Natural Selection and Biological Progress

By

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On the last page of *On the Origin of Species* Darwin wrote: " as Natural Selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection ". Thus the *Origin* put forward not only the view that species as we now find them result from processes of evolutionary change and that this change was directed by " Natural Selection ", but also the view that such evolution must necessarily be progressive. It appeared to Darwin inevitable that natural selection must promote progress towards ever higher states.

There have of course been difficulties with this view. Not only is it logically assailable, but to many it is and has been emotionally objectionable, because it has been tied up with the concept of individuals struggling for survival: " nature red in tooth and claw " does not seem too nice a basis for progress towards perfection. Such difficulties were felt by T. H. Huxley who found it impossible to reconcile his concepts of human progress with this concept of biological progress, and found himself forced to deny the applicability of biological progress to man [6]. Progress for man required that he turn his back on nature's " Cosmic Code ", and actively oppose it with the " Ethical Code " that man has made or part-made for himself.[1]

In effect, Huxley was forced to deny that knowledge of the mechanism of evolution can have any ethical message for us, which of course he was entitled to do because any argument of ethics from evolution must be based on the *a priori* premise that what evolution does is desirable. We may either deny this premise or accept it. We cannot justify it. Huxley denied the premise, but others accepted it and some still do, and it is

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[1] [Huxley's ethical views are more fully discussed in chapter 15.—Ed.]

therefore important that, at the biological level, we should try to be clear what such acceptance might imply in the light of contemporary knowledge, for this knowledge may lead to conclusions differing from those that Huxley reached. To be so clear requires that we have some carefully considered concept of biological progress and of the mechanisms that may bring such progress about.

This is an important, though negative, incentive for thought about biological progress. The biologist must do his best to ensure that those who are prepared to base ethical conclusions on evolutionary concepts do not base them on erroneous biological concepts. Some feel, however, that there are positive reasons too. As Dampier has written:

> Regarded as a whole, as in natural history, any organism shows a synthetic unity as its characteristic expression of life, and man, carrying further what is seen in other animals, displays a higher unity in his mind and consciousness—a new aspect of life. The theory of evolution carries this synthetic process a step onward, and discloses an underlying unity in the whole organic creation. Life from a single cell of protoplasm to that infinitely complex structure, fearfully and wonderfully made, which we call man, is linked in all its parts by evolutionary ties. It forms one problem . . . the solution of which, could we reach it, would give us also the solution of subordinate problems, and give us a firm basis for ethics, æsthetics and metaphysics, the inner meaning of the Good, the Beautiful and the True. And one clue to the solution is the theory of evolution elucidated by Darwin's principle of natural selection. [1, p. 344]

Defining biological progress is essential to following that clue.

T. H. Huxley's grandson, Julian Huxley, with such considerations in mind, has done much to develop discussion of biological progress, taking into account our modern knowledge of the course and of the mechanism of evolution, and our knowledge that man is placed in a special position by his ability to learn from the experience of previous generations [4, 5].

Able to weigh the great body of evidence that has accumulated since Darwin's times concerning the course that evolution has actually taken, he has abstracted certain general trends which he calls progressive. These are broadly three: first, increasing adaptation to the more general aspects of the environment; second, increasing independence of the environment or increasing ability to maintain internal conditions despite external variation; and third, increasing rate of evolutionary change. Huxley derives this definition of progress from a consideration of the differences that have at various times distinguished the dominant groups of animals from their less successful contemporaries, and that have distinguished particular successful groups from those that they replaced; he has explicitly departed from Darwin's original attitude that progress must be inevitable and hence universal.

While Huxley's has been a notable contribution to the study of our problem, it has an inherent weakness which leaves many dissatisfied. The weakness is that in essence it defines the progressive as that which has generally (though not always) occurred. Huxley, in effect, assumes that progress has occurred, and then in masterly fashion shows us what we must on this assumption label as progressive. But it needs to be demonstrated that this basic assumption is sound.[1]

Some feel all attempts to define progress must be open to some such objection. Haldane has said " When we speak of progress in evolution we are already leaving the relatively firm ground of scientific objectivity for the shifting morass of human values " and these values are themselves the product of evolution [3]. However, it seems to me, as it seemed to Julian Huxley, that there is no need to involve human values in defining progress *biologically* and that it is possible to stick to the firm ground of objectivity, though of course there is need to involve human logic which itself involves value judgments at a different level.

