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TELEOLOGICAL EXPLANATIONS IN EVOLUTIONARY BIOLOGY*

FRANCISCO J. AYALA†

The Rockefeller University

The ultimate source of explanation in biology is the principle of natural selection. Natural selection means differential reproduction of genes and gene combinations. It is a mechanistic process which accounts for the existence in living organisms of end-directed structures and processes. It is argued that teleological explanations in biology are not only acceptable but indeed indispensable. There are at least three categories of biological phenomena where teleological explanations are appropriate.

Early in the nineteenth century, William Paley in his *Natural Theology* [6] pointed out the obvious functional design of the human eye. For Paley, it was absurd to suppose that the human eye, by mere chance, "should have consisted, first, of a series of transparent lenses (very different, by and by, even in their substance from the opaque materials of which the rest of the body is, in general at least, composed; and with which the whole of its surface, this single portion of it excepted, is covered) secondly of a black cloth or canvas (the only membrane of the body which is black) 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, namely at the concourse of the refracted rays: thirdly, of a large nerve communicating between this membrane and the brain."

The adaptive character of the structures, organs, and behavior of plants and animals is an incontrovertible fact. The vertebrate eye, with its complicated anatomy of highly specialized tissues, is obviously adapted for vision; the hand of man is made for grasping, and the bird's wing for flying. Organisms show themselves to be adapted to live where they live and the way they live. To explain the phenomenon of the adaptation of life is one of the main objectives of natural science and of natural philosophy.

Before 1859, the year Darwin published *The Origin of the Species*, the adaptation of organisms was either accepted as a fact without any explanation of its origin, or more frequently, it was attributed to the omniscient design of the Creator. God

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had given wings to birds so that they might fly, and had provided man with kidneys to regulate the composition of his blood. For Paley, living nature is a manifestation of the existence and wisdom of the Creator.

In *The Origin of the Species* Darwin accumulated an impressive number of observations supporting the evolutionary origin of living organisms. Moreover, and perhaps most importantly, he provided a causal explanation of evolutionary processes—the theory of natural selection. The principle of natural selection, as Darwin saw it, makes it possible to give a natural explanation of the adaptation of organisms to their environment. With *The Origin of the Species* the study of adaptation, the problem of design in nature came fully into the domain of natural science.

Darwin recognized, and accepted without reservation, that organisms are adapted to their environments, and that their parts are adapted to the functions they serve. Fish are adapted to live in water, the hand of man is made for grasping, and the eye is made to see. Darwin accepted the facts of adaptation, and then provided a natural explanation for the facts. One of his greatest accomplishments was to bring the teleological aspects of nature into the realm of science. He substituted a scientific teleology for a theological one. The teleology of nature could now be explained, at least in principle, as the result of natural laws manifested in natural processes, without recourse to an external Creator or to spiritual or non-material forces. At that point biology came into maturity as a science.

1. Hereditary Variability. About the time Darwin published *The Origin of the Species*, Gregor Mendel was performing in his Augustinian monastery in Brünn (Austria) experiments with peas. The results of such experiments, published in 1866, provided the fundamental principles of heredity. The Mendelian principles remained generally unknown until 1900, when they were independently and nearly simultaneously rediscovered by three biologists. The principles of heredity were extended during the nineteen hundreds to a considerable number of species of plants and animals. A whole body of knowledge concerning heredity blossomed. The biological or synthetic theory of evolution as we know it today is a synthesis of Darwin's principle of natural selection and genetic knowledge. It is in essence a two-factor theory. Mutation is the ultimate source of hereditary variability; natural selection is the directional factor that results in organized complexes of hereditary material and in adaptation.

Heredity is the transmission, from parent to offspring, of the information that directs the development of the fertilized egg to its adult stage and controls the living activity of the organism. The hereditary information is carried in a chemical substance known as deoxyribonucleic acid (DNA). Molecules of DNA exist in discrete but complexly interacting units called genes. The genes are organized in chromosomes, which exist in sets. One or more sets of chromosomes—most frequently two in higher organisms—exist in the fertilized egg cell (zygote) from which the adult individual develops. In sexually reproducing organisms, one of the two sets of chromosomes is inherited from each parent via the sex cells.

