THE
DIALECTICAL
BIOLOGIST

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To Frederick Engels,
who got it wrong a lot of the time
but who got it right where it counted

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.

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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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In contrast, Darwin proposed a *variational* principle, that individual members of the ensemble differ from each other in some properties and that the system evolves by changes in the proportions of the different types. There is a sorting-out process in which some variant types persist while others disappear, so the nature of the ensemble as a whole changes without any successive changes in the individual members. Thus variation among objects in space is transformed qualitatively into temporal variation. A dynamic process in time arises as the consequence of a static variation in space. There is no historical process other than the evolution of living organisms that has this variational form, at least as far as we know.

In transformational theories the individual elements are the *subjects* of the evolutionary process; change in the elements themselves produces the evolution. These subjects change because of forces that are entirely internal to them; the change is a kind of unfolding of stages that are immanent in them. The elements "develop," and indeed the word "development" originally meant an unfolding or unrolling of a predetermined pattern, a meaning it still retains in photography and geometry. The role of the external world in such developmental theories is restricted to an initial *triggering* to set the process in motion. Even Lamarck's theory of organic evolution did not make the environment the creator of change but only the impetus for the organism to change itself through will and striving. Two characteristics flow from such a transformational view. First, the stages through which each individual passes are themselves the precondition for the next stage. There are no shortcuts possible, no reordering of the transformation, and only one possible end to the process. Indeed, the tensions and contradictions of one stage are actually the motive forces of the change to the next stage. Marx's theory of history is precisely such a theory of well-ordered historical stages, each of which gives rise to the next as a consequence of forces internal to each step. Theories of psychic development, such as those of Freud and Piaget, are derived from theories of embryological development of the nineteenth century. Each stage, whether of the body or of the psyche, is a necessary precondition of the next stage and leads to it because of forces that are purely internal at each moment. The role of the outer world is to set the process in motion and to allow the successful completion of each step.

This role of the environment provides the second characteristic of transformational theories, the possibility of arrested development. If external forces block the unrolling, the system may become permanently fixed at an early stage, and it is this premature fixation that explains any observed variation from individual to individual. In Freudian theory the personality may become fixed at an anal or oral erotic stage or at the stage of Oedipal resolution and so give rise to the manifest variations among neurotic symptoms.

In the theory of *neoteny,* evolutionary theory retains notions of linear arrays of stages and arrested development. According to this view organisms that appear later in evolution have the form of earlier developmental stages of their ancestral species. Gorilla and human embryos resemble each other much more than the adults do, and adult humans are morphologically like the gorilla fetus. Humans are thus gorillas born too soon and fixed at a gorilla fetal stage. It follows from such a theory that if the development of a human being could somehow be unblocked, it would develop the long arms, receding jaw, and sagittal crest of the adult gorilla that is present but hidden. It seem obvious that a neotenic view of evolution is severely limited in its scope, since adult humans cannot be said to resemble the early embryonic stages of fish. Indeed, evolution cannot be any kind of simple unfolding, for such a homunculus theory implies the absurdity that mammals are already completely contained in the earliest single-celled organisms.

Darwin's variational theory is a theory of the organism as the *object,* not the subject, of evolutionary forces. Variation among organisms arises as a consequence of internal forces that are autonomous and alienated from the organism as a whole. The organism is the object of these internal forces, which operate independently of its functional needs or of its relations to the outer world. That is what is meant by mutations being "random." It is not that mutations are uncaused or outside of a deterministic world (except as quantum uncertainty may enter into the actual process of molecular change), but that the forces governing the nature of new variations operate without influence from the organism or its milieu. Once variation has occurred, some variants survive and reproduce while others are lost to the species, according to the relation between the variant types and the environment in which they live. Once again the organism is the object, this time of external forces, which are again autonomous and alienated from the organism as a whole. The environment changes as a consequence of cosmological, geological, and meteorological events that have their own laws, independent of the life and death of the species. Even when the environment of a given species includes other species, the histories of those species are autonomous and independent of the species being considered.

The roles of the external and the internal are not symmetrical in Darwinism. Pre-Darwinian variational theories placed the internal forces of development in the dominant position and understood history as a consequence of development. Neoteny belongs to this Platonic, pre-Darwinian tradition for it portrays the evolution of organisms as nothing but various stages of arrested development; ontogeny dominates history. In Darwinian theory the reverse is true. Historical forces are dominant, and development does nothing but provide the raw material for the forces of natural selection. The external chooses which of many possible internal states shall survive. Thus the developmental pathways that we see are the consequence of history, not its cause. Ernst Haeckel's theory of recapitulation is, in this sense, truly Darwinian, for it holds that the embryonic stages through which an organism passes are the trace of its evolutionary past, not the image of its evolutionary future. Human embryos have gill slits because their fish and amphibian ancestors had them, but in human beings the gill slits disappear because human beings have evolved further. Through evolution, new stages of development have been added, stages that were not immanent in Devonian fish. So history in Darwinism dominates ontogeny.

