Title
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Journal
History and Philosophy of the Life Sciences, 21(1)

ISSN
0391-9714

Author
Ayala, FJ

Publication Date
1999

Hist. Phil. Life Sci., 21 (1999), 3-33

Adaptation and Novelty: Teleological Explanations in Evolutionary Biology

Francisco J. Ayala

Department of Ecology and Evolutionary Biology
University of California
Irvine, CA 92697-2525, USA

ABSTRACT – Knives, birds' wings, and mountain slopes are used for certain purposes: cutting, flying, and climbing. A bird's wings have in common with knives that they have been 'designed' for the purpose they serve, which purpose accounts for their existence, whereas mountain slopes have come about by geological processes independently of their uses for climbing. A bird's wings differ from a knife in that they have not been designed or produced by any conscious agent; rather, the wings, like the slopes, are outcomes of natural processes without any intentional causation. Evolutionary biologists use teleological language and teleological explanations. I propose that this use is appropriate, because teleological explanations are hypotheses that can be subject to empirical testing. The distinctiveness of teleological hypotheses is that they account for the *existence* of a feature in terms of the function it serves; for example, wings have evolved and persist because flying is beneficial to birds by increasing their chances of surviving and reproducing. Features of organisms that are explained with teleological hypotheses include structures, such as wings; processes, such as development from egg to adult; and behaviours, such as nest building. A proximate explanation of these features is the function they serve; an ultimate explanation that they all share is their contribution to the reproductive fitness of the organisms. I distinguish several kinds of teleological explanations, such as natural and artificial, as well as bounded and unbounded, some of which but not others apply to biological explanations.

Darwin's Devolution

The steering wheel of a car has been designed for turning; the human eye has been designed for seeing. Most of us would be willing to accept these two statements, but would probably balk if somebody claimed that a mountain has been designed for climbing. We might note that mountain slopes are there whether or not there is anybody to climb them, but steering wheels would never have been produced if it were not for the purpose they serve. Mountain slopes and steering wheels have in common that they are used for certain purposes, but differ because steering wheels, but not mountain slopes, have been specially created for the purpose they serve. This is what we mean when we say that steering wheels are 'designed' for turning; the reason steering wheels exist at all and exhibit certain features is that they have been designed for turning the car. This is not so with mountain slopes. But what about eyes? I will expound in the pages that follow the proposition that human eyes share something in common with steering wheels and something with mountain slopes. Human eyes, like steering wheels, have been 'designed,' because were it not for the function of seeing they serve, eyes would have never come to be; and the features exhibited by eyes specifically came to be in order to serve for seeing. But eyes share in common with mountain slopes that both came about by natural processes, the eyes by natural selection, the mountain slopes by geological movements and erosion. Steering wheels, on the contrary, are designed and produced by human engineers. The issue at hand is, then, how to account for design, as in the design of the eye, without a designer. This conundrum was solved by Charles Darwin.[1]

In *The Origin of Species* Darwin accumulated an impressive number of observations supporting the evolutionary origin of living organisms. Moreover, and most importantly, he advanced a causal explanation of evolutionary change – the theory of natural selection, which provides a natural account of the design of organisms, or as we say in biology, their adaptation. Darwin accepted that organisms are adapted to live in their environments, and that their parts are adapted to the specific functions they serve. Penguins are adapted to live in the cold, the wings of birds are made to fly, and the eye is made to see. Darwin accepted the facts of adaptation, but advanced a scientific hypothesis to account for the facts. It may count as Darwin's greatest accomplishment that he brought the design aspects of nature into the realm of science. The wonderful designs of myriad plants and animals could now be explained as the result of natural laws manifested in natural processes, without recourse to an external Designer or Creator.

Before Darwin, the obvious adaptations of organisms and their organs were commonly attributed to the design of an omniscient Creator. In the nineteenth century the English theologian William Paley in his *Natural Theology* (1802) elaborated the argument-from-design as a forceful demonstration of the existence of the Creator. The functional design of the human eye, argued Paley, provides conclusive evidence of an all-wise Creator. It would be absurd to suppose, he wrote, that the human eye by mere chance 'should have consisted, first, of a se-

[1] Thomas H. Huxley, Darwin's younger contemporary, wrote that 'perhaps the most remarkable service to the philosophy of Biology rendered by Mr. Darwin is the reconciliation of Teleology and Morphology, and the explanation of the facts of both which his views offer ... There is a wider Teleology, which is not touched by the doctrine of Evolution, but is actually based upon the fundamental proposition of Evolution' (Huxley 1873, p. 272).

ries 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.' Similarly, the Bridgewater Treatises, published between 1833 and 1840, were written by eminent scientists and philosophers to set forth 'the Power, Wisdom, and Goodness of God as manifested in the Creation.' The complex functional organisation of the human hand was, for example, cited as incontrovertible evidence that the hand had been designed by the same omniscient Power that had created the world.

The strength of the argument-from-design to demonstrate the role of the Creator is easily set forth. Wherever there is function or design we look for its author. A steering wheel is made for turning, a knife is made for cutting, and a clock is made to tell time; their functional designs have been contrived by an engineer, a blacksmith, and a watchmaker. The exquisite design of Leonardo da Vinci's *Mona Lisa* proclaims that it was created by a gifted artist following a preconceived purpose. Organisms and their structures, organs, and behaviours are also precisely designed to serve certain functions. The functional design of organisms and their features would therefore seem to argue for the existence of a designer. It was Darwin's greatest insight to discover that the directive organisation of living beings can be explained as the result of a natural process, natural selection, without a need to resort to a Creator or other external agent. The origin and adaptations of organisms in their profusion and wondrous variations were thus brought into the realm of science, having been explained as the result of natural laws manifested in natural processes. The presence of design in living organisms is a distinctive consequence of natural selection in the unending sequence of interactions between organisms and their environments.

