EVOLUTION
ABOVE THE SPECIES LEVEL

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EVOLUTION ABOVE THE SPECIES LEVEL

Bernhard Rensch

Professor of Zoology
in the University of Münster

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Foreword

It is very fitting to have the English translation of Rensch's *Evolution Above the Species Level* published in 1959, the centenary year of Darwin's classic *On the Origin of Species.* The work of Professor Rensch is one of the great books which have appeared since 1940 and which may fairly be said to have given shape to the modern biological, or synthetic, theory of evolution. The biological theory is the heir to and direct descendant of Darwin's seminal discovery. The intellectual continuity between them is evident and unbroken, but this does not diminish the importance of the radical changes which the century and particularly the last two decades of biological research, thought, and discussion have brought. Apart from the discovery of a great mass of facts, some of them of cardinal importance, there has been a remarkable movement towards synthesis of previously very nearly disconnected lines of investigation and speculation. Instead of the scarcely related 'theories' put forward by systematists, geneticists, paleontologists, and others, we have now a theory of evolution which embraces biology. Together with an attempt by Huxley (1942) which fell rather short of synthesis, we have had the works of Mayr (1942) stemming from zoological and of Stebbins (1950) stemming from botanical systematics and genetics, of Simpson (1944, further developed in 1953) from paleontology, of Schmalhausen (1946 in Russian, 1949 in English) from comparative morphology, of Darlington (1939) and White (1945, 1954) from cytology and genetics, and of Rensch (the two German editions in 1947 and 1954) from systematics, comparative morphology, and paleontology. Notwithstanding their having been based primarily on different bodies of evidence, all these works came to substantially identical conclusions. It is, indeed, a grand synthesis.

This should not be taken to mean that the theory of evolution is now complete except for some emendation. On the contrary, radical changes and major upsets are not only possible but almost certain to occur. The progression of science is, however, uneven; periods of broadening of the evidential base alternate with tides of generalization and forward leaps of understanding. It is our privilege to live in a period of the latter kind, in which the book of Rensch marks one of the forward leaps.

Columbia University
in the City of New York
1 *January*, 1959

THEODOSIUS DOBZHANSKY

Preface

The greater part of this book was written in the last years of the war. My intention was not to present a compilation of known facts brought to light by evolutionary research, but rather to outline the major rules governing the processes of evolution. I wanted to attempt a causal explanation, partly based on new material, with the intention of proving that very probably the major trends of evolution are brought about by the same factors that bring about race and species formation. The first German edition, which came out in 1947, could refer to the works by J. S. Huxley (1942), Simpson (1944), and Mayr (1942), published in England and the United States during the war, only in an addendum after final proof-reading was completed. It was not until the second edition (Stuttgart, 1954) was prepared that the material in these books, as well as in those by Dobzhansky, Haldane, Lack, Edinger, A. H. Miller, and others could be incorporated. The authors were so kind as to place their books at my disposal. I was surprised to find that many scientists, though working independently and using quite different materials as the bases of their studies, had arrived at the same conclusions. For the first time in this century there was a rather general agreement among paleontologists, geneticists, systematists, and comparative anatomists.

The present English translation is based upon the second German edition, and only a few alterations and additions have been made. These consist chiefly of the abridgement of material that is of minor importance and the inclusion of quotations from recent literature. It has not been possible, however, to deal with all the numerous special evolutionary studies available in the most recent literature, as this would have increased too greatly the size of the book.

The rules governing transspecific alterations of the structural type (Chapters 4 and 6) which – in part – have been newly established are treated in more detail, because they represent a sound means of appreciating organic evolution as a whole and because they exemplify the regularities of the major lines of evolution. The chapter on the evolution of phenomena of consciousness has been reworded so as to be intelligible to those readers who are not too well acquainted with philosophical and epistemological considerations. In spite of its somewhat hypothetical character, I have not omitted this chapter because the majority of the readers of the German edition – insofar as their written and spoken comments have reached me – considered it essential and stimulating.

It is my pleasant duty to express my cordial gratitude to Professor Theodosius Dobzhansky for suggesting this translation of my book and for going through the manuscript. Thanks are also due to the Manager of the Publication Department of Columbia University Press, Mr Henry H. Wiggins, for his obliging cooperation in bringing out the American edition. Finally, I wish to thank Dr Altevogt for translating the German text, which was not too easy in places.

B. RENSCH

Münster, Westphalia
March, 1956

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Introduction

The concepts of mutation and selection developed in modern genetics have supplied an increasingly sound basis for an understanding of race and species formation. Not a few biologists have found this a possible explanation of evolution as a whole. It has been proved, however, that certain rules govern the major trends of phylogeny; these can be traced in the gradual differentiation of genera, families, orders, and categories, and also in the formation of new organs and new anatomical patterns. These rules ('laws') cannot be immediately derived from the genetic, taxonomic, and paleontologic study of race and species formation. Indeed, the progressive evolution of many characteristics suggests the existence of special, not fully understood, phylogenetic agents. Moreover, it was the regularity of the phylogenetic course in evolution in some groups that led some paleontologists to the assumption of such unknown agents. One of the regularities of evolution has been claimed to be an explosive formation of many types at the beginning of a new family or order, then a slowly decreasing speciation that parallels increasing specialization, and finally a degeneration before the extinction of species. These facts were interpreted as due to autonomous factors, creative principles (e.g. Osborn, 1934; Lillie, 1945), or even as an expression of a 'will to individual and free development' (Beurlen, 1937).

With regard to such findings, it has become customary to distinguish between problems of 'macro-evolution' and 'micro-evolution'. As these two terms merely designate 'larger' and 'smaller' events without any clear borderline, and as they are linguistic mixtures of Greek and Latin roots, I prefer to use the terms 'infraspecific' and 'transspecific' evolution. Thus I hope to indicate a little more clearly the difference between those phylogenetic processes that occur within a species or lead to a new species and those that occur beyond the species limit and lead to new genera, families, and lesser divisions, and thus to new constructional types.

At present, transspecific evolution is one of the central problems of evolutionary thinking. A number of biologists and paleontologists say that undirected mutation, selection, and isolation are not sufficient for a workable explanation or the causation of major phylogenetic phenomena and their regularity. Thus far, however, we have not been able to discover or analyze in detail any additional evolutionary agents. Nor can one expect quick agreement on this problem, as those who hold different opinions must finally ask the same important question: have organisms which stand high on the evolutionary scale – including man – arisen through the action of autonomous vital factors, or through undirected mutation and accidents of selection? There can be no doubt that this latter view is somewhat 'unsatisfactory' to those who otherwise look entirely to the cause-and-effect principle in their research work.

The various opinions regarding evolution are, to a certain extent, heterogeneous; the fact is that for valuable evolutionary work a thorough knowledge of different branches of the biological sciences (such as genetics, embryology, comparative anatomy, ecology, and paleontology) is necessary. Because scientific literature is huge in extent and because some important papers are difficult to come by, this desirable universality of knowledge can only rarely be obtained. Thus the discrepancy of opinions arises primarily out of the differing scientific backgrounds of the authors and is not due to the whole bulk of scientifically proved facts.

In contributing the present book to the study of transspecific evolution, I am well aware of the difficulties. I have, however, tried to avoid a one-sided view. My main object has been to examine critically all special factors and rules concerning transspecific evolution to determine their validity and to explore the possibility of interpreting them by evolutionary mechanisms known to science. (I already tried to do this in a brief survey in *Biological Reviews*, vol. 14, 1939, and in a short summary in *Biologia generalis*, vol. 17, 1943.) At the same time, however, I wish to show that these problems can also be studied successfully in recent animals. The methods employed are mainly those of comparative anatomy, because in most cases genetical studies cannot be made; most hybrids of species and genera are sterile, and hybridizing members of families and orders is impossible.

Today one fact can be mentioned which was not obvious when I finished the first edition of this book (1947). A certain optimistic view of the future development of evolutionary theories seems to be justified; there are striking similarities of ideas and results in the works of three authors who worked independently and reached the same conclusions. Wartime conditions prevented sufficient – or indeed any – communication when J. S. Huxley (1942) and I compiled our comparative evolutionary and ontogenetic studies and when Simpson (1944, 1949) prepared his paleontologic treatise. These books and the works of many others seem to indicate by similarity of views and findings that the problems of transspecific evolution rest upon a common ground, with an increasingly firm basis for infraspecific evolutionary studies (Dobzhansky, 1937, 1951; Mayr, 1942; Schmalhausen, 1949; Stebbins, 1950).

To me it seems essential for the understanding of transspecific evolution to realize that there are various ways by which races and species may be formed, and that all possible intermediate links between a race, a species, and a genus can be observed frequently in nature. Hence, two introductory chapters on this subject precede the main treatise.

