FACTORS OF EVOLUTION

SCHMALHAUSEN

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THE THEORY OF STABILIZING SELECTION

BY

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Preface

The problem of the factors of evolution was analyzed in part in my previous books, "The Organism as a Whole," in which the historical development of the ideas in this field was briefly surveyed, and "Ways and Laws of the Process of Evolution." However, this analysis was only incidental since our main interest was directed toward other aspects of special importance for these problems. Because these problems are so complex, it might be inferred from the incomplete analysis that the exposition is not only inadequate but also contradictory. This contradiction, however, is not due to the subjective evaluation of facts from different points of view, but is inherent in the facts themselves, for thoroughly objective contradictory processes underlie the evolution of the organic world. This is true of the basic materials of evolution—namely, heritable and noninheritable variability—and even more true of the causative forces of the process of evolution.

As F. Engels has remarked, heredity itself appears as a negative factor hindering the historical transformation of organisms, and, conversely, as a positive factor preserving the organization and rendering new elements capable of entering firmly into this organization.

In many respects variation appears as a negative factor disturbing the stability of organization. Mutations disrupt the organism. Those which have accumulated in a specific direction favored by natural selection either destroy such features, whose importance has been lost, or create new organic forms. Under given conditions of existence, single mutations upset established relations between the organism and its environment and at the same time unsettle adjustments among its different parts. Mutations are usually harmful. But under other conditions, especially in certain combinations, they become new acquisitions beneficial to the organism. The capacity for adaptive modification is of positive value in a variable environment. However, when brief and accidental changes predominate in the external environment, individual variability may become harmful. Indeed, the advantage may be on the side of the more stable forms.

The struggle for existence is always associated with the destruction of less viable, less well adapted individuals (elimination), and the destruction of entire populations, species, and obsolete forms of organization (extinction). But the same struggle for existence is connected also with racial survival—i.e., with the appearance of more adaptive individuals, species, and organic forms as a result of individual and intergroup competition. Finally the displacement and redistribution of species in place and time, in biocoenoses, in floras and faunas, are manifestations of intergroup competition.

Herein lies the creative role of natural selection. Many authors have correctly pointed out the importance of natural selection both in the mere segregation of viable forms (out of many occurring variations) and also in their distribution over the surface of the earth (neo-Lamarckians, neo-Darwinians: among Soviet authors especially L. S. Berg). Charles Darwin also has called attention to the *conserving role* of natural selection which preserves the structure and function of normal organization (L. S. Berg) under given conditions of existence. Again, some authors have indicated the importance of natural selection in firmly establishing useful adaptations by means of appropriate heritable variations. This is the stabilizing role of organic or harmonious selection (L. Morgan, J. Baldwin, H. F. Osborn).

These diverse conceptions of natural selection have a real basis in the variety of conditions under which the struggle for existence is taking place. According to these conditions, selection appears now in a causal, now in a distributing role, and sometimes in a conserving or fixating role. Usually, authors stress only one of these aspects of natural selection and ignore the others, particularly the most important feature, which is the role of selection as the basic creative factor of evolution. It is precisely this one-sidedness which distinguishes not only the anti-Darwinians but also the modern neo-Darwinians, and which brings them into conflict with the logically impeccable concept of the immortal creator of the theory of evolution.

Both neo-Darwinians and mutationists regard selection as a mere sifting of individual mutations. In contrast to this I have pointed out the importance of natural selection as an integrating factor; one always operating with complex individual variations of different origins and creating more stable and integrated forms of organization (the creative role of evolution). Moreover, I distinguish between the mobile and the conserving forces of natural selection. The former reshapes the entire individual in accordance with its new relation to the external environment. The latter produces new forms of ontogenesis which are more protected against the disturbing influence of the environment, and the organization therefore becomes more stable in the given environment. Furthermore, while the mobile form of selection is based upon the selective advantage of certain variations over the former "norm," the stabilizing form of selection rests upon the selective advantage of the established definitive norm over all deviations from it.

This "fixation" of modifications that have attained permanent significance in the life of a species may be regarded as a special case of the stabilization of forms in a certain variable environment (accidental variation). The conservation or immobilization of species, however, may be regarded as due to stabilization under other, more constant and limited, environmental conditions. Even if in certain cases stabilizing selection does not produce a perceptible change in organization, it is still a factor of great integrating and creative importance. For it creates a stable ontogenesis through its more or less autonomous mechanisms that regulate individual development.

