

**THE LIFE OF
VERTEBRATES**

SECOND EDITION

I. Z. YOUNG

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THE LIFE OF VERTEBRATES

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SECOND EDITION

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PREFACE TO THE SECOND EDITION

FOR this edition every part of the book has been revised and corrected, but the basic plan and balance of interests have not been altered. Changes of arrangement and emphasis might have suited some types of reader but I have thought it better that the book should continue to show the idiosyncracies and interests of the author. One of the dangers of a textbook is, surely, that unsophisticated readers may suppose that they are getting the authentic and complete treatment of the subject. Some obvious imbalances may, therefore, even be an advantage as reminders of the relativity of all statements.

Nevertheless, I have attempted to make the treatment rather more complete and systematic than before. For example, the descriptions of the parts of the body are now arranged more nearly similarly for all groups. With the help of many friends mistakes have been removed and accounts of recent work added. The anatomy of Mammals is not dealt with in the same detail as that of other groups, being covered separately in *The Life of Mammals* (Clarendon Press, 1957), where also there is a fuller account of the comparative embryology of vertebrates.

During the revision I have become even more conscious of the defects of the work, both in general form and detailed treatment. It is still not possible to see more than the vaguest outlines of a proper science of comparative biology. We are faced with a great series of wonderful systems, differing slightly from each other and maintaining themselves in slightly different surroundings. But we have no proper scientific words with which to talk about them. For example, it is absurd that this book contains so little reference to genetics, biochemistry, or control theory. No doubt this is partly my fault, but the fact is that these more exact sciences have yet to show us how to treat the organization of a whole creature.

Fortunately, the animals remain as fascinating as ever, indeed the search for exact ways of describing makes them even more so. Those of us who have revised the book will be well rewarded for our trouble if others are helped to look and think for themselves. If they do they will find a really astonishing array of experiments made by natural selection with every part of the vertebrate organization. To take one example, we are offered the opportunity to learn how the endocrine

control system works by examining hundreds of different variants of it. The more one thinks of it the more surprising it is that biology has made so little use of the experiments that have been done for us by nature. Surely soon someone will come along with sufficient knowledge and logical and mathematical ingenuity to show us how to study vertebrate organization.

Besides those mentioned below who have assisted in the revision of particular sections, I should like to thank the many people, including teachers and students, who have written about particular points, and especially Professor J. Lever of Amsterdam for his many detailed comments. My grateful thanks are also due to Mrs. J. Astafiev, who has redrawn many of the figures, Mr. C. Marmoy for assistance with the Bibliography, Mr. P. N. Dilly, who has helped throughout, also my secretaries and especially Miss S. Thistleton and Miss J. Everard, for continuous help with the manuscript. It is also a pleasure to thank the members of the Clarendon Press and in particular Miss M. Gregory for the help with the revision.

J. Z. Y.

February 1962

PREFACE TO THE FIRST EDITION

THE history of textbooks is often dismissed by the contemptuous assertion that they all copy each other—and especially each other's mistakes. Inspection of this book will quickly confirm that this is true, but there is nevertheless an interest to be obtained from such a study, because textbooks embody an attitude of mind; they show what sort of knowledge the writer thinks can be conveyed about the subject-matter. It may be that they are more important than at first appears in furthering or preventing the change of ideas on any theme.

The results of the studies of scholars on the subject of vertebrates have been summarized in a series of comprehensive textbooks during the past hundred years. Most of these works are planned on the lines laid down by the books of Gegenbaur (1859), Owen (1866), and Wiedersheim (1883), lines that derive from a pre-evolutionary tradition. This partly explains the curiosity that in spite of the great importance of evolutionary doctrine for vertebrate studies, and vice versa, vertebrate textbooks often do not deal directly with evolution. They derive their order from something even more fundamental than the evolutionary principle. The essential of any good textbook is that it should be both accurate and general. As Owen puts it in his Preface: 'In the choice of facts I have been guided by their authenticity and their applicability to general principles.' The chief of the principles he adopted was 'to guide or help in the power of apprehending the unity which underlies the diversity of animal structures, to show in these structures the evidence of a predetermining Will, producing them in reference to a final purpose, and to indicate the direction and degrees in which organisation, in subserving such Will, rises from the general to the particular'. He confessed 'ignorance of the mode of operation of the natural law of their succession on the earth. But that it is an "orderly succession"—and also "progressive"—is evident from actual knowledge of extinct species.'

