

Philosophical Issues

The study of biological evolution begets more, as well as more urgent, philosophical questions than any other branch of the natural sciences. Problems such as the origin and future of man and man's relationships with the rest of nature are the subject of evolutionary biology but also raise important philosophical questions. A question may be regarded as philosophical if it cannot be approached by the methods characteristic of the empirical sciences but is nevertheless amenable to rational investigation. (The methodological trademarks that distinguish the empirical sciences from other forms of knowledge will be identified below.)

Various kinds of philosophical questions arise from the study of evolutionary biology: epistemological questions, dealing with the sources and grounds of knowledge in evolutionary biology; metaphysical questions, concerned with the nature and ultimate significance of man and the universe; ethical questions, concerned with right and wrong human conduct; and questions of aesthetics, concerned with the nature of beauty and the criteria for artistic judgment.

Chapters 14 and 15 dealt more or less incidentally with the ethical implications of man "engineering" his own biological future and man's management of nature, questions that also have important sociological and political implications. A systematic treatment of the ethical issues arising in evolutionary biology would take us far afield and will not be attempted here. This chapter is primarily concerned with epistemological questions, such as the goals of science and its characteristic methodology, the relationships between biology and the physical sciences, the role of teleological explanations in evolutionary biology, and the logical structure of the theory of natural selection. The notion of biological progress, a metaphysical question, will also be discussed. Evolution appears to be obviously progressive, at least in some sense, and evolutionary

biologists often speak of evolutionary progress. The first issue to be discussed is the nature of the scientific method and its application to the study of evolution. Some scientists as well as philosophers erroneously assume that the scientific method used in evolutionary biology is different from that used in the physical sciences.

EMPIRICAL SCIENCE

The Greek philosopher and scientist Aristotle said that man naturally desires to know. Man seeks understanding of natural phenomena and of himself because of sheer intellectual curiosity and also because such understanding gives him the means to manipulate and utilize the environment for his benefit, because it improves his strategic position in the world. Man's manipulation of the environment can be traced to the first tools constructed by *Australopithecus*, and much later to the discovery of fire and other achievements by *Homo erectus*.

All human cultures, including primitive ones, develop explanations for natural phenomena. At least since the discovery of agriculture, mankind has understood certain causal relationships between rain, sunlight, the seasons, and the life cycles of plants and animals. Yet the birth of empirical science (or simply science) is commonly traced to the sixteenth and seventeenth centuries. What are the traits that distinguish science from the common-sense knowledge of primitive cultures and from nonscientific forms of knowledge?

One distinguishing characteristic is that science seeks the systematic organization of knowledge. Science formulates statements about observable phenomena. Common sense also provides knowledge about natural phenomena, and often is correct. Common sense tells one that children resemble their parents and that good seeds produce good crops. Common sense, however, shows little interest in systematically establishing connections between phenomena that do not appear to be obviously related. By contrast, science is concerned with formulating general laws and theories that manifest patterns of relations between very different kinds of phenomena. Science develops by discovering new relationships, and particularly by integrating statements, laws, and theories, which previously seemed to be unrelated, into more comprehensive laws and theories.

Another distinguishing characteristic of science is that it strives to explain why observed events do in fact occur. Although knowledge acquired in the course of ordinary experience is frequently accurate, it seldom provides explanations of why phenomena occur as they do. Practical experience tells us that children resemble one parent in some traits and the other parent in other traits, or that manure increases crop yield. But it does not provide explanations for these phenomena. Science, on the other hand, seeks to formulate explanations for natural phenomena by identifying the conditions that account for their occurrence.

Seeking the systematic organization of knowledge and trying to explain why events are as observed are characteristics that distinguish science from common-sense knowledge. However, these characteristics are also shared by other forms of knowledge, such as mathematics and philosophy. The characteristic that distinguishes the empirical sciences from other systematic forms of knowledge is that scientific explanations must be subject to the possibility of *empirical falsification*. Falsifiability is indeed the criterion of demarcation that sets science apart from other forms of knowledge (Popper, 1934). A scientific hypothesis (or theory) must be empirically testable. A hypothesis is tested by ascertaining whether or not precise predictions derived as logical consequences from the hypothesis agree with the state of affairs found in the empirical world. A hypothesis that is not subject to the possibility of rejection by observation and experiment cannot be regarded as scientific.

Science may be defined as the systematic organization of knowledge about the universe on the basis of explanatory principles subject to the possibility of empirical falsification. Another definition is the following: "Science is an exploration of the material universe that seeks natural, orderly relationships among observed phenomena and that is self-testing" (Simpson, 1964, p. 91). Many other definitions have been proposed, but seeking a "perfect" definition is a futile endeavor. Science is a complex enterprise that cannot be adequately defined in a compact statement. Thus, rather than attempt to formulate an adequate definition, we shall further examine the methodology of science.

THE SCIENTIFIC METHOD

The idea that induction is the method of science is a common misconception, which can be traced to the English statesman and essayist Francis Bacon (1561–1626). Bacon had an important and influential role in shaping modern science by his criticism of the prevailing metaphysical speculations of medieval scholastic philosophers. In the nineteenth century the most ardent and articulate proponent of inductivism was John Stuart Mill (1806–1873), an English philosopher and economist.

Induction was proposed as a method of achieving *objectivity* while avoiding subjective preconceptions, and of obtaining *empirical* rather than abstract or metaphysical knowledge. In its extreme form, inductivism holds that the scientist should observe any phenomena that he encounters in his experience, and record them without any preconceptions as to what to observe or what the truth about them might be—truths of universal validity are expected eventually to emerge. The methodology proposed may be exemplified as follows. A scientist measuring and recording everything that confronts him observes a tree with leaves. A second tree, and a third, and many others, are all observed to have leaves. Eventually, he formulates a universal statement, "All trees have leaves."

The inductive method fails to account for the actual process of science.

First of all, no scientist works without any preconceived plan as to what kind of phenomena to observe. Scientists choose for study objects or events that, in their opinion, are likely to provide answers to questions that interest them. Otherwise, as Darwin (1903) wrote, "one might as well go into a gravelpit² and count the pebbles and describe the colours." A scientist whose goal was to record carefully every event observed in all waking moments of his life would not contribute much to the advance of science; more likely than not, he would be considered mad by his colleagues.

Moreover, induction fails to arrive at universal truths. No matter how many singular statements may be accumulated, no universal statement can be logically derived from such an accumulation of observations. Even if all trees so far observed have leaves, or all swans observed are white, it remains a logical possibility that the next tree will not have leaves, or the next swan will not be white. The step from numerous singular statements to a universal one involves logical amplification. The universal statement has greater logical content—it says more—than the sum of all singular statements.

Another serious logical difficulty with induction as a scientific method is that scientific hypotheses and theories are formulated in abstract terms that do not occur at all in the description of empirical events. Mendel observed in the progenies of hybrid plants that alternative traits could be segregated into certain ratios. Repeated observations of these ratios could never have led inductively to the formulation of his hypothesis that "factors" (genes) exist in the sex cells and are arranged according to certain rules. These "factors" were not observed, and thus could not be included in observational statements. The most interesting and fruitful scientific hypotheses are not simple generalizations. Instead, scientific hypotheses are creations of the mind, imaginative suggestions as to what might be true.

Induction fails in all three counts pointed out: as a method that insures objectivity and avoids preconceptions, as a logical method to reach universal truths, and as a description of the process followed by scientists in the formulation of hypotheses.*

A more nearly correct concept of the methods of science is provided by the so-called *hypothetico-deductive* model. The explicit formulation of this model may be traced to William Whewell (1794–1866) and William Stanley Jevons (1835–1882) in England, and to Charles S. Peirce (1839–1914) in the United States. The most precise characterization of the scientific method has been expounded by Karl R. Popper (1934). Scientists, of course, practiced the hypothetico-deductive method long before it was adequately defined by philosophers. Eminent practitioners of this method include Blaise Pascal (1623–1662) and Isaac Newton (1642–1727) in the seventeenth century, and, among nineteenth-century biologists, Claude Bernard (1813–1878) and Louis Pasteur (1822–1895) in France, Charles Darwin (1809–1882) in England, and Gregor Mendel (1822–1884) in Austria. These and other suc-

*For more extensive criticisms of inductivism see, for example, Popper (1934), Kuhn (1962), Hempel (1966), and the very readable account of Medawar (1969).

cessful scientists practiced the hypothetico-deductive method even if some of them claimed to be inductivists in order to conform to the claims of contemporary philosophers.

Science is a complex enterprise that essentially consists of two interdependent episodes, one imaginative or creative, the other critical. To have an idea, advance a hypothesis, or suggest what might be true is a creative exercise. But scientific conjectures or hypotheses must also be subject to critical examination and empirical testing. Scientific thinking may be characterized as a process of invention or discovery followed by validation or confirmation. One process concerns the acquisition of knowledge, the other concerns the justification of knowledge.

Scientists like other people *acquire* knowledge in all sorts of ways: from conversation with other people, from reading books and newspapers, from inductive generalizations, and even from dreams and mistaken observations. Newton is said to have been inspired by a falling apple. Kekulé had been unsuccessfully attempting to devise a model for the molecular structure of benzene. One evening he was dozing in front of the fire. The flames appeared to Kekulé as snake-like arrays of atoms. Suddenly one snake appeared to bite its own tail and then whirled mockingly in front of him. The circular appearance of the image inspired in him the model of benzene as an hexagonal ring. Darwin proposed his hypothesis of the origin of coral reefs before he had ever seen a coral reef. The model to explain the evolutionary diversification of species came to Darwin while tiding in his coach and observing the countryside. "I can remember the very spot in the road . . . when to my joy the solution came to me. . . . The solution, as I believe, is that the modified offspring . . . tend to become adapted to many and highly diversified places in the economy of nature" (Darwin, 1958).

Hypotheses and other imaginative conjectures are the initial stage of scientific inquiry. It is the imaginative conjecture of what might be true that provides the incentive to seek the truth and a clue as to where we might find it (Medawar, 1967). Hypotheses guide observation and experiment because they suggest what to observe. The empirical work of scientists is guided by hypotheses, whether explicitly formulated or simply in the form of vague conjectures or hunches about what the truth might be. But imaginative conjecture and empirical observation are mutually interdependent processes. Observations made to test a hypothesis are often the inspiring source of new conjectures or hypotheses.

Although the conception of an idea is the starting point of scientific inquiry, this process is not the subject of investigation of logic or epistemology. The complex conscious and unconscious events underlying the creative mind are properly the interest of empirical psychology. The creative process is obviously not unique to scientists. Philosophers as well as poets, novelists, and other artists are also creative; they too advance models of experience and they also generalize by induction. What distinguishes science from other forms of knowledge is the process by which this knowledge is justified or validated.

THE CRITERION OF DEMARCATION

Testing a hypothesis (or theory) involves at least four different activities. First, the hypothesis must be examined for internal consistency. A hypothesis that is self-contradictory or not logically well-formed in some other way should be rejected. Second, the logical structure of the hypothesis must be examined to ascertain whether it has explanatory value, i.e., whether it makes the observed phenomena intelligible in some sense, whether it provides an understanding of why the phenomena do in fact occur as observed. A hypothesis that is purely tautological should be rejected because it has no explanatory value. Third, the hypothesis must be examined for its consistency with hypotheses and theories commonly accepted in the particular field of science, or to see whether it represents any advance with respect to well-established alternative hypotheses. Lack of consistency with other theories is not always ground for rejection of a hypothesis, although it will often be. Finally, the hypothesis must be tested empirically.

A hypothesis (or theory) is tested empirically by ascertaining whether or not predictions about the world of experience derived as logical consequences from the hypothesis agree with what is actually observed. The critical element that distinguishes the empirical sciences from other forms of knowledge is the requirement that scientific hypotheses be empirically falsifiable. Scientific hypotheses cannot be consistent with all possible states of affairs in the empirical world. A hypothesis is scientific only if it is consistent with some but not with other possible states of affairs not yet observed in the world, so that it may be subject to the possibility of falsification by observation. The predictions derived from a scientific hypothesis must be sufficiently precise that they limit the range of possible observations with which they are compatible. If the results of an empirical test agree with the predictions derived from a hypothesis, the hypothesis is said to be provisionally corroborated; otherwise it is falsified.

The requirement that a scientific hypothesis be falsifiable has been appropriately called the *criterion of demarcation* of the empirical sciences because it sets apart the empirical sciences from other forms of knowledge (Popper, 1934). A hypothesis that is not subject, at least in principle, to the possibility of empirical falsification does not belong in the realm of science.

