GENETICS AND THE ORIGIN OF SPECIES

BY

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CONTENTS

ILLUSTRATIONS

I: ORGANIC DIVERSITY

THE EXTENT OF DIVERSITY

FOR CENTURIES man has been interested in the diversity of living beings. The multitude of the distinct "kinds" or species of organisms is seemingly endless, and within a species no uniformity prevails. In the case of man himself it is generally taken for granted that every individual is unique, different from every other one who now lives or has lived. The same is probably true for individuals of species other than man, although our methods of observation are frequently inadequate to show this. Attempts to understand the causes and significance of organic diversity have been made ever since antiquity; the problem seems to possess an irresistible aesthetic appeal, and biology owes its existence in part to this appeal.

The true extent of organic diversity can only be surmised at present. In 1758 Linnaeus knew 4,236 species of animals. The recent estimates of described species (Pratt 1935) are as follows:

Arthropoda	640,000	Total of Column 1	794,500
Mollusca	70,000	Annelida	6,500
Chordata	60,000	Plathelminthes	6,000
Protozoa	15,000	Echinodermata	4,800
Coelenterata	9,500	All others	10,965
. . . . .		Total	822,765

The number of described species of flowering plants is around 133,000, and of lower plants 100,000, a total of 233,000. That these totals fall short of the actually existing number of species is clear enough. For although in some groups—such as mammals and birds—most species are known already, in other groups—notably among insects, which make up more than a half of the species of animals—many new species are described every year, and large additions may be expected in the future. A million and a half species of animals and plants combined is a conservative estimate. Of course, this does not take into account the intraspecific variation, which is commensurate only with the number of living individuals.

DISCONTINUITY

Organic diversity is an observational fact more or less familiar to everyone. It is perceived by us as something apart from ourselves, a phenomenon given in experience but independent of the working of our minds. A more intimate acquaintance with the living world discloses another fact almost as striking as the diversity itself. This is the discontinuity of the organic variation.

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 a single probability distribution or any other kind of continuous distribution. Instead, a multitude of separate, discrete, distributions are found. In other words, the living world is not a single array of individuals 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, usually possessing some common characteristics and gravitating to a definite modal point in their variations. Small clusters are grouped together into larger secondary ones, these into still larger ones, and so on in an hierarchical order.

The discontinuity of organic variation has been exploited to devise a scientific classification of organisms. Evidently the hierarchical nature of the observed discontinuity 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 remains for the investigator to choose, within limits, which cluster is to be designated a genus, family, or order. But the same classification is natural so far as it reflects the objectively ascertainable discontinuity of variation, and the dividing lines between species, genera, and other categories are made to correspond to the gaps between the discrete clusters of living forms. Therefore the 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 this point.

Any two cats are individually distinguishable, and the same probably holds for any two lions. And yet no living individual has ever been seen about which there could be a doubt as to whether it belongs to the species-cluster of cats (*Felis domestica*) or to the species-cluster of lions (*Felis leo*). The two clusters are discrete because of the absence of intermediates, and therefore one may safely affirm that any cat is different from any lion, and that cats as a group are distinct from lions as a group. 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 the existing individuals of these species, but to certain modal points toward which these species gravitate. The modal points are statistical abstractions having 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 species as naturally existing units is not thereby impaired.

What has been said above with respect to the species *Felis domestica* and *Felis leo* holds for innumerable pairs of species, genera, and other groups. Discrete groups are encountered among animals as well as plants, in those that are structurally simple as well as in those that are very complex. 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.

MORPHOLOGICAL AND PHYSIOLOGICAL METHODS

A scientific study of organic diversity may proceed in two methodologically distinct ways. First, one may describe the diversity by recording as accurately as possible the multitudinous structures and functions of the beings now living and of those preserved as fossils; the descriptions are then catalogued and the regularities revealed in the process are formulated and generalized. Second, an analysis of causes underlying the diversity and determining its properties may be made. These two methods are known as the generalizing and the exact induction, respectively (Hartmann).