2

The Causative Factors of Infraspecific Evolution

Numerous studies on race and species formation, especially those based on genetics, have shown that infraspecific evolution can generally be considered as a complex function of the following factors: (1) mutations, (2) recombination of genes and gene flow, (3) fluctuations of population, (4) processes of isolation, and (5) processes of selection. All these factors have been so thoroughly analyzed that fairly generally accepted ideas of race and species formation could be advanced. It has been found, however, that each of these five main factors involves a series of single processes of quite a different character. Due to these special factors infraspecific evolution can proceed along quite different lines. For further studies of these phenomena the excellent surveys by Dobzhansky (1951; 1st ed. 1937), J. S. Huxley (1942), Mayr (1942), and Stebbins (1950) should be referred to, as well as the detailed genetical works by East (1936), N. W. Timoféeff-Ressovsky (1937, 1935), Stubbe (1938), Bauer and Timoféeff-Ressovsky (1943), White (1954), and the evaluation of modern systematics by various authors (J. S. Huxley, ed., 1940). A brief discussion of the main topics with which I shall deal follows.

A. MUTATION

The sudden alteration of inherited characters is the fountainhead of all evolution. It can occur as the mutation of a gene, a chromosome, a genome, a plastid, or a plasmon. Most important in race formation seems to be gene mutation. Normally the effects of genes are only known by mutations of an allele. Genes are considered to be large nucleoprotein molecules or small groups of molecules. They are capable of identical self-reproduction. The main component of the genic material seems to be nucleoproteins capable of many catalytic functions (Butenandt, 1953; Haldane, 1954). They are capable of self-reproduction (see also Chapter 8), and their constancy and stability are extremely great, so that alterations occur only after a relatively long time. This constancy is a necessary condition for the developmental differentiation needing stable interactions of numerous reactions. How spontaneous gene mutations are brought about we do not know. Recent investigations indicate that chemical analysis of these events may not be impossible.

Spontaneous mutations can happen in every gene and can thus produce alterations of every possible morphological and physiological character. Hence, there is no directed mutation at all. But of course the number of mutations of a nucleoprotein is not unlimited, and certain identical or very similar mutations occur from time to time in different populations. Because of this, homologous mutants can be seen in related animal groups, such as the short head in dogs, pigs, and the like.

The mutation rate generally is very low, but different in various genes. (In *Drosophila melanogaster* the rate of lethal mutations is estimated as about $2\text{–}2{\cdot}5 \times 10^{-5}$ per gene per generation. Cf. Dobzhansky, 1951.) The possibility of exact calculations of mutation rates shows that mutation is time proportional. Hence the frequency of spontaneous mutations is higher in older than in just ripened spermatozoa (cf. *Drosophila*, H. J. Muller, 1946). It is of interest that the mutation rates as a whole are similar in bacteria, animals and plants. The instability of a gene can also be caused by a special 'mutator gene' (Mampell, 1946) or even – in *Epilobium* – by certain qualities of the cytoplasm (Michaelis, 1949).

As far as is now known, only one allele is affected in all gene mutations, and the mutants thus arise as heterozygotes only.

It is very probable that genes act primarily as enzymes. Sometimes they affect the earliest stages of development of the whole body or of a special organ. In such cases a mutation may have a quite striking effect, as in homeotic mutants in which a part of the antenna or of the mouth parts of *Drosophila* are changed into leg-like organs (Villee, 1942; Hadorn, 1953; Stern, 1954).

Other mutations affect only a certain step in a chain of later biochemical reactions. This applies to the process of pigmentation of ommatidia in insects, to the formation of anthocyanines in phanerogams, and especially to the synthesis of aminoacids in *Neurospora* (A. Kühn, 1932, 1950; Haldane, 1940; Beadle, 1947; Glass and Plaine, 1950; Hadorn, 1953, and others). On the other hand, it is quite evident that many mutations cause simultaneous alterations of many morphological and physiological traits. Such pleiotropism of gene action apparently is quite frequent (see also Chapter 6, B III) and must be given special consideration in the evaluation of processes of selection.

Manifold and various as a given mutation may be, mutations usually result in pathological alterations, defects, and abnormalities, that is to say, the normal development is more or less severely disturbed by them. In *Drosophila* about 90 percent of all morphologically sharply distinct mutants prove to be lethal (lethal zygotic genes; besides these there are lethal gonic and lethal gametic genes which can hardly be demonstrated because they eliminate themselves immediately after arising). Most mutations cause a decrease in viability (e.g. a general weakness in the struggle for survival) or fertility. One should not think, however, that gene mutations usually result in nothing but the destruction of alleles, as numerous back-mutations to the original type have been reported.

A small number of mutants shows full or even increased viability or superiority in special fields of competition. There is, for instance, a melanistic mutant (At) of the moth *Ptychopoda sericata* in which the mortality during the development is lower than in the normal type. Many other melanistic mutants show an increased viability. Some mutants are less viable than the normal type but have advantages under special conditions (preadaptation). The white mutant of *Drosophila* is more resistant to higher and lower temperatures than the normal type, and hence it is favored during strong shifts of climatic conditions and in possible migrations and expansions into different climatic areas (see also A. Kühn, 1935). Usually only a few favorable mutants arise under laboratory conditions, because in nature nearly all favorable mutations possible within the reaction limits of the genic material concerned have already occurred previously and have been incorporated into the 'normal' set of genes. There is no decrease of viability in certain micromutants, which apparently occur quite frequently. They produce no perceptible morphological alterations; yet often they can be detected by physiological methods. In the process of speciation they seem to play quite an important part.

A mutation can be either recessive or more or less dominant. Recessive mutations are considerably more frequent, as mutation usually causes an irregularity in the normal process and very often renders the gene inactive. Fully expressed dominance is definitely rarer than was previously supposed. It should be noted that similar phenotypic traits can be brought about by dominant as well as by recessive genes. There is, for instance, a dominant and a recessive white in fowl and pigs, and a dominant and a recessive black in mice. The intensity of the dominance of an allele can be altered by changes in the genotypic environment or by external conditions. Probably such an alteration in the degree of dominance is usually brought about by the effects of genetic modifiers during various processes of selection (Fisher, 1931). It can also be due, however, to a crossing-over or to any other dislocation by which the gene is brought into a different genotypic environment. Such a position effect can result in changes of viability and fertility. It can also shift the degree of phenotypic manifestation of some genes ('expressivity': N. W. Timoféeff-Ressovsky) and alter the frequency of the manifestation ('penetrance': Timoféeff-Ressovsky). Such alterations in penetrance and expressivity, however, also depend on alterations in the genotypic and external environment. In other cases alleles producing similar phenotypical effects are located at adjacent loci. Such 'pseudo-alleles' suggest a close biochemical interaction of small complexes of genes in the chromosomes (Lewis, 1954). Characters showing a graded series of intensity, as in color or size, are frequently brought about by multiple alleles acting successively or additively.

As with many other physiological processes, the rate of mutation within biological limits is proportional to temperature. It follows Van't Hoff's Rule to some extent as it is increased by higher temperatures; in *Drosophila* , for instance, a rise of temperature of 10° C. produces two and a half to five times as many mutations as would be produced at lower temperatures. It is not yet clear whether or to what extent indirect effects act upon the genes via the simultaneously altering physiological conditions of the body. Chemical agents can also act upon the germ cells as mutagens (mustard gas, formaldehyde, urethane, ethyl ether, etc.; Auerbach, 1949, summary in Dobzhansky, 1951; Herskowitz, 1955).

Finally, in all animal and plant groups the rate of mutation can be increased by ionizing radiations. It is not the kind of rays but the degree of ionization produced which causes the increase (up to 200 times the normal rate). According to our present knowledge, it is improbable that spontaneous mutations are caused by ionizing radiations occurring under natural conditions. The chitinous tergites of *Drosophila* (or a mash of *Drosophila* bodies, ½ mm. high) will absorb most of the ultraviolet radiation, and the natural radio-active and cosmic rays are by no means intense enough to produce the rates of spontaneous mutation observed in nature (Hanson and Keys, 1930; Rajewsky and N. W. Timoféeff-Ressovsky, 1939) though they may, of course, have their share in effecting them. Species of Copepoda and Ostracoda from radioactive waters did not show any special variants (Pax, 1942).

Thus, a gene mutation can be spontaneous or induced, recessive or more or less dominant; it can result in an absolute loss or in an increase or a decrease of viability and fertility; it can produce marked alterations or minute changes; it can affect mainly a single character or a single process in a genetically caused chain of reactions or it can produce a pleiotropic effect; and finally, it can appear as a reverse mutation causing a restitution of the normal allele. But gene mutation is always a nondirected process limited only by molecular potentiality.

The effects of chromosome mutations are no less manifold than those of gene mutations. Like the latter, they are non-directed and can be spontaneous or induced by external factors, especially by ionizing radiations. They are caused by fragmentations and abnormal rearrangements of parts of chromosomes. The simplest case is the translocation of a part of a chromosome to another chromosome. By reciprocal translocation of two acrocentric chromosomes one metacentric chromosome may arise. Thus the number of chromosomes may be altered. By this process some genes are brought into a new neighborhood (position effect) and new combinations arise (thus, causing change of dominance).

If a chromosome breaks twice and the part between the two breaks rotates through 180° and is then fastened again to the rest of the chromosome, an inversion has taken place. Such inverted chromosomal parts usually disturb the pairing with the homologous chromosome at meiosis, and there is no recombination in the inverted parts, which are thus preserved in their original position. By this means chromosomal compounds with favorable combinations of genes can be kept together.

