken as *defining* the adaptation, irrespective of its net benefit to the organism. Such a solution would decouple adaptation from evolution and make it into a purely intellectual game.

EVOLUTIONARY CONVERGENCE

The serious methodological and epistemological difficulties in the use of adaptive explanations should not blind us to the fact that many features of organisms clearly seem to be convergent solutions to obvious environmental problems. It surely is no accident that fish have fins; that aquatic mammals have altered their appendages to form finlike flippers; that ducks, geese, and seabirds have webbed feet; that penguins have paddlelike wings; and even that sea snakes, lacking fins, are flattened in cross-section. All these traits are obviously adaptations for aquatic locomotion, and the reproductive fitness of the ancestors of these forms must have been increased by the gradual modification of their appendages in a similar way. Yet it seems pure mysticism to suppose that swimming was a major "problem" held out before the eyes of the terrestrial ancestors of all these animals before they actually had to cope with locomotion through a liquid medium. It must be that the problem of swimming was posed in a rudimentary and marginal form, putting only marginal demands on an organism, whose minor adaptive response resulted in a yet deeper commitment of the evolving species to the water.

But this coevolution of the organism and of the environment it was creating for itself continued over long times in the same direction, producing fishlike animals from doglike ones and swimmers from fliers, all with flattened appendages. It follows that the *ceteris paribus* argument must be true reasonably often, or else no progressive alteration to form such structures could occur. Therefore, the mapping of character states into net reproductive fitness must have two characteristics: *continuity* and *quasi-independence*. By continuity we mean that very small changes in a character result in very small changes in the ecological relations of the organism and therefore very small changes in reproductive fitness. Neighborhoods in character space map into neighborhoods in fitness space. So a very slight change in the shape of a mammalian appendage to make it finlike does not cause a dramatic change in the sexual recognition pattern or make the organism attractive to a completely new set of predators. By quasi-independence we mean that there exists a large variety of paths by which a given character may change; although some of these paths may give rise to countervailing changes in other organs and in other aspects of the ecological relations of the organism, in a reasonable proportion of cases the countervailing effects will not be of sufficient magnitude to overcome the increase in fitness from the adaptation. In genetic terms, quasi-independence means that a variety of mutations may occur, all with the same effect on the primary character but with different effects on other characters, and that some set of these changes will not be at a net disadvantage.

NONADAPTIVE CHARACTERS AND THE FAILURE OF ADAPTATION

While the principles of continuity and quasi-independence can be used to explain adaptive trends in characters that have actually occurred, they cannot be used indiscriminately to assert that all characters are adaptive or to predict the appearance of some character that ought to evolve because it would be adaptive. The lack of continuity and quasi-independence may, in fact, be powerful deterrents to adaptive trends. That adaptation has occurred seems obvious. But it is not at all clear that most changes, or even many, are adaptive. The adaptationist program is so much a part of the vulgarization of Darwinism that an increasing amount of evolutionary theory consists in the uncritical application of the program to both manifest and postulated traits of organisms.

A paradigm is the argument by Wilson (1975) that indoctrinability ("human beings are absurdly easy to indoctrinate . . . they seek it", p. 562) and blind faith ("men would rather believe than know," p. 561) are adaptive consequences of human evolution since conformist individuals will more often submit to the common goals of the group, guaranteeing support rather than hostility and thus increasing their reproductive fitness. This view universalizes two socially determined behaviors, makes them part of "human nature," and then argues for their adaptive evolution. Putting aside the question of the universality of indoctrinability and blind faith, the claim that they are the product of adaptive evolution requires that there has been heritable variation

for these traits in human evolutionary biology, that conformists really would leave more offspring, all other things being equal and, finally, that all other things *are* equal. None of these propositions can be tested. There is no evidence of any present genetic variation for conformism, but that is not compelling since the question concerns genetic variation in the evolutionary past. Nor is there any reason to suppose that conformism is a separate trait and not simply a culturally defined concept that has been reified by the biologist. The alternative is to recognize that "conformism" is a "trait" only by abstract construction, that it is one of the possible ways of describing some aspect of the behavior of some individuals at some times and that it is a consequence of the evolution of a complex central nervous system. That is, the adaptive trait is the extremely highly developed central nervous organization; the appearance of conformity as a manifestation of that complexity is entirely epiphenomenal.

