Animal Species and Evolution

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Preface

The steadily rising flood of scientific publications makes it increasingly difficult for a scientist to keep up with developments outside his own narrow area of specialization. The need for surveys of selected areas of science has never been greater than today. The present work is an attempt to summarize and review critically what we know about the biology and genetics of animal species and their role in evolution.

Friends have suggested that I go a step further and incorporate the relevant information on plants, expanding this account into a "species and evolution." I have resisted the temptation to yield to this suggestion. Having worked with animal species for some 35 years, in the field and in the laboratory, I believe that I have acquired some understanding of their species structure and evolutionary behavior. Lacking a similar familiarity with plants, I might come up with absurd generalizations if I tried to apply my findings to plants. Each of the kingdoms has its own evolutionary peculiarities and these must be worked out separately before a balanced synthesis can be attempted. Accordingly, I have also refrained from referring to numerous phenomena recently discovered in microorganisms that do not seem to have equivalents among higher organisms. When I speak of species, chromosomes, and gene pools, I refer to those of animals, particularly of the higher animals, even where this is not stated specifically. On the other hand, the findings derived from the higher animals concerning the population structure of their species and the mechanisms controlling their genetic variation are directly applicable to man. A study of the species of higher animals is, therefore, of the utmost importance, particularly in view of the impossibility of experimenting with man. An understanding of the biology of the species *Homo sapiens* is an indispensable requisite for the safeguarding of its future.

Evolutionary biology has been exceedingly active in recent years. I have endeavored in the present volume to concentrate on topics that have not been thoroughly discussed in recent works. Only a summary treatment is given here of cytology, of the more formal aspects of taxonomy, of paleontology, and of some areas of population genetics, because recent and comprehensive treatments are already available. This is a volume on the species and its role in evolution rather than on the evolutionary theory itself.

I have attempted to present a continuous story, with each chapter based on the preceding chapters. My aim has been to integrate and interpret rather than to present raw data. Interpretation is necessarily subjective; it requires the setting up of models and the testing of them with additional data. Where the issue is controversial I have not hesitated to choose the interpretation that seems most consistent with the picture of the evolutionary process as it now emerges. To take an unequivocal stand, it seems to me, is of greater heuristic value and far more likely to stimulate constructive criticism than to evade the issue. I have called attention whenever possible to unsolved problems. Where it helped the interpretation I have related the evolutionary subject matter to relevant material from other fields, such as physiology and biochemistry. Integration has been my major goal throughout.

Comparing two such different fields as, let us say, the evolutionary biology of species and enzyme chemistry brings home the enormous contrasts within science. In chemistry we deal with repeatable unit phenomena and with actions that, once correctly described, are known forever. In evolutionary biology we deal with unique phenomena, with intricate interactions and with balances of selection pressures—in short, with phenomena of such complexity that an exhaustive description is beyond our power. We can approach the truth only by a trial-and-error process of increasing accuracy. As in the humanities, and in contrast to many of the physical sciences, a thorough knowledge of the classical literature of the field is a prerequisite in evolutionary biology for a full understanding of the total conceptual framework.

I share the curiosity of those who are interested in the origin of the ideas in which we currently believe. It is for this reason that I have made an attempt in this work to trace whenever possible the history of concepts. Most references to publications antedating 1940 are included for historical reasons. It is well to remember that the main concepts of the biological role of species and of the process of species formation were established empirically by naturalists long before the turn of the century, but that a precise causal analysis became possible only after the rise of population genetics. The extraordinary vitality of the area of research covered by this book may seem surprising, considering that it has been active for more than a century. Yet anyone comparing the current interpretations with those prevailing even as recently as 1930, for example, will be struck by the clarification of ideas and change in emphasis.

The first draft of this work served as the text for a course given in 1949 at the University of Minnesota, and the ensuing years have been devoted to the seemingly never-ending task of improvement. The final version was completed in 1961, and it has not been feasible to include more than a fraction of the literature published since then.

