Vertebrate Life

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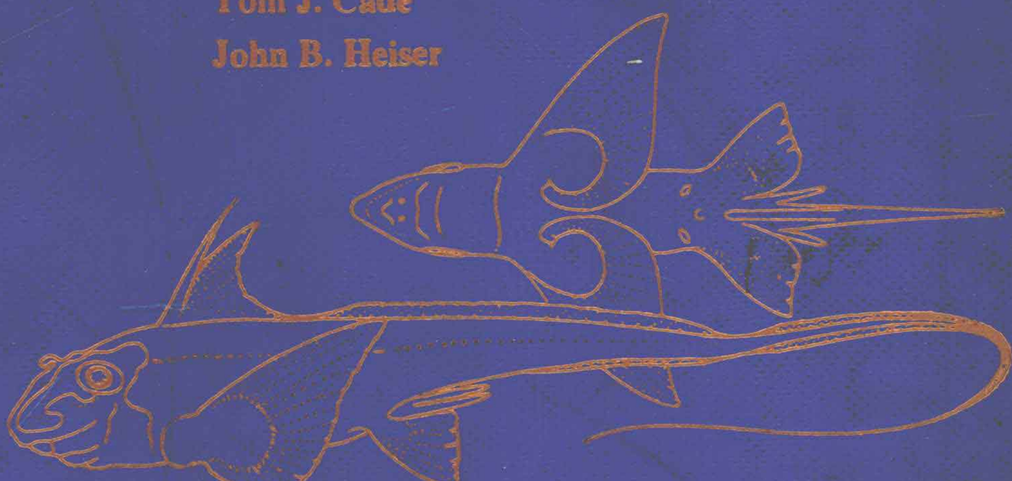

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Preface

A considerable time ago, perhaps longer than it should have been, several students in our course "The Vertebrates" suggested that we write this book. The course, which continues today, is structured around two themes—the evolution and the ecology of vertebrates. In spite of the several excellent textbooks of vertebrate morphology and evolution that are available, we could not find a text that underscored our view that a broad-based approach integrating traditionally separate specializations such as physiology and behavior or ecology and morphology is necessary to understand how animals function in their environment. This text, therefore, is an attempt to fill that gap. It is intended to provide students with a broad and detailed view of vertebrate biology. By better understanding the similarities of all vertebrates, one can also develop an appreciation of why vertebrates are so diverse. Our hope is that students who use this book will gain a keener perspective of themselves and, by doing so, develop a lasting reverence for living things—a commitment that is essential if vertebrate life, including human life, is to be sustained in our world.

The book's themes—evolution and ecology—are presented in phylogenetic order from fishes to mammals. In addition, other functional aspects of vertebrates are spread through several chapters. As a consequence, it is not possible to read in one chapter all we have said about kidney function and osmoregulation, or about social behavior and reproduction, or about body form and locomotion. Instead, aspects of these subjects are introduced in the context of the vertebrate taxa that best illustrate them. Major subjects such as these have been indexed for easier reference.

In addition to the phylogenetic sequence of chapters, five chapters are devoted to discussion of the geology and paleoecology of the time periods when major vertebrate groups arose. Because familiarity with the geological time record is so central to understanding the evolution of vertebrates, a time scale listing the various periods and eras is presented inside the front cover. A short Latin-Greek glossary is provided inside the back cover to assist students in deciphering the many compound words encountered in biology. Familiarity with only a few dozen Latin and Greek roots vastly simplifies the task of remembering and distinguishing the seemingly bewildering array of technical terms and animal names. In addition to the Latin-Greek glossary, a glossary of specialized English terms is included.

