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SYSTEMATICS

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EDITED BY
JULIAN HUXLEY

MUTATIONS AND GEOGRAPHICAL VARIATION

By N. W. TIMOFEEFF-RESSOVSKY

1. *Introduction*

THIS article will deal with one of the topics of the inter-relations of modern genetics with taxonomy and evolutionary studies. This special topic is the question of the role of mutations in geographical variability.

The present author regards this question as a fundamental one in the attempt at introducing modern genetic viewpoints into studies of the mechanism of evolution. Darwin formulated in a wonderfully clear and precise way the principle of natural selection and showed that this principle is the basic explanation of the mechanism of evolution. Since Darwin much very extensive and ingenious work has been done in the field of evolutionary studies, using palaeontological, morphological, embryological, and biogeographical data; these studies have allowed us to picture the main historical steps and events of the evolutionary process. The efficacy of these classical methods, which give a picture of what we may call 'macro-evolution', seems now to be more or less exhausted. Relatively much less work has been done in the field of what we may call 'micro-evolution', i.e. the evolutionary processes taking place within shorter limits of time, smaller groups of organisms, and lower systematic categories. But 'micro-evolution' is the evolutionary process in which we may expect to get exact scientific evidence regarding its mechanism; 'macro-evolution' is only accessible to descriptive historical methods, the conclusions regarding its mechanism being always deduced from other sources of evidence. And the main phenomenon of 'micro-evolution' is geographical variability and speciation.

It is curious that exactly at the moment when modern minor systematics, minor biogeography, and experimental ecology started their present development (at the end of the nineteenth and the beginning of the twentieth century) many evolutionists apparently became disappointed with Darwinism

and returned to various modifications of Lamarckian views on the mechanism of evolution. The cause of this reaction may perhaps lie in peculiarities of the development of our knowledge of organic variability. At the time of Darwin almost nothing was known about the distinction between heritable and non-heritable variation. During the whole period of classical evolutionism following Darwin very little attention was paid to an exact analysis of variability. Attention was concentrated on the major steps of evolution, neglecting the evolutionary material as such. Most evolutionists, taxonomists, and biogeographers also neglected the rapid development of experimental genetics since the beginning of this century, although the exact knowledge of the main traits and characteristics of heritable and non-heritable variability provided by this new branch of biology undoubtedly constitutes the most important advance in our knowledge with direct bearing on the mechanism of evolution, since Darwin. The neglect was reciprocal: most of the experimental geneticists, absorbed in their experimental analytical work, did not pay much attention to taxonomic and evolutionary problems. Only recently have both sides begun to feel that closer co-operation and reciprocal exchange of information will be of the greatest value for the further development of systematics, biogeography, and evolutionary theory.

Thus we regard as the main contribution of modern biology to the problem of evolution the knowledge of the mechanism of organic heredity and variability, which was provided by the development of experimental genetics. In Darwin's time and during the subsequent development of the theory of evolution, the mode of action of the known evolutionary factors, especially that of natural selection, could be considered and discussed only in a rather general and unspecified way. This was because almost nothing was known about the nature of the evolutionary material. To-day we are able to test in a precise and concrete way two questions which are important in this respect: (1) whether the variability of organisms, which provides the raw material for the evolutionary processes of adaptation and differentiation, is based merely on known genetic phenomena, or, in other terms, whether the genetically known and analysable units of variation constitute the only source of evolutionary raw material; and (2) whether these genetically known units of

variation have all those qualities which must be assumed and required in order to explain their role as evolutionary material.

In the following sections these two questions will be briefly considered, followed by an examination of the actual participation of mutations in the formation of taxonomic units, and an evaluation of the various known evolutionary factors.

The author is much indebted to the editor, Dr. J. S. Huxley, for his help in correcting the English, and for his critical revision of the manuscript.

2. *Mutation as the Source of Evolutionary Material*

We know that the variability of organisms has two distinct components: the non-heritable modifications and the heritable variations. Only the latter ones are of primary importance in the process of evolution, the former being important merely in regard to the plasticity of the type and in being, in the last instance, based on its type of hereditary constitution. Almost all cases of well-analysed hereditary differences between individuals or groups of individuals have proved to depend upon combinations of Mendelian 'unit-characters'. And we know that all segregating unit-differences are due, in respect to their origin, to mutations in the broadest sense of the word. We thus can say that mutations and their combinations constitute the basis of almost all analysable hereditary differences. The only known exceptions are certain plastid and plasmon differences in plants. The non-Mendelian plastid-characters are due to the far-reaching autonomy of plant plastids in regard to reproduction, variation, and segregation. We have good reason to believe that such heritable, extra-nuclear plastid-differences originate as sudden, reproducible changes of single plastids. If we define the term 'mutation' as sudden changes of heritable units, transmitted in a more or less constant new form to subsequent cell-generations, we may speak of these as plastid-mutations. If so, the only cases of heritable differences which in their origin cannot yet be regarded as due to mutation are certain plasmatic differences, found in some species and varietal crosses in plants; these so-called plasmon-differences seem to be more or less independent of the genetical factors localized in the chromosomes, and nothing is yet known about their origin. But this phenomenon of autonomous plasmon-differences does

not seem to be of very general importance, since it has been found in only a few cases.

Thus we can say that by far the most important source of the origin of heritable variation is mutation. We must accordingly examine the following three questions: (1) whether the general character of the known and genetically analysable process of mutation may explain the whole of the heritable variability of organisms; (2) whether mutations and their combinations produce such differences in the relative viability of individuals as to enable a sufficiently differentiated action of natural selection to take place; and (3) whether mutations are present in sufficient numbers in free-living populations of organisms. This examination will show us whether the mutation-process can really be regarded as the sole or main source of evolutionary raw material. If this question can be answered in the affirmative, the same examination will also show us the real characters and qualities of the evolutionary material, thus permitting a much more specialized and exact consideration of the mechanism of action and the relative value of the various factors of evolution.

(a) *Types of mutations, mutant characters, and mutation-rates.* As mutations we design sudden changes of heritable characters, leading from one more or less stable condition to another. Mutations have been found to occur spontaneously, i.e. without the application of any special mutation-inducing factors, in all species of protista, plants, and animals so far analysed in this respect. We thus have good reason to believe that spontaneous mutation is a general character of all living beings.

Cytogenetic work has revealed several different distinct types of mutational change in the hereditary material. According to the unit of change mutations can be classified into the following three groups: (1) gene-mutations, i.e. changes or losses of single genes; (2) chromosome-mutations, i.e. structural changes in single or several chromosomes (deletions, duplications, inversions, translocations); and (3) genome-mutations, i.e. changes in the number of single, several, or all chromosomes (haplo- or polysomy, heteroploidy, polyploidy). In plants, plastid-mutations may occur besides these three types.

All hypoploid chromosome-mutations (i.e. those lacking a piece of one or more chromosomes), and many of the hyperploid ones, are lethal in homozygous condition. Deficiencies for one

or more genes often produce phenotypic character-changes even when heterozygous. Some of the chromosome-rearrangements show so-called 'position-effects' of the gene or genes near the point of breakage of the chromosomes; these 'position-effects' consist in character-changes, brought about by the abnormal functioning of the genes near the point of breakage and rearrangement, due to their proximity to other genes than in normal chromosomes.

Extensive observations of the mutation-process in different plants and animals show that all types of morphological and physiological character-changes can be produced by mutations. Mutant characters vary from ones so slight, that they can be detected only by means of special methods, up to changes so profound that they can be regarded as of more than normal specific value or produce death or serious pathological symptoms. All species of plants and animals extensively analysed in respect to their mutability show that mutations and their combinations are capable of producing the whole range of morphological and physiological character-variability of the species in question.

In genetically well-analysed species quantitative studies of their mutability have been made. They showed the following traits of spontaneous mutability. The total mutation rates[1] per generation are rather low, lying in the order of magnitude of 1–10 per cent. Variation in the factors of the normal environment of the organisms have little or no influence upon the mutability. Different single mutation-steps have different rates of change, lying in the order of magnitude of 0·001–0·00001 per cent.

(b) *The relative viability of mutations.* It was mentioned in the preceding paragraph that all possible kinds of character-changes may be produced by mutations. This already shows that different mutant characters and their combinations must show pronounced differences in their biological value. In all species extensively enough analysed in respect of their mutability, a

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[1] By the 'rate of mutation' we understand the percentage of gametes or haploid genomes containing a mutation. In this case, by 'total mutation rate' is meant the percentage of gametes (of one generation) containing any kind of mutation. In other cases the rates of single definite mutation-steps, or of mutations of a certain gene or group of genes, or of mutations producing a certain type of character-changes may be analysed. For details and difficulties of determination of mutation-rates see Timofeeff-Ressovsky, 1937.

very large proportion of newly arising mutations show a more or less pronounced decrease of viability (many of them being even lethal when homozygous). This characteristic of mutation is not at all surprising: we must admit that by a permanent natural selection the 'best' mutations are taken up into the so-called normal type of the species or race in question, so that most mutations (i.e. alleles and chromosome-structures not belonging to the 'normal' type) must be rather 'worse' than the 'normal' type, which by natural selection is permanently kept in harmonious relation to its environment. The fact that most mutations are more or less deleterious has often led to the conclusion that mutability is of no importance as providing the raw material of evolution. But this conclusion is evidently wrong. The deleterious nature of many mutant homozygotes merely decreases the mutation-rate which is of evolutionary significance.

In order to get more information on the viability relations of mutations and their combinations special experiments can be performed. In such experiments some special aspect of the general phenomenon of 'viability' must be chosen and studied quantitatively. It is, for instance, possible to study the relative viability of different genotypes by comparing their hatching-, survival-, or fertility-rates under definite constant conditions. In *Drosophila funebris* and *melanogaster* experiments on the relative viability of mutations and their combinations were performed by studying the hatching-rates of a normal and various mutant genotypes, in culture-bottles started with equal numbers of the two types of eggs and kept under definite conditions of crowding, food, and temperature.

Some examples of the results are shown in Fig. 1. The upper row of this figure shows the viability of several single mutations as compared with that of the normal type: most of the mutations have a lower, but some a higher, viability than the normal type under given conditions. The viability of combinations shows sometimes a purely additive effect of the viabilities of the single mutations in question; but in other cases it may be lower or higher than is to be expected on the assumption of an additive effect of the single genes—three different typical cases are shown in the lower row of Fig. 1. The viability of a 'large' mutation may be specifically changed not only by the presence of another large mutation but also by many 'small' mutations or so-called

modifiers, as is shown by the action of plus- and minus-selection upon the relative viability of a definite single mutation in heterogeneous cultures. Thus the general statement can be made that the relative viability of single mutations is partly
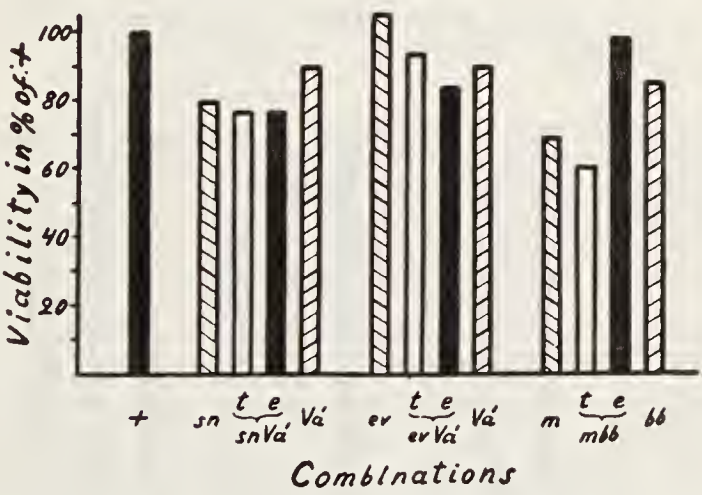

FIG. 1. The relative viabilities of eight mutations and three combinations in *Drosophila funebris* (hatching-rates in percentage of the normal type, in constantly crowded cultures held at 25° C.). For combinations two values are given: the empirical (*e*), and that calculated on the assumption of a purely additive effect of the two genes (*t*). (Timofeeff-Ressovsky, 1934.)

dependent upon the 'genotypical environment' provided by the gene-complex in which they find themselves.

The relative viability of different mutations and combinations may also differ under different environmental conditions. The upper row of Fig. 2 shows some typical examples: the viability

of the three mutations behaves differently with change of temperature. Similar differences were also found in the reactions of the relative viabilities of different mutations to other environmental factors.
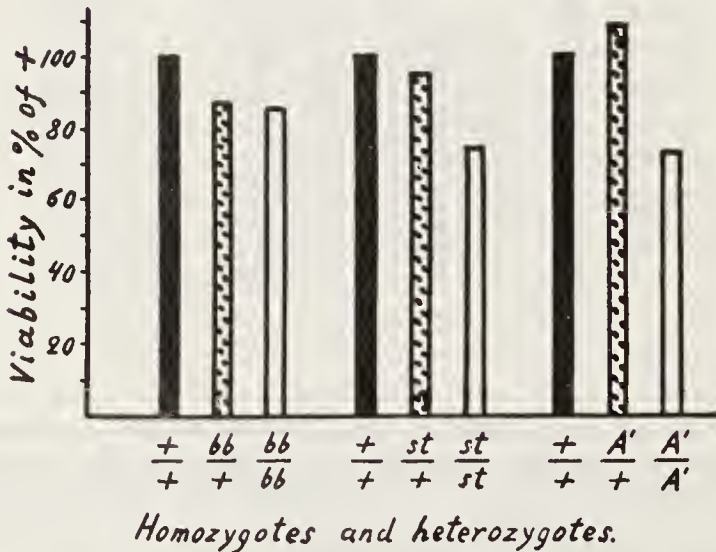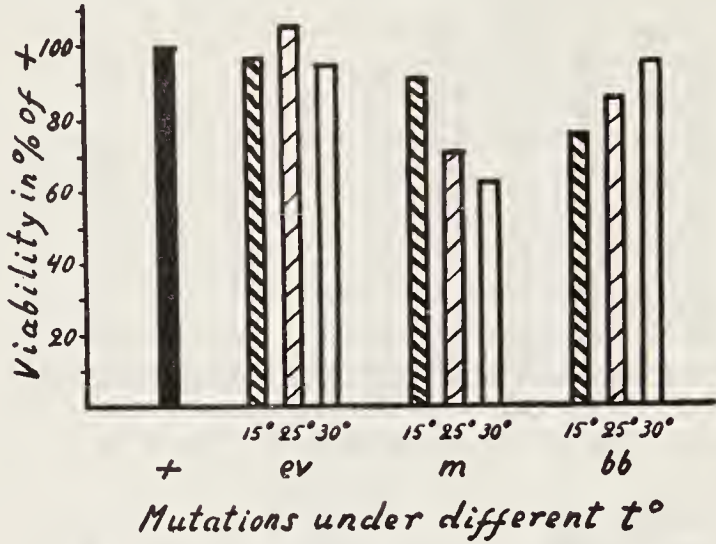

FIG. 2. The relative viabilities of three mutations at different temperatures, and the comparison of the relative viabilities of heterozygotes and homozygotes of three mutations at 25° C. in *Drosophila funebris* (all the experiments at constant degree of crowding of the cultures). (Timofeeff-Ressovsky, 1934.)