If a chromosome fraction gets lost in the course of a mitotic division a deletion occurs which usually proves to be lethal – when homozygous – even with very small losses of chromosomal material. Furthermore, there can be multiple breaks of chromosomes and correspondingly much more complicated recombinations. If, for instance, two homologous chromosomes break at different points and exchange their end parts duplications can happen.

Genome mutations have been observed only as a doubling of some chromosomes (heteroploidy), or as a multiplication of all chromosomes (polyploidy). The latter phenomenon is quite frequent in the plant kingdom, but seems to be of less importance in the animal world. In the heterogametic sex of animals polyploidy apparently causes too many disturbances in the balance of sex chromosomes and autosomes; often these disturbances lead to disturbances in ontogenetic development. Polyploid variants do appear in animals with parthenogenetic reproduction, as in some cases of *Artemia salina*, a small euphyllopod of inland salt waters, with di-, tetra-, and octoploid variants (F. Gross, 1932), in the isopod *Trichoniscus provisorius*, the moth *Solenobia triquetrella* (Seiler, 1938), some curculionids, such as *Otiorhynchus dubius* (Vandel, 1934; Suomalainen, 1947), and others. In the last two groups polyploid generations can be found only in the northern portions of their distribution area, a fact that proves that there is a geographic race formation. This, however, will not lead to the formation of new species, as all races with normal sexual reproduction are diploid.

On the other hand it must not be forgotten that there are closely related animal groups with normal sexual reproduction in which the total numbers of chromosomes indicate speciation by polyploidy. This applies to some butterflies (Lorkovič, 1941), Dermaptera (Bauer, 1947), Orthoptera (E. Goldschmidt, 1952, 1953), Lumbricidae (Omodeo, 1952), Triclada (Aeppli, 1952; Benazzi, 1949), and possibly to some Salmonidae (Svärdson, 1945; Kupka, 1950; compare also White, 1954).

Since Geitler's first reports in 1939 it has become more and more evident that there is also a 'somatic polyploidy' in which the zygote and the embryonic tissue are diploid as usual, but in which during ontogenetic development certain parts of the body become polyploid. This is brought about by endomitosis, a process in which chromosome division occurs in the nucleus without formation of the normal spindle and with a reduced spiraling of the chromosomes during the process. So, in the pond skater *Gerris* (Heteroptera) the muscles are tetraploid, the fat body is 4–32 ploid, the Malpighian tubes are 32–64 ploid and the salivary glands 1024–2048 ploid. Similar cases of endomitotic polyploidy were found not only in Diptera (nurse cells of the ovaries, salivary glands), in Odonata (fat and connective tissue), and in beetles and butterflies, but also in Ciliata (macronucleus), Radiolaria, and especially in Mammalia (liver and spleen, d'Ancona, 1939). By endomitosis the evolutionary advantages of polyploidy (certain reactions being controlled by several identical genes, possible increase of viability and resistance to certain factors of selection, greater adaptability and preadaptation) can become effective without causing any hazards in the mechanism of sexual reproduction. It cannot be told as yet to what extent the rhythmic nuclear growth in any other animals is also due to endomitosis.

Finally the mutations of cytoplasm and plastids should also be mentioned. The study of these has commenced only recently (Michaelis, 1949, 1954; Sonneborn, 1950; McCarty, 1946; and others). It has long been assumed that there is identical self-replication in certain cytoplasmic organelles. In other words, the cytoplasm is race and species specific. The interest of evolutionists has been aroused by the recent findings that self-replicating plasmatic structures can mutate. In contrast to the chromosomal genes that initiate and control certain chains of reactions, mutations of plasmatic genes result in direct hereditary alterations of the reaction systems proper. Cytoplasmic mutations can be important in hybrids of races and species, because the normal interactions of the genes of the chromosomes and the cytoplasm can be altered or disturbed to such a degree that sterility or death may result (Lamprecht, 1944; Michaelis, 1954).

The multitude of gene, chromosome, genome, and plasmatic mutations is further increased by the fact that some mutative alterations cause only minor, but others quite complex, evolutionary effects, which are often important for basic processes of individual development. Such constructive mutations (B. Rensch, 1947; also compare Chapter 6, B III) can be caused either by a single gene process or by a mutative change in a balanced system of gene combinations (e.g. main gene and modifier genes). In the case of the single gene mutation, various characters can be altered that control whole systems of physiological processes: e.g. mutational alterations in the quantity of active tissue of a hormone gland like the pituitary, or a mutational change of body size which causes a long series of correlated alterations in various proportions and functions of the body.

And, finally, the recombination of genes by sexual reproduction, by crossing over, and by translocations and inversions produces various gene combinations in a population which form a sort of genetic 'individual' of a higher order ('gene pool': Dobzhansky, 1951). By recombination, genes or chromosomes can form new gene combinations and may develop new effects. It can even happen that heterozygotes for lethal and normal chromosomes are in some cases more viable than heterozygotes of normal chromosomes (proved in the case of *Drosophila willistoni* by Cordeiro and Dobzhansky, 1954). Heterosis, i.e. hybrid vigor, is one of these effects. Evolution normally acts upon these genetic systems of higher orders, a fact to which taxonomists first paid attention by describing not 'types' of races or species but the whole variability (B. Rensch, 1929, 1934).

The mutants resulting from these various types of changes can lead to the formation of new races or species only in those cases where they can spread over several populations or at least over one large population in the course of generations. If the spreading process is sufficiently rapid, the variants will finally replace the larger part of the population. This end result is rendered possible by factors of selection and is favored by fluctuations in the size of populations and by processes of isolation.

B. FLUCTUATIONS OF POPULATION SIZE

Through the course of generations singly occurring mutations can spread. If it represents a variant without selective importance, only the polymorphism of the population is increased. High mutation rates can alter small populations considerably in a relatively short time. If the mutation rate is 0·01 percent of the population, the mutation pressure can be more important than the selection pressure (Ludwig, 1942). Mutants with minor selective disadvantages can escape extinction if they happen to find a 'niche' in their biotope which has not yet been taken by competitors (this is called 'annidation' of mutants with characters that are neutral or slightly disadvantageous to selection: Ludwig, 1950). In a rapidly increasing population rare mutants and rare combinations of genes and chromosomes will not encounter too much selection pressure and may spread fairly rapidly (Elton, 1930; Ford, 1949). Hence the genic material of the whole population ('gene pool': Dobzhansky, 1951) is the decisive basis of race and species formation. In this connection it is interesting to mention that song in birds not only denotes territory but also serves as a means of keeping the groups of populations together (Kullenberg, 1946).

The length of time elapsing between the first appearance of a selectively favored mutant and its spread and establishment within a population largely depend on the number of individuals belonging to that population and on the speed of the gene flow, i.e. the possible dispersal of the mutant. The number of generations necessary for a new mutant to reach a frequency of 1 permille in the population is extremely great in very large populations and relatively small in small ones; in the latter a new mutation comes to represent a higher percentage more quickly than in large populations, provided that nothing limits cross fertilization. In a small population random pairings will lead rather quickly to many homozygous alleles, because the risk of extinction is large, and loss of rare and new mutants is extremely great. Normally, reproductive animal populations are relatively small or medium-sized, of the order of 1,000 to 10,000 individuals.

Medium-sized populations also show marked numerical fluctuations (less distinct in pelagic animals). Any notable reduction of the number of individuals accelerates evolution and decreases variability.

Often the fluctuations occur periodically (in so-called 'population waves': Tschetverikov, Timoféeff-Ressovsky), bring about severe reductions in the number of individuals during harsh climatic seasons (winter, dry period in summer), and act as an ever-active force of evolution. Besides, there are irregular fluctuations caused by various factors, such as floods, epidemics, extreme cold or heat waves, and so on. If a population increases greatly, its parasites and natural enemies normally also grow in number (thus, the cycles of abundance in insects, especially pest insects).

Changes in the habitat of a species also frequently cause fluctuations in the size of populations. Such populations become especially important if the inhabited area shrinks and certain insular relict populations are cut off from the main population. It is in these relict populations that the principle of reducing the variants becomes obviously effective. But within the main population similar conditions can prevail, especially on the borders of specialized habitats (e.g. where a forest recedes and a steppe gains ground, or where a lake gradually is transformed into a swamp or solid land). If the process of shifting the habitat in the same spatial direction is continued for several generations, certain alleles of a population's gene pool may be lost, because the individuals migrating across the former habitat borders represent only a small fraction of the whole population; thus, they do not preserve the full number of genes. (This is elimination in Reinig's sense. It is not necessary to accept Reinig's assumption of 'single migrations'). Finally, all these numerical fluctuations of populations caused by temporal or spatial factors may combine in various patterns.

C. SELECTION

The speed and extent of race formation and speciation depend on processes of selection rather than on the variability of the material produced by mutation. This could also be demonstrated in the lines of descent of fossil types (Simpson, 1944). If environmental conditions remain constant, selection eliminates mutant genes in which harmful qualities preponderate. If the environment changes or the inhabited area is shifted to another place, variants and individual traits that were neutral in the preceding state can become quite important with regard to selection. Such a preadaptation may also cause major evolutionary steps, e.g. the loss of wings in insects living near the seashore or on islands (proved experimentally by l'Héritier, Neefs, and Teissier, 1937), or the formation of characters typical of cave dwellers, or the origin of terrestrial animals (see also Kosswig, 1948; Cuénot, 1951).