Thus classical Darwinism places the organism at the nexus of internal and external forces, each of which has its own laws, independent of each other and of the organism that is their creation. In a curious way the organism, the object of these forces, becomes irrelevant for the evolutionist, because the evolution of organisms is only a transformation of the evolution of the environment. The organism is merely the medium by which the external forces of the environment confront the internal forces that produce variation. It is not surprising, then, that some vulgar Darwinists make the gene the only real unit of selection and see evolution as a process of differential survival of *genes* in response to the external world. In *The Selfish Gene* Richard Dawkins (1976) speaks of organisms as "robots . . . controlled body and mind" by the genes, as nothing but a gene's way of making another gene. If the species is indeed the passive nexus of gene and selective environment, if the genes propose and the environment disposes, then in a deep sense organisms really are irrelevant, and the study of evolution is nothing but a combination of molecular biology and geology.

But such a view gives a false picture of organic evolution and cannot successfully cope with the problems posed by evolutionary biology, for it ignores two fundamental properties of living organisms that are in direct contradiction to a superficial Darwinism. First, it is not true that the development of an individual organism is an unfolding or unrolling of an internal program. At a symposium in 1982 commemorating the hundredth anniversary of Darwin's death, a leading molecular biologist expressed the belief that if the complete sequence of an organism's DNA were known and a large enough computer were available, it would be possible, in principle, to compute the organism. But that is surely false, because an organism does not compute itself from its DNA. The organism is the consequence of a historical process that goes on from the moment of conception until the moment of death; at every moment gene, environment, chance, and the organism as a whole are all participating. Second, it is not true that the life and death and reproduction of an organism are a consequence of the way in which the living being is acted upon by an autonomous environment. Natural selection is not a consequence of how well the organism solves a set of fixed problems posed by the environment; on the contrary, the environment and the organism actively codetermine each other. The internal and the external factors, genes and environment, act upon each other through the medium of the organism. Just as the organism is the nexus of internal and external factors, it is also the locus of their interaction. The organism cannot be regarded as simply the passive object of autonomous internal and external forces; it is also the subject of its own evolution.

GENE AND DEVELOPMENT

It is common, even in textbooks of genetics, to speak of genes determining traits, as if knowing the gene means the trait of the organism is given. This notion derives from several historical sources. First, since the nineteenth century, embryologists have taken their problematic to be explaining how a fertilized egg of a frog always becomes a frog, while that of a chicken always develops into another chicken. Even when the environment in which development is taking place is severely disturbed, a process of regulation often assures that the final outcome is the same. If the developing limb bud of an amphibian embryo is cut out, the cells disaggregated, then put back together again, and the lump of cells reimplanted in the embryo, a normal leg will develop. And no environmental disturbance has ever caused an amphibian embryo to develop into a chicken. Thus there is an overwhelming impression that a program internal to the cells is being expressed and that the development of the adult is indeed the unfolding of an inevitable consequence.

Second, the laws of inheritance were discovered by following simple traits that have a one-to-one correspondence to genes. Mendel succeeded where others had failed partly because he worked with horticultural varieties in which major differences in phenotype resulted from alternative alleles for single genes. Mendel's peas had a single gene difference between tall and short plants, but in the usual natural populations of most plant species there is no simple relation at all between height and genes. So when Mendel tried to understand the inheritance of variation in the wild species *Hieracium,* he failed completely.

Third, modern molecular biology deals with the direct products of gene action, the proteins produced by the cell using specific sequence information from the structure of DNA. As with Mendel's peas, there is a one-to-one correspondence between a simple genetic difference and a discrete observable difference in phenotype. Indeed, the problematic of molecular biology is to give a complete description of the machinery that is responsible for assembling the unique correspondence. It is impossible to work out the details of the machinery if the correspondence between gene and phenotype is poor, so molecular biology, by the necessary demands of its research methods, concentrates all its attention on the simplest relations between gene and trait. If, however, one examines the more general relations between gene and organism, it becomes immediately apparent that the situation is more complex.

In general, the morphology, physiology, metabolism, and behavior—that is, the phenotype—of an organism at any moment in its life is a product both of the genes transmitted from the parents and of the environment in which development has occurred up until that moment. The number of light-receptor cells, or facets, in the compound eye of the fruit fly, *Drosophila,* is usually about 1,000, but certain gene mutations severely reduce the number of facets. For example, flies carrying the mutation *Ultrabar* have only about 100. However, the number of eye cells also depends upon the temperature at which the flies develop; flies of the normal genotype produce about 1,100 cells at 15°C, but only 750 cells at 30°C.

