AN OUTLINE OF THE PROCESS OF ORGANIC EVOLUTION

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THE NATURE OF EVOLUTION

Organic evolution is descent with change. Present-day organisms differ from their ancestors of the past, and the differences between past and present organisms have come about slowly. The organisms now on the earth are related through descent, and the degree of similarity between them is an indication of the recentness of their common ancestry. Evolution is a process which results in dissimilarities between ancestral and descendent populations. It is a process of change, from generation to generation, in the genetic composition of species populations. The factors which bring about organic evolution have been in operation for many millions of years and are still operative, and some of them can be studied experimentally.

Certain features of the evolutionary process may be deduced from the data of paleontology and other fields. Evolutionary change in a species is usually very slow; the differences in organisms found in the fossil record have been occurring over millions of years. However, this process is not equally slow in all groups of organisms; it is in general slower in aquatic than in terrestrial organisms, and slower in more constant evironments. The changes which occur result in differences in physiology, structure (gain, loss, or modification of a structure, or a change in size), and behavior, and may result in a change of habitat by the organism. Evolutionary changes in organisms sometimes occur as the environmental conditions change; sometimes environmental changes are not accompanied by evolutionary changes in the organism, and it becomes extinct. Evolutionary changes in an animal may proceed in a given direction (for example, increase in size) for a long period of time (orthogenesis). On the other hand, a species may undergo evolutionary change even when living under constant environmental conditions. Evolution in isolated groups living under similar conditions often occurs in different directions, and the amount of difference which develops between them usually increases the longer they are isolated. Evolutionary changes in species generally proceed in the direction of increased specialization. On the basis of data from various sources it is often possible to determine the evolutionary changes that have occurred in the phylogeny of a particular present-day animal.

There are two more or less distinct phases of the evolutionary process, (1) the nature and sources of genetic change in the cells of the organism (sometimes spoken of as evolutionary statics), and (2) the factors which influence the trend or direction of evolutionary change in species populations (sometimes spoken of as evolutionary dynamics).

THE NATURE AND SOURCES OF GENETIC CHANGE

Changes in the evolution of a sexually reproducing animal must be genetic, otherwise they do not pass to succeeding generations. The Lamarckian hypothesis of the inheritance of acquired characters is not adequate to explain the origin of genetic changes. An organism cannot respond to environmental conditions by producing corresponding genetic changes. Somatic changes, that is, changes in the body of an organism but not in the germ plasm, which are induced by direct environmental stimuli do not produce corresponding changes in the germ plasm. A gene which controls a particular somatic character is not correspondingly changed by an environment-induced change in that somatic character.

Genetic differences between individuals or generations may come about as a result of recombinations of genes, chromosomal aberrations, or changes in genes.

Recombinations of genes result from independent assortment during sexual reproduction. Two parents with the genotype Cc may produce offspring of three different genotypes, CC, Cc, or cc, one or two of which may be visibly different from the parents. Similarly, two parents with the genotype $AaBb$ may produce offspring of nine different genotypes, $AABB$, $AABb$, $AAbb$, $AaBB$, $AaBb$, $Aabb$, $aaBB$, $aaBb$, or $aabb$, some of which may be visibly different from the parents. It is obvious, however, that the amount of genetic difference between parents and offspring that can come about by this process is limited by the number of heterozygous pairs of genes in the parents (if n represents the number of heterozygous pairs of genes in the two parents, these parents can produce offspring of 3^n different genotypes). The evolutionary change that has taken place in the past, as indicated by the fossil record, cannot have taken place by this process alone.

New or different combinations of genes may also result from chromosomal changes or aberrations. Chromosomal aberrations are changes in the number of chromosomes or changes in the structure of individual chromosomes. Chromosomal changes usually involve many genes, and hence a greater amount of genetic change can come about by this process than by independent assortment.

The chromosomes of an animal are normally present in pairs, one of each pair having come from each parent, or it may be said that the animal has two sets of chromosomes; this condition is spoken of as *diploid*, and the chromosome number is represented by the symbol $2n$ ($n=$the number of chromosomes in a set, $2=$the number of sets). Numerical changes in chromosomes are either an increase in the number of sets (*polyploidy*), or a change in the number of chromosomes in a particular set (*heteroploidy*). A polyploid condition in which there are three sets is called *triploid*, or $3n$; one in which there are four sets is called *tetraploid*, or $4n$. In heteroploidy one of a set may be missing ($2n-1$), or one set may contain an extra chromosome ($2n+1$); a $2n-1$ organism usually does not survive. Structural changes in the chromosomes may be *losses* (a section of a chromosome missing), *duplications* (a section of a chromosome present at its normal location and also present elsewhere), *translocations* (two non-homologous chromosomes exchanging parts), or *inversions* (a block of genes on a chromosome rotating through 180°). Chromosomal aberrations may often be detected by microscopic examination; inversions result in a peculiar behavior of the chromosomes at synapsis. Chromosomal changes of these various types have often been observed.