The requirement that scientific hypotheses be falsifiable rather than simply verifiable may seem surprising at first. It might seem that the goal of science is to establish the "truth" of hypotheses rather than attempt to falsify them. It is not so. There is an asymmetry between falsifiability and verifiability of universal statements that derives from the logical nature of such statements. A universal statement can be shown to be false if it is found inconsistent with even one singular statement, i.e., a statement about a particular event. But, as was pointed out in the discussion of induction, a universal statement can never be proven true by virtue of the truth of particular statements, no matter how numerous these may be.

Consider a hypothesis, H_1 , from which a certain number of consequences,

C_1, C_2, \dots, C_n , are logically derived. Assume that it is found that C_1, C_2, \dots, C_n are true. It does not necessarily follow that H_1 is true. Consider the argument: If H_1 is true, then C_1 must also be true; it is the case that C_1 is true. Therefore H_1 is true. This erroneous kind of inference is called by logicians the *fallacy of affirming the consequent*. The conclusion is invalid even if both premises are true. It may in fact be the case that there is some other hypothesis, H_2 , from which the same consequences or predictions can be derived. Then C_1, C_2, \dots, C_n might still be true because H_2 is true, even if H_1 is false.

The proper form of logical inference for conditional statements is what logicians call the *modus tollens* (*modus* = mode; *tollens* = to take away, to reject). It may be represented by the following argument. If H_1 is true, then C_1 must also be true; but evidence shows that C_1 is not true; therefore H_1 is false. This is a correct form of inference; if both premises are true, the conclusion necessarily follows. It is possible to show the falsity of a universal statement, but it is never possible to demonstrate conclusively the truth of a universal statement concerning the empirical world.

The asymmetry between verification and falsification is recognized in the statistical methodology of testing hypotheses. The hypothesis subject to test, the *null hypothesis*, may be rejected if the observations are inconsistent with it. If the observations are consistent with the predictions derived from the hypothesis, the proper conclusion is that the test has failed to falsify the null hypothesis, not that its truth has been established. The requirement that scientific hypotheses be falsifiable has another parallel in statistical inference, namely in the requirement that the power of the test be greater than zero. Statisticians recognize two kinds of errors: a Type I error, the probability of rejecting the null hypothesis when it is true, usually represented as α ; and a Type II error, the probability of not rejecting the hypothesis when it is false, symbolized as β . Scientists pay considerable attention to Type I errors, and thus choose α levels sufficiently low. It is unfortunate that many scientists pay little attention to Type II errors. Yet the power of the test depends on the probability, $1 - \beta$, of rejecting the null hypothesis when it is wrong. Thus, small levels for both α and β are desirable. Although for any given test the magnitudes of α and β are inversely related, the value of β may be reduced by increasing the sample size or the number of replications in a test.

Just as the power of a statistical test must be greater than zero, so it is more generally required of tests of scientific hypotheses that they have a positive probability of resulting in the rejection of the hypothesis if it is false. A scientific hypothesis divides all particular statements of fact into two nonempty subclasses. First, we have the class of all statements with which it is inconsistent, the class of the "potential falsifiers" of the hypothesis. Second, there is the class of all statements that the hypothesis does not contradict, the class of "permitted" statements. A hypothesis is scientific only if the class of its potential falsifiers is not empty, because it makes assertions only about its potential falsifiers—it asserts that they are false. "Not for nothing do we call the laws of nature 'laws': the more they prohibit the more they say" (Popper, 1934).

The empirical or information content of a hypothesis is measured by the class of its potential falsifiers. The larger this class, the greater the information content of the hypothesis. A hypothesis asserts that its potential falsifiers are false; if any of them is true, the hypothesis is proven false. A hypothesis or theory consistent with all possible states of affairs in the natural world lacks empirical content, and thus does not belong in the realm of science.

Scientific hypotheses can only be accepted provisionally, since their truth can never be conclusively established. This does not mean that we have the same degree of confidence in all hypotheses that have not yet been falsified. A hypothesis that has passed many empirical tests may be said to be "corroborated." The degree of corroboration is not simply a matter of the number of tests, but rather their severity. Severe tests are precisely those that are very likely to have outcomes incompatible with the hypothesis if the hypothesis is false. The more precise the predictions being tested, the more severe the test. A so-called critical or crucial test is an experiment for which competing hypotheses predict alternative, mutually exclusive outcomes. A critical test thus will corroborate one hypothesis and falsify the others.

The larger the variety of severe tests withstood by a hypothesis, the greater its degree of corroboration. Hypotheses or theories may thus become established beyond reasonable doubt. The hypothesis of evolution, that new organisms come about by descent with modification from dissimilar ancestors, is an example of a hypothesis corroborated beyond reasonable doubt. This is what is claimed by biologists who state that evolution is a fact rather than a theory or hypothesis. In ordinary usage, the terms "hypothesis" and "theory" sometimes imply a lack of sufficient corroboration. The evolutionary origin of organisms is compatible with virtually all known facts of biology, and has passed a wide variety of severe tests.

The *modus tollens* is a logically conclusive method—if a necessary consequence of a premise is false, then the premise must also be false. Nevertheless, the process of falsification is subject to human error. It is possible, for example, that an observation or experiment contradicting a hypothesis may have been erroneously performed or erroneously interpreted. Thus, it is usually required, particularly in the case of important or well-corroborated hypotheses, that the falsifying observation be repeatable.

The *modus tollens* may lead to erroneous conclusions if the prediction tested is not a necessary logical consequence from the hypothesis. The connection between a hypothesis and specific predictions derived from it is often not a simple matter. The logical validity of an inference may depend not only on the hypothesis being tested, but also on other hypotheses, whether explicitly stated or not, as well as on assumptions concerning the particular conditions under which the deduced inferences obtain (boundary conditions). If a particular prediction is falsified, it follows that the hypothesis tested as well as other hypotheses necessarily implied and the boundary conditions cannot all jointly be true. The possibility exists that one of the subsidiary hypotheses or some assumed condition may be false. A proper test of a hypothesis thus tests the validity of all the hypotheses and conditions involved.

MENDEL AND THE SCIENTIFIC METHOD

Gregor Mendel's classic paper, "Experiments in Plant Hybridization," is an eminent example of the use of the scientific method in biology. First published in 1866, this paper established single-handedly the basic principles and fundamental theory of heredity, from which a whole new branch of science, genetics, would develop. The paper is also remarkable because of Mendel's explicit and lucid awareness of the requirements of the scientific method. Mendel formulated hypotheses, examined their consistency with previous results, then submitted the hypotheses to severe empirical tests and suggested additional tests that might be performed.

Mendel's genius is evident in his recognition of the conditions required to formulate and test a theory of inheritance: different traits should be considered individually, alternative states of the traits should differ in clear-cut ways, and ancestry of the plants should be precisely known (which, in turn, requires that only true-breeding lines be used in the experiment, and that the origin of the pollen, and not only the eggs, be controlled). Mendel's hypotheses were formulated in probabilistic terms; accordingly, he obtained large samples and subjected them to statistical analysis.

Mendel studied the transmission of seven different traits in the garden pea, *Pisum sativum*, including the color of the seed (yellow versus green), the configuration of the seed (round versus wrinkled), and the height of the plant (tall versus dwarf). The results of Mendel's experiments are too well known to need detailed presentation here, but it is worth pointing out the various stages of his methodology. His first series of experiments was with plants that differ in a single trait. The regularities observed led to certain generalizations having the form of law-like statements: only one of the two traits (the *dominant* trait) appears in the F_1 progenies; after self-fertilization, three-fourths of the F_2 progenies exhibit the dominant trait, and one-fourth exhibit the other (*recessive*) trait; the F_2 plants exhibiting the recessive trait breed true in the F_3 and following generations, but the plants exhibiting the dominant trait are of two kinds, one-third breed true, the other two-thirds are hybrids. Mendel tested these generalizations by repeating his experiments for each of the seven characters. These generalizations were summarized in a law, later called the Principle of Segregation: hybrid plants produce seeds that are one-half hybrid, one-fourth pure breeding for the dominant trait, and one-fourth pure breeding for the recessive trait.

Mendel tested the hypothesis of segregation by deriving and verifying additional predictions. For example, he predicted that after n generations of self-fertilization the ratio of true-breeding to hybrid plants in the progeny of a hybrid should be $2^n - 1$ to 1. He explicitly stated that this prediction would obtain only if the following condition obtained, that all plants have "an average quality of fertility . . . in all generations."

The study of the offspring of crosses between plants differing in two traits (e.g., round and yellow seeds in one parent, wrinkled and green seeds in the

other parent) led him to formulate a second law-like statement, later called the Principle of Independent Assortment: "The principle applies that [in] the offspring of the hybrids in which several essentially different characters are combined . . . the relation of each pair of different characters in hybrid union is independent of the other differences in the two original parental stocks." He corroborated this principle by examining progenies of plants differing in various combinations of two traits, as well as in plants differing in three and four traits. He correctly predicted and corroborated experimentally that in the progenies of plants hybrid for n characters there will be 3^n different classes of plants.

Textbooks give credit to Mendel for having formulated the principles of segregation and independent assortment, often called Mendel's First and Second Law of Inheritance. The formulation and experimental testing of these two laws take up only approximately the first half of Mendel's paper. Midway through the paper Mendel advanced what he properly called a hypothesis or theory to account for his previous results and for the two laws. In the second half of the paper predictions are derived from the theory and tested.

Mendel's theory of inheritance contains the following elements: (1) for each character in any plant, whether hybrid or not, there is a pair of hereditary "factors"; (2) these two factors are inherited one from each parent; (3) the two factors of each pair segregate during the formation of the sex cells, so that each sex cell receives only one factor; (4) each sex cell receives one or the other factor of a pair with a probability of one-half; (5) alternative factors for different characters associate at random in the formation of the sex cells. Mendel's well-deserved eminence as a scientist rests particularly on the formulation of this theory of heredity. Mendel was also quite aware of the logical status of his proposal, namely that it was a hypothesis and therefore required experimental corroboration. In the paragraph following the formulation of his theory, Mendel wrote that "this hypothesis would fully suffice to account for the development of the hybrids in the separate generations," i.e., the hypothesis is consistent with his previous observations. But, quite appropriately, he recognized that further experimental tests were called for: "In order to bring these assumptions to an experimental proof the following experiments were designed." The experiments are two series of back-crosses that confirm segregation and independent assortment in the egg cells, and then in the pollen cells.

The theory was further tested with experimental crosses using a different plant, *Phaseolus*. The ratios observed in the progenies of hybrids were the same as in *Pisum* and thus consistent with the theory. With respect to two traits, flower and seed color, Mendel observed in the F_2 progenies "a whole series of colors . . . from purple to pale violet and white." Mendel correctly conjectured that "these enigmatic results . . . might be explained . . . if we might assume that the color of the flowers and seeds of *Ph [aseolus] multiflorus* is a combination of two or more entirely independent colors, which individually act like any other character in the plant." After showing how this hypothesis accounts for the gamut of colors, Mendel added: "It must, never-

theless, not be forgotten that the explanation here attempted is based on a mere hypothesis, only supported by the very imperfect result of the experiment just described. It would, however, be well worthwhile to follow up the development of color in hybrids by similar experiments." To the very end, Mendel was fully aware of the demand of the scientific method.

Some authors have suggested that Mendel must have had a fairly clear conception of what he expected to find even before he began the first experiments reported in his paper. The experiments appear too well designed for things to be otherwise. Indeed, it might be the case that Mendel had performed some previous experiments, or that he came upon the idea of the binary determination of traits from considerations of the existence of two sexes, or in some other way. Whether or not Mendel had a preconception of what the results of his experiments would be is irrelevant to the integrity of his scientific accomplishments or his masterly understanding of the requirements of the scientific method. Mendel's paper remains a model of the scientific method.

DARWIN AND THE SCIENTIFIC METHOD

Few scientists in the nineteenth century or at any earlier time equal Mendel's clear delineation of the scientific method he was pursuing. In the English-speaking countries, scientists advanced hypotheses and tested them in their work, but often claimed in their writings to be following the orthodoxy of inductionism proclaimed by philosophers as the method of good science. Darwin is a remarkable example of this discrepancy.