The relationship between the phenotype and the environment is expressed in the *norm of reaction,* which is a table or graph of correspondence between phenotypic outcome of development and the environment in which the development took place. Each genotype has its own norm of reaction, specifying how the developing organism will respond to various environments. In general, a genotype cannot be characterized by a unique phenotype. In some cases the norm of reaction of one genotype is consistently below that of another in all environments. So, for example, we can say unambiguously that *Ultrabar* flies have smaller eyes than normal flies because that is true at every temperature of development. However, another mutation, *Infrabar,* also has fewer cells than normal, but it has an opposite relation to temperature, and its norm of reaction crosses that of *Ultrabar* (see Fig. 3.1). Clearly we cannot ask, "Which mutation has more eye cells?" because the answer de-

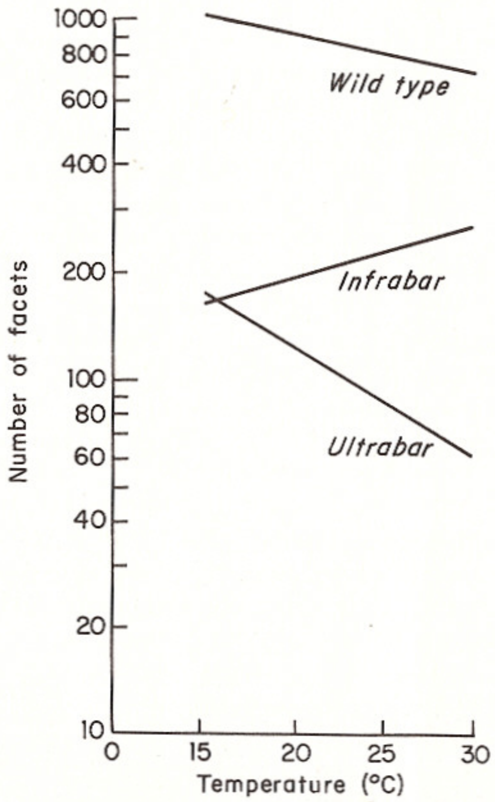

Fig. 3.1. Reaction norms for the number of eye cells as a function of temperature in *Drosophila.*

pends upon temperature. Fig. 3.2 shows the reaction norms for the probability of survival of immature stages in *Drosophila* as a function of temperature. The different lines represent genotypes taken from a natural population, and they are more typical of norms of reaction than are the mutations of eye size. There is no regularity at all to be observed. Some genotypes decrease survival with temperature, some increase it, some have a maximum at intermediate temperatures, some a

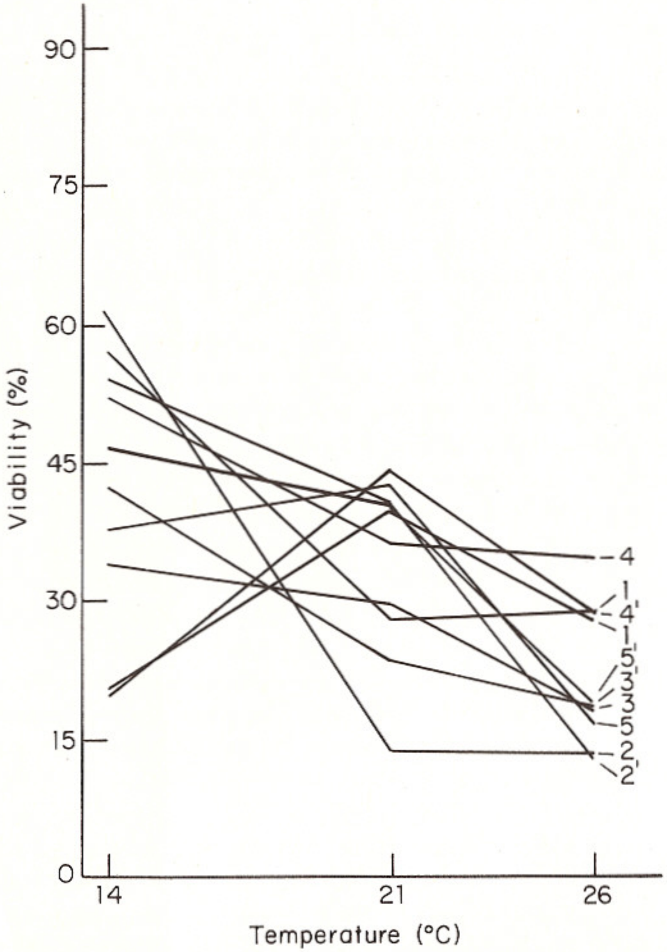

Fig. 3.2. Reaction norms for viability in genotypes from natural populations of *Drosophila,* as a function of temperature.

minimum. The genotype 2′, which has the third highest survival at 14°C, has the lowest at 26°C. The experiments illustrated in Figs. 3.1 and 3.2, carried out in a variety of organisms for a variety of traits and a variety of environments, establish three characteristics for the relationship among gene, environment, and organism. First, there is no unique phenotype corresponding to a genotype; the phenotype depends on both genotype and environment. Second, the form and direction of the environment's effect upon development differs from genotype to genotype. Third, and reciprocally, there is no unique ordering of genotypes such that one can always be characterized as "superior" or "inferior" to another.