Many colleagues have provided suggestions, critical comments, and additional material in various stages of the development of the book. Dr. Frederick Test read the introductory chapters and the final chapter as well as the chapters on birds. Dr. Edwin Colbert reviewed the chapters covering geological events and paleoclimates, and Dr. Keith Thompson read these chapters as well as those concerned with fishes. Drs. George Bartholomew, Robert Carroll, Carl Gans, Rodolfo Ruibal, and Margaret Stewart reviewed the chapters on amphibians and reptiles. Dr. Dean Amadon read the chapters on birds, and Dr. Brian McNab those on mammals. Dr. John Repetski kindly provided the scanning electron micrographs of *Anatolepis* used in Figure 5–1. Our gratitude to Mary Beth Hedlund Marks is profound. She was involved in the book from its inception and typed large portions of the manuscript. More importantly she detected errors and inconsistencies and managed to bring a semblance of order to the diverse styles of the four authors.

Several students and former students, particularly Dr. Kentwood Wells, Willy Bemis, and Elaine Burke, read portions of the manuscript. Especially helpful was a review of the entire manuscript by Fredrica van Berkum, then a senior at Cornell. Rickie's perspective was valuable because she detected ambiguities that would bother a student but escape the notice of a professional biologist. Dr. Alan Savitzky reviewed the glossary. Margaret Pough read much of the text, and Amanda Pough was a great help in compiling the index.

—William N. McFarland, F. Harvey Pough, Tom J. Cade , John B. Heiser

SOURCES AND ADDITIONAL READING

Assisting students to become acquainted with the literature of a field is an important function of an introductory textbook. To this end, we have cited a great variety of primary and secondary materials. The following books are important general references and any student of vertebrate biology should become familiar with them. We have cited these books in the text by author and date only—e.g. Romer 1966.

Colbert, E. H. 1969. *Evolution of the Vertebrates*, 2nd ed. John Wiley & Sons, New York.

Hildebrand, M. 1974. *Analysis of Vertebrate Structure.* John Wiley & Sons, New York.
Kluge, A. G. et al. 1977. *Chordate Structure and Function*, 2nd ed. Macmillan Publishing Co., Inc., New York.
Romer, A. S. 1966. *Vertebrate Paleontology*, 3rd ed. University of Chicago Press, Chicago.
Romer, A. S. 1968. *Notes and Comments on Vertebrate Paleontology.* University of Chicago Press, Chicago.
Romer, A. S. and T. S. Parsons. 1977. *The Vertebrate Body.* W. B. Saunders Co., Philadelphia.
Stahl, B. J. 1974. *Vertebrate History: Problems in Evolution.* McGraw-Hill, New York.
Young, J. Z. 1962. *The Life of Vertebrates*, 2nd ed. Oxford University Press, New York.

Several hundred additional references are provided at the ends of the chapters and in figure captions. To avoid repetition we have used the following system of coding for citations:

1. For references that appear only figure captions, the full citation is given in the caption.
2. Citations in figure captions that appear in the list of references at the end of the same chapter are indicated by a number—e.g. Noble [4].
3. Citations that appear in the list of references in a different chapter are indicated by the chapter number and reference number—e.g. Olson Ch. 5[7].

Contents

1

The Basic Plan of Vertebrate Organization

Synopsis: The history of vertebrates covers a span of 500 million years or more. We think of the human as the most highly evolved vertebrate—specialized in many structures, hands, feet, vertebral column, cerebrum—but the structure and organization of the human body have been determined by a long and complex course of evolution. When we strip away all the special features of humans and compare the result with other vertebrates we can identify a "basic body plan," presumably the ancestral plan, which consists of a bilateral, tubular organization, possessing such characteristic features as notochord, pharyngeal slits, dorsal hollow nerve cord, vertebrae, and cranium, as well as other essential systems. One of the protochordates, amphioxus, and the ammocoete larva of lampreys offer suggestions of what the earliest vertebrates were like.

1.1 INTRODUCTION: OVERVIEW OF VERTEBRATE BIOLOGY AS A SUBJECT

The scientific study of vertebrates is a vast subject with a rich literature going back to the classical writings of Aristotle in the fourth century B.C. Among many other original contributions to our knowledge of vertebrates, Aristotle reported that whales are mammals and not fish, and he accurately described the peculiar reproductive system of the placental dogfish. Our subject also covers 500 million years or more of evolutionary history, as the earliest vertebrate fossils occur in the Cambrian Period. Biologists have described and studied tens of thousands of different vertebrate species, both living and fossil forms, each with a morphology and life of its own. Little wonder, then, that students making their first serious approach to vertebrate biology may hesitate, unsure how or where to begin.