In his *Autobiography* Darwin says that he proceeded "on true Baconian principles and without any theory collected facts on a wholesale scale" (1958, p. 119). The opening paragraph of *Origin of Species* conveys the same impression:

When on board H. M. S. *Beagle*, as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent. These facts seemed to me to throw some light on the origin of species—that mystery of mysteries, as it has been called by one of our greatest philosophers. On my return home, it occurred to me, in 1837, that something might perhaps be made out on this question by *patiently accumulating and reflecting on all sorts of facts which could possibly have any bearing on it*. After five years' work I allowed myself to speculate on the subject, and drew up some short notes; these I enlarged in 1844 into a sketch of the conclusions, which then seemed to me probable: from that period to the present day I have steadily pursued the same object. [Emphasis added]

Darwin claims in many other writings to have followed the inductivist canons. The facts are very different from these claims, however. Darwin's notebooks and private correspondence show that he entertained the hypothesis of the evolutionary transmutation of species shortly after returning from the

voyage of the *Beagle*, and that the hypothesis of natural selection occurred to him in 1838—several years before he claims to have allowed himself for the first time "to speculate on the subject." Between the return of the *Beagle* on October 2, 1836, and publication of *Origin of Species* (and, indeed, until the end of his life) Darwin relentlessly pursued empirical evidence to corroborate the evolutionary origin of organisms, and to test his theory of natural selection.

Why this disparity between what Darwin was doing and what he claimed? There are at least two reasons. First, in the temper of the times "hypothesis" was a term often reserved for metaphysical speculations without empirical substance. This is the reason why Newton, the greatest theorist of all scientists, also claimed, *Hypotheses non fingo* ("I fabricate no hypotheses"). Darwin expressed distaste and even contempt for empirically untestable hypotheses. He wrote of Herbert Spencer: "His deductive manner of treating any subject is wholly opposed to my frame of mind. His conclusions never convince me . . . His fundamental generalizations (which have been compared in importance by some persons with Newton's Laws!) which I daresay may be very valuable under a philosophical point of view, are of such a nature that they do not seem to me to be of any strictly scientific use. They partake more of the nature of definitions than of laws of nature. They do not aid me in predicting what will happen in any particular case" (1958, p. 109).

There is another reason, a tactical one, why Darwin claimed to proceed according to inductive canons. He did not want to be accused of subjective bias in the evaluation of empirical evidence. Darwin's true colors are shown in a letter to a young scientist written in 1863: "I would suggest to you the advantage, at present, of being very sparing in introducing theory in your papers (I formerly erred much in *Geology* in that way); *let theory guide your observations*, but till your reputation is well established, be sparing of publishing theory. It makes persons doubt your observations" (F. Darwin, 1903, 2:323; see also Hull, 1973). Nowadays scientists, young or not, often report their work so as to make their hypotheses appear as conclusions derived from the evidence at hand, rather than as preconceptions tested by empirical observations.

Darwin rejected the inductivist claim that observations should not be guided by hypotheses. The statement quoted earlier, "A man might as well go into a gravel-pit and count the pebbles and describe the colours," is followed by this telling remark: "How odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service!" (F. Darwin, 1903, 1:195). He acknowledged the heuristic role of hypotheses, which guide empirical research by telling us what is worth observing, what evidence to seek. He confesses: "I cannot avoid forming one [hypothesis] on every subject" (1958, p. 141).

Darwin was an excellent practitioner of the hypothetico-deductive method of science, as modern students of Darwin have abundantly shown (De Beer, 1964; Mayr, 1964; Ghiselin, 1969; Hull, 1973). Darwin advanced hypotheses in multiple fields, including geology, plant morphology and physiology, psychology, and evolution, and subjected his hypotheses to empirical test. "The

line of argument often pursued throughout my theory is to establish a point as a probability by induction and to apply it as a hypothesis to other parts and see whether it will solve them" (Darwin, 1960). Popper (1934) has not only made clear that falsifiability is the criterion of demarcation of the empirical sciences from other forms of knowledge, but also that falsification of seemingly true hypotheses contributes to the advance of science. Darwin recognized this: "False facts are highly injurious to the progress of science, for they often endure long; but false views, if supported by some evidence, do little harm, for every one takes a salutary pleasure in proving their falseness; and when this is done, one path towards error is closed and the road to truth is often at the same time opened" (Darwin, 1871, 2nd ed., p. 606).

Some philosophers of science have claimed that evolutionary biology is a historical science that does not need to satisfy the requirements of the hypothetico-deductive method. The evolution of organisms, it is argued, is a historical process that depends on unique and unpredictable events, and thus is not subject to the formulation of testable hypotheses and theories. Such claims emanate from a monumental misunderstanding. There are two kinds of questions in the study of biological evolution (Dobzhansky, 1951, pp. 11-12). One concerns history: the study of phylogeny, the unraveling and description of the actual course of evolution on earth that has led to the present state of the biological world. The scientific disciplines contributing to the study of phylogeny include systematics, paleontology, biogeography, comparative anatomy, comparative embryology, and comparative biochemistry. The second kind of question concerns the elucidation of the mechanisms or processes that bring about evolutionary change. These questions deal with causal, rather than historical, relationships. Population genetics, population ecology, paleobiology, and many other branches of biology are the relevant disciplines.

There can be little doubt that the causal study of evolution proceeds by the formulation and empirical testing of hypotheses, according to the same hypothetico-deductive methodology characteristic of the physicochemical sciences and other empirical disciplines concerned with causal processes. This book contains numerous examples of hypotheses, and their tests, advanced to account for the various processes underlying biological evolution (see also Ayala, 1975b). But even the study of evolutionary history is based on the formulation of empirically testable hypotheses. Consider a simple example. For many years specialists proposed that the evolutionary lineages leading to man separated from the lineage leading to the great apes (chimpanzee, gorilla, orangutan) before the lineages of the great apes separated from each other. Some recent authors have suggested instead that man, chimpanzees, and gorillas are more closely related to each other than the chimpanzee and the gorilla are to the other apes. A wealth of empirical predictions can be derived logically from these competing hypotheses. One prediction concerns the degree of similarity between enzymes and other proteins. It is known that the rate of amino acid substitutions is approximately constant when averaged over many proteins and long periods of time (Chapter 9). If the first hypothesis is correct,

the average amount of protein differentiation should be greater between man and the African apes than among these and orangutans. On the other hand, if the second hypothesis is correct, man and chimpanzees should have greater protein similarity than either one has with orangutans. These alternative predictions provide a critical empirical test of the hypotheses. The available data favor the second hypothesis. Man, chimpanzees, and gorillas appear to be phylogenetically more closely related to each other than any one of them is related to orangutans (Goodman, 1976).

Certain biological disciplines relevant to the study of evolution are largely descriptive and classificatory. Description and classification are necessary activities in all branches of science, but play a greater role in certain biological disciplines, such as systematics and biogeography, than in other disciplines, such as population genetics. Nevertheless, even systematics and biogeography occasionally use the hypothetico-deductive method and formulate empirically testable hypotheses.

MECHANISM AND VITALISM

The relationships between the biological and physical sciences, and between organisms and inorganic matter, are of considerable interest to the philosophy of science. Many papers, books, and symposia have been devoted to these relationships in recent years (e.g., Koestler and Smythies, 1969; Ayala and Dobzhansky, 1974). The issue at stake is sometimes called "the problem of reductionism" or "the question of reduction." Few philosophical issues have been more actively debated in recent years, particularly among scientists, than the question of reduction. The debate, however, involves several different issues, not always properly distinguished. Issues about the relationship between the biological and physical sciences fall into at least three domains, which may be called "ontological," "methodological," and "epistemological." We shall identify the issues in each domain, and then consider each domain in turn.

Reductionistic questions arise, first, in what may be called the ontological, the structural, or the constitutive domain. The issue here is whether or not physicochemical entities and processes underlie all living phenomena. Are organisms constituted of the same components as those making up inorganic matter? Or do organisms consist of other entities besides molecules, atoms, and ultimately subatomic particles? Other questions are related to these. Are organisms nothing else than aggregations of atoms and molecules? Do organisms exhibit properties other than those of their constituent atoms and molecules?

Second, there are reductionist questions that might be called methodological, procedural, or strategic. These questions concern the strategy of research and the acquisition of knowledge, the approaches to be followed in the investigation of living beings. The general question is whether biological problems should always be investigated by studying the underlying (ultimately, physical)

processes, or whether they should not also be studied at higher levels of organization, such as the cell, the organism, the population, and the community.

The third type of reductionistic question concerns issues that may be called epistemological, theoretical, or explanatory. The fundamental issue here is whether or not the theories and laws of biology can be derived from the laws and theories of physics and chemistry. Epistemological reductionism is concerned with the question whether biology may not be a separate science, but simply a special case of physics and chemistry.

Distinguishing the various kinds of questions being asked in the debate over reductionism is the first step towards solving the issues. Much argument and confusion has resulted from a failure to identify the type of question being argued in particular instances. It is not untypical, for example, to see a reductionist concerned primarily with the ontological question accusing a self-proclaimed anti-reductionist of being a vitalist, while the latter may be an epistemological anti-reductionist but also in fact an ontological reductionist.

In the ontological domain reductionism versus anti-reductionism, in its extreme form, resolves into mechanism versus vitalism. The mechanist position is that organisms are ultimately made up of the same atoms that make up inorganic matter, and nothing more. Vitalists argue that organisms are made up not only of material components (atoms, molecules, and aggregations of them) but also of some nonmaterial entity, variously called *entelechy*, *vital force*, *élan vital*, *radial energy*, and the like. Aristotle (384–322 B.C.), the great Greek philosopher who was also the best biologist of his time, is sometimes said to be the first systematic proponent of vitalism. The modern controversy over mechanism versus vitalism dates from the seventeenth century, when René Descartes (1596–1650) proposed that animals are nothing else than complex machines. Early in the twentieth century vitalism was defended by such philosophers as Henri Bergson (1859–1941), and by some biologists, notably Hans Driesch (1867–1941). At present vitalism has no distinguished proponents among biologists, and few if any among philosophers.

Vitalism has been excluded from science because it does not meet the requirements of a scientific hypothesis. Vitalism is not a hypothesis subject to the possibility of empirical falsification and therefore leads to no fruitful observations or experiments. Moreover, all available evidence indicates that organisms and life processes can be explained without recourse to any substantive nonmaterial entity.

Ontological reductionism claims that organisms are exhaustively composed of nonliving parts. No substance or other residue remains after all atoms making up an organism are taken into account. Ontological reductionism also implies that the laws of physics and chemistry fully apply to all biological processes at the level of atoms and molecules.

Ontological reductionism does not necessarily claim, however, that organisms are nothing but atoms and molecules. The idea that because something consists of "something else" it is nothing but this "something else" is an erroneous inference, called by philosophers the "nothing but" fallacy. Organisms

consist exhaustively of atoms and molecules, but it does not follow that they are nothing but heaps of atoms and molecules. A steam engine may consist only of iron and other materials, but it is something other than iron and the other components. Similarly, an electronic computer is not only a pile of semiconductors, wires, plastic, and other materials. Organisms are made up of atoms and molecules, but they are highly complex patterns, and patterns of patterns, of these atoms and molecules. Living processes are highly complex, highly special, and highly improbable patterns of physical and chemical processes.

A much debated reductionist question that belongs in the ontological domain is whether organisms exhibit *emergent properties*, or whether their properties are simply those of their physical components. For example, are the functional properties of the kidney simply the properties of the chemical constituents of that organ? It must be pointed out, first, that the question of emergent properties is not exclusive to biology, but applies to all complex systems. The general formulation of this question is whether the properties of a particular object are simply the properties of its component parts, organized in certain ways.

Whether complex systems exhibit emergent properties is largely a spurious issue that can be solved as a matter of definition. Consider the following question. Are the properties of common salt, sodium chloride, simply the properties of sodium and chlorine when they are associated according to the formula NaCl? If among the properties of sodium and chlorine we include their association into table salt and the properties of the latter, the answer is yes. In general, if among the properties of an object we include the properties that the object has when associated with other objects, it follows that the properties of complex systems, including organisms, are also the properties of their component parts. However, this is simply a definitional maneuver that contributes little to understanding the relationships between complex systems and their parts.

In common practice the properties of an object do not include the properties of systems of which the object may form a part. There is a good reason for this. No matter how exhaustively an object is studied in isolation, there is usually no way to ascertain all the properties that it may have in association with any other object. Among the properties of hydrogen we do not usually include the properties of water, ethyl alcohol, proteins, and human beings. Nor do we include among the properties of iron those of the steam engine.