I have accordingly defined biological progress by basing the definition on objective consideration of the general conditions of living [10]. This approach does not directly involve the " morass of human values " for it leads to a definition of biological progress that does not depend on our preferences. At the same time the approach does not involve the assumption that progress has actually occurred in evolution.

THE DEFINITION OF BIOLOGICAL PROGRESS

Since Darwin's time we have obtained a great deal of knowledge, based on critical experiment, concerning the nature of

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[1] [See also chapter 15.—ED.]

the inheritable individual differences upon which natural selection must operate if it is to produce evolutionary change. In the process, the belief that the inheritance of acquired characters can supply any important part of such variation has receded.[1] The raw material on which natural selection operates is mutation, largely undirected change in the heritable properties of the individual.

This process of mutation provides the basis from which an array of genetically different individuals are produced. In any particular set of environmental conditions some of the kinds of individual will succeed in producing more offspring than others. Their kinds will therefore multiply more than the others and, since the numbers that can survive are limited, will gradually replace the others. This is the basis of evolution by natural selection.

In the classic phrase, this process of natural selection promotes the survival of those relatively more fit to survive. The only form of progress, therefore, that it can promote is progress in fitness to survive, an apparent dilemma that has often been pointed out. For example, Dampier [1] writes: " Herbert Spencer's phrase for natural selection, the survival of the fittest, standing alone begs the question. What is the fittest? The answer is: The fittest is that which best fits the existing environment . . . that which is fit survives, and that which survives is fit." The dilemma, however, is not real and does not need evading. Progress by natural selection can only be increase of fitness for survival, but fitness itself requires elucidation. We can begin to understand the nature of biological progress only if we can satisfactorily answer the question " What does fitness for survival mean? " In particular, is it true to say " The fittest is that which best fits the existing environment "? And if it is true, is this the whole truth?

Defining biological progress as increase in fitness for survival requires some quantitative definition of fitness. The quantity involved will be the probability that, after a given lapse of time, the organism or organisms under consideration will be alive or have left descendants, that is to say, will have been naturally selected. Biological progress involves increase of this probability and any evolutionary change that leaves this

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[1] [See also chapter 1, pp. 6 *et seq.*, and chapter 3.—Ed.]

probability unaffected will be neutral in regard to biological progress, no matter how large it may be in other respects. In seeking to understand biological progress, therefore, we must look into the factors that may favourably or adversely affect the probability of survival.

The actual value of this probability will clearly depend upon the time we choose to consider. The probability that the author will be alive or have live descendants tomorrow is high. The probability that he will be represented by live descendants 1,000 years hence is lower. The probability that he will be represented by live descendants after a million years is lower still. Our choice of time scale is, however, limited, for we are considering progress in evolution and must consider fitness in terms of a time-scale that can permit significant evolution. We are therefore involved in long periods of time such as a million or ten million years.

This being so, we see at once that " The fittest is that which best fits the existing environment " is probably untrue, and is certainly not the whole truth. Environments change, and that which best fits the existing environment will not necessarily fit the future environment at all. That which best fits the existing environment will succeed temporarily, but unless it can also adapt to future environments it will in time fail completely. That which fits the present environment merely adequately may be well equipped to survive the change that is going to occur. *The fit are those who fit their existing environments and whose descendants will fit future environments.*

Environmental change and ability to accommodate to that change are therefore the keys to understanding the nature of fitness and progress. Relative adaptation to the contemporary environment is comparatively unimportant. Here lies the weakness of much thought on our subject and of arguments, frequently met, which claim to show natural selection cannot be the source of biological progress. Such argument was well expressed by Joad, who felt forced to reject natural selection as the source and directive agent of evolutionary change, because he believed natural selection must have an end point when all organisms fit the environment perfectly and no further natural selection is possible [7]. With natural selection Joad threw out all materialist philosophy as well.

> Why, then, it may be asked, does life still develop? [he wrote] Why does evolution go on, and go on to complicate our structure so unnecessarily that, instead of becoming more fitted to our physical environment than we used to be, we are less? A degree of adaptation which, from the purely physical point of view, would put the average human being to shame has been achieved by living organisms thousands of years ago.
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> The inference is irresistible, that the achievement by life of mere adaptation is not enough, but that living beings are evolved at more complicated and therefore more dangerous levels, in the endeavour to attain *higher* forms of life. The amœba, in short, is superseded by the man, not because the man is better-adapted life, but because he is better-quality life. In making this inference, however, we are admitting the suggestion that evolution is not a haphazard but a purposive process—an admission which is incompatible with Materialism.