A parallel situation for morphological characters has long been recognized in the phenomenon of *allometry.* Different organs grow at different rates, so that if growth is prolonged to produce a larger individual not all parts are proportionately larger. For example, in primates tooth size increases less from species to species than does body size, so large primates have proportionately smaller teeth than small primates. This relationship of tooth size to body size is constant across all primates, and it would be erroneous to argue that for some special adaptive reason gorillas have been selected for relatively small teeth. Developmental correlations tend to be quite conservative in evolution, and many so-called adaptive trends turn out on closer examination to be purely allometric.

Reciprocally, the increase of certain traits in a population by natural selection is not in inself a guide to adaptation. A mutation that doubled the egg-laying rate in an insect, limited by the amount of food available to the immature stages, would very rapidly spread through the population. Yet the end result would be a population with the same adult density as before but twice the density of early immatures and much greater competition among larval stages. Periodic severe shortages of food would make the probability of extinction of the population greater than it was when larval competition was less. Moreover, predators may switch their search images to the larvae of this species now that they are more abundant, and epidemic diseases may more easily spread. It would be difficult to say precisely what environmental problem the increase in fecundity was a solution to.

ADAPTATION AS IDEOLOGY

The caricature of Darwinian adaptation that sees all characteristics, real or constructed, as optimal solutions to problems has more in common with the ideology of the sixteenth century than with that of the nineteenth. Before the rising power and eventual victory of the bourgeoisie, the state and the unchanging world were seen and justified as manifestations of divine will. The relations among people, and between humankind and nature, were unchangeably just and rational because the author of all things was unchanging and supremely just and rational. There was, moreover, an organic unity of relationships, for example, of lord and serf and of both to the land, which could not be broken, since they were all part of an articulated plan. This ideology, which was both a conscious legitimation of the social order and its unconscious product, necessarily came under attack by the ideologues of the increasingly powerful commercial bourgeoisie. The success of commercial and manufacturing interests made it necessary for men to be able to rise as high in status and power as their entrepreneurial activities took them and required freeing money, land, and labor power from their traditional rigid relationships. It had to be possible to alienate land for primary production and by the same process to allow the laborer to own his own labor power and to carry it to the centers of manufacturing where he could sell it in the labor market. Thus the ideology of the Enlightenment emphasized progress rather than stasis, becoming rather than being, and the freedom and disarticulation of parts of the world, rather than their indissoluble unity. Voltaire's Dr. Pangloss, who believed that even the death of thousands in the Lisbon earthquake proved that this was the "meilleur des mondes possibles," symbolized the foolishness of the old ideology. Descartes' *bête machine* and La Mettrie's *homme machine* provided the program for the analysis of nature by dissecting and disarticulating it into separate causes and effects.

Darwin's work came at the end of the successful struggle of the bourgeoisie to make a world appropriate to its own activities. The middle of the nineteenth century was a time of immense expansion of production and wealth. Darwin's maternal grandfather, Josiah Wedgwood, started as a potter's apprentice and became one of the great Midland industrialists, epitomizing the flowering of an exuberant capitalism. Mechanical invention and a free labor market underlay the required growth of capital and the social and physical transformation of Europe. Herbert Spencer's *Progress: Its Law and Cause,* expressed the mid-nineteenth-century belief in the inevitability of change and progress. Darwin's theory of the evolution of organic life was an expression of these same ideological elements. It emphasized that change and instability were characteristic of the living world (and of the inorganic world as well, since the earth itself was being built up and broken down by geological processes). Adaptation, for Darwin, was a process of becoming rather than a state of final optimality. Progress through successive improvement of mechanical relations was the characteristic of evolution in this scheme.