The question of emergent properties may also be formulated in a somewhat different manner. Can the properties of complex systems be *inferred* from knowledge of the properties that their component parts have in isolation? For example, can the properties of benzene be predicted from knowledge about oxygen, hydrogen, and carbon? Or, at a much higher level of complexity, can the behavior of a cheetah chasing a deer be predicted from knowledge about the atoms and molecules making up these animals? Formulated in this manner, the issue of emergent properties is an epistemological question, not an ontological one. It asks whether the laws and theories accounting for the behavior of complex systems can be derived as logical consequences of the laws and theories

that explain the behavior of their component parts. (Epistemological questions of reductionism are discussed later in this chapter, p. 491ff.)

REDUCTIONISM VERSUS COMPOSITIONISM

One outstanding characteristic of living beings is the complexity of organization connoted by the name "organism." A hierarchy of levels of complexity runs from atoms, through molecules, macromolecules, organelles, cells, tissues, multicellular organisms, populations, and communities. Some biological disciplines focus on one or a few of these levels of complexity of organization: cytology is the study of cells, histology the study of tissues, and ecology the study of populations and communities. Yet biological disciplines are identified more by the kinds of questions asked, and the kinds of answers sought, than by the level of organization investigated.

Methodological reductionism claims that living phenomena are best studied at lower levels of complexity, ultimately at the level of atoms and molecules. For example, genetics should seek to understand heredity ultimately in terms of the behavior and structure of DNA, RNA, enzymes, and other macromolecules, rather than in terms of whole organisms, the level at which the Mendelian laws of inheritance are formulated. Methodological reductionism has its counterpart in what may be called methodological compositionism (Simpson, 1964), which claims that to understand organisms we must first explain their organization—not only how organisms and groups of organisms are organized, but also what functions the organization serves. Accordingly, organisms and groups of organisms should be studied as wholes, as well as in their component parts.

Methodological reductionism in its extreme form claims that biological research should be conducted only at the level of physicochemical component parts and processes. Research at other levels, it is argued, is not worth pursuing since biological phenomena can ultimately be understood only at the molecular and atomic levels. Methodological compositionism in its extreme form makes the opposite claim, namely, that biological research is worth pursuing only at the level of whole organisms, populations, and communities. Research at lower levels of organization may be good physics or good chemistry, but it has no biological significance.

It is unlikely that any thoughtful scientist would advocate the extreme form of either compositionism or reductionism. Extreme methodological reductionism would imply the unreasonable claim that genetic investigations should not have been undertaken until the discovery of DNA as the hereditary material, or that a moratorium should be declared in ecology until we can investigate the physicochemical processes underlying ecological interactions. Similarly, extreme methodological compositionism would imply that understanding the structure of DNA or the enzymatic processes involved in replication is of no significance to the study of heredity, or that the investigation of physicochemical reactions in the transmission of nerve impulses is of no importance to the understanding of animal behavior.

The moderate version of methodological reductionism emphasizes the success of the analytical method in science, and the obvious fact that the understanding of living processes at any level of organization is much advanced by knowledge of the underlying processes. Moderate methodological reductionists claim that the best strategy of research is to investigate any given biological phenomenon at increasingly lower levels of organization as this becomes possible, and ultimately at the level of atoms and molecules.

These claims of moderate methodological reductionists are legitimate. Reductionist analysis is of great heuristic value, i. e., it serves to discover and to stimulate investigation; much can be learned about a phenomenon through the investigation of its component elements or processes. In biology the most impressive achievements of the last few decades have been those of molecular biology. But there is little justification for any exclusionist claim that research should always proceed by investigation of increasingly lower levels of integration. The only criterion of validity of a research strategy is its success. Compositionist as well as reductionist approaches, synthetic as well as analytic methods of investigation, are justified if they further our understanding of a phenomenon, if they increase knowledge. Reductionist and compositionist approaches to the study of a biological problem are complementary; often the best strategy of research is an alternation between analysis and synthesis.

Investigation of a biological phenomenon at higher levels of complexity often contributes to the understanding of the phenomenon itself. Compositionist investigations are also heuristic. It is doubtful that the structure and functions of DNA would have been known as readily as they were if there had been no previous knowledge of Mendelian genetics. The problem of the specificity of the immune response of antibodies proved refractory to a satisfactory solution as long as the structure alone of antibodies and antigens was taken into consideration. The natural selection theory of antibody function emerged only when antibodies were considered in their organismic milieu. Although the idea of clonal selection was logically inadequate and quite vague at first, it had an enormous heuristic value in helping to understand how the specificity of antibodies comes about (Edelman, 1974).

THE REDUCTION OF THEORIES

When philosophers of science speak of reductionism, they are generally referring neither to ontological nor to methodological issues, but to epistemological reductionism. In biology the central question of epistemological (theoretical, explanatory) reductionism is whether the laws and theories of biology can be shown to be special cases of the laws and theories of the physical sciences.

Science seeks to discover patterns of relations among vast kinds of phenomena in such a way that a number of principles explain a large number of propositions concerning those phenomena. Science advances by developing gradually more comprehensive theories, i. e., by showing that theories and laws that had hitherto appeared as unrelated can in fact be integrated in a single theory of greater

generality. For example, Mendel's theory of heredity can explain diverse observations about many kinds of organisms, such as the proportions in which traits are transmitted from parent to offspring, why progenies exhibit some traits inherited from one parent and some from the other parent, and why the offspring may exhibit traits not present in their parents. The discovery that the behavior of chromosomes during meiosis is connected with the Mendelian principles made possible the explanation of many additional observations concerning heredity; for example, why certain traits are inherited independently from each other, while other traits are more often transmitted together. Further discoveries made possible the development of a unified theory of inheritance of great generality, which explains many diverse observations, including the distinctness of individuals, the adaptive nature of organisms and their traits, and the discreteness of species.

The connection among theories has sometimes been established by showing that the tenets of a theory or branch of science can be explained by the tenets of another theory or branch of science of greater generality. The less general theory (or branch of science), called the secondary theory, is then said to have been reduced to the more general or primary theory. Epistemological reduction of one branch of science to another takes place when the theories or experimental laws of a branch of science are shown to be special cases of the theories and laws formulated in some other branch of science. The integration of diverse scientific theories and laws into more comprehensive ones simplifies science and extends the explanatory power of scientific principles, and thus conforms to the goals of science.

The reduction of a theory or even a whole branch of science to another has occurred repeatedly in this history of science (Nagel, 1961; Popper, 1974). One of the most impressive examples is the reduction of thermodynamics to statistical mechanics, made possible by the discovery that the temperature of a gas reflects the mean kinetic energy of its molecules. Several branches of physics and astronomy have been to a large extent unified by their reduction to a few theories of great generality, such as quantum mechanics and relativity. A large sector of chemistry was reduced to physics after it was shown that the valence of an element bears a simple relation to the number of electrons in the outer orbit of the atom. Parts of genetics were to some extent reduced to chemistry after discovery of the structure and mode of replication and action of the hereditary material, DNA.

The impressive successes of these reductions have led some authors to claim that the ideal of science is to reduce all the natural sciences, including biology, to a comprehensive physical theory that would provide a common set of principles of maximum generality capable of explaining all observations about natural phenomena.

Nagel (1961) has formulated the two conditions that are necessary and sufficient to effect the reduction of one theory or branch of science to another. These are the condition of derivability and the condition of connectability. The *condition of derivability* states simply that in order to reduce a branch of science to another it is necessary to show that the laws and theories of the

secondary science can be derived as logical consequences from the laws and theories of the primary science.

The *condition of connectability* is based on the rule that no terms can appear in the conclusion of a demonstrative argument that do not appear in the premises. The reduction of one science (theory) to another takes the form of a deductive argument in which one of the premises is the primary science (theory), and the conclusion the secondary. Generally, however, the experimental laws and theories of a branch of science contain distinctive terms that do not appear in other branches of science. For the deduction to be logically valid there must be another premise that establishes the connection between the terms of the primary and secondary sciences. For example, the reduction of thermodynamics to statistical mechanics required the definition of "temperature" in terms of "kinetic energy." The reduction of the theories or experimental laws of genetics to those of chemistry requires that such terms as "gene" and "chromosome" be defined in terms of "hydrogen bond," "nucleotide," "deoxyribonucleic acid," "histone protein," and the like.

Whenever the conditions of connectability and derivability are satisfied, the epistemological reduction of a theory to another becomes logically feasible. If all the experimental laws and theories of one branch of science can be reduced to those of another, the former science is said to have been completely reduced to the latter.

It bears repetition that epistemological reduction is not a question of whether the *properties* of certain kinds of objects, such as organisms, result from the properties of other kinds of objects, such as inorganic compounds. Scientific laws and theories consist of propositions about the natural world. The reduction of one science to another is a matter of deriving one set of *propositions* from another. It is therefore a legitimate epistemological question to ask whether the *statements* concerning the properties of organisms, but not the properties themselves, can be logically deduced from statements concerning the properties of their physical components. The question of epistemological reduction can only be settled by empirical investigation of the logical consequences of propositions, and not by discussions about the "nature" of things or their properties.

It follows from the previous comments that questions of epistemological reduction can only be properly answered by referring to the actual state of development of the scientific disciplines involved. Certain parts of chemistry were reduced to physics after the modern theory of atomic structure was advanced half a century ago. That reduction could not have been accomplished before such a development. If the reduction of one science to another is not possible at the present stage of development of the two disciplines, claims that such a reduction will be accomplished in the future carry little weight, since such claims are not based on developments from existing theories but are merely expressions of hope.

There are some extreme positions about the question of epistemological reductionism that can be easily discounted. Some vitalists claim that biology is in principle irreducible to the physical sciences because living phenomena are

the manifestation of nonmaterial principles, such as vital forces, entelechies, and so on. Epistemological anti-reductionism is thus predicated on ontological anti-reductionism. Vitalism is not an empirical hypothesis because it does not lend itself to the possibility of empirical falsification.

At the other end of the spectrum is the claim that the epistemological reduction of biology to the physical sciences is not only possible but the most important task of biologists at present. The impressive successes of molecular biology during recent decades have moved some people to claim that the only worthy and truly scientific biological investigations are those leading to the explanation of biological phenomena in terms of their underlying physicochemical components and processes. *Nevertheless, epistemological reduction of biology to the physical sciences is not possible at present.* In the current stage of scientific development a great many biological terms, such as "organ," "species," "consciousness," "mating propensity," "fitness," "competition," and "predator," cannot be defined adequately in physicochemical terms. Nor is there any class of statements and hypotheses in physics and chemistry from which every biological law can be derived logically. Therefore, neither the condition of connectability nor the condition of derivability—the two necessary conditions for epistemological reduction—can be satisfied.

A moderate reductionist position is probably not uncommon among biologists. Although the reduction of biology to chemistry cannot be effected at present, it is claimed that it is possible in principle and therefore a goal to be actively sought; actual reduction of biology to the physical sciences is made contingent upon further progress in the biological or physical sciences or both. This moderate form of epistemological reductionism is often based on convictions about ontological reductionism. It is generally accepted by biologists that living beings are exhaustively made up of physical components. It does not follow, however, that organisms are *nothing but* physical systems. Ontological reductionism does not entail epistemological reductionism. From the fact that organisms are exhaustively composed of atoms and molecules, it does not follow that the behavior of organisms can be exhaustively explained by the laws advanced to explain the behavior of atoms and molecules.

The claim that the reduction of biology to chemistry will eventually be possible is contingent upon unspecified, and at present *unspecifiable*, scientific advances. It is, therefore, a position that cannot be convincingly argued rationally. Moreover, there are reasons to believe that complete reduction of biology to physics will never be possible. Popper has shown that no major case of epistemological reduction (including such model cases as the reduction of thermodynamics to statistical mechanics) "has ever been *completely* successful: there is almost always an unresolved residue left by even the most successful attempts at reduction" (Popper, 1974, p. 260; see also Hull, 1974). It does not follow, however, that scientists should not attempt to reduce biological theories to those of the physical sciences, whenever such an undertaking seems likely to be successful. On the contrary, epistemological reductions are very successful forms of scientific explanation. A great deal is learned from

epistemological reductions even when they are unsuccessful or incomplete, because much understanding is gained by the partial success, and valuable problems arise from the partial failure (Popper, 1974). The reduction of Mendelian genetics to molecular genetics has been far from completely successful (Hull, 1974). Yet there can be little doubt that much has been learned from what has been accomplished up to the present.