While the phenotype depends on both genotype and environment, it is not determined by them. If one counts the eye cells or the large hairs on the left and right side of a *Drosophila* raised in the laboratory, one finds that the fly is usually asymmetrical but that there are as many right-sided flies as left-sided. That is, there is no average difference between left and right for the species as a whole, but there is a large variation among individuals. The genes of the left and right side of a fly are the same. Moreover, each fly began as a larva that burrowed through a homogeneous artifical medium and then completed its development as a pupa 2 to 3 millimeters long attached to the surface of a glass vial. No sensible definition of environment would allow that it was different on the left and right sides, yet the two halves of the organism did indeed develop differently. This random asymmetry is a consequence of *developmental noise,* the random events at a cellular and molecular level that influence cell division and maturation and that especially may result in small differences in the time when critical changes occur. If a cell divides too early, it may give rise to an extra hair; if too late, it may not differentiate at all. Such random developmental events contribute a significant amount of the variation of an organism. For very complex organs like the brain, in which small structural variations may be reflected in large functional differences, random developmental noise may be an important source of individual variation.

At present the connections among gene, environment, and such traits as shape, size, and behavior are known only at a superficial, phenomenological level. The actual mechanisms of interaction are unknown, but some simple cases of control of enzyme production and activity provide a model for the more complex cases. Information from the environment plays a role at four levels. At the lowest level the synthesis of a particular enzyme or protein is turned on or off because the gene specifying that protein is either blocked or made available to the machinery of protein synthesis by the very substances on which the enzyme will operate. For example, in bacteria the gene for the enzyme that splits lactose is normally blocked, but if lactose is present in the environment, it combines in the cell with the blocking molecule and opens the gene to the protein synthetic machinery. Conversely, in the same bacteria the genes for enzymes that synthesize the essential amino acid tryptophane are normally turned on, but as tryptophane accumulates, it combines with a blocking molecule and turns the gene off. At a higher level, substances acted upon by enzymes may combine with the enzymes to stabilize them and so prevent their degradation, thus guaranteeing an adequate supply when the enzyme is in high demand. At yet a higher level, the normal kinetics of chemical reactions slow down a chain of synthetic events if the end product accumulates and speed it up if the end product is rapidly removed. At the highest level, the rate of protein synthesis in general is modulated by temperature, nutrients, and inorganic ions by changes in the rate of production of the enzymes necessary for synthesis.

Each of these mechanisms except the last has the property that information from the environment modulates the biosynthetic pathways in a way that matches the rate of activity to the demand for the product. The sensitivity of total biosynthetic activity to temperature and nutrients cannot really be regarded as adaptive, however, but is a mechanical consequence of general properties of chemical systems.

The consequence of the interaction of gene, environment, and developmental noise is a many-to-many relationship between gene and organism. The same genotype gives rise to many different organisms, and the same organism can correspond to many different genotypes. That does not mean that the organism is infinitely plastic, or that any genotype can correspond to any phenotype. Norms of reaction for different genotypes are different, but it is the norms of reaction that are the proper object of study for developmental biologists rather than some ideal organism that is supposed to be produced deterministically by the genes.

The view of development as the inevitable unfolding of successive stages, although incorrect, does incorporate an important feature of ontogeny, that it is a historical process in which the next event is influenced by the previous state. Development is then a contingent process in which the effect of a force cannot be specified in general but only in a

particular context. One consequence of this contingency is that the environment as it is relevant to a developing organism is a temporal sequence of events in which the exact order is critical. If a heat shock is given to some strains of *Drosophila* during a critical four-hour period of their development, the pattern of veins in the wing will be altered. A shock given before or after this critical period will not change the wing veins but may affect other traits such as eye size. But this temporal contingency is also contingent on genotype, since genetically different individuals may develop identically in some environmental sequences but differ from each other in other environments. Most flies develop a normal wing pattern at 25°C, but only some genotypes produce abnormal wing veins under heat shock.

A second consequence of developmental contingency is that the effect of genetic variation on development of a trait depends upon genes other than those directly concerned with the character. The experiments of Rendel (1967) and Waddington (1957) on so-called "canalized" characters have shown that, paradoxically, traits that do not vary from individual to individual nevertheless have a genetic basis for variation. The number of scutellar bristles, four, on the back of a *Drosophila* is extremely constant from fly to fly. If, however, the development of the fly is severely upset experimentally, flies under the same treatment will develop different numbers of bristles. These differences turn out to be heritable, so there is indeed genetic variation among individuals that would affect bristle number if the normal developmental system did not damp out the variation. Moreover, the buffered developmental system itself turns out to be a consequence of yet other genes, so it is possible genetically to remove the damping or to alter its characteristics so that it buffers around six bristles instead of four.

Yet another consequence of developmental contingency is that ontogeny is not a linear array of stages, one leading always to a particular next stage, but a branched set of pathways. At one extreme, the leaves and stems of tropical vines take a variety of shapes and thicknesses, depending upon where the growing tip is in relation to the ground. There is one form while the vine is growing along the ground, a second when it begins to climb a tree, a third when it reaches a great height, and a fourth when it descends from the tree branches, hanging freely in the air. Any one of these forms will succeed any other, depending upon environmental cues of light, gravity, and contact, so each state is accessible from all the others, and the transition from one state to another has only a weak dependence on the previous history of growth. Such vines are at one extreme of the structure of developmental pathways in which the probability of entering any developmental sequence is essentially independent of the present state or past history. At the other extreme are unique transitions in which a given developmental step can only be taken from a particular state, and the system is irreversible. Once a developing bud is committed to floral development, the process cannot be reversed to make a leaf.