The selective agencies are quite diversified.

1. Many factors of the inanimate world act as forces of selection by wiping out those individuals that cannot stand extreme or harsh conditions caused by environmental factors (minima and maxima of temperature in winter and summer, droughts and floods, rapid or extreme changes of exposure to light, of salinity and hydrogen-ion concentration, and so on). All these factors may act periodically or only occasionally. The same holds for changes due to spatial shifts of the area inhabited, which are especially effective on borders of a biotope. Besides this negative selection there is also a positive one, as some variants may possess preadaptations which become genuine adaptations in the new situation, and as many animals actively move into suitable habitats. Dobzhansky (1948), for instance, stated that the percentage of three different gene arrangements in the third chromosome of *Drosophila pseudoobscura* differs strongly in populations inhabiting different altitudinal levels. The standard type prevails at low elevations, the arrowhead type at higher

altitudes. Other evidence on selection by factors of the inanimate environment is to be found in the papers by Alexander (1941); Errington (1943); Dobzhansky and Spassky (1944); Stalker and Carson (1948); Spiess (1950), etc.

2. Among the selective factors of the biotic environment is it the predators that maintain a steady process of selection by preying more frequently on those individuals with a more conspicuous coloration than the rest of the species, an imperfect state of camouflage and mimesis, an insufficient warning color, poor hiding or flight instincts, poor sense organs, and so on. Numerous relevant experiments proved the paramount importance of selection by predators. One should consult, for instance: Poulton and Sanders (1898); Heller (1928); Cesnola (1904); Sumner (1935); Steiniger (1937*a*,*b*); d'Ancona (1939); Cott (1940); Dice (1947); Blair (1948); Cain and Sheppard (1954); and others. It is interesting to note that there is a mutual relation of predator and prey which causes periodic fluctuations in population size (Lotka, Volterra, and d'Ancona, 1939; Gause, 1935). These again influence the intensity of selection among the variants preyed upon, and lead to a similarly periodic fluctuation of selective intensity.

3. A special type of such 'enemies' is represented by parasites and infectious diseases (animals, bacteria, fungi, viruses). If they act on a large scale, in the form of an epidemic, their selective importance can hardly be underrated. At the same time they contribute to the population fluctuations which are so important in evolution.

4. Furthermore, a continuous selection is at work in the competition for food, territory, nesting sites (e.g. among birds nesting in holes), and so on. This daily 'struggle for life' also causes an interspecific selection. This is especially effective, as usually species differ more markedly from each other than do races of a species. Such a selection by rivalry has been studied experimentally in a number of cases. Usually the inferior type was wiped out, if it could not manage to find a niche not competed for (annidation, see below on p. 119). For further details see l'Héritier and Teissier (1934); d'Ancona (1939); Dobzhansky and Spassky (1947); Park (1948); Birch, Park, and Frank (1951); Birch (1954); and others.

5. Finally, sexual selection is effective in many more cases than was supposed by zoologists three decades ago. Here, too, we may find positive selection by ritualized or non-ritualized fighting, or by preference for certain mating partners (including homogamy), or extinction because of aberrant or less vigorous mating instincts, abnormalities of the sexual organs, or insufficient strength of sexual odor. Sexual selection is especially effective in developing and maintaining characters with a releasing function in display or the recognition of the other sex, the young, the parents, or the members of a social group (Tinbergen, 1951). This is evident, for instance, in closely related sympatric species, e.g. species of 'Darwin's finches' on the Galapagos islands. Here a marked sexual pattern is an important means of attracting and recognizing a sexual partner of the same species. If a species differentiation by such means is not necessary – as is the case on lonely islands inhabited by only

one species of a genus – the sexual difference between male and female can become greatly reduced (Lack, 1947).

All these types of selection can act together on the same species, and the daily struggle for life causes a continuous selection. The intensity of the latter can best be estimated from the enormous overproduction of progeny in nearly any type of organism, which was pointed out convincingly by Charles Darwin. Animals with periodic fluctuations of population size are subjected to a series of selective examinations, as Elton (1930) has impressively demonstrated. The increase of a population causes a more intense infraspecific competition; the decrease is characterized by selection through parasites and diseases, and in the cold season by selection through low temperatures. These changing situations of selection always maintain a certain essential level of polymorphism in the population. Such polymorphism can also be favored by the fact that heterozygous individuals have a greater adaptive value in consequence of an increased vigor (heterosis). On the importance of polymorphism, consult Ford (1945) and Dobzhansky (1951).

Selection processes usually affect certain characters. Thus, for instance, the smallest variants of warm-blooded animals are extinguished by the low winter temperatures, and carnivorous animals prey on those individuals in which fleeing and hiding instincts are less well developed than in others, etc. Most such characters are brought about by combinations of genes rather than by single genes. Hence, selection usually eliminates gene combinations or increases or decreases their frequency. Due to the pleiotropic effects of many of these genes, characters will be affected that do not seem to have any connection at all with the particular factors of selection. This is an important fact, as it explains that unfavorable characters may also arise or be intensified by selection in those cases where these negative traits belong to a gene complex in which the positive selectional characteristics prevail. Such complex effects of gene combinations provide a good interpretation of the causation of hypertrophy of some organs (see Chapter 6, B IV).

In this context it is not necessary to deal in detail with the much discussed mathematical foundations of selectional processes and results (compare the papers by Haldane, 1924, 1954: Fisher, 1930, 1936; Wright, 1932; d'Ancona, 1939; Ludwig, 1954). It should be mentioned, however, that with a normal mutation rate (1/100,000) and a selectional advantage of only 1 percent a mutant dominant allele will have totally displaced the original one after about 4,800 generations in an infinitely large population. With recessive alleles, a very long time will pass before the mutation reaches a 1 permille frequency (about 100 million generations). As we have seen, however, these figures are subject to strong alterations with diminishing size of populations, and hence increase and decrease of allele frequency may be influenced by random factors as well as by mutation and selection rates. In smaller populations the time to reach a certain level of frequency (1 permille) is shorter, lasting from about some hundred to a few thousand generations for a mutation with a 1 percent selective advantage, and thus even recessive mutants may gain complete preponderance within a relatively short time. Normally, the mating populations in nature are fairly small in number of individuals, or at least they show marked fluctuations in numbers, during which a temporary numerical minimum is reached. Furthermore, the selective advantage of a mutation is often more than 1 percent. This is especially so in interspecific competition, where the characteristics of the rival species are definitely more marked. Hence – except among the fairly large populations of pelagic animals and in the stable environment of the deep seas – mutations may reach certain levels of frequency within a fairly short time, and selection leads to evolutionary changes within periods that are in accord with those proved for race and species formation by paleontology (see Chapter 5).

Haldane (1954) pointed out that the intensity of natural selection for a special character can be defined as the logarithm of the ratio of the fitness of the optimal phenotype to that of the whole population. Sometimes these values, ranging from near zero to about 12 percent, can be determined from frequency distributions.

D. ISOLATION

The evolutionary factors dealt with in the foregoing chapters may give rise to new races and species in the course of generations. In addition to this historical evolution there is a complicating differentiation into races, due to spatial or physiological segregation. Young phylogenetic differentiations cannot be kept apart from continuous gene flow (panmixia) unless historical isolation is displaced by different isolation types of races *in statu nascendi*. This can happen in various ways.

1. Populations or parts of populations become separated spatially. This is especially clear in those cases where one large area of distribution is torn apart by climatic shifts or other environmental changes, or where an expansion beyond separating barriers takes place (e.g. if terrestrial animals spread or are transported to islands, or if water birds carry a new species to a lake where it was previously unknown simply by having eggs or larvae on their legs. This spreading process leads to the formation of geographic races. However, such isolation need not be complete. Quite a number of animal types show relatively little vagility, which may be due to limited mobility (in land snails, Myriapoda, wingless insects) or to ecological and behavioral (or 'psychic') linkage to the biotopes (e.g. territoriality in birds and mammals). In such cases there is often a continuous area of distribution over a wide range, but the gene flow will be limited to a narrow zone near the border line of the single races. In such relative geographic isolation the reproductive communities are relatively small in number of individuals, a fact which is often neglected in mathematical treatises on selection. Quite often this type of race formation – the arrangement of various races in a sort of geographic mosaic or a chain with more or less marked differences – can be observed in nature, and in many groups of birds, mammals, and insects it is the rule.

Spatial separation can also occur in microhabitats, as various factors of ecological or physiological importance differ within the general habitat. Thus, the small alternating areas of forest, steppe, mountain peaks, isolated lakes, colonies of food plants (in monophagous animals) and of hosts of parasitic species sometimes bring about spatial separation within the borders of fairly small habitats, and may lead to the formation of new races. Hence ecological races can arise within a geographic distribution area.

2. Furthermore, gene flow (panmixia) can be markedly reduced or rendered impossible by sexual isolation. This can be due to differences in mating seasons, different behavior patterns of mating and display (such as special calls to attract the sex partner, or methods of copulation), differences in sex odors, or anatomical deviations of copulatory organs. Incomplete, but quite efficient in the long run, is the sexual isolation provided by the phenomenon of assortative mating (homogamy), which means that similar partners prefer each other for copulation, as has been shown to occur in some cases. Sexual isolation is important, too, as an additional means of forming ecological and geographic races.