Some authors have claimed that even if some parts of biology can be reduced to physics and chemistry now or in the future, a complete reduction is impossible in principle because biological disciplines employ patterns of explanation that do not occur in the physical sciences (Simpson, 1964; Ayala, 1968b). Historical explanations are sometimes mentioned as distinctive of the biological and social sciences. They are not, however, because they also occur in some physical sciences, such as astronomy and geology. Although historical explanations do play a role in evolutionary theory, the theory is primarily concerned with causal explanations of evolutionary processes. Teleological explanations, as expounded below, are appropriate in biology but appear to be neither necessary nor appropriate in the explanation of physical phenomena.

DARWIN'S CONCEPTUAL REVOLUTION

The publication in 1859 of Darwin's *Origin of Species* opened a new era in the intellectual history of mankind. The discoveries of Copernicus, Kepler, Galileo, and Newton had gradually led to a conception of the universe as a system of matter in motion governed by natural laws. The earth was found to be not the center of the universe but a small planet rotating around an average star; the universe appeared as immense in space and in time; the motions of the planets around the sun could be explained by simple laws—the same laws that accounted for the motion of objects in our planet. These and many other discoveries greatly expanded human knowledge. But the conceptual revolution that went on through the seventeenth and eighteenth centuries was the realization that the universe obeys immanent laws that can account for natural phenomena. The workings of the universe were brought into the realm of science—explanation through natural laws. Physical phenomena could be reliably predicted whenever the causes were adequately known. Darwin completed the Copernican revolution by drawing out for biology the ultimate conclusions of the notion of nature as a lawful system of matter in motion. The adaptations and diversity of organisms, the origin of novel and highly organized forms, even the origin of man himself could now be explained by an orderly process of change governed by natural laws.

Before Darwin, the origin of organisms and their marvelous adaptations was most frequently attributed to the design of an omniscient Creator. God had created the birds and bees, the fish and corals, the trees in the forest, and best of all Man. God had given man eyes so that he might see, and had provided fish with gills to breathe in water. Philosophers and theologians often argued

that the functional design of organisms evinced the existence of an all-wise Creator. In the thirteenth century St. Thomas Aquinas had used the argument-from-design as his "fifth way" to demonstrate the existence of God. In the nineteenth century the English theologian William Paley argued in his *Natural Theology* (1802) that the functional design of the human eye provided conclusive evidence of an all-wise Creator. It would be absurd to suppose, wrote Paley, that the human eye by mere chance "should have consisted, first, of a series of transparent lenses . . . ; secondly of a black cloth or canvas spread out behind these lenses so as to receive the image formed by pencils of light transmitted through them, and placed at the precise geometrical distance at which, and at which alone, a distinct image could be formed . . . ; thirdly of a large nerve communicating between this membrane and the brain." The eight Bridgewater Treatises, written by eminent scientists and philosophers, were published between 1833 and 1840 to set forth "the Power, Wisdom, and Goodness of God as manifested in the Creation." The mechanisms and vital endowments of man's hand gave, according to Sir Charles Bell, author of one Bridgewater Treatise, incontrovertible evidence that the hand had been designed by the same omniscient Power that had created the world.

The apparent strength of the argument-from-design to demonstrate the existence of a Creator is obvious. Wherever there is function or design we look for its author. A knife is *made* to cut and a clock is *made* to tell time; their functional designs are contrived by a knifemaker and a watchmaker. The structures, organs, and behaviors of living beings are directly organized to serve certain functions. Thus the functional design, or teleology, of organisms and their features would seem to argue for the existence of a designer. Darwin showed that the directive organization of living beings could be explained as the result of a natural process—natural selection. There was no need to resort to a Creator or other external agent. The origin and adaptation of organisms were thus brought into the realm of science.

Darwin recognized that organisms are teleologically organized. Organisms are adapted to certain ways of life and their parts adapted to perform certain functions. Fish are adapted to live in water, kidneys are designed to regulate the composition of blood, the hand of man is made for grasping. Darwin accepted the facts of adaptation and then provided a natural explanation for those facts. He brought the teleological aspect of living beings into the realm of science: he provided ample evidence for the occurrence of evolution, and for this he is appropriately given credit. More revolutionary, however, was the fact that he extended the Copernican revolution to the world of living things. The origin and adaptive nature of organisms could now be explained, like the phenomena of the inanimate world, as the result of natural laws manifested in natural processes. Darwin's theory was opposed in certain religious circles, not so much because he proposed the evolutionary origin of living things (this had been proposed many times before, even by Christian theologians), but because he excluded God from the explanation of the adaptation of organisms. The Roman

Catholic church's opposition to Galileo in the seventeenth century was similarly motivated.

The central argument of the theory of natural selection was eloquently summarized by Darwin in *Origin of Species*:

As more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. . . . Can it, then, be thought improbable, seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should sometimes occur in the course of thousands of generations? If such do occur, can we doubt (remembering that more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind? On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favorable variation and the rejection of injurious variations, I call Natural Selection.

Darwin's argument addresses the problem of explaining the adaptive nature of organisms. Darwin argues that adaptive variations ("variations useful in some way to each being") must occasionally appear, and that these are likely to increase the reproductive chances of their carriers. Over the generations favorable variations will be preserved, injurious ones will be eliminated. In one of the few places where he uses the term "adaptation" or its cognates in *Origin of Species*, Darwin adds: "I can see no limit to this power [natural selection] in slowly and beautifully *adapting* each form to the most complex relations of life." Natural selection was proposed by Darwin primarily to account for the adaptive organization of living beings; it is a process that promotes or maintains adaptation. Evolutionary change through time (anagenesis) and evolutionary diversification (cladogenesis) are not directly promoted by natural selection, but they often ensue as by-products of natural selection fostering adaptation. "One problem of great importance . . . is the tendency in organic beings to diverge in character as they become modified. . . . The solution [to this problem] is that the modified offspring of all dominant and increasing forms tend to become *adapted* to many and highly diversified places in the economy of nature" (Darwin, 1958).

TELEOLOGICAL EXPLANATIONS

Teleology (from the Greek *telos* = end) is "the use of design, purpose, or utility as an explanation of any natural phenomenon" (*Webster's Third New International Dictionary*, 1966). An object or a behavior is said to be teleological or telic when it gives evidence of design or appears to be directed toward certain ends. The behavior of human beings is often teleological. A

person who buys an airplane ticket, reads a book, or cultivates the earth is trying to achieve a certain end: getting to a given city, acquiring knowledge, or getting food. Objects and machines made by people also are usually teleological: a knife is made for cutting, a clock is made for telling time, a thermostat is made to regulate temperature. Features of organisms are teleological as well: a bird's wings are *for* flying, eyes are *for* seeing, kidneys are constituted for regulating the composition of the blood. The features of organisms that may be said to be teleological are those that can be identified as adaptations, whether they are structures like a wing or a hand, or organs like a kidney, or behaviors like the courtship displays of a peacock. Adaptations are features of organisms that have come about by natural selection because they serve certain functions and thus increase the reproductive success of their carriers.

Inanimate objects and processes (other than those created by men) are not teleological because they are not directed toward specific ends, they do not exist to serve certain purposes. The configuration of a sodium chloride molecule depends on the structure of sodium and chlorine, but it makes no sense to say that that structure is made up so as to serve a certain end. The shape of a mountain is the result of certain geological processes, but it did not come about so as to serve a certain end. The motion of the earth around the sun results from the laws of gravity, but it does not exist in order to satisfy certain ends or goals. We may use sodium chloride as food, a mountain for skiing, and take advantage of the seasons, but the use that we make of these objects or phenomena is not the reason why they came into existence or why they have certain configurations. On the other hand, a knife and a car exist and have particular configurations precisely in order to serve the ends of cutting and transportation. Similarly, the wings of birds came about precisely because they permitted flying, which was reproductively advantageous. The mating display of peacocks came about because it increased the chances of mating and thus of leaving progeny.

The previous comments point out the essential characteristics of telic phenomena, i. e., phenomena whose existence and configuration can be explained teleologically. We may now propose the following definition. *Teleological explanations account for the existence of a certain feature in a system by demonstrating the feature's contribution to a specific property or state of the system.* Teleological explanations require that the feature or behavior contribute to the existence or maintenance of a certain state or property of the system. Moreover, and this is the essential component of the concept, the contribution must be the reason why the feature or behavior exists at all.

The configuration of a molecule of sodium chloride contributes to its property of tasting salty and therefore to its use as food, not vice versa; the potential use of sodium chloride as food is not the reason why it has a particular molecular configuration or tastes salty. The motion of the earth around the sun is the reason why seasons exist; the existence of the seasons is not the reason why the earth moves about the sun. On the other hand, the sharpness of a knife can be explained teleologically because the knife has been created precisely to serve

the purpose of cutting. Motorcars and their particular configurations exist because they serve transportation, and thus can be explained teleologically. (Not all features of a car contribute to efficient transportation—some features are added for aesthetic or other reasons. But as long as a feature is added because it exhibits certain properties—like appeal to the aesthetic preferences of potential customers—it may be explained teleologically. Nevertheless, there may be features in a car, a knife, or any other man-made object that need not be explained teleologically. That knives have handles may be explained teleologically, but the fact that a particular handle is made of pine rather than oak might simply be due to the availability of material. Similarly, not all features of organisms have teleological explanations.)

Many features and behaviors of organisms meet the requirements of teleological explanation. The hand of man, the wings of birds, the structure and behavior of kidneys, the mating displays of peacocks are examples already given. In general, as pointed out above, those features and behaviors that are considered adaptations are explained teleologically. This is simply because adaptations are features that come about by natural selection. Among alternative genetic variants that may arise by mutation or recombination, the ones that become established in a population are those that contribute more to the reproductive success of their carriers. The effects on reproductive success are usually mediated by some function or property. Wings and hands acquired their present configuration through long-term accumulation of genetic variants adaptive to their carriers. An alternative feature may be due to a single gene mutation, e.g., the presence of normal hemoglobin rather than hemoglobin S in humans. One amino acid substitution in the beta chain in humans results in hemoglobin molecules less efficient for oxygen transport. The general occurrence in human populations of normal rather than S hemoglobins is explained teleologically by the contribution of hemoglobin to effective oxygen transport and thus to reproductive success. The difference between peppered-gray and melanic moths is due to one or only a few genes. The replacement of gray moths by melanics in polluted regions is explained teleologically by the fact that melanism decreases the probability of predation in such regions. The predominance of peppered forms in nonpolluted regions is similarly explained.

Not all features of organisms need to be explained teleologically, since not all come about as a direct result of natural selection. Some features may become established by genetic drift, by chance association with adaptive traits, or in general by processes other than natural selection. Proponents of the neutrality theory of protein evolution argue that many alternative protein variants are adaptively equivalent. Most evolutionists would admit that at least in certain cases the selective differences between alternative protein variants must be virtually nil, particularly when population size is very small. The presence in a population of one amino acid sequence rather than another adaptively equivalent to the first would not then be explained teleologically. Needless to say, in such cases there would be amino acid sequences that would not be

adaptive. The presence of an adaptive protein rather than a nonadaptive one would be explained teleologically; but the presence of one protein rather than another among those adaptively equivalent would not require a teleological explanation.

NATURAL AND ARTIFICIAL TELEOLOGY

In the previous section some man-made objects and adaptive traits of organisms served as examples of teleological phenomena. We may now distinguish several kinds of teleological phenomena (Ayala, 1968b, 1970). Actions or objects are *purposeful* when the end-state or goal is consciously intended by an agent. Thus, a man mowing his lawn is acting teleologically in the purposeful sense; a lion hunting deer and a bird building a nest have at least the appearance of purposeful behavior. Objects resulting from purposeful behavior exhibit *artificial* (or *external*) teleology. A knife, a table, a car, and a thermostat are examples of systems exhibiting artificial teleology: their teleological features were consciously intended by some agent.

Systems with teleological features that are not due to the purposeful action of an agent but result from some natural process exhibit *natural* (or *internal*) teleology. The wings of birds have a natural teleology; they serve an end, flying, but their configuration is not due to the conscious design of any agent. We may distinguish two kinds of natural teleology: *determinate* or necessary, and *indeterminate* or nonspecific. Determinate natural teleology exists when a specific end-state is reached in spite of environmental fluctuations. The development of an egg into a chicken, or of a human zygote into a human being, are examples of determinate natural teleological processes. The regulation of body temperature in a mammal is another example. In general, the homeostatic processes of organisms are instances of determinate natural teleology. Two types of homeostasis are usually distinguished—physiological and developmental—although intermediate conditions exist. Physiological homeostatic reactions enable organisms to maintain certain physiological steady states in spite of environmental shocks. The regulation of the concentration of salt in blood by the kidneys, or the hypertrophy of muscle owing to strenuous use, are examples of physiological homeostasis. Developmental homeostasis refers to the regulation of the different paths that an organism may follow in the progression from fertilized egg to adult. The process can be influenced by the environment in various ways, but the characteristics of the adult individual, at least within a certain range, are largely predetermined in the zygote.