At the beginning of its existence as a science, biology was forced to take cognizance of the seemingly boundless variety of living things, for no exact study of life phenomena was possible until the apparent chaos of the distinct kinds of organisms had been reduced to a rational system. Systematics and morphology, two predominantly descriptive and observational disciplines, took precedence among biological sciences during the eighteenth and nineteenth centuries. More recently physiology has come to the foreground, accompanied by the introduction of quantitative methods and by a shift from the observationalism of the past to a predominance of experimentation. The great significance of this change is readily apparent and has been stressed in the writings of many authors, some of whom went to the length of ascribing to the quantitative and experimental methods almost magical virtues. Another characteristic of modern biology, which has been emphasized perhaps less than its due, is the prevalence of interest in the common properties of living things instead of in the peculiarities of separate species. This attitude is important, for it centers the attention of investigators on the fundamental unity of all organisms.

The problem of organic diversity falls within the provinces of morphological as well as of physiological biology, but it is treated differently by the two. Morphology is predominantly an order-creating and historical discipline. It is concerned first of all with the recording of the fact of organic diversity as it appears to our senses, and with the description of this diversity in terms of ideal prototypes (the modal points of the species, genera, families, etc.). Next, morphology traces the development of individuals (ontogeny) and of groups (phylogeny), striving to secure an understanding of the present status of the living world through a knowledge of its past. Genetics, being a branch of physiology concerned in part with the

problem of organic diversity, is a nomothetic (law-creating) science. To a geneticist organic diversity is one of the most general and fundamental properties of living matter; diversity is here considered, so to speak, as an aspect of unity through a study of the mechanisms which may be responsible for the production and maintenance of variation, an analysis of the conflicting forces tending to increase or to level off the differences between organisms. The aim of the present book is to review the genetic information bearing on the problem of organic diversity; it is not concerned with the morphological aspect of the problem.

EVOLUTION

Since Darwin any discussion of organic diversity unavoidably involves a consideration of the theory of evolution, which represents the greatest generalization advanced in this field. Here again morphological and physiological biology are interested in different aspects of the matter.

The theory of evolution asserts that the beings now living have descended from different beings which have lived in the past; that the discontinuous variation observed at our time-level, the gaps now existing between clusters of forms, have arisen gradually, so that if we could assemble all the individuals which have ever inhabited the earth, a fairly continuous array of forms would emerge; that all these changes have taken place due to causes which now continue to be in operation and which therefore can be studied experimentally. The evolution theory was arrived at through generalization and inference from a body of predominantly morphological data and may be regarded as one of the most important achievements of morphological biology. However, the evolutionists of the morphological school have concentrated their efforts on proving the correctness of the first and second of the three assertions listed above, leaving the third rather in abeyance. They are interested primarily in demonstrating that evolution has actually taken place, in "bridging the gap," in filling up the discontinuities between the existing groups of organisms, in understanding the relationships between the branches of phylogenetic trees, and not so much in elucidating the nature of the discontinuities themselves or of the mechanisms through which they originated. As a matter of fact, Darwin was one of the very few nineteenth-century evolutionists whose major interests lay in studies of the mechanisms of evolution, in the causal rather than the historical problem. It was exactly this causal aspect of evolution which toward the close of the last century began to attract more and more attention, and which has now been taken up by genetics. In this sense genetics rather than evolutionary morphology is heir to the Darwinian tradition.

How neglected were the studies of the mechanisms of evolution is apparent from the fact that in 1922 Bateson was able to write: "In dim outline evolution is evident enough. But that particular and essential bit of the theory of evolution which is concerned with the origin and nature of species remains utterly mysterious." As recently as 1934 Goldschmidt expressed similar opinions. To most biologists these views seemed unduly pessimistic. Be that as it may, the fact remains that among the present generation no informed person entertains any doubt of the validity of the evolution theory in the sense that evolution has occurred, and yet nobody is audacious enough to believe himself in possession of the knowledge of the actual mechanisms of evolution. Evolution as an historical process is established as thoroughly as science can establish a fact witnessed by no human eye. The mass of evidence bearing on this subject does not concern us in this book; we take it for granted. But the understanding of causes which may have brought about this evolution, and which can bring about its continuation in the future, is still in its infancy. Much work has been done already to secure such an understanding and undoubtedly more remains to be done. In the following pages an attempt will be made to evaluate the present status of knowledge in this field.