A scholar can broach the subject in various ways, depending on a particular interest, but we have chosen to begin with some facts and concepts that are likely to be familiar to most biology students. From this general and familiar starting point, we can move into more specific, less well-known aspects of vertebrate life.

1.1.1 Some Familiar Facts About Vertebrates

Most students know that vertebrates belong to the Subphylum Vertebrata and that their name derives from the serially arranged vertebrae, which comprise a major portion of an axial endoskeleton that vertebrates share as a common diagnostic character (Figure 1-1). Anteriorly skeletal elements have been elaborated into a cranium or skull, which houses various sense organs and a complex brain. Another name sometimes used for the group is Craniata, because the cranium is also characteristic as, for that matter, is the tripartite brain inside. In fact, there is reason to believe that the distinctive vertebrate cranium and brain evolved before the vertebral column and are, therefore, more fundamentally characteristic of vertebrates than the backbone.

Most students no doubt also know that the vertebrates share some fundamental morphological features with certain marine invertebrates, and that by virtue of these common structures they are classified in the Phylum Chordata. These common chordate structures are the notochord, dorsal hollow nerve cord, and pharyngeal slits. Only the nerve cord remains as a definitive and functional entity in the adult stage of many vertebrates, but all three chordate features are clearly evident at some stage in the development of all vertebrates.

We now have the minimum information needed to define a **vertebrate.** A vertebrate is a special kind of chordate animal that has a cartilaginous or bony endoskeleton. The axial components of this endoskeleton consist of a cranium housing a brain, which is divided into three basic parts, and a vertebral column through which the nerve cord passes. No other group of animals possesses this constellation of fundamental and related characters which have existed in vertebrates since the late Cambrian and Ordovician.

1.1.2 The Diversity of Vertebrates

What about the different kinds of vertebrates? Everyone knows that humans are vertebrates, that dogs and cats and cows and chickens are all vertebrates, but few people realize that there are some 40,000 living species that share this distinction, not to mention the many extinct fossil forms. Most biology students know that there are different major groups of vertebrates—jawless fishes, cartilaginous fishes, bony fishes, amphibians, reptiles, birds, and mammals—each possessing certain distinctive features that set it apart from the others. In our system of zoological classification, these groups correspond to the Classes of Vertebrates (Table 1-1).