The lower row of Fig. 2 shows some different typical examples of the dominance-relations of the relative viability of different

mutations. Just as in the case of morphological character, the viability effects of different mutations can show different degrees of dominance or recessiveness, which do not always correspond to those of the morphological character. Attention is drawn to the fact that in some cases mutations having low viability in homozygous condition may show a significant increase of relative viability when heterozygous.
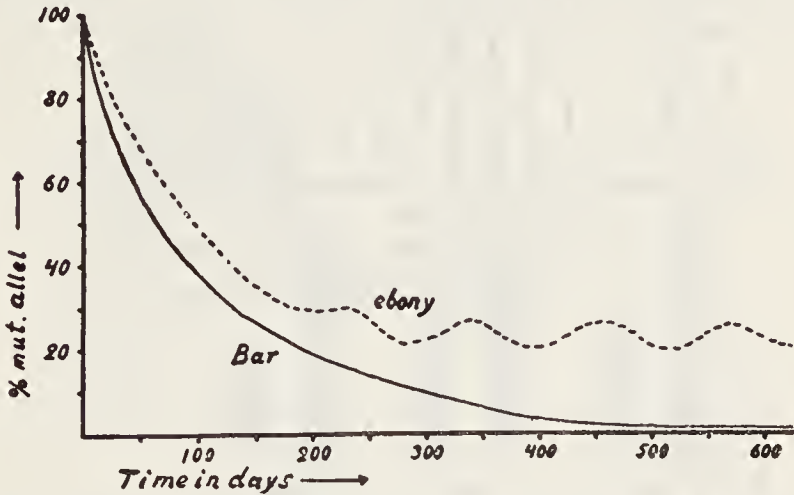

FIG. 3. The negative selection of two mutations in *Drosophila melanogaster*, one which has a lowered relative viability both in homozygous and heterozygous condition (Bar), and another whose relative viability is lowered in homozygous, and increased in heterozygous condition (ebony). Quantitatively stable 'artificial' populations (containing about 4,000 individuals each) of the mutations in question, were 'infected' by small amounts of normal flies. (L'Héritier and Teissier, 1937.)

The relative viability of mutants can be studied also in another way. L'Héritier and Teissier developed a method of keeping quantitatively stable artificial populations of *Drosophila* (in large boxes, supplied with dishes containing food, of which one is changed every day). Such stable populations of different mutants can be 'infected' by normal flies, and the relative numbers of mutants and normals can then be counted every few weeks over a long period of time. Fig. 3 shows the result of such experiments with the mutants Bar and ebony of *Drosophila melanogaster*. Both mutants decrease rapidly in number at first; then Bar continues to be gradually replaced by normal, finally disappearing from the population; ebony is after a while stabilized at a certain, rather low percentage. This latter effect is due to the counter-action of the negative selection of homo-

zygotes by the positive selection of heterozygotes. It is interesting
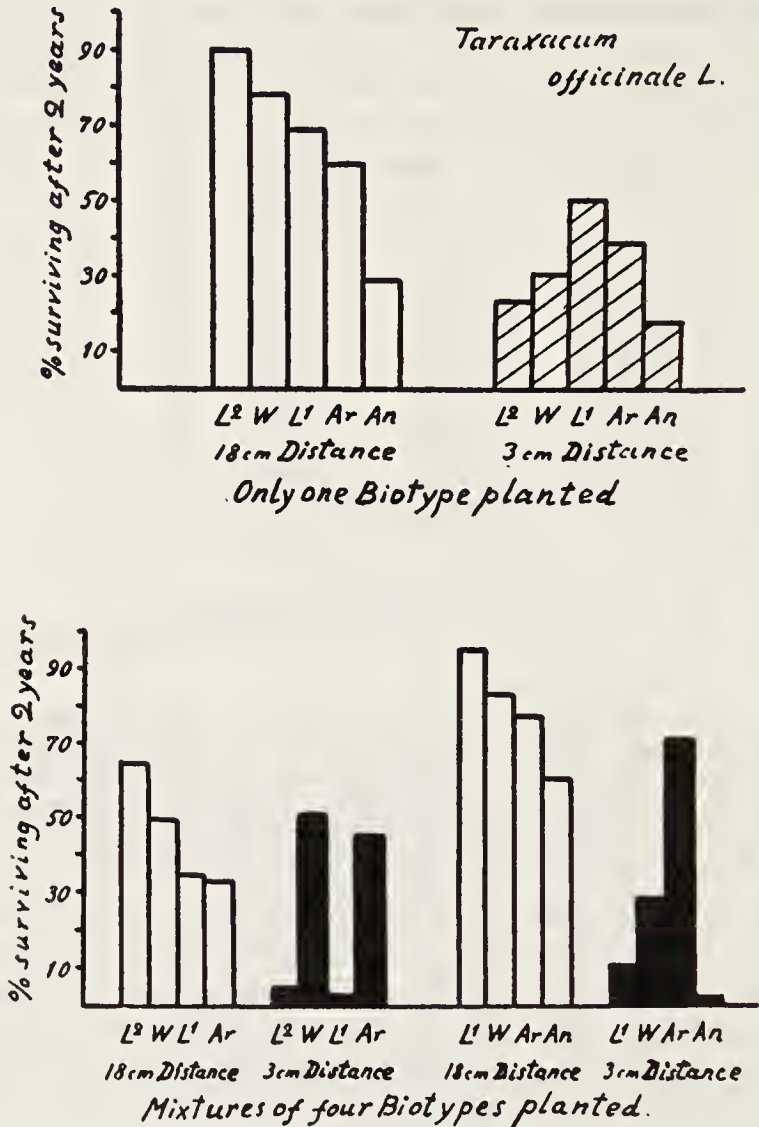to note that in our own previous, quite independent, experi-

Fig. 4. Survival rates in artificial populations of five different biotypes of *Taraxa-
cum officinale* L. (Compositae) from: Leningrad 1, Leningrad 2, Archangelsk,
Wologda, and Askania-Nova. The populations were planted in two densities:
3 cm. and 18 cm. distance between the plants; above—each population contained
only one of the biotypes; below—each population contained a mixture of four
biotypes in equal numbers. (Sukatschev, 1928.)

ments on the relative viability of mutations it was found that
ebony behaved in the same way as the mutation A on the right
side of the lower row of Fig. 2: it showed a lowered relative

viability in homozygous condition but increased relative viability of the heterozygote.

Still further tests of the relative viability of different genotypes can be performed in nature. Fig. 4 shows the results of an experiment of Sukatschev on the survival rates of five different biotypes of the dandelion, *Taraxacum officinale*; these experiments clearly show that the relative viability of a certain genotype may differ both under different conditions of population-density and in combinations with different other genotypes. Fig. 5
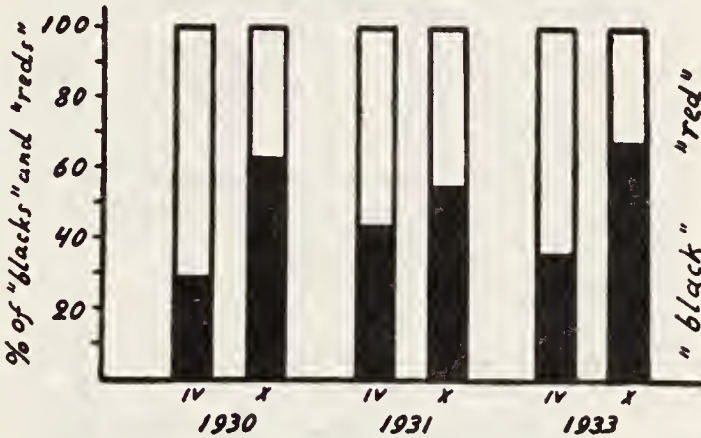

FIG. 5. The relative frequencies of two groups of colour-pattern-forms ('black' and 'red') of *Adalia bipunctata* L. (Coleoptera, Coccinellidae) in the early spring population (IV; just after hibernation) and in the late autumn population (X; just before hibernation) during three seasons near Berlin. (Timofeeff-Ressovsky, unpubl.)

shows the results of counting the relative numbers of two different monogenic colour-pattern types of the lady-beetle *Adalia bipunctata* in the early spring and the late autumn populations near Berlin during three years: this beetle has about three generations a year in this locality and shows a decrease of one of the genotypes after hibernation and of the other one just before it. This result shows that during different seasons of the year these two genotypes have different, opposite selective values; this is probably the cause of the permanent polymorphism of almost all populations of the species.

All the above-cited experiments were performed on 'large' mutations. Our experience of intraspecific variability shows us that the latter is in most cases due to 'small' mutations, slightly affecting some quantitative characters. It is thus important to

know whether 'small' viability mutations, not causing pronounced character changes, also occur in organisms. Special experiments can be performed in *Drosophila* on the production of sex-linked mutations, differently affecting the relative viability of males. Fig. 6 shows the results of such experiments;
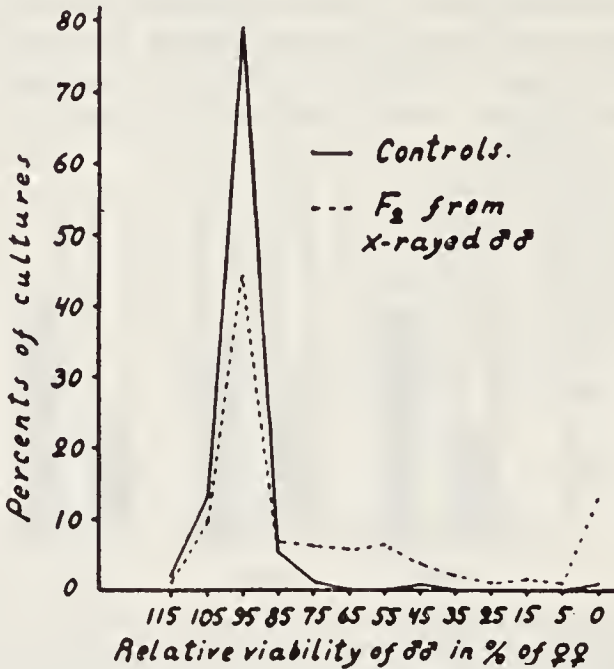

FIG. 6. Production of sex-linked mutations with lowered viability by X-rays in *Drosophila melanogaster*. Distribution of the sex-ratios in control cultures and in F₂-cultures from X-rayed ♂♂. (Timofeeff-Ressovsky, 1935.)

they clearly proved that 'small' viability mutations are the most frequent group of mutations in *Drosophila*. These results were confirmed by similar experiments of Kerkis (1938).

We thus see that mutations and their combinations may affect the relative viability of the organism in an extremely manifold and plastic way, permitting a most variable, specialized, and delicate action of natural selection. Fig. 7 shows schematically different types of mutational changes of viability in respect to an environmental factor; some of these changes do not replace the optimum, others do. The first type of viability changes may be classified as changes of 'resistance' to a certain environmental factor; the second as 'adaptational' changes. Anyhow, we see that as regards viability, mutations fulfil all requirements expected from the raw material of evolution.

(c) *Mutations in free-living populations.* We have now to prove whether mutations fulfil the last requirement: Are they present in sufficient frequency in free-living populations? Many incidental observations in different species of plants and animals have shown that mutations of the same type as those found in genetic experiments may be present in heterozygous condition in wild material. Nevertheless, many biologists still believe that
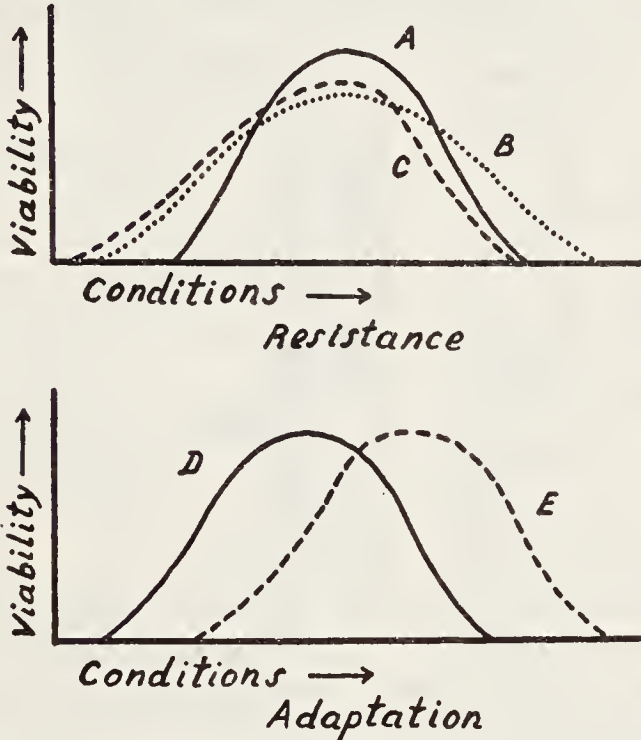
FIG. 7. Graphical representation of the different possible changes of the relative viability produced by mutations. Above: the optimum in respect to a certain environmental factor (e.g. temperature) is not changed in B and C; they differ from A merely in respect to their resistance to extreme conditions (change of 'resistance'). Below: E differs from D in its optimum in respect to the environmental factor ('adaptational' change). (Timofeeff-Ressovsky, 1934.)

mutations are of no evolutionary importance, since mutation-rates are so low and since most mutations are of no biological value. There are even some biologists who still think that mutations are a kind of 'artefacts' produced in the laboratory or under conditions of domestication in 'genetical' objects. Our whole knowledge of the mutation-process together with the numerous incidental observations of mutations in wild popula-

tions speak against these views, and show that mutation must occur in nature just as in our laboratory cultures.