These principles were essentially sound, and Owen's treatment was to a large extent the basis of the work that appeared after the Darwinian revolution. In English, following the translation of Wiedersheim's book by W. N. Parker (1886) we have H. J. Parker and Haswell's work, now in its 6th edition. The books of Kingsley and Neal and Rand are in essentially the same tradition, though they

incorporate much new work, especially from the neurological studies of Johnston and Herrick. Further exact studies on these same general morphological lines made possible the books of Goodrich (1930) and de Beer (1935), which have provided the morphological background for the present work. Throughout these works on Comparative Anatomy the emphasis is on the evolution of the form of each organ system rather than on the change of the organization of the life of the animal as a whole.

Meanwhile many other treatises appeared dealing with the life and habits of the animals, rather than with morphological principles. Among these we may mention Bronn's *Tierreich* (1859 onwards), the *Cambridge Natural History*, and many works dealing with particular groups of vertebrates. The palaeontologists produced their own series of textbooks, mainly descriptive, such as those of Zittel and Smith Woodward, culminating in Romer's admirably detailed and concise book, to which the present work owes very much. The results of embryological work have been summarized by Graham Kerr (1919), Korscheldt and Heider (1931), Brachet (1935), Huxley and de Beer (1934), and Weiss (1939), among others. Unfortunately there has been little summarizing of what is commonly called the comparative physiology of vertebrates. Winterstein's great *Handbuch der vergleichenden Physiologie* (1912) covers much detailed evidence, but comes no nearer than do the comparative anatomists to giving us a picture of the evolution of the life of the whole organism.

All of these books deal in some way with the evolution of vertebrates, and yet curiously enough they speak of it very little. It is hardly an exaggeration to say that they leave the student to decide for himself what has been demonstrated by their studies. Huxley's *Anatomy of Vertebrated Animals* (1871) is an exception in that it deals with the animals rather than their parts, and at a more popular level. Brehm's *Thierleben* (1876) gives a picture of the life of the animals, though in this case not of their underlying organization. Kükenthal's great *Handbuch der Zoologie* has the aim of synthesizing a variety of knowledge about each animal-group, and some of the volumes dealing with vertebrates make fascinating reading—notably that of Streseman on birds. But the size of the work and the multiplicity of authors make it impossible for any general picture of vertebrate life to appear from the mass of details.

The position is, then, that we have good descriptions of the structure, physiology, and development of vertebrates, of the discoveries of the palaeontologists and accounts of vertebrate natural history, but

that there is no work that attempts to define the organization of the whole life and its evolution in all its aspects. Indeed, none of these works defines what is being studied or tries to alter the direction of investigation—all authors seem prepared to agree that biological study is adequately expressed through the familiar disciplines of anatomy, physiology, palaeontology, embryology, or natural history. In passing, we may note the extraordinary fact that there are no detailed works on the comparative histology or biochemistry of vertebrates—surely most fascinating fields for the future, as is, indeed, hinted by the attempts that have been made in older works, such as that of Ranvier (1878), and the newer ones of Baldwin (1937 and 1945).

The present book has gradually grown into an attempt to define what is meant by the life of vertebrates and by the evolution of that life. Put in a more old-fashioned way, this represents an attempt to give a combined account of the embryology, anatomy, physiology, biochemistry, palaeontology, and ecology of all vertebrates. One of the results of the work has been to convince me more than ever that these divisions are not acceptable. All of their separate studies are concerned with the central fact of biology, that life goes on, and I have tried to combine their results into a single work on the way in which this continuity is maintained.

A glance through the book will show that I have not been successful in producing anything very novel—others will certainly be able to go much farther, and in particular to introduce to a greater extent facts about the evolution of the chemical and energy interchanges of vertebrates, here almost omitted! However, I have very much enjoyed the attempt, which has provided the stimulus to try to find out many things that I have always wanted to know.

For any one person to cover such a wide field is bound to lead to inexactness and error in many places. I have tried to verify from nature as often as possible, but a large amount has been copied, no doubt often wrongly. Throughout, the aim has been to provide wherever possible an idea of the actual observations that have been made, as well as the interpretations placed upon them. A proper appraisal of general theories can only be reached if there is first a knowledge of the actual materials, which is the characteristic feature of scientific observation. A book such as the present has value only in so far as it leads the reader to make his own observations and helps him to know the world for himself.

Mammalian organization requires more detailed treatment than that of other groups, and in providing this the work grew to beyond

the length of a single book. Mammalian structure, function, and development will therefore be dealt with in a separate volume, which will also include a survey of comparative embryology.