3. Genetic isolation can be caused by mutations which prevent fertile interbreeding of the variants, for instance, by severe disturbances in certain stages of development (e.g. after a mutative alloploidy). However, there may be hybrids of normal or even increased viability which are sterile or less fertile than the ancestors. Such types of genetic isolation are often combined with geographic race formation. Hence, the end links of chains of geographic races sometimes show a decreased fertility.

On genes causing sterility in hybrids, consult above all Dobzhansky (1951), Steiner (1942, 1945), Hadorn (1949). For interspecific genes and the inability of hybrids to reproduce possible 'progenes', see the papers by Lamprecht (1948, 1949).

E. HYBRIDIZATION

Sexuality supported by the processes of crossing over has a great revolutionary effect by continuously causing gene recombination. Even without mutation, recombination may produce new races. Furthermore, hybridization of races occurs when formerly separated types come into secondary contact. This can be seen from the examples of some European races of animals that originated during the Ice Age and took refuge in western and southeastern Europe, coming into secondary contact in central Europe in postglacial times. Normally, such events lead to the formation of hybrid races, but sometimes additional types with new characters arise by selection of special hybrid types.

F. INTERACTION OF THE EVOLUTIONARY FACTORS

Up to now there has been no reason to assume that further factors are active in infraspecific evolution. The joint action of mutation, gene recombination, changes of the population size, processes of selection and isolation, and occasional secondary hybridization is a sufficient explanation of all known types of race and species formation. There is quite a number of cases in which this fact has been proved by careful analysis.

As has been pointed out, the evolutionary factors mentioned usually act together in various combinations. Mutation produces new evolutionary materials; by fluctuations of population size it is sometimes given a certain preponderance, but usually only to such a degree that selection can have a more rapid effect on the frequency of the varients. By isolation swamping of any racial differentiation which may have begun is prevented. Depending on the efficiency of these factors, the evolutionary effect may be quite different. If there is a considerable number of new mutants due to a high mutation rate ('mutation pressure') a strong individual variability will result. If there is an extreme reduction of population size, a quite uniform race will emerge. If selection is very harsh and intense, highly specialized types will result. Even in cases where race formation is checked mainly by isolation and where population shifts and selection are less effective, undirected mutation leads to a marked variability not dependent upon environmental conditions, and eventually to the excessive development of certain structures. This is often found to apply to evolutionary processes on small islands.

Finally, we must not forget that animals are not only passively subjected to selection and isolation but that they find their choice of habitat actively guided by inherited releasers for habitat and food. Normally such releasers are only adapted to certain very limited characters of the habitat. Hence, if such characters also occur in a neighbouring area, where climatic conditions may be rather different, the species may enlarge their normal territory.

3

Types of Race and Species Formation occurring in Nature

Judging from the manifold effects of the various evolutionary factors and their combinations, it seems to go without saying that we should not expect to find a universal mode of infraspecific evolution, such as some geneticists have occasionally tried to establish. On the contrary, quite a number of different types of speciation exist (first outlined: B. Rensch, 1939). So we should try to demonstrate the various modes of speciation as they can be traced in free nature, and should evaluate their approximate effect on the sum total of evolutionary processes.

In spite of the theoretical possibility of finding a large number of combinations of evolutionary factors and interactions, it is relatively simple to find a suitable order in which to arrange the types of race formation, because only two of the five evolutionary factors mentioned above are strictly necessary: mutation and isolation. The special types of mutation effective in race formation have been analyzed in only a few cases, and in most animal forms it is hardly possible to analyze them, as many animal species are difficult to breed in captivity or their generations are too long to permit experiments. Since the types of isolation, on the other hand, can more readily be observed, we can distinguish six main types of races: (1) historical races, prevented from panmixia by their temporal succession; (2) geographic races in more or less discrete geographic areas; (3) ecological races living in the same geographic area but separated at least during the mating season; (4) races separated by physiological mechanisms affecting sexual activities; (5) genetic races which cannot produce fully viable or fully fertile hybrids; (6) hybrid races, which result from the secondary contact of formerly isolated (normally geographic) races.

A. HISTORICAL RACES

All well-known fossil animal groups show that the species have a relatively limited period of existence in time. Recent species of mammals and birds can usually be traced back only to the Pleistocene, whereas the respective types of the Pliocene must be considered as species of their own. Some species of Prosobranchia have remained unchanged since the early part of the Tertiary, but in still lower geological horizons they are replaced by different older species. Thus, all animal types show a continuous change of certain features, and from this general rule one can infer that historical race formation and speciation is by far the most frequent and important type of evolution. Considering the effects of time-proportionate mutation and of processes of selection, population shifts, and isolation, one arrives at the same conclusion. All favorable mutants, especially those causing an increased viability or fertility, will increase in frequency as time passes, and hence races and species as a whole will change with time. Of necessity there is also a time factor in all processes of geographic, ecologic, or sexual race formation.

In contrast to possible expectation, the number of paleontologic series proving such a historical race formation and speciation is not very large. The main reason for this fact seems to be that four premises must be successfully met: (1) a totally undisturbed succession of sediments; (2) organisms with structures capable of fossilization; (3) organisms with a sufficiently large number of individuals; and (4) able paleontologists taking the trouble to carefully collect and evaluate hundreds and thousands of fossil specimens.

There is a model example of such work based on the study of more than 4,000 specimens and illustrating the problems of historical race formation: the races of the Ammonite genus *Kosmoceras* from the Callovian (*Jurassic*) (Brinkmann, 1929). Here, in three parallel lines of descent a gradual change of races could be demonstrated, showing differentiations of single ancestral forms into several species as a phylogenetic bifurcation. Usually the changes of one race into the other and of races into species occurred gradually, the variability of characters in one form overlapping that of the successive form to a certain extent. Nevertheless, it seems clear that morphologically stable types lasted longer than unstable forms. Thus it is easier than might be expected to arrive at a correct and adequate grouping of the various forms of historical races. This is also the opinion of the experienced Swiss paleontologist E. Kuhn (1948). In *Kosmoceras*, furthermore, Simpson (1949) could prove, as the coefficients of variation in five characters bear evidence, that the differentiation of the *pollux–ornatum* from the *castor–aculeatum* line was probably due to the divergence of a population which had only some of the genes typical of the ancestral forms. In this divergent group individual variability seems to have been increased later on. It is not known whether this divergence was caused by temporary geographic isolation and possible remigration, or by some ecological or sexual isolation.

There is one more carefully analyzed example: the Trilobite genus *Olenus*. It is fairly probable that in this group repeated geographic isolations and remigrations occurred. R. Kaufmann (1933, 1934) studied six successive species of this genus in an Upper Cambrian profile of alum slate near Andrarum in Southern Sweden (see Figure 71). All species show a change from 'Artfrühformen' (early species forms) to 'Artspätformen' (late species forms), and in one case a whole transformation of three species in temporal succession could be demonstrated: *O. transversus–truncatus–wahlenbergi*. Otherwise, the species are separated by evolutionary gaps ('saltations'). Some paleontologists consider these gaps to be evidence of corresponding gaps in the phylogenetic course ('macromutation', see Chapter 6, A and E). However, Kaufmann seems to be more correct in assuming that these 'gaps' were caused by reimmigrations and differentiations of a 'conservative strain' from a habitat located elsewhere. In expounding this, he drew attention to the fact that all geographic 'Rassenkreise' show horizontal race and species formation. The shifts of population habitats in the case of *Olenus* may have been caused by the oceanic transgressions of the Upper Cambrian.

As it is difficult properly to judge geographic variation in fossil animals, paleontologists are often unable to determine whether the successive changes in a series of fossil types from a certain succession of sediments are due to historical race and species formation or to secondary immigration (or reimmigration). Usually the dating of geological horizons is done by using the fossils contained in them and, if the fossils of two horizons are alike, the horizons themselves are considered to be alike. Hence, with geographic variation taken into account, one is never sure whether the horizons in question are older or younger. This uncertainty is increased by the fact that primitive and more advanced geographic races may live at the same time, which can be seen from various examples in the Recent fauna.

It is fairly certain that there were geographic races in the fossil horse *Anchitherium aurelianense*, the evolutionary tempo of which was increased during the Miocene. There was a larger race in France, a smaller race in Switzerland, and a dwarf type in southern Germany (Wehrli, 1938).

It will remain difficult for research to prove that gaps in geological series of fossils from a certain stratigraphy are due to geographic race formation. One may, however, infer from the common fact of geographic race formation in our present times that this process has also happened in former eras. Moreover, one should not forget that some of the evolutionary gaps from undisturbed horizons (Waagen's 'mutations') may be a result of gaps in collecting or of disturbances and gaps of sedimentation. Such irregularities in sedimentation apparently are more frequent than has hitherto been assumed. Hennig (1932) states that the more one studies the details of paleontology and stratigraphy, the more probable it seems that there are irregularities in sedimentation. This is so even in profiles with an apparently undisturbed stratigraphy.