Natural Selection and Adaptation

The central argument of the theory of natural selection is summarised by Darwin in *The Origin of Species* as follows:

'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 favourable variations and the rejection of injurious variations, I call Natural Selection' (Darwin 1967, ch. 3, p. 63; ch. 4, pp. 80-81).

Darwin's argument addresses the problem of explaining the adaptive features of organisms. Darwin argues that adaptive variations ('variations useful in some way to each being') occasionally appear, and that these are likely to increase the reproductive chances of their carriers. Over the generations, favourable variations will be preserved, injurious ones will be eliminated. In one place, Darwin avers: 'I can see no limit to the amount of change, to the beauty and infinite complexity of the coadaptations between all organic beings, one with another and with their physical conditions of life, which may be effected in the long course of time by nature's power of selection' (Darwin 1967, ch. 4, p. 109). Natural selection was proposed by Darwin primarily to account for the adaptive organisation, or 'design' of living beings; it is a process that promotes or maintains adaptation. Evolutionary change through time and evolutionary diversification (multiplication of species) are not directly promoted by natural selection, but they often ensue as by-products of natural selection fostering adaptation to diverse and ever-changing environments.

Darwin formulated natural selection primarily as differential survival. The modern understanding of the principle of natural selection is formulated through gene arrays and statistical terms as differential reproduction. Natural selection implies that some genes and gene arrays are transmitted more frequently, on the average, to the following generations than their alternates. Such genetic units will become more common in each subsequent generation and their alternates less common. Natural selection is simply a statistical bias in the relative rate of reproduction of alternative genetic units. But the reproductive bias, argued Darwin, will likely favour the variants that are useful to the organisms, precisely because it is this usefulness that increases the reproductive chances of their carriers. Gazelles that run swifter will better escape their predators and so gazelles come to have swift legs.

Evolutionary Novelty

Natural selection has been compared to a sieve which retains the rarely arising useful genes 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 thus creative in a way. It does not 'create' the entities upon which it operates, but it produces adaptive genetic combinations which would not have existed otherwise owing to the enormous improbability of their coming about by chance.

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*, require, in order to be able to reproduce in a culture medium, 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 resistance for streptomycin occur in normal (i.e., sensitive) bacteria at rates on 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 or thirty 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 a culture with streptomycin but with no histidine. Most of them will not be able to reproduce, but about a hundred will start reproducing until the available medium is saturated.

Natural selection has produced bacterial cells resistant to streptomycin and not requiring histidine for growth in two steps. The probability the two mutational events happening in the same bacterium is 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.[2]

As illustrated by the bacterial example, natural selection produces combinations of genes that would otherwise be highly improbable because natural selection proceeds stepwise. The vertebrate eye did not suddenly appear in all its present perfection. Its formation requires the appropriate integration of many genetic units, and thus the eye could not have resulted from random processes alone. The ancestors of today's vertebrates had for more than half a billion years some kind of organs sensitive to light. Perception of light, and later vision, were important for the survival of organisms and for their reproductive success. Sunlight is, and has been for millions of years, a pervasive feature of the environments in which many animals live.[3] Accordingly, natural selection has favoured genes and gene combinations promoting the functional efficiency of the eye. Such genetic units gradually accumulated, eventually leading to the highly complex and efficient vertebrate eye.[4] 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. In this sense, natural selection is a creative process, although it does not create the raw materials – the atoms – upon which it acts.

Natural selection has no foresight, nor does it operate according to some preconceived plan. Rather it is a purely natural process resulting from the interacting properties of physicochemical and biological entities. Natural selection is simply a consequence of the differential multiplication of living beings. It may appear purposeful because it is

[2] The process described in this example is indeed *natural* selection, in contrast with the artificial selection when an animal breeder selects, for example, the cows that produce the most milk in order to breed the next generation. In the bacterial selection, human intervention is restricted to changing the environments in which the bacteria breed, rather than selecting the bacteria that breed best in each particular case. In nature, environments change endlessly from place to place and from one time to the next. This persistent environmental variation prompts evolution by natural selection, as variations favoured in one environment become replaced by those favoured in the next.

[3] 'The sun provided not only the energy to drive the chemical cogwheels of life. It also offered the chance of a remote guidance technology. It pummelled every square millimetre of the Earth's surface with a fusillade of photons: tiny particles travelling in straight lines at the greatest speed the universe allows, criss-crossing and ricocheting through holes and cracks so that no nook escaped, every cranny was sought out. Because photons travel in straight lines and so fast, because they are absorbed by some materials more than others and reflected by some materials more than others, and because they have always been so numerous and so all-pervading, photons provided the opportunity for remote-sensing technologies of enormous accuracy and power. It was necessary only to detect photons and – more difficult – distinguish the directions from which they came. Would the opportunity be taken up? Three billion years later you know the answer, for you can see these words (Dawkins 1996, pp. 138-139).

[4] Eyes have evolved in animals in at least forty different types. The human (vertebrate) eye is one type; others are the squid's, the snail's, and the fly's. R. Dawkins has discussed the evolution of eyes, authoritatively and with beautiful prose, (Dawkins 1996, pp. 138-197).

conditioned by the environment: which organisms reproduce more effectively depends on which variations they possess that are useful in the environment where they live.

Natural selection does not strive to produce predetermined kinds of organisms, but only organisms that are adapted to their present environments. Which characteristics are selected depends on which variations happen to be present at a given time in a given place. This in turn depends on the random process of mutation, as well as on the previous history of the organisms (i.e., on the genetic make-up they have as a consequence of their previous evolution). Natural selection is an 'opportunistic' process. The variables determining in what direction it will go are the environment, the preexisting constitution of the organisms, and the randomly arising mutations. Because natural selection does not anticipate the environments of the future, drastic environmental changes may be insuperable to organisms that were previously thriving.

