SYSTEMATICS AND THE ORIGIN OF SPECIES

MAYR

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FROM THE VIEWPOINT OF A ZOOLOGIST

By ERNST MAYR

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INTRODUCTION

A NEW AND SIGNIFICANT trend has become discernible in biology during the last decade. The excessive specialization which had prevailed in the recent past seems slowly to be giving way to a greater unity; a science of general biology appears to be emerging. In a way this trend represents a partial reversal of a historic tendency of much greater duration. For more than a century the field of biology was so extensive and growing so rapidly that no single investigator, no matter how broad might be his grasp, could keep abreast with the developments in all the numerous branches. The response of biology to this challenge was a subdivision of the general field into many disciplines, each endowed with its own materials, methods, and techniques. Instead of being biologists, most of us became systematists, physiologists, geneticists, embryologists, biochemists, pathologists, etc. Inevitably, secondary subdivisions have arisen in the course of time. Nobody could any longer be at home in, for example, the systematics of all animals or of all plants. The systematists split into mammalogists, ornithologists, entomologists, helminthologists, protozoologists, etc., and finally into specialists on separate families, genera, and even smaller groups. The genetics of, let us say, Oenothera threatened to become incomprehensible to those engaged in studies on the genetics of Drosophila or of man. This extreme compartmentalization of biological knowledge proved fruitful in that it led to an enormous accumulation of factual information; it has been deleterious in so far as it resulted in a lack of understanding between the representatives of the various disciplines and a consequent lowering of the efficiency of biological research. It stands to reason that the exigencies of the situation continue, and probably will continue, to demand that each biologist be a specialist in some small portion of the general field. During the last decade the conclusions reached by many of the specialists have begun to converge toward a set of general principles applicable to the entire realm of living matter. One can now hope that this will occur in increasing measure in the future. Biology, it seems, is no longer in its childhood; as a science, it is approaching maturity.

Obviously, it would be out of place to attempt to discuss here the results of the unifying trend in modern biology as a whole. Suffice it to

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say that Dr. Mayr's *Systematics and the Origin of Species* is one of the manifestations of this trend. Dr. Mayr is an outstanding zoological systematist; his specialty is ornithology, and he is the foremost authority on the birds of Oceania and Indonesia. The results of his preoccupation with the subject matter of his special investigations are amply evident in his choice of examples in many chapters of the book. Yet it is equally evident that this book has not been written from the point of view of a specialist on the systematics of a certain group of animals inhabiting a certain part of the world. It has been written by a general biologist. Although this book contains a critical reassessment of the evidence furnished by zoological systematics regarding the course and the mechanisms of the biological evolution, that is not what makes it unique. Such critical reassessments have been published from time to time by many systematists and they are undoubtedly interesting and necessary. But Dr. Mayr's chief accomplishment in this book has been to correlate the evidence and the points of view of modern systematics with those of other biological disciplines, particularly genetics and ecology. A correlation of this sort has been necessary for some time; even in the recent past there existed a notorious lack of mutual comprehension between the systematists on one hand and the representatives of the experimental biological disciplines on the other. That this lack of mutual comprehension was due in part to an unfamiliarity with each other's factual materials and methods, and in part to a sheer misunderstanding of the respective points of view, was felt by many systematists as well as by experimentalists. But it remained for a systematist of Dr. Mayr's caliber, possessing a wide familiarity with and a perfect grasp of the apparently conflicting disciplines, to demonstrate conclusively that this conflict is spurious.

TH. DOBZHANSKY

Mount San Jacinto, California
July, 1942

PREFACE

DURING the past fifty years animal taxonomy has undergone a revolution almost as fundamental as tha which occurred in genetics after the rediscovery of Mendel's laws. It is true that the change from the static species concept of Linnaeus to the dynamic species concept of the modern systematist has not entirely escaped the attention of progressive students of genetics and evolution. However, the whole significance of the polytypic species, of the phenomena of geographic variation, of the differences between geographic and other forms of isolation are by no means as widely appreciated among students of evolution and even among taxonomists as they deserve. I have attempted in this book to summarize our knowledge in the field of systematics, and to subject to a searching analysis the principal concepts on which taxonomic work is based. Finally I have tried to present some of the evidence of the systematist on the question of the origin of species. A discussion of general evolution and of such specific subjects as the evolution of sex, degeneration, and parasitism has been considered outside the scope of this book. The extreme scattering of taxonomic literature makes it inevitable that some publications worthy of detailed discussion have been overlooked. Special emphasis has been placed on the most recent literature and on the field with which I personally am most familiar, the ornithology of the Pacific Islands.

