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VERTEBRATE LIFE

Second Edition

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SECOND EDITION

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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** 1
1.1 Introduction: Overview of Vertebrate Biology as a Subject 1
1.2 The Human as a Familiar Example of a Vertebrate 4
1.3 The Basic Vertebrate Body Plan 8

2 **Vertebrate Ancestors and Origins** 16
2.1 Introduction: Earliest Known Vertebrates 16
2.2 A Search for the Ancestors of the First Vertebrates 19
2.3 Lophophorates, Deuterostomes, and Chordates 29
2.4 Environment in Relation to Vertebrate Origins 32

3 **Diversity and Classification of Vertebrates** 36
3.1 Introduction: Goals of the Chapter 36
3.2 Linaean System of Classification 36
3.3 Phylogenetic and Evolutionary Interpretation of Classification Begun by Darwin 38
3.4 Modern Uses of Classification 38
3.5 Classification and Phylogeny of Vertebrates 44
3.6 Species and Speciation in Vertebrates 48

4 **Geology and Ecology During Vertebrate Origins** 62
4.1 Earth History, Changing Habitats, and Vertebrate Evolution 63
4.2 Why the Continents Move 63
4.3 Evidence for Continental Drift 65
4.4 Continental Positions in the Early Paleozoic 65
4.5 The Early Habitat of Vertebrates 69
4.6 Early Paleozoic Climates 70

5 **Earliest Vertebrates** 72
5.1 The First Evidence of Vertebrates 73
5.2 Living Agnathans 82
5.3 The First Jawed Vertebrates 85
5.4 Chondrichthyes — The Cartilaginous Fishes 97

6 **The Bony Fishes — Osteichthyes** 113
6.1 Major Groups of Bony Fishes 114
6.2 The Evolution of the Actinopterygii 120
6.3 Living Actinopterygii 125
6.4 Adaptations to the Deep Sea 136

7 **Life in Water: Its Influence on Basic Vertebrate Functions** 145
7.1 Locomotion in Water 145
7.2 Special Senses of Fishes 156
7.3 Regulation of Ions and Body Fluids: Ion-Osmoregulation 166
7.4 Responses to Temperature 173
7.5 Gills, Lungs, and Preadaptations to Life on Land 177

8 **Geology and Ecology of Tetrapod Origin** 183
8.1 Continental Geography in the Late Paleozoic 183
8.2 Devonian Climates 183
8.3 Terrestrial Habitats of the Devonian 185

9 **Origin and Radiation of Amphibians** 189
9.1 Introduction 191
9.2 Origin of Amphibians 191
9.3 Evolution of Terrestrial Vertebrates 196
9.4 Structural Adaptations for Terrestrial Life 198
9.5 Radiation of Paleozoic Amphibians 202

10 **Modern Amphibians** 212
10.1 Introduction 214
10.2 Evolutionary Origin of Lissamphibians 218
10.3 Diversity of Life Histories of Lissamphibians 223
10.4 Apodans 223
10.5 Urodeles 224
10.6 Anurans 226
10.7 Amphibian Metamorphosis 231
10.8 Lissamphibian Life History as a Model for Paleozoic Amphibians 234
10.9 Water Relations of Amphibians 234
10.10 Skin Glands of Amphibians 236

11 **Geology and Ecology during the Mesozoic** 242
11.1 Continental Geography During the Mesozoic 242
11.2 Climatic Prelude to the Mesozoic — Habitats during the Late Paleozoic 244
11.3 Mesozoic Climates and Habitats 246
11.4 Flora and Land Animals of the Cretaceous 249
11.5 Mesozoic Extinctions 251

12 **Origin and Early Radiation of Reptiles** 254
12.1 The Events Leading to the Evolution of Reptiles 254
12.2 The Amniotic Egg 257
12.3 The Pelycosaurs 261
12.4 Therapsids 264