Determinism and Contingency

Adaptation to a given environment may occur in a variety of different ways. An example may be taken from the adaptations of plant life to desert climate. The fundamental adaptation is to the condition of dryness, which involves 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 on 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. Ephemeral plants germinate from seeds, grow, flower, and produce seeds – all within the space of the few weeks while rainwater is available; the rest of the year the seeds lie quiescent in the soil.[5]

The opportunistic character of natural selection is also well-evidenced by the phenomenon of adaptive radiation. The evolution of drosophila flies in Hawaii is a relatively recent adaptive radiation. There are

[5] I cited earlier another example of the different ways in which organisms adapt to the same environmental features. Very diverse types of eyes have evolved in different kinds of animals, taking advantage of the ubiquitous presence of sunlight for finding food and shelter, escaping predators, directing daily or seasonal rhythms, and so on. The detailed steps in the evolution of several eye types can be found in R. Dawkins' *Climbing Mount Improbable* (Dawkins 1996).

about 1,500 drosophila species in the world. Approximately 500 of them have evolved in the Hawaiian archipelago, although it has a small area, about one twenty-fifth the size of California. Moreover, the morphological, ecological, and behavioural diversity of Hawaiian *Drosophila* exceeds that of *Drosophila* in the rest of the world.

Why should such 'explosive' evolution have occurred in Hawaii? The overabundance of drosophila flies there contrasts with the absence of many other insects. The ancestors of Hawaiian drosophila reached the archipelago before other kinds of insects did, and thus they found a multitude of unexploited opportunities for making a living. They responded by a rapid adaptive radiation; although they are all probably derived from a single colonising species, they adapted to the diversity of opportunities available in diverse places or at different times by developing appropriate adaptations, which range broadly from one to another species.

The process of natural selection can explain the adaptive organisation of organisms, as well as their diversity and evolution, as a consequence of their adaptation to the multifarious and ever changing conditions of life. The fossil record shows that life has evolved in a haphazard fashion. The radiations, expansions, relays of one form by another, occasional but irregular trends, and the ever present extinctions, are best explained by natural selection of organisms subject to the vagaries of genetic mutation and environmental challenge.

Natural selection accounts for the design of organisms, as expounded earlier, because adaptive variations tend to increase the probability of survival and reproduction of their carriers at the expense of maladaptive, or less adaptive, variations. The arguments of Paley and other natural theologians against the incredible improbability of chance accounts of the origin of organisms are well taken within their limits. But neither these scholars, nor any other authors before Darwin, were able to discern that there is a natural process (namely, natural selection) that is not random but rather is oriented and able to generate order or 'create.' The traits that organisms acquire in their evolutionary histories are not fortuitous but determined by their functional utility to the organisms.

Chance is, nevertheless, an integral part of the evolutionary process. The mutations that yield the hereditary variations available to natural selection arise at random, independently of whether they are beneficial or harmful to their carriers. This random process (as well as others that come to play in the great theatre of life) is counteracted by natural selection, which preserves what is useful and eliminates the harmful. Without mutation, evolution could not happen because there would be no variations that could be differentially conveyed from one to another generation. Without natural selection, the mutation process would yield disorganisation and extinction because many mutations are disadvantageous. Mutation and selection have jointly driven the marvelous process that starting from microscopic organisms has spurted orchids, birds, and humans.

The theory of evolution manifests chance and necessity jointly intertwined in the stuff of life; randomness and determinism interlocked in a natural process that has brought forth the most complex, diverse, and beautiful entities in the universe: the organisms that populate the earth, including humans who think and love, endowed with free will and creative powers, and able to analyse the process of evolution itself that brought them into existence. This was Darwin's fundamental discovery, that there is a natural process that is creative, though not conscious.

Teleological Explanations

As I have written elsewhere (Ayala 1998), the biological literature abounds in statements such as the following (*emphasis* added): 'Any biological mechanism produces at least one effect that can properly be called its *goal*: vision for the eye or reproduction and dispersal for the apple ... Thus I would say that reproduction and dispersal are the *goals*, or *functions* or *purposes* of apples and that the apple is a means or mechanism by which such *goals* are realized by apple trees' (Williams 1966, pp. 8-9). 'Generation by generation, step by step, the *designs* of all the diverse organisms alive today – from redwoods and manta rays to humans and yeast – were permuted out of the original, very simple, single-celled ancestor through an immensely long sequence of successive modifications' (Tooby and Cosmides 1992, p. 52). '[T]he *design* of eyes reflects the properties of light, objects, and surfaces; the *design* of milk reflects the dietary requirements of infants ...; the *design* of claws reflects things such as the properties of prey animals, the strength of predator limbs, and the task of capture and dismemberment (Tooby and Cosmides 1992, p. 68). 'Fig wasps don't transport pollen for food. They deliberately take it on board, using special pollen-carrying pockets, *for the sole purpose* of fertilizing figs (which benefits the wasps only in a more indirect way)' (Dawkins 1996, p. 302). 'Our mouth, throat, and larynx ... were originally '*designed*' for swallowing food and breathing. They were modified *so that* we could produce sounds that were easy to understand' (Lieberman

1998, p. 20). These statements refer in one way or other to the functional organisation of organisms and their constituent parts that comes about by natural selection, as Darwin saw it. Nobel Laureate Peter Medawar and Jeanne Medawar have written that 'It is folly or ignorance to deny that the purpose of nests is to protect the relatively helpless young of birds and mammals ... The purpose of teeth ... is mastication; of eyes to see, and of ears to hear' (Medawar and Medawar 1983, p. 256).