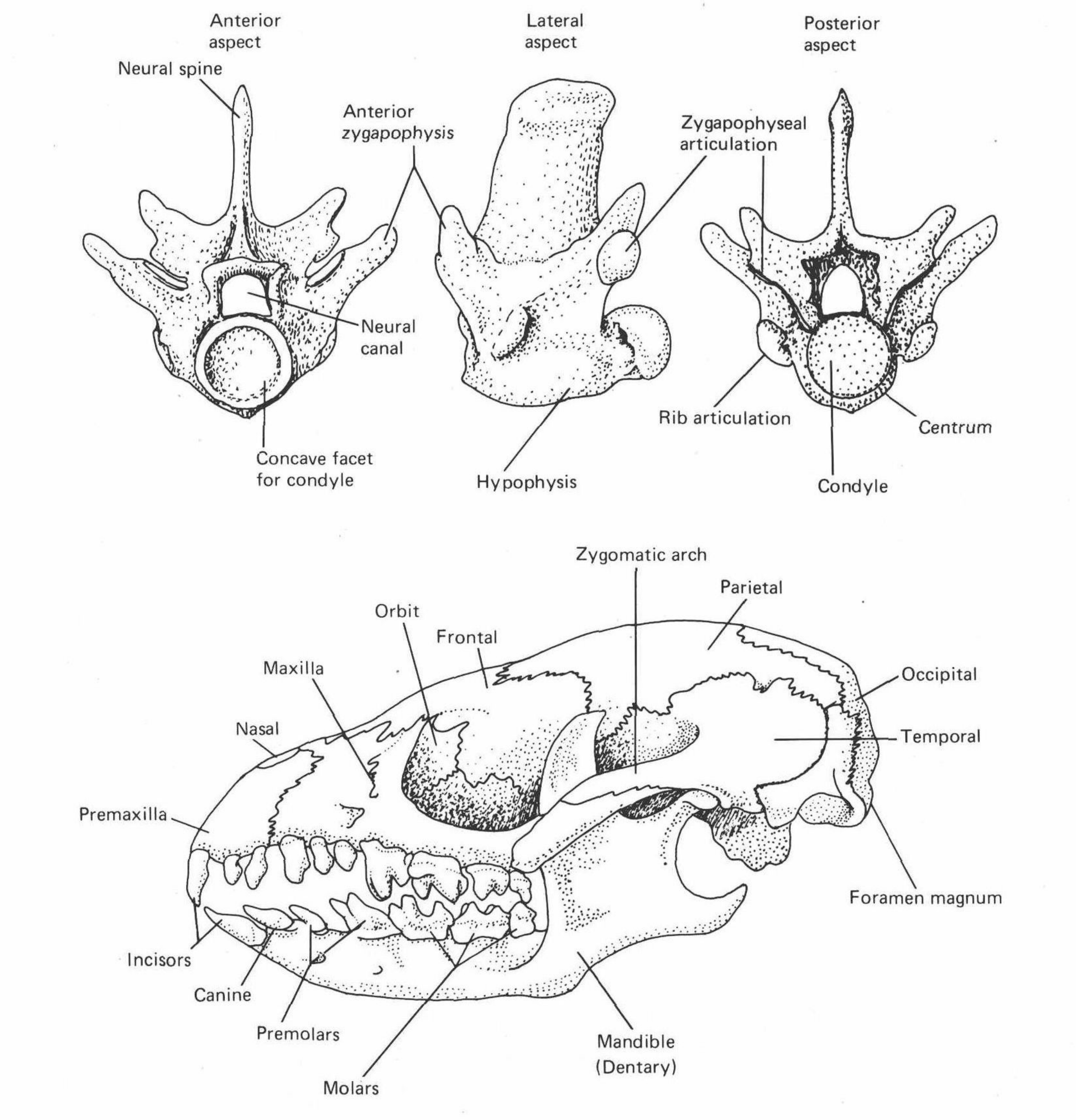

Figure 1-1 Examples of a typical reptilian vertebra and a mammalian cranium.

1.1.3 The Significance of Similarity and Differences

Each of the major groups or classes of vertebrates differs from the others in some fundamental way, but all share the common chordate-vertebrate characters, which in turn set them apart from all other animals. What is the meaning of the underlying similarity? Since Darwin's *Origin of Species* we have understood that the sharing of such fundamental similarities, or **homologs**, among widely different groups of species indicates that they all evolved from a common ancestor that also possessed the same features. In general the more homologs two species share, the more closely related they are (see Chapter 3).

Table 1-1. Selected Characteristics of the Living Vertebrate Classes

<table>
<tr><th></th><th>Jaws</th><th>Endoskeleton</th><th>Locomotory Appendages</th><th>Respiratory Surface</th><th>Extra-Embryonic Membranes</th><th>Body Temperature Energetics</th><th colspan="2">Integument</th></tr>
<tr><td>AGNATHA</td><td>AGNATHA</td><td rowspan="2">CARTILAGE</td><td rowspan="3">FINS (Pisces)</td><td rowspan="2">GILLS</td><td rowspan="4">ANAMNIOTA (Yolk sac and chorion)</td><td rowspan="5">ECTOTHERMAL</td><td rowspan="4">GLANDULAR (Mucous secretions)</td><td>Naked</td></tr>
<tr><td>CHONDRICHTHYES</td><td rowspan="6">GNATHOSTOMATA</td><td>Placoid Scales</td></tr>
<tr><td>OSTEICHTHYES</td><td rowspan="5">BONE</td><td>Note 1</td><td>Dermal Scales</td></tr>
<tr><td>AMPHIBIA</td><td rowspan="4">LIMBS (Tetrapoda)</td><td>Note 2</td><td>Naked</td></tr>
<tr><td>REPTILIA</td><td rowspan="3">LUNGS</td><td rowspan="3">AMNIOTA (Yolk sac, chorion, allantois and amnion)</td><td rowspan="2">AGLANDULAR (Dry)</td><td>Epidermal Scales</td></tr>
<tr><td>AVES</td><td rowspan="2">ENDOTHERMAL</td><td>Feathers and Epidermal Scales</td></tr>
<tr><td>MAMMALIA</td><td>SECONDARILY GLANDULAR (Oily and watery secretions)</td><td>Hair</td></tr>
</table>