THE BEARING OF GENETICS ON EVOLUTION

It should be reiterated that genetics as a discipline is not synonymous with the evolution theory, nor is the evolution theory synonymous with any subdivision of genetics. Nevertheless, it remains true that 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. Taken as a group, a population, every succeeding generation of a species resembles but is never a replica of the preceding generation. Evolution is a process resulting in the development of dissimilarities between the ancestral and the descendant populations. The mechanisms that determine the similarities and dissimilarities between parents and offspring constitute the subject matter of genetics. Genetics is physiology of inheritance and variation. This is the reason why the quest for an understanding of the mechanisms of evolutionary continuity or change has devolved upon genetics. But inheritance and variation may be studied on their own account, as general physiological functions, without reference to their bearing on the problem of organic diversity in any of the ramifications of the latter.

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 essentially discontinuous, composed of discrete particles known as genes. Quantitative and qualitative characters, fluctuating variability as well as discontinuous differences between individuals, normal and pathological, intraspecific and interspecific, "superficial" and "fundamental" characters of organisms are determined by the genes carried in the sex cells, or, to be more exact, in the chromosomes of these cells. Chromosomes as carriers of genes have been studied in detail, with the result that the physical basis of hereditary transmission has been revealed. 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. In *Drosophila melanogaster*, and to a lesser extent in certain other forms, hereditary types possessing a desired set of characteristics may, within limits, be synthesized at will, and the schemes of such "syntheses" worked out in theory are almost always realized in minute detail in the actual experiments.

The elegance and precision of methods devised by genetics to control the results of experiments involving crosses of individuals differing in many hereditary characteristics have led to claims that the problem of heredity has been solved. Although a large amount of work still remains to be done in this field, it is indeed fair to say that the genetics of the transmission of hereditary characters is, by and large, understood now. But the problem of heredity is much wider. Knowing the rules governing the distribution of the hereditary characteristics of an organism among the sex cells, one is in a position to predict what constellations of genes are likely to be present in the zygotes coming from the union of such sex cells. Between the genes of a fertilized egg and the characters of the adult organism arising from it there lies, however, the whole of individual development during which the genes exert their determining action. The mechanisms of gene action in development constitute the central problem of the second major subdivision of genetics, which has been variously labeled as the genetics of the realization of the hereditary characters, phenogenetics, or developmental genetics.

The problem of gene action is far from having been solved. It is known in some instances that the formation of adult characteristics, such as size or coloration of the body or its parts, is preceded by the appearance in the developing organisms of chemical substances of the hormone type which are operative in the processes that produce the adult characters. The great interest of such information is self-evident, although a physiologically minded biologist always would have taken it for granted that chemical precursors of the visible morphological traits must be active in development. The disappointing feature of this work is that to date it has failed to give a clear insight into the gene action proper. A gene is a particle located in a chromosome in the cell nucleus. Its effects on development must of necessity start with intracellular processes, which are subsequently translated into more or less long chains of reactions, culminating in the appearance of visible adult characters. Regarding those intracellular processes, the first links in the reaction chains, nothing is known at present. Are all genes continuously active, or does each gene exert its determining function at a certain period of development and remain in a quiescent state at other periods? Is gene action merely a by-product of the process of self-reproduction of the genes

in the course of cell division? Are genes specialized, in the sense of being concerned each with a single or a few reactions taking place in the body, or is their action of a more general sort? No answers are available to these and many related questions, and, what is still more important for further work, no reliable methods have been devised for investigations in this field.

The genetics of the transmission, and the genetics of the realization of hereditary materials are concerned with individuals as units. The former establishes the rules governing the formation of the gene constellation in individual zygotes, and the latter deals with the mechanisms of gene action in ontogeny. The third subdivision of genetics has as its province the processes taking place in groups of individuals—in populations—and therefore is called the genetics of populations. A population may be said to possess a definite genetic constitution, which is evidently a function of the constitutions of the individuals composing the group, just as the chemical composition of a rock is a function of that of the minerals entering into its make-up. The rules governing the genetic structure of a population are, nevertheless, distinct from those governing the genetics of individuals, just as rules of sociology are distinct from physiological ones, in spite of being merely integrated forms of the latter. Imagine, for example, that some factors have arisen in the environment which discriminate against too tall or too short individuals of a species. From the standpoint of an individual, some growth genes would have acquired lethal properties, and the effects of these genes might be described adequately by stating the precise nature of the physiological reactions leading to death. From the viewpoint of population genetics, death of this category of individuals is merely the beginning of a complex chain of consequences; the relative frequencies of individuals homozygous and heterozygous for certain growth genes and for genes located in the same chromosomes would be altered; some genetic factors which previously were being eliminated because of their harmfulness might become neutral or even favorable; after some generations the genetic constitution of the whole species may be changed.