Genetic differences which come about by recombinations of genes or by chromosomal aberrations are always of a minor nature; judging from the fossil record, evolutionary changes have taken place which are greater in extent than can be accounted for by these processes alone. These more extensive changes in evolution must have come about by changes in genes, or mutations. The

term "mutation" as used here refers to a change in a gene[1], though some writers use the term to include also chromosomal aberrations; in actual practice it is sometimes difficult to determine whether a particular change in an organism has come about by a gene change or by a chromosomal change.

Mutations have been repeatedly detected in organisms, and quite a bit is known of their nature. A mutation may result in any of a number of changes in an organism—in physiology, and in the resultant visible structures, or in behavior. The change may be very marked, or it may be so slight that it can be detected only by special techniques. In its effect on the organism's ability to survive, a mutation may vary all the way from lethal (causing death) to increasing survival ability. Mutations apparently always occur in only one gene of an allelic pair at a time. They may occur in either body cells or germ cells; except in the case of animals which reproduce asexually, only mutations in the germ cells are of significance in evolution. Mutations may occur at any time in the life cycle of the organism. They occur "spontaneously." They occur under conditions favorable to the organism, and their causes are not well understood. They occur largely at random; when a mutation occurs in an organism it may be in almost any gene, and it may be in any of a number of different directions. The frequency with which genes mutate is very low; genes are generally very stable. Mutations resulting in marked effects on the organism usually occur less frequently than those resulting in only slight effects. The frequency of mutation varies with the gene (some genes mutate more frequently than others), with the allele produced (for example, the gene A may mutate more often to the gene a_1 than to the gene a_2), or with the race, strain, or species of organism involved. Certain environmental agents, such as X-rays and some temperature conditions, may influence the frequency of mutation; X-rays, for example, may increase the frequency some 150 times, but the mutations occurring are still at random. There is no known set of environmental conditions which will always produce only a specific mutation.

EVOLUTIONARY TREND-INFLUENCING FACTORS

A species or race which becomes altered in a particular direction by genetic or evolutionary changes does so either because of a restricted variety of mutations or recombinations, or as a result of differences in the survival of many random mutations. Continued evolutionary change in a given direction for a long period of time has taken place in the past, as indicated by the fossil record of many groups, but there is little genetic evidence that the variety of mutations is thus restricted. Such genetic evidence consists of the variation in the frequency of mutation of different genes, or of a given gene to different alleles, which in turn may be due to the inherent nature of the genes concerned or to the influence of other genes. Known mutations occur largely at random, hence evolution in a given direction must be principally a matter of certain mutations persisting in, and others disappearing from, a species population.

GENETIC DRIFT

Let us suppose that we have a species population in which all the genes of a particular allelic pair are the same, and we designate this gene type as A; this would mean that all individuals of this population are homozygous AA. Now, suppose that the mutation A to a occurs in one gene, with the result that the individual with this gene becomes heterozygous (Aa). We would then have a population consisting of one Aa individual and all the others AA. If the a gene in the Aa individual prevented that individual from mating, obviously the gene a would never get to the next generation (in a sexually reproducing animal),

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[1]Following Dobzhansky, T., 1941, Genetics and the Origin of Species, Columbia University Press, New York, p. 22.

and there would be no evolution in this direction. If the Aa individual can mate, it must mate with an AA individual, and such a mating will result in either AA or Aa offspring or both.

These two parents might have almost any number of surviving offspring, depending on the species and on chance (let us assume that the a in the Aa individual is completely recessive, and hence the Aa individual has no greater survival or reproductive ability than the AA individuals). If they have no offspring surviving long enough to reproduce, the gene a is lost to the next generation. If they have one surviving offspring, there is a .50 chance of a being lost in the next generation; if there are two surviving offspring, there is a .25 chance of a being lost in the next generation; if there are r surviving offspring, there is a 2^{-r} chance of a being lost in the next generation. With the population remaining constant, generation after generation, the aggregate possibility of the gene a being lost in the next generation, considering varying numbers of surviving offspring, is .3679; the probability of its being in one individual in the next generation is .3679, in two individuals .1839, in three individuals .0613, etc.

