GENETICS AND THE ORIGIN OF SPECIES

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Third Edition, Revised

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Preface to the Third Edition

TEN YEARS have elapsed since the publication of the second edition of this book. This decade witnessed the convulsion of the War and the gloom of the postwar reaction. And yet, it has proved to be the most fruitful decade in the history of evolutionary thought since the appearance of Darwin's classic in 1859.

The earlier conclusions reached by the different biological disciplines bearing on evolution had often seemed inconsistent with each other. There seemed to be no common language spoken by geneticists, systematists, paleontologists, ecologists, embryologists, and comparative anatomists interested in evolutionary problems. This is no longer the case. Mayr's *Systematics and the Origin of Species* (1941) and Stebbins's *Variation and Evolution in Plants* (1950) showed that the findings of animal and plant systematics are wholly compatible with the theory of the mechanisms of evolution developed by geneticists. Simpson's *Tempo and Mode in Evolution* (1944) and *Meaning of Evolution* (1949) ended the belief which used to have a surprisingly wide currency, that paleontology has discovered some mysterious "macroevolution" which is inexplicable in the light of the known principles of genetics. The long pageant of evolution extending over one billion years appears to have been brought about by fundamental causes which are still in operation and which can be experimented with today. Rensch (1947) and Schmalhausen (1949) generalized the facts of comparative morphology and comparative and experimental embryology, and integrated them with genetics. A similar integration of the findings of ecology and natural history was given by Huxley (1942), Lack (1947), and Emerson (in Allee et al., 1949), and of cytology by White (1945). Only the fields of physiology and biochemistry still remain relatively little influenced by the evolutionary approach. However that may be, instead of the varied theories of evolution which arose in different branches of biology, we are now witnessing the emergence of a new science of life unified by the great evolutionary idea. It is quite possible to analyze and to describe the processes of life one by one. But biology is becoming more than a branch of technology concerned with organic materials and processes. It aspires towards understanding life and man. Such an understanding requires knowledge of the organism as a part of the constantly changing and developing pattern of nature. Evolutionary biology is a study of the dynamics of life.

The amount of new data bearing on evolution published in recent years is very large. In preparing a third edition of the present book it has been even more necessary than in the past to avoid submerging the fundamental principles of the evolutionary thought in a review of the current literature. In numerous instances this has meant that some valuable papers could not be adequately discussed or even mentioned. More than in the first two editions the economy of space required that the presentation be made assertive rather than polemic.

This book owes much to the critical reading of the manuscript by my colleagues and friends Drs. A. B. da Cunha, M. Demerec, L. C. Dunn, E. Mayr, J. A. Moore, and T. Prout. My greatest appreciation goes to Mrs. N. P. Sivertzev-Dobzhansky for her advice, criticism, and her help in the preparation of the manuscript and in reading the proofs. The adroit editorial pencil of Miss Elizabeth Adams, of the Columbia University Press, has efficiently removed numerous rough spots in the original manuscript.

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DIVERSITY AND ADAPTEDNESS

MAN HAS ALWAYS been fascinated by the great diversity of organisms which live in the world around him. Many attempts have been made to understand the meaning of this diversity and the causes that bring it about. To many minds this problem possesses an irresistible aesthetic appeal. Inasmuch as scientific inquiry is a form of aesthetic endeavor, biology owes its existence in part to this appeal.

Organisms are amazingly varied in the gross and in the microscopic structure of their bodies. They are equally varied in their ways of life. Several generations of morphologists and anatomists have worked to describe the structures of recent organisms, and the end of this work is not yet in sight. Paleontologists keep discovering a tremendous variety of fossils. Ecologists have only begun to explore the multiform relationships between organisms and their environments. The extent of the diversity of physiological and biochemical traits in living beings is still quite imperfectly known.

All this diversity is at first sight staggering and bewildering. The greatest achievement of biological science to date is the demonstration that the diversity is not fortuitous. It has not arisen from a whim or caprice of some deity. It is a product of evolution, an outcome of a long historical process of development, the duration of which is surmised to be of the order of two billion years (Simpson 1949). Biology can not fathom whether life may be a part of some Cosmic Design. But biology does show that the evolution of life on earth is governed by causes that can be understood by human reason. Darwin was the first to infer that organic diversity is a response of the living matter to the diversity of environments on our planet.

