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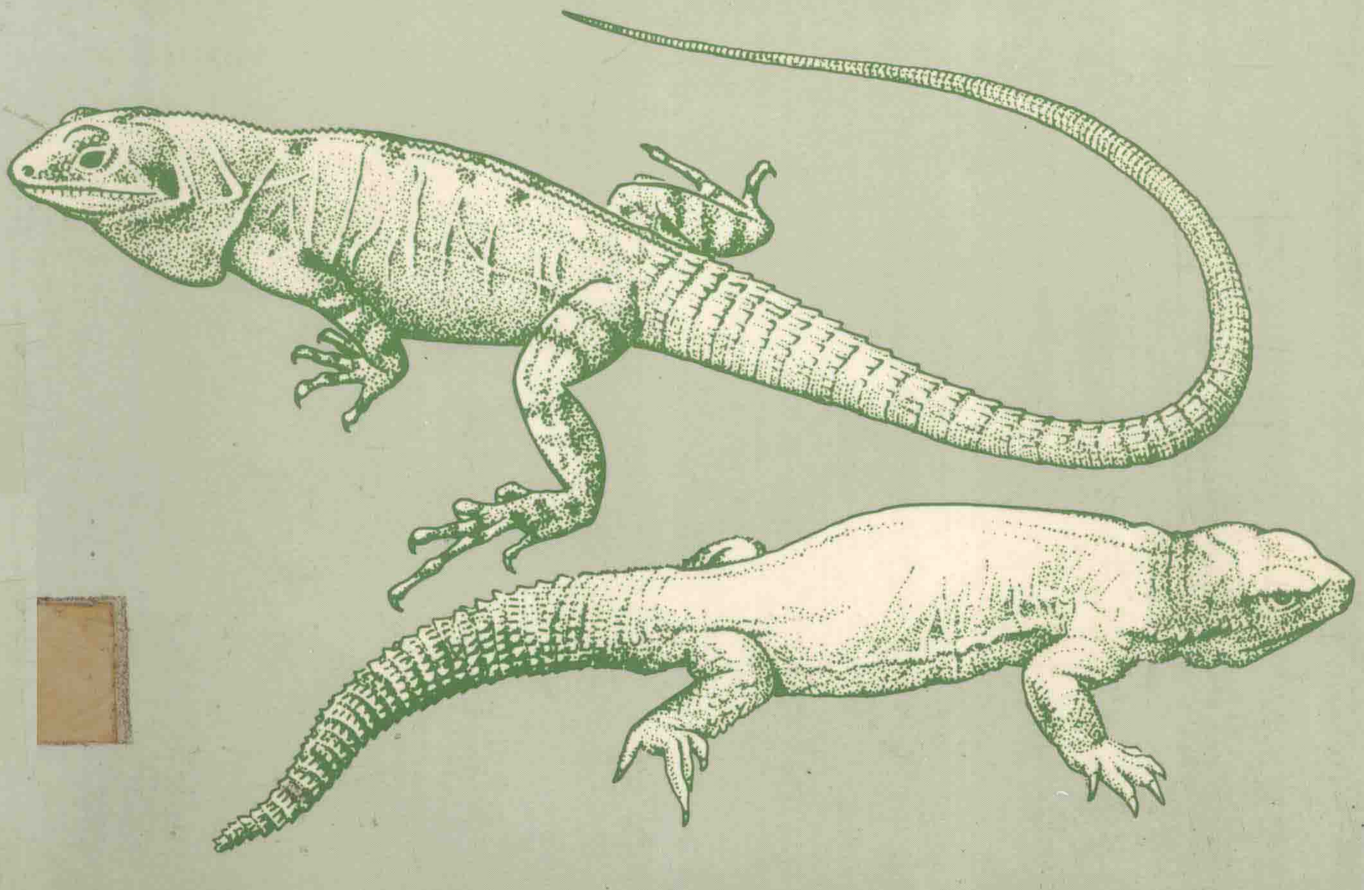
VERTEBRATE LIFE