The genes of a population are shuffled and combined in different ways every generation. In the process of genetic recombination during the formation of the sex cells (gametes), the two sets of hereditary material received by each individual from its parents are combined in different ways. The sex cells carry a single set of genes each, representing combinations in different proportions of the two sets possessed by the individual. Fertilization brings together two sex cells in the zygote from which the mature individual develops. Gametic recombination and fertilization create new combinations of genes and chromosomes every generation. These new sets of information are tested against the environment where the individual lives. Thus, genetic experimentation, so to speak, occurs in all natural populations every generation.

The sum total of genetic information in a population of sexually interbreeding individuals can be thought of as the "gene pool" of the population. The gene pool of a population is characterized by the totality of genes in the population, their combinations, and the relative frequencies of both among the individuals of the population. Evolution consists in changes in the gene pool of a population. Recombination produces new combinations of genes but by itself it does not change the gene pool. There are four known processes which can do so—mutation, random fluctuation of genetic frequencies known as "sampling errors," migration of individuals in and out of the population, and natural selection. The first three of these processes are essentially random. Although the relative importance for evolution of random genetic sampling has been questioned, it must have played a role in certain instances—in particular, when a new environment is colonized by a small number of individuals and when populations are reduced to few individuals in their usual environments by drastic environmental stresses. For our present purpose we need consider neither random sampling nor migration.

Genes are fairly stable entities but not completely so. Occasionally, mutations occur. The frequencies of mutations vary for different genes and for different organisms. It is probably fair to estimate the frequency of a majority of mutations in higher organisms between one in ten thousand, and one in a million per gene per generation. Mutations in a broad sense include not only changes in the hereditary information of single genes, but also changes in the arrangement and distribution of genes in chromosomes, and in the number of chromosomes and sets of chromosomes. Mutations have sometimes been described as "errors" in the replication of the hereditary material. Such a description may be misleading, since the alleged "errors" are the ultimate source of evolutionary change. Mutation provides the raw materials of evolution, i.e., mutation is the ultimate source of genetic variability.

Mutations are random changes of the hereditary material. They are random in the sense that they occur independently of the needs of the organism in which they happen. Most new mutations are in fact harmful to the organism. If mutation were the only factor promoting genetic change in a population, it would result in an array of freaks and finally in total disorder. The genetic information stored in the DNA of the population would ultimately disintegrate. However, there is a directive process that counteracts mutation and results in order and adaptation—natural selection. Natural selection is able to produce and to preserve the stored information transmitted by the hereditary process.

2. Natural Selection. Natural selection was Darwin's major contribution to the explanation of the evolution of life. For Darwin, natural selection was primarily differential survival. The modern understanding of the principle of natural selection derives from Darwin's concept, although it is formulated in a somewhat different way. Natural selection is understood today in genetic and statistical terms as differential reproduction. Differential reproduction is a compound process, the elements of which are differential survival, differential mating success, and differential fecundity. Natural selection implies that some genes and genetic combinations are transmitted to the following generation on the average more frequently than their alternates. Such genetic units will become more common in every subsequent generation and their alternates less common. Natural selection is a statistical bias in the relative rate of reproduction of alternative genetic units.

Genes and gene combinations are the entities subject to natural selection. Genes do not exist by themselves but in organisms. Genes increase or decrease in relative frequency depending on their average effects in the organisms which carry them. The process of natural selection can be also predicated of individual organisms—and in a less precise sense, of populations of organisms as well—in the sense that some organisms leave more progeny than others. Individual organisms are not lasting, however. Genes persist in the progenies of the organisms which carry them.

Natural selection is a process determined by the environment. The selective advantage of certain genetic variants must be understood in relation to the environment where the population lives. A genetic unit which is favorably selected in one environment may be selected again in a different one. A trivial example is that wings—and therefore the genes responsible for the development of wings—may increase the reproductive success of a bird, but will probably be of no advantage, and presumably will be disadvantageous, to a deep sea fish. To speak of the environment of a population is, however, an oversimplification. The environment is highly heterogeneous both in the dimension of time and in the dimension of space. The environment of a population includes all the physical and biotic elements affecting the individuals of the population in the whole range of their geographic distribution. Small or large differences in climate, food resources, competitors, etc. exist within the spatial distribution of any population. Moreover, no environment remains constant in time. It changes from morning to night, from one season to another, from one year to the next. The reproductive fitness of a genetic variant is then the average result of the effects of that genetic unit in all the environments where the population lives. It may change from one to another generation as the biotic and physical environments of the population change. Environmental diversity and environmental change are responsible for the continuous evolution of natural populations. If life existed in only a single uniform and constant environment, evolution might conceivably have produced a genotype optimally fitted to that environment with no further change. An absolutely uniform and constant environment is an abstraction; it does not exist in nature.