The adaptedness of organisms to their environments is striking. The structures, functions, and modes of life of every species are at least tolerably consonant with the demands of its environment. Every organism is adjusted to occupy and to exploit certain habitats. But habitats vary in space. Evolution has, accordingly, brought about the diversity of allopatric organisms, which inhabit different territories. Diverse habitats occur also within territories which are accessible to an individual organism in its wanderings during its lifetime, or in which the sex cells or seeds of an individual are dispersed. Adaptation to such local diversities of habitats brings about the diversity of sympatric organisms. Finally, the habitats change with time, and the inhabitants often change hand in hand with the environmental changes. The evolutionary changes not only enable life to endure the shocks emanating from the environment; they permit life to conquer ever new habitats, and to establish progressively firmer control of the older ones.

DISCONTINUITY

Organic diversity is an observational fact more or less familiar to everyone. It is perceived by us as something apart from ourselves, independent of the working of our mind. Experience shows that every person whom one meets differs from all met before. Every human individual is unique, different from all others who live or lived. This is probably true also of individuals of organisms other than man.

The uniqueness and unrepeatability of individuals are aspects falling primarily within the province of philosophers and artists. Although individuals, limited in existence to only a short interval of time, are the prime reality with which a biologist is confronted, a more intimate acquaintance with the living world discloses a fact almost as striking as the diversity itself. This is the discontinuity of the variation among organisms. If we assemble as many individuals living at a given time as we can, we notice at once that the observed variation does not form any kind of continuous distribution. Instead, a multitude of separate, discrete, distributions are found. The living world is not a single array in which any two variants are connected by unbroken series of intergrades, but an array of more or less distinctly separate arrays, intermediates between which are absent or at least rare. Each array is a cluster of individuals which possess some common characteristics. Small clusters are grouped together into larger secondary ones, these into still larger ones, and so on in an hierarchical order.

Biologists have exploited the discontinuity of variation to devise a scientific classification of organisms. The hierarchical nature of the observed discontinuity evidently lends itself admirably to this purpose. For the sake of convenience the discrete clusters are designated races, species, genera, families, and so forth. The classification thus arrived at is to some extent an artificial one, because it is a matter of convenience and convention which cluster is to be designated a genus, family, or order. But the clusters themselves, and the discontinuities observed between them, are not, as sometimes contended, abstractions or inventions of the classifier. Classification is natural and not artificial, in so far as it reflects the objectively ascertainable discontinuity of variation, and in so far as the dividing lines between species, genera, and other categories are made to correspond to the gaps between the discrete clusters of living forms. Biological classification is simultaneously a man-made system of pigeonholes, devised for the pragmatic purpose of recording observations in a convenient manner, and an acknowledgment of the fact of organic discontinuity. A single example will suffice to illustrate the point.

Any two cats are individually distinguishable, and this is probably equally true of any two lions. And yet no individual has ever been seen about which there could be a doubt as to whether it belongs to the species of cats (*Felis domestica*) or to the species of lions (*Felis leo*). The two species are discrete because of the absence of intermediates. Therefore, one may safely affirm that any cat is different from any lion. Any difficulty which may arise in defining the species *Felis domestica* and *Felis leo,* respectively, is due not to the artificiality of these species themselves, but to the fact that in common as well as in scientific parlance the words "cat" and "lion" frequently refer neither to individual animals nor to all existing individuals of these species, but to certain modal, or average, cats and lions. These modes and averages are statistical abstractions which have no existence apart from the mind of the observer. The species *Felis domestica* and *Felis leo* are evidently independent of any abstract modal points which we may contrive to make. No matter how great may be the difficulties encountered in finding the modal "cats" and "lions," the discreteness of these species is not thereby impaired.

