

## Natural Selection and Evolutionary Progress\*

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### MULTIFORMITY OF EVOLUTION

THE students of a particular aspect of evolution are prone to think that their conclusions are generally applicable, whereas they usually are not. The palæontologists unearth long evolutionary series and claim that evolution is always gradual. However, their conclusions apply almost entirely to abundant and mostly to marine animals. In some land plants, on the contrary, we now have evidence of a wholly different method of evolution—namely, the discontinuous and abrupt formation of new species. In rare forms the course of evolution will not run in the same way as in abundant and dominant types.

Meanwhile the naturalist and the comparative physiologist are struck by the adaptive characters of animals and plants: to them the problem of evolution becomes synonymous with the problem of the origin of adaptation. The systematist, on the other hand, is struck by the apparent uselessness of the characters on which he distinguishes species and genera.

The palæontologist, confronted with his continuous and long-range trends, is prone to misunderstand the implications of a discontinuous theory of change such as mutation, and to invoke orthogenesis or Lamarckism as explanatory agencies: and, since there exist more rare than abundant species, the biogeographer will have to discount the fact that he is dealing mainly with processes irrelevant to the major trends of evolution regarded as a long-range process.

### SELECTION IN A MENDELIAN WORLD

In our attack upon the problem, we must first mention some implications of recent genetics. Essentially, the modern conception may be put as follows. The notion of Mendelian *characters* has been entirely dropped. Instead of a given gene having a constant effect, its actual effect is dependent upon the co-operative action of a number of other genes. Mutations which in one gene-complex are pathological, in another may be perfectly harmless, and in yet another advantageous. The adjustment of such mutations to the needs of the organism may occur entirely through recombination of existing modifiers, or, after a preliminary

and partial buffering by this means, the final adjustment may have to wait upon further mutation.

Thus, evolution need not occur by a series of sharp single steps; each such step is immediately buffered by ancillary changes in genes and gene-combinations. What evolves is the gene-complex; and it can do so in a series of small if irregular steps so finely graded as to constitute a continuous ramp.

Nor is the pathological character of many mutations at their first appearance necessarily a bar to their final evolutionary utilization by the species. The mutant gene *eyeless* in *Drosophila* was originally described as considerably reducing the size of the eyes, in some cases to complete absence, markedly decreasing fertility, and depressing viability. When, however, a stock for *eyeless* was inbred for a number of generations, it was found that practically all had normal eyes and showed little reduction in either fertility or viability. On outcrossing to the normal wild type and re-extracting the recessives in *F*<sub>2</sub>, it was found that these once more manifested the original characters of *eyeless*, though in even more variable degree.

The explanation of these facts is that the manifestations of *eyeless* are readily influenced by other genes, and that in general those modifiers which make for normal viability and fertility also make for normality in eye-size. Thus, natural selection acting upon the recombinations of modifiers present in the stock speedily saw to it that the combinations making for the manifestation of reduced eyes were eliminated. In competition with the wild-type allelomorph, *eyeless* would be eliminated; but in stocks pure for *eyeless*, the genes to be eliminated will be the plus modifiers of the mutation.

Selection of this type, it now appears, is a constant and indeed normal process. It has become almost a commonplace in animals used for genetic analysis to find that mutant types which at first are extremely difficult to keep going, after a few generations become quite viable. This has repeatedly occurred in *Gammarus*, for example, as well as in *Drosophila*, and is also known in mice and nasturtiums. R. A. Fisher has extended this concept to explain dominance and recessiveness in general. These are to be regarded as modifiable

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characters, not as unalterable inherent properties. Dominant genes, or most of them, are not born dominant: they have dominance thrust upon them. Mutations *become* dominant or recessive, through the action of other genes in the gene-complex.

In addition to the initial or intrinsic usefulness of a few small mutations, we have also the fact that mutations which are initially deleterious may become advantageous either in an altered environment or in an altered genic background, and the further fact that many mutations or Mendelizing variations cannot be described as intrinsically useful or harmful, but vary in their selective effects with variation in environmental conditions.

We must now discuss the processes of evolution and the role which selection may play in them. Darwin himself happened to confuse the issue by calling his greatest book the "Origin of Species". Evolution, however, must be dealt with under several rather distinct heads. Of these, one is the origin of species—or we had better say the origins of minor systematic diversity. Another is the origin of adaptations. A third is extinction. A fourth, and in many ways the most important, is the origin and maintenance of long-range evolutionary trends.

#### THE ORIGINS OF SPECIES

First, then, we have the origin of species. It is logically obvious that every existing species must have originated from some pre-existing species, but equally clear on the basis of recent research that it may do so in one of several quite different ways. A single species as a whole may become transformed gradually until it comes to merit a new specific name. Or it may separate, also gradually, into two or more divergent lines. Or it may hybridize with another species and the hybrid product then, by doubling of the chromosomes (allopolyploidy), give rise at one bound to a new species. Here, instead of one species diverging to form two, two converge to form one. So far, convergent species-formation is known only in plants. In these cases hybridization, apparently involving many more than two forms, together with recombination, chromosome-doubling and apogamy, appears to have been, and still to be, at work. A similar process, but without chromosome-doubling and apogamy, occurs in man. Thus species-formation may be continuous and unilinear; continuous and divergent; abrupt and convergent; or what, following a recent writer, we may call reticulate, dependent on constant intercrossing and recombination between a number of lines, and thus both convergent and divergent at once.