On the other hand, it is self-evident that geographic race formation involves a time component and that this type of speciation is linked with historical race formation. I wish only to emphasize that cases of a strictly historical race and species formation – one species per geological era without splitting into races – seem to be relatively rare. Further examples of historical race formation may be treated in a more cursory way.

The phylogenetic stages in ammonites discovered by Waagen in 1869 from the Brown Jurassic which belong to the group of *Ammonites subradiatus* are not now considered as racial stages, but at best as a successive line of species.

From these series the paleontological term 'mutation' was coined to distinguish historical from spatial race formation (variation). In the modern view the 'racial stages' of Waagen represent different genera ranging from *Stephanoceras* to *Parkinsonia-Perisphinctes-Oppelia* and *Macrocephalites* (see H. Schmidt, 1935). There is a gradual change of characters also in the successive species found in the Liassic Zones 2*c* to 1 *d* which cover the species from *Scamnoceras angulosum* to *Sc. angulatum*, on to *Saxoceras praecursor–S. costatum–S. angersbachense*, and at last to *S. schroederi* (Lange, 1941).

In 1856 Hoernes discussed a phylogenetic lineage in the snail *Cancellaria cancellata L.* (Prosobranchia), which starts with small Miocene types (Vienna, and Tortona, Italy) having narrow and flat shell structures and leading to the Recent race (see Abel, 1929, pp. 3–5, Figure 1). In 1866 Hilgendorf demonstrated lines of descent in the snail *Gyraulus multiformis* collected from the Upper Miocene of the Steinheim area, and in 1875 and 1880 Neumayr studied a similar lineage in forms of *Viviparus* (*Paludina*) from the Upper Pliocene of western Slavonia and the Isle of Kos. Judged in the light of today's knowledge these lines are often considered to be mere local variants. The transformation of flat to more cone-shaped shells in *Gyraulus* was probably due to a sudden or progressive effect of warm waters, and in *Viviparus* the gradual development of smooth shell surfaces into more sculptured ones was possibly due to an increase of salinity caused by brackish water (see Abel, 1929). However, I would not exclude the possibility that this gradual transformation might involve a genetic shift. What has been proved (especially in *Gyraulus*) is merely a causal connection between change of environment and shape of shell. Hence, it may well be possible that the formation of hereditary ecological races was caused by a change in selection in addition to the modificatory effect. Races of this type have been shown to occur in recent fresh-water snails (Rumjancev, 1928). Moreover, varieties of sculpture among Melaniidae which Neumayr chose for comparison can be modified to only a small degree. On the isles of the Malay Archipelago there are four variants of *Melania tuberculata* showing strong differences of shell structures, but only one is usually found in the wide range of distribution across Africa (this is so in 98 percent of all relevant specimens in the collections of the Zoological Museum of Berlin). From this fact it is quite clear that in these cases there is no modification by ecological factors, but that the differences are hereditary (see B. Rensch, 1934, pp. 401–4). As a last example of historical race formation in fresh water, mussels, belonging to the species *Anthrocomyia modiolaris* from the Carboniferous, may be mentioned (Sylvester-Bradley, 1951).

Among the corals, temporal successions of races have been described in the genus *Zaphrentis* from the Carboniferous by Carruthers (1910) and Sylvester-Bradley (1951). An especially elaborate treatise on lineages of races and species in the genus *Bolivinoides* (Foraminifera) from the Senon was presented by Hiltermann and Koch (1950) and Hiltermann (1951). This study, too, based on thousands of specimens, shows that the periods of phylogenetic splitting are relatively short.

Concerning historical races in mammals, a few examples must serve. The rather strongly differing mastodons, *Bunolophodon angustidens* (Middle and Upper Miocene), *B. longirostris* (Lower Pliocene), and *B. arvernensis* (Middle Pliocene and Lower Upper Pliocene), are perfectly connected by intermediate types, morphologically and temporally. Hence, one can agree with Abel's opinion (1929) that this is a genuine line of descent. A still clearer situation shows up with the racial stages of the cave bear (pre-, eu- and hyper-spelaeoid stages) as they were discovered in the Drachenhöhle of Mixnitz (Styria, Austria) in layers of fossil bones of about 12 m. depth (Ehrenberg, 1928). A probable racial lineage can also be seen in the ancestry of the red deer from the recent *Cervus elaphus elaphus*, which is linked by *C. e. angulatus* with the early Pleistocene *C. e. priscus*, and possibly with the still earlier *C. acoronatus*.

As regards the ancestry of man, there is a historical race formation at least in the transformation of more or less Cro-Magnon-like types (*Homo sapiens fossilis*) to the recent *H. s. sapiens*. The same is possibly true in the racial change of *Pithecanthropus* into the types of Ngandong (Java)–Cohuna (Australia). It seems probable that the situation will prove to be quite similar in the general lineage of the Neanderthal type from the *Pithecanthropus* forms (including *Sinanthropus* and perhaps *Africanthropus*), though the direct lines of descent have not yet been elucidated in detail.

Numerous as the cases of historical race formation may seem to be, their number is not yet as large as would be expected taking into account the huge number of generic and species lineages. Perhaps this may best be explained by the assumption that in former geological periods the bulk of speciation happened in the same way as in our present time: by geographic variation, i.e. by spatial isolation of types.

In some cases the historical transformation of geographic races and the gradual change of a recent race can be observed even during the relatively short time of a few decades. In the moth *Pachys* (*Amphidasis*, *Biston*) *betularia* a dominant melanic mutant originated (*carbonaria*) which spread so rapidly that in some parts of the range in northwestern Europe it is the prevalent or even the only type (Ford, 1954, 1955). On the isles of Rügen, Usedom, Wolin, in the neighboring coastal districts, in some parts of central and southern Germany, and in the Brandenburg provinces this mutant appeared as late as between 1890 and 1925, and today this spreading is still under way (see Schneider, 1935; Schneider and Wörz, 1939). The map in Figure 1 showing this was drawn after the findings by Ule (1925) and some other entomologists. There is a similar situation in the gypsy moth *Lymantria monacha L.*, in which an increasing number of melanic variants (caused by three genetic factors) could be observed during the last 30 to 40 years (Gäbler, 1939). About 50 species of moths are now known in northwestern Europe in which the normal color phases have been replaced by melanic mutants (Ford, 1955).

Among birds this phenomenon may have occurred in the New Zealand flycatcher *Rhipidura flabellifera* (Figure 2) and in the sugar bird *Coereba*

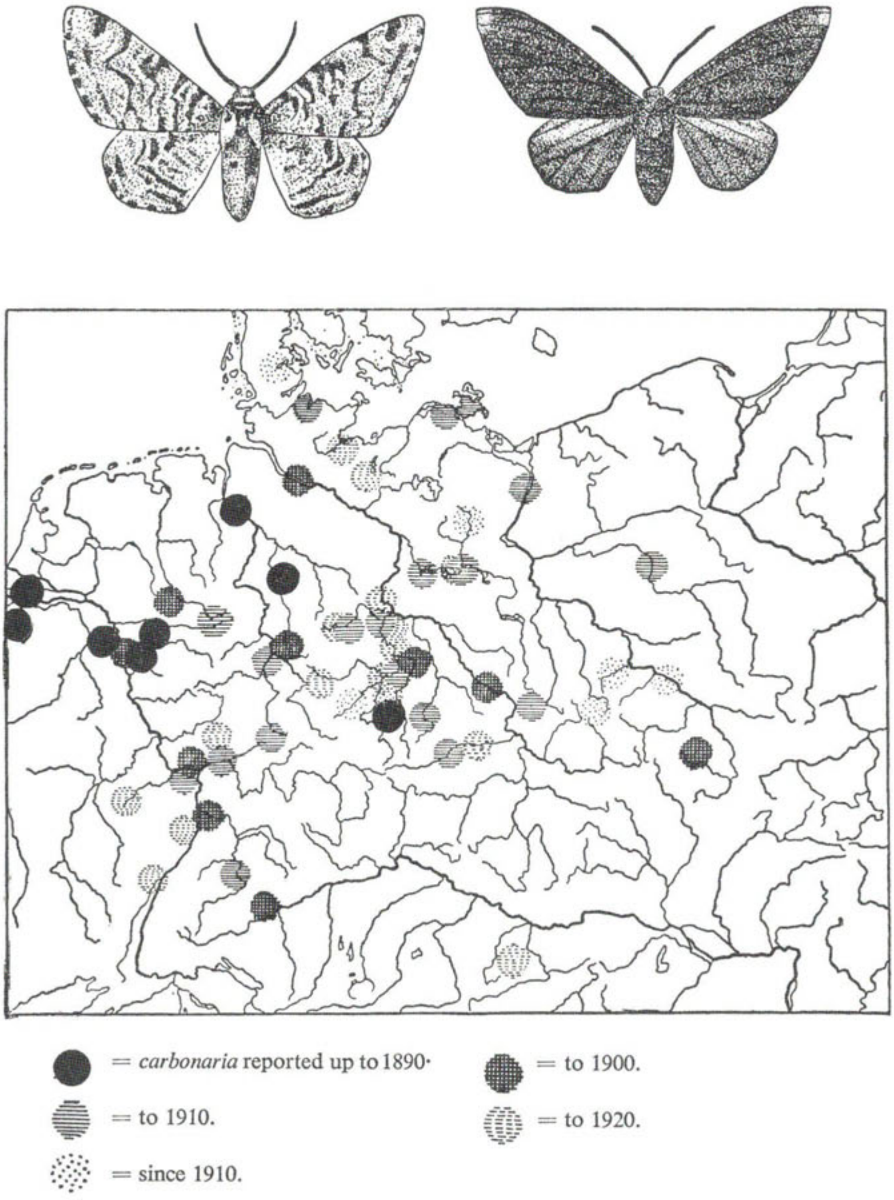

FIGURE 1. Spreading of the melanic mutant (*carbonaria*) of the moth *Amphidasis betularia*, after reports by Ule, Blasche, A. Bergmann, and others.