Developmental processes in general fall between these extremes, with early stages in development being both reversible and multiply branched. As development proceeds, many traits become irreversibly fixed. In *Drosophila* clumps of embryonic tissue normally destined to become genitalia, legs, wings, or eyes of adults, can develop into a different adult tissue if they are held long enough in an embryonic, undifferentiated state. Genital cells can change to either legs or antennae, but the reverse cannot happen. Embryonic leg and antenna cells can change reversibly to wing, and wing reversibly to eye, but embryonic eye will never change to antenna. So there is a topology of possible developmental transitions that puts constraints on developmental pathways without making them unique.

Finally, the processes of development are Markovian. That is, the probability of transition to a given state depends upon the state of the organism at the time of the transition but not on how it came into that state. Small seeds give rise, in general, to small seedlings, which grow slowly because they are shaded by competitors. It does not matter whether the seed was small because of the maternal plant's genotype or because it set seed in an unfavorable habitat. Small animals, with large surface-to-volume ratios, lose a great deal of heat by radiation, irrespective of the causes of their small size. Thus the organism, irrespective of the internal and external forces that influenced it, enters directly into the determination of its own future. The view of development that sees genes as determinative, or even a view that admits interaction between gene and environment as determining the organism, places the organism as the end point, the object, of forces. The arrows of causation point from gene and environment to organism. In fact, however, the organism participates in its own development because the outcome of each developmental step is a precondition of the next. But the organism also actively participates in its own development because, as we shall see, it is the determinant of its own milieu.

ORGANISM AND ENVIRONMENT

The classical Darwinian view of the process of evolution places the problem of adaptation as one of the two aspects of nature that must be understood: "In considering the Origin of Species, it is quite conceivable that a naturalist . . . might come to the conclusion that species had not been independently created, but 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 justly excites our admiration."(Darwin 1859). Darwin's solution, of course, was that different variants within a species possess properties that make them more or less successful in the struggle for existence. There are two ways in which this differential success can be viewed. The first, purely kinetic, view is that different variants simply have different reproductive rates and probabilities of survival, so in the end one type will come to characterize the species. Nothing in this description, however, predicts that "perfection which so excites our admiration." One genotype having a slightly higher egg-laying rate than another at high temperatures would result in evolution but not in any impression of the marvelous fit between organism and the external world.

The second view, however, does explain the apparent fit. It is that the external world poses certain well-defined "problems" for organisms; those that best survive and reproduce are those whose morphological, physiological, and behavioral traits represent the best solutions to the problems. So locomotion is a problem that swimming animals have solved by developing flattened appendages such as fins, flukes, and webbed feet; terrestrial animals have solved it by developing hooves, paws, and articulated legs; and flying animals have solved it by developing wings. This view of adaptation acquired credibility not only from an appeal to the findings of common sense and engineering—that fins really do help movement through water, and wings through air—but also from the fact that insects, bats, and birds have all developed wings from quite different anatomical features. Such convergent homologies make it seem obvious that flying is a problem and that independent solutions have evolved through natural selection. Organisms are the objects of the force of natural selection. This force sorts out the form that is the best solution to the problem posed by the external world. The word "adaptation" reflects this point of view, implying that the organism is molded and shaped to fit into a preexistent niche, given by the autonomous forces of the environment, just as a key is cut and filed to fit into a lock.

There are two difficulties with this formulation of evolution, one conceptual and the other factual. The conceptual problem is how to define the niche of a potential organism before the organism exists. The physical world can be put together is an uncountable infinity of ways to create niches. One can construct an arbitrary number of menus of food items, say particular frequencies of different plant species which would nourish an insect, but which no insect actually eats. No animal crawls on its stomach, lays eggs, and eats grass, although snakes live in the grass. No bird eats the leaves at the tops of trees, although lots of insects do. If evolution is now going on, as we assume it is, then what marks out the combinations of physical and biotic factors that make the niches into which organisms are evolving? Is this a natural class? Could we somehow discover physical rules that would delimit the niches for us and show us that all other conceivable combinations of physical and biological factors for some reason do not constitute niches? An insight into this question can be gained by consulting the description of ecological niches in works on ecology. The description of the niche of a bird, for example, is a list of what the bird eats, of what and where it builds its nest, how much time it spends foraging in different parts of the trees or ground, what its courtship pattern is, and so on. That is, the niche is described always in terms of the life activity of the bird itself. This is not simply a convenience but an implicit recognition that niches are defined *in practice* by the organisms in the process of their activities. But there is a contradiction here. If the metabolism, anatomy, and behavior of an organism define its niche, how can a niche exist *before* the species, so that the species can evolve into it? This contradiction is not resolved in the classical Darwinian theory of adaptation, which depends absolutely on the problem preexisting the solution.