It must be remembered that for Darwin, the existence of "organs of extreme perfection and complication" was a difficulty for his theory, not a proof of it. He called attention to the numerous rudimentary and imperfect forms of these organs that were present in living species. The idea that the analysis of living forms would show them, in general, to have optimal characters would have been quite foreign to Darwin. A demonstration of universal optimality could only have been a blow against his progressivist theory and a return to ideas of special creation. At the end of *Origin of Species* (1859) he wrote: "When I view all beings not as special creations, but as lineal descendants of some few beings which lived long before the first bed of the Cambrian system was deposited, they seem to me to become ennobled. Judging from the past, we may safely infer that not one living species will transmit its unaltered likeness to a distant futurity . . . And as natural selection works solely by and for the good of each being, all corporeal and mental endowments *will tend to progress toward perfection"* (p. 489).

Even as Darwin wrote, however, a "spectre was haunting Europe." The successful revolutions of the eighteenth century were in danger of being overturned by newer revolutions. The resistance by the now dominant bourgeoisie to yet further social progress required a change in the legitimating ideology. Now it was claimed by their advocates that the rise of the middle classes had indeed been progressive but that it was also the last progressive change; liberal democratic entrepreneurial man was the highest form of civilization, toward which the development of society had been tending all along. Dr. Pangloss was right after all, only a bit premature. The liberal social theory of the last part of the nineteenth century and of the twentieth has emphasized dynamic equilibrium and optimality. Individuals may rise and fall in the social system, but the system itself is seen as stable and as close to perfect as any system can be. It is efficient, just, and productive of the greatest good for the greatest number. At the same time the Cartesian mechanical analysis by disarticulation of parts and separation of causes has been maintained from the earlier world view.

The ideology of equilibrium and dynamic stability characterizes modern evolutionary theory as much as it does bourgeois economics and political theory; Whig history is mimicked by Whig biology. The modern adaptationist program, with its attempt to demonstrate that organisms are at or near their expected optima, leads to the consequence that although species come into existence and go extinct, nothing really new is happening in evolution. In contrast to Darwin, modern adaptationists regard the existence of optimal structures, perfect adaptation, as the evidence of evolution by natural selection. There is no progress because there is nothing to improve. Natural selection simply keeps the species from falling too far behind the constant but slow changes in the environment. There is a striking similarity between this view of evolution and the claim that modern market society is the most rational organization possible, that although individuals may rise or fall in the social hierarchy on their individual merits, there is a dynamic equilibrium of social classes, and that technological and social change occur only insofar as they are needed to keep up with a decaying environment.

3

The Organism as the Subject and Object of Evolution

THE MODERN theory of evolution is justly called the "Darwinian" theory, not because Darwin invented the idea of evolution, which he certainly did not, nor because Darwin's invention, natural selection, is the only force in evolution. Rather, Darwin realized that the process of evolutionary change of living organisms is radically different from any other known historical process and because his formulation of that process was a radical epistemological break with past theories. Before Darwin, theories of historical change were all *transformational.* That is, systems were seen as undergoing change in time because each element in the system underwent an individual transformation during its life history. Lamarck's theory of evolution was transformational in regarding species as changing because each individual organism within the species underwent the same change. Through inner will and striving, an organism would change its nature, and that change in nature would be transmitted to its offspring. If the necks of giraffes became longer over time, it was because each giraffe attempted to stretch its neck to reach the top of the trees. An example of a transformational theory in modern natural science is that of the evolution of the cosmos. The ensemble of stars is evolving because every star, after its birth in the initial explosion that produced the matter of the universe, has undergone the same life history, passing into the main sequence, becoming a red giant, then a white dwarf, and finally burning out. The evolution of the universe is the evolution of every star within it. All theories of human history are transformational; each culture is transformed through successive stages, usually, it is supposed, by transformation of the individual human beings that make up the society.

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