No similar statements are found in the writings of physical scientists. The configuration of sodium chloride depends on the structure of sodium and chlorine, but no chemist is likely to write that sodium chloride has been *designed* for certain purposes, such as tasting salty. The earth's continents move, but geologists do not claim that this is for the *purpose* of facilitating vicariate evolution. The motion of the earth around the sun results from the laws of gravity, but astrophysicists do not state that this happens *in order to* produce the seasons.

Biologists need to account for the functional features of organisms, their 'design,' in terms of the goals or purposes they serve, which is accomplished by means of teleological hypotheses or teleological explanations. Physical scientists do not face similar demands. A dictionary definition of 'teleology' is 'the use of design, purpose, or utility as an explanation of any natural phenomenon' (*Merriam Webster's Collegiate Dictionary*, Tenth Edition 1994). The same dictionary defines 'teleological' as 'exhibiting or relating to design or purpose esp. in nature.' The *Oxford Dictionary* includes virtually identical definitions: 'teleological', 'dealing with design or purpose, esp. in natural phenomena'; 'teleology,' 'such design as exhibited in natural objects or phenomena'.

An object or a behaviour can be said to be teleological, or telic, when it provides evidence for design or appears to be directed towards certain ends, goals, or purposes.[6] For example, the behaviour 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 goal: getting to a given city, acquiring knowledge, or getting food.

[6] In the pages that follow and to the extent that I do not specify otherwise in a particular case, I shall use the terms 'ends,' 'goals' and 'purposes' as largely equivalent and/or complementary. Obviously, in this context, I do not mean by 'end' simply the point of termination, as in 'the end of the line' or 'the end of a book,' but rather something to be achieved as in the phrases 'the means to an end,' or 'the end sought' or 'the end served.' 'Purpose' and to a lesser extent 'goal' often implies intention, or conscious pursuit; I do not intend this more restricted meaning, except when explicitly stated or obvious from the context. I also consider 'telic' and 'teleological' to have largely overlapping meanings so that they can often be used interchangeably, but I will mostly limit myself to using the terms 'teleological' and 'teleology.'

Objects and machines made by people are also usually teleological: a knife is made for cutting, a clock is made for telling time, a thermostat is made to regulate temperature. In a similar fashion, I have argued, features of organisms have come to be because they serve certain purposes or functions, and in this sense they can be said to be teleological: 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, organs like a kidney, or behaviours like the courtship displays of a peacock. Adaptations are features of organisms that have come about by natural selection because they increase the reproductive success of their carriers.

Inanimate objects and processes (other than those created by humans) are not teleological because they are not directed toward specific ends, they do not exist to serve certain purposes. The configuration of sodium chloride 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. Similarly, the slopes of a mountain are the result of certain geological processes and weather erosion, but did not come about so as to serve a certain end, such as skiing. 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, such as producing the seasons.

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 they came into existence or have certain configurations. On the other hand, a knife and a car exist and have particular configurations precisely in order to serve the respective 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 observations point out the essential characteristics of teleological phenomena, i.e., phenomena whose existence and configuration can be explained teleologically. I 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, in such a way that this contribution is *the reason why the feature or behaviour exists at all*.' Teleological explanations require that the feature or behaviour being explained contributes to the existence or maintenance of a certain state or property of the system. But, the essential component of my definition is that teleological explanations apply only to features or behaviours that could not have come about were it not for the particular end or purpose they serve. The end, goal, or purpose served is, therefore, the explanatory reason for the existence of the feature or behaviour and its distinctive characteristics. A teleological hypothesis purports to identify the function or purpose that accounts for the evolution of a particular feature.

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. The motion of the earth around the sun is the reason seasons exist; the existence of the seasons is not the reason 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. Automobiles exist and have particular configurations because they serve for transportation, and thus can be explained teleologically. (Not all features of a car contribute to the purpose of 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 human-made object that need not be explained teleologically. That knives have handles is to 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.[7])

Many features and behaviours of organisms meet the requirements of teleological explanations. The human hand, the bird's wings, the structure and behaviour of kidneys, the mating displays of peacocks are examples already given. In general, as pointed out above, those features and behaviours that are considered adaptations are explained teleologically. This is simply because adaptations are features that come about by natural selection. As I have indicated above, an account of natural selection says that among alternative genetic variants that

[7] G.C. Williams has noted in *Adaptation and Natural Selection* that teleological, or adaptationist hypotheses are onerous and thus should be used with restraint (Williams 1966). He has in mind, particularly, 'group selection' accounts. The facile recourse to or even abuse of teleological explanations (adaptational accounts, in their terminology) has been criticised by S.J. Gould and R.C. Lewontin, (Gould and Lewontin 1979).

arise by mutation or recombination, the ones that become propagated in a species are those that contribute more to the reproductive success of their carriers. The effects on reproductive success are mediated by a certain function or property. Wings and hands acquired their present configuration through long-term accumulation of genetic variants adaptive to their carriers.

How natural selection yields adaptive features may now be reiterated with a simple human example, where the adaptation arises as a consequence of a single gene mutation, such as the presence of normal hemoglobin rather than hemoglobin S in most people. An amino acid substitution in the beta hemoglobin chain results in hemoglobin molecules which are less efficient for oxygen transport. The general occurrence in human populations of normal rather than S hemoglobin is explained teleologically by the contribution of hemoglobin to effective oxygen transport and thus to reproductive success. A simple and well known nonhuman example concerns the difference between peppered-gray moths and melanic moths. The replacement of gray moths by melanics in polluted regions is explained teleologically by the fact that in such regions melanism decreases the probability that a moth be eaten by a bird. The predominance of peppered forms in nonpolluted regions is similarly explained.[8]

But it must also be reiterated that 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 random genetic drift, by chance association with adaptive traits, by physical constraint, by historical contingency, or in general by processes other than natural selection. Proponents of the neutrality theory of protein evolution, for example, argue that many alternative protein variants are adaptively equivalent. Most evolutionists would admit that at least in certain sites the selective differences between alternative nucleotides in DNA or amino acids in proteins must be virtually nil, particularly when population size is very small. The presence of one nucleotide or amino acid rather than another adaptively equivalent to the first, would not be explained then teleologically, but as a consequence of chance and historical contingency.