In *Drosophila* and some other objects special experiments have been performed in order to test quantitatively the presence and concentration of different mutations in free-living populations. The method of these experiments is very simple and consists in arranging for the segregation of all recessives present in individuals taken from wild populations. The simplest way is the
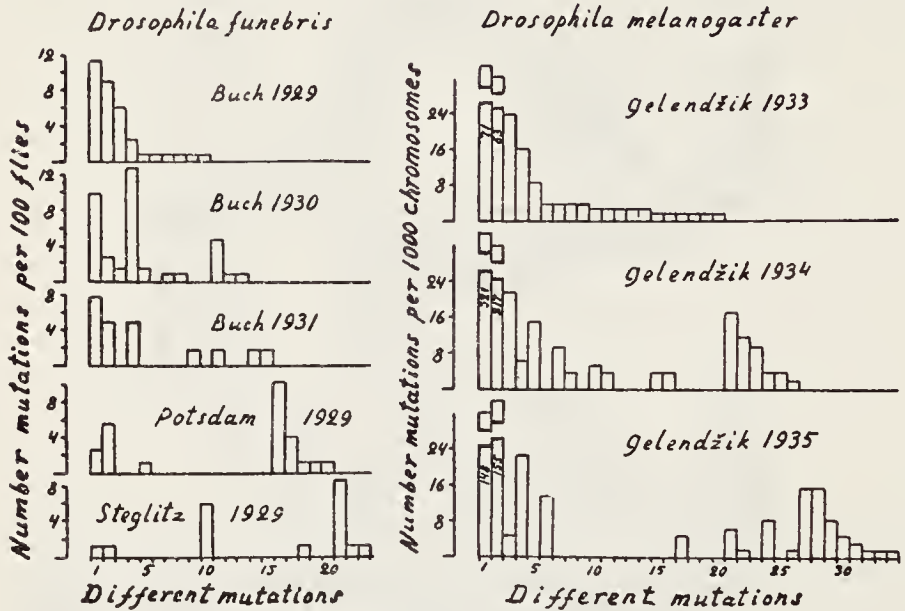
FIG. 8. Concentrations of mutations in different free-living populations of *Drosophila melanogaster* (Dubinin and associates, 1936), and *D. funebris*. (Timofeeff-Ressovsky, 1939a.)

inbreeding of wild-caught females, already fertilized in nature, for two generations, by making a large number of single pair-crossings from the F_1; any recessive present in heterozygous condition in either of the wild parents will then segregate in one of the F_2 crosses. Using this method, extensive tests of free-living populations of *Drosophila melanogaster* from Berlin (Timofeeff-Ressovsky, 1927) and from the Caucasus (Tschetverikov, 1928) showed that numerous mutations were present in different concentrations in these populations. Substantially similar results have later been found in other populations of the same species (Dubinin and co-workers, 1934, 1936, 1937; Gordon, 1935; Timofeeff-Ressovsky, unpubl.) in different populations

of *Drosophila funebris* (Romashoff, Timofeeff-Ressovsky), of *D. obscura* (Gershenson, 1934), *D. subobscura* (Gordon, 1936), *D. pseudo-obscura* (Dobzhansky and Queal, 1938), *D. phalerata*, *D. transversa*, and *D. vibrissina* (Balkashina and Romashoff, 1935), and of the amphipod *Gammarus chevreuxi* (Sexton and
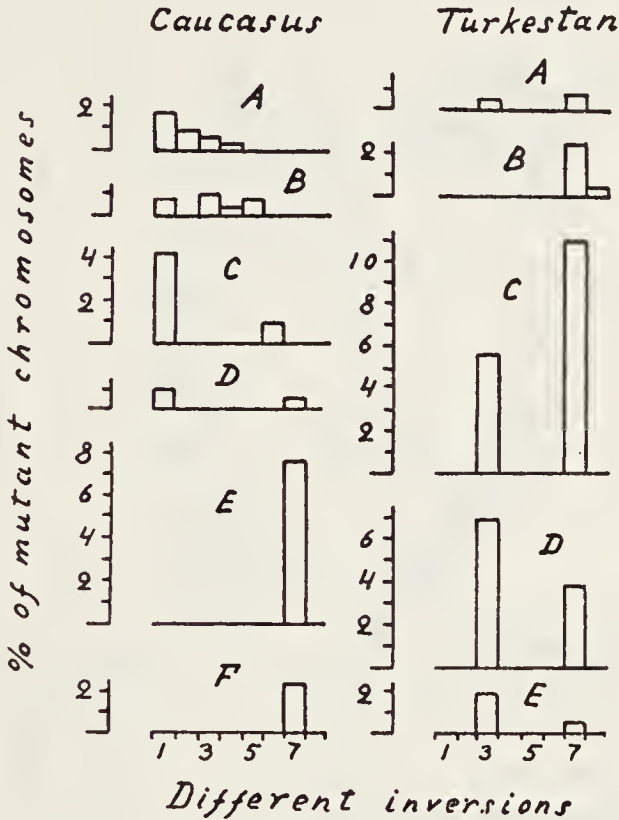
FIG. 9. Concentrations of inversions in different free-living populations of *Drosophila melanogaster*. Caucasus: A, Kutais; B, Gori; C, Batum; D, Baku; E, Gelendžik; F, Derbent. Turkestan: A, Osh; B, Samarkand; C, Bukhara; D, Stalinabad; E, Leninabad. (Dubinin and associates, 1937.)

Clark, 1936). Different populations may contain different, or sometimes the same mutations, the concentrations of different mutations within the same populations being sometimes very different. The content of mutations in the same population in successive years may vary very much; but the mutations present in high concentrations may persist in the populations for several years, i.e. for many generations of *Drosophila*. Fig. 8 shows the results of such experiments in *Drosophila funebris* and *D. melanogaster*. All these experiments thus show that numerous muta-

tions of the same type as those studied in genetical experiments are present in wild populations, sometimes in surprisingly high concentrations. Special experiments in *D. pseudo-obscura* (Dobzhansky and Queal, 1938) showed that 'small' mutations
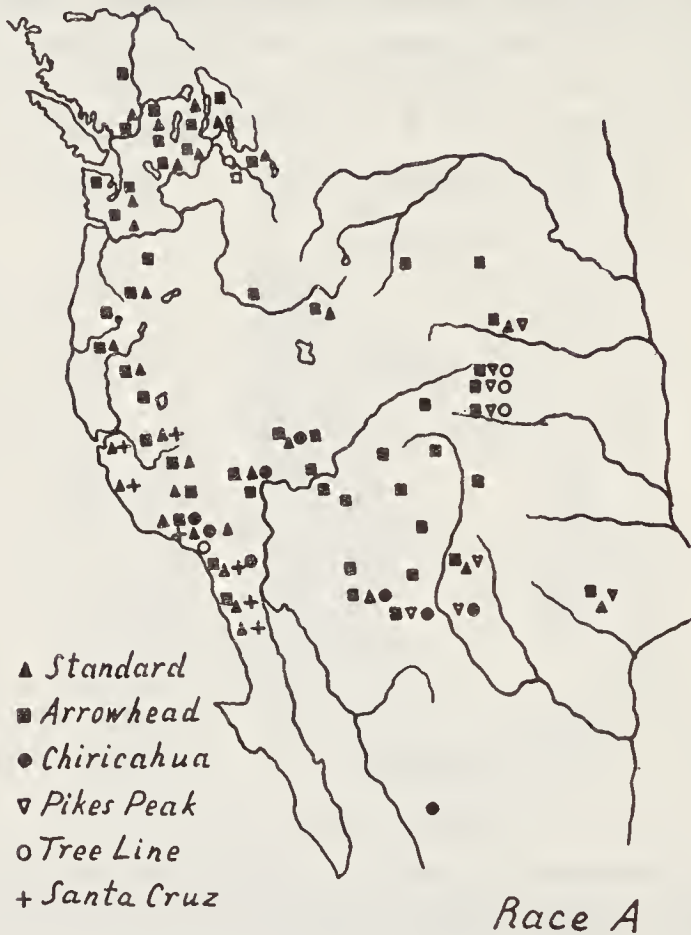
Fig. 10. Geographical distribution of different types of gene-arrangements (inversions and combinations of inversions) in the III-chromosome of *Drosophila pseudo-obscura* race A, in North America. (From Dobzhansky, 1937*b*.)

are also abundantly present in wild populations. In *D. melano-gaster* and in *D. pseudo-obscura* special experiments were designed in order to test the presence of chromosome-mutations in free-living populations. Fig. 9 shows the concentration of inversions in different *D. melanogaster* populations. Figs. 10 and 11 show the geographical distribution of different inversions and combinations of inversions in one of the chromosomes of *D. pseudo-*

obscura A and B in North America. Both of these extensive sets of experiments show that inversions especially are present in rather high concentration in all populations examined.

Thus both the *ad hoc* analysis in *Drosophila* and the whole evidence from other species shows that mutations are abundantly

▲ *Standard*

● *Klamath*

■ *Sequoia 1*

◉ *Sequoia 2*   ○ *Cowichan*   + *Wawona*

Race B

FIG. 11. Geographical distribution of different types of gene-arrangements in the III-chromosome of *Drosophila pseudo-obscura* race B, in North America. (From Dobzhansky, 1937*b*.)

present in free-living populations, so that the second requirement also is fulfilled. The study of inversions and combinations of inversions of a certain chromosome is of interest also in another respect. A special analysis of inversions and different combinations of inversions in the giant chromosomes of the salivary glands of *Drosophila* may show the sequence of their origin (Sturtevant and Dobzhansky, 1936), so that following up their geographical distribution, the accurate phylogenetic relations of the different types may be found. Fig. 12 shows the

result of such investigations in *D. pseudo-obscura* A and B and *D. miranda*.

(*d*) *Mutations as the raw material of evolution.* We thus have seen that gene-mutations, chromosome-mutations, genom-mutations, the position effects accompanying some of the chromosome-mutations, and the plastid-mutations in plants are the only known sources of heritable variation of organisms. Even if other still unknown sources of heritable variation exist, the
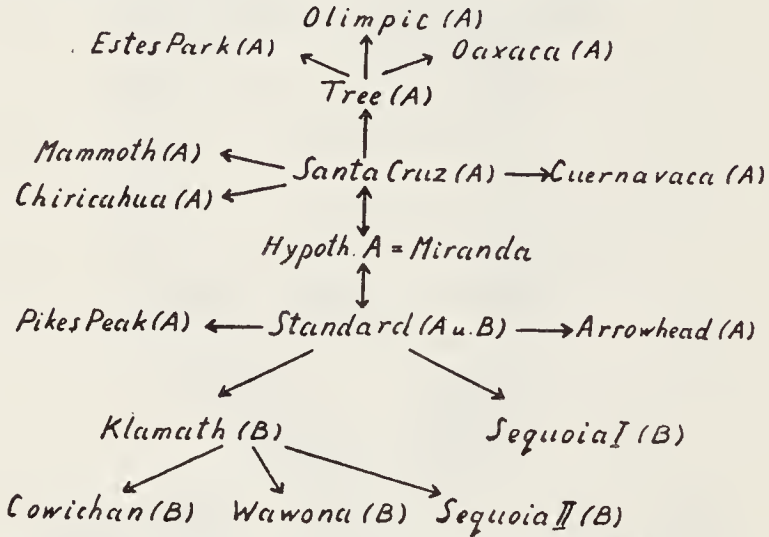
FIG. 12. Scheme of the phylogenetic relations of the different populations of *Drosophila pseudo-obscura* race A, race B, and *D. miranda*, constructed according to the assumed sequence of origin of repeated inversions in the III-chromosomes contained in these populations. (From Dobzhansky, 1937*b*.)

known ones and their combinations undoubtedly constitute by far the majority. The general features of the mutation-process, the special experiments on the relative viability of mutations and their combinations, and the analysis of the mutation-content of free-living populations, show that the assumption that mutation, as made known by modern genetics, is the only source of evolutionary material, fulfils all necessary requirements. It is thus legitimate to consider evolutionary questions and problems on the basis of this assumption.

3. *Mutations and the Formation of Taxonomic Groups*

If we consider mutations as the only source of evolutionary material, we must expect that the analysis of the genetic constitution of different subspecific and specific taxonomic groups

will show that the differences between those groups are merely due to different combinations of mutations (i.e. show Mendelian segregation); furthermore, we should expect to find cases of the formation of taxonomic groups *in statu nascendi*, due to the spread of single mutations or of definite combinations of mutations.

In this chapter some examples will be given proving that mutations and combinations are in point of fact the basis of geographical variability and of the differences between taxonomic groups. But first we must briefly consider the definition of 'real systematic groups'.

With the exception of really pure lines, clones, and identical twins, all individuals are genotypically different. Thus a biotype, even if classified and identified only in respect to rather few of the more important heritable characters, cannot be regarded as a group of taxonomic value. A 'real systematic group' of some taxonomic value must be characterized in two ways: It is a group of individuals (1) possessing a number of heritable characteristics in common, and (2) having, as a group, an historical reality in the process of evolution. The simplest definition of a 'real systematic group' would then be as follows: A group of individuals characterized by one or several common heritable characters and having a common area of distribution. The definition of an area of distribution should not be limited merely to a closed geographical territory, but extended to cover cases of ecological areas: in the latter case, two or more areas may overlap within a larger geographical area.

According to the above definition, a clear detection of the lowest intraspecific systematic categories can be made. The relative taxonomic evaluation of higher groups remains very difficult in particular cases, and must depend upon the general knowledge and 'biological tact' of the systematist. These difficulties already arise in connexion with any general definition of the species. This question can be here considered only very briefly. I believe that we have no reason to doubt the reality of species as natural taxonomic units; but, on the other hand, I doubt whether it is possible to give a general and simple definition of the species, applicable in all the larger groups of organisms. The most general but at the same time cautious definition of a species may perhaps be given as follows: a species is

a group of individuals that are morphologically and physiologically similar (although comprising a number of groups of the lowest taxonomic category), which has reached an almost complete biological isolation from similar neighbouring groups of individuals inhabiting the same or adjacent territories. Under biological isolation we understand the impossibility or non-occurrence of normal hybridization under natural conditions.[1] The practical difficulties of a general definition of the term species, and of using one or two simple criteria in distinguishing what is a species and what is not, may be seen from some examples of 'good' species which practically show no pronounced morphological differences (e.g. *Drosophila melanogaster* and *D. simulans*, *D. miranda*, and *D. pseudo-obscura*), and on the other side also 'good' species showing typical specific traits in their morphology, physiology, and distribution, but producing fertile hybrids with other species under laboratory conditions (e.g. some Lepidoptera, birds, and many plants).