Here is implied an idea of progress independent of fitness and resulting from some force, mystical in kind, opposed to natural selection. But the argument on which it is based is invalid, for environmental change is in the nature of life and there is no evidence that a stable equilibrium is yet established. The origin of life was itself a change, and since life involves the removal of raw materials from the environment and their return in changed form, it must involve perpetual change of the environment. Furthermore, every evolutionary change involves change in the way the environment is exploited with consequent change of the environment. Since living things are important components of each other's environment, every evolutionary change is a change of the environment to which all organisms must be able to adapt if they are to survive. Evolution must therefore continue if life is to continue ; for, quite apart from inorganically caused change, organisms must always be catching up with the change caused by their own and each other's evolution. If organisms do not continue to evolve, their probability of survival must necessarily fall as environmental changes leave life behind. Failure to evolve must be retrogressive.

Clearly, then, evolution is inevitable if life is to go on. But equally clearly evolution does not inevitably involve biological progress, for much of evolutionary change must be discounted as merely maintaining adaptation as the environment changes.

Progressive evolution can occur only if evolutionary changes do more than this, that is, if they actually increase the probability of survival. There has, on our definition, been biological progress in the last million years only if the probability of survival for a million years from now is greater than the probability of survival for a million years was a million years ago.

One question that has caused difficulty must be made clear at this point. It is the probability of survival, not the fact of survival, that is relevant to our discussion. Our primitive ancestor in whom life on this planet originated has living descendants now. This does not mean that its probability of survival was high. A low probability of survival means a high probability of extinction, but it does not mean inevitable extinction. Likewise a high probability of survival does not imply inevitable survival.

GENERAL FACTORS INFLUENCING THE PROBABILITY OF SURVIVAL

Let us now consider what is required of a solitary individual organism if it is to survive in any way for a million years. First, it must be adapted to the existing environment. Since it is alive we must suppose that it is. Second, it must reproduce, or sooner or later, purely by chance, it will be extinguished by a flash of lightning or some other " random " environmental fluctuation. The first progressive step in evolution, which some would define as the origin of life, is the establishment by reproduction of a *population* of individuals.

Now it seems most unlikely that such reproduction at its origin could be perfect: there would be bound to be mistakes (mutations). The population produced would therefore contain a variety of related types, and natural selection would automatically come into force.

The population must now maintain itself in a slowly changing environment, change partly inorganic in cause, partly determined by the activities of the population itself. Natural selection will first operate so that the members of the population become more and more adapted to contemporary conditions. The more perfectly adapted they become, the greater will be the advantage of their producing offspring adapted like themselves and natural selection will consequently tend to reduce the frequency and the magnitude of reproductive errors (mutations). The probability of survival, therefore, will depend upon the ability of individuals to produce offspring exactly or very like themselves, which we may refer to as the *genetical stability* of the population. However, during any long period considerable environmental change will occur and, unless it too can change, the population will find itself in an environment to which it is not adapted. It can change and, therefore, can survive, only if its individuals are capable of producing offspring unlike themselves, that is to say, if there is *variability*. The probability of survival therefore depends both on the ability of organisms to produce offspring *like* their parents and upon the clearly opposite ability to produce offspring *unlike* their parents. Progress must depend upon the establishment of the best compromise between these antagonistic needs, and upon any resolution of the antagonism that may be possible. The probability of survival will also depend upon the amount of change that will occur in environmental conditions during the period under consideration.

The probability of survival of the population, therefore, will depend upon adaptation, the genetical stability of the population (its capacity to remain adapted), the variability of the population (its capacity to change) and the stability of the population's environment (which determines its need to change). Increase of any of these, provided it does not involve corresponding decrease of another, will be biological progress as defined.

Clearly, genetical stability must depend upon the mechanisms controlling the similarity of parent and offspring—the " genetic system " as Darlington called it [2]. But variability too will be affected by this genetical system, that is to say, by the *genetical versatility* of the population...(Closely similar is the *genetical diversity* of the population. The environment is heterogeneous, that is, there are many environments. If a population includes different kinds of individuals these may be adapted to different adjacent environments. The probability that an environment in which the population can survive will be available in the future will then be relatively large.)