[8] I have selected the two particular examples in this paragraph because we know of environmental variations that shift their adaptive value. In regions of tropical Africa where malaria is rife and a major debilitating disease and cause of mortality, the incidence of S hemoglobin is high, because it protects against malarial infection. Starting in the mid-nineteenth century, the frequency of melanic moths rapidly increased in English regions heavily polluted by burning industrial coal. Since the mid 1960s, pollution controls have gradually eliminated the soot covering tree trunks, and the incidence of peppered-gray moths has concomitantly increased at the expense of the melanics.

Teleological Features and Behaviours in Organisms

I will now identify three categories of biological phenomena where teleological explanations are pertinent, although the distinction between the categories need not always be clearly delimited, and it is also possible to subdivide them or reformulate them in a different or more prolific array. These three classes of teleological phenomena are established according to the mode of relationship between the structure or process and the property or end-state that accounts for its presence. Other classifications of teleological phenomena are possible according to other principles of distinction, including some that are suggested below.

(1) A behaviour such that the end-state or goal is consciously anticipated by the agent. This is purposeful activity which, if it is understood in a strict sense, probably occurs only in humans. With a lesser degree of intentionality, behaviours initiated in order to reach a goal also occur in other animals. I am acting teleologically when I buy an airplane ticket to fly to Mexico City. A cheetah hunting a gazelle gives at least the appearance of purposeful behaviour. We may notice that according to those who believe in 'special' creation, the existence of organisms and their adaptations is the result of the consciously intended activity of a Creator seeking to create specifically each kind. Biologists recognise purposeful activity in the living world, at least in humans; but the existence of the living world, including humans, need not be explained as the result of purposeful behaviour.[9]

(2) Self-regulating of 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 a teleological mechanism of this kind. In general, the homeostatic reactions of organisms belong to this category of teleological phenomena.

Biologists usually distinguish between two types of homeostasis – physiological and developmental homeostasis – although intermediate and additional types do exist.[10] Physiological homeostatic reactions

[9] A very common reason for which biologists do not use the term 'teleology' is that they believe it necessarily implies that function and design must be attributed to an external agent; i.e., that the design features of organisms have been created by God. I take up this matter below. It is in any case amusing to read statements of denial of teleology in articles and books pervaded with teleological language and teleological explanations. One is reminded that 'a rose by any other name is still a rose.' It has been informally attributed to one or another distinguished evolutionist the witticism: 'Teleology is like a mistress. A man does not want to be seen in her company, but he cannot do without her.'

[10] For instance, the persistence of a genetic polymorphism in a population due to heterosis (advantage of individuals who inherit a different allele from each parent) may be considered a homeostatic mechanism acting at the population level. One example is the presence of the 'normal' and the S forms of hemoglobin in human populations severely infected with malaria. The S form protects against malaria and the 'normal' variant prevents falciform anemia.

enable the organism to maintain a certain physiological steady state in spite of environmental shocks. The regulation of the composition of the blood by the kidneys, or the hypertrophy of muscle in case of 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. The development of a chicken from an egg is a typical example of developmental homeostasis. 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 fertilised egg.[11]

Self-regulating systems or servo-mechanisms built by humans belong to this second category of teleological phenomena. A simple servo-mechanism is a thermostat unit that maintains a specified room temperature by turning on and off the source for heating or cooling. Self-regulating mechanisms of this kind, living or human-made, are controlled by feed-back information. Robots programmed to perform certain functions are additional examples.

(3) Organs, limbs, and other features anatomically and physiologically constituted to perform a certain function. The human hand is made for grasping, and the eye for vision. Tools and human-made machines are teleological in this third sense. A watch, for instance, is made to tell time, and a faucet to draw water. The distinction between the (2) and (3) categories of teleological systems is sometimes blurred. Thus, the human eye is able to regulate itself within a certain range according to the conditions of brightness and distance so as to perform its function more effectively.

Adaptation and Teleology

The adaptations of organisms – whether organs, homeostatic mechanisms, or patterns of behavior – are explained teleologically as a consequence of natural selection, because their existence is ultimately accounted for in terms of their contribution to the reproductive fitness of the organisms. A feature of an organism that increases its reproductive fitness will be selectively favoured. Given enough generations it will extend to the whole species.

[11] Aristotle, Saint Augustine, and other ancient and medieval philosophers, took developmental homeostasis as the paradigm of all teleological natural processes. According to Saint Augustine, God did not create directly all living species of organisms, but these were implicit in the primeval forms created by Him. The existing species arose by a natural 'unfolding' of the potentialities implicit in the primeval forms or 'seeds' created by God. These ancient or medieval views are not intended here, of course.

Patterns of behaviour, such as the migratory habits of certain birds or the web-spinning of spiders, have developed because they favoured the reproductive success of their possessors in the environments where the population lived. Similarly, natural selection can account for the existence of homeostatic mechanisms. Some living processes can be operative only within a certain range of conditions. If the environmental conditions oscillate frequently beyond the functional range of the process, natural selection will favour self-regulating mechanisms that maintain the system within the functional range. In humans, 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 the dissipation of heat in warm environments through perspiration and dilation of the blood vessels in the skin. In cool weather the loss of heat is minimised, and additional heat is produced by increased activity and shivering. Finally, the adaptation of an organ or feature to its function is also explained teleologically by natural selection in that the existence of the organ or feature is accounted for in terms of the contribution it makes to the reproductive success of its carriers. The vertebrate eye arose because genetic mutations responsible for its development occurred, and were gradually combined in progressively more efficient patterns, the successive changes increasing the reproductive fitness of their possessors in the environments in which they lived.