Genes act in concert with other genes. The average effect of a gene in a population may vary depending on the other genes and genetic combinations existing in the population. The reproductive fitness of a genetic unit must be understood as the average effect it has on all the individuals carrying it. That average effect is likely to change as the genetic composition of the population changes from generation to generation.

The numbers of alternative genetic variants existing in a natural population is a debated question, but they vary widely for different kinds of organisms. If two variants, A_1 and A_2, of a gene exist in a population, there are in diploid organisms three possible different genotypes with respect to that gene, namely A_1A_1, A_1A_2, and A_2A_2. If the number of genes existing in two alternative forms is n, 3^n different genotypes are possible. That number becomes very large as n increases. For instance, if n equals 10, the number of possible different genotypes is nearly one hundred thousand; if n equals 20, there are more than one billion potential genotypes; and if n equals 30, there are nearly one million billion possible different genotypes. The number of possible genetic combinations in a population of diploid organisms, even in those organisms carrying relatively few alternative genetic units, is enormous. Most of them will never occur because the number of individuals in the population is much less than the number of possible different genetic combinations. Natural selection operates exclusively on the genetic combinations actually realized in the population.

If a gene or genetic combination increases on the average the reproductive success of the individuals carrying it, its frequency in the population will increase gradually. It has been shown both theoretically and experimentally that a newly arisen genetic unit will swamp the population in relatively few generations, even if the advantage over its alternative forms is moderately small.

Natural selection has been compared to a sieve which retains the rarely arising useful and lets go the more frequently arising harmful mutants. Natural selection acts in that way, but it is much more than a purely negative process, for it is able to generate novelty by increasing the probability of otherwise extremely improbable genetic combinations. Natural selection is creative in a way. It does not "create" the genetic entities upon which it operates, but it produces adaptive genetic combinations which would not have existed otherwise. The creative role of natural selection must not be understood in the sense of the "absolute" creation that traditional Christian theology predicates of the Divine act by which the universe was brought into being *ex nihilo*. Natural selection may be compared rather to a painter which creates a picture by mixing and distributing pigments in various ways over the canvas. The canvas and the pigments are not created by the artist but the painting is. It is conceivable that a random combination of the pigments might result in the orderly whole which is the final work of art. Some modern paintings look very much like a random association of materials, to be sure. But the probability of, say, Leonardo's *Mona Lisa* resulting from a random combination of pigments is nearly infinitely small. In the same way, the combination of genetic units which carries the hereditary information responsible for the formation of the vertebrate eye could have never been produced by a random process like mutation. Not even if we allow for the three billion years plus during which life has existed on earth. The complicated anatomy of the eye like the exact functioning of the kidney are the result of a nonrandom process—natural selection.

How natural selection, a purely material process, can generate novelty in the form of accumulated hereditary information may be illustrated by the following example. Some strains of the colon bacterium, *Escherichia coli*, to be able to reproduce in a culture medium, require that a certain substance, the amino acid histidine, be provided in the medium. When a few such bacteria are added to a cubic centimeter of liquid culture medium, they multiply rapidly and produce between two and three billion bacteria in a few hours. Spontaneous mutations to streptomycin resistance occur in normal, i.e., sensitive, bacteria at rates of the order of one in one hundred million (1×10^{-8}) cells. In our bacterial culture we expect between twenty and thirty bacteria to be resistant to streptomycin due to spontaneous mutation. If a proper concentration of the antibiotic is added to the culture, only the resistant cells survive. The twenty plus surviving bacteria will start reproducing, however, and allowing a few hours for the necessary number of cell divisions, several billion bacteria are produced, all resistant to streptomycin. Among cells requiring histidine as a growth factor, spontaneous mutants able to reproduce in the absence of histidine arise at rates of about four in one hundred million (4×10^{-8}) bacteria. The streptomycin resistant cells may now be transferred to an agar-medium plate with streptomycin but with no histidine. Most of them will not be able to reproduce, but about a hundred will start dividing and form colonies until the available medium is saturated. Natural selection has produced in two steps bacterial cells resistant to streptomycin and not requiring histidine for growth. The probability of the two mutational events happening in the same bacterium is of about four in ten million billion ($1 \times 10^{-8} \times 4 \times 10^{-8} = 4 \times 10^{-16}$) cells. An event of such low probability is unlikely to occur even in a large laboratory culture of bacterial cells. With natural selection cells having both properties are the common result.