I am deeply indebted to numerous friends and colleagues for encouragement, suggestions, and assistance of every kind. Having discussed almost every aspect of the subject matter with them, I find it quite impossible to separate their intellectual contribution from my own. Draft versions of certain chapters were read and criticized by Carleton Coon (20), J. F. Crow (part of 9), Th. Dobzhansky (1, 7, 8, 9, 10, 17), J. J. Hickey (4), L. B. Keith (4), R. H. MacArthur (4), F. A. Pitelka (4), G. G. Simpson (1), Bruce Wallace (7, 8, 9, 10, 17), M. J. D. White (15), and E. O. Wilson (5). All have made numerous suggestions, most of which though not all I have incorporated. Any remaining errors are strictly my own responsibility. I owe special thanks to Richard Lewontin for a penetrating analysis of chapters 1, 7, 8, 9, 10, and 17. I am indebted to Dr. Arthur Steinberg for making some unpublished data on the genetics of the Hutterites available to me. I am obliged to various authors and publishers for permission to republish illustrations, as acknowledged in the captions of these figures. Various assistants have helped in the preparation of the numerous drafts of the manuscript, particularly Sophie Prywata, Carmela Berrito Rosen, and, more recently, Lorna Levi and Emily Witte. Without their devoted services this volume would never have been completed.

E. M.

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1 ~ Evolutionary Biology

The theory of evolution is quite rightly called the greatest unifying theory in biology. The diversity of organisms, similarities and differences between kinds of organisms, patterns of distribution and behavior, adaptation and interaction, all this was merely a bewildering chaos of facts until given meaning by the evolutionary theory. There is no area in biology in which that theory has not served as an ordering principle. Yet this very universality of application has created difficulties. Evolution shows so many facets that it looks alike to no two persons. The more different the backgrounds of two biologists, the more different have been their attempts at causal explanation. At least, so it was through the history of evolutionary biology (Heuts 1952; Simpson 1949, 1960b; Eiseley 1958), until the many dissenting theories were almost suddenly fused, in the 1930's, into a broad unified theory, the "synthetic theory."

Many of the earlier evolutionary theories were characterized by heavy emphasis, if not exclusive reliance, on a single factor (Table 1-1). The synthetic theory has selected the best aspects from the earlier hypotheses and has combined them in a new and original manner. It attempts to evaluate the respective roles of the numerous interacting factors responsible for evolutionary change. In essence it is a two-factor theory, considering the diversity and harmonious adaptation of the organic world as the result of a steady production of variation and of the selective effects of the environment. It is thus basically a synthesis of mutationism and environmentalism.

Attempting to explain evolution by a single-factor theory was the fatal weakness of the pre-Darwinian and most 19th-century evolutionary theories. Lamarckism with its internal self-improvement principle, Geoffroyism with its induction of genetic change by the environment, Cuvier's catastrophism, Wagner's evolution by isolation, De Vries' mutationism, all were deficient through focusing on only one aspect of a complex set of interacting factors. These hypotheses tried to explain evolution by a single principle to the exclusion of all others. Even Darwin occasionally fell into this error, as when he wrote, late in his life, that natural selection

Table 1–1. Theories of evolutionary change (in part after Heuts 1952).

A. Monistic (single-factor explanations)
   1. Ectogenetic: changes directly induced by the environment
      (a) Random response (for example, radiation effects)
      (b) Adaptive response (Geoffroyism)
   2. Endogenetic: changes resulting from intrinsic forces
      (a) Finalistic (orthogenesis)
      (b) Volitional (genuine Lamarckism)
      (c) Mutational limitations
      (d) Epigenetic limitations
   3. Random events ("accidents")
      (a) Spontaneous mutations
   4. Natural selection
B. Synthetic (multiple-factor explanations)
   1(b) + 2(a) + 2(b) = most "Lamarckian-type" theories
   1(b) + 2(b) + 2(c) + 4 = some recent "Lamarckian" theories
   1(b) + 3 + 4 = late Darwin, Plate, most nonmutationists during first three decades of 20th century
   3 + 4 = early "Modern Synthesis"
   1(a) + 2(c) + 2(d) + 3 + 4 = recent "Modern Synthesis"

rather than isolation was responsible for the origin of species, as if the two forces were mutually exclusive (Mayr 1959c). Yet on the whole Darwin was the first to make a serious effort to present evolutionary events as due to a balance of conflicting forces. Indeed, he often went too far in compromising. It has been claimed, not without justification, that one can find support in Darwin's writings for almost any theory of evolution: speciation with geographic isolation or without it, direct effect of the environment or merely selection by the environment, evolutionary importance of large genetic changes or of small ones, and so on. This explains the paradox that the term "Darwinism" means such different things to an American, a Russian, or a French biologist. To be sure, the current theory of evolution—the "modern synthesis," as Huxley (1942) has called it—owes more to Darwin than to any other evolutionist and is built around Darwin's essential concepts. Yet it incorporates much that is distinctly post-Darwinian. The concepts of mutation, variation, population, inheritance, isolation, and species were still rather nebulous in Darwin's day. To avoid confusion, it has been suggested, particularly by Simpson