In organisms which reproduce sexually and by cross-fertilization, the reality of species as biological units can also be demonstrated by a quite different method. If mating and procreation are observed, it will soon be found that organisms form usually quite discrete reproductive communities. These communities consist of individuals united by the bonds of sexual unions, as well as of common descent and common parenthood. It will doubtless be discovered that one of these reproductive communities consists of animals which, on the basis of previous morphological study, were called cats, while another community will consist of lions. No lion cub is ever born to a pair of cats, nor is the converse ever observed. A species is, consequently, not merely a group and a category of classification. It is also a supraindividual biological entity, which, in principle, can be arrived at regardless of the possession of common morphological characteristics.

What has been said above with respect to the species *Felis domestica* and *Felis leo* holds for innumerable other pairs of species. Discrete groups are encountered among animals as well as plants, among structurally simple as well as among very complex ones. Formation of discrete groups is so nearly universal that it must be regarded as a fundamental characteristic of organic diversity. An adequate solution of the problem of organic diversity must consequently include, first, a description of the extent, nature, and origin of the differences between living beings, and, second, an analysis of the nature and the origin of the discrete groups into which the living world is differentiated.

The true extent of organic diversity can only be surmised at present. In 1758 Linnaeus knew 4,235 species of animals. How many species are known at present, and how many remain to be discovered, can be estimated only very roughly. According to Mayr (1946a), 8,616 species of birds have been described, and it seems doubtful that even as many as 100 remain to be discovered. The systematics of birds is, however, known better than that of any other group of comparable size, not only because collections have been made in most parts of the world but also because the evaluation of the taxonomic status of the described forms as species or as races and subspecies has acquired a fair degree of reliability and internal consistency. In other groups—notably among insects—many new species are described every year, large additions may be expected in the future, and some forms now regarded as species will be eventually reduced to subspecific status and vice versa. The estimates of numbers of species known have, therefore, quite different margins of error in different groups. They are relatively more reliable for the vertebrates, for which Mayr gives the following figures:

Mammals	3,500
Birds	8,600
Reptiles and Amphibians	5,500
Fishes	18,000
Total Vertebrates	35,600

Mayr's estimates for the phyla of the animal kingdom are:

Vertebrates	35,600
Tunicates and Prochordates	1,700
Echinoderms	4,700
Arthropods	815,000
Mollusks	88,000
Worms and related groups	25,000
Coelenterates and Ctenophores	10,000
Sponges	5,000
Protozoans	15,000
Total	1,000,000

Among the estimated 815,000 known arthropod species, some 750,000 are insects. These numbers are growing rapidly, and may eventually be more than doubled. The number of plant species is smaller than that of animals. The following estimates have been kindly furnished by Professor Carl Epling:

Angiosperms	150,000
Fungi	70,000
Mosses	15,000
Algae	14,000
Pteridophytes	10,000
Liverworts	6,000
Gymnosperms	500
Total	265,500

A million and a half species of animals and plants combined is, therefore, a minimal estimate of the number now living on earth.

ADAPTIVE PEAKS

Organic diversity and discontinuity of organic variation are perceived by direct observation. Similarly, we recognize, through observation and experiment, that living beings with different body structures occur in different habitats, and that they possess organs, traits, and forms of behavior which permit them to secure food, shelter, protection from enemies, and to care for the offspring in countless different ways. It is a natural surmise as well as a profitable working hypothesis, that the diversity and discontinuity on one hand, and the adaptation to the environment on the other, are causally related. The present book is devoted to an inquiry into the nature of this relationship. It may, however, be useful at the outset, as an aid in arriving at clear-cut statements of the problems involved, to consider a symbolic picture of the relations between the organism and the environment devised by Wright (1932).

Every organism may be conceived as possessing a certain combination of organs or traits, and of genes which condition the development of these traits. Different organisms possess some genes in common with others and some genes which are different. The number of conceivable combinations of genes present in different organisms is, of course, immense. The actually existing combinations amount to only an infinitesimal fraction of the potentially possible, or at least conceivable, ones. All these combinations may be thought of as forming a multi-dimensional space within which every existing or possible organism may be said to have its place.[1]

The existing and the possible combinations may now be graded with respect to their fitness to survive in the environments that exist in the world. Some of the conceivable combinations, indeed a vast majority of them, are discordant and unfit for survival in any environment. Others are suitable for occupation of certain habitats and ecological niches. Related gene combinations are, on the whole, similar in adaptive value. The field of gene combinations may, then, be visualized most simply in a form of a topographic map, in which the

[1] A more precise and realistic version of Wright's symbolic picture will be given in chapter X of this book.