As a result of this process, based as it is on chance, 36.79 percent on the average of all the new genes appearing in each generation by mutation are passed to the next generation unchanged in frequency, 36.79 percent are lost, and the rest are increased in frequency. It may be calculated that out of every 10,000 mutations, only 153 may be expected to survive 127 generations, assuming equal ability to survive and reproduce of AA, Aa, and aa individuals; these are the "lucky" genes, which increase in frequency instead of being lost.

It may be of interest at this point to note certain theoretical considerations concerning infinitely large populations in which the breeding is at random and in which there is no selection[2].

It can be shown mathematically that, in the absence of mutations, gene frequencies in such populations remain constant. This concept is usually known as the Hardy-Weinberg Law, and may be expressed by the equation

$$q^2AA + 2q(1\text{-}q)Aa + (1\text{-}q)^2aa = 1 \tag{1}$$

where $q =$ the frequency of the gene A and $(1\text{-}q) =$ the frequency of the gene a. This law means that if, for example, half the genes of a particular allele in the population are A and the other half are a, the ratio of the two genes will remain constant generation after generation.

It can also be shown that if the mutation A to a occurs in such a population, and if the reverse mutation a to A does not occur, then the gene A will eventually be eliminated from the population and all the individuals will become homozygous aa.   The time in terms of the number of generations required for the gene A to be eliminated depends on the frequency with which the mutation A to a occurs.

It can further be shown that if both mutations, A to a and a to A, occur in such a population, then the frequencies of the genes A and a will reach a certain value and remain stable there.   The frequencies at this stable point can be calculated; if we let u represent the frequency of the mutation A to a (which might, for example, be 1 in 100,000) and v represent the frequency of the mutation a to A (which, let us say, is 1 in 1,000,000), then the frequency of the gene A at the stable point is represented by q in the formula $q = \dfrac{v}{u + v}$ $\qquad(2)$

With the values of u and v mentioned, the value of q would be 1/11, that is, at the stable point one gene out of every eleven of this allele would be A and the other ten would be a.

These theoretical considerations suggest that in very large populations mutation (or "mutation pressure") would increase the frequency of occurrence of new

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[2]Selection is discussed below, p. 325.

(mutant) genes in the population, and this would occur even if the new gene had an unfavorable effect on the organism, especially if the new gene were recessive. As a matter of fact, natural populations contain many recently mutated genes, even including lethals. This accumulation of new genes in a population results in what may be called *genetic variability*. If conditions change, the genotypes of a species population with high genetic variability may be reorganized and the species survive; populations with low genetic variability may be unable to effect reorganization of the genotype with changing conditions, and die out.

Populations of infinite size and with random breeding do not exist in nature; natural populations vary greatly in size, and those in which there is random breeding may be small. It can be shown mathematically that gene frequencies in small populations fluctuate at random, and some genes become fixed (homozygous in the entire population) while others become lost, purely by chance, and selection has very little effect. Evolution (changes in gene frequencies) is rapid until the genetic variability is lost, and selection is unimportant in influencing the direction of evolution. In large populations gene frequencies remain at or near a stable point, which is determined by mutation pressure (formula (2), above) and selection; evolution is slow or nil, and only severe selection is operative. The genetic variability is constant and high. Selection is of more importance in populations of intermediate size. There is abundant ecological, taxonomic, and genetic evidence that population size is often a very important factor influencing the fate of newly mutated genes and the genetic variability of populations, and hence in influencing evolutionary trends.

By population size is meant the size of the effective breeding population, which is not necessarily the same as the total number of adults. This value is influenced by many factors, including the extent of the movements of individuals during the mating or breeding season, territoriality and homing behavior, breeding behavior, and other factors. The biological significance of genetic drift in small populations lies in the fact that if a species is broken up into small isolated groups, these groups will become differentiated—by chance—even with similar environmental (and selectional) factors operating in the isolated groups.

It therefore appears that whether or not a new gene survives in a population and replaces the gene from which it mutated depends to a certain extent on chance, the chance being influenced by population size and the frequency with which the new gene is produced. However, in the preceding paragraphs we have spoken of *selection*; let us now consider the nature of this mechanism in influencing evolutionary trends.

