THE LIFE OF VERTEBRATES

J. Z. YOUNG

THIRD EDITION

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Preface to the Third Edition

In the last twenty years there has been an immense addition of knowledge on nearly all aspects of vertebrate life, especially of physiology and ecology. In this new edition we have introduced much new detail, especially about the nervous and endocrine systems and behaviour. It has been found possible to incorporate many new facts within the original framework of the book and this has confirmed my belief that the best way to study animals is to look at all aspects of their lives. To understand the special features of the carpus or the cortex of an animal you need to know how it lives.

Fortunately there have not been great changes in knowledge of gross anatomy and we have kept the descriptions of skeletons and dissections of a few types, and the beautiful drawings made by the late Miss E.R. Turlington. The facts set out in these sections of the book are hard to obtain elsewhere. We have also retained the systematic classifications; even though controversial they provide a framework for which many workers may be grateful. We have not always followed recent cladistic revisions since we believe that classifications that emphasize grades of organization are useful, at least for the beginner.

The whole book is organized around the theme that mechanisms of homeostasis have become increasingly more complex during vertebrate evolution, allowing life to continue under conditions not possible before. Discussion of this involves questions of value about the aims of life and the meanings of 'higher' and 'lower'. Such topics are often avoided by scientists but no honest treatment of living organisms can avoid them. I believe that emphasis on the pervasive tendency to self-maintenance (homeostasis), and its progressive evolution, allows us to organize our study of the life of vertebrates and also provides a much-needed guiding light in considering the life of man.

A synoptic view of the lives of animals can perhaps be given only in a work produced by a single author, but this necessarily involves the limitations imposed by his ignorance, of which I have been acutely conscious. I must apologize to those scientists who find their work misquoted (or omitted altogether) and also to any students who are consequently misled. We have added many more bibliographical references so that readers can consult original sources.

In mitigating the dangers of inaccuracy I have been fortunate to have the advice of those listed on page vi on their special topics. Several of them found it hard to accept my point of view, but they have all helped to remove many errors; I alone am responsible for those that remain. It may be some consolation that a single author can provide his own point of view on controversial topics.

Above all I am grateful to Dr M. Nixon. Without her help this revision would not have been possible. She has sought out the most recent papers on an immense variety of topics and has undertaken all the laborious work of editing and correcting. We are both of us grateful to Miss P.R. Stephens for help in many ways, and also to R.M. Young who acts as our secretary.

As usual we have to thank all those at the Oxford University Press who have given us so much kindly help.

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From the 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.

J.Z.Y.

1950

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1 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 existed. Thinking of the great numbers of types that have lived 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 is evolution?

The superficial answer to the question 'Why are there so many different vertebrates?' is that they have been generated by a process of Evolution. Unfortunately this much-used word is ambiguous and even the best biologists seem unwilling to define it. Darwin did not use it in the first edition of the *Origin*. Indeed it was used to refer to ontogeny (literally 'unfolding') until nearly the end of the nineteenth century.

A simple definition sometimes used is that 'Evolution is a change in the genetic make-up of populations'. But every population changes its genes from minute to minute as individuals are born and die. Is all this to be called 'evolution'? We more commonly use the word to talk about sequences of adult forms, that is of phenotypes, especially about the series of animals and plants revealed by palaeontology. What is the connection between these long-term alterations and changes of the genotype that are going on all the time?

Living things are improbable steady-state systems. They exist in environments that change from minute to minute, day to day and over the years and centuries. What enables them to continue on this unlikely course? Briefly, it is the information they inherit which allows them to take actions to prevent death. They can do this on various scales. Each individual is an *agent* selecting from minute to minute what is best to do in the changing circumstances. He can choose 'wisely' because his DNA (deoxyribonucleic acid) provides him with receptors tuned to respond to changes that are likely to occur. With this information he sets in action the enzymes, muscles, glands, and many other organs that are provided by the DNA. How this system came into being is the question of the Origin of Life, which we cannot discuss here (see *Introduction to the Study of Man*). Its result is that every form of life, bacterium, plant, or animal, can continue to meet the demands of its varying environment if it shows adequate variety of actions and sufficient capacity to collect the information needed to act correctly. Each individual is able to do this by virtue of its particular range of sensory and motor capacities.