"contours" symbolize the adaptive values of various combinations (Fig. 1). Groups of related combinations of genes, which make the organisms that possess them able to occupy certain ecological niches, are then, represented by the "adaptive peaks" situated in different parts of the field (plus signs in Fig. 1). The unfavorable combinations of genes which make their carriers unfit to live in any existing environment are represented by the "adaptive valleys" which lie between the peaks (minus signs in Fig. 1).

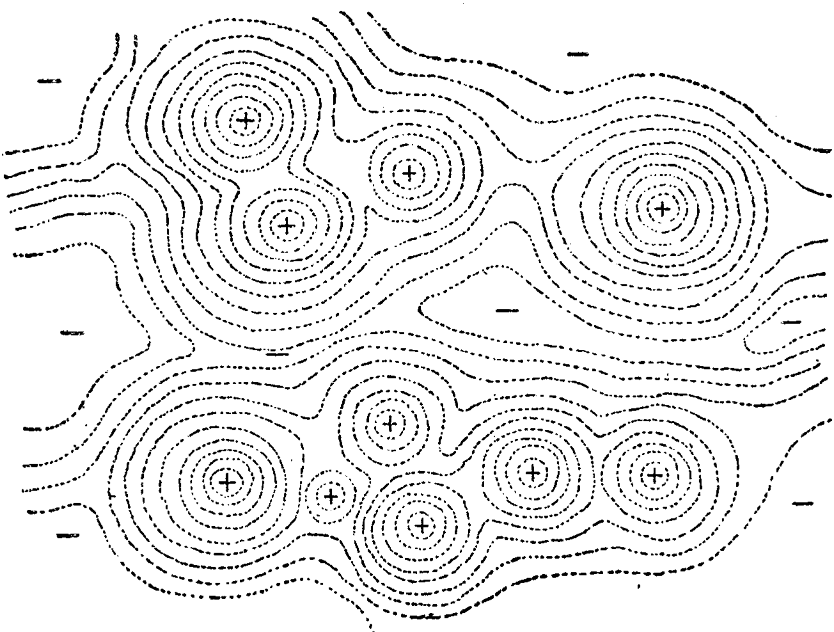

FIG. 1. The "adaptive peaks" and "adaptive valleys" in the field of gene combinations. The contour lines symbolize the adaptive value (Darwinian fitness) of the genotypes. (After Wright.)

The enormous diversity of organisms may be envisaged as correlated with the immense variety of environments and of ecological niches which exist on earth. But the variety of ecological niches is not only immense, it is also discontinuous. One species of insect may feed on, for example, oak leaves, and another species on pine needles; an insect that would require food intermediate between oak and pine would probably starve to death. Hence, the living world is not a formless mass of randomly combining genes and traits, but a great array of families of related gene combinations, which are clustered on a large but finite number of adaptive peaks. Each living species may be thought of as occupying one of the available peaks in the field of gene combinations. The adaptive valleys are deserted and empty.

Furthermore, the adaptive peaks and valleys are not interspersed at random. "Adjacent" adaptive peaks are arranged in groups, which may be likened to mountain ranges in which the separate pinnacles are divided by relatively shallow notches. Thus, the ecological niche occupied by the species "lion" is relatively much closer to those occupied by tiger, puma, and leopard than to those occupied by wolf, coyote, and jackal. The feline adaptive peaks form a group different from the group of the canine "peaks." But the feline, canine, ursine, musteline, and certain other groups of peaks form together the adaptive "range" of carnivores, which is separated by deep adaptive valleys from the "ranges" of rodents, bats, ungulates, primates, and others. In turn, these "ranges" are again members of the adaptive system of mammals, which are ecologically and biologically segregated, as a group, from the adaptive systems of birds, reptiles, etc. The hierarchic nature of the biological classification reflects the objectively ascertainable discontinuity of adaptive niches, in other words the discontinuity of ways and means by which organisms that inhabit the world derive their livelihood from the environment.