A weak claim is sometimes made that there are indeed preferred organizations of the external world, but that we simply do not know how to find them, although organisms do so in their evolution. Once again, convergence of unrelated forms is offered as evidence. The marsupial fauna of Australia has a number of forms that closely resemble placental mammals, although their evolution has been totally independent. There are marsupial "wolves," "moles," "rabbits," "bears," and "rats," and sometimes the superficial resemblance to the placental mammal is striking, as in the case of the "rats" and "wolves." On the other hand, there are no marsupial whales, bats, or ungulates, so niches are not inevitably filled. Nevertheless, if niches do not exist independently of organisms, some other explanation of convergence must be found.

The factual difficulty of formulating evolution as a process of adapting to preexistent problems is that the organism and the environment are not actually separately determined. The environment is not a structure imposed on living beings from the outside but is in fact a creation of those beings. The environment is not an autonomous process but a reflection of the biology of the species. Just as there is no organism without an environment, so there is no environment without an organism. The construction of environments by species has a number of well-known aspects that need to be incorporated into evolutionary theory.

Organisms determine what is relevant. The bark of trees is part of the woodpecker's environment, but the stones at the base of the tree, even though physically present, are not. On the other hand, thrushes that break snail shells include the stones but exclude the tree from their environment. If breaking snail shells is a problem to which the use of a stone anvil is a thrush's solution, it is because thrushes have evolved into snail-eating birds, whereas woodpeckers have not. The breaking of snail shells is a problem created by thrushes, not a transcendental problem that existed before the evolution of the Turdidae.

Not only do organisms determine their own food, but they make their own climate. It is well known in biometeorology that the temperature and moisture within a few inches of the soil in a field is different from the conditions on a forest floor or at the top of the forest canopy. Indeed, the microclimate is different on the upper and lower surfaces of a leaf. Which of these climates constitutes an insect's environment depends upon its habitat, a matter that, in a gross sense, is coded in the insect's genes. All terrestrial organisms are covered with a boundary layer of warm air created by the organism's metabolism. Small ectoparasites living in that boundary layer are insulated from the temperature and moisture conditions that exist a few millimeters off the surface of their host. If the ectoparasite should evolve to become larger, it will emerge from the warm, moist boundary layer into the cold stratosphere above, creating a totally new climatic environment for itself. It is the genes of lions that make the savannah part of their environment, and the genes of sea lions that make the ocean their environment, yet lions and sea lions have a common carnivore ancestor. When did swimming, catching fish, and holding air in its lungs become problems for the terrestrial carnivore from which sea lions evolved?

Organisms alter the external world as they interact with it. Organisms are both the consumers and the producers of the resources necessary to their own continued existence. Plant roots alter the physical structure and chemical composition of the soil in which they grow, withdrawing nutrients but also conditioning the soil so that nutrients are more easily mobilized. Grazing animals actually increase the rate of production of forage, both by fertilizing the ground with their droppings and by stimulating plant growth by cropping. Organisms also influence the species composition of the plant community on which they depend. White pine trees in New England make such a dense shade that their own seedlings cannot grow up under them, so hardwoods come in to take their place. It is the destruction of the habitat by a species that leads to ecological succession. On the other hand, organisms may make an environment more hospitable for themselves, as when beavers create ponds by felling trees and building dams; indeed, a significant part of the landscape in northeastern United States has been created by beavers.

The most powerful change of environment made by organisms is the gas composition of the atmosphere. The terrestrial atmosphere, consisting of 80 percent nitrogen, 18 percent oxygen, and a trace of carbon dioxide, is chemically unstable. If it were allowed to reach an equilibrium, the oxygen and nitrogen would disappear, and the atmosphere would be nearly all carbon dioxide, as is the case for Mars and Venus. It is living organisms that have produced the oxygen by photosynthesis and that have depleted the carbon dioxide by fixing it in the form of carbonates in sedimentary rock. A present-day terrestrial species is under strong selection pressure to live in an atmosphere rich in oxygen and poor in carbon dioxide, but that metabolic problem has been posed by the activity of the living forms themselves over two billion years of evolution and is quite different from the problem faced by the earliest metabolizing cells.

Organisms transduce the physical signals that reach them from the outside world. Fluctuations in temperature reach the inner organs of a mammal as chemical signals, not thermal signals. The regulatory system in mammals alters the concentration of sugar and various hormones in the blood in response to temperature. Ants that forage only in the shade detect temperature changes as such only momentarily, but over a longer term will experience sunshine as hunger. When a mammal sees and hears a rattlesnake, the photon energy and vibrational energy that fall on its eyes and ears are immediately transformed by the neurosecretory system into chemical signals of fear. On the other hand, another rattlesnake will react very differently. It is the biology of each species that determines what physical transformation will occur when physical signals impinge on the organism or whether these signals are even perceived. Bees can see light in the ultraviolet range, but mammals cannot. For bees, ultraviolet light leads to a source of food, while for us it leads to skin cancer. One of the most striking aspects of evolution is the way in which the significance of physical signals has been completely altered in the origin of new species.