Another question must still be briefly considered. Some biogeographers assume a fundamental difference between individual and geographical variation. This assumption is based on the obvious fact that not all the characters of the individual variation seen in a single local population are included in the geographical variability. But deductions about fundamental differences between geographical and individual variation based on these facts are wrong. The individuals differ in all those characters which are included in the geographical variation, but not vice versa, since the geographical variation is the result of the selection of only a few possible character-differences and character-combinations. The mutations and their combinations form the basis of the individual heritable variability; but only a few of them are used in the process of evolution to build up what were above described as 'systematically real groups'; and it is these latter which exhibit geographical variability. In many cases the same character may in different groups of organisms behave as an individual aberration, as a characteristic of a geographical race, or even as a species-character. Fig. 13 shows an example of this kind: a mutant wing-vein character in the genus *Andrena* (Hymenoptera).

[1] A more detailed classification and description of the various types of isolation is given in the next section (p. 107).

(a) *Taxonomic groups in statu nascendi.* We will now first examine the question whether cases can be found, in which certain mutations or combinations of mutations are just beginning to produce geographical races. If mutations really participate in the formation of taxonomic groups, such cases of races *in statu nascendi* should be found.

FIG. 13. A mutant character ('second cubital crossvein') in the populations of six different species of the genus *Andrena* (Hymenoptera): as a rare aberration (*A. albicans, A. praecox, A. vaga*), as a frequent aberration (*A. serica, A. argentata*), and as a species-character (*A. neglecta*). (Zimmerman, 1933.)

The participation of mutations in the formation of geographical races can be directly observed in the following cases. First of all when races, distinguishable in some other respects, show pronounced differences in the concentration of certain alternative heritable characters. Next, when species are polymorphic in respect of certain alternative heritable characters, and show pronounced differences in the concentrations of some of these characters in different populations (some of these populations reaching monomorphism by the total elimination of some of the character-alternatives). And finally in cases where a certain mutation, spreading around its centre of origin, occupies a definite distribution area, and thus can be designed as a good geographical race. There are undoubtedly many cases of all these types, but only a few of them have been described, because

of our lack of knowledge of the minor systematics and bio-geography even of our commonest species.

Cases of the first two types are nevertheless well known, especially amongst birds and beetles. In birds such cases were described by Stresemann in his *Mutationsstudien* (1926). In beetles a thoroughly analysed case has been described by Dobzhansky in *Harmonia axyridis* (1924, 1937). Fig. 14 shows
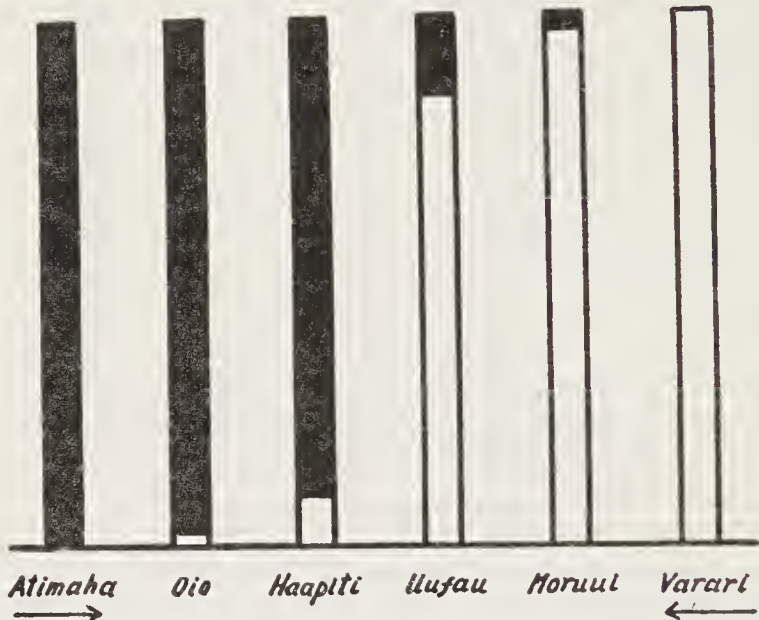
FIG. 14. Relative frequencies of an alternative heritable character, dextrality (black, →) and sinistrality (white, ←) of coiling in the mollusc *Partula suturalis*, in different populations on the island Moorea. (Crampton, 1916.)

a similar case in the mollusc *Partula suturalis*, analysed by Crampton, and showing different frequencies of an alternative heritable character in different populations on Moorea. Many other cases are known in the *Carabid bettles* from mountainous regions. Population-statistical studies on various of our most common species of plants and animals would reveal a large volume of interesting data on the distribution of single heritable characters, their dynamics, and their participation in the process of geographical variability.

The following figures will show some cases of the formation of geographical races by single mutations. Fig. 15 shows the present geographical distribution of the semi-dominant mutation *Elaterii* in a part of the north Mediterranean population of

the lady-beetle *Epilachna chrysomelina*. This mutation causes a conspicuous, specific colour-pattern, and must be classified as a good geographical race. The *Elaterii*-population also shows some differences in minor heritable characters, genetically inde-

Fig. 15. Geographical distribution of the semidominant gene 'Elaterii' in the north Mediterranean populations of *Epilachna chrysomelina* F. (Coleoptera, Coccinellidae).

pendent of the *Elaterii*-mutation; this is to be expected according to our knowledge of the relative viability of mutations and combinations: every mutation selected or distributed for any reason must automatically 'select' a genotypical environment which is optimal for its relative viability. Fig. 16 shows the distribution of a recessive mutation affecting the structure of the molar teeth in the north German population of *Microtus arvalis* (Zimmerman, 1935). From Schleswig-Holstein the concentration of this mutation decreases southwards. Fig. 17 shows the distribution of three heritable colour-types, the normal and two different recessive mutations, in the German population of the squirrel *Sciurus vulgaris*; both mutations seem to be limited, so far as any considerable frequency is concerned, to northern or mountainous regions (they frequently recur in northern
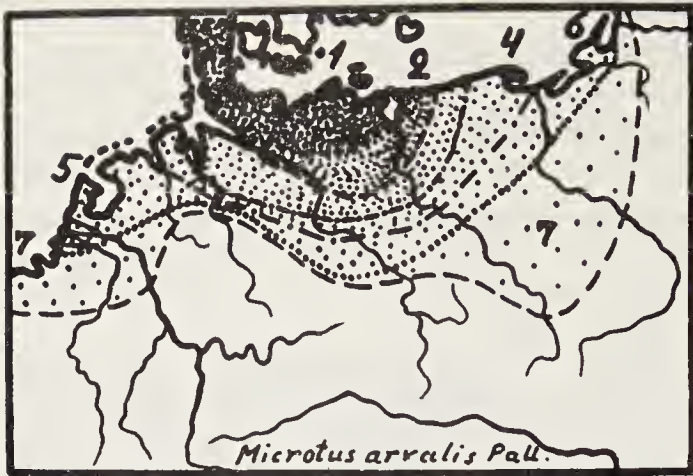
FIG. 16. Geographical distribution of the recessive mutant character 'simplex' (molar teeth) in the population of *Microtus arvalis* Pall. (Rodentia) from northern Germany. Concentrations of phenotypically detectable homozygotes: 1 = over 85 per cent.; 2 = 65–85 per cent.; 3 = 50–65 per cent.; 4 = 25–50 per cent.; 5 = 10–25 per cent.; 6 = 5–10 per cent.; 7 = less than 5 per cent. (Zimmerman, 1935.)
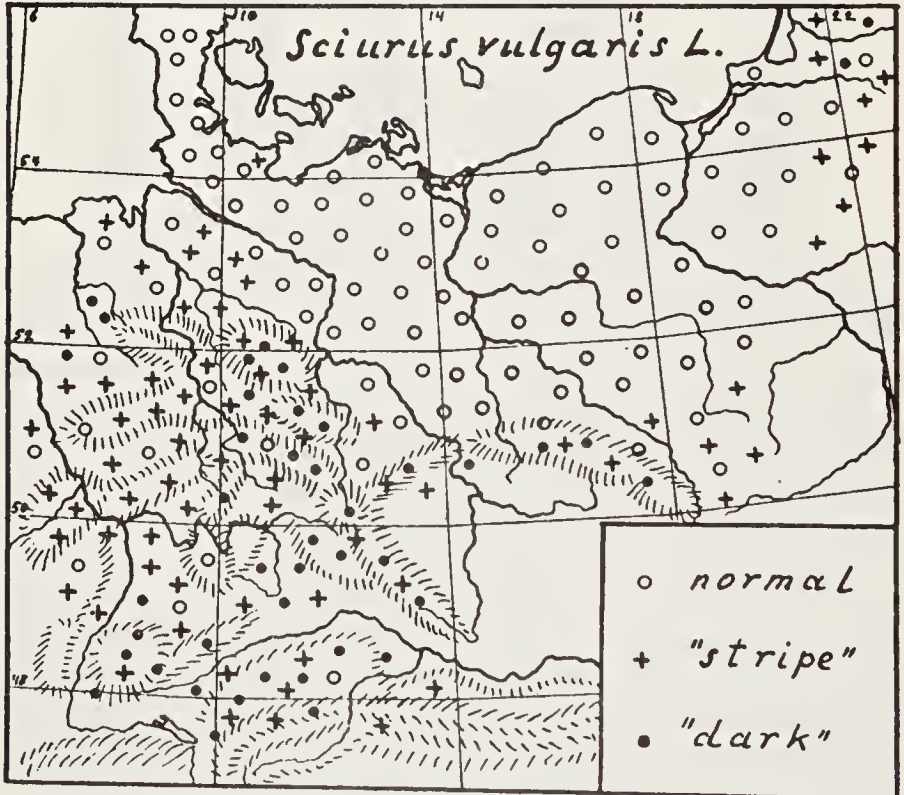
FIG. 17. Geographical distribution of three heritable colour-types ('normal', dark dorsal 'stripe', and 'dark' colour) in the squirrel, *Sciurus vulgaris* L. (Rodentia) in Germany. (Lühring, 1928.)

Russia and the Ural district), but as single aberrations may be found anywhere. Figs. 18 and 19 show definite, limited distribution areas of high concentrations of recessive colour-mutations within the populations of the polecat *Putorius putorius* and of the hare *Lepus timidus* in western Russia; as rare aberrations

Putorius putorius L.
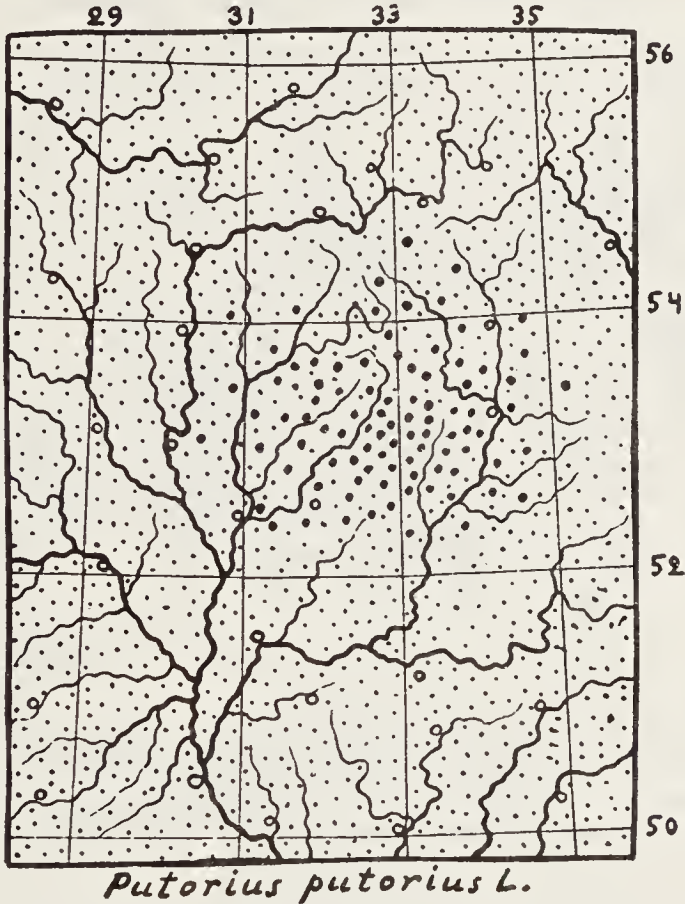
FIG. 18. Geographical distribution of a recessive erythristic mutant colour-character (subspec. *Stanchinskii* Mel.) in the polecat, *Putorius putorius* L. (Carnivora) in western Russia. (According to the data of Melander, 1926, and other sources.)

this erythristic mutation in the polecat and this melanistic mutation in the hare are also found in other parts of the respective species-areas.