Indeterminate or nonspecific teleology occurs when the end-state served is not specifically predetermined, but rather is the result of selection of one from among several available alternatives. For teleology to exist, the selection of one alternative over another must be deterministic and not purely stochastic. But what alternatives happen to be present may depend on environmental and/

or historical circumstances and thus the specific end-state is not generally predictable. Indeterminate teleology results from a mixture of stochastic (at least from the point of view of the teleological system) and deterministic events. The adaptations of organisms are teleological in this indeterminate sense. The wings of birds require teleological explanations: the genetic constitutions responsible for their configuration came about because wings serve to fly and flying contributes to the reproductive success of birds. But there was nothing in the constitution of the remote ancestors of birds that would necessitate the appearance of wings in their descendants. Wings came about as the consequence of a long sequence of events, where at each stage the most advantageous alternative was selected among those that happened to be available; but what alternatives were available at any one time depended at least in part on chance events. In spite of the role played by stochastic events in the phylogenetic history of birds, it would be mistaken to say that wings are not teleological features. Again, there are differences between the teleology of an organism's adaptations and the nonteleological potential uses of natural inanimate objects. A mountain may have features appropriate for skiing, but those features did not come about so as to provide skiing slopes. On the other hand, the wings of birds came about precisely because they serve flying. The explanatory reason for the existence of wings and their configuration is the end they serve—flying—which in turn contributes to the reproductive success of birds. If wings did not serve an adaptive function they would have never come about or would gradually disappear over the generations.

The indeterminate character of the outcome of natural selection over time is due to a variety of nondeterministic factors. The outcome of natural selection depends, first, on what alternative genetic variants happen to be available at any one time. This in turn depends on the stochastic processes of mutation and recombination, and also on the past history of any given population. (What new genes may arise by mutation and what new genetic constitutions may arise by recombination depend on what genes happen to be present—which depends on previous history.) The outcome of natural selection depends also on the conditions of the physical and biotic environment. Which alternatives among available genetic variants may be favored by selection depends on the particular set of environmental conditions to which a population is exposed.

Some evolutionists have rejected teleological explanations because they have failed to recognize the various meanings that the term "teleology" may have (Pittendrigh, 1958; Mayr, 1965, 1974b; Williams, 1966; Glüselin, 1974). These biologists are correct in excluding certain forms of teleology from evolutionary explanations, but they err when they claim that teleological explanations should be excluded altogether from evolutionary theory. In fact, they themselves often use teleological explanations in their works, but fail to recognize them as such, or prefer to call them by some other name, such as "teleonomic." Teleological explanations, as explained above, are appropriate in evolutionary theory, and are recognized by most evolutionary biologists and

philosophers of science who have thoughtfully considered the question (Beckner, 1959; Nagel, 1961; Simpson, 1964; Dobzhansky, 1970; Ayala, 1968b, 1970; Wimsatt, 1972; Hull, 1974). Which kinds of teleological explanations are appropriate and which ones are inappropriate with respect to various biological questions may be briefly specified.

Mayr (1965) has pointed out that teleological explanations have been applied to two different sets of biological phenomena. "On the one hand is the production and perfection throughout the history of the animal and plant kingdoms of ever-new and ever-improved DNA programs of information. On the other hand is the testing of these programs and their decoding throughout the lifetime of each individual. There is a fundamental difference between end-directed behavioral activities or developmental processes of an individual or system, which are controlled by a program, and the steady improvement of the genetically coded programs. This genetic improvement is evolutionary adaptation controlled by natural selection." The "decoding" and "testing" of genetic programs of information are the issues considered, respectively, by developmental biology and functional biology. The historical and causal processes by which genetic programs of information come about are the concern of evolutionary biology. Grene (1974) uses the term "instrumental" for the teleology of organs that act in a functional way, such as the hand for grasping; "developmental" for the teleology of such processes as the maturation of a limb; and "historical" for the process (natural selection) producing teleologically organized systems.

Organs and features such as the eye and the hand have determinate (and internal) natural teleology. These organs serve determinate ends (seeing or grasping) but have come about by natural processes that did not involve the conscious design of any agent. Physiological homeostatic reactions and embryological development are processes that also have determinate natural teleology. These processes lead to end-states (from egg to chicken) or maintain properties (body temperature in a mammal) that are on the whole determinate. Thus, Mayr's "decoding" of DNA programs of information and Grene's "instrumental" and "developmental" teleology, when applied to organisms, are cases of determinate natural teleology (Mayr prefers to use the term "teleonomy" for this type of teleology). Human tools (such as a knife), machines (such as a car), and servomechanisms (such as a thermostat) also have determinate teleology, but of the artificial kind, since they have been consciously designed.

The process of natural selection is teleological but only in the sense of indeterminate natural teleology. It is not consciously intended by any agent, nor is it directed towards specific or predetermined end-states. Yet the process is far from random or completely indeterminate (Chapter 4). Among the genetic alternatives available at any one time, natural selection favors those that increase the reproductive success of their carriers in the particular environmental circumstances in which the organisms live. Reproductive success is, of course, mediated by some adaptive function, say flying, that is determined by the genetic variants that are favored by natural selection.

Some authors exclude teleological explanations from evolutionary biology because they believe that teleology exists only when a specific goal is purposefully sought. This is not so. Terms other than "teleology" could be used for natural (or internal) teleology, but this might in the end add more confusion than clarity. Philosophers as well as scientists use the term "teleological" in the broader sense, to include explanations that account for the existence of an object in terms of the end-state or goal that they serve.

The process of evolution by natural selection is not teleological in the purposeful sense. Thomas Aquinas and the natural theologians of the nineteenth century erroneously claimed that the directive organization of living beings evinces the existence of a Designer. The adaptations of organisms can be explained as the result of natural processes without recourse to consciously intended end-products. There is purposeful activity in the world, at least in man; but the existence and particular structures of organisms, including man, need not be explained as the result of purposeful behavior.

Lamarck (1809) erroneously thought that evolutionary change necessarily proceeded along determined paths from simpler to more complex organisms. Similarly, the evolutionary philosophies of Bergson (1907), Teilhard de Chardin (1959), and such theories as *homogenesis* (Berg, 1926), *aristogenesis* (Osborn, 1934), *orthogenesis*, and the like are erroneous because they all claim that evolutionary change necessarily proceeds along determined paths. These theories mistakenly take embryological development as the model of evolutionary change, regarding the teleology of evolution as determinate. Although there are teleologically determinate processes in the living world, like embryological development and physiological homeostasis, the evolutionary origin of living beings is teleological only in the indeterminate sense. Natural selection does not in any way direct evolution toward any particular organisms or toward any particular properties.

Teleological explanations are fully compatible with causal explanations (Nagel, 1961; Ayala, 1970). It is possible, at least in principle, to give a causal account of the various physical and chemical processes in the development of an egg into a chicken, or of the physicochemical, neural, and muscular interactions involved in the functioning of the eye. It is also possible in principle to describe the causal processes by which one genetic variant becomes eventually established in a population. But these causal explanations do not make it unnecessary to provide teleological explanations where appropriate. Both teleological and causal explanations are called for in such cases.

One question biologists ask about features of organisms is "What for?" That is, "What is the function or role of a particular structure or process?" The answer to this question must be formulated teleologically. A causal account of the operation of the eye is satisfactory as far as it goes, but it does not tell all that is relevant about the eye, namely that it serves to see. Moreover, evolutionary biologists are interested in the question why one particular genetic alternative rather than others came to be established in a population. This question also calls for teleological explanations of the type: "Eyes came into existence because

they serve to see, and seeing increases reproductive success of certain organisms in particular circumstances." In fact, eyes came about in several independent evolutionary lineages: cephalopods, arthropods, vertebrates.

There are two questions that must be addressed by a teleological account of evolutionary events. First, there is the question of how a genetic variant contributes to reproductive success; a teleological account states that an existing genetic constitution (say, the allele coding for a normal hemoglobin beta chain) enhances reproductive fitness better than alternative constitutions. Then there is the question of how the specific genetic constitution of an organism enhances its reproductive success; a teleological explanation states that a certain genetic constitution serves a particular function (for example, the molecular composition of hemoglobin has a role in oxygen transport).

Both questions call for teleological hypotheses that can be empirically tested. It sometimes happens, however, that information is available on one or the other question but not for both. In population genetics the fitness effects of alternative genetic constitutions can often be measured while the mediating adaptive function responsible for the fitness differences may be difficult to identify. We know, for example, that in *Drosophila pseudoobscura* different inversion polymorphisms are favored by natural selection at different times of the year (Chapter 4) but we are largely ignorant of the physiological processes involved. In a historical account of evolutionary sequences the problem is occasionally reversed: the function served by an organ or structure may be easily identified, but it may be difficult to ascertain why the development of that feature enhanced reproductive success and thus was favored by natural selection. One example is the large brain of man, which makes possible culture and other important human attributes. We may advance hypotheses about the reproductive advantages of increased brain size in the evolution of man, but these hypotheses are notoriously difficult to test empirically.

Teleological explanations in evolutionary biology have great heuristic value. They are also occasionally very facile, precisely because they may be difficult to test empirically. Every effort should be made to formulate teleological explanations in a fashion that makes them readily subject to empirical testing. When appropriate empirical tests cannot be formulated, evolutionary biologists should use teleological explanations only with the greatest restraint (see Williams, 1966).

THE THEORY OF NATURAL SELECTION

According to the theory of evolution expounded in this book, natural selection is the process responsible for the adaptations of organisms, and also the main process by which evolutionary change comes about. The principle of natural selection, together with some subsidiary and generally well-corroborated hypotheses (such as the Mendelian theory of inheritance), can explain a large number of phenomena in the living world, such as the diversity of organisms, their gradual change through time, and their remarkable adaptations to

their environments. The theory of evolution is indeed the single most encompassing biological theory.

Two criticisms of the theory of evolution by natural selection have been raised. One is that the theory can explain all conceivable states of affairs in the living world and therefore is not subject to the possibility of empirical falsification. The other criticism is more fundamental. It claims that the principle of natural selection is circular; it is able to explain all conceivable evolutionary outcomes because it lacks empirical content. This alleged circularity would explain why the theory of natural selection is not empirically falsifiable.

These criticisms are mistaken. We shall show that the theory of natural selection is not circular and that it can be properly tested empirically.

Claims of circularity may imply circularity of either definition or argumentation. Circularity of definition occurs when the terms to be defined appear in the definition. Circularity of argumentation occurs when the conclusion is logically included in one of the premises. Circularity of definition is not a serious criticism in empirical science. It can be resolved by replacing the circular definition by a noncircular one. Natural selection is often defined as "differential reproduction of alternative genetic variants," which is not a circular definition. Definitions of natural selection need not be circular.

Recently, some philosophers have leveled the more serious charge against the theory of natural selection that it is purely tautological (Himmelfarb, 1962; Smart, 1963; Manser, 1965; Flew, 1967; Barker, 1969; Grene, 1974). According to these critics, arguments for natural selection proceed approximately as follows. One premise states that alternative genetic variants that confer higher fitness to their carriers will increase in frequency over the generations at the expense of genetic variants with lower fitness. The second premise is empirical, establishing that a particular genetic variant confers high fitness in a particular situation. The conclusion drawn is that the particular genetic variant (observed to have higher fitness) will gradually increase in frequency. The catch, it is claimed, is the empirical premise. Since evolutionists measure fitness by observing which genetic variants leave greater numbers of progeny, the conclusion of the argument is not a conclusion at all: the conclusion has been used to establish the second premise of the argument. Grene (1974, p. 86) writes: "What have we? Once more, tautology: well, after all, what survives survives. . . . When the theory [of natural selection] is summed up in a formula for measuring differential gene ratios, you have a theorem universally applicable because empty, totally comprehensive because it expresses a simple identity."

These criticisms are mistaken. First, the critics erroneously equate fitness with changes in gene frequencies. Although fitness differences are likely to lead to changes in gene frequencies, not all gene frequency changes are due to fitness differences. Gene frequencies change by natural selection, but also by drift, mutation, and migration. Whether a particular evolutionary change is due to fitness differences, i.e., to natural selection, can be tested empirically. Second, the critics err because they fail to consider a critical premise in the

argument. Natural selection, as Darwin saw it, is postulated to explain *adaptation*—why organisms exhibit features that are end-directed. Evolutionary change is simply a consequence of natural selection promoting the adaptation of organisms to their environments.