This book contains a more specialized and complete discussion of the role of the stabilizing form of natural selection. First there is an examination of variation as the basis of evolution, which serves as an introduction. It is a survey of materials well known to biologists, particularly to geneticists. Special attention is given those facts (Chapters 7 and 8) that are significant for a subsequent discussion of evolutionary problems.

Following the examination of variation is an analysis of the causative forces of evolution on the lower level, especially the transformation of the genetic composition of population. From the point of view of population genetics this may appear as an incomplete survey of its contemporary achievements. However, I did not propose to write a review of this field, nor do I dwell on the problem of species formation, for all these problems are treated comprehensively in the books of Academician Komarov and in the review of Sinskaia, and in the recent publications of Dobzhansky, Timofeeff-Ressovsky, and Dubinin. Instead I wish to analyze only the elementary processes of general importance. The causative forces of evolution are discussed more fully here but, as in my previous books, only in so far as they are necessary for the main task. We are interested primarily in justifying our emphasis upon the stabilizing aspect of natural selection. Since the basic evolutionary processes occur only in populations of interbreeding individuals, it was necessary to consider the subject of population genetics. Special emphasis is placed upon the processes involved in the accumulation of hidden reserves of variability. This portion of the book concludes with a discussion of these processes, and the entire analysis contained in subsequent parts of the book is based upon this discussion.

Next there is a discussion of fundamental processes involved in the transformation of the individual organism during its historical development. In it are treated a series of topics which are immediately related to the issues discussed in my earlier books. The problem of the origin of the adaptive reactions of organisms serves as a natural introduction to the problems of the ways and laws of evolution (Schmalhausen, 1939, 1940). The problem of the origin of regulating mechanisms leads to an understanding of the organism as a whole (Schmalhausen, 1937, 1942). Finally, the rate of evolution and the factors determining it at the various stages are dealt with in the last part of the book.

Because of the War this book was written almost without recourse to any library (including my own). Accordingly, the modern literature, even the most recent Soviet literature, could not be sufficiently utilized. This affected chiefly the contents of the early chapters which are merely a survey of the literature from the point of view of the author. In the fourth and fifth chapters of this part I made extensive use of Dobzhansky's well-known book.

Only after the re-evacuation to Moscow, at the end of 1943, when the manuscript was completely ready for publication, did I have the opportunity to read the article of C. H. Waddington published in *Nature* in 1942. It is regrettable that I was unable to make use of this interesting work, for Waddington suggests a solution of the problem of the role of individual adaptation in evolution. His solution is very close to ideas I had previously evolved in a series of books and articles beginning in 1938. The difference between Waddington and myself amounts to a somewhat different terminology. I employ the terms "autoregulation" and "autoregulating mechanism" in approximately the same sense as Waddington uses the term "canalization" of development. Moreover, I believe that the mechanism of transition from a development depending on the environment (in which a definite proportion exists between the factors of the environment and the morphogenetic reactions), to a self-regulating type ("canalized" with the establishment of threshold levels of normal tissue reactivity), and finally to autonomous development, is accomplished through a particular form of natural selection which I designate as the stabilizing form.

THE AUTHOR

Foreword

An upsurge of activity unprecedented since the time immediately following the publication of Darwin's "Origin of Species" has taken place in the last ten to fifteen years in the field of evolutionary biology. This upsurge is caused by convergence and unification of the contributions to evolutionary thought coming from various biologic disciplines. For evolution does not constitute the subject matter of any one biologic science. Genetics, systematics, comparative morphology and embryology, paleontology, and ecology have all been profoundly influenced by and have made important contributions to evolutionary thought. Among the major subdivisions of modern biology only physiology and biochemistry still remain largely unaffected by evolutionary ideas, doubtless to mutual detriment.

The different biologic disciplines which bear on evolution have, however, remained isolated from each other until recent years. A geneticist interested in evolution spoke a language unfamiliar to most systematists and paleontologists, and vice versa. Owing to this unfamiliarity, theories sprang up which were contradictory to each other, and were based on allegedly incompatible findings of the different disciplines. This sterile bickering is now, very fortunately, a thing of the past. A trend toward unification and synthesis has set in, which clearly leads toward confluence of the separate currents of evolutionary thought in a single stream. Several synthetic treatments of evolution have appeared in recent years. That by Dobzhansky (1937–1941) has as its starting point the contributions of genetics; that by Mayr (1942) springs from modern systematics and biogeography; Simpson (1944) builds on the foundation of paleontology; Huxley (1943) contributes a magnificent literature review; Rensch (1947) uses comparative morphology as a point of departure. But the view of evolution which emerges from all these several treatments is very largely the same. We have arrived at a biologic synthesis.