<div align="center">SELECTION</div>

The basic concept of selection as a trend-influencing mechanism in evolution is that the genetic characters of the better adapted individuals will become more frequent in the population in succeeding generations ("favored" by selection), while those of less adapted individuals will become less frequent. "Better adapted" means greater reproductive ability or greater survival ability, or both. Greater reproductive ability means higher fecundity or greater mating success; greater survival ability involves greater ability to resist such environmental hazards as enemies, competition, and other environmental factors that are not optimum. The trend of evolution, if influenced by selection, is thus in the direction of adaptation.

The effect of selection is proportional to its intensity, or what for purposes of mathematical treatment may be termed the selection coefficient. For example, if s is the coeffiicient of selection favoring the gene A over its recessive allele a (that is, favoring AA or Aa over aa), then for every offspring produced by the dominants the recessives produce 1-s offspring, on the average. If the frequencies are A and a are .5 in one generation, and the value of s is .01, the value of q (fre-

quency of the gene A) in the next generation would be .5012; with an s value of 1 (which would mean that the gene concerned is a recessive lethal) the value of q in the next generation would be .67.

The effect of selection varies with the frequency of the genes concerned. With a constant selection coefficient, the effect of selection decreases as the frequency of the favored gene increases. For example, starting with q (the frequency of the favored gene A) equal to .5 and a selection coefficient of 1 (a recessive lethal), the value of q in the second generation would be .67 (an increase of .17), in the third generation .75 (an increase of .08), in the fourth generation .80 (an increase of .05), and so on; in the nth generation q would be $\dfrac{n}{n+1}$. The increase each generation in the frequency of the dominant allele favored by selection may be calculated by the formula

$$q_2 = \frac{q_1}{1 - s(1 - q_1)^2} \tag{3}$$

The above discussion of the effect of the intensity of selection (s) is based on the assumption that there are no mutations; mutations alter the picture slightly. With mutation away from a favored allele, an equilibrium will be established; for example, with A mutating to the less favorable allele a with a frequency of u, the equilibrium frequency of a (q_a) may be calculated by the formula

$$q_a = \sqrt{\frac{u}{s}} \quad (s = \text{the selection coefficient}) \tag{4}$$

Where $s = 1$ (a recessive lethal) the formula becomes

$$q_a = \sqrt{u} \tag{5}$$

If the selection coefficient is high, mutation has little effect, and the frequency of the gene selected against remains low. If the selection coefficient is low, the mutation frequency is more important in determining gene frequencies, which tend to remain at equilibrium at a point determined by the mutation rates to and from the favored allele (formula (2), above).

In cases where selection favors heterozygotes over homozygotes—and such cases are known—the proportions of heterozygotes and homozygotes reach a balance; this situtation is sometimes referred to as a *balanced polymorphism.*

Selection may also play a role in the evolution of non-adaptive characters. Neutral or even slightly deleterious traits may be favored by selection if they happen to be connected with favorable ones; selection acts on the *over-all* adaptive value of the genotype. Further, a seemingly neutral trait may be only one effect of a gene, the other effects of which may be favored by selection. Due to the relationships between developing parts of the organism, a change in one organ may result in changes in developmentally related organs.

As a result of mutation, traits may appear which are adaptively neutral in one environment, but which may be of adaptive value in another environment; this phenomenon is sometimes termed *preadaptation.* Evolution by selection occurs because some genotypes happen to have adaptive value in environments encountered by the species. Mutations do not occur when needed, but if they happen to be present when needed, selection will favor them.

Evolution by selection may be centripetal, centrifugal, or linear. In centripetal evolution, selection favors the average condition, and variants tend to be eliminated; there is an increase in specialization, with a reduction in the variation in the species. In centrifugal evolution the variants are more adaptive; this process might be compared to an expanding ring, and if the variants become isolated further divergence and speciation may occur. Linear evolution occurs with a slow shift in environmental conditions (selection factors), with the average of the population shifting. With a constant shift in selection factors (orthoselection), the evolution is linear or orthogenetic.

ISOLATION

Natural populations of organisms exhibit discontinuous variation. The world fauna and flora consist of many different populations which differ in non-integrading characters, that is, all the individuals of one population are different from all the individuals of the other populations. These population units are called species or races, the term used depending somewhat on the populations; they usually differ in many genes, and often also in chromosome structure. The maintenance of this discontinuous variation depends upon the different populations being prevented from interbreeding. The interbreeding of races or species (where such interbreeding is possible) results in a breakdown of the racial or specific differences, though the individual genes remain unchanged. The discontinuous variation of races and species can come about only when population groups are *isolated*, that is, when they are prevented from interbreeding.