Proximate and Ultimate Teleology of Natural Selection

There are in all organisms two levels of teleology that may be labeled *proximate* (or *particular*) and *ultimate* (or *generic*). There usually exists a specific and proximate end for every feature of an animal or plant. The existence of the feature is thus explained in terms of the function or property that it serves, which function or property can be said to be the particular or proximate end of the feature. Thus, seeing is a particular, specific, or proximate end served by an eye, and flying is a particular, specific, or proximate end served by a wing. There is also an ultimate goal to which all features contribute or have contributed in the past – reproductive success. The general or ultimate end to which all features and their functions contribute is increased reproductive efficiency. The presence of the functions themselves – and therefore of the features which serve them – is ultimately explained by their contribution to the reproductive fitness of the organisms in which they exist. It is in this sense that the ultimate source of teleological explanation in biology is the principle of natural selection.

It is because of the reasoning just advanced that I suggested in the past that natural selection can be said to be a teleological process in a *causal* sense, namely as a distinctive process, occuring only in the living world, which accounts for the adaptive features of organisms. (Ayala 1968, 1970). I could have said instead that natural selection is a *teleology-inducing* process, intending to convey the same idea. But this might also be misunderstood and it might be best to discard these designations. Natural selection is not an entity or an agent, and thus it is not a cause in the usual sense. Nor does natural selection result in pre-determined or pre-conceived features or organisms, as I will further expound. To reiterate the point, natural selection is not an entity but a purely material or natural process governed by the laws of physics, chemistry, and other natural laws. To designate it as a 'teleological process' would be to exclusively convey the meaning that natural selection results in the production and preservation of end-directed organs and behaviours, when the functions these serve contribute to the reproductive effectiveness of the organisms.

In any case, the process of natural selection is not at all teleological in a different sense. Natural selection is not in any way directing toward the production of specific kinds of organisms or toward organisms having certain specific properties. The over-all process of evolution cannot be said to be teleological in the sense of proceeding toward certain specified goals, preconceived or not. Natural selection is nothing more than the outcome of differential reproduction. 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 changes.

I have argued that the presence of organs, processes, and patterns of behaviour can be explained teleologically by exhibiting their contribution to the reproductive fitness of the organisms in which they occur. This does not imply that reproductive fitness is a consciously intended goal. Such intent must be denied except in the case of the voluntary behaviour of humans. In teleological explanations the end-state or goal is not to be understood as the efficient cause of the object or process that it explains. The end-state is causally posterior, the outcome of a process, not its cause.

Natural versus Artificial Teleology; and Bounded versus Unbounded Teleology

I have already identified several kinds of biological phenomena that call for teleological accounts, and have pointed out that such accounts also apply to purposeful behaviour and to human made objects. It will be helpful to characterise some differentiating features of these categories of teleological entities; particularly, the biological in general and the distinctively human.

Actions are *purposeful* when an end-state or goal is consciously intended by an agent. Thus, a person mowing a lawn is acting teleologically in the purposeful sense; a lion hunting deer and a bird building a nest manifest at least the appearance of purposeful behaviour. A knife, a car, and a thermostat are objects or systems intended for (and produced) by humans. Actions or objects resulting from purposeful behaviour may be said to exhibit *artificial* (or *external*) teleology. Their teleological features have come about because they were consciously intended for and by some agent.

Systems with teleological features that are not due to the purposeful action of an agent but result from natural process may be said to 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. The development of an egg into a chicken is a teleological process also of an internal or natural kind, since it comes about as a natural process, both in terms of its proximate causation, the concatenation of events by which the egg develops into a chicken; and its remote causation, the evolutionary process by which chicken and their developmental processes came to be.

We may distinguish between two kinds of natural teleology: *determinate* (or *bounded* or *necessary*) and *contingent* (or *indeterminate* or *unbounded*). This distinction applies as well to purposeful objects and behaviours, but human actions are predominantly determinate, in the sense that they are consciously intended. Humans can of course walk randomly or act aimlessly and can produce objects, such as a die, that behave randomly, but for the most part these are nevertheless products of intentionality.

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.

Indeterminate or unbounded teleology occurs when the end-state served is not specifically intended or predetermined, but is rather the result of a natural process selecting one among several available alternatives. For teleology to exist, the selection of one alternative over another must be deterministic and not purely stochastic. But what alternative happens to be selected 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.

Many features of organisms are teleological in the indeterminate sense. The evolution of birds' wings requires teleological explanation: the genetic constitutions responsible for their configuration came about because wings serve for flying and flying contributes to the reproductive success of birds. But there was nothing in the constitution of the remote reptilian 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, at each stage of which the most advantageous alternative was selected among those that happened to be available; which alternatives were available at any one time depended at least in part on contingent 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. As pointed out earlier, 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 are used for flying. One 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 the purpose of an adaptive function they would have never come about, and 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, firstly, 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. (Which new genes may arise by mutation and which new genetic arrays may arise by recombination depend on which 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 favoured by selection depends on the particular set of environmental conditions to which a population is exposed. The historical process of evolution is contingent, but at each step there is a predominantly deterministic component, provided by the natural selection of favourable variants among those that happen to be present. Organisms are adapted to their environments and exhibit adaptive features owing to this deterministic component. The contingency of history and environment makes long term evolution undetermined or unbounded. There can be little doubt that if the process of evolution on earth were to start again from where it was three billion years ago, the evolved organisms would be conspicuously different from the ones that came about in the first run of the process.