In this way survival is possible under a limited range of change of circumstances. But the information in the DNA also provides for *reproduction*, producing continually a series of slightly different individuals. This allows for life to continue much longer, by producing new types capable of meeting the situations that result from variations that occur in the climate or other factors (p. 23). This continual change of living organization is the process that we call evolution.

The basic 'cause' of evolution is therefore the tendency of all living things to strive to survive. They succeed in spite of varying conditions because every part inherits information that allows it to *adapt* to the circumstances it is likely to find. A bacterium can switch on production of a new enzyme, a muscle grows stronger with use and a brain learns a new response. The DNA provides every individual with many such ways of 'learning' during its lifetime. But information acquired in this way during life is not passed on to the next generation. The major changes in evolution depend upon differential survival of those genotypes that provide the best information.

The pressure to acquire better sources of information and ways to adapt is thus itself a factor making for change. We shall find evidence that animal types rarely remain stable, there has been a continuous series of extinctions and replacements throughout vertebrate history. These are partly due to the repeated alterations of climate and other conditions (p. 25). But at each stage there are signs that the new types had capacities that made them more efficient than the old. New means of coping with the environment appear, involving greater complexity of organization. In particular vertebrates have developed increasing powers of *adapting* their tissues especially through their senses and nervous systems. This increase of information as to how to survive is the main sense in which there has been progress during evolution (p. 584).

3. Questions about evolution

Nearly all biologists believe that evolution has been the result of some form of natural selection of hereditary variations as postulated by neo-Darwinism (Mayr 1976; Dobzhansky, Ayala, Stebbins, and Valentine 1977). But palaeontologists, who follow both the large and small changes of organisms, have long felt that some questions remain to be answered. Recently molecular biologists, geneticists, and ethologists have raised further problems. Everybody agrees that evolution has occurred, that living forms have changed, but there are still many questions about the agencies that have produced the change (Gould 1977; Stanley 1980). Study of the life of vertebrates should help to answer these questions. We may list them as follows:

(1) We readily understand that evolution involves alteration of the genetic make-up of populations. But is *any* change 'evolution'?
(2) Is all evolutionary change adaptive, or may some of it be due to random chance?
(3) Can small microevolutionary changes explain macroevolution, large alterations of the whole plan of organisms, as when fishes became amphibians or reptiles became birds?
(4) At the opposite extreme can selection explain the numerous small differences that molecular biologists have found between proteins and other macromolecules?
(5) Do the changes follow any clearly defined sequence or direction? Can we detect progress in evolution? What is meant by referring to 'higher' and 'lower' organisms?
(6) As Gould asks, 'What is the tempo of organic change? Does it proceed gradually in a continuous and stately fashion, or is it episodic?'

We shall hope to find answers to some of these and other 'eternal questions' as we study each group of vertebrates in turn and try to understand the processes that have been at work, modifying the basic vertebrate organization.

4. Is variation between demes the basis of evolution?

Every species contains a number of distinct groups of inter-breeding individuals or demes, more or less isolated from each other by mere distance or physical barriers. Thus the western rattlesnake *Crotalus viridis* shows nine 'geographic races' (Savage 1977) (Fig. 1.1). They differ in body stripe, scales, and colour and where races meet there are intergradations. Endless examples of this sort could be given and often it is possible to identify the character of each deme as due to adaptation to local conditions. Sometimes a character changes gradually with distance and this is known as a 'cline'.