Natural selection produces highly improbable combinations of genes by proceeding step-wise. The human eye did not appear suddenly in all its present perfection. It requires the appropriate integration of many genetic units, and thus it could not have resulted from a random process. Our ancestors have had for at least the last half billion years some kind of organs sensitive to light. Perception of light, and later vision, were important for their survival and reproductive success. Natural selection accordingly favored genes and gene combinations increasing the functional efficiency of the eye. Such genetic units gradually accumulated eventually leading to the highly complex and efficient human eye.

Natural selection can account for the rise and spread of genetic constitutions, and therefore of types of organisms, that would never have existed under the uncontrolled action of random mutation and recombination of the hereditary materials. In this sense, although it does not create the raw materials, that is, the genes, selection is definitely creative.

3. Natural Selection and Adaptation. Evolutionary changes in the gene pool of a population frequently occur in the direction of increased adaptation. The organisms likely to leave more descendants are those whose variations are most advantageous as adaptations to the environment. Natural selection, however, occurs in reference to the environment where the population presently lives. Evolutionary adaptations are not anticipatory of the future. The environmental challenges that a population may meet in the future cannot affect in any way the reproductive fitness of the organisms in the present environment. If the population is unable to react adaptively to a new environmental challenge, the result may be extinction. The fossil record bears witness that a majority of the species living in the past became eventually extinct without issue.

The evolutionary course of a population is conditioned by the past history of the population. The genetic configuration of a population is determined by the environments where the population has lived in the past. Those genes and genetic combinations were favorably selected which increased the reproductive fitness of their carriers in the environments where the population lived. The present configuration of its gene pool sets limits to the evolutionary potentialities of a population. The only genes that may be favored by natural selection are those actually present in the population. An obvious example is the colonization of the land by organisms. The colonization of the land by plants occurred during the Silurian geological period, and by animals during the Devonian period. New and diversified environments were open to the evolution of life. New forms of plants evolved, but the basic adaptations to plant life remained in all of them. These adaptations had occurred in the past and set limits to the evolutionary potentialities of their descendants. The considerable diversification of anatomic and physiological characteristics that occurred in animals were not open to plants and vice versa.

Natural selection is thoroughly opportunistic. A new environmental challenge is responded to by appropriate adaptations in the population or results in its extinction. Adaptation to the same environment may occur in a variety of different ways. An example may be taken from the adaptations of plant life to desert climate (Dobzhansky [1]). The fundamental adaptation is to the condition of dryness which carries the danger of desiccation. During a major part of the year, sometimes for several years in succession, there is no rain. Plants have accomplished the urgent necessity of saving water in different ways. Cacti have transformed their leaves into spines, having made their stems into barrels containing a reserve of water. Photosynthesis is performed in the surface of the stem instead of in the leaves. Other plants have no leaves during the dry season, but after it rains they burst into leaves and flowers and produce seeds. A third type of adaptation exists. Ephemeral plants germinate from seeds, grow, flower, and produce seeds—all within the space of the few weeks while water is available. The rest of the year the seeds lie quiescent in the soil.

Natural selection can explain the facts of the adaptation of living organisms to their environments and to their ways of life. The account of natural selection given here is also consistent with the history of life as obtained from the fossil record and with the diversity of plants and animals existing today (Simpson [10]). The fossil record shows that the evolution of life occurred in a haphazard fashion. The phenomena of radiation, expansion, relaying of one form by another, diversification, occasional trends and extinction shown by the fossil record, are best explained by the synthetic theory of evolution. They are not compatible with a preordained plan whether imprinted from without by an omniscient Creator, or the result of the orthogenetic activity of any immanent nonmaterial force, be it called "élan vital," "radial energy" or "vital force."

4. Teleological Explanations in Biology. Nagel ([5], p. 24) has written that "the notion of teleology is neither hopelessly archaic nor necessarily a mark of superstition." The concept of teleology is in general disrepute in modern science. The main reason for this discredit is that the notion of teleology is equated with the belief that future events are active agents in their own realization. Such belief, however, is not necessarily implied in the concept of teleology. Teleological explanations are appropriate in certain areas of natural science. In particular, I shall attempt to show that teleological explanations are appropriate and indispensable in biology, and that they are fully compatible with causal accounts, although they cannot be reduced to nonteleological explanations without loss of explanatory content.