The book of I. I. Schmalhausen advances the synthetic treatment of evolution starting from a broad base of comparative embryology, comparative anatomy, and the mechanics of development. It supplies, as it were, an important missing link in the modern view of evolution. For

Schmalhausen is by no means content to restrict himself to anatomy and embryology. His grasp is remarkably inclusive. His command of genetics permits him to give a penetrating as well as inclusive analysis of the developmental relationships in terms of genetic causation. His knowledge of paleontology and systematics supplies not merely some illustrations of his fundamental ideas but leads to important new generalizations. Finally, his mature and incisive philosophic and epistemologic outlook makes his insight profound as well as logically impeccable. This is not a book written by a mere specialist but is the work of a scholar.

Ivan Ivanovich Schmalhausen is perhaps the most distinguished among the living biologists in USSR. A son of a professor of botany at the University of Kiev, he has had the advantage of biologic training with the best biologists in Russia. Foremost among his teachers and advisers was A. N. Severtsov, professor of the University of Moscow, an eminent comparative anatomist and a lifelong student of the phylogeny of vertebrates. I. I. Schmalhausen held professorial positions at the Universities of Voronezh and Kiev. Having been elected member of the Ukrainian Academy of Sciences in Kiev, he organized a research institute of biology. In this he built a school of experimental morphologists and embryologists from which came some of the most brilliant younger workers in these fields. Shortly before the Second World War, Schmalhausen was elected member of the Academy of Sciences of USSR. He moved to Moscow, and became director of the Institute of Evolutionary Morphology founded some years earlier by Severtsov. During the War he worked in the eastern part of European Russia; the present book was written during this enforced sojourn away from the large scientific centers. This is important to keep in mind, since, as stated by Schmalhausen himself, he did not have access to some of the current biologic literature during this period.

Schmalhausen's original research has made important contributions to several biologic disciplines. His early work has been in the field of comparative anatomy and phylogeny of vertebrates, dealing particularly with the origin of fins in fishes. Later he inclined more toward embryologic research, first descriptive and then experimental. He made important studies on regeneration and on rates of growth of various organs. He and his students have worked with much success on the phenomena of embryonic induction and on organizers.

But the diversity of problems investigated by Schmalhausen is more apparent than real. The leitmotif in all his studies has been a lifelong interest in the problems of evolution. Among other things, his work represents a culmination and a synthesis of the attainments of the

Russian school of comparative morphology, particularly those of the group headed by his erstwhile teacher Severtsov. In the present and in earlier books, Schmalhausen uses a number of concepts and terms evolved by this school, which are not familiar to many English-speaking evolutionists. Perhaps the most important among these concepts is a classification of types of evolutionary changes, which can be summarized under the following five headings.

Aromorphosis is an evolutionary transition to a more complex morphologic type, which represents a progression to a higher level of organization. This is caused by acquisition of new adaptations of a generalized character, which permit the organism to exploit new kinds of environments. Examples—the phylogenetic development of body temperature regulation in higher vertebrates, development of feathers in birds or of the hair or teeth in mammals, etc.

Allomorphosis—adaptive changes connected with alterations in the environment which leave the interrelations between the organism and the environment at about the same level of limited adaptation. Example—adaptive radiation of different types of teeth in different orders of mammals.

Telomorphosis—adaptive specialization which leads the organism to become restricted to a narrower part of the environment. Example—foot and body structure specializations in the sloth, development of the enormous canine teeth in the saber-tooth tigers (*Machairodus*, *Smilodon*).

Katamorphosis—regressive changes which lead to simplification of the connections between the organism and the environment. Examples—development of the Rotatoria and Bryozoa among the worms, of Cirripedia among the crustaceans, of mites among the arachnoids, of Apterygota among the insects. Neotenic changes (or *hypomorphoses*) are a special type of katamorphosis.

The present translation has been made from a manuscript which was received in this country before the appearance in print of the Russian edition (1947). The translation has been checked against this printed version, but the generally small differences between the two were mostly disregarded. It seemed expedient to eliminate, in the English edition, some pages dealing with purely genetic phenomena which are sufficiently familiar to most prospective readers. Some minor cuts have been made also in other parts of the book where repetition seemed to occur.

TH. DOBZHANSKY

Contents

CHAPTER 1 *Individual Variability as a Source of Historic Change in Organic Nature*

Individuals of any plant or animal species differ from one another in many ways. An analysis of these differences discloses certain regularities in their distribution among individuals descending from definite ancestral forms and also among individuals living in a specific environment. Laboratory experiments make it possible to penetrate more deeply into the nature of these differences. Some, originating in a single individual, are encountered later in approximately the same form among the offspring of that individual. Others, appearing in all individuals exposed to certain conditions, disappear either at once or gradually in their offspring, if the latter develop in different environments.