This book is based on the Jesup lectures delivered at Columbia University in March, 1941. The writer presented the evidence of the zoologist, and Dr. Edgar Anderson, of Washington University and of the Missouri Botanical Garden, St. Louis, that of the botanist. The present volume includes only the material of the zoological lectures. Parts of the manuscript were read by Edgar Anderson, Charles M. Bogert, Mont A. Cazier, James P. Chapin, Kenneth Cooper, J. Eric Hill, George G. Simpson, Herman Spieth, George M. Sutton and John T. Zimmer, to all of whom I owe many valuable suggestions. A. E. Emerson, Julian Huxley, and other friends have discussed a number of problems with the author and have helped him in crystallising his ideas. Most of all I am indebted to Th. Dobzhansky and L. C. Dunn, who aided in countless ways in the preparation of the manuscript and who encouraged and

inspired me throughout. I dedicate this work to the army of taxonomists who have unselfishly devoted their lives to the task of describing and classifying the animals of the world.

ERNST MAYR

The American Museum of Natural History
New York, May, 1942

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I am deeply indebted to Mr. Roger T. Peterson for drawing the originals of Figs. 10 and 11. Science Press permitted the reproduction of Figures 2, 13, 17, 19, 20, and 23 from Mayr (1940a) (*The American Naturalist*) and supplied the cuts of Figures 2, 13, 19, and 23. This assistance is gratefully acknowledged. The American Museum of Natural History supplied the cuts of Figures 27 and 28. Figures 1, 3, 5, 12, 14 also are reproductions of previously published illustrations, the other 16 figures are original.

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CHAPTER I

THE METHODS AND PRINCIPLES OF SYSTEMATICS

THE RISE of genetics during the first thirty years of this century had a rather unfortunate effect on the prestige of systematics. The spectacular success of experimental work in unraveling the principles of inheritance and the obvious applicability of these results in explaining evolution have tended to push systematics into the background. There was a tendency among laboratory workers to think rather contemptuously of the museum man, who spent his time counting hairs or drawing bristles, and whose final aim seemed to be merely the correct naming of his specimens. A welcome improvement in the mutual understanding between geneticists and systematists has occurred in recent years, largely owing to the efforts of such men as Rensch and Kinsey among the taxonomists, Timofeeff-Ressovsky and Dobzhansky among the geneticists, and Huxley and Diver among the general biologists.

It was realized by these workers that only some of the problems of the origin of species can be solved by the geneticist, while other aspects are more accessible to such branches of biology as ecology and biogeography, paleontology, and taxonomy. A satisfactory understanding of intricate evolutionary phenomena can be attained only through the coöperation of all these disciplines, and systematics is willing and able to contribute its share.

The importance of systematics in the study of evolution was perhaps better realized in the last century than it is now. Darwin's conclusions in his *Origin of Species* were based largely on the results of contemporary taxonomic work, and I can see no reason why modern systematics should not yield even greater results. After all, systematics has grown tremendously since Darwin's day. The number of species of animals known to us, eighty years after Darwin, is probably tenfold and the number of specimens in collections a thousandfold. But not only the number of known species has grown; the degree to which they are known has also increased. With this vast body of material before us—and I

might confess, from my own museum experience, with an equally large or even greater amount of work still to be done—it is very easy to lose sight of the final aims of such work. It is therefore necessary to pause once in a while in order to make a survey of its present status.

THE STATUS OF SYSTEMATICS

Systematics is in a more difficult position than most other sciences. It seems as if all the conclusions and generalized laws derived from a study of taxonomic material were dependent to a very high degree on the nature of this material and the background of the student. The result is that—partly from the variety of the material, too—we have an almost unlimited diversity of opinion in answer to such questions as: What is a species? How do species originate? Are the systematic categories natural? and so forth. There is no uniform point of view among taxonomists; in fact, in regard to many of these questions there may not even be a majority opinion. This situation is revealed rather clearly if we study the discussions of the twenty-two contributors to *The New Systematics* (Huxley 1940) or the various recent species and speciation symposia in *The American Naturalist* (1940, 1941). This is true not only for the plant taxonomist versus the animal taxonomist, or the parasitologist versus the zoölogist, but also for the opinions of the taxonomist of fresh-water organisms as compared with those of the student of terrestrial animals, or of the students of continental and insular faunas, and even of different taxonomic groups—let us say the opinions of the taxonomist of diptera and mollusca, as compared to those of the ornithologist. This situation indicates clearly that no one taxonomist can yet attempt a broad outline of the generalisations deducible from systematics that is acceptable to all his fellow taxonomists.