The notion of teleology arose most probably as a result of man's reflection on the circumstances connected with his own voluntary actions. The anticipated outcome of his actions can be envisaged by man as the goal or purpose towards which he directs his activity. Human actions can be said to be purposeful when they are intentionally directed towards the obtention of a goal.

The plan or purpose of the human agent may frequently be inferred from the actions he performs. That is, his actions can be seen to be purposefully or teleologically ordained towards the obtention of the goal. In this sense the concept of teleology can be extended, and has been extended, to describe actions, objects or processes which exhibit an orientation towards a certain goal or end-state. No requirement is necessarily implied that the objects or processes tend consciously towards their specific goals, nor that there is any external agent directing the process or the object towards its end-state or goal. In this generic sense, teleological explanations are those explanations where the presence of an object or a process in a system is explained by exhibiting its connection with a specific state or property of the system to whose existence or maintenance the object or process contributes. Teleological explanations require that the object or process contribute to the existence of a certain state or property of the system. Moreover, they imply that such contribution is the explanatory reason for the presence of the process or object in the system. It is appropriate to give a teleological explanation of the operation of the kidney in regulating the concentration of salt in the blood, or of the structure of the hand obviously adapted for grasping. But it makes no sense to explain teleologically the falling of a stone, or a chemical reaction.

There are at least three categories of biological phenomena where teleological explanations are appropriate, although the distinction between the categories need not always be clearly defined. These three classes of teleological phenomena are established according to the mode of relationship between the object or process and the end-state or property that accounts for its presence. Other classifications of teleological phenomena are possible according to other principles of distinction. A second classification will be suggested below.

(1) When the end-state or goal is consciously anticipated by the agent. This is purposeful activity and it occurs in man and probably in other animals. I am acting teleologically when I pick up a pencil and paper in order to express in writing my ideas about teleology. A deer running away from a mountain lion, or a bird building its nest, has at least the appearance of purposeful behavior.

(2) In connection with self-regulating or teleonomic systems, when there exists a mechanism that enables the system to reach or to maintain a specific property in spite of environmental fluctuations. The regulation of body temperature in mammals is of this kind. In general the homeostatic reactions of organisms belong to this category of teleological phenomena. Two types of homeostasis are usually distinguished by biologists—physiological and developmental homeostasis, although intermediate situations may exist. Physiological homeostatic reactions enable the organism to maintain certain physiological steady states in spite of environmental shocks. The regulation of the composition of the blood by the kidneys, or the hypertrophy of a structure like muscle due to strenuous use, are examples of this type of homeostasis. Developmental homeostasis refers to the regulation of the different paths that an organism may follow in its progression from zygote to adult.

Self-regulating systems or servo-mechanisms built by man are teleological in this second sense. The simplest example of such servo-mechanisms is a thermostat unit that maintains a specified room temperature by turning on and off the source of heat. Self-regulating mechanisms of this kind, living or man-made, are controlled by a feed-back system of information.

(3) In reference to structures anatomically and physiologically designed to perform a certain function. The hand of man is made for grasping, and his eye for vision. Tools and certain types of machines made by man are teleological in this sense. A watch for instance, is made to tell time, and a faucet to draw water. The distinction between this and the previous category of teleological systems is sometimes blurred. Thus the human eye is able to regulate itself within a certain range to the conditions of brightness and distance so as to perform its function more effectively.

Teleological mechanisms in living organisms are biological adaptations. They have arisen as a result of the process of natural selection. The adaptations of organisms—whether organs, homeostatic mechanisms, or patterns of behavior—are explained teleologically in that their existence is accounted for in terms of their contribution to the reproductive fitness of the population. As explained above, a feature of an organism that increases its reproductive fitness will be selectively favored. Given enough time it will extend to all the members of the population.

Patterns of behavior, such as the nesting habits of birds or the web-spinning of spiders, have developed because they favored the reproductive success of their possessors in the environments where the population lived. Similarly, natural selection can account for the presence of homeostatic mechanisms. Some processes can be operative only within a certain range of conditions. If the conditions are affected by the environment, natural selection will favor self-regulating mechanisms that maintain the system within the function range. In man death results if the body temperature is allowed to rise or fall by more than a few degrees above or below normal. Body temperature is regulated by dissipating heat in warm environments through perspiration and dilatation of the blood vessels in the skin. In cool weather the loss of heat is minimized and additional heat is produced by increased activity and shivering. Finally, the adaptation of an organ or structure to its function is explained teleologically in that its presence is accounted for in terms of the contribution it makes to reproductive success in the population. The vertebrate eye arose because genetic mutations responsible for its development arose and increased the reproductive fitness of their possessors.