In the former case, we may conjecture that some environmental influence has affected the organism and its germ cells. If such a change of the organism or its germ cells be regarded as its reaction to the environment, it has, until now, been impossible to establish a causal connection between the environment and the specific hereditary reaction of the organism or its germ cells. Darwin thought that the specific nature of the reaction is determined principally by the individual characteristics of each organism and designated such changes as individual or "indeterminate." Today they are termed mutations. The kinds of mutations depend upon the individual hereditary properties of the organism itself.

In the second case, however, a relationship between certain environmental factors and the nature of the changes in the organism is easily established. The particular character of the reaction clearly is determined primarily by the organism itself. Darwin has called these changes "determinate." Today, they are termed modifications. Their nature clearly depends upon the heritable characteristics of the organism, and, even more, upon the common heritable characteristics of the organism as the representative of a certain species than upon its purely individual properties, although these are still important. The usual modifications are adaptive in nature and recur regularly among different individuals of a given species. The capacity for certain adaptive modification, as well as other characteristics of organisms and their entire organization with all its functions, is the result of an age-long historic development of organisms in diverse but definite environments.

A. ROLE OF EXTERNAL AND INTERNAL FACTORS IN ORIGIN OF CHANGE

Modifications as well as mutations are changes of organisms which depend in origin and manifestation both upon the genotype of the organism and the environment.

In the development of any individual, environmental factors act only as agents releasing form building processes and providing conditions necessary for their realization. This should be regarded as the result of phylogenetic development of the organism in certain environments. The forms of interaction between organism and environment have altered during this historic development. Evolution has, on the whole, been a liberation of the developing organism from accidental environmental changes. It has been accompanied by the elaboration of internal regulating mechanisms controlling processes of individual development. Liberating the organism from the *determining* influence of environment involves establishment of a system of internal factors of development which determine the specific course of morphogenetic processes.

During the early stages of organic evolution, life was completely at the mercy of accidental environmental changes which determined its form and elementary vital processes. However, the entire further evolutionary development consisted of a gradual liberation from dependence upon environment. Organisms became, to a certain extent, independent carriers of life, controlling their own form (size, structure) and their own functions. Environmental influences were directed gradually into definite channels and were transformed within the organism by means of its specific responses. Thus, the organism developed either passive or active defenses against unfavorable influences. On the other hand, it benefited from favorable influences and changes resulting from these influences were canalized into the most profitable forms of reaction. All this was associated with differentiation of the organism, for every act of differentiation involves a utilization by the organism of specific connections with its environment. In this way, environmental factors are more and more controlled by the organism. At present, the organism itself determines its relationship to its environment, thus protecting itself against some influences and utilizing others. This relationship to the environment varies for different organisms. Modes of defense and utilization of environmental factors are not identical in different organisms. Every species profits from environment in its own way and responds to changes in environment in different ways. Reactions of the organism to basic environmental factors to which it has become adapted are always strictly specific. This specificity of reaction is determined by the historically developed nature of the organism, by its evolution in a certain environment, and by the constant interaction of the latter with internal factors of the organism. On the other hand, environmental factors that do not usually occur in the normal environments of the organisms can, to the extent that they influence the organism, produce only indeterminate effects, manifested in a more or less profound disturbance of its normal structure and function.

The organism's adaptation to environmental factors is expressed in protective reactions against harmful influences emanating from the environment and in utilization of favorable elements. In both cases, responses may be either easily and quickly reversible physiologic reactions or more slowly reversible morphogenetic reactions. The latter are termed adaptive morphologic modifications.

The *uncontrolled environmental factors*, as far as they exert an influence, do not elicit an adaptive response in the organism. The organism developed historically without having interacted with certain factors (e.g., x-ray, highly concentrated ultraviolet radiation, unusual chemical substances in food, etc.), or with certain intensities (e.g., temperature, humidity, salt concentrations, etc.), to which it was not accustomed. Therefore, the organism evolved neither adequate means of protection against such environmental agencies nor ways of utilizing them. Hence, a defenseless organism is unable to respond to such influences by adaptive change. The influence of such factors would be determined, first, by their nature and, secondly, by specific structural and physiologic characteristics of the organism. Such influences can be only nonspecific so that all new changes in the organism that are not historically determined would also be indeterminate. However, this category of indeterminate changes includes not only heritable variations or mutations, but also all new modifications arising for the first time. Such modifications are nonadaptive and are termed morphoses. Morphoses can have a two-fold origin: either the modifying factor is new (x-rays, unusual chemical substances, etc.) or the organism itself is to a certain extent new as a result of having been changed by a recent mutation. In the latter case, modifications of the mutant will appear as morphoses.