One of the most interesting cases of the geographical distribution of single mutations is represented in Fig. 20. Here is shown the present distribution of a recessive melanistic colour-mutation in the hamster *Cricetus cricetus*. This mutation occurs sporadi-

cally as an aberration in various populations of the hamster. The well-known Russian geographer Lepekhin, at the end of the eighteenth century (in the years 1771–2), during his scientific journey to northern Bashkiria, observed that in a certain region between the rivers Kama and Belaia the hamster population contained a high percentage of melanistic animals. Since then
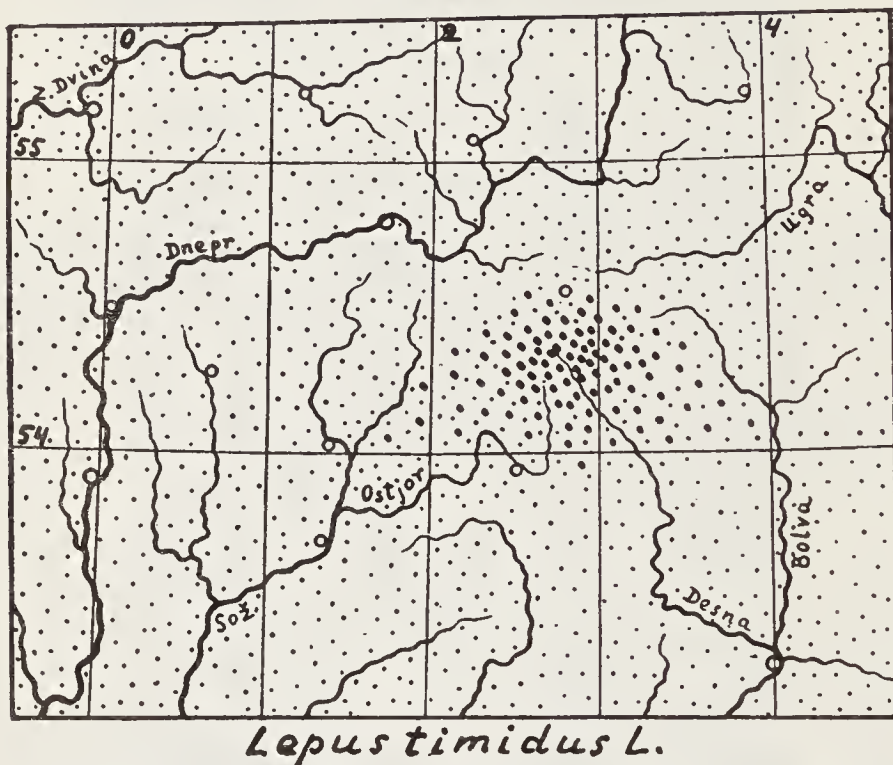
Lepus timidus L.

FIG. 19. Geographical distribution of a recessive melanistic mutant colour-character in the hare, *Lepus timidus* L. (Rodentia), in western Russia. (According to the data of Melander, 1930, and other sources.)

up till the present the distribution of this black mutant has been followed up (Kirikov, 1934, and additional data). An exact study of its distribution was possible because hamsters play an important role on the fur-markets in eastern Russia. In the course of the last 150 years this mutation has spread from its original centre of high concentration along the northern border of the species-area. To-day the populations of northern Bash-kiria and in the adjacent western parts of eastern Russia are almost homogeneous for this mutation; and populations with rather high concentrations of this gene are spread westwards as

far as the river Dnieper. The hamster is a typical rodent of the xerophytic zone of the steppes; but this melanistic mutation seems to be better adapted than the normal form to the cooler and moister climate of the wood-steppe subzone along the northern border of the distribution area of this species.

FIG. 20. Geographical distribution of a recessive melanistic colour-mutation in the hamster, *Cricetus cricetus* L. (Rodentia), along the northern limit of its distribution-area in eastern and middle Russia. (According to the data of Kirikov, 1934, and other sources.)

What appears to be a very similar case is that of the spread of the melanic mutant of the opossum *Trichosurus vulpecula* in its Tasmanian subspecies (Pearson, 1938), except that the area in which the black form is abundant is geographically isolated from the main area of the species, in which melanics occur only as rare aberrations. As with the previously cited case of the tooth-mutant in *Microtus arvalis*, the geographical distribution of the frequencies of the mutant type provide evidence that it is still in process of spreading, the spread being totally prevented or partially held up by such features as mountains, large rivers,

or narrow isthmuses. It is also to be noted that the region in which the black form has been favoured is cooler and moister than the rest of the range, in *Trichosurus* as well as in *Cricetus*.

These examples show clearly enough that although our knowledge of the population-statistics of wild plants and animals is rather meagre, nevertheless enough direct cases of the participation of mutations in the origination of geographical races may be observed. That this refers not only to gene-mutations but also to chromosome-rearrangements is shown by the *Drosophila pseudo-obscura* work, some results of which are shown in Figs. 10 and 11.

(*b*) *The genetic structure of races and species.* Another way of proving the participation of mutations in the origin of taxonomic groups is to test the genetic nature of the differences between these groups.

In many different cases, involving different groups of plants and animals, different geographical races or subspecies or even different species have been crossed. Although a thorough monographic analysis of the whole intraspecific variability has been carried out only in a few cases, the general impression of all such genetic experiments is that all heritable differences between races and even species are dependent upon segregating units of genetically familiar type, the origin of which is known to be due to gene- or chromosome-mutations. Only in a few cases, as was mentioned before, some plant crosses show plasmatic differences the origin of which is not yet known. In any case we may state that the great majority of the differences between taxonomic groups are due to mutations and their combinations.

The experiments show that most of the 'good' geographic races, even the closely related ones, differ in a large number of genes, most of which cause only very small quantitative character-deviations. Thus we get typical multifactorial segregations, like the one shown in Fig. 21. But this is just what is to be expected according both to our knowledge of the history of species and races and to our knowledge of the interrelations of the relative viabilities of mutations and combinations.

In many cases it is still impossible to discover the detailed relations between the biological values of single race characters or their combinations and the local environmental conditions. But in some cases the local biological value of the geographical

$F_2 \quad M = 69.1 \quad \sigma = 13.9$

$F_1 \quad M = 68.9 \quad \sigma = 6.5$

P. leucocephalus $\quad$ P. polionotus

$M = 45.5 \quad p \quad M = 93.0$

40 $\quad$ 60 $\quad$ 80 $\quad$ 100
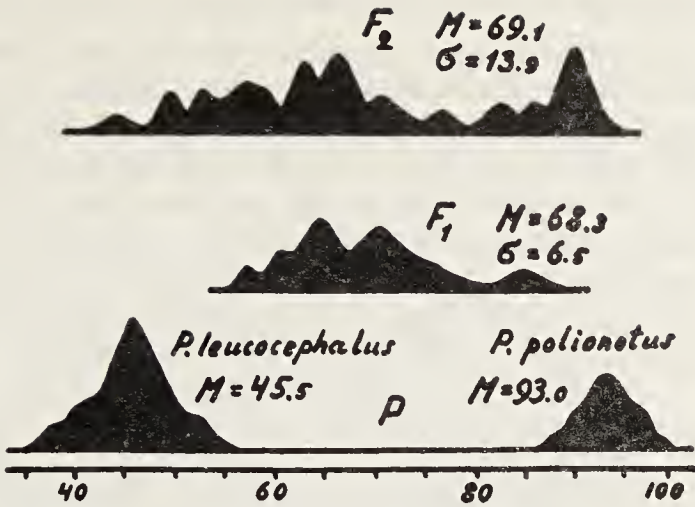
FIG. 21. Polygenic segregation of the extension of dark colour in a cross between two subspecies of deer-mouse, *Peromyscus polionotus polionotus* × *Peromyscus polionotus leucocephalus*. (Sumner, 1932.)
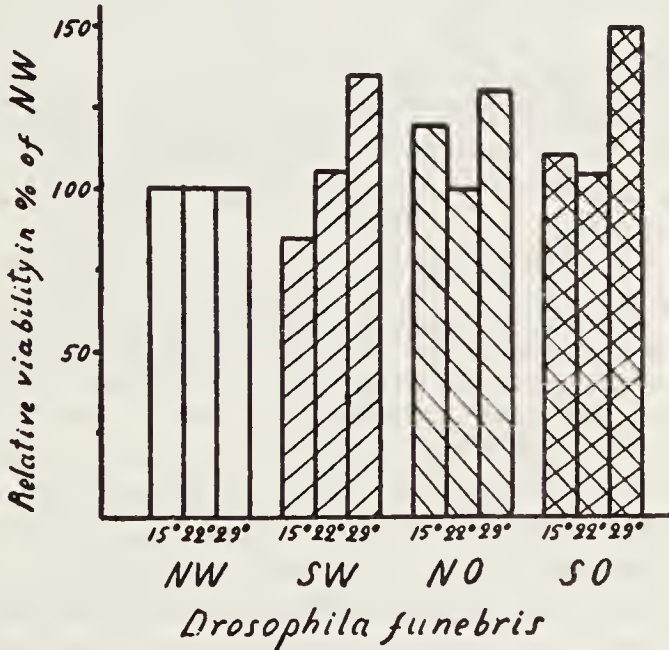
FIG. 22. Relative viabilities of *Drosophila funebris* from various regions of the western Palaearctic: the north-west (seven populations from: Germany, Sweden, Norway, Denmark, Scotland, England, and France), the south-west (six populations from: Portugal, Spain, Italy, Gallipoli, Tripolis, and Egypt), the north-east (six populations from: Leningrad, Kiev, Moscow, Saratov, Perm, and Tomsk), and the south-east (five populations from: Crimea, northern Caucasus, southern Caucasus, Turkestan, and Semiretchje), in different temperatures (15°, 22°, and 29°), expressed in percentage of the viability of the north-western form. (Timofeeff-Ressovsky, 1935a.)

races can be shown experimentally. The relative viability of *Drosophila funebris* flies from twenty-four different populations of the western Palaearctic was studied at three different temperatures (15°, 22°, and 29° C.). A summary of the results is shown in Fig. 22; the north-western and south-western populations differ clearly in respect to their viabilities at low and high
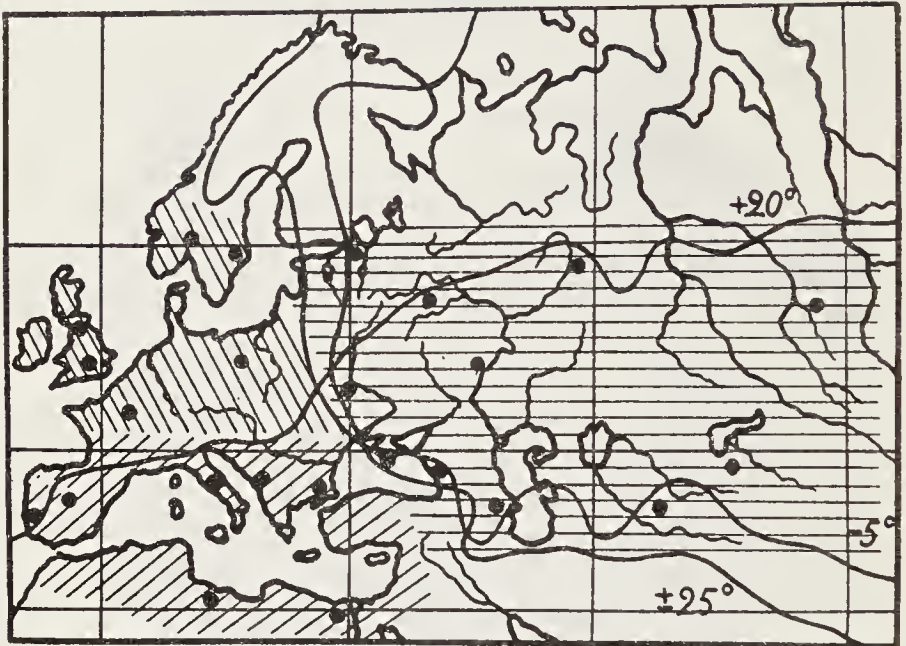
FIG. 23. Map of the approximate distribution of the three 'temperature-races' in *Drosophila funebris*; the distribution fits the climatic peculiarities of this region, characterized by the isotherms of July (+20° C.), and January (−5° C.), and by the isoline of a difference of 25° C. between the mean temperatures of July and January (±25°). (Timofeeff-Ressovsky, 1935*a*).

temperatures, the northern population being more resistant to low, the southern more resistant to high temperatures. All the eastern populations, the north-eastern as well as the south-eastern ones, show higher resistance both at low and at high temperatures. At first glance the results for the eastern populations do not show the same correspondence with the local climate as the western ones. But if, as it is shown on Fig. 23, we consider the climatic peculiarities in this part of the palaearctic region, we find an excellent correspondence of all populations with the climates of their habitats. As is seen on the map of Fig. 23, the January isotherm of −5° C. runs from the northernmost part of Norway to the south-west point of Russia on the

Black Sea coast; on the other hand, the July isotherm of $+20°$ C. runs from Lisbon in the west up to about $63°$ latitude in the east. These isotherms characterize the continental climate of eastern Europe and northern Asia, with both extremely high and low temperatures. Thus these 'temperature races' of *Drosophila funebris*, which are due to the accumulation by selection of small mutations, show excellent correspondence to their environments. Dobzhansky (1935, 1937) obtained similar results in studying the fertility of different populations of *Drosophila pseudo-obscura* at different temperatures.

Thus, the whole analysable evidence is in favour of the assumption that the origin of taxonomic groups is due to the accumulation and combination of genetically known variations.

4. Evolutionary Factors

In the preceding two sections the evolutionary material was examined from the viewpoint of experimental genetics. Now a brief examination of the evolutionary factors will be added.

An infinitely large panmictic population consisting of a mixture of genes having equal biological value will, in the absence of mutation and under constant environmental conditions, be stabilized in a certain state of equilibrium of the different allelomorphs. Exact mathematical investigations (R. A. Fisher, J. B. S. Haldane, S. S. Tschetverikov, S. Wright, and others) show that three different factors may disturb this equilibrium and lead to a change of the relative gene-frequencies, i.e. to an evolution of the previously stable population. These factors are: (1) mutability, introducing, by mutation, changes into the genetic constitution, the amount of the change being expressed by the mutation-pressure depending upon the rate of mutation; (2) selection, depending upon differences in the biological value of the different genotypes, and quantitatively characterized by selection-pressure; and (3) the limitation of panmixy, leading to accidental fluctuations of the concentration of single genotypes, and, in cases of continued isolation, to a statistical divergence of the different parts of a mixed population. The interrelation of these three factors constitutes the mechanism of adaptation and differentiation, i.e. the mechanism of evolution.

Mathematical analysis shows the quantitative values and

limitations of the efficiency of each of these three factors and their interrelations under various arbitrary conditions and values of mutation-pressure, selection-pressure, and isolation. This type of mathematical work is of the greatest importance, showing us the relative efficacy of various evolutionary factors under the different conditions possible within the populations (Wright, 1932). It does not, however, tell us anything about the real conditions in nature, or the actual empirical values of the coefficients of mutation, selection, or isolation. It is the task of the immediate future to discover the order of magnitude of these coefficients in free-living populations of different plants and animals; this should form the aim and content of an empirical population-genetics (Buzzati-Traverso, Jucci, and Timofeeff-Ressovsky, 1938). Here we can consider the evolutionary factors only in a rather general way, with the aim of testing whether the known qualities of the evolutionary material and of the conditions in natural populations are of such a nature that the known evolutionary factors, applied to the known evolutionary material, are capable of explaining the mechanism of evolution.