The reasons for this vast diversity of opinion are not yet quite clear. It is unquestionably true that species limits are strongly affected by ecological factors and that consequently parasites and other ecologically specialized forms show a taxonomic behavior and course of speciation different from that of widespread, polyphagous animals, such as birds. The influence of these ecological factors will be discussed in greater detail in a later chapter. However, equally or even more important for the opinions of a taxonomist on speciation is the degree to which the group with which he is working is known. It can be claimed without exaggeration that lasting generalisations can be based only on systematic groups that are well known. Recent work on the mosquitoes of the *Anopheles*

maculipennis group, on fresh-water fishes, on "biological races" of certain plant pests, and the like have proven this point abundantly.

There is little doubt that birds are better known taxonomically than any other class of animals and that in consequence taxonomic interpretation in ornithology has reached a degree of refinement which is not equaled in any other group. It is estimated that less than 2 percent of the total number of species of birds of the entire world remain still unknown. Nearly every species is well represented in one or another museum, and for the last forty years most of the work has centered on a study of infraspecific groups. A few genera of mammals, butterflies, beetles, mollusks, and so forth are as well known as the most thoroughly studied avian genera, but our knowledge of most systematic groups of animals is very incomplete; this is particularly true of most invertebrates.

How little we know of certain groups of animals is best indicated by the many recent discoveries in the field of systematic zoölogy, such as the living Coelacanthid fish, *Latimeria* (1939), or the new class of animals, the Pogonofora (Johansson 1937). But in addition to these spectacular novelties, new discoveries are made daily, even in comparatively well-explored areas. A striking illustration of this is presented by Remane's work on the microscopic marine fauna of the Kieler Bucht, an area previously considered to be exhaustively known (Remane 1933). By thorough search and with the application of new methods, Remane found in ten years 300 new species, including representatives of 15 new families. Among them were several entirely new types. In a revision of the small red mites (Amystidae) that are so common in gardens, Oudemans (1936) added 10 new genera to the known 5, and 14 new species to the well-known 12; 24 additional species of the family are insufficiently known, and nobody knows how many species are still undiscovered. In his monograph on the South American weevil genus *Conotrachelus*, K. Fiedler (1940) lists a total of 547 species, of which 404 (74 percent) are described by him as new. A reviewer of the work (Marshall) estimated that this amounted to approximately one-fourth of the probable 2,000 species of this genus. Kinsey (1936) added to the known 50 species of a subgroup of American Cynipid gall wasps no less than 36 additional species during two collecting trips. Dr. Gertsch, of the American Museum, has described some 500 new species of North American spiders during the last eight years and he, as well as three or four other arachnologists, find every year some additional new species, even in such well-worked areas as New England or New Jersey. He estimates that altogether less than 25 percent of the spiders of the earth have so far

been described. In the fruit fly genus *Drosophila* only 28 Nearctic species were known in 1921, as compared to more than 75 known today. Of the 44 species which are known to occur in Texas only 7 were known in 1921, the other 37 being discovered during the last four years, and no less than 21 of these were new to science (Patterson in litt., Feb., 1941; see also Patterson 1942). Had not this genus such prominence in genetics, we would not even suspect this abundance of species. There are many large taxonomic groups, such as the parasitic hymenoptera and certain families of flies and of minute tropical beetles, in which the number of known species is estimated to be less than 10 percent of those probably existing.

The specialist who deals with such groups is happy if he can keep step with the unworked material that continues to pour in. Only seldom does he have time to go beyond the purely descriptive phase of work and try his hand at putting some order into the growing "heap" of species. Newly discovered species are likely to upset his ideas any day. He is forced by necessity to do "old" systematics.

The Old and the New Systematics

Huxley recently introduced the happy term "New Systematics" (Huxley 1940: Foreword) and even though he says: "the new systematics is not yet in being: before it is born, the mass of new facts and ideas which the last two or three decades have hurled at us must be digested, correlated, and synthesized," I feel that the outlook and the technique in the more mature taxonomic groups might well be characterized by the term "new systematics."[1] Naturally, there is no sharp line of demarcation between the two, for no taxonomic work is all old or all new systematics. The two are always mixed in varying proportions.

If we had to characterize the differences between old and the new systematics, we might do it as follows:

The old systematics is characterized by the central position of the species. No work, or very little, is done on infraspecific categories (subspecies). A purely morphological species definition is employed. Many species are known only from single or at best a very few specimens; the individual is therefore the basic taxonomic unit. There is great interest in purely technical questions of nomenclature and "types." The major problems are those of a cataloguer or bibliographer, rather than those of a biologist.

[1] The terms systematics and taxonomy are considered by me as approximately synonymous. In America the term taxonomy seems to be preferred, in the rest of the world the term systematics seems to be more widely used. The expression "new systematics" had been used by Hubbs (1934) already 6 years earlier.

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