Second Edition



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SECOND EDITION

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CORNELL UNIVERSITY

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GEOLOGICAL TIME SCALE

Relative Time Span
Cenozoic
Mesozoic
Paleozoic
Precambrian

ERA	PERIOD		EPOCH	Approximate time since start in millions of years before the present. In parentheses, duration in millions of years.
CENOZOIC	QUATERNARY		Recent	0.01
			Pleistocene	1.5
	TERTIARY		Pliocene	12 (10)
			Miocene	25 (13)
			Oligocene	34 (9)
			Eocene	56 (22)
			Paleocene	63 (7)
MESOZOIC	CRETACEOUS		No consistent system of epochs earlier than the Cenozoic is recognized because of the difficulty of correlating strata on different continents.	135 (70)
	JURASSIC			180 (45)
	TRIASSIC			225 (45)
PALEOZOIC	PERMIAN			280 (55)
	CARBONIFEROUS	PENNSYLVANIAN		310 (30)
		MISSISSIPPIAN		350 (40)
	DEVONIAN			400 (50)
	SILURIAN			430 (30)
	ORDOVICIAN			500 (70)
	CAMBRIAN			570-600 (70-100)
PRECAMBRIAN	PROTEROZOIC			2,500 (2,000)
	ARCHEOZOIC			4,600 (2,000)

MAJOR GEOLOGICAL, CLIMATIC, AND BIOLOGICAL EVENTS

Culmination of mountain-building followed by erosion and moderate, short-lived invasions of the sea. Early warming trends were reversed by the middle of the period to cooler and finally to glacial conditions. Subtropical forests gave way to temperate forests and finally to extensive grasslands. Transition from primitive mammals to modern orders and eventually families. Evolution of humans during the last 5-8 million years. (See Figures 16-2 and 16-3, pp 378 and 379.)
Last great spread of epicontinental seas and shoreline swamps. At the end of the period extensive mountain building cooled the climate worldwide. Angiosperm dominance began. Extinction of archaic birds and many reptiles by the end of the period. (See Figure 11-5, p. 250.)
Climate was warm and stable with little latitudinal or seasonal variation. Modern genera of many gymnosperms and advanced angiosperms appeared. Reptilian diversity was high in all habitats. First birds appeared. (See Figure 11-4, p. 249.)
Continents were relatively high with few shallow seas. The climate was warm; deserts were extensive. Gymnosperms dominated; angiosperms first appeared. Mammal-like reptiles were replaced by precursors of dinosaurs and the earliest true mammals appeared. (See Figure 11-3, p. 248.)
Land was generally higher than at any previous time. The climate was cold at the beginning of the period but warmed progressively. Glossopterid forests developed with the decline of the coal swamps. Mammal-like reptiles were diverse; widespread extinction of amphibians at the end of the period. (See Figure 11-2, p. 245.)
Generally warm and humid, but some glaciation in the Southern Hemisphere. Extensive coal-producing swamps with large arthropod faunas. Many specialized amphibians and the first appearance of reptiles. (See Figure 11-1, p. 243.)
Mountain-building produced locally arid conditions, but extensive lowland forests and swamps were the beginning of the great coal deposits. Extensive radiation of amphibians; extinction of some fish lineages and expansion of others.
The land was higher and climates cooler. Freshwater basins developed in addition to shallow seas. The first forests appeared and the first winged insects. There was an explosive radiation of fishes, followed by the disappearance of many jawless forms. The earliest tetrapods appeared. (See Figure 8-1, p. 184.)
The land was slowly being uplifted, but shallow seas were extensive. The climate was warm and terrestrial plants radiated. Eurypterid arthropods were at their maximum abundance in aquatic habitats and the first terrestrial arthropods appeared. The first gnathostomes appeared among a diverse group of marine and freshwater jawless fishes. (See Figure 4-4, p. 68.)
The maximum recorded extent of shallow seas was reached and the warming of the climate continued. Algae became more complex, vascular plants may have been present, and there was a variety of large invertebrates. Jawless fish fossils from this period are fragmentary but more widespread. (See Figure 4-3, p. 67.)
There were extensive shallow seas in equatorial regions. The climate was warm. Algae were abundant and there are records of trilobites and brachipods. The first remains of vertebrates are found at the end of this period.
Changes in the lithosphere produced major land masses and areas of shallow seas. Multicellular organisms appeared and flourished—algae, fungi, and many invertebrates.
Formation of the earth and slow development of the lithosphere, hydrosphere, and atmosphere. Development of life in the hydrosphere.

Preface to the First Edition

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, Rudolfo 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 Frederica 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.

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Preface to the Second Edition

Since 1979 we, and others around the world, have used this text in teaching vertebrate biology. As a result we have received comments and suggestions from students and colleagues. In addition, in the past six years new information and new hypotheses about vertebrate evolution and ecology have modified many concepts of vertebrate biology. For example, new interpretations of the significance of a unique vertebrate tissue, the neural crest, have appeared. The group of fishes from which tetrapods arose is once again a subject of controversy. Evidence of coevolution of plants, invertebrates, and vertebrates has become stronger, and new interpretations of extinctions have been widely debated.