Although we know only the three above-mentioned groups of mechanisms leading to changes in the genetic constitution of populations, we may distinguish four different evolutionary factors: mutation, selection, isolation, and population-waves. For biological reasons (which will be mentioned in due course) we differentiate the 'mathematical' factor of isolation into two biological factors, that of isolation proper and that of population-waves.

(a) *Mutation.* The biological content and significance of this first evolutionary factor are at present better known than those of the other factors, due to the extensive genetical experiments on the process of mutation in different plants and animals.

As we have seen in the previous sections, mutation is the sole, or in any case the most important, source of new evolutionary material. In this sense the significance of mutation as an evolutionary factor is quite clear. But it is often asserted that mutation may also act as a directing factor in evolution. Even some geneticists have thought that, for instance, some of the so-called orthogenetic series in palaeontological evolution may be explained by 'directed' mutations (Jollos). However, there are

two general features of mutation which make it impossible to explain directed evolutionary series simply by correspondingly directed mutation—first, the random nature of mutation and, secondly, the relatively very low rate of mutation. These two properties show that the process of mutation as such could influence the direction of evolutionary change only in the extremely improbable event of mutation-pressure being high enough over long periods of time to override the effects of the other factors, selection and isolation. The evolutionary fate of two mutations A and B will thus normally depend not upon the very small difference in their very low mutation-rates but upon their relative selective value and the structure and history of the populations. This being so, even cases of strictly directed mutations (which are so far unknown from exact experimental data) would have no importance as an explanation of chronologically or territorially 'directed' series of phenotypes. A directive influence of mutation is possible only in so far as the mutability of any species is limited, and in so far as any step in differentiation at the same time constitutes a certain limitation of further possibilities of variation.[1]

Mutation as an evolutionary factor is thus of importance as the source of new heritable variation; it has no, or at best very little, importance as a directive factor in evolution.

(b) *Selection*. The significance of natural selection as an evolutionary factor is well known, so that we need here only examine whether and to what extent the genetically known evolutionary material may be subject to selective processes.

In a mixture of two or more different genotypes, that one which under given conditions has the highest total probability of producing mature offspring will gradually increase its relative frequency within the population: this is the general process of natural selection. Selection-pressure can be numerically expressed in the form of selection-coefficients which represent the relative probabilities of reproduction of the genotypes in ques-

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[1] Perhaps some cases of the reduction of vestigial organs which no longer retain the selective value which they possessed when fully developed can be ascribed to an automatic accumulation of mutations, most of which would produce a reduction of the organ. But this would be only a special case of a very general phenomenon: without the sifting, and thus directive, action of natural selection, mutation alone would lead to a general regression of highly differentiated organisms (since most mutations are 'deleterious' or 'regressive').

tion. It has been shown by numerous mathematical studies (Fisher, Gause, Haldane, Tschetverikov, Volterra, Wright, and others) that even very small selective advantages may, although only within large populations and over long periods of time, significantly increase the concentration of genotypes previously present in low concentrations, and thus change the genotypic constitution of the population. Most evolutionists have been very cautious in their assumptions concerning the quantitative values of selection-coefficients, and seem in general to have rather underestimated the amount of selection-pressure to be found in nature. All that we know about the relative viability of different mutations and combinations under different environmental conditions shows that we can, in point of fact, reckon with quite high positive and negative selective values for different genotypes under different conditions and in combination with different other genotypes. Experiments on the relative viability of mutations and combinations have shown that the selective values of mutations may be very different in the heterozygous and the homozygous condition, in different combinations with other genes, and in different environments. From these findings a highly differentiated and plastic action of natural selection may be deduced.

Our present knowledge of the relative viability of mutations readily explains the possibility of the differentiation by natural selection of different 'harmonious' genotypic combinations in different regions within the geographical range of a species; they are due to the fact that every process of selection automatically involves (even in cases when one character is mainly being selected) many different genes connected with the primary character by their viability interrelations. This is the way in which many so-called physiological correlations arise, and the apparently 'neutral' characters that often are diagnostic of species and subspecies. It is evident that not only positive but also negative selection will be of importance in building up physiologically correlated gene-combinations. The heterogeneity of almost all natural populations provides the species with potential 'candidates' for evolution, ready to undergo positive or negative selection in different regions of the species area. The same mutation may clearly have different selective values in different populations, due to differences in the external

or the genotypic environments. The genetic heterogeneity of a species constitutes a reservoir of potential adaptability to heterogeneous and fluctuating environments.

Thus, the properties of the genetically known material of evolution permit an extremely powerful, plastic, and differentiated action of natural selection, leading to the most specialized and minute adaptations. And different selective adaptations, when combined with isolation, may lead to differentiation. We know that rather high selection coefficients may occur; but we still know very little concerning the actual intensities of selection-pressures to be found in nature.

(c) *Isolation.* For biological reasons we must distinguish two evolutionary factors, which are rather similar in the mechanism of their action: first, isolation, and, secondly, population-waves. The essential properties of both these factors are the limitation of panmixy, leading to a limitation of interbreeding between neighbouring groups of organisms, and the restriction of population-size. The limitation of interbreeding and mixture hinders the dissipation of incipient local processes of differentiation and localizes them; the reduction of population-size significantly increases the relative importance of accidental fluctuations of gene-concentrations.

Isolation we define as the more constant, longer-lasting limitations of panmixy, their most essential result being a partial or total prevention of interbreeding between two or more groups of organisms. A definition of population-waves will be given later.

Various different forms of isolation exist. Isolation as a whole comprises two main kinds—biological and territorially-geographical (hereinafter simply called geographical). Biological isolation may be subdivided (without pretending to give a definitive classification) into the following main groups: (1) genetic isolation *sensu stricto*, consisting in the lowering of hybrid viability or fertility (in extreme cases producing complete hybrid sterility or inviability), and brought about by genetic differences between the parental groups of organisms; (2) physiological isolation, consisting in a limitation (by sexual or gametic incompatibility) on the production of hybrids, although the hybrids themselves, if produced, are more or less normal; (3) ecological isolation, limiting the possibility of interbreeding

through ecological differences between the parental groups of organisms. It is evident that all types of biological isolation are in the last resort due to genetic differences. Geographical isolation, on the other hand, is brought about by unequal distribution of the individuals within the species area, by disjunction between different parts of the distribution area, or by unsurmountable geographical obstacles within the species area.

All the types of biological isolation above mentioned have been observed in different plants and animals, although sometimes it is rather difficult to say which type is primary. The problem of genetic and physiological isolation has been extensively analysed by Dobzhansky, Sturtevant, and their colleagues in *Drosophila pseudo-obscura* A and B, *D. miranda*, *D. athabasca*, and *D. azteca* (Dobzhansky, 1935, 1937; Dobzhansky and Koller, 1938; Sturtevant and Dobzhansky, 1936). Physiological and ecological isolations have been extensively studied in *Trichogramma* (Harland and Attek, 1933) and in Aphids (Cholodkowsky, 1910). Sexual selection leading to partial physiological isolation has been experimentally tested in some mutant stocks of *Drosophila melanogaster* and *funebris* (Nikoro and collaborators, 1935; Spett, 1931; Sturtevant, 1915; Timofeeff-Ressovsky unpublished), and in different strains of *Drosophila pseudo-obscura*, *D. miranda*, *D. azteca*, *D. athabasca* (Dobzhansky and Koller, 1938). Apart from *Drosophila*, the limitations of the fertility and viability of hybrids due to differences in the structure and number of chromosomes are especially well known in Lepidoptera and plants (Federley, 1915–16; Karpechenko, 1935).

In many, if not in most cases, the various types of biological isolation are secondary, the primary isolation being geographical. The latter type of isolation may occur in very different forms. Fig. 24 shows an extreme case of a geographical disjunction of a species area; such cases are known in different groups of plants and animals, and are due to post-diluvial disjunction during the reimmigration of the species into their previous area from the south-western and south-eastern refuges into which Palearctic organisms were driven during the glacial period. Fig. 25 shows an example of a territorially fractionated species area, due to the lack of suitable biotopes between the various occupied parts of the total distribution area; such cases

of geographical isolation are also very frequent. An example of
secondary fragmentation, due to partial extermination by man,

FIG. 24. Postdiluvial disjunction of the distribution-area of *Cyanopica cyanus* Pall.
(Aves, Corvidae). (Meinertzhagen, 1928.)

FIG. 25. Ecological disjunction of the distribution-area of *Nesokia* (Rodentia) in
middle Asia. (Geptner, 1936.)

is shown in Fig. 26. Territorial fragmentation of the population
of a species may occur also on a smaller geographical scale, as
shown on Fig. 27.

An examination of the real distribution of individuals within

the species-area shows that total or partial territorial isolation may occur on a still smaller scale, even within small local popula-

FIG. 26. Secondary fragmentation of the distribution-area of *Martes zibellina* L. (Carnivora), by extermination. (Ognev, 1931.)

FIG. 27. Orographical disjunction of the populations of *Chionomys nivalis* Mart. (Rodentia) in the Alps. (Mohr, 1930, from Geptner, 1936.)

tions. The distribution of individuals is never quite uniform, and shows either small isolated population-areas or at least more or less pronounced differences in population-density in different parts of the inhabited territory; this is schematically

shown in the upper row of Fig. 28. But such minor fragmentations of the population do not always lead to isolation. Isolation, in the sense of a limitation of panmixy, depends upon the relation between territorial fragmentation of the population and what we may call the 'range of activity' of the individuals of the species in question. By the term 'range of activity' we mean the area within which individuals of one generation may move
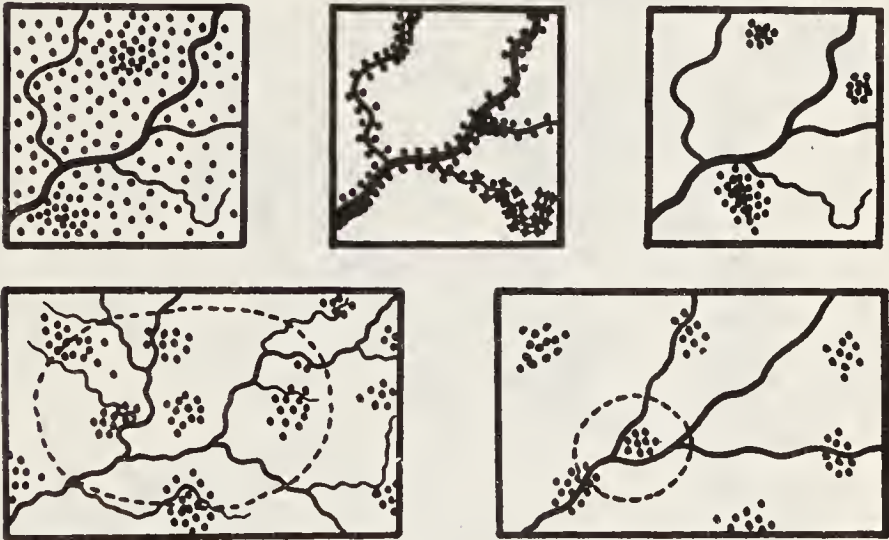

FIG. 28. Schemes of the distribution of individuals within the population of different species, and of its relation to the 'activity-regions' of the individuals. (Original.)

or be passively but regularly transported; it thus defines the regular potential breeding-ground of individuals of the species in question. Two different possible relations of these two variables are diagrammatically shown in the lower row of Fig. 28. If territorial fragmentation is small compared with the size of the range of activity, then isolation in the sense of a limitation of panmixy will not necessarily occur. The following example shows how misleading conclusions concerning the degree of geographical isolation may be, if based merely upon territorial fragmentation of the population. The common teal, *Nettion crecca*, occurs in widely separated biotopes within the distribution area of the species, so that a pronounced degree of geographical isolation of the various single populations might be assumed. But, as shown on Fig. 29, young birds taken from

the nest and ringed in central England were already in their next year caught as nesting-birds in different parts of a huge region, extending from Iceland and the northern Urals in the north to central France and central Russia in the south. This implies a tremendous dissipation of the young birds in every generation, i.e. a very large range of activity, so that territorial

FIG. 29. The nest-regions ('activity-regions'): of the common teal, *Nettion crecca* L. (Aves, Lamellirostres), marked as young birds in England and caught as nesting birds during the next year; of *Sturnus vulgaris* L. (Aves, Passeres), marked as young birds in Denmark and caught during the subsequent eight years. (Original, according to the data of Schütz and of Promptov.)

fragmentation is of no importance as an isolating factor. The same figure shows the considerably smaller activity-range found in the starling *Sturnus vulgaris*.

Our knowledge of the real distribution of individuals within populations, and of their ranges of activity, is still very limited, so that we know little about the relative importance and frequency of small-scale territorial isolation. In suitable objects both questions can be easily studied. Fig. 30 shows the results of a study of the distribution of individuals in three different species of *Drosophila* on a small area near Berlin. Fig. 31 shows the result of an experiment on the determination of the activity-range in one of the species, using non-deleterious mutations as

markers. These studies show that the regular activity-ranges in *Drosophila* are rather small, so that even small territorial fragmentations of the population may result in partial isolation. Further experiments of this type should be carried out, both in *Drosophila* and in other organisms.
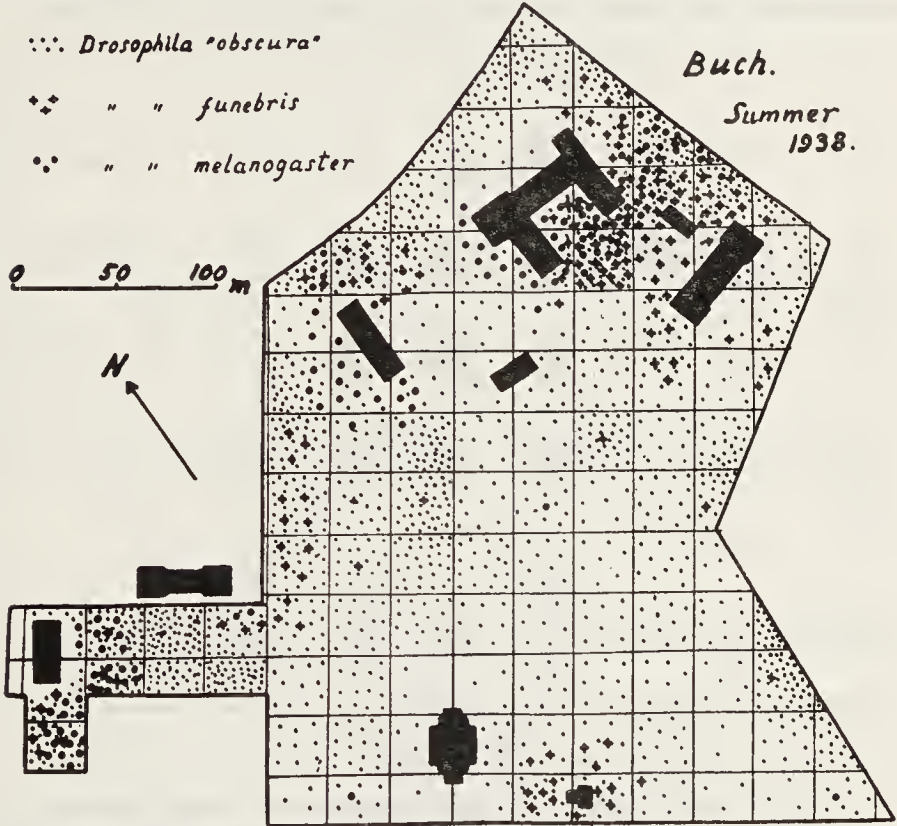
FIG. 30. The distribution of three species of *Drosophila* on a tenement in Buch. In the middle of each square a bottle with food was placed for 3–4 days; these bottles were inspected twice on each day, and the flies caught in them were counted and recorded; such experiments were repeated every 3–4 weeks during the whole season. (Original, according to the data of H. A. Timofeeff-Ressovsky.)

