

CAN EVOLUTION BE EXPLAINED IN TERMS OF KNOWN
GENETICAL FACTS?

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The facts to be explained are mainly derived from two sources. On the one hand the paleontologists describe successive faunas, and in some cases are able to construct extremely plausible lineages. The best of such lineages, such as the Micrasters of the English chalk, show quite continuous evolution, the populations at successive levels overlapping. Where, as in the case of the horse, apparent discontinuities exist, it is possible to postulate continuous evolution in an unexplored area. But many of the trends displayed by such series are hard to explain. Such a trend is the tendency to evolve certain characters, for example, large size, whose full development was a prelude to extinction. Equally difficult to explain is the trend well shown in certain Ammonite lineages and deduced elsewhere by embryologists, for tachygenesis, that is to say, the appearance at progressively earlier stages in the life cycle of a character at first only found in the adult. This leads to the phenomenon of recapitulation, which could readily be explained on such an hypothesis as racial memory, were any genetical facts available to support such a hypothesis.

The systematists, on the other hand, describe groups of closely related species of such genera as *Crepis* or *Partula*, each with its characteristic habitat. It is moreover hard to escape from the arguments brought forward by such workers as WILLIS that many of these species have originated quite suddenly within recent times. Thus while the paleontologist often proves, and never disproves, continuous evolution the systematist makes the existence of discontinuous evolution almost certain. It may be that these two types of evolutionary phenomena are due to different causes. It is at least noteworthy that, while the paleontologist deals with species which were very common in their own time, and often lived in a constant environment such as the sea bottom, the systematist is mostly concerned with rare species, often occupying rather small ecological niches. The two types of species, dominant and rare, may therefore evolve under rather different sets of causes.

The answer to our original question must fall into two parts. First, are interspecific differences similar to intervarietal, and thus explicable by the accumulation of differences of known types? Second, if the first question is answered in the affirmative, can we account for observed evolutionary trends?

When we are able to analyze the differences between two species we oc-

asionally find cases which are fully explicable by gene differences. Thus CHITTENDEN analyzed the differences between *Primula acaulis* and *P. Juliae*. The yellow flower pigment of the former and the purple of the latter are each determined by separate dominant genes. The F_1 possessed both pigments, and approximately one-sixteenth (four out of sixty-eight) of the F_2 had neither and were therefore white. Other differences seemed to be due to relatively small numbers of genes.

In mammals the color differences between related species and subspecies (*Mus musculus* and *M. bactrianus*; *Mus rattus rattus*, *M. rattus alexandrinus* and *M. rattus tectorum*; *Cavia porcellus* and *C. rufescens*) are found to be due to small changes at the *a* (black) and *e* (recessive yellow) loci, less pronounced than those found in mutants of domestic forms such as the black mouse or the cream *Mus rattus*. This is so even when, as in the case of *Cavia*, the species are so far removed from one another as to give sterile male F_1 hybrids. GREEN'S analysis of the above mouse cross not merely makes it probable that the size difference between these species is due to genes, but identifies the chromosome carrying one of these genes.

In plants at any rate cytoplasmic differences between species sometimes occur, but the work of BLEIER shows that they may be negligible. In hybrids between *Lens esculenta* and *Vicia faba* (the latter as pollen parent) the *Lens* chromosomes are eliminated, and the resulting plants can not be distinguished from *Vicia*.

Commonly, however, the results of species crossing are dominated by cytological differences. These may be in the number of chromosomes (for example in polyploid series), in the arrangement of the chromatin (for example, segmental interchange in *Datura* species) or both. Both these types of difference can be produced experimentally within a species. Further, by hybridization new amphidiploid species can be made, such as *Primula Kewensis*, or old ones recreated, as in MUNTZING'S synthesis of *Galeopsis tetrahit*. More complex results can also be obtained by hybridization, as in the case of CLAUSEN'S synthetic *Viola arvensis*.

We can to some extent extrapolate this analysis to the case of species which will not cross. This may be done, as by ANDERSON in *Dianthus*, by the use of a third species as a bridge, by comparing the chromosome arrangement, as in different *Drosophila* species and so on. There is no suggestion of a qualitatively new type of difference not found in more closely related species. Semisterility of hermaphrodites or of both sexes, and sterility of the heterogametic sex, may be produced between varieties by chromosome rearrangement. Death of all F_1 hybrids has not yet been observed between

varieties, but almost all the other phenomena once thought to be characteristic of species crosses have now been observed after varietal crosses. There is no strong reason to doubt that DARWIN was correct in regarding varieties as incipient species.