In this second edition we have attempted to respond to the suggestions of students and colleagues and to incorporate much that has excited us in the recent literature. The basic theme of the text remains a phylogenetic approach to vertebrates. Our goal has been to integrate morphology, physiology, behavior, and natural history to produce an organismal approach to the ecology and evolution of vertebrates.

A major structural change in the text has been the incorporation of citations to the primary and secondary literature. Because this book is intended as an introductory text, we have chosen citations that will give students an entry into the literature on a subject, but not necessarily papers that were key steps in the historical development of those topics. In particular, we have cited as many recent reviews and symposia as possible. Within the bibliographies at the end of each chapter we have sometimes provided notations helpful in guiding students to the next level of information. A major addition that readers will find useful is a complete author index, and the subject index, glossary, and list of Latin and Greek roots of biological terms have been substantially expanded.

Although we take full responsibility for any errors of fact or interpretation in the text, the following individuals have been especially helpful in providing information and suggestions during preparation of the second edition: Albert F. Bennett; Daniel G. Blackburn; Edward Brothers; Robert L. Carroll; Jack A. Cranford; James A. Hopson; Farrish A. Jenkins, Jr.; Leslie K. Johnson; Robert K. Johnson; Suzanne Kamel; Kenneth A. R. Kennedy; Karel Liem; R. Eric Lombard; Karl Niklas; Mary J. Packard; Pamela J. Parker; William Roertgen; John A. Ruben; Thomas J.M. Schopf; James R. Spotila; Margaret M. Stewart; Katherine E. Troyer; Marvalee H. Wake; and Kentwood D. Wells. We are especially indebted to Frances Zweifel for the many new illustrations throughout the text.

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Contents

1

The Basic Plan of Vertebrate Organization

Synopsis: The history of vertebrates covers a span of more than 500 million years. 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 the special features of humans and compare the result with other vertebrates we can identify a "basic body plan." Presumably ancestral, the plan consists of a bilateral, tubular organization, possessing such characteristic features as notochord, pharyngeal slits, dorsal hollow nerve cord, vertebrae, and cranium. One of the photochordates, amphioxus, and the ammocoete larva of lampreys provide glimpses of what the earliest vertebrates were like.

1.1 INTRODUCTION: OVERVIEW OF VERTEBRATE BIOLOGY AS A SUBJECT

The scientific study of vertebrates has a rich literature going back to the classical writings of Aristote in the fourth century B.C. Among many other original contributions, Aristotle reported that whales are mammals and not fish, and he accurately described the peculiar reproductive system of the placental dogfish [Singer, 1959]. Our subject covers more than 500 million years 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, 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 of how or where to begin.

We have chosen to begin with some facts and concepts that are familiar to most biology students. From this general starting point, we can move into more specific, less well-known aspects of vertebrate life.

1.1.1 Some Familiar Facts About Vertebrates

Vertebrates belong to the Subphylum Vertebrata, a name that derives from the serially arranged vertebrae, or 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 for the vertebrates is Craniata. In fact, the distinctive vertebrate cranium and tripartite brain may have evolved before the vertebral column and are, perhaps, more fundamentally characteristic of vertebrates than the backbone.

Vertebrates also share some fundamental morphological features with certain marine invertebrates and by these common structures are classified in the Phylum Chordata. These common chordate structures are **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 evident at some stage in the development of all vertebrates.