There are two levels of teleology in organisms. There usually exists a specific and proximate end for every feature of an animal or plant. The existence of the feature is explained in terms of the function or end-state it serves. But there is also an ultimate goal to which all features contribute or have contributed in the past—reproductive success. The ultimate end to which all other functions and ends contribute is increased reproductive efficiency. In this sense the ultimate source of explanation in biology is the principle of natural selection.

Natural selection can be said to be a teleological process in two ways. Firstly, natural selection is a mechanistic end-directed process which results in increased reproductive efficiency. Reproductive fitness can, then, be said to be the end result or goal of natural selection. Secondly, natural selection is teleological in the sense that it produces and maintains end-directed organs and processes, when the function or end-state served by the organ or process contributes to the reproductive fitness of the organisms.

However, the process of natural selection is not at all teleological in a different sense. Natural selection does not tend in any way towards the production of specific kinds of organisms or towards organisms having certain specific properties. The over-all process of evolution cannot be said to be teleological in the sense of proceeding towards certain specified goals, preconceived or not. The only nonrandom process in evolution is natural selection understood as differential reproduction. Natural selection is a purely mechanistic process and it is opportunistic in the sense discussed above. The final result of natural selection for any species may be extinction, as shown by the fossil record, if the species fails to cope with environmental change.

The presence of organs, processes and patterns of behavior can be explained teleologically by exhibiting their contribution to the reproductive fitness of the organisms in which they occur. This need not imply that reproductive fitness is a consciously intended goal. Such intent must in fact be denied, except in the case of the voluntary behavior of man and perhaps of some animals. In teleological explanation the end-state is not to be understood as the efficient cause of the object or process that it explains. The end-state is causally—and in general temporally also—posterior.

Mayr (cf. [3], p. 42) has pointed out that the term "teleology" has been applied to two different sets of phenomena. "On 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." The behavioral activities or developmental processes of an individual are controlled by the program of information encoded in the DNA inherited by the organism from its parents. The decoding of the DNA programs of information can properly be said to be a teleological—or as Mayr prefers to call it, teleonomic—process. Teleology has also been applied to the evolution of organisms, that is, to the production and perfection of DNA codes of information. The overall process of evolution cannot be said to be teleological in the sense of directed towards the production of specified DNA codes of information, i.e., organisms. But it is my contention that it can be said to be teleological in the sense of being directed towards the production of DNA codes of information which improve the reproductive fitness of a population in the environments where it lives. The process of evolution can also be said to be teleological in that it has the potentiality of producing end-directed DNA codes of information, and has in fact resulted in teleologically oriented structures, patterns of behavior, and self-regulating mechanisms.

Three categories of teleological systems have been distinguished above, according to the nature of the relationship existing between the object or process and its end-state or goal. Another classification of teleology may be suggested in reference to the agency giving origin to the teleological mechanism. The end-directedness of living organisms and their features may be said to be "internal" teleology, while that of man-made tools and servo-mechanisms may be called "external" teleology. It might also be appropriate to refer to these two kinds of teleology as "natural" and "artificial," but the other two terms, "internal" and "external," have already been used (cf. [2], p. 193). Internal teleological systems are accounted for by natural selection which is a strictly mechanistic process. External teleological mechanism are products of the human mind, or more generally, are the result of purposeful activity consciously intending specified ends.

Living organisms, then, exhibit internal teleology, but do not in general possess external teleology. The overall process of evolution is not teleological in the external sense. Evolution can be explained without recourse to a Creator or planning agent external to the organisms themselves. There is no evidence either of any vital force or immanent energy directing the process towards production of specified kinds of organisms. The evidence of the fossil record is against any necessitating force, external or immanent, leading the process towards specified goals.