Notes: [1]Primarily gills; secondarily gut and integument specializations
[2]Primarily lungs; secondarily integument and neotenic retention of gills

What is the meaning of the diversity within a lineage of related groups and species? The differences relate to adaptation to different environmental conditions or opportunities. Each species has an ecological niche that is different from all others and that is expressed, at least in part, by altered body form and function, and the diversity of species in the higher taxa, at the level of genera, families, orders, and even classes, gives an indication of the genetic plasticity or responsiveness of that group to environmental differences.

Evolution and adaptation are the major themes of this book. Throughout the subsequent pages we shall be directing attention to the following sorts of questions. What were the historical, ancestral precursors of any structure, behavior, or function under consideration? How does the structure, function, or behavior promote survival and reproduction of the organism in its natural environment?

1.1.4 Teleology Versus Teleonomy

Adaptations can be tricky subjects to write about in a textbook, because one of the most obvious features of adaptation is functional design. An adaptation, presumably, serves some useful purpose in the life of the organism possessing it. Because human beings are purposive animals, perceive the means to ends, and anticipate results prior to their achievement, some philosophers and even scientists of an earlier era ascribed a guiding principle or divine purpose as the cause for useful adaptations and for organic evolution. This philosophy, which is not widely held by scientists today, is called *teleology*. Teleologic explanations for adaptations are based on the assumption that final causes exist and that design in the universe presupposes the existence of a designer.

When biologists discuss adaptations they are referring to alterations in structure or function that result from natural selection operating on the random genetic variability of organisms. These alterations confer improved fitness for survival and reproduction on the altered individuals. By this process, adaptive design results from mechanistic interactions between the inheritable variability of organisms and selective pressures from the environment. Design emerges without the existence of a prior purpose for it. This scientific explanation of adaptations has been termed *teleonomy*.

In this book where we use word-saving phrases such as "legs evolved for jumping," "wings adapted for flight," "feathers that function to conserve heat," and so forth, our meaning is teleonomic, not teleological. Since we humans are so accustomed to think in anthropomorphic and teleological terms, it will be necessary for most students to make a conscious effort to keep these distinctions in mind.

1.2 THE HUMAN AS A FAMILIAR EXAMPLE OF A VERTEBRATE

Most of us are fairly conversant with the human body, and we can therefore consider ourselves as a familiar example of a vertebrate and examine some of our structural and functional details in relation to other vertebrates as a starting point for the study of vertebrate biology. We all know that the human is a "highly evolved" and unique form of life, and the beginning student therefore may wonder whether there is any meaning to be derived from a view of the human as a vertebrate animal.

1.2.1 The Relevance of Vertebrate Biology as a Science

Even a hundred years after Darwin, man's exalted view of himself still persists. It has very deep roots in the Judeo-Christian religious view of western civilization and has been buttressed historically by the idea that man was created in the image of God—a little lower than the angels—but with very clear dominion over the beasts of the field. Such arrogance has been further strengthened by human achievements in modern technology—atomic bombs, space travel to the moon, green revolutions, and the like. Can we human beings find meaningful roots among the lower animals when our philosophy and technology have transported us so far beyond them?

It is a curious anthropological fact that even aboriginal people have much the same ethnocentric view of themselves. Most tribal names—"Navajo," for example—translate to mean something equivalent to "the people," "the chosen ones," or "those set apart." In fairness to these peoples, it must be said that in many cases they also feel a certain kinship with animals, usually in a religious or mystical sense.