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other instances it is the refutation of an erroneous theory that vacates the field for new ideas. An excellent illustration of this is Louis Agassiz's neglect of what seem to us most convincing evolutionary facts because they were inconsistent with his well-organized, harmonious world view (Mayr 1959d). Darwin, who had started the voyage of the *Beagle* with views similar to those of Agassiz, began to think seriously about evolution only after he had found overwhelming evidence that was completely irreconcilable with the idea of an origin of the world fauna and flora by creation. Or, to cite another example, as long as spontaneous generation and the instantaneous conversion of one species into another were universally believed in, even for higher animals and plants (Zirkle 1959), there was no room for a theory of evolution. By insisting on the fixity of species, Linnaeus did more to bring about the eclipse of the concept of spontaneous generation than did Redi and Spallanzani, who disproved it experimentally. Indirectly, Linnaeus did as much to prepare the ground for a the ory of evolution as if he had proposed such a theory himself. Weismann, through his theoretical analysis of the relation between germ cells and soma cells, eliminated many of the misconceptions and errors that until then had prevented the recognition of the work of Mendel. These are merely a few illustrations of the importance of eliminating erroneous theories. The refutation of an erroneous idea thus is not a purely negative activity, and in this volume I often give considerable space to the analysis of that alternative of two opposing theories that I consider to be the less well-founded one.

More important for the development of the synthetic theory than the rejection of ill-founded special theories of evolution was the rejection of two basic philosophical concepts that were formerly widespread if not universally held: preformism and typological thinking. Preformism is the theory of development that postulates a preformed adult individual in miniature "boxed" into the egg or spermatozoon, ready to "unfold itself" during development. The term evolution is derived from this concept of unfolding, and this connotation continued well into the post-Darwinian period. It was perhaps the reason Darwin did not use the term "evolution" in his *Origin of Species.* Transferred from ontogeny to phylogeny, evolution meant the unfolding of a built-in plan. Evolution, according to this view, does not produce genuine change, but consists merely in the maturation of immanent potentialities. This, for instance, was Louis Agassiz's theory of evolution (Mayr 1959d). Some of the orthogenetic and finalistic theories of evolution are the last remnants of this type of thinking. The underlying erroneous assumption that the development of the "type" is essentially the same phenomenon as the development of the individual has also been the reason for much of the search for "phylogenetic laws." Mutationism was the extreme in the reaction to these orthogenetic concepts. The current theory compromises by admitting that genotype and phenotype of a given evolutionary line set severe limits to its evolutionary potential (Table 1-1, A2*c,d*), without, however, prescribing the pathway of future evolutionary change.

Typological thinking is the other major misconception that had to be eliminated before a sound theory of evolution could be proposed. Plato's concept of the *eidos* is the formal philosophical codification of this form of thinking. According to this concept the vast observed variability of the world has no more reality than the shadows of an object on a cave wall, as Plato puts it in his allegory. Fixed, unchangeable "ideas" underlying the observed variability are the only things that are permanent and real. Most of the great philosophers of the 17th, 18th, and 19th centuries were influenced by the idealistic philosophy of Plato and the modifications of it by Aristotle. The thinking of these schools dominated the natural sciences until well into the 19th century. The concepts of unchanging essences and of complete discontinuities between every *eidos* (type) and all others make genuine evolutionary thinking well-nigh impossible. I agree with those (such as Reiser 1958) who claim that the typological philosophies of Plato and Aristotle are incompatible with evolutionary thinking.

> The assumptions of population thinking are diametrically opposed to those of the typologist. The populationist stresses the uniqueness of everything in the organic world. What is true for the human species, that no two individuals are alike, is equally true for all other species of animals and plants . . . All organisms and organic phenomena are composed of unique features and can be described collectively only in statistical terms. Individuals, or any kind of organic entities, form populations of which we can determine the arithmetic mean and the statistics of variation. Averages are merely statistical abstractions; only the individuals of which the populations are composed have reality. The ultimate conclusions of the population thinker and of the typologist are precisely the opposite. For the typologist, the type (*eidos*) is real and the variation an illusion, while for the populationist the type (average) is an abstraction and only the variation is real. No two ways of looking at nature could be more different (Mayr 1959c).

The replacement of typological thinking by population thinking is perhaps the greatest conceptual revolution that has taken place in biol-