Mutations and their modifications are more or less profound changes of the organism resulting from interaction with the environment. The specific character of both types of changes depends essentially upon the nature of the organism. However, mutations can manifest themselves in some of the offspring even if the environment is not altered. Modifications, however, always depend upon specific environmental factors and will not recur if these factors change. Mutations are always new acquisitions of the organism, while modifications are merely a superstructure or a new version of the already existing organization.

The transmission of mutations from generation to generation is an extremely regular process controlled by the principle of segregation discovered by Mendel. The phenomena of segregation demonstrate the discreteness of the mutational steps and the immiscibility of the hereditary traits.

The statement that modifications are not heritable is not precise. The ability to undergo modification is strictly hereditary. Every organization, the typical as well as the variant (including mutants), does not pre-exist but develops on a specific hereditary foundation (genotype). This development is determined not only by the genotype but also by environmental factors. Therefore, the genotypic expression of both normal organisms and mutants is different in diverse environments. Those *differences of expression* which depend for their development upon different environmental factors are termed modifications. The process that causes corresponding changes of the typical organization or of the expression of a mutation is also called modification. Consequently, modification is both an individual and a historically determined superstructure resulting from specific reactions of the organism to changes in its environment.

Environmental factors always modify only those processes of individual development dependent on them. In its role of dependent development, environment produces its effect either directly or through the functions of the organism. The quality of effect is determined, however, by the basic hereditary organization, by the capacity of the organism to undergo specific modification. Geneticists, therefore, speak of a hereditary "norm of reaction." All dependent reactions are characterized by dependence upon environmental factors during individual development. Since these reactions are determined by the genotype, they can be realized in the offspring only in the presence of definite environmental factors; otherwise neither reactions nor their resulting modifications will recur.

The individual modification is nonheritable because its hereditary foundation is unchanged; its reappearence requires a certain intensity of environmental factors. Its recurrence in the offspring under different conditions signifies that the inherited norm of reaction has changed, i.e., a mutation has arisen. In the seldom occurring persistent modifications ("dauer-modifications"), the results of individual reaction to environment are observable in the offspring. In contrast to mutations, persistent modifications are transmitted in sexually reproducing organisms to all the offspring, not to just a certain proportion of them; such modifications are not transmitted discretely and gradually fade from generation to generation. Available data indicate that persistent modifications are inherited through the germ plasm but not through the chromosomes, which are responsible for the discrete inheritance of mutations. In the inheritance of persistent modifications, the living substance exhibits a certain inertness which is expressed in the ultimate reversibility of the modifications and in their final disappearance.

The specificity and adaptiveness of the majority of reactions, including modifications, can be explained by the fact that the entire organization with all its reactions is historically established. The random nature of structure changes (mutations) and the nonadaptiveness of reactions are due to encroachments upon the historically established hereditary foundation. Mutations and their various expressions, however, are not yet historically established. They represent new characters of the organism which, in certain cases, can be utilized in evolution. It is precisely these new useful traits that are fully inheritable. Thus, mutations are the foundation upon which new reactions are built. Mutations bring about not only new traits of organization but also its various expressions in different environments, namely, modifications.

B. MODIFICATIONS—THEIR EXPRESSION AND REVERSIBILITY

Modifications involve either single traits or organs. The color of young salamanders (*Salamandra maculosa*, Kammerer) changes to conform with the color of the environment. Again, different intensities of light cause changes in size, structure, and shape of the leaves of many plants.

In some cases, the entire organism is altered. Differences in the nutrition of larvae bring about significant differences in the size of adult insects. The capacity for modification sometimes causes a thorough reconstruction of the entire organism. Resultant changes are adaptive and the organism becomes polymorphic in accordance with the environment. Such an organism, therefore, has several definite adaptive norms. Where ecological conditions are markedly different, the so-called ecophenes (Turesson) are observed. An example is the lowland and alpine modifications of certain plants. Sometimes these different norms correspond to different seasons, i.e., seasonal polymorphism and cyclomorphism; less often polymorphism is expressed through sexual differences (*Bonellia*) or through differences, as of caste, within certain insect societies (bees, ants, termites).

Modifications differ also in mode of reaction. Sometimes the reaction