Unless some genotypes are fitter than others, a population in which polymorphism is due to genes is in equilibrium, apart from effects of mutation and random extinction. The latter can be shown to be unimportant as an evolutionary agent in large populations, but may have acted on small populations (for example, in oceanic islands). Mutation, though needed to account for initial polymorphism, will not cause a gene to spread through a population in the face of any but the very feeblest natural selection working in the opposite direction. It would seem that the main burden of causing evolution must be thrown on natural selection.

Observation shows that it occurs. Calculation shows that it would produce changes fast enough to account for the speed of evolution recorded in the rocks. But many difficulties remain. Individual mutations are generally harmful, as is inevitable if a species is in equilibrium. Otherwise the mutant forms would displace the type. And a successful change in such an organ as the eye requires the compresence of several mutant genes (coaptation). GONSALEZ described a case in *Drosophila* where a double recessive had a longer expectation of life than either single recessive. In such a case more than one stable equilibrium is possible in a population. It is possible that species of a related swarm may represent different stable equilibria, each having a combination of genes such that changes in only one or two at a time would lower fitness. To pass from one such equilibrium to another, either an unrepresentative fraction of a population must be isolated, or as the result of a chromosomal rearrangement two genes must come to be so closely linked as to be inherited together. The possibilities of gene recombination are enormous. Assuming 400 loci in *Drosophila* and only two allelomorphs at each (both underestimates) we should have 2^{400} possible combinations. It is highly probable that many of these are fitter than the wild-type.

The evolutionary appearance of apparently useless characters can often be tentatively explained by the multiple effects of genes (DARWIN'S "correlation") and the fact that apparently irrelevant genes restore a physiological balance. Thus in order to be hairy *Matthiola incana* must have colored flowers. If arc wing were selected for in *Drosophila melanogaster* the addition of an axillary spot would increase the fitness.

Characters actually detrimental to a species may spread as the result of

natural selection when competition is largely between members of the species, that is, whenever there is crowding at any stage of the life cycle. Thus where a gene for a somatic character slows down pollen-tube growth (as in *Zea* and *Oenothera*) such a somatic character will be eliminated even if moderately advantageous. And there will be no compensatory advantage to the species due to the gain of a few hours between pollination and fertilization of the ovules. Competition between male animals may be expected to lead to an increase in size which may be detrimental to a species for other reasons. Again in polytalous mammals we may expect that genes favoring rapid embryonic growth will spread, as slower growing embryos are at a disadvantage. Such genes will not necessarily or even generally produce characters advantageous in the adult. We can thus understand the orthogenetic evolution of characters which make the species as a whole less fit and may lead to its extinction. This tendency will however be in abeyance in a relatively rare species where competition usually occurs with other species rather than between members of the same species.

Where characters are very nearly neutral from the point of view of fitness, mutation may be expected to determine evolutionary trends. It is capable of explaining the slow reduction of useless but not harmful organs, such as the pelvis of the whale. It can also explain certain cases of tachygenesis, for the following reason. Wild-type genes will tend to increase in dominance for two causes. On the one hand, as FISHER pointed out, this will lead to partial protection against harmful mutations; on the other hand, mutation in this direction will not be prevented by natural selection. According to GOLDSCHMIDT dominant genes produce their effects more rapidly than recessives. The characters produced by them will thus tend to appear progressively earlier in the life cycle.

While we cannot yet explain all evolutionary phenomena in terms of known genetical facts, the number of phenomena so explicable increases every year, and there is no sign that the possibilities of explanation are reaching a limit. We may reasonably hope for a fairly complete explanation.

It would seem that we must envisage the possibility that there are two rather different types of evolution. The first, primarily studied by the paleontologist, is that of dominant species in a fairly stable environment. Such species change slowly by the gradual spread of genes each with a relatively slight effect. It is hard to study in practice, but can be theoretically treated on lines laid down by WRIGHT, FISHER, and HALDANE. Such species are peculiarly liable to unfavorable evolutionary changes.

The second type is characteristic of species whose members exist in quite

small and nearly or quite isolated groups. Such a group may undergo a cytological change or a change in several genes at once. Such changes, while they must ultimately stand the test of natural selection, are not themselves due to natural selection. The new variants so produced are not likely, as in the first type, to be swamped by hybridization before they have a chance to develop into new species. Nor is the probability of harmful orthogenetic evolution due to competition so great.

Until recently man was divided into small tribes, and human evolution was predominantly of the second type. Under modern conditions of large communities and increased mobility man is becoming subject to evolutionary influences of the first type.