Teleology and Causality

Teleological explanations are fully compatible with causal explanations (see Nagel 1961, 1965; Ayala 1970, 1995). 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. (I use the 'in principle' clause to imply that any component of the process can be elucidated as a causal process if it is investigated in sufficient detail and in depth, but I know of no developmental process for which all the steps have been so investigated, with the possible exception of the flatworm *Caenorhabditis elegans*. The development of *Drosophila* fruitflies has also become known in much detail, but not yet completely.) It is also possible in principle to describe the causal processes by which one genetic variant eventually becomes established in a population. But these causal explanations do not make it unnecessary to advance teleological explanations where appropriate. Both teleological and causal explanations are called for in evolutionary biology.

According to Nagel, 'a teleological explanation can always be transformed into a causal one.' Consider a typical teleological statement in biology, 'The function of gills in fishes is respiration.' This statement is a telescoped argument the content of which can be unraveled approximately as follows: Fish respire; if fish have no gills, they do not respire; therefore fish have gills. According to Nagel, 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 organisation and activities.'[12]

Nagel's account, however, misses an essential feature of teleological explanations, which invalidates his claim that they are equivalent to (even if less cumbersome than) causal accounts. Although a teleological explanation can be reformulated into a nonteleological one, the teleological explanation connotes something more than the equivalent nonteleological one. In the first place, a teleological explanation implies that the system under consideration is directively organised. For that reason teleological explanations are appropriate in biology and in the domain of human creations but make no sense when used in the physical sciences to describe phenomena like the fall of a stone or the slopes of a mountain. Teleological explanations imply, while nonteleological ones do not, that there exists a distinctive, or specific means-to-an-end relationship in the systems under description: the eye is for seeing, the egg develops into a chicken, the knife is used for cutting.

In addition to connoting that the system under consideration is directively organised, and most importantly, teleological explanations account for the existence of specific functions in a system and more generally for the existence of the directive organisation itself. A teleological explanation accounts for the presence in an organism of a certain feature, say the gills, because it contributes to the performance or maintenance of a certain function, respiration in this example. The teleological explanation also connotes, in the case of organisms, that the function came about because it contributes to the reproductive fitness of the organism. In the nonteleological translation given above, the major premise states that 'fish respire.' Such a formulation assumes the presence of a specified function, respiration, but it does not account for its existence. A teleological explanation implicitly (or explicitly) accounts for the presence of the function itself by connoting (or stating explicitly) that the function in question contributes to the reproductive fitness of the organism in which it exists and that *this is the reason why the function and feature came about in evolution.* The

[12] 'The function of gills in fishes is respiration, that is the exchange of oxygen and carbon dioxide between the blood and the external water.' A statement of this kind, according to Nagel, accounts for the presence of a certain feature *A* (gills) in every member of a class of systems *S* (fish) which possess a certain organisation *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 unraveled 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 organisation *C* is to enable *S* in environment *E* to engage in process *F*' can be formulated more explicitly: 'Every system *S* with organisation *C* and in environment *E* engage in function *F*; if *S* with organisation *C* and in environment *E* does not have *A*, then *S* cannot engage in *F*; hence, *S* must have *A*.' According to Nagel, the difference between a teleological explanation and a nonteleological one is, thus, one of emphasis rather than of asserted content.

teleological explanation gives the reason why the system is directively organised. The apparent purposefulness of the ends-to-means relationship existing in organisms is a result of the process of natural selection which favours the development of any organisation that increases the reproductive fitness of the organisms.

It follows that teleological explanations are not only acceptable in biology, but are also indispensable as well as distinctive of the discipline. It further follows that for this reason alone (and I have suggested others) biology cannot be reduced to the physical sciences (Ayala 1968, 1977).

Teleological Explanations as Testable Hypotheses

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 indicate all that is relevant about the eye, namely that it is useful to the organism because it serves to see. Evolutionary biologists are interested in the question of why one particular genetic alternative rather than another came to be established in a species. 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 (Dawkins 1996, pp. 138-197).

There are two questions that must be addressed by a teleological account of evolutionary events. First, there is the question of whether a genetic variant contributes to reproductive success; a teleological account states that an existing genetic constitution (say, the gene 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 specific teleological hypotheses that can be empirically tested.[13] It sometimes happens, however, that information

[13] This point has been belaboured, for example by J. Tooby and L. Cosmides (Toby and Cosmides 1992).

is available for 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 the fruitfly *Drosophila pseudoobscura* different inversion polymorphisms are favoured by natural selection at different times of the year, 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 favoured by natural selection. One example is the large human brain, 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 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 (Williams 1966; Gould and Lewontin 1979).

It has been argued 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 teleological is alleged rather than arbitrary. A chemical buffer, an elastic solid or a pendulum at rest are examples of physical systems that appear to be goal directed. I suggest using the criterion of utility to determine whether an entity is teleological or not. The criterion of utility can be applied to both natural and artificial teleological systems. Utility in an organism is defined in reference to the survival and reproduction of the organism itself. A feature of a system will be teleological in the sense of natural (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 system. Operationally, then, a structure or process of an organism is teleological if it can be shown to contribute to the reproductive efficiency of the organism itself, and if such a contribution accounts for the existence of the structure or process. Eyes, gills, and homeostatic developmental processes are features beneficial to the organisms in which they exist.

In artificial (external) teleology, utility is defined in reference to the creator of the object or system. Human-made tools and machines are teleological with external teleology 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 in 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 is a teleological feature of the peacock because it serves the peacock in its attempt to find a mate. The beautiful display is not teleologically directed toward pleasing our human aesthetic sense. That it pleases the human eye is accidental, because this does not contribute to the reproductive fitness of the peacock (except, of course, in the case of traits selected by humans, such as milk production by cows, or dog breeds).