5. Teleology and Causality. Nagel ([5], p. 24, 25) has convincingly argued that "teleological explanations are fully compatible with causal accounts. . . . Indeed, a teleological explanation can always be transformed into a causal one." Teleological explanations can be reformulated, without loss of explicit content, to take the form of nonteleological ones. A typical teleological statement in biology is the following, "The function of gills in fishes is respiration, that is the exchange of oxygen and carbon dioxide between the blood and the external water." Statements of this kind account for the presence of a certain feature A (gills) in every member of a class of systems S (fish) which possess a certain organization C (the characteristic anatomy and physiology of fishes). It does so by declaring that when S is placed in a certain environment E (water with dissolved oxygen) it will perform a function F (respiration) only if S (fish) has A (gills). The teleological statement, says Nagel, is a telescoped argument the content of which can be unravelled approximately as follows: When supplied with water containing dissolved oxygen, fish respire; if fish have no gills, they do not respire even if supplied with water containing dissolved oxygen; therefore fish have gills. More generally, a statement of the form "The function of A in a system S with organization C is to enable S in environment E to engage in process F" can be formulated more explicitly; "Every system S with organization C and in environment E engage in function F; if S with organization C and in environment E does not have A, then S cannot engage in F; hence, S must have A." The difference between a teleological explanation and a nonteleological one is, then, one of emphasis rather than of asserted content. A teleological explanation directs our attention to "the *consequences* for a given system of a constituent part or process." The equivalent nonteleological formulation focuses attention on "some of the *conditions* . . . under which the system persists in its characteristic organization and activities" ([4], p. 405).

Although a teleological explanation can be reformulated in a nonteleological one, the teleological explanation connotes something more than the equivalent nonteleological one. A teleological explanation imples that the system under consideration is directively organized. For that reason, teleological explanations are appropriate in biology and in the domain of cybernetics but make no sense when used in the physical sciences to describe phenomena like the fall of a stone. Moreover, and most importantly, teleological explanations imply that the end result is the explanatory reason for the *existence* of the object or process which serves or leads to it. A teleological account of the gills of fish implies that gills came to existence precisely because they serve for respiration.

If the above reasoning is correct, the use of teleological explanations in biology is not only acceptable but indeed indispensable. Biological organisms are systems directively organized towards reproductive fitness. Parts of organisms are directively organized towards specific ends that, generally, contribute to the ultimate goal of reproductive survival. One question biologists ask about organic structures and activities is "What for?" That is, "What is the function or role of such structure or such process?" The answer to this question must be formulated in teleological language. Only teleological explanations connote the important fact that plants and animals are directively organized systems. That such connotation—or, in Nagel's expression, "surplus meaning"—can always be expressed in nonteleological language is beside the point. As Nagel ([4], p. 423) has written questions about the value of an explanation "can be answered only by examining the effective role an explanation plays in inquiry and in the communication of ideas."

It has been noted by some authors that the distinction between systems that are goal-directed and those which are not is highly vague. The classification of certain systems as end-directed is allegedly rather arbitrary. A chemical buffer, and elastic solid or a pendulum at rest are examples of physical-systems that appear to be goal-directed. I suggest the use of the criterion of utility to determine whether an entity is teleological or not. The criterion of utility can be applied to both internal and external teleological systems. A feature of a system will be teleological in the sense of internal teleology if the feature has utility for the system in which it exists and if such utility explains the presence of the feature in the systems. Utility in living organisms is defined in reference to survival or reproduction. A structure or process of an organism is teleological if it contributes to the reproductive efficiency of the organism itself, and if such contribution accounts for the existence of the structure or process. Man-made tools or mechanisms are teleological with external teleology if they have utility, i.e., if they have been designed to serve a specified purpose, which therefore explains their existence and properties. If the criterion of utility cannot be applied, a system is not teleological. Chemical buffers, elastic solids and a pendulum at rest are not teleological systems.

The utility of features of organisms is with respect to the individual or the species in which they exist at any given time. It does not include usefulness to any other organisms. The elaborate plumage and display of the peacock serves the peacock in its attempt to find a mate. The beautiful display is not teleologically directed towards pleasing man's aesthetic sense. That it pleases the human eye is accidental, because it does not contribute to the reproductive fitness of the peacock (except, of course, in the case of artificial selection by man). The criterion of utility introduces needed objectivity in the determination of what biological mechanisms are end-directed. Provincial human interests should be avoided when using teleological explanations, as Nagel says. But he selects the wrong example when he observes that "the development of corn seeds into corn plants is sometimes said to be natural, while their transformation into the flesh of birds or men is asserted to be merely accidental" ([4], p. 424). The adaptation of corn seeds have developed to serve the function of corn reproduction, not to become a palatable food for birds or man. The role of wild corn as food is accidental, and cannot be considered a biological function of the corn seed in the teleological sense.

Some features of organisms are not adaptive nor useful by themselves. They have arisen because they are concommitant of other features that are adaptive or useful. Features of organisms may also be present because they were useful to the organisms in the past although they are no longer adaptive. Vestigial organs like the vermiform appendix of man are features of this kind. If they are neutral to reproductive fitness they may remain in the population indefinitely.