Since evolution is a change in the genetic composition of populations, the mechanisms of evolution constitute problems of population genetics. Of course changes observed in populations may be of very different orders of magnitude, from those induced in a herd of domestic animals by the introduction of a new sire to phylogenetic changes leading to the origin of new classes of organisms. The former are obviously trifling in scale compared with the latter, and it may not be convenient to have all of them subsumed under the name "evolution." Experience seems to show, however, that there is no way toward an understanding of the mechanisms of macro- evolutionary changes, which require time on a geological scale, other than through a full comprehension of the micro-evolutionary processes observable within the span of a human lifetime and often controlled by man's will. For this reason we are compelled at the present level of knowledge reluctantly to put a sign of equality between the mechanisms of macro- and micro-evolution, and, proceeding on this assumption, to push our investigations as far ahead as this working hypothesis will permit.

EVOLUTIONARY STATICS AND EVOLUTIONARY DYNAMICS

Since the middle of the last century the organic diversity observed in nature has been considered a result of the evolutionary process. The principal tenet of the evolutionary doctrine is that the living world as seen by us at present has not always been as it is now; what we study at our time level is a cross section of the phylogenetic lines, the beginnings of which are lost in the dim past. But evolution is a process of change or movement. Description of any movement may be logically and conveniently divided in two parts; statics, which treats of the forces producing a motion and the equilibrium of these forces, and dynamics, which deals with the motion itself and the action of forces producing it. Following this scheme, we shall discuss, first, the forces which may come under consideration as possible factors bringing about changes in the genetic composition of populations (evolutionary statics), and second, the interactions of these forces in race and species formation and disintegration (evolutionary dynamics).

In bare outline, the mechanisms of evolution as seen by a geneticist appear as follows. Gene changes, mutations, are the most obvious source of evolutionary changes and of diversity in general. Next come

the changes of a grosser mechanical kind involving rearrangements of the genic materials within the chromosomes. It seems probable at present that such rearrangements may at least occasionally entail changes in the functioning of the genes themselves (position effects), since the effects of a gene on development are determined not only by the structure of that gene itself but also by that of its neighbors. Finally, reduplications and losses of whole chromosome sets (polyploidy) are important as evolutionary forces, especially among some plants.

Mutations and chromosomal changes arise in every sufficiently studied organism with a certain finite frequency, and thus constantly and unremittingly supply the raw materials for evolution. But evolution involves something more than origin of mutations. Mutations and chromosomal changes are only the first stage, or level, of the evolutionary process, governed entirely by the laws of the physiology of individuals. Once produced, mutations are injected in the genetic composition of the population, where their further fate is determined by the dynamic regularities of the physiology of populations. A mutation may be lost or increased in frequency in generations immediately following its origin, and this (in the case of recessive mutations) without regard to the beneficial or deleterious effects of the mutation. The influences of selection, migration, and geographical isolation then mold the genetic structure of populations into new shapes, in conformity with the secular environment and the ecology, especially the breeding habits, of the species. This is the second level of the evolutionary process, on which the impact of the environment produces historical changes in the living population.

Finally, the third level is a realm of fixation of the diversity already attained on the preceding two levels. Races and species as discrete arrays of individuals may exist only so long as the genetic structures of their populations are preserved distinct by some mechanisms which prevent their interbreeding. Unlimited interbreeding of two or more initially different populations unavoidably results in an exchange of genes between them and a consequent fusion of the once distinct groups into a single greatly variable array. A number of mechanisms encountered in nature (ecological isolation, sexual isolation, hybrid sterility, and others) guard against such a fusion