The theory of evolution by natural selection advances arguments of the following general form. Among alternative genetic variants, some result in features that are useful to their carriers as adaptations to the environment. Individuals possessing useful adaptations are likely to leave, on the average, greater numbers of progeny than individuals lacking them (or having less useful adaptations). Therefore useful adaptations become established in populations.

To explain a particular adaptation, a valid selectionist argument has to show (1) that natural selection is involved at all; and (2) that natural selection favors the particular adaptation. These two claims can be tested empirically. Those who claim that the theory of natural selection is circular erroneously claim two identities: that changes in gene frequencies are the same as differences in fitness, and that fitness is the same as adaptation. These identities do not always obtain. Whether natural selection is involved in a particular genetic change, and whether natural selection favors a particular adaptation are questions to be resolved empirically. As pointed out in the previous section, there are two kinds of problems encountered in explanations of evolution by natural selection. One is to determine whether natural selection is involved in a certain genetic change; the second is to identify the particular adaptation involved in the genetic change.

Many examples of adaptations have been given in previous sections of this chapter and elsewhere in the book. Adaptation is, nevertheless, a concept difficult to define (Bock and Wahlert, 1965; Williams, 1966; Dobzhansky, 1968; Ayala, 1969). Adaptations can be recognized in individuals—whether physiological, morphological, or behavioral—as well as at the level of the population. Some operational ways of measuring the adaptation of populations have been considered by Dobzhansky (1968), Ayala (1969b), and others. Williams (1966) has proposed that a useful criterion for identifying individual adaptations is whether an analogy can be established between some human artifact and the feature presumed to be an adaptation. A mammalian oviduct may be seen as a mechanism for conveying an early embryo to the uterus; the uterus may be seen as designed for the protection and nourishment of the embryo. Ayala (1968b, 1970) has suggested utility as a criterion for identifying adaptations. A feature of an organism is regarded as an adaptation if it has utility for the organism and if such utility explains the presence of the feature.

Adaptation and fitness are in any case different concepts. Fitness is simply a measure of the reproductive efficiency of one genetic constitution relative to alternative ones in the same population. Fitness does not always go hand-in-hand with adaptation. One example is provided by the *t* alleles in the house mouse. Homozygotes for these alleles are lethal or sterile. The *t* alleles distort segregation in heterozygous males in such a way that a majority (up to 95 percent) of the spermatozoa carry the mutant rather than the normal allele. A *t* allele introduced in a population by either mutation or migration will increase in

frequency due to natural selection. Yet this increase reduces the adaptation of the individual carriers and the population. Other examples of genetic variants with high fitness that decrease adaptation can be given (Ayala, 1969).

The theory of evolution proposes natural selection as the process that accounts for the structural and functional adaptation of organisms to their environments. The observed adaptations of organisms were the facts that Darwin set himself to explain as the result of natural processes. The connection between fitness, i.e., systematic differences in reproductive efficiency that result in natural selection, and adaptation needs to be demonstrated for each particular case of adaptation. This is done by means of empirically falsifiable hypotheses claiming that carriers of a given adaptation have greater reproductive efficiency than organisms lacking that adaptation.

It is surprising that critics of the theory of natural selection would argue that evolutionists measure fitness simply by observing changes in gene frequencies from one generation to the next in a given population. Changes in gene frequencies may be due to any of the variety of causes discussed in other chapters of this book. For example, genetic drift may result in substantial genetic evolution over generations, particularly in small populations (Chapter 4). Also, the neutrality theory of molecular evolution postulates that much protein evolution is not due to natural selection (Chapter 9). In natural selection arguments, the claim that a given genetic change is due to fitness differences is a hypothesis empirically falsifiable by appropriate observations and experiments. Many examples have been given in earlier chapters of this book; two will be briefly summarized here. Certain chromosomal arrangements are observed to change in frequency throughout the year in natural populations of *Drosophila pseudoobscura* (Dobzhansky, 1971). One possible explanation is that these changes are due to seasonal changes in the fitness of the chromosomal arrangements. This hypothesis is subject to empirical tests in the laboratory (Wright and Dobzhansky, 1946), as well as in nature, e.g., by observing whether the seasonal changes are repeated from one year to the next (Dobzhansky and Ayala, 1973). Populations of *Biston betularia* and other moths have experienced considerable evolution throughout the last hundred years. In some localities melanic forms have totally replaced the typical grayish moths. A great variety of empirical observations and tests have corroborated the hypothesis that the evolution of melanic forms is due to fitness changes associated with industrial pollution of the environment. The particular adaptation involved has also been identified as the cryptic coloration of melanic forms that are more likely to escape predation than light gray moths when resting on blackened trees.

THE CONCEPT OF PROGRESS

The earliest organisms living on earth were no more complex than some bacteria and blue-green algae. Three billion years later their descendants include the orchids, the bees, the dolphins, and man. Thus, biologists sometimes speak

of "evolutionary progress" to refer to certain evolutionary trends, such as advances in complexity of organization, increased homeostasis, or the development of social organization. The evolutionary literature abounds in such terms as "lower (or higher) organisms," "more (or less) advanced," and the like. Yet evolutionary lineages may be "progressive" with respect to one or a few attributes but not with respect to others. Or they may not be "progressive" at all by any reasonable definition; bacteria and blue-green algae today are not very different from their ancestors of two or three billion years earlier. Moreover, many evolutionary lineages have become extinct.

What do we mean by "biological progress"? In what sense, if any, can we say that evolution is progressive? The term "progress" may be clarified by comparing it with other related terms used in biological discourse. These terms are "change," "evolution," and "direction."

"Change" means alteration, whether in the location, the state, or the nature of a thing. Progress implies change, but the opposite is not true—not all changes are progressive. Molecules of oxygen and nitrogen in the air of a room change locations continuously; such change would not generally be regarded as progressive. The mutation of a gene from a functional allele to a nonfunctional one is a change of state, but definitely not a progressive one.

"Evolution" can also be distinguished from "progress," although both terms imply that *sustained* change has occurred. Evolutionary change is not necessarily progressive. The evolution of a species may lead to its extinction, a change that is not progressive, at least not for that species.

"Direction" and "progress" are also distinguishable. The concept of "direction" implies that a series of changes have occurred that can be arranged in a linear sequence, with respect to some property or feature, such that elements in the later part of the sequence are more different from early elements of the sequence than from intermediate elements. Directional change may be "uniform" or "net" (see below), depending on whether each succeeding member is invariably more different from the first than each preceding member is, or whether directional change occurs only on the average.

In discussions of evolution "directionality" is sometimes equated with "irreversibility": the process of evolution is said to have a direction because it is irreversible. Evolutionary changes are irreversible (see Chapter 1), except perhaps in some trivial sense, as when a previously mutated gene mutates back to its former allelic state. Direction, however, implies more than irreversibility. Consider a new pack of cards with each suit arranged from ace to ten, knave, queen, king, and with the suits arranged in the sequence spades, clubs, hearts, diamonds. If we shuffle the cards thoroughly, the order of the cards changes, and the change cannot be reversed by shuffling. We may shuffle again and again until the cards are totally worn out without ever restoring the original sequence. The change of order of the cards is irreversible but not directional.

Irreversible and directional changes occur in the inorganic as well as the living world. The second law of thermodynamics describes sequential changes that are irreversible but also directional, and indeed uniformly directional. Within a closed system, entropy always increases; that is, a closed system passes con-

tinuously from less to more probable states. The concept of direction applies to what in paleontology are called "evolutionary trends." A trend occurs in a phylogenetic sequence when a feature persistently changes through time in the members of the sequence. Trends are commonly seen in fossil sequences that are sufficiently long to be called "sustained" (Simpson, 1953).

Consider the trend toward a gradual reduction of the number of dermal bones in the skull roof in the evolutionary sequence from fish to man, or the trend toward increased molarization of the last premolars in the phylogeny of the Equidae from *Hyracotherium* in early Eocene to *Haplohippus* in early Oligocene. These trends represent directional change, but it is not obvious that they should be labeled progressive. To label them progressive we would need to agree that the directional change had been in some sense for the better. To consider a directional sequence progressive, we need to add an evaluation, namely that the condition in the later members of the sequence represents a *betterment* or improvement. Directionality in a sequence may be accepted without any such evaluation being added. Progress implies directional change, but the opposite is not true.

The concept of progress contains two elements: one descriptive—that directional change has taken place; the other axiological (= evaluative)—that the change represents a betterment (Gould, 1961). The notion of progress requires that a value judgment be made of what is better and what is worse. However, the axiological standard of reference need not be a moral one; not all forms of progress are moral. To recognize progress, an evaluation of better versus worse is required, but not necessarily one of right versus wrong, or of good versus evil. "Better" may simply mean more efficient, or more abundant, or more complex, without any reference to moral values or standards.

Progress, then, may be defined as *systematic change in a feature belonging to all members of a sequence in such a way that posterior members of the sequence exhibit an improvement of that feature*. More simply, progress may be defined as directional change toward the better. The antonym of progress is "retrogression," or directional change for the worse. The two elements of the definition, namely directional change and improvement according to some standard, are jointly necessary and sufficient for the occurrence of progress. Directional change (and progress) may be observed in sequences that are spatially rather than temporally ordered. *Clines* are examples of directional change recognized along a spatial dimension. In evolutionary discourse, however, temporal (historical) sequences are of greatest interest.

Various kinds of progress can be distinguished by attending to either one of the two essential elements of the definition. We shall later refer to different types of evolutionary progress based on different standards. Here we shall further clarify the concept of progress by making two distinctions that relate to the descriptive element of the definition, namely the requirement of directional change. These distinctions also apply, therefore, to the concept of direction.

If we attend to the *continuity* of the direction of change, we can distinguish two kinds of progress: uniform and net. *Uniform progress* takes place whenever

every later member of a sequence is better than every earlier member of the sequence according to a certain standard. Let m_i represent the members of a sequence, temporally ordered from 1 to n , and let p_i measure the state of the feature under evaluation. There is uniform progress if it is the case for every m_i and m_j that $p_j > p_i$ for every j greater than i . *Net progress* does not require that every member of a sequence be better than all previous members of the sequence and worse than all its successors; it requires only that later members of the sequence be better *on the average* than earlier members. Net progress allows for temporary fluctuations of value. If the members of a sequence, m_i , are linearly arranged over time, net progress occurs whenever the regression (in the sense used in mathematical statistics) of p on time is significantly positive.

Some authors have argued that progress has not occurred in evolution because, no matter what standard is chosen, fluctuations of value can be found in every evolutionary lineage. This criticism is valid against uniform, but not net evolutionary progress. Also, neither uniform nor net progress require that progress continue forever, or that any specified goal be achieved. The *rate* of progress may decrease with time; progress means only a gradual improvement in the members of a sequence. It is possible that a progressive sequence may tend asymptotically toward a finite goal, that is, continuously approach but never reach the goal.

The distinction between uniform and net progress is similar but not identical to the distinction between uniform and perpetual progress made by Broad (1925) and Goudge (1961). Simpson (1949, 1953) implicitly makes a distinction between uniform and net progress in his enlightening discussion of evolutionary progress. He uses terms like "universal," "invariable," "constant," and "continuous" for what we have called uniform progress (although he also uses these terms with other meanings).

Other types of progress (and directional change) can be distinguished. With respect to the *scope* of the sequence considered, progress can be either general or particular. *General progress* is that which occurs in all historical sequences of a given domain of reality, and from the beginning of the sequences until their end. *Particular progress* is that which occurs in one or several, but not all historical sequences, or progress that takes place during part but not all of the duration of the sequence or sequences.

In biological evolution general progress would be any kind of progress that can be predicated of the evolution of all life from its origin to the present. If a type of progress is predicated of only one or several lines of evolutionary descent, it is a particular kind of progress. Progress that embraces only a limited period of the existence of life is also a particular kind of progress. Some writers have denied that evolution is progressive because not all evolutionary lineages exhibit advance. Some evolutionary lineages, like those leading to certain parasitic forms, are retrogressive by certain standards; and many lineages have become extinct without issue. These considerations may be valid criticism against the idea of general progress, but not necessarily against that of particular forms of progress.