If a group formed by selection or in any other way remains isolated for a sufficient length of time its genetic make-up is likely to become incompatible with that of other demes; they become mutually infertile and a new species is formed. This may happen quite rapidly. Lake Nabugabob in Africa has been separated from Lake Victoria for less than five thousand years but contains five endemic species of the cichlid fish *Haplochromis*, each derived from a different parent species in the main lake (Greenwood 1965). This rapid speciation may have occurred because the numbers are small. Conversely many species are the same on both sides of the Isthmus of Panama although the Caribbean and Pacific Oceans have been separated for 5–6 million years. This is especially true of the pelagic species, with numerous individuals. Many of the intertidal and shallow water animals have formed geminate (twin) species, slightly different on the two sides of the isthmus. Evidently isolation and small numbers are among the conditions that promote change. Clearly they are not the only factors determining the *direction* of change, if indeed can it be said to have a direction at all?

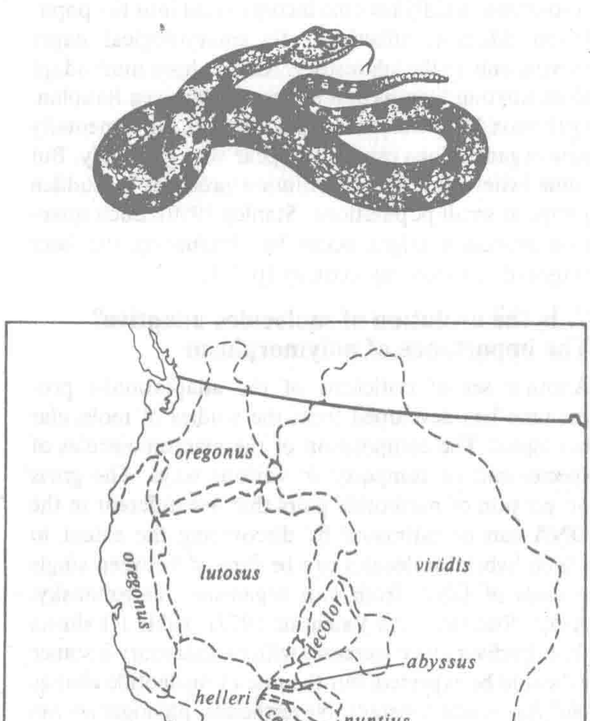

FIG. 1.1 Geographic variation in the Western rattlesnake (*Crotalus viridis*). (After Savage 1977.) (Narrow regions within broken lines indicate areas of intergradation of races.)

5. Genetic drift

The orthodox neo-Darwinian adaptationist position is that natural selection decides which phenotypes and hence which genotypes shall survive. The varieties of organic form according to this view have been produced by the changing demands of the physical and biological environment upon each deme. This is still the basic assumption of the great majority of biologists, even including some who wish nevertheless to emphasize that other factors are also at work in determining organic organization (Gould and Lewontin 1979). These alternative agencies undoubtedly play a part, some in accelerating, others in retarding evolutionary change. The most thoroughly established of them is *genetic drift*. Isolated populations are often small and the first step to speciation may occur in them by pure chance without the action of any selective force at all (Wright 1931, 1968–1978; see Gould and Eldredge 1979). A deme founded by a small number of colonists may continue to maintain the characteristics of the founders and such random differences may persist if the group remains isolated and if there is no strong selection against any of them. Computer modelling has shown that distinctions between groups at least as great as those found in nature can occur purely by a Markov chain of random stochastic changes, that is a sequence where each event is partly dependent on the outcome of previous ones. Figure 1.2 shows how a sort of model trilobite, a 'triloboid', changed by random steps on a computer in five traits, two of its 'head', one of the 'thorax', and two of the 'tail'. If fossils like these were found it would be concluded that taxa A and B had been selected for large size, while absence of tail had evolved separately in C and D and so on. Such simulations do not show that evolution *has* been random, but they warn that the hypothesis of randomness needs to be carefully excluded by appropriate tests of its probability. Palaeontological series can sometimes be tested in this way, but it is not easy (Feller 1968).