Resolution of the antagonism between stability and variability must therefore be, at least, in part a function of evolving genetical systems, and we must look at these systems for evidence of progress. Variability, however, is not solely to be achieved by genetical variation. It also depends upon the *versatility of individuals*, that is, on the capacity of individuals to accommodate themselves to environmental differences. If they can do so they can survive corresponding environmental change, and their probability of survival is correspondingly large. Our definition of biological progress requires us to call the evolution of such versatility progressive.

Such individual versatility must depend upon a measure of physiological complexity, a complexity that permits the organism to survive unaffected by certain environmental changes; in effect this enables the organism, by becoming independent of some environmental variables, to reduce the effective rate of environmental change. In addition, rather similar complexity may permit the individual organism, or more often a community of organisms, so to *control the environment* that the rate of environmental change is actually reduced. This too will increase the probability of survival, as also will control of the environment directed towards adapting the environment to the organism and making adaptation of the organism itself less necessary.

Biological progress then may be in principle brought about by any evolutionary change that so improves the genetical system that the antagonism between genetical stability and genetical versatility is reduced, any change that increases individual versatility, any change that increases the diversity of types and hence the number of environments to which there are adapted forms, and any change that permits the organism to control its environment in such a way that the environment remains suitable or becomes more suitable for the organism.

GENETICAL STABILITY AND GENETICAL VERSATILITY

Studies of the mechanism of heredity in a wide variety of organisms are beginning to show us that organisms have in the past developed genetical systems (systems controlling heredity and variation) that go a long way to resolving the antagonism between the conditions of survival they have had to meet.

Mutation is the source of the variation that a population must exploit if it is to be genetically adaptable, but mutation, a sudden change of hereditary properties, is necessarily a breakdown of genetical stability. Organisms have, however, evolved mechanisms that permit them to carry potential variation without showing corresponding actual variation, and thus to retain genetical versatility while increasing stability.

There are several ways of doing this [9], all dependent upon the organism having sexual reproduction (or some such means of combining genes from different individuals), but only one will be described here. It depends on the organism possessing a number of pairs of alternative genes affecting the same character. (The difference between the members of such a pair of genes will have been produced by mutation.) Stability is achieved as a result of these genes being tied together in the same mechanical system, the chromosomes.

We will illustrate the principle in greatly simplified form. Suppose the character is size (though less evident physiological characters are likely to be far more important). Then we have what we may call "plus" $(+)$ genes that increase size, and "minus" $(-)$ genes alternative to them which decrease size. We will suppose the system to comprise only two pairs of alternative genes, both equally effective, and that the optimum size of the organism is given by the combination of two $+$ and two $-$ genes. There are four kinds of chromosome $\underline{++}$, $\underline{+-}$, $\underline{-+}$ and $\underline{--}$, and, since each individual has a pair of the relevant chromosomes, these can be combined in four different ways to give adaptive sizes, thus:

$$\frac{++}{--}, \frac{+-}{+-}, \frac{-+}{-+} \text{ and } \frac{+-}{-+}.$$

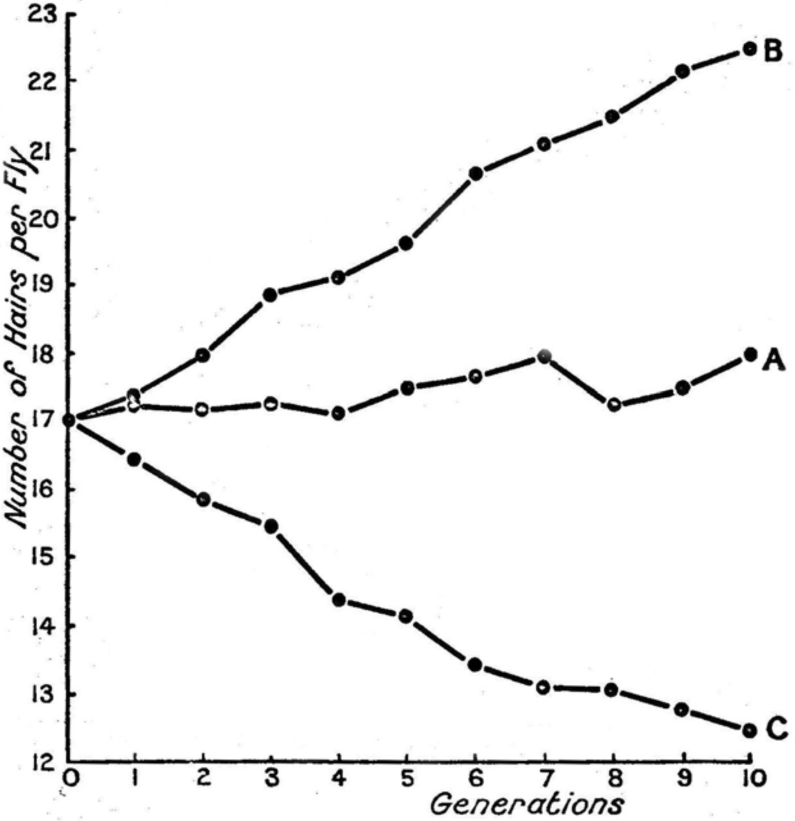
The first of these is a variable arrangement. When an organism reproduces sexually, each of the gametes (eggs or sperm) it forms receives one member of each of the pairs of chromosomes it contains. Thus a $\frac{++}{--}$ individual will form $\underline{++}$ and $\underline{--}$ gametes. Two such individuals mating will therefore produce a proportion (one-quarter) of offspring by combination of a $\underline{++}$ egg and a $\underline{++}$ sperm. These will be $\frac{++}{++}$ and will be too large. Likewise a proportion (one-quarter) of the offspring will be $\frac{--}{--}$ and will be too small. Only half the offspring will be $\frac{++}{--}$. This arrangement of the genes therefore produces a wide variety of offspring. It is versatile but unstable.

By contrast the $\frac{+-}{-+}$ arrangement of genes is one which is both stable and versatile. Individuals of this type will form two kinds of gamete, $\underline{+-}$ and $\underline{-+}$, and these can be combined to produce offspring of three types, $\frac{+-}{+-}$, $\frac{-+}{-+}$ and $\frac{-+}{+-}$. Each of these types has two + and two − genes, and all of them will therefore have the same genic size properties as their parents. The size is stable in heredity. However, in gamete production there are exchanges of material (crossovers) between members of a pair of chromosomes, such that a $\frac{-+}{+-}$ individual will produce a few gametes carrying $\underline{++}$ chromosomes and a corresponding number containing $\underline{--}$ chromosomes. These provide a source of variability that can be exploited to produce $\frac{++}{++}$ or $\frac{--}{--}$ individuals if and when a change of size is necessitated by a change in environmental conditions. The system is therefore in principle stable but, at the price of regularly producing a few ill-adapted variants (the crossovers), permits the maintenance of adaptability that can be exploited rapidly if the need arises. This model is grossly over-simplified, but it illustrates how the principle works, and how the tying together of genes in chromosomes permits some resolution of the antagonism between stability and variability to which we have referred.

It is in fact quite astonishing how stable and at the same time how versatile their genetical systems permit some natural species to be. An example from the author's own work will suffice to illustrate this. The figure on page 325 shows the results of experiments on some flies, all of which were the descendants of one fertilized female captured in the wild. The character studied, chosen purely because it is experimentally convenient, was the number of hairs on a certain part of each fly. Graph A shows the average number of hairs per fly in a population in which the parents of each generation (four pairs of flies) were selected at random. The number of hairs remains fairly steady, showing the stability of the character. Graph B shows the average number of hairs per fly in a population in which the 5 per cent of flies with most bristles were deliberately selected in each generation to be parents of the next generation. Graph C shows a population artificially selected for low bristle-number in the same way. It is clear from these graphs that the population responded readily to artificial selection in either direction. Further, the artificial selection produces something new. The fly with the most hairs found in generation 0 had 23 hairs; that with the least had 13. By generation 10 artificial selection for high hair-number had produced a fly with 32 hairs, and artificial selection for low hair-number had produced a fly with only 9 hairs. The selection has not only changed average hair-number but has produced new types of fly.

It is known that mutations occurring during the experiment cannot account for these responses. The genetical make-up of the original wild female and its mate, from whom all these populations were descended, was therefore such as to determine a high stability of hair-number but yet to preserve great potential variation; so that hair-number could be altered quickly if new conditions (here the artificial selection) required it. The system is both stable and versatile. The antagonism between stability and variability is partially resolved.