Divergent splitting must clearly be postulated on a large scale, if only to account for the rapid increase of the number of forms in newly evolved groups such as the higher placental orders. What without question are different stages of the process are yielded by a study of geographical distribution. Physiological subspecies are of a similar nature.

In all these cases isolation, whether geographical or physiological, is involved. We cannot be sure whether isolation simply makes it easier for selection to cause adaptive divergence in relation to local conditions, or whether in some cases at least, by some method as yet obscure, it permits the fruition of mere random and biologically useless variation. It does not matter in principle whether isolation is effected gradually or abruptly; in any case subsequent divergence will be gradual (except the cases of convergent species-formation, where the isolating process itself produces marked differences in appearance).

Biologists have realized for some time that the term *species* is loose and difficult of definition. However, whether we can define species or not, or whether we ought to emphasize the distinctions between different kinds of species by refinements of terminology, it remains true that species are genuine biological units. On the other hand, we can distinguish in principle between the causes of their isolation and the causes of their divergence.

From the point of view of natural selection, species will then fall into two contrasted categories. On one hand we have those in which natural selection can have had nothing to do with the origin of the basic specific characters, but merely acts upon the species as given, in competition with its relatives. These include all species in which character-divergence is abrupt and initial. On the other hand, we have those forms in which character-modification is gradual. Here natural selection may, and on both deductive and inductive grounds often must, play a part in producing the characters of the species. This helps to bring home the heterogeneity of the processes which we lump together as 'evolution'.

#### ADAPTATION AND SELECTION

We next come to the origin of adaptations. How has adaptation been brought about? Most biologists look askance at orthogenesis *sensu stricto*, and also at Lamarckism. As Fisher has cogently pointed out, the implications both of Lamarckism and of orthogenesis run directly counter to the observed fact that the great majority of mutations are deleterious.

There remains natural selection. We must invoke natural selection whenever an adaptive structure involves a number of separate steps for its origin. A one-character, single-step adaptation might clearly be the result of mutation. But when several or many steps are involved, it becomes inconceivable that they shall have originated simultaneously. The improbability is therefore enormous that they can have arisen without the operation of some agency which can gradually accumulate and combine a number of contributory changes: and natural selection is the only such agency that we know. Natural selection achieves its results by giving probability to combinations which would otherwise be in the highest degree improbable.

This important principle clearly removes all force from the 'argument from improbability' used by many anti-Darwinians, such as Bergson. It helps us also to detect the fallacy sponsored by T. H. Morgan, who has asserted that natural selection merely preserves certain among the hosts of recombinations, and that, in the absence of natural selection, in addition to the known forms of life a vast assemblage of other types would exist which have been destroyed by selection.

According to the view of the pre-adaptationists, variations occur which would be adaptive in some new environment or way of life, and their possessors then find their way into that environment or take up that way of life. What we have previously said makes it clear that this can only apply to the early stages of an elaborate adaptation, not to its whole history. Mutations, however, do occur which may be described as *potentially pre-adaptive*.

In general, the evidence that we possess goes to show, first, that selection can be very efficacious in altering the mean of a population within the range of existing variability; secondly, that a relaxation of selection will allow the type to deviate away from adaptive perfection, quite outside the range of variability to be found where selection is more stringent; and thirdly, that adaptive characters may advantage their possessors in such a way as to exert definite selection-pressure in their favour, and that accordingly selection can have a continuous guiding effect towards adaptive perfection.

#### EVOLUTIONARY TRENDS

We must now consider long-range evolutionary trends. It is quite clear that many of these are adaptive. So obvious is this fact that it has found expression in the current phrase *adaptive radiation*.

It is hard to understand why the trends seen in adaptive radiation have been adduced as proof of internally determined orthogenesis. Whenever they lead to improvement in the mechanical or neural basis for some particular mode of life, they will confer advantage on their possessors and will come under the influence of selection; and the selection will continue to push the stock further and further along the line of development until a limit of perfection, usually determined by quite simple mechanical principles, has been reached.

The only feature inviting orthogenetic explanation is the directive character of the trends. But on reflection this too is seen to be not only explicable but also expected on a selectionist point of view. Specialization, in so far as it is a product of natural selection, automatically protects itself against the likelihood of any change save further change in the same direction.

However, that this apparent orthogenesis is determined functionally is excellently shown by the evolution of the elephants, during which the effective reach of the animals for their food was continuously increased, but the structural basis was wholly altered. It is impossible to stretch the principle of internal orthogenesis to cover a process of this type.

The same principles would seem to apply in general to small-scale adaptations as to long-range adaptive trends, except that since such adaptations frequently concern only one particular function and not the organism's main way of life, it should be easier for evolutionary direction to be changed, and for adaptation to set off on a new tack.

An important difference will be found between abundant and scarce species. In the latter, competition will be more with other species, while in the former it will be more between members of the species itself. In general, this latter or *intra-specific* type of selection is more widespread than the inter-specific.

It is a common fallacy to think of natural selection as first and foremost a direct struggle with adverse weather, with enemies, or with the elusive qualities of prey. The most important feature of the struggle for existence is intra-specific competition.

It is another fallacy to imagine that because the major elimination of individuals occurs in one period of life, therefore selection cannot act with any intensity on the phase of minimum numbers. Selection, in fact, can, and does, operate equally effectively at any stage of the life-cycle. Further, elimination is far from being the only tool with which selection operates. Differential fertility of the survivors is also important, and in man and many plants is probably the more influential.

(To be continued.)