The original plan was that the palaeontological parts of the book would be written by J. A. Moy-Thomas. Had he lived this aspect of the work would have been very much better, and his common sense and laughter would have lightened the whole. I have tried to give some compensation at least by the speculation that is possible from a single point of view. To protect the reader against the limitations of my ignorance I have consulted specialists on every part of the work, and my deepest thanks are due to those who have helped in this way. They have done wonders in correcting mistakes, but, of course, are not responsible for any that remain, or for views expressed. Among those who have helped in this way with particular parts are Professor G. R. de Beer, Mr. R. B. Freeman, the late Professor W. Garstang, Dr. A. Graham, Professor J. B. S. Haldane, Professor W. Hollingworth, Dr. W. Holmes, Dr. J. S. Huxley, Dr. D. Lack, Mr. Maynard Smith, Dr. F. S. Russell, Dr. Tyndell Hopwood, Mr. H. G. Ververs, Professor D. M. S. Watson, and Professor S. Westoll. They have been patient and severe critics, and the reader and I owe them very much.

One of the main problems of such a work is its illustration, and here I have been extraordinarily fortunate in having the help of Miss E. R. Turlington, who has not only provided brilliantly clear and beautiful pictures, but has taken extremes of care to ensure their accuracy by drawing from live animals, from dissections, and from skeletons, as well as by research into the illustrations of others. Miss J. de Vere has also given much help with drawing. We have borrowed good pictures unhesitatingly and should like to thank those who have given permission for their reproduction.

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J. Z. Y.

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I

EVOLUTION OF LIFE IN RELATION TO CLIMATIC AND GEOLOGICAL CHANGE

1. The need for generality in zoology

THE aim of any zoological study is to know about the life of the animals concerned. Our object in this book is, therefore, to help the reader to learn as much as possible about all the vertebrate animal life that has ever been. Thinking of the great numbers of types that have existed since the first fishes swam in the Palaeozoic seas, one might well be appalled by such a task: to describe all these populations in detail would indeed demand a huge treatise. However, in a well-developed science it should be possible to reduce the varied subject-matter to order, to show that all differences can be understood to have arisen by the influence of specified factors operating to modify an original scheme. Animal and plant life is so varied that it has not yet proved possible to systematize our knowledge of it as thoroughly as we should wish. Thinking, again, of the variety of vertebrate lives, it may seem impossible to imagine any general scheme and simple set of factors that would include so many special circumstances. Yet nothing less should be the aim of a true science of zoology. Too often in the past we have been content to accumulate unrelated facts. It is splendid to be aware of many details, but only by the synthesis of these can we obtain either adequate means for handling so many data or knowledge of the natures we are studying. In order to know life—what it is, what it has been, and what it will be—we must look beyond the details of individual lives and try to find rules governing all. Perhaps we may find the task less difficult than expected. Even an elementary anatomical and physiological study shows that all vertebrates are built upon a common plan and have certain similarities of behaviour. Our object will be to come to know the nature of this plan of life, of structure, and action, to show how it is modified in special cases and how each special case is also an example of a general type of modification.

Since the problem arises from the variety of animals that have lived and live today, our central task is obviously to inquire into the reason for the existence of so much difference. If vertebrate life began as one single fish-like type, why has it not continued as such until now? Why, instead of numerous identical fishes, are there countless

different kinds, while descendants of most unfish-like form are found living out of the water and even in the air and under the ground?

To put it in a way more familiar, though perhaps less clear: what are the forces that have produced the changes of animal form? Knowing these forces, and the original type, it would be possible to construct a truly general science of zoology, with sure premisses and deductions. Even if we cannot reach this end, we should at least try, hoping that after investigation of the biology of vertebrates it will be possible to retain something more than a mass of detailed information. At the end of such a study, if we deal with the subject right, we should surely be better able to answer some of the fundamental biological questions. We should be able to say something about the nature of evolution and of the differences between types, to know whether there have been rhythms of change at work to produce these differences, and also—the acid test of any true science—to forecast how these changes are likely to proceed in the future.

2. What do we mean by the life of an animal?

In biology we make much use of analogies, attempting to grasp the nature of the processes at work by comparison with man-made machines. We have a science of anatomy, which we are told is concerned with the 'structure' of animals, and we feel that we understand what 'structure' means. Physiology is the study of 'function', and this, too, we seem to understand. We take the analogies from our machines, which have what we call 'structure' and 'function'. However, the difficulty at once arises that the living things make and control themselves. The whole scheme fails us when we ask what is it, then, that we call the 'life' of the animal, and what is it that is passed on from generation to generation, and that changes through the ages by the process we call evolution? It has gradually become apparent that the body is not a fixed, definite 'structure' as it appears to casual observation or when dissected. In life there is ceaseless activity and change going on within the apparently constant framework of the body. The movement of the blood is one sign of this activity, and since Harvey's discovery of the circulation (1628) we have learnt of innumerable others. Everyone knows that the skin is continually being renewed by growth from below, and many other types of cell are similarly replaced; for instance, red blood-cells last only for a few weeks in man. Even in the cells that are not completely destroyed and replaced, such as the nerve-cells, there is continual change of the molecules that make up their substance. The full extent of this exchange has been