We thus see that various forms of isolation are widespread in all organisms, down to the territorially smallest populations. But, just as in the case of selection, we still possess very few exact data about the real amount and the relative significance of biological and small-scale geographical isolation.

(d) *Population-waves.* The fourth evolutionary factor, population-waves, consists in quantitative fluctuations of the number of individuals and of the territorial distribution of single

populations. As with isolation, the mechanism of action of population waves consists essentially in the limitation of panmixy and population-size; but population-waves differ from isolation in not being definitely-directed and long-period processes, but accidental short-period fluctuations in both directions. Their
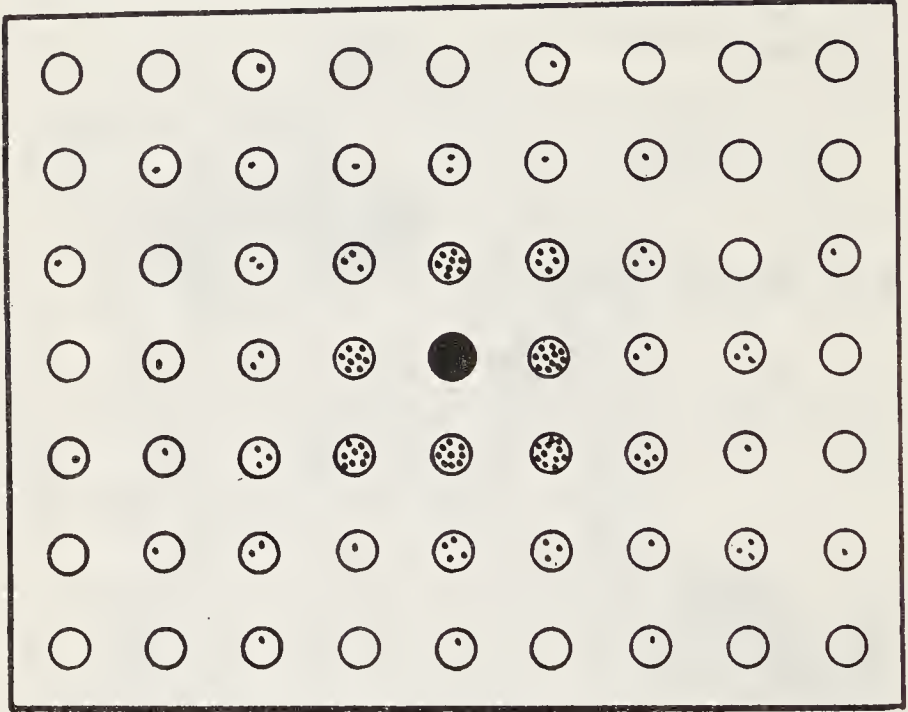
ca 25 m

FIG. 31. The 'activity-region' of *Drosophila funebris*. 1,200 marked flies were put with a supply of food at the place marked with a black circle; 99 bottles with food were placed at regular distances around this place, and the marked flies caught in these bottles were counted and recorded once a day during a period of two weeks. The circles represent the bottles, and the black dots the marked flies caught in these bottles. (Original.)

most important effect consists in the production of accidental fluctuations of gene concentrations. The evolutionary importance of these processes was first recognized by Tschetverikov (1905, 1915), who called them 'life-waves'; Elton (1930), Dubinin (1931), and Dubinin and Romaschoff (1932) pointed out their evolutionary significance under the name of 'genetically-automatic processes', and Wright (1932) gave an exact mathematical analysis of the mechanism of their action.

In all organisms, the population-size is not constant but is

subject to more or less pronounced quantitative fluctuations, usually periodic (Elton, 1930). It is, for instance, well known that only a small fraction of the young produced in each generation reaches maturity; this indeed implies only a difference in the numbers of individuals of different ages. But it is also well known that in organisms with several generations per year the population-size at different seasons of the year may be very
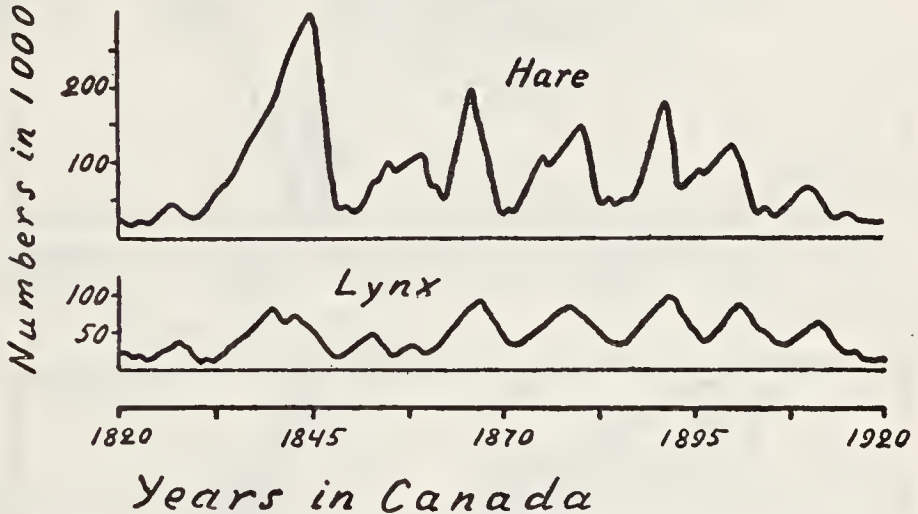
FIG. 32. Quantitative fluctuations of the populations of the hare *Lepus americanus* and the lynx *Lynx canadensis* in eastern Canada, as shown by the fur-market data of the Hudson Bay Company. (Hewitt, 1921.)

different; in some insects of the temperate zone the differences in number of individuals before and after hibernation may be of the order of magnitude of 1 : 1,000 or even more. Finally, in many organisms non-seasonal fluctuations recurring at more or less regular periodic intervals of several years are also known; Fig. 32 shows such correlated fluctuations of the populations of hare and lynx in Canada during the last century.

In most cases fluctuations in number of individuals are accompanied by corresponding fluctuations of the 'micro-territories' of the sub-populations. In addition, there may occur larger and more permanent increases or decreases, both periodic and aperiodic, of the territory occupied by larger populations (species or subspecies); the causes of these fluctuations are in most cases not yet exactly known. Fig. 33 shows the rapid expansion of the European cornborer *Pyrausta nubilalis* in North America; and Fig. 34 the expansion of the American musquash

FIG. 33. Expansion of *Pyrausta nubilalis* Hb. (Lepidoptera) in North America in the years 1926–7. ▨—territory occupied before 1926. (Felt (1928), from Geptner (1936).)
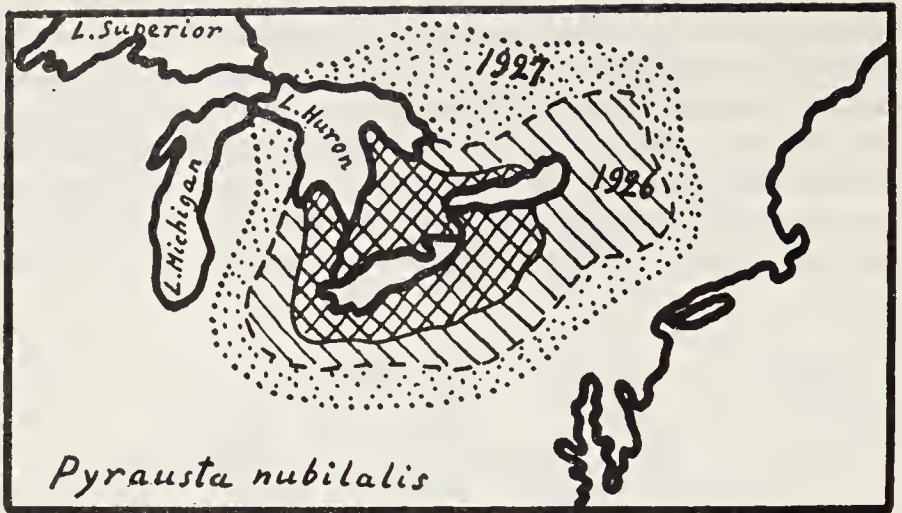

FIG. 34. Expansion of the musquash (muskrat), *Fiber (Ondathra) zibethicus* L. (Rodentia) in central Europe since its introduction in 1905. (Ulbrich, 1930.)

(muskrat) *Fiber zibethicus* in central Europe since its introduction in the first years of the present century. Fig. 35 shows the expansion of the common hare, *Lepus europaeus*, in a north-eastern direction during the last century; and Fig. 36 that of the Siberian bunting, *Emberiza aureola*, in a western direction during

FIG. 35. North-eastward expansion of the hare *Lepus europaeus* L. (Rodentia) and of the Serin finch *Serinus canaria serinus* L. (Passeres) from 1825 to 1925, and from 1800 to 1925 respectively. (From the data of Folitarek, Mayr, and other sources.)

the same period. A case of northward expansion in the roller (*Coracias garrula*) is shown in Fig. 37.[1]

Many similar cases are known, especially in insects, game-birds, and mammals, of changes in distribution area; but only a few have been studied quantitatively. All gradations occur from small and short territorial fluctuations up to prolonged

[1] Another well-known case is the rapid expansion round the coasts of the British Isles from the island of St. Kilda, of the breeding-range of the Fulmar Petrel (*Fulmarus glacialis*) which, starting in about 1887, has now reached southern Yorkshire on the east, and Pembrokeshire and southern Ireland in the west. See S. Gordon (1936).

and pronounced range-changes, gradually leading over to processes of historical expansions or migrations of species. Most important from our present point of view are the small quantitative fluctuations of single populations, especially at the limits of the distribution areas of subspecies and species. Every field-naturalist is aware that at the margins of distribution areas the
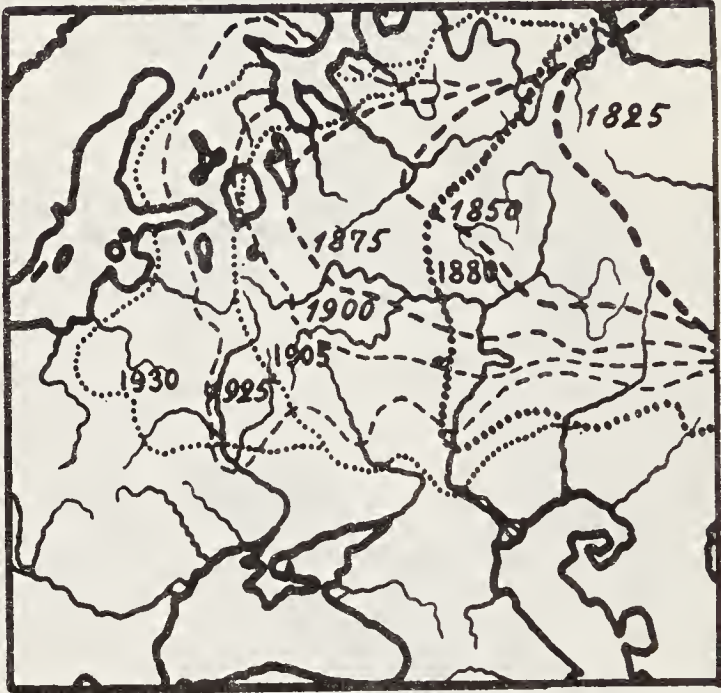
Fig. 36. Westward expansion of the bunting *Emberiza aureola* Pall. (Passeres, - - - - 1825) and of the warbler *Acanthopneuste viridana* Blyth. (Passeres, · · · · 1880), from 1825 to 1925, and from 1880 to 1930 respectively. (From the data of Promptov, and other sources).

waves of population may result in what we may call 'breakers'. Fig. 38 shows diagrammatically such 'population-breakers' at the margin of a distribution area. As an evolutionary factor, both numerical and territorial population-waves are of great importance.

The periodic numerical fluctuations of small populations will produce a pronounced accidental fluctuation of the concentration of single genotypes. They may lead to the total disappearance of many genotypes present in low concentrations (irrespective of their selective value), while other rare genotypes may also irrespective of their selective value reach rather

high concentrations. This process is of the greatest importance. The action of selection (even with high selection-coefficients) can be shown to be very slow in the case of low concentrations of a genotype; it becomes very much more rapid when the concentration is higher. Thus only the genotypes which reach higher

FIG. 37. The northward expansion of the roller, *Coracias garrula* L. (Aves, Coraciiformes) during a period of fifty years.

concentrations as a result of accidental fluctuations become exposed to a really effective selection. Further, the selection of homozygotes can only begin when the concentration of heterozygotes has reached a rather high level. Population-waves are thus important as an historical factor in the fixation or disappearance of mutations. The high concentration of many mutations in free-living populations is undoubtedly due to population-waves. On the other hand, the further fate of those genotypes which have already reached a higher concentration

depends mainly on selection and not on accidental fluctuations.