The mechanisms which prevent the interbreeding of groups of individuals, and thus bring about isolation, are very diverse. Groups may be isolated by geographic barriers (*geographic isolation*), and hence never meet. Two groups may occur in different ecological situations in the same general region, yet never come together during the breeding season (*ecological isolation*). Two groups may occur in the same habitat and interbreeding may not occur because the breeding periods of the two groups are at different times (*seasonal* or *temporal isolation*). Two groups may occur together and not interbreed because of a lack of mutual attraction of the two sexes (*sexual isolation*), or copulation may be difficult or impossible due to the physical incompatibility of the reproductive organs (*mechanical isolation*). In some cases mating between two groups may occur, with no resulting offspring due to a failure of fertilization or development, or with the offspring sterile.

One effect of isolation is that the isolated groups evolve in different directions in certain respects. As we have seen, the mutations occurring in a population are largely random in nature, and whether a particular new gene that appears in a population persists or is lost depends on chance and selection. In some cases, particularly in small populations, selection has relatively little effect. Therefore, because of the random nature of mutations, and the role of chance in determining the fate of new genes, one would expect that in general the new genes which appear and persist in isolated populations would be different, and hence the isolated populations would evolve in different directions. The longer the period of isolation, the more the isolated populations would diverge. In cases where selection is particularly severe, and similar in the isolated populations, these isolated populations would probably exhibit similar evolutionary trends.

The data of geographic distribution furnish considerable evidence to support the role of isolation in species formation. A species' nearest relative is usually to be found in an adjacent area separated by a barrier; exceptions may be due to some type of isolation other than geographic, or the related forms may have come together by migration subsequent to their divergence. The degree of isolation of any given area for different species varies inversely with the vagility (ability to extend the range) of the species. A species of high vagility may be represented in a given area by a single form, while another, of low vagility, may be split into a number of geographic races in the same area. The amount of endemism (a species is endemic to an area when it occurs there and nowhere else) in various groups in a given area usually varies inversely with the vagility of the groups. The amount of differentiation of a group in an isolated area is influenced by the duration of its isolation, population size, and selection. Long-continued isolation of a group may be accompanied by its evolving into ecological types, similar in adaptations but different taxonomically, from species in similar habitats elsewhere. Similar areas, such as deserts, mountains, and grasslands, in different

parts of the world are in general occupied by different species. Each species is usually restricted to particular geographic areas, and does not occupy all the geographic areas in the world where conditions are suitable for its existence.

RATES OF EVOLUTION

The rate of evolution may be defined as the amount of change per unit of time. It may be measured in terms of the amount of morphological change, as evidenced by the taxonomic units applied to the different stages of the evolving line. Data on evolutionary rates are largely from the field of paleontology.

Many variations occur in rates of evolution. In a given line, the rate may vary in different geological periods. Characters in a given evolving line which are developmentally correlated may evolve at similar rates, but characters not developmentally correlated may evolve at different rates. In some cases, at least for short periods, a given character may evolve at a constant rate. It would seem that evolution should be faster in forms with more generations per unit of time, but the fossil record shows no correlation between rate of evolution and generation length (compare the fossil records of flies and elephants during the Cenozoic).

Different lines within a group such as a class, order, or family, may evolve at different rates; some (*tachytelic*) may have a high rate of evolution, while others (*bradytelic*) may have a low rate. Tachytely is usually of short duration, and often ushers in a new major group; then the rate is more moderate (*horotelic*).

The fossil record contains many examples of bradytelic lines—groups which have evolved relatively little over long periods, for example, horseshoe crabs (Triassic to present), opossums (late Cretaceous to present), and many molluscan genera (Carboniferous to present). Bradytely is likely in groups with continuously high populations and stable environmental conditions, even with normal mutation rates. Such forms usually have a high range of tolerance, and are not over-specialized.

SUMMARY

By the process of organic evolution present-day organisms have descended, with changes, from the organisms of the past. Some of the characteristics of the evolutionary process can be inferred from the data of paleontology and geographic distribution. The changes which occur in evolution involve genetic changes in individuals and populations, and come about largely through mutation. The direction in which a population evolves may be influenced by its inherent mutability, the population size, selection, and isolating mechanisms. Evidence of the nature and mechanism of evolution is to be found in the data of paleontology, observations of mutations in experimental animals and plants, the results of experimental breeding, studies of the genetics of natural populations, and the data of geographic distribution.