flaveola, which show a predominant melanic mutant in some parts of their areas. But the supposed spread of these blackish mutants during the last century is not sufficiently proved, as the observational data of earlier reports are incomplete (Mayr, 1942). There are similar situations among birds of various orders, but here the details of spreading have received even less study (melanic mutants in the blackcap *Sylvia atricapilla heineken* on the Canary Islands and Madeira, in the shrike *Lanius schach schach* in southern China, in the weaver bird *Coliuspasser ardens* in western and central Africa, leucistic mutants in the hawk *Accipiter novae-hollandiae* of Australia – the exclusive type of Tasmania [Figure 2] – in the goose *Chen hyperboreus*, and others [Stresemann, 1926]). There has been a spreading of a melanic mutant in the hamster *Cricetus cricetus* since the end of the eighteenth century, with the center at the lower part of the Belaja River in the southern Ural region and the main spreading direction towards the west, finally crossing the Dnieper to take its course along the northern boundary of the area inhabited (N. W. Timoféeff-Ressovsky, 1939). A remarkably quick spreading of a gene could also be reported in a colony of the butterfly *Panaxia dominula* by Fisher and Ford (1947). It is a striking fact that in all these cases more or less aberrant and dominant (often melanic) types are concerned, which are clearly beyond the normal range of variation ('exotypes' in the sense of Remane, 1928); possibly this type of a relatively quick racial transformation is restricted to certain vital forms of mutations.

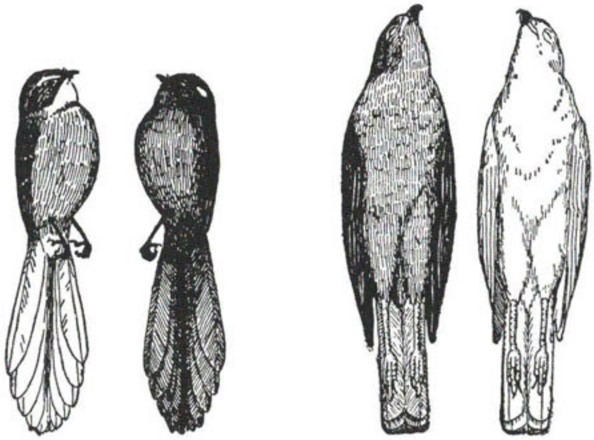

FIGURE 2. *Left:* New Zealand flycatcher *Rhipidura flabellifera* and its melanic mutant, '*fuliginosa*' (after Stresemann, 1926). *Right:* New Guinea hawk *Accipiter novae-hollandiae etorques* and its white mutant, '*leucosomus*' (after Stresemann, 1926).

B. GEOGRAPHIC RACES

In contrast to the cases of strictly historical race formation there is a quite different situation to be observed when the geographic races are studied. Here we need not search for suitable examples, as geographic variation can be observed in nearly every group, and there are even extremely large numbers of geographic variants, at least in those groups of terrestrial and fresh-water animals that present a great diversity of forms. (It should be noted that usually the races that have been studied have differed in morphological traits only, and that the numerous physiological variations have not yet been dealt with sufficiently.)

In many cases it has proved useful to designate large polymorphic species comprising several geographic races as 'Rassenkreise' (mosaics of races; B. Rensch, 1926, 1929, 1934). This term was introduced because strongly differentiated members of a 'Rassenkreis' do not differ less from each other than do closely related 'good species' (in the old sense) without geographic variation, and because such races when getting into secondary contact either do not hybridize or produce a more or less infertile offspring. Nevertheless, 'Rassenkreise' and species differ only by degrees, and in most cases the terms are synonymous.

The systematic study of geographic race formation has not yet been completed in any animal group, but in several cases the situation is now fairly clear, as the following data will show. When Hartert and Steinbacher finished their well-known work (1938), 1,715 geographic races of the palearctic Oscines had been described (doubtful forms not included), which were grouped into 363 'Rassenkreise' (comprising from 2 to 31 races each, with an average of 4·7 per 'Rassenkreis'). There were 153 more 'species' in the old sense which could not be grouped into 'Rassenkreise' (8·2 percent of all forms mentioned), many of which, however, represent borderline cases between race and species. A similar situation is found on other continents.

Species of larger birds with a wider distribution often covering several continents show a considerably weaker geographic variation. So the five bird families of herons (Ardeidae), storks (Ciconiidae), ibises (Ibididae), bustards (Otididae), and cranes (Gruidae) of the palearctic region show a total of only 32 races in 20 species or 'Rassenkreise' (making an average of 1·6 races per 'Rassenkreis' if the extra-palearctic races are excluded) and 24 species without any geographic race differentiation. The decrease in geographic race formation in such larger birds is probably caused by their greater vagrancy. In the species of smaller birds, migrating and nonmigrating birds also show typical differences as to their number of geographic subspecies. The palearctic families of ravens (Corvidae), tree creepers (Certhiidae), nuthatches (Sittidae), titmice (Paridae), wrens (Troglodytidae), and woodpeckers (Picidae), most species of which are more or less sedentary, comprise a total of 586 races in 81 'Rassenkreise' and only 34 species without geographic variations. The migratory families of shrikes (Laniidae), flycatchers (Muscicapidae s. lat.), hedge sparrows (Accentoridae), swallows (Hirundinidae), wagtails (Motacillidae), and orioles (Oriolidae) present 550 races in 173 'Rassenkreise' besides 115 species not varying geographically. Thus, the average number of species per 'Rassenkreis' is 7·2 in the sedentary and 3·2 in the migratory bird families, and the percentage of geographically nonvarying species is 5·5 in the nonmigratory and 17·3 in the migratory form.

The European mammals have not yet been studied sufficiently as to their 'racial systematics'. Up to 1937, however, the critical list by Oekland enumerated 399 mammalian races in 88 'Rassenkreise' (an average of 4·5 races per 'Rassenkreis'). Unfortunately Oekland did not mention the 'species' that showed no geographic variation. They amount to 90, which is 18 percent of all forms concerned. In studying Eurasiatic and Indo-Australian bats Tate (1941 *a,b*) applied the 'Rassenkreis' principle successfully (up to 18 races per 'Rassenkreis'). Mertens and Müller (1940), working on the European reptiles, could enumerate 205 geographic races forming 54 'Rassenkreise' (up to 24 races per 'Rassenkreis') and 50 nonvarying species (19·6 percent). In the European amphibians they could establish 20 'Rassenkreise' comprising 62 races. Twenty-one species (25·3 percent of all forms described) did not show geographic variation. (It is interesting to note that in 1928, when the first edition of the check list was published, 26·5 percent of the reptiles and 28·4 percent of the amphibian forms were considered to be species.)

In a zoogeographic survey of the European fresh-water fishes, Berg (1933) classified 207 geographic races (besides numerous subraces and ecologic races) in 64 'Rassenkreise' and 186 species without geographic variation (47 percent of the total number of forms mentioned in the study, and 40 percent of this total if the said subraces are included).

Breuning's monograph (1932–6) on the ground beetles of the genus *Carabus* enumerates 366 geographic races in Europe (Caucasian and East Russian border countries excluded) in 62 'Rassenkreise' (comprising from 1 to 42 races each) and 27 (6·9 percent) geographically nonvarying species. (Besides the geographic races mentioned by Breuning there are many types referred to as 'natio' which can well be considered as genuine geographic races with relatively small distribution areas.) Inside the German borders (northern Alps included) there are 63 races in 22 'Rassenkreise' and only 3 nonvarying species (4·6 percent). Evidently, then, these ground beetles which have lost their ability to fly and show only a very limited vagrancy generally tend to geographic race formation. And if in Breuning's survey the Asiatic forms are nearly all considered as species, this is due only to our incomplete knowledge of the systematic and faunistic characters of these types.

Quite a similar situation prevails in many other insect groups. Numerous 'Rassenkreise' have already been established as the result of studies on beetles, butterflies, Hymenoptera (especially bumblebees and ants), Orthoptera, and others. It is certain, however, that we are far from knowing enough about the geographic variation (except in bumblebees and in some groups of butterflies). The collections often do not include material that represents the series of specimens from all possible localities, and in some cases the specialist's interpretation points in a different direction from the principle of geographic 'Rassenkreise'. In some groups, such as the Drosophilae, genetically clear-cut races cannot be separated morphologically from each other (Dobzhansky, 1951). Therefore the extent to which speciation via the geographic variation occurred in the other insect groups cannot yet be defined precisely. Geographic variation in European butterflies cannot be surveyed as completely as that in Indo-Australian forms, because in describing the latter types the authors, K. Jordan *et al.*, in the great work on butterflies by Seitz (1927) applied the principle of geographic 'Rassenkreise' systematically. Among the Papilionidae, Pieridae, and Danaidae they listed 2,268 geographic races in 412 'Rassenkreise' and 283 nonvarying species (11 percent of all forms mentioned). So we may now say that in nearly all insect groups the geographic race is probably the most frequent stage of formation of new species.