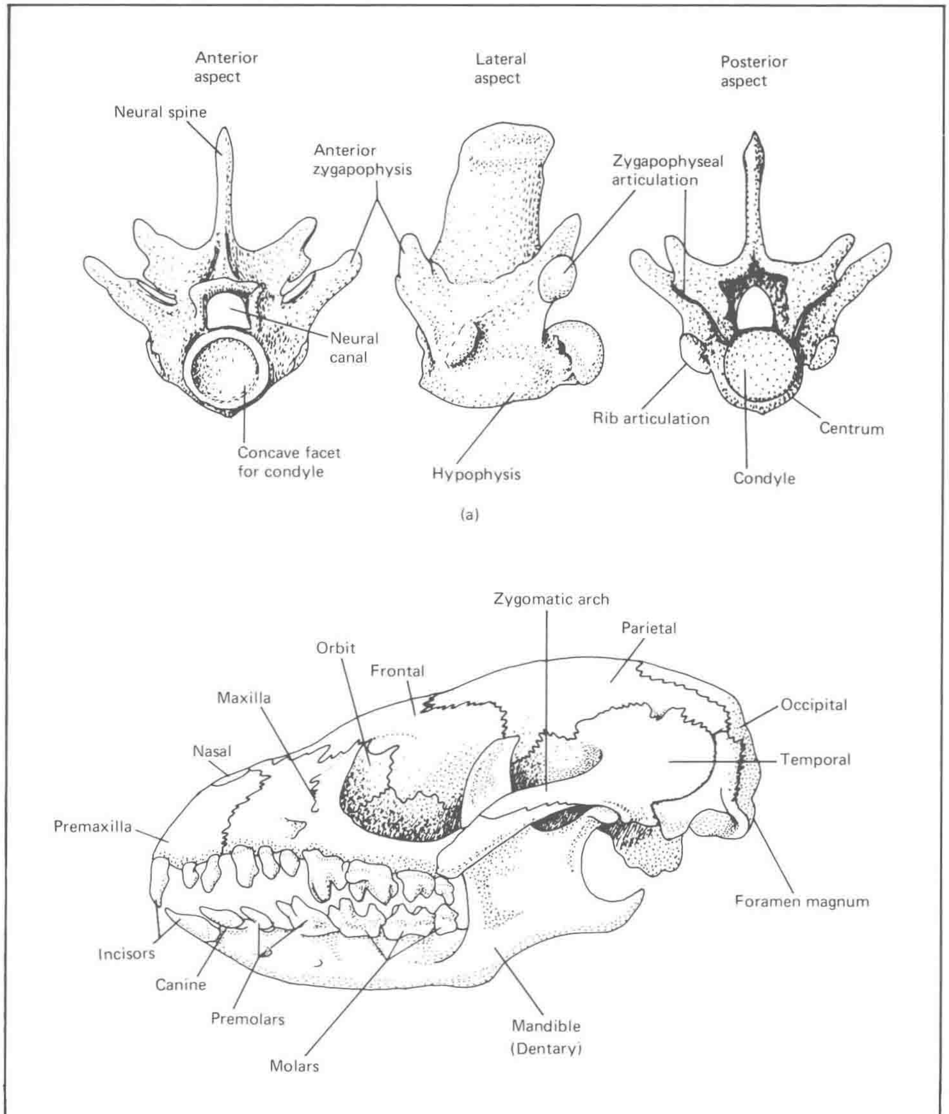

Figure 1-1 Examples of a typical reptilian vertebra and a mammalian cranium.

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

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 vertebrates, but few people realize 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 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).

1.1.3 The Significance of Similarity and Differences

Each class of vertebrates differs in some fundamental way, but all share the common chordate-vertebrate characters that 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 fundamental similarities, or **homologs,** among widely different groups of species indicates that they evolved from a common ancestor that possessed the same features. In general the more homologs two species share, the more closely related they are (see Chapter 3).

What is the meaning of the diversity within a lineage

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

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 often expressed by altered body form and function. The diversity of species in the higher taxa, at the level of genera, families, orders, and even classes, is indicative of the genetic responsiveness of each group and its distinctive constellation of traits to environmental differences.

Evolution and adaptation are the major themes of this book. We shall direct attention therefore 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, because one obvious feature of adaptation is function. An adaptation, presumably, has some useful function in the life of the organism possessing it. Because humans 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 [Singer, 1959]. This philosophy 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 refer to alterations in structure or function that result from natural selection operating on the 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** [Williams, 1966].

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.

1.1.5 The Relevance of Vertebrate Biology as a Science

More than a hundred years after Darwin, our exalted view of ourselves persists. It has deep roots in the Judeo-Christian religious view of western civilization and has been buttressed historically by the idea that humans were created in the image of God—a little lower than the angels—but with 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 humans find meaningful roots among the lower animals when our philosophy and technology have transported us so far beyond them?

It is a curious fact that many aboriginal people have much the same ethnocentric view of themselves. Most tribal names—''Navajo,'' for example—translate to ''the people,'' ''the chosen ones,''or ''those set apart.'' In fairness to these peoples, in many cases they feel a kinship with animals, usually in a religious or mystical sense.

When biologists look at humans as an animal species they quickly see that human anatomy and physiology, and much of human behavior and social organization, have counterparts in other living vertebrates and in some cases antecedents that trace back hundreds of millions of years in vertebrate evolution. ''Know thyself,'' is an old Greek injunction that humanists are fond of invoking; however, to pursue it fully requires not only a study of humans as a distinctive species, but also the study of all forms of life to which humans are related by direct, lineal ancestry. Most particularly, it requires knowledge of our closest relatives, the vertebrates.

From that perspective, there is no need for questioning the ''relevance'' of biology. Biology does not have to be made relevant by some gimmick, because biology provides natural bridge between the "hard sciences" and the humanities.

1.2 THE HUMAN AS A FAMILIAR EXAMPLE OF A VERTEBRATE

Most of us are fairly conversant with the human body and can therefore consider and examine our structural and functional details in relation to other vertebrates.