This stability and versatility depend upon what we call "balanced heterozygosity". $\frac{+}{+}$ and $\frac{-}{-}$ individuals are said to be homozygous, and can each produce only one kind of gamete. $\frac{+}{-}$ individuals are said to be heterozygous and can produce two kinds of gamete. Genetical versatility is promoted by heterozygosity, but balanced heterozygous systems permit stability as well. Homozygous systems also permit stable populations but cannot preserve versatility, which we consider to be the reason why populations with heterozygous systems are the more usual. Natural selection may and does establish species with homozygous systems (for instance, self-fertilizing species), but in *the long run* it must eliminate these and preserve only the versatile heterozygous species. These depend for their heterozygosity on *out-breeding* (cross-breeding) systems which limit the amount of mating between near relatives: we must regard the origin of such genetical and breeding systems, and of sexual reproduction and the chromosome mechanism that are part of them, as having involved evolutionary progress.



55.—Changes in average hair-number resulting from artificial selection in populations of flies. For explanation see text.

A—average hair-numbers in a population not selected (the "control").

B—average hair-numbers in a population selected for high hair-number.

C—average hair-numbers in a population selected for low hair-number.

Each point is the average obtained from 160 flies.

GENETICAL DIVERSITY

A population can also partially resolve the antagonism between stability and variability by splitting into two populations. Let us take the same simplified example as before, two pairs of genes affecting size. These, it will be recalled, can exist together in a number of combinations giving intermediate size, namely $\frac{+-}{+-}$, $\frac{-+}{-+}$, $\frac{+-}{-+}$ and $\frac{++}{--}$. Now a population can achieve a stable intermediate size, and yet preserve all these genes by splitting up into two separate populations one of which is $\frac{+-}{+-}$ and the other $\frac{-+}{-+}$. Each of these is homozygous and will be genetically stable apart from mutation, but each has lost its genetical versatility. However, if individuals from the two new populations occasionally cross, they will reconstitute the versatile $\frac{+-}{-+}$ type and thus, *provided that the two subpopulations do not separate completely*, genetical versatility may be preserved. The separation of a population into two populations that can never cross with one another is the sort of thing that is involved in the formation of new species. We therefore see that the origin of species is not necessarily evolutionary progress by our definition. To be progress it must produce something that compensates for the loss of genetical versatility that in some measure it must involve.

A further principle may be illustrated to strengthen this point, though it is necessary to consider more pairs of genes for this purposes. Four pairs will do. $\frac{+-+-}{-+-+}$ may be regarded as our starting point. Let us suppose a population contains these two types of chromosome, and lives in an environment where 4 + and 4 − genes together give adaptive size. Now let us suppose that this environment changes so as to produce two different environments in one of which 6 + and 2 − genes would give optimal size, and in the other 2 + and 6 − genes. Our population is versatile, since it contains heterozygous individuals, and these can produce new kinds of chromosome by exchange of parts between the old kinds, for example, $\underline{++-+}$ and $\underline{--+-}$. Natural selection will pick these out and may produce two sub-populations of different sizes, occupying the two new environments, namely, $\frac{++-+}{++-+}$ and $\frac{--+-}{--+-}$. The old types will be eliminated. Complete separation of these two new populations would form two species. However, they would retain greater probability of survival if they did not separate completely. For suppose the change in the two environments were to continue until 8 + genes were needed in the one, and 8 − genes in the other. Apart from mutation, only a cross between the two populations could produce the type, namely $\frac{++-+}{--+-}$, that could produce these. The two populations would therefore have a higher probability of survival if they retained the tendency to cross.

Such environmental situations are common in nature. In fact, most species occupy heterogeneous environments. Hence we would expect natural selection to ensure corresponding genetical diversity. Such diversity provides a source of genetical versatility. But it also ensures that a species shall consist of a number of types each adapted to different environments. The probability that all these environments will disappear is smaller than the probability that one of them will. Such genetical diversity therefore increases the probability of survival in two ways, first by providing individuals adapted to a number of environments and second by preserving genetical versatility in a stable system.

