# THE LIFE OF VERTEBRATES

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OXFORD
AT THE CLARENDON PRESS

*Oxford University Press, Amen House, London E.C.4*

GLASGOW NEW YORK TORONTO MELBOURNE WELLINGTON
BOMBAY CALCUTTA MADRAS KARACHI KUALA LUMPUR
CAPE TOWN IBADAN NAIROBI ACCRA

FIRST PUBLISHED 1950
REPRINTED LITHOGRAPHICALLY IN GREAT BRITAIN
AT THE UNIVERSITY PRESS, OXFORD
FROM CORRECTED SHEETS OF THE FIRST EDITION
1952, 1955, 1958

# PREFACE

THE history of text-books 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 text-books 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 text-books 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 text-books 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 text-book is that it should be both accurate and general. As Owen put 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 text-books, 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. Kukenthal'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 makes 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. Vevers, 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.

I should also like to thank particularly my secretary, Miss P. Codlin, who has played a large part in making the book possible, and my daughter Cordelia for help with the index.

Finally, I have to thank the Secretary and members of Oxford University Press for the care with which the book has been produced, and for their friendly co-operation, which has made the work a pleasure.

J. Z. Y.

1950

# ACKNOWLEDGEMENTS

THANKS for permission for reproductions of illustrations are due to:

G. C. Aymar, E. J. W. Barrington, J. Berrill, T. H. Bullock, A. J. E. Cave, W. E. Le Gros Clark, E. Crosby, F. G. Evans, Helen Goodrich, A. Gorbman, J. Gray, W. K. Gregory, W. J. Hamilton, J. E. Harris, L. Hogben, A. Holmes, E. Hoskings, W. W. Howells, J. H. Huxley, F. Knowles, D. Lack, N. A. Mackintosh, G. H. Parker, A. T. Phillipson, R. J. Pumphrey, E. C. R. Reeve, A. R. Romer, E. S. Russell, F. K. Sanders, A. H. Schultz, G. G. Simpson, N. Tinbergen, G. L. Walls, L. Waring, S. Westoll, E. I. White, F. F. Zeuner, Lieut.-Col. W. P. C. Tenison.

and to the following publishers and other bodies:

The American Museum of Natural History; Balliere, Tindall and Cox; E. Benn, Ltd.; *Biological Reviews*; the *British Medical Journal*; the British Museum; the Cambridge University Press; the Company of Biologists, Ltd.; Dodd, Mead & Co.; Editors of the *Ibis*; Longmans, Green & Co., Ltd.; the Physiological Society; Putnam, Ltd.; the *Scientific Monthly*; the Wilson *Bulletin*; the Wistar Institute; Zoological Society of London.

# NOTE

THE arrangement of this book is systematic, proceeding from the earliest chordates to the mammals. In every group the organization is described in the same way, beginning with the external features and proceeding then to the skeleton, muscles, and locomotion, followed by feeding and digestion, circulation, respiration, excretion, reproduction, the nervous and sensory organization and behaviour. Each system is dealt with in special detail where it is first met with. The index has been arranged so as to make it possible to survey any organ-system, or subject—say, the skull or osmoregulation, throughout the vertebrates.

# CONTENTS

# 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 take into mind 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 particular facts. It is splendid to be aware of many details, but only by the synthesis of these can we obtain either an adequate means of 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 which have lived and live to-day, 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 fishes all alike in the seas, are there countless different kinds even in one mass of water, 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 the rhythms of change that have been at work to produce these differences, and also—the acid test of any true science—to forecast how these rhythms are likely to operate in the future.

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

Much obscurity comes in biology from inconsidered use of analogies in attempting to grasp the nature of life. 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. In both cases we take the implied analogies from our man-made machines; they have what we call 'structure' and they 'function'. But further examination of living things has made these visions of biological science much less clear than they have seemed in past centuries. 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 we have learnt of innumerable others. Everyone knows that the skin is continually being renewed by growth from below, and very 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 very rapid change of the molecules that make up their substance. The full extent of this exchange has been shown by using isotopes to discover for how long individual atoms remain in the body; the work of Schoenheimer (1942), which by this means first clearly established the rapidity of the turnover, is a classic of modern biology.

If the matter of the body is continually changing we cannot expect to be able to describe the characteristics of life in terms of the properties of particular substances. Life is characterized by activities or processes and by the particular molecules that are engaged. Different types of life involve different processes, and each sort of life therefore produces certain types of molecules and certain visible structures. Specification of these chemical and visible units that we can abstract from the living organism is at present our only means of studying the system as a whole. We have to take our science as we find it, and as yet we have no means of grasping the enormously complicated network of activities that constitutes a single life. Throughout this book, however, an attempt will be made to approach that end by use of certain clues to help us to concentrate on significant features, to see the rhythms or patterns common to the lives of the animals, and thus to carry in mind many details. It is possible in this way to bring together information collected by morphologists, geneticists, embryologists, physiologists, biophysicists, and biochemists to give a single view of the life of the organisms concerned. The task is admittedly a hard one and the success achieved only partial. Continually one slips into the discussion and imagination of particular structures, substances, or processes, forgetting the whole life. A detail of form or of chemical composition attracts, and thus distracts, attention; perhaps it can hardly be otherwise if we are to describe exactly. But it is surprising how practice improves the powers of selecting and emphasizing those patterns or details of knowledge that are significant for the study of each life as a whole.

The first difficulty is to force oneself to remember all the time that a living animal or plant system is in a continual state of change. When making any observations, whether by dissection or with the microscope, with a test-tube, oscillograph, or respirometer, it is necessary continually to think back to the time when the tissue was active in the living body, and to frame the observation so that it shall reveal something significant of that activity. *This means that every biologist must know as much as possible of the life of the whole organism with which he*