THE EXPANSION OF LIFE

We have established that the concept of "progress" involves an axiological element. Discussions of evolutionary progress require that a choice be made of the standard by which organisms and evolutionary events are to be evaluated. A decision must also be made as to what direction of change represents improvement. These decisions are in part subjective, but they should not be arbitrary; biological knowledge should guide them. A standard is valid if it enables one to say enlightening things about the evolution of life. The choice of appropriate standards depends on how much relevant biological information is available, and whether the evaluation can be made.

There is no standard according to which *uniform* progress can be said to have occurred in the evolution of life. Changes of direction, slackening, or reversals have occurred in all evolutionary lineages, no matter what feature is considered (Simpson, 1949, 1953). The question, then, is whether *net* progress has occurred in the evolution of life, and in what sense.

The next question is whether there is any criterion by which net progress can be said to be a *general* feature of evolution, or whether identifiable progress applies only to particular lineages or during particular periods. One conceivable standard of progress is the increase in the amount of genetic information stored in organisms. DNA contains the information that, in interaction with the environment, directs the development and behavior of organisms. Net general progress can be said to have occurred if organisms living at a later time have, on the average, greater content of genetic information than their ancestors. One difficulty, insuperable at least for the present, is that there is no way in which the genetic information contained in the whole DNA of an organism can be measured. The amount of information is not simply related to the amount of DNA, since we know that many DNA sequences are repetitive. There are ways to measure, at least approximately, the "complexity" of DNA in a given organism, i.e. the total length of different DNA sequences (see Chapter 3). But a large fraction of the DNA does not encode information in the form of codon triplets, and much DNA may have nonsense messages.

Another possible criterion of general progress is the expansion of life. According to Simpson (1949) there is in evolution "a tendency for life to expand, to fill in all the available spaces in the livable environments, including those created by the process of that expansion itself." In principle, the expansion of life can be measured by at least four different though related criteria: (1) the number of *kinds* of organisms, i.e., the number of species; (2) the number of individuals; (3) the bulk of living matter (biomass); and (4) the total rate of energy flow. Increases in the number of individuals or their total bulk may not be an unmixed blessing, as is the case now for mankind, but they can be a measure of biological progress. Net progress might be a general feature of the evolution of life by any one of these four standards of progress.

Living organisms have a tendency to multiply exponentially ad infinitum without intrinsic constraints. This is simply a consequence of the process of

biological reproduction: each organism is capable of producing, on the average, more than one progeny throughout its lifetime. However, the tendency of life to expand encounters extrinsic constraints of various sorts. Once a certain species has come to exist, its expansion is limited at least in two ways. First, the supply of resources accessible to organisms is limited. Second, favorable conditions for multiplication do not always occur. Predators and competitors, together with climatic conditions, are the main factors interfering with the multiplication of organisms. Drastic and gradual changes in the weather, as well as geological events, at times lead to vast decreases in the size of some populations and even of the whole of life. Because of these constraints the tendency of life to expand has not always succeeded. Nevertheless, it appears certain that life has, on the average, expanded throughout most of the evolutionary process.

The number of extant biological species is almost certainly greater than two million, and may be as large as six million. Although it is difficult to estimate the number of plant species that existed in the past (since well-preserved plant fossils are rare), the number of animal species can be roughly estimated. Approximately 150,000 animal species live in the seas today, probably a larger number than the total number of animal species that existed in the Cambrian (600 million years ago), when no animal or plant species lived on land. The number of land animal species is probably at a maximum now, even if we exclude the insects. Insects make up about three-quarters of all animal species, and about half of all species, including plants. Insects did not appear until the Carboniferous, some 350 million years ago. More species of insects exist now than at most, probably all, times in the past. On the whole, it appears that the number of living species is probably greater in recent times than it ever was before, and that at least on the average a gradual increase in the number of species has characterized the evolution of life (chapter 13).

The expansion of the number of species operates as a positive feedback process. The greater the number of species, the greater the number of environments that are created for new species to exploit. Once plants came into existence it was possible for animals to exist; and animals sustain large numbers of species of other animals, as well as parasites and symbionts.

The number of individuals living on earth today is not known with any reasonable approximation, even if we exclude microorganisms. The median number of individuals for insect species is estimated to be around 2×10^8 , but some species may consist of more than 10^{16} individuals—and there are more than one million insect species! The number of individuals of *Euphausia superba*, the small krill eaten by some whales, may be greater than 10^{20} . There can be little doubt that the number of individual animals and plants and their total biomass are greater now than they were in the Cambrian. Very likely they are also greater than they have been at most times since the beginning of life. Even if we include microorganisms, it is probable that the number of living individuals has increased, on the average, throughout the evolution of life. The total bulk of living matter has also probably increased, on the average, since larger organisms have generally appeared later in time.

The rate of energy flow has probably increased in the living world faster than the total biomass. One effect of living things is to retard the dissipation of energy that covers the earth's surface. Green plants store radiant energy from the sun that would otherwise be converted into heat. Animals, although they dissipate energy individually, since they have higher rates of catabolism than of anabolism, provide a new path for the flow of energy; their interactions with plants increase the total rate of energy flow through living matter.

PARTICULAR FORMS OF EVOLUTIONARY PROGRESS

As stated above, the concept of progress is based on an evaluation of better versus worse relative to some criterion. Particular forms of evolutionary progress, which obtain only in certain evolutionary sequences and usually for only a limited span of time, may be identified using a variety of criteria. Simpson (1949) has examined several criteria, including dominance, invasion of new environments, replacement, improvement in adaptation, adaptability and possibility of further progress, increased specialization, control over the environment, increased structural complexity, increase in general energy or level of vital processes, and increase in the range and variety of adjustments to the environment. For each of these criteria, Simpson has shown in what evolutionary sequences and for how long progress has taken place. Stebbins (1969) has proposed a law of "conservation of organization" that accounts for evolutionary progress as a small bias towards increased complexity of organization. Other criteria of progress have been examined by Huxley (1942, 1953), Rensch (1947), Williams (1966), and Ayala (1974b).

No single criterion is a priori the best. Any criterion that furthers understanding of the evolutionary process is valid. Different criteria illuminate different features of evolution. As an example, let us consider the ability of organisms to obtain and process information about the environment (Ayala, 1974b). This ability is of evolutionary interest because it contributes to the biological success of organisms, particularly animals. It is particularly relevant to the evolution of man, since, among the differences that mark off man from all other animals perhaps the most fundamental is man's greatly developed ability to perceive the environment, and to react flexibly to it. Whereas all organisms become genetically adapted to their environments, man is also able to create environments that suit his genetic constitution.

Increased ability to gather and process information about the environment is sometimes expressed as evolution towards "independence from the environment." This latter expression is misleading. No organism can be truly independent of the environment. Allegedly, the evolutionary sequence fish \rightarrow amphibian \rightarrow reptile is an example of evolution towards independence from the environment. Reptiles, birds, and mammals are indeed independent of *water* as a living medium, but their lives depend on the conditions of the land.

They have not become independent of the environment, but rather have exchanged dependence on one environment for dependence on another.

"Control over the environment" has been linked to the ability to gather and use information about the state of the environment. However, in the strictest sense, control over the environment is exercised only by the human species.

All organisms *interact* with the environment, but not all can *control* it. Nest-building among birds, the construction of beehives, or the building of dams by beavers do not represent control over the environment except in a trivial sense. The ability to control the environment started with the australopithecines, the first group of organisms that can be called human. They are considered to be men precisely because they were able to produce devices such as rudimentary pebble and bone tools to manipulate the environment. The ability to obtain and process information about the conditions of the environment enables organisms to avoid unsuitable environments and to seek suitable ones. It has developed in many organisms because it is a useful adaptation.

All organisms interact selectively with the environment. The cell membrane of a bacterium permits certain molecules but not others to enter the cell; selective molecular exchange occurs also in the inorganic world. But this can hardly be called a form of information processing. Certain bacteria when placed on an agar plate move about in a zig-zag pattern that is almost certainly random. The most rudimentary ability to gather and process information about the environment can be found in certain single-celled eukaryotes. A *Paramecium* swims in a sinusoid path, ingesting the bacteria that it encounters as it swims. Whenever it meets unfavorable conditions, like unsuitable acidity or salinity in the water, the *Paramecium* checks its advance, turns, and starts in a new direction. Its reaction is purely negative. The *Paramecium* apparently does not seek food or a favorable environment, but simply avoids unsuitable conditions.

A somewhat greater ability to process information about the environment occurs in the single-celled *Euglena*. This organism has a light-sensitive spot by which it can orient itself in the direction from which the light originates. *Euglena*'s motions not only avoid unsuitable environments but actively seek suitable ones. An amoeba represents further progress in the same direction; it reacts to light by moving away from it, and also actively pursues food particles.

An increase in the ability to gather and process information about the environment is not a general characteristic of the evolution of life. Progress in this respect occurred in certain evolutionary lines but not in others. Today's bacteria are not more progressive by this criterion than their ancestors of one billion years ago. In many evolutionary sequences some very limited progress took place in the early stages, without further progress through the rest of their history. By this criterion, animals are in general more advanced than plants; vertebrates are more advanced than invertebrates; mammals are more advanced than reptiles, which are more advanced than fish. The most advanced organism by this criterion is man.

The ability to obtain and process information about the environment has progressed little in the plant kingdom. Plants generally react to light and to

gravity. Geotropism is positive in the root, but negative in the stem. Plants also grow toward light; the parts of some plants, such as the sunflower, follow the daily course of the sun. Plants are also hydrotropic, that is, the roots tend to grow toward water. The response to gravity, water, and light is basically due to differential growth rates; a greater elongation of cells takes place on one side of the stem or root than on the other side. Some plants react also to tactile stimuli; their tendrils twine around whatever they touch. *Mimosa* and carnivorous plants, like the Venus flytrap (*Dionaea*), have leaves that close rapidly when touched.

In multicellular animals the ability to obtain and process information about the environment is mediated by the nervous system. All major groups of animals, except the sponges, have nervous systems. The simplest nervous system among living animals occurs in coelenterates, which include hydra, corals, and jellyfishes. Each tentacle of a jellyfish reacts individually, and only if it is directly stimulated; there is no coordination of the information received by different parts of the animal. Moreover, jellyfishes are unable to learn from experience. A limited form of coordinated behavior occurs in echinoderms, which include starfishes and sea urchins. Whereas coelenterates possess only an undifferentiated nerve net, echinoderms possess a nerve ring and radial nerve cords in addition to a nerve net. When the appropriate stimulus is encountered, a starfish reacts with direct and unified actions of the whole body.

The most primitive form of a brain occurs in such organisms as planarian flatworms, which also have numerous sensory cells and eyes without lenses. The information gathered by these sensory cells and organs is processed and coordinated by the central nervous system and the rudimentary brain. A planarian worm is capable of some variability of responses and some simple learning—similar stimuli do not always produce similar responses. In the ability to gather and process information about the environment, planarian flatworms have progressed further than starfishes, and starfishes have progressed further than sea anemones and other coelenterates. But none of these organisms has progressed very far by this criterion. Among invertebrates, the most progressive groups of organisms are arthropods, but vertebrates have progressed much further than any invertebrates.

Arthropods, which include the insects, have complex forms of behavior. Precise visual, chemical, and acoustic signals are obtained and processed by many arthropods, particularly in their search for food and their selection of mates. Vertebrates are generally able to obtain and process much more complicated signals and to produce a much greater variety of responses than the arthropods. The vertebrate brain has an enormous number of neurons with an extremely complex arrangement. Among vertebrates, progress in the ability to deal with environmental information is correlated with development of the neopallium. The neopallium is involved in the association and coordination of all kinds of impulses from all receptors and brain centers. It first appeared in reptiles; in mammals it has expanded to become the cerebral cortex, which covers most of the cerebral hemispheres. The larger brain of vertebrates permits them

also to have a large number of neurons involved in information storage or memory.

The ability to perceive the environment, and to integrate, coordinate, and react flexibly to what is perceived, has developed in its most advanced state in man. This incomparable advancement is perhaps the most fundamental characteristic that marks off *Homo sapiens* from all other animals. Symbolic language, complex social organization, control over the environment, the ability to envisage future states and work toward them, values and ethics are all developments made possible by man's greatly developed capacity to obtain and organize information about the state of the environment.

The ability to obtain information about the environment and react to it is useful to organisms as an adaptation. It is an acceptable criterion of progress because it illuminates certain features of the evolution of life. However, it is not necessarily better or worse than other criteria of progress. Other criteria may help to discern other features of evolution, and thus be worth examining. Needless to say, organisms are more or less progressive depending on what criterion of progress is used. By certain criteria, flowering plants are more progressive than many animals.

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