That the taxonomic method applied in studying a certain animal group is quite decisive for the evaluation of the systematic situation can clearly be seen from the revision of the Cypraeidae (Prosobranchia) by F. A. and M. Schilder (1939). Here formerly only a few 'variants' that could be considered as geographic races had been described. The monograph by Schilder and Schilder revealed 279 geographic races forming 84 'Rassenkreise', and only 77 species in the former sense (21 percent of all forms mentioned). Such a surprising change in the classification of an animal group of great geological age should inspire us to caution when evaluating other animal classes in which geographic variation has not yet been studied sufficiently, if at all.

Thus, it may not be superfluous to give a brief mention of those animal groups in which geographic 'Rassenkreise' have recently been established and in which formerly only species and nongeographic 'variants' had been described: Tunicata (Eisentraut, 1926: 3 'Rassenkreise' in *Ciona* and *Botryllus*), Echinodermata (Döderlein, 1902; Engel, 1934; Heding, 1942; Vasseur, 1952; Mayr, 1954), Cephalopoda (Adam, 1941: e.g. 4 races in *Sepia officinalis*), Brachiopoda (Helmcke, 1940), Phyllopoda (Wesenberg Lund, 1904–8, in Cladocera; Colosi, 1923, in *Apus cancriformis*), Copepoda (Ekman, 1917–20, in *Limnocalanus*; Baldi, 1941, even in pelagic Diaptomidae within the same lake; Tonolli, 1949, in diaptomids from high altitudes; Pirocchi, 1951, in cosmopolitan Copepoda and Cladocera; Kiefer, 1952, in many African and often pelagic species), Cumacea (C. Zimmer, 1930, 6 races in *Diastylis glabra*, 3 in *D. rathkei*), Amphipoda (d'Ancona, 1942, in Italian races of *Niphargus*), Hydracarina (Viets, 1926), Scorpionidae (Meise, 1933: 8 'Rassenkreise' in the genus *Rhopalurus*), Diplopoda (Karl, 1940), Trematoda (Erhardt, 1935), Turbellaria (Benazzi, 1945), Anthozoa (Pax, 1936: 4 European and American [Pacific coast] races of *Metridium senile* form one 'Rassenkreis'; Jaworski, 1938, in *Actinia*; Frenzel, 1937, in *Alcyonium*), and salt-water Spongiae (W. Arndt, 1943: 17 'Rassenkreise').

In the plant kingdom geographic race formation is not a rare phenomenon, though systematists do not yet seem to pay sufficient attention to it and sometimes get into trouble, since the recognition of geographic speciation can be difficult because of hereditary ecologic race formation and hybridization. For further study, see Von Wettstein, 1898 (e.g. *Gentiana*, *Euphrasia*); B. Rensch, 1929, 1939; Du Rietz, 1930 (e.g. *Pinus*, *Picea*, *Silene*, *Celmisia*, etc.); Geyr von Schweppenburg, 1935 (*Larix*, *Abies*); W. Zimmermann, 1935 (*Pulsatilla*); O. Schwarz, 1936 (*Pinus*); Stebbins, 1950; Baker, 1953 (*Armeria maritima*).

Summing up, we may state that geographic race formation has been proved to occur in nearly all animal groups and in several plant groups. It is evident that the number of examples studied recently and showing this mode of speciation is rapidly increasing, and that in many groups with an abundant variety of forms the taxonomic situation is ruled by this principle. This means that the large number of existing species may be considered to be mainly the result of geographic speciation.

Such a conclusion, of course, requires that the characteristics of the geographic races be hereditary. Modification and mutation often act in the same direction, giving similar phenotypic results (phenocopy), and they – in spite of their totally different causation – often seem to react to the same environmental conditions (because modification and mutation are the two possible ways by which the organisms adapt themselves to their environment). Therefore, a safe judgment of the possible heritability of the phenotype *in situ* cannot generally be given. Experimental tests on geographic races have been carried out in a relatively small number of cases, but these cases dealt with very different groups of animals. And all these cases showed clear cut genotypic differences in their essential racial characteristics. This has been proved in the North American rodents of the genus *Peromyscus* (Sumner, 1930, 1932; Dice, 1935; Svilha, 1935), in the European mouse *Arvicola scherman* (Müller-Böhme, 1935), and in the European hedgehogs (*Erinaceus europaeus* and *E. roumanicus*), which must be considered as strongly differing races (Herter, 1935). It was shown to be true in the European and American bison (*Bison europaeus* and *B. americanus*; the latter is a borderline case, see below) (Iwanow and Philipschenko, 1916), in red and silver foxes (*Vulpes*) (e.g. Demoll, 1930, p. 42), in the races of the African ostrich, *Struthio camelus*, (Duerden, 1919), in the races of the parrot, *Agapornis* (Duncker, 1929), in doves of the genus *Streptopelia* (Whitman, 1919), and in the races of the pheasant *Phasianus colchicus* (e.g. Cronau, 1902; Poll, 1911; Thomas and J. S. Huxley, 1927; and others: some races are still termed species). Additional examples are found in races of frogs (Porter, 1941; Moore, 1954) and of newts (Wolterstorff and Radovanovic, 1938; Callan and Spurway, 1951; Spurway, 1953); in races of the lady beetle *Epilachna* (K. Zimmermann, 1934, 1936); in bees and bumblebees (Armbruster, Nachtsheim, and Roemer, 1917); in flies, genus *Volucella* (Gabritschewsky, 1924); in the geographic races of butterflies, genus *Lymantria* (R. Goldschmidt, 1924–33), *Callimorpha* (R. Goldschmidt, 1924), *Spilosoma* (Federley, 1920; R. Goldschmidt, 1924), *Phragmatobia* (Seiler, 1925), *Colias* (Lorkovič, 1928), *Dicranura* (Federley, 1937: here the numbers of chromosomes vary in different races), *Leucodonta* (Suomalainen, 1941), *Zygaena* (Bovey, 1941), and *Pieris* (Petersen, 1947); in Diptera, genus *Drosophila* (in which the detection of racial differences is based on the pattern of the giant chromosomes, since in other structural and morphologic details there are only slight differences: Dobzhansky, 1950); and finally, in races of the land snail, *Murella* (B. Rensch, 1937).

This short survey of the relevant literature could be considerably increased by carefully examining all entomological and game-management periodicals, and those published by zoological gardens (for example, see Beninde, 1940, on hybridization in the red deer). Furthermore, one should mention the observations on the constancy of characteristics in different races kept under equal environmental conditions, as in all zoological gardens, where the strikingly different races of giraffes, zebras, lions, ostriches, cassowaries, and pheasants keep their respective differences through many generations. How far, however, modificatory alterations can proceed is shown, for instance, by the coregonid fishes (*Coregonus*), which, if they have been transported from their native lake to another one, develop quite a different pattern of gill structure after a few generations (Surbeck, 1920; Kreitmann, 1927; Thienemann, 1928).

Another proof of the heritability of geographic racial characteristics can be given if two races get into secondary contact under natural conditions (hybrid populations). This can be studied in central Europe in the hooded and the carrion crow (*Corvus corone corone* and *C. corone cornix*), and in the races of longtailed titmice (*Aegithalos c. caudatus* and *Ae. c. europaeus*); in southern Europe in the sparrows *Passer domesticus* and *Passer hispaniolensis*; in North America in two races of *Melospiza melodia* near San Francisco Bay (A. H. Miller, 1949), in two races of *Junco caniceps* in Arizona (A. H. Miller, 1941), and in other forms. Such cases are very numerous (for detailed study see also Meise, 1928, 1936; G. Dementiev, 1936, 1938; B. Rensch, 1936, 1945, pp. 42–3; Mayr, 1942; Johannsen, 1944). A typical feature of such regions with hybrid populations due to secondary contact is the extent of variation, which comprises the variability of both contacting races.

Finally, heritability of geographic characters can be considered to be fairly certain in the numerous cases where marked racial boundaries are not accompanied by any conspicuous environmental alterations, as is so often found where uniform races are distributed over a large area with strongly differing environmental conditions.

All such experiments and studies on populations have emphasized the fact that the characteristics used by systematists as typical features of geographic races generally have a genotypic background. Nevertheless, one should never forget that in all cases which have not been analyzed genetically one can deduce the possible heritability of characters only by analogy, although the probability may be fairly great. Concerning the problems dealt with in the present chapter we may state that geographic race formation based on genotypic variation can be a prelude to speciation.

In most cases geographic races differ from each other in several genes. By the formation of various geographic races, each of which is a more or less harmonious unit, a species becomes a very complicated genetic system capable of adapting in various directions, and thus possessing an enormous evolutionary plasticity (cf. Wright, 1939). It is apparently because of this plasticity that geographic variation became such a general phenomenon in speciation.

A further requirement for the assumption of geographic races as the most