When biologists look at humankind as an animal species they quickly see that every feature of human anatomy and physiology, and much of the behavior and social organization, have quite clear counterparts in other living vertebrates and direct antecedents in the history of vertebrate evolution tracing back hundreds of millions of years in some cases. "Know thyself," is an old Greek injunction that humanists are fond of invoking; however, to pursue it in the fullest biological sense requires not only a study of yourself as an individual organism and human beings as a distinctive species but also a study of all forms of life to which the human is related by direct, lineal ancestry. Most particularly, it requires knowledge of the human's closest relatives, the vertebrates.

Viewed in that perspective, there is no need for questions about the "relevance" of biology. Biology does not have to be made relevant by some gimmick, such as creating a new course, because by the very nature of its subject—life in all its myriad aspects—it is relevant to the human condition. Biology is the one study that makes a natural bridge between the "hard sciences" and the humanities.

Humans have always prided themselves in their uniqueness, in their *humanness*, in what some have even referred to as our godlike qualities. But how unique is humankind really?

1.2.2 The Uniqueness and Nonuniqueness of *Homo sapiens*

In more than a metaphorical sense the history of vertebrate evolution is reflected in the structure and organization of the human body. We can begin to see how this assertion is true by examining some of our unique and some not-so-unique features.

Table 1-2 lists some of the most distinctive anatomical and behavioral traits of humans. As far as our structural features are concerned, the most crucial anatomical development for the evolution of the human condition was the acquisition of a fully upright posture and a strictly bipedal mode of locomotion. As we shall see later, many other vertebrates have independently evolved bipedalism, but only the human has become a fully erect bipedal strider. The other main peculiarities of human anatomy, such as the manipulative hand, the S-shaped vertebral column, and the oversized brain, follow from that posture or are coadaptations with it. The major behavioral traits in human adaptive achievement have no doubt been tool making and language, which in turn have been dependent upon the evolution of the human hand and brain.

The scientific name that humans have given to themselves—*Homo sapiens*—

Table 1-2. Distinctive Traits of *Homo sapiens*

Anatomical	*Behavioral and Psychological*[1]
1. Normal posture upright	1. Curiosity, imitation, attention, memory, imagination all more highly developed than in other animals
2. Legs longer than arms	2. Ability to improve adaptive nature of behavior by rational thought
3. Toes short, the first usually longest and not divergent	3. Uses and makes tools in great variety
4. Vertebral column with S curve	4. Self-conscious—reflects on past, future, life, death, consequences of own behavior, etc.
5. Hands prehensile and thumb strongly opposable	5. Makes mental abstractions and develops related symbolism—especially language
6. Body mostly bare with only short, sparse, inconspicuous hair	6. Sense of beauty
7. Joint for neck in middle of base of skull	7. Religious emotions in broad sense—awe, superstition, animism, belief in supernatural spirit
8. Brain uniquely large for body size with very large, complex cerebrum	8. Moral and ethical values
9. Face short, almost vertical under front of brain	9. Culture and social organization unique in complexity
10. Jaws short, with rounded dental arch	
11. Canines usually no larger than premolars, normally not separated by gaps in tooth row.	
12. First premolar like the second, tooth structure generally distinctive	
Most crucial anatomical development for the evolution of the human condition: acquisition of upright posture and strictly bipedal locomotion; the other main peculiarities of human anatomy follow from that or are coadaptations with it.	Major factors in human adaptive achievement have been toolmaking and language.

[1] Based on Charles Darwin, *The Descent of Man,* 1871.

suggests one set of traits that we consider unique, our wisdom. Humans know more about themselves and their world than does any other animal. Consequently we can do an infinite number of things and think an infinite number of thoughts. We can predict or know the consequences of an action before it happens, and this prescience, together with our highly social nature, has led to the development of a moral conscience. We may be the only animal that has a conscience, although some canids and apes act as though they may have.

All our vaunted intelligence we owe to a large, complex brain, the intricate workings of which are just beginning to be understood. Especially we owe it to our forebrain, the cerebral hemispheres, which have become so enlarged with