The criterion of utility introduces needed objectivity in the determination of which biological mechanisms are end-directed. Provincial human interests should be avoided when using teleological explanations, as Nagel has written. 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' (Nagel 1961, p. 424). The adaptations of corn seeds have developed to serve the function of corn reproduction, not to become a palatable food for birds or humans. The role of wild corn as human food is indeed accidental to the corn, and cannot be considered a biological function of corn seeds in the teleological sense.[14]

Some features of organisms are not useful by themselves. They have arisen as concomitant or incidental consequences of other features that are adaptive or useful. In some cases, features which are not adaptive in origin may become useful at a later time. For example, the sound produced by the beating of the heart has become adaptive for modern humans because it helps the physician to diagnose the health of the patient. The origin of such features is not explained te-

[14] This point was clearly and repeatedly made by Darwin. For example 'Natural selection will modify the structure of the young in relation to the parent, and of the parent in relation to the young. In social animals it will adapt the structure of each individual for the benefit of the community; if each in consequence profits by the selected change. What natural selection cannot do, is to modify the structure of one species, without giving it any advantage, for the good of another species; and though statements to this effect may be found in works of natural history, I cannot find one case which will bear investigation' (Darwin 1967, ch. 4, pp. 86-87).

leologically, although their preservation might be so explained in certain cases.

Features of organisms may 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, these features may remain in a species indefinitely. The origin of such organs and features, although not their preservation, is accounted for in teleological terms.

Objections, Responses, and Interpretations

Some evolutionists have rejected the teleological mode of explanation in evolutionary biology because they have failed to recognise the various meanings that the term 'teleology' may have (Ghiselin 1974; Mayr 1965, 1974; Pittendrigh 1958; Williams 1966). These biologists are correct in excluding certain forms of teleological explanations from biology, 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 recognise them as such, or prefer to call them by some other name, such as 'teleonomic.' Teleological explanations, as expounded above, are appropriate in evolutionary theory, and are recognised by evolutionary biologists and philosophers of science (Beckner 1959; Christensen 1996; Binswanger 1990; Dobzhansky 1970; Goudge 1961; Hull 1974; Nagel 1961; Simpson 1964; Wimsatt 1972). Some kinds of teleological explanations that are appropriate and some that are inappropriate with respect to various biological questions may be briefly specified.

According to Mayr teleological explanations have been applied to two different sets of biological phenomena (Mayr 1965). '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 uses the term 'instrumental' for the teleology of organs that act in a functional way, such as the hand and the eye, 'developmental' for the teleology of such processes as the maturation of a limb, and 'historical' for the process (natural selection) producing teleologically organised systems (Grene 1974).

In the terminology that I have proposed, organs and features such as the eye and the hand have natural and determinate 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. 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.

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 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.

It is important, for historical reasons, to reiterate that the process of evolution by natural selection is not teleological in the purposeful sense. The natural theologians of the nineteenth century erroneously claimed that the directive organisation of living beings evinces the existence of a Designer. The adaptations of organisms can be explained as results of natural processes without recourse to conscious intention. There is purposeful activity in the world, at least in humans, but the existence of particular organisms, including humans, and their features need not be explained as a result of purposeful behaviour.

Some scientists and philosophers who held that evolution is a natural process erred, nevertheless, in seeing evolution as a determinate, or bounded, process. Lamarck thought that evolutionary change necessarily proceeds along determined paths from simpler to more complex organisms (Lamarck 1963). Similarly, the evolutionary philosophies of Bergson, Teilhard de Chardin, and the theories of *nomogenesis, aristogenesis, orthogenesis*, and the like, are erroneous because they all claim that evolutionary change necessarily proceeds along determined paths (Berg 1969; Bergson 1911; Osborn 1934; de Chardin 1959). 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 kind of organism or toward any particular properties.

Teleology and Teleonomy, Aristotle and Aquinas

I want to take up two more issues. The first is a semantic question, the second a historical one. Pittendrigh (Pittendrigh 1958), Simpson (Simpson 1964), Mayr (Mayr 1965), Williams (Williams 1966) and others, have proposed to use the term 'teleonomic' to describe end-directed processes that do not imply that future events are active agents in their own realisation, or that things or activities are conscious agents or the product of such agents. These authors 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 Dobzhansky, Simpson, and Nagel (Dobzhansky 1970; Simpson 1964; Nagel 1961) employ the term 'teleology' without implying a preordained relationship of means to an end. Thus, it might produce 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 useful is to clarify the notion of teleology by explaining the various uses of the term. One may then explicitly express in which sense the term is used in a particular context.

As I have written elsewhere, should the term 'teleology' eventually be discarded from the scientific vocabulary, or restricted in its meaning to preordained end-directed processes, I would welcome such an 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 (Ayala 1970).

Pittendrigh 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' (Pittendrigh 1958, p. 394). The Aristotelian concept of teleology allegedly implies that future events are active agents in their own realisation. 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 (see Mayr 1965; Simpson 1960, p. 125).

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 from these questions are Aristotle's 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 given in answer 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 it serves 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 organised 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 realisation. For Aristotle, ends 'never do anything. Ends do not act or operate, they are never efficient causes' (Randall 1960, 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 (Ross 1949; see also Randall 1960). There is no God designer of nature. According to Aristotle, if there is a God, He cannot have purposes (Randall 1960, 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 it exists. 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 insight concerning this matter surpasses Nagel's.[15]

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 non-living world. In the Middle Ages, Aristotle was 'Christianised,' particularly in the works of the great theologian St. Thomas Aquinas (1225-1274). It was Aquinas, not Aristotle, who accounted for the teleology of organisms, and of nature in general, as the intended purpose of an Omniscient Creator.

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[15] See above, p. 26 about the teology of corn seeds.

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