Organisms transform the statistical pattern of environmental variation in the external world. Both the amplitude and the frequency of external fluctuations are transformed by biological processes in the organism. Fluctuations are damped by various storage devices that average over space and time. An animal with a wide home range averages food availability over smaller spatial patches. Fat or carbohydrate storage averages the fluctuating availability of resources in time. All seeds store solar energy during the growing season in order to provide it to seedlings, which are at first unable to photosynthesize. Animals in turn store the seeds and thus capture the plant storage mechanism, while converting the storage cycle to their own biological rhythms. Human beings have added yet a third form of damping by engaging in planned production that responds to fluctuations in demand.

Conversely, organisms can magnify small fluctuations, as when birds use a small change in the abundance of a food item as a signal to shift their search images to another item. Living beings can also integrate and differentiate signals. Plants flower when a sufficient number of degree-days above a critical temperature have been accumulated, irrespective of the detailed day-to-day fluctuations in temperature. On the other hand, *Cladocera* change from asexual to sexual reproduction in response to a rapid change in temperature, food availability, or oxygen concentration, irrespective of the actual level itself. An animal's visual acuity depends upon the rate of change of light intensity at the edges of objects, rather than on the total intensity itself. The frequency of external oscillations can even be converted to a cycle having a different frequency. The thirteen- or seventeen-year periodic cicadas hatch out after thirteen or seventeen successive seasonal cycles in the temperate zone, so somehow they are able to count up to a prime number.

The organism-environment relationship defines the "traits" selected. Suppose, for example, that a lizard lives in an equable climate in which food is abundant but must be caught by stalking and pouncing. Since the lizard must expend energy carrying its whole weight as it hunts—and its effectiveness in catching prey may depend on its size—the size spectrum of insect prey may be a major selective force acting on lizard size, while the spatial distribution of prey may determine the lizard's preferences for certain locations over others. The size and preference together form a trait, "predation effectiveness." Now if the climate becomes hotter, the lizard faces a physiological problem, the danger of overheating. Since the rate of heating is affected by body color and the surface- volume relation, body size and color are now linked as part of the physiological trait "heat tolerance." Genes affecting color and size will show epistatic interaction in their effect on this trait, even if the biochemical products of these genes' activity never meet and even if temperature does not affect growth rate. The course of selection, the degree of change in size against that in color, will depend on the available genetic variance for color and size, the other selection forces operating on both of these, and the intensity or frequency of heat stress. This last factor depends on exposure, where the lizard spends its time. Its preference for certain locations becomes part of its ecological heat tolerance, which includes physiological tolerance and exposure. So now location preference, which may have evolved in relation to prey habitat selection, and body size, related to prey size, become linked together with color in "heat tolerance" and continue to be linked in the trait "predation effectiveness."

Suppose now that a predator enters the scene. The lizard may avoid the predator by camouflaging itself or by changing its haunts. Now color and site selection have become linked as part of the trait "predator avoidance," while still forming part of "heat tolerance." Furthermore, a change in where the lizard spends its time can either intensify or diminish selection for "heat tolerance" and, by changing the color of the substrate where it is found, alter the camouflage significance of body color and therefore its effectiveness in heat tolerance. If a second lizard species is present, feeding on the same array of insects, then size, location, and possibly heat tolerance become part of the new trait "competitive ability."

Thus, under natural conditions, aspects of phenotype are constantly joining together and coming apart to create and destroy "traits," which are then selected. The opposite side of organisms constructing their environment is that the environment constructs the traits by means of which the organisms solve the problems posed to them by the environments they created.

Of course, under conditions of artificial selection, the selectors define the traits. Any arbitrary combination of measurements may be defined as a trait. If the price of soybean cake is favorable, the dry weight of soybeans may be the defined "yield" and thus be a trait for selection. With a change in the market, "yield" may become oil per hectare. Or an experimenter may find that some laboratory rats, when picked up by their tails, bite the technician. The experimenter might define the frequency of biting the technician as "aggressivity" and report that he has selected for increased or diminished "aggression" in rats, even if the causal pathway is that the rats with more sensitive tails bite more.

Therefore, when we talk about the traits of organisms fitting their environments, we have to remember that neither trait nor environment exists independently. Nothing better illustrates the error of the problem-solution model than the seemingly straightforward example of the horse's hoof given by Lorenz (1962). The "central nervous apparatus does not prescribe the laws of nature any more than the hoof of the horse prescribes the form of the ground . . . But just as the hoof of the horse is adapted to the ground of the steppe which it copes with, so our central nervous apparatus for organizing the image of the world is adapted to the real world with which man has to cope . . . The hoof of the horse is already adapted to the ground of the steppe before the horse is born and the fin of the fish is adapted to the water before the fish hatches. No sensible person believes that in any of these cases the form of the organ 'prescribes' its properties to the subject."