Natural selection, therefore, is not to be expected to give rise to uniformity, a best, ideal type. Fitness, which natural selection must promote, depends upon diversity. Further, species formation, though it involves increased diversity, is not necessarily progressive, for it involves some loss of genetical versatility. Progress is more likely if diversity can be achieved without speciation, that is, by the formation of separate races which to some extent interbreed. This is a conclusion strikingly different from that of Darwin's followers to whom speciation was of the essence of evolutionary progress, a view that has been held by many thinkers on the subject ever since. Sir Arthur Keith, for instance, wrote: " If a tribe loses its integrity : . . by free interbreeding with neighbours and thus scattering its genes, then that tribe as an evolutionary venture has come to an untimely end. For evolutionary purposes it has proved a failure " [8]. There is no warrant for a statement of this generality. A tribe is at least as likely to increase as to decrease its fitness by mixing genetically (and culturally) with others. Even if purity of race were achievable, it would not be desirable.

INDIVIDUAL VERSATILITY

As indicated above, the probability, that a population of organisms will survive a given amount of environmental change, is not only dependent upon the versatility of its genetical system, but may also be influenced by the versatility of the individuals comprising the population. If the individuals can cope only with a restricted range of environmental conditions, the amount of environmental change the population can survive without genetical versatility will be correspondingly restricted. If, on the other hand, the individuals comprising the population can each cope with a wider range of environmental conditions, not only will the population be able at any one time to occupy a wider range of environments (and hence to exist in larger numbers), but the probability that all the environments the individuals can occupy will disappear will be correspondingly smaller.

There can therefore be no doubt that, unless it be achieved at the expense of a greater amount of genetical versatility, any increase in individual versatility is progressive. It is this aspect of progress that has most attracted the attention of biologists. Reptiles are capable of withstanding a greater range of humidity than are amphibians. Mammals and birds are capable of functioning in a greater range of temperatures than are reptiles. The reader is referred to the writings of Julian Huxley [4] for detailed discussions of such biological progress.

Such individual versatility must depend upon a certain measure of physiological complexity. Complexity therefore may be essential to this aspect of biological progress, and some authors have in fact regarded increasing complexity as itself evidence of progress, though there seems to be no warrant for this. Increased complexity of a particular kind (such as to result in increased individual versatility) is biological progress, but not increased complexity of any kind.

ENVIRONMENTAL CONTROL

Progressive increase of individual versatility, an increase itself dependent on genetical versatility, has in time brought some organisms to a degree of complexity permitting them not only to become independent of some aspects of environmental change, but also to control the environment so as to render it less liable to change.

All organisms affect their environment, but this is not to say that all organisms affect their environment in such a way as to increase their fitness or probability of survival by reducing the rate at which the environment becomes unsuitable for them. The fungus attacking an apple rots the apple and destroys it. The parasite may kill the host on whom it depends, and may even extinguish the host species and hence its own. On the other hand beavers build and maintain dams and birds build nests, thus altering the environment to make it more suitable for themselves. Likewise, as we have learnt at some cost, the stability of most, if not all, soils depend upon the vegetation, especially trees and grasses, whose roots bind the soil together and prevent it from being blown or washed away. Such control of the environment depends to a great degree on co-operation between individuals (and between species), for a single grass plant can seldom hold any soil on a slope. It requires a sward. Thus, once such capacity to control the environment is evolved, natural selection will tend to promote co-operation.

Supreme in ability to control his environment is man, because his ability to communicate information renders him able to co-operate in the control of nature in an entirely new way. It is this that determines man's dominance in contemporary nature.

BIOLOGICAL AND HUMAN PROGRESS

As we have seen, the organisms that have the greatest probability of survival are those which are not only adapted to their contemporary environment but which also to the greatest degree possess genetical stability and versatility, racial and individual diversity, individual versatility and the capacity to control their environment so as to maintain its suitability for them. There can be no doubt that man is one of the species that possesses these attributes in most marked degree, and it seems unlikely that any other species can match man in fitness as defined here. Increasing, though very limited, knowledge of human genetics leaves little doubt that man's genetical system provides considerable versatility and diversity within most human populations, and there is also considerable racial diversity so that potential variation may be exploited through racial hybridization provided that those with wrong-headed ideas of the biological function of races do not prevail.