Population-waves may also exert an influence upon the mechanism of selective action. The territorial fluctuations of a population increase environmental variability, thus making it

FIG. 38. Territorial progression (↓) and regression (↑), building of 'drop'- or 'island'-populations, their growth and disappearance, at a border (southern) of the distribution-area of a species. - - - - - - former conditions; ——— present conditions. Roughly diagrammatic, but based on actual data.

possible for some of the 'evolutionary candidates', in the shape of mutations and recombinations, to find a specially suitable environment. Of especial importance in this respect are the 'breakers' at the margin of distribution areas; and an extensive geno-geographical analysis of cultivated plants has shown that many recessive mutants are actually found at the periphery of the distribution areas of species (Vavilov, 1927). In cases of pronounced numerical fluctuations extending over several generations, the intensity of selection is also affected, rising while the population is decreasing and vice versa; its type also will change at different points in the cycle (Elton, 1930, p. 27). Thus one method of studying the real intensity of natural selec-

tion will be by careful and exact population-statistical analysis of the total number of individuals and the relative frequency of various characters through the course of several periodic population-waves; a rough approximation to this type of analysis is shown in Fig. 5. Ford and Ford (1930) have given an example of the working of this principle in nature in the butterfly *Melitaea aurinia*. An extreme diminution in numbers in an isolated colony of the species was followed by rapid increase and final stabilization. During the period of rapid increase (and therefore presumably low selection-intensity) the variability was extreme, including even forms approximating to the pathological. This excessive variability disappeared when the numbers were again stabilized, but the new modal type was distinctly different from that found in the previous stable period prior to the decrease in numbers.

Finally, the larger and more prolonged territorial population-waves, approximating in extension to the historical migrations of species and races, may be of evolutionary importance by permitting previously separated groups of organisms to interbreed, and by subjecting large and heterogeneous parts of the original population to new constellations of external environment and biological association. More or less rapid migrations or extensions of previously rather small populations may be accompanied by gradual elimination of some of the geno-types: this possibility was recently used by Reinig (1938) to explain cases of geographical character-gradients ('clines' according to the new terminology of Huxley, 1939).

(*e*) *Relative evaluation of evolutionary factors.* It is obvious that all four evolutionary factors are necessary in the process of evolution. Thus their relative importance can only be evaluated in respect of their particular significance for different parts of the complex evolutionary mechanism.

As already mentioned, three basic mechanisms can be distinguished which may alter the genetic composition of a population: mutation-pressure, selection-pressure, and limitations of panmixy and population-size. We must now discuss how far the single evolutionary factors, with the aid of these three mechanisms, are able to exert a directive influence upon the evolutionary process.

Mutation cannot be regarded as a directive factor in adapta-

tion and differentiation, because, as we have seen, mutations arise at random and individual mutation-rates are extremely low; a directive influence of the mutation-process is possible only in those few cases where mutation-pressure is for some reasons greater than the pressures of selection and of accidental fluctuations in the concentrations of single genotypes. Mutation must thus be regarded mainly as a factor supplying new evolutionary material. We must assign essentially the same significance to population-waves. By rapid changes in the concentrations of single genotypes they produce pronounced changes in the genotypic content of populations, and expose some of the mutations more intensively to selective action by rapid accidental increase of their concentrations; and by territorial fluctuations of populations (range-changes) they create permanently new environmental constellations for the process of adaptation by natural selection.

The directive factors are selection and isolation. Selection permanently maintains an optimal relation between organisms and their surroundings, and also produces an adaptive morphophysiological differentiation in time. The first result we normally call adaptation, the second specialization or evolutionary progress. Isolation is the main factor of differentiation in space. The latter may be also produced by selection, acting on different parts of the population under different conditions; but here too differentiation is markedly accelerated by isolation. Different forms of biological isolation, especially genetical isolation *sensu strictu*, constitute the most important step in the process of speciation.

The four evolutionary factors may thus be divided into two groups: mutation and population-waves are providers of evolutionary material; and selection and isolation are the directive factors of evolution, the first being the only factor in adaptation and progressive differentiation, and the latter the most important factor in regard to differentiation in space. Other suggested evolutionary factors, such as, for instance, a direct Lamarckian influence of the environment upon organisms, or immanent heritable orthogenetic variation, have never been proved; conversely, the whole evidence of experimental genetics disproves their existence and shows that there is really no need to assume it to explain the mechanism of evolution.

5. *Conclusions*

The facts set forth in the preceding sections lead to the conclusion that in the known and genetically analysable material of evolution (mutations and combinations), and in the known evolutionary factors (mutability, selection, isolation, and population-waves) we possess all the theoretical premisses at present needed to explain the mechanism of micro-evolution and of geographical variation. No attempt is here made to give a complete theory of the mechanism of micro-evolution; only certain features regarding geographical variation will be briefly discussed.

The examination of groups exhibiting geographical variation shows that they may be characterized by three types of characters and character-combinations: neutral characters, clearly adaptive ones, and harmonious character-combinations (i.e. characters which in a specific combination have a specifically adaptive relation to a local environment and to each other). On the basis of the known properties of mutations and combinations, and of the mechanism of action of different evolutionary factors, it is easy to understand the origin of all three types of geographically varying characters. The first group undoubtedly includes, on the one hand, really 'neutral' characters, whose origin has nothing to do with selective adaptation, but is due to historically accidental plus-fluctuations of the relevant gene-concentrations. On the other hand, many characters appear to us to be 'neutral' merely because we cannot find any plausible relation between them and the local environment; in many cases a selective value must be ascribed not to a character as such, but to the influence of the gene responsible for it upon the relative viability of a specific gene-combination in a specific local environment. The obvious cases of adaptive characters or character-combinations owe their origin to the selective advantage of the morphological or physiological properties of the character as such under given environmental conditions, mimicry and protective coloration being extreme examples of this type. We should not forget that the selective advantage or the survival-rate represents the numerical sum of a large complex of different biological properties (such as, for instance, degree of sexual affinity, fertility-rate, spontaneous embryonic

mortality, resistance of different developmental stages to diseases or enemies, specific qualities in the struggle for existence, and competition with other groups of organisms, &c.), influencing the relative viability of a genotype under given conditions. It is thus evident that the selective value of a mutation may in some cases be connected with the obvious main morphological or physiological character phenotypically manifested by the gene, while in others it will not be. This leads us to the question of harmonious character-combinations. Their origin is based on automatic simultaneous selection of several ancillary genes by any one selected for some specific reason; this simultaneous selection is due to the specific viability-interrelations of the various genes (see section 2 (b)). Even the fixation of a mutant character by chance (accidental plus-fluctuation of the gene-concentration) must inevitably induce the selection of an optimal genotypic environment for itself. A mutation producing a character, which as such, morphologically, is of importance for the organism under local conditions, may be positively selected, although its spontaneous 'physiological' viability may be lower than that of the original type; but after a while it will improve its physiological viability by selection of other genes, leading to an optimal, harmonious combination. These selective interrelations of genes assuredly explain some at least of the cases of relatively narrow zones of interbreeding, and relatively few natural hybrids between two 'good' and numerically large subspecies: both optimal gene-combinations lose their selective value if destroyed by crossing and subsequent segregation of their components. On the other hand, some zones of mixture may sometimes give origin to many new combinations of positive selective value.

The methods of geographical differentiation may be very various. In section 3 (a) were described some cases of the geographical expansion of single mutations. This is undoubtedly one of the methods by which geographical races (subspecies) originate; while *in statu nascendi*, such races differ primarily in one character, but soon, by the above-mentioned process of simultaneous selection, 'good' races differing in several characters must result. Another method by which geographically localized polygenic character-combinations originate is the meeting and overlapping of originally independent distribu-

tion- and expansion-areas of different single mutations or combinations; in some cases this will simply lead to an irregular polymorphism of the population, but in others it may result in the formation of a harmonious combination having a local selective advantage. Such cases are probably not infrequent, but their detection demands a detailed 'phenogeographic' and if possible 'genogeographic' analysis of the species—i.e. an analysis of the distribution and concentration of single, more or less elementary, characters and of the genes responsible for them. Studies of this type in lady-beetles (*Epilachna*, *Coccinella*) and mice, which are still in progress, have revealed such cases.

Both these methods of subspeciation occur within species-areas which are more or less geographically continuous; pronounced and long-continued intraspecific isolation will certainly lead to a corresponding differentiation; such cases of 'historical' subspecies-formation are well known in biogeography. Another 'historical' mechanism leading to the origin of new races is the migration and crossing of previously separated and already well-differentiated groups. Probably many of the local races of the northern Palearctic are in their origin partly due to such mixture after reimmigration of subspecies which were differentiated in separate isolated refuges during the glacial period.

In many cases the intraspecific (and sometimes also the interspecific) variability shows the phenomenon of geographical character-gradients, for which Huxley (1939) has recently proposed the term 'cline'. A special case of geographical clines is represented by those characters which follow the so-called 'geographical rules' (the rules of Bergmann, Gloger, Allen, &c.). Clines, and especially the cases embodied in the 'geographical rules', are a favourite field of research and discussion in modern biogeography. Such cases are of interest in two respects: (1) They present certain purely technical difficulties to the taxonomist, sometimes making it difficult to distinguish and describe the different geographical forms. But this will present really serious difficulty only in a few cases and in a few groups of organisms, since it is rather seldom that we encounter a really continuous geographical variation, without any sharp steps of difference, within the whole area of a species. Geographical clines without more or less well-marked 'steps' are found only

for single quantitative characters; and to the different popula-
tions within a continuous cline concerned with a single charac-
ter, no names of taxonomic value should be given, if they do
not also show other characters allowing them to be described
as races. (2) There is much discussion about the validity and
the mechanism of origin of the geographical rules. Some bio-
geographers undoubtedly exaggerate the frequency of the cases
which obey these rules; others try to deny the reality of almost
all of them. The explanation of this controversy may lie in the
rather curious phenomenon that some of the most radical
upholders of the zoogeographical rules have used them as argu-
ments in support of their Lamarckian views (e.g. Rensch, in his
earlier work, 1929).[1] Many cases of parallel geographical clines
and of geographical convergence undoubtedly exist within
larger systematic categories. Their explanation on selectionist
lines encounters no fundamental theoretical difficulties, although
we know very little about the special ecological and physio-
logical relations of the characters in question to their environ-
ments; a selectionist explanation of geographical convergence
is much facilitated by the well-known fact that related species
and genera show a far-reaching parallelism in their heritable
variation (phenomenologically summarized by Vavilov (1922)
in his 'law of homologous series in variation'). But equally
undoubtedly the exceptions to the geographical rules are much
more numerous than is admitted by their most radical up-
holders; we should always keep in mind that only relatively few
groups of organisms have been analysed extensively enough on
a large enough scale, and including the whole area of distribu-
tion, in respect of their geographical variation. Many clines
appear to have no relation at all to the geographical rules, but
to represent phenotypic gradients of polygenic quantitative
characters around the centre of their highest development, or
along the paths of distribution, migration, or expansion of the
mutations or groups of organisms in question; in some cases
such clines may be due to what Reinig (1938) called 'elimina-
tion', i.e. a reduction of the genetic heterogeneity of populations
from the centre of origin or of diversity, to the periphery of the
species-area. But this explanation too should not be overstressed,

[1] In later publications (e.g. 1939, *Arch. Naturgesch.* N.F. **8**, 89) Rensch has
adopted a selectionist interpretation of the 'geographical rules.'

since geographical convergences and geographical clines prob-
ably originate in quite a different way.

The last question to be mentioned concerns the relation of
intraspecific variability to speciation. Here, too, opinions differ
markedly. Although, as pointed out in an earlier section, it is
very difficult to give a definition of the species which would be
of general value and of practical use in all groups of organisms,
we nevertheless know that a high degree of biological isolation
is the most important criterion. Since, as we have seen, there
are many types of biological isolation, all due to genetic differ-
ences of the parental groups, we may expect also different
mechanisms of speciation. The one extreme would be the
origin of biological isolation, and thus of full speciation, by
long-continued geographical isolation. The groups which in
this way reached a certain degree of biological isolation may
then, by migration or expansion, penetrate into each other's
territories without crossing; or they will occupy adjacent regions
without forming a hybrid population in the zone of transgres-
sion or common border of their distribution areas (geographi-
cally vicariant species). The other possible extreme would be
the local origin and expansion of a genotype biologically
isolated in some way from the surrounding genotypes; the
degree of biological isolation would increase by accumulation
of further genetic differences. And we can imagine all inter-
mediates between these two extremes. We still know very little
about species *in statu nascendi* in nature.

As an example of the first type of speciation may serve the
subspecies *major* and *minor* of *Parus major*; these two geographi-
cally extreme races (*major* being the north-eastern, and *minor*
being the south-eastern in the ring of subspecies around the
great Asian deserts) meet in Manchuria and the Ussuri district
without showing any tendency to hybridization. The second
type is perhaps realized in the origin of different species in the
'*obscura*'-group in *Drosophila*. In genetic experiments 'good'
species have been produced experimentally in *Drosophila* (Dubi-
nin, 1936; Kozhevnikov, 1936) and in *Datura* (Blakeslee, 1932),
in using chromosome-mutations.

The general impression obtained by a review of the relations
of modern genetics to geographical variability and micro-
evolution is first, that by now we are sufficiently supplied with

general, fundamental principles and mechanisms for the explana-
tion of micro-evolution. But there is still very little empirical
material from field biology and micro-systematics to supply
coefficients and numerical values in our general formulae.
The immediate future should be devoted to intensive work in
the field of empirical population-genetics. Modern taxonomy,
ecology, and biogeography should devote special attention to
the study of phenogeography, population-statistics, and popula-
tion-waves in suitable common species of plants and animals.
In these studies the results and viewpoints of modern genetics
must be taken into account, in order to avoid *a priori* fruitless
work and methodologically incorrect conclusions. Only when
the mechanisms and explanatory principles of present-day
experimental genetics have been exhausted (and they are still
not fully understood or appreciated by the majority of taxo-
nomists, biogeographers, and ecologists) must we search for
new ones; and they then must be analysed with the aid of exact
experimental methods. Anti-selectionist and anti-genetical
evolutionary speculations have to-day no scientific value, even
in connexion with the problems of macro-evolution.

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