EVOLUTION

Scientific study of the organic diversity and adaptation begins of necessity with description and classification. At the beginning of its existence as a science, biology was forced to reduce to a rational system the seemingly boundless variety of living things. In the eighteenth and nineteenth centuries systematics and morphology, two predominantly descriptive disciplines, took precedence among biological sciences. But description is only the first step in scientific inquiry. However great may be the satisfaction which an investigator derives from observation and accurate recording of facts, sooner or later he feels a desire to inquire into the causal connections between the phenomena observed. The theory of evolution arose in the nineteenth century through generalization and inference from a body of predominantly systematic and morphological data. It has furnished a rational framework for biological thought.

The theory of evolution asserts that (1) the beings now living have descended from different beings which lived in the past; (2) the evolutionary changes were more or less gradual, so that if we could assemble all the individuals which have ever inhabited the earth, a fairly continuous array of forms would emerge; (3) the changes were predominantly divergent, so that the ancestors of the now living forms were on the whole less different from each other than these forms themselves are; (4) all these changes have arisen from causes which now continue to be in operation, and which therefore can be studied experimentally.

Evolutionists of the nineteenth century were interested primarily in demonstrating that evolution has actually taken place. They succeeded eminently well. Evolution as a historical process is established as thoroughly and completely as science can establish facts of the past witnessed by no human eyes. At present, an informed and reasonable person can hardly doubt the validity of the evolution theory, in the sense that evolution has occurred. The very rare exceptions (such as Marsh 1947) prove only that some people have emotional biases and preconception strong enough to make them reject even completely established scientific findings. However that may be, the mass of evidence which can be adduced to show that evolution has indeed taken place in the history of the earth does not concern us in this book; we take it for granted.

Two distinct approaches to evolutionary problems became crystallized rather early in the development of evolution theory. The first concentrated on unraveling and describing the actual course which the evolutionary process took in the history of the earth, and which has led to the status of the organic world which we find at our time level. The historical process, phylogeny, is the central theme for the exponents of this approach, while their methods are mainly those of systematics, comparative morphology, comparative embryology, and paleontology. The second approach emphasizes studies on the mechanisms that bring about evolution, causal rather than historical problems, phenomena that can be studied experimentally rather than events which happened in the past. In general, the phylogenetic approach to evolutionary problems was predominant during the second half of the nineteenth century, while in the twentieth century the attention shifted toward the causal aspects, which were taken up by genetics and related biological disciplines. In fact, Darwin was one of the very few nineteenth-century evolutionists whose major interests lay in studies on the mechanisms of evolution, in the causal rather than the historical problems. In this sense, genetics and not evolutionary morphology is heir to the Darwinian traditions. Finally, the most recent developments indicate a trend toward synthesis of what were often divergent historical and causal approaches, and toward emergence of a unified evolutionary biology.

GENETICS AND EVOLUTION

Genetics as a discipline is not synonymous with the evolution theory, nor is the evolution theory synonymous with any subdivision of genetics. Nevertheless, genetics has so profound a bearing on the problem of the mechanisms of evolution that any evolution theory which disregards the established genetic principles is faulty at its source. Every individual resembles its parents in some respects but differs from them in others. Every succeeding generation of a species resembles but is never a replica of the preceding generation. Evolution is the development of dissimilarities between the ancestral and the descendant populations. The mechanisms which determine the similarities and dissimilarities between parents and offspring constitute the subject matter of genetics. Genetics is the physiology of inheritance and variation.

The signal successes of genetics to date have been in studies on the mechanisms of the transmission of hereditary characteristics from parents to offspring, that is, on the architectonics of the germ plasm of the sex cells. The germ plasm has been shown to be composed of discrete particles known as genes. Chromosomes as carriers of genes have been studied in detail. The transmission of hereditary characters has been brought under human control, in the sense that in organisms which have been well studied genetically the characteristics of the offspring are frequently predictable, with a rather high degree of accuracy, from a knowledge of the characteristics of the parents.

The elegance and precision of methods devised by genetics to control the results of experiments which involve crosses of individuals