In addition, man possesses a degree of individual versatility and environmental control that no other species can equal. He is capable of functioning successfully in a wider variety of environments than any other species. He can function in the arctic and the tropics, he can cross the sea and penetrate its depths, he can climb mountains and burrow into the earth, and he can fly in the air. A lot of nonsense is written about man's unfitness by comparison with other animals. No other species can be warm in the arctic and cool in the tropics: stoves and air conditioners are adaptations just as much as are hair and sweat glands. In fact, man can travel along the ground faster than any animal, on water faster than any fish, and fly the air faster than any bird. It is nonsense to deny these facts just because they depend upon machines not limbs, and because these attributes of man have been evolved by social, not biological, means. If all the factors involved in fitness as here defined had to be measured by one approximate empirical measure, that measure would be the range of environmental conditions in which the species can function, for this is closely related to the range of environmental change the species could survive and hence to its probability of survival. Man with his aids is at least as fit as and probably far fitter than any other species by this measure.

Man has reached this stage because, with his evolution by natural selection, a new form of evolution became effective. Man evolves not only by natural selection of genetical constitution (biological evolution) but by the non-biological inheritance of acquired environment (social evolution). What one man learns can be taught to others without the necessity of biological relationship, and what each generation achieves can be handed to the next by the path of social inheritance. Man has thus acquired a degree of control of the environment that could not otherwise have been achieved.

In this new phase of evolution man has not escaped the biological necessities. Adaptation, genetical stability and versatility are still required for maximum fitness. But stability and versatility are now also to be considered in a new context, social evolution, in which stability is maintained by tradition, and versatility by the continuous production of new ideas. Once again we have the old antagonism at a new level, and progress will be much dependent upon resolution of the antagonism within political systems in which new ideas and old traditions can react upon one another with minimum discord so that change may be harmonious. Thus man may come into increasing harmony with his environment, living and non-living.

However, fitness, or the probability of survival, is not necessarily increased and may be decreased by environmental control. Control of the environment not only permits stabilization of the environment and the improvement of the environment in the directions that will increase the probability of survival, but also permits the exploitation of the environment for short-term ends that make long-term survival less probable. For fitness to be increased the control must be directed to the right end. In the main the end must be increasing harmony between the controlling organism and the environment, which of course includes all other organisms. This requires not only the intention that the end shall be attained, but also increasing knowledge of the environment such that the results of attempts to control it shall become more predictable.

Once knowledge of the environment has reached this predictive level man may be ready to embark upon a third phase of evolution, in which not only the environment, but also genetical constitution is controlled, so that, by genetical and environmental control, both the genetical constitution of the species and the environment are brought into ever more perfect harmony. Once again such control will be biologically progressive only if directed to the right end, increasing harmony with an increasing range of environments. And since a most important component of the environment for each man is other men, this includes harmony amongst ourselves. Such control of evolution would seem to be the natural outcome of natural selection.

PROGRESS OF LIFE

So far we have only considered biological progress with respect to the probability of survival of a population or species. We have not considered the general progress of life itself. By the same argument that we applied to a population we must here be concerned with the probability that any life at all will survive after the lapse of a long period of time. This probability is clearly related to the probabilities of survival of all the separate species of which life is composed. Life therefore progresses as each of its component species progresses in adaptation, in stability, in versatility, and in their control of the environment towards its improvement for their own long-term ends. It will also tend to progress as the diversity of species increases.

It does not, however, follow that mere increase of number of species is necessarily biological progress for life, for species interact on one another because they are components of each other's environment. They therefore determine one another's probability of survival. The origin of a new species, therefore, may or may not be progressive. It will be progressive in so far as the new species does not reduce the probability of survival of old species by as much as the probability of survival of the new species itself.

This will be so if the new species occupies a new environment to which hitherto no species had been adapted, as occurred when aquatic forms gave rise to others capable of living in land marshes, and when the marsh forms gave rise to those living on dry land. (In the same way the conquest of space may be progress for life.) This will also be so if the new species occupies an old environment, but exploits that environment in a way that harmonizes with its use by old species, and even, as do the various species involved in the nitrogen cycle, makes that environment more suitable for the other species that occupy it. On the other hand, the origin of new species will not involve biological progress for life as a whole if the new species merely competes with the‸species for limited environmental ‸old resources.

Biological progress, therefore, not only involves increasing versatility of individual species, but also increasing diversity of species *harmoniously adapted to one another*. It would seem therefore that nature's code is far nearer to Huxley's " ethical code" than to the "cosmic code" of struggle which he rejected. As was pointed out at the beginning of this article, we cannot justify any argument of ethical principles from evolutionary principles. If, however, we were to accept the premise that what evolution does is desirable, the conclusions we would reach today would be the opposite of those that T. H. Huxley reached.