Indeed, there is a real world out there, but Lorenz makes the same mistake as Ruskin, who believed in the "innocent eye." It is a long way from the "laws of nature" to the horse's hoof. Rabbits, kangaroos, snakes, and grasshoppers, all of whom traverse the same ground as the horse, do not have hooves. Hooves come not from the nature of the ground but from an animal of certain size, with four legs, running, not hopping, over the ground at a certain speed and for certain periods of time. The small gracile ancestors of the horse had toes and toenails, not hooves, and they got along very well indeed. So, too, our central nervous systems are not fitted to some absolute laws of nature, but to laws of nature operating within a framework created by our own sensuous activity. Our nervous system does not allow us to see the ultraviolet reflections from flowers, but a bee's central nervous system does. And bats "see" what nighthawks do not. We do not further our understanding of evolution by general appeals to "laws of nature" to which all life must bend. Rather we must ask how, within the general constraints of the laws of nature, organisms have constructed environments that are the conditions for their further evolution and reconstruction of nature into new environments.

It is difficult to think of any physical force or universal physical law that represents a fixed problem to which all organisms must find a direct solution. We think of gravitation as universal, but because it is such a weak force, it does not apply in practice to very small organisms suspended in liquid media. Bacteria are largely outside the influence of gravity as a consequence of their size, that is, as a consequence of their genes. On the other hand, they are subject to another universal physical force, Brownian motion of molecules, which we are protected from by our large size, again a result of our evolution. The most remarkable property of living organisms is that they have avoided biologically the chemical laws of mass action and the high energy needed to initiate most chemical reactions; both have been accomplished by structure. The structure of the genes themselves, and the way they are held together in very large macromolecular structures, makes it possible for gene replication and protein synthesis to take place even though there is only a single molecule of each gene in each cell. The structure of enzymes, in turn, makes it possible to carry out at ambient temperatures chemical reactions that would otherwise require great heat.

It is impossible to avoid the conclusion that organisms construct every aspect of their environment themselves. They are not the passive objects of external forces, but the creators and modulators of these forces. The metaphor of adaptation must therefore be replaced by one of construction, a metaphor that has implications for the form of evolutionary theory. With the view that the organism is a passive object of autonomous forces, evolutionary change can be represented as two simultaneous differential equation systems. The first describes the way in which organism O evolves in response to environment E, taking into account that different species respond to environments in different ways:

$$\frac{dO}{dt} = f(O,E).$$

The second is the law of autonomous change of the environment as some function only of environmental variables:

$$\frac{dE}{dt} = g(E).$$

A constructionist view that breaks down the alienation between the object-organism and the subject-environment must be written as a pair of *coupled* differential equations in which there is coevolution of the organism-environment pair:

$$\frac{dO}{dt} = f(O,E) \quad \text{and}$$

$$\frac{dE}{dt} = g(O,E).$$

There is already a parallel for such a coevolutionary system in the theory of the coevolution of prey and predator or host and parasite. The prey is the environment of the predator, and the predator the environment of the prey. The coupled differential equations that describe their coevolution are not easy to solve, but they represent the minimum structure of a correct theory of the evolution of such systems. It is not only that they are difficult to solve, but that they pose a conceptual complication, for there is no longer a neat separation between cause (the environment) and effect (the organism). There is, rather, a continuous process in which an organism evolves to solve an instantaneous problem that was set by the organism itself, and in evolving changes the problem slightly. To understand the evolution of the sea lion from a primitive carnivore ancestor, we must suppose that at first the water was only a marginal habitat putting only marginal demands on the animal. A slight evolution of the animal to meet these demands made the aquatic environment a more significant part of the energetic expenditure of the proto-sea lion, so a shift in selective forces operated instantaneously on the shape of its limbs. Each change in the animal made the environment more aquatic, and each induced change in the environment led to further evolution of the animal.

The incorporation of the organism as an active subject in its own ontogeny and in the construction of its own environment leads to a complex dialectical relationship of the elements in the triad of gene, environment, and organism. We have seen that the organism enters directly and actively by being an influence on its own further ontogeny. It enters by a second indirect pathway through the environment in its own ontogeny. The organism is, in part, made by the interaction of the genes and the environment, but the organism makes its environment and so again participates in its own construction. Finally, the organism, as it develops, constructs an environment that is a condition of its survival and reproduction, setting the conditions of natural selection. So the organism influences its own evolution, by being both the object of natural selection and the creator of the conditions of that selection. Darwin's separation of ontogeny and phylogeny was an absolutely necessary step in shaking free of the Lamarckian transformationist model of evolution. Only by alienating organism from environment and rigorously separating the ontogenetic sources of variation among organisms from the phylogenetic forces of natural selection could Darwin put evolutionary biology on the right track. So, too, Newton had to separate the forces acting on bodies from the properties of the bodies themselves: their mass and composition. Yet mass and energy had to be reintegrated to resolve the contradictions of the strict Newtonian view and to make it possible for modern alchemy to turn one element into another. In like manner, Darwinism cannot be carried to completion unless the organism is reintegrated with the inner and outer forces, of which it is both the subject and the object.

TWO

On Analysis