6. Teleology, Teleonomy, and Aristotle. I want to take up, very briefly, two more issues; the first is a semantic question, the second a historical one. Pittendrigh [7], Simpson [10], Mayr [3], Williams [11], and others, have proposed to use the term "teleonomic" to describe end-directed processes which do not imply that future events are active agents in their own realization, nor that things or activities are conscious agents or the product of such agents. They argue that the term "teleology" has sometimes been used to explain the animal and plant kingdoms as the result of a preordained plan necessarily leading to the existing kinds of organisms. To avoid such connotation, the authors argue, the term teleonomy should be used to explain adaptation in nature as the result of natural selection.

Although the notion of teleology has been used, and it is still being used, in the alleged sense, it is also true that other authors, like Nagel [4], [5], Goudge [2], etc., employ the term "teleology" without implying a preordained relationship of means to an end. Thus, it might originate more confusion than clarity to repudiate the notion of teleology on the grounds that it connotes an intentional relationship of means to an end. The point is that what is needed is to clarify the notion of teleology by explaining the various meanings the term may have. One may then explicitly express in which sense the term is used in a particular context.

Should the term "teleology" eventually be discarded from the scientific vocabulary, or restricted in its meaning to preordained end-directed processes, I shall welcome such event. But the substitution of a term by another does not necessarily clarify the issues at stake. It would still be necessary to explicate whatever term is used instead of teleology, whether teleonomy or any other. It may further be noted that the term "teleonomic" is commonly employed in the restricted sense of self-regulating mechanisms. There are phenomena in biology that are end-directed without being self-regulating mechanisms in the usual sense. The hand of man, for example.

Pittendrigh ([7], p. 394) has written that "It seems unfortunate that the term 'teleology' should be resurrected.... The biologists' long-standing confusion would be more fully removed if all end-directed systems were described by some other term, like 'teleonomic,' in order to emphasize that the recognition and description of end-directedness does not carry a commitment to Aristotelian teleology as an efficient causal principle." The Aristotelian concept of teleology allegedly implies that future events are active agents in their own realization. According to other authors, Aristotelian teleology connotes that there exists an overall design in the world attributable to a Deity, or at least that nature exists only for and in relation to man, considered as the ultimate purpose of creation (cf. Simpson [10], Mayr [3]).

Science, for Aristotle, is a knowledge of the "whys," the "reasons for" true statements. Of a thing we can ask four different kinds of questions: "What is it?", "Out of what is it made?", "By what agent?", "What for?" The four kinds of answers that can be elicited to these questions are his four causes—formal, material, efficient, and final. Only the third type of answer is causal in the modern scientific sense. *Aition*, the Greek term that Cicero translated "cause" (*causa*, in Latin) means literally ground of explanation, i.e., what can be answered to a question. It does not necessarily mean causality in the sense of efficient agency.

According to Aristotle, to fully understand an object we need to find out, among other things, its end; what function does it serve or what results it produces. An egg can be understood fully only if we consider it as a possible chicken. The structures and organs of animals have functions, are organized towards certain ends. Living processes proceed towards certain goals. Final causes, for Aristotle, are principles of intelligibility; they are not in any sense active agents in their own realization. For Aristotle, ends "never do anything. Ends do not act or operate, they are never efficient causes." (cf. Randall, [8], p. 128).

According to Aristotle there is no intelligent maker of the world. The ends of things are not consciously intended. Nature, man excepted, has no purposes. The teleology of nature is objective, and empirically observable. It does not require the inference of unobservable causes. (cf. Ross [9], Randall [8]) There is no God designer of nature. According to Aristotle, if there is a God, He cannot have purposes (Randall [8], p. 125).

Finally, for Aristotle, the teleology of nature is wholly "immanent." The end served by any structure or process is the good or survival of that kind of thing in which they exist. Animals, plants, or their parts do not exist for the benefit of any other thing but themselves. Aristotle makes it clear that nutritious as acorns may be for a squirrel, they do not exist to serve as a squirrel's meal. The natural end of an acorn is to become an oak tree. Anything else that may happen to the acorn is accidental and may not be explained teleologically.

Aristotle's main concern was the study of organisms, and their processes and structures. He observed the facts of adaptation and explained them with considerable insight considering that he did not know about biological evolution. His error was not that he used teleological explanations in biology, but that he extended the concept of teleology to the nonliving world.

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