13 **Mesozoic Reptiles** 273
13.1 Introduction 274
13.2 Phylogenetic Relationships and Radiations of Mesozoic Reptiles 275
13.3 Subclass Anapsida, Order Testudinata 276
13.4 Subclass Euryapsida 277
13.5 The Diapsid Reptiles: Subclasses Lepidosauria and Archosauria 281
13.6 Subclass Lepidosauria 281
13.7 Subclass Archosauria 286
13.8 Suborders Saurischia and Ornithischia 291
13.9 Saurischians 294
13.10 Ornithischians 296
13.11 The Ecology of Dinosaurs 302
13.12 Other Terrestrial Reptiles of the Late Mesozoic 306
13.13 Were Dinosaurs Endotherms? 307
13.14 The End of the Age of Reptiles 310

14 **Modern Reptiles** 315
14.1 Introduction 316
14.2 Order Crocodilia (Crodilians) 316
14.3 Order Testudinata (Turtles) 318
14.4 Order Squamata (The Scaly Reptiles) 323
14.5 Evolutionary Origin and Specializations of Snakes 330
14.6 Reptilian Thermoregulatory Mechanisms 339
14.7 Role of Thermoregulation in the Lives of Reptiles 345
14.8 Water Relations of Reptiles 346
14.9 Reproduction and Parental Care 348
14.10 The Role of Ectothermal Vertebrates in Terrestrial Ecosystems 350

15 **Vertebrate Energetics: The Costs and Benefits of Temperature Regulation and Motility** 357
15.1 Energy Utilization — A Challenge to All Vertebrates 357
15.2 The Regulation of Body Temperature 361
15.3 The Cost of Motility 365
15.4 Adaptive Significance of Migration 368
15.5 Nitrogen Excretion in Vertebrates 370

16 **Geology and Ecology of The Cenozoic** 375
16.1 Cenozoic Time — The Age of Mammals 375
16.2 Early Tertiary Mammals in Laurasia 378
16.3 Tertiary Mammals of the Southern Continents 381

17 **The Origin of Birds and the Function of Feathers** 389
17.1 Introduction: Diversity of Birds 390

17.2 Birds and Reptiles Compared 390
17.3 Origin and Evolution of Birds 390
17.4 Structure and Evolution of Feathers 397
17.5 Feathers and Thermoregulation 401
17.6 Avian Flight 404
17.7 Other Functions of Feathers 415

18 The Diversity of Locomotion and Feeding in Birds 421
18.1 Introduction: Adaptive Radiation and Convergence in Birds 422
18.2 Flying Adaptations 422
18.3 Foraging Behavior of Birds: The Concept of Optimalization 429
18.4 Divergence and Convergence in Feeding Adaptations 432
18.5 Reproductive Biology 441

19 Origin and General Characteristics of Mammals 443
19.1 Mammalian Beginnings 443
19.2 Recent Mammals: Characterization of Major Groups 449
19.3 The Mammalian Integument 449
19.4 The Mammalian Kidney 462

20 Diverse Adaptations of Mammals 471
20.1 Mammalian Trophic Biology 472
20.2 The Mammalian Nervous and Sensory Systems 487
20.3 Reproduction in Mammals 513
20.4 Sex Determination and Sexual Dimorphism 523
20.5 Genetic Events in Vertebrate Evolution 525

21 Adaptations of Endotherms to Rigorous Habitats 530
21.1 Advantages of Endothermy 530
21.2 Adaptations of Endotherms to Cold Climates 531
21.3 Torpor as a Response to Low Temperature and Limited Food 534
21.4 Endotherms in Deserts 537
21.5 Migratory Movements of Vertebrates 545

22 Review of Earth History and the Geologic and Ecologic Settings during the Pleistocene 553
22.1 Review of Continental Drift 553
22.2 Vertebrate Changes during the Pleistocene 559

23 Homo sapiens and the Vertebrates 563
23.1 Introduction: The Biological Origin of *Homo sapiens* 564
23.2 The Human Race and the Future of Vertebrates 582

Glossary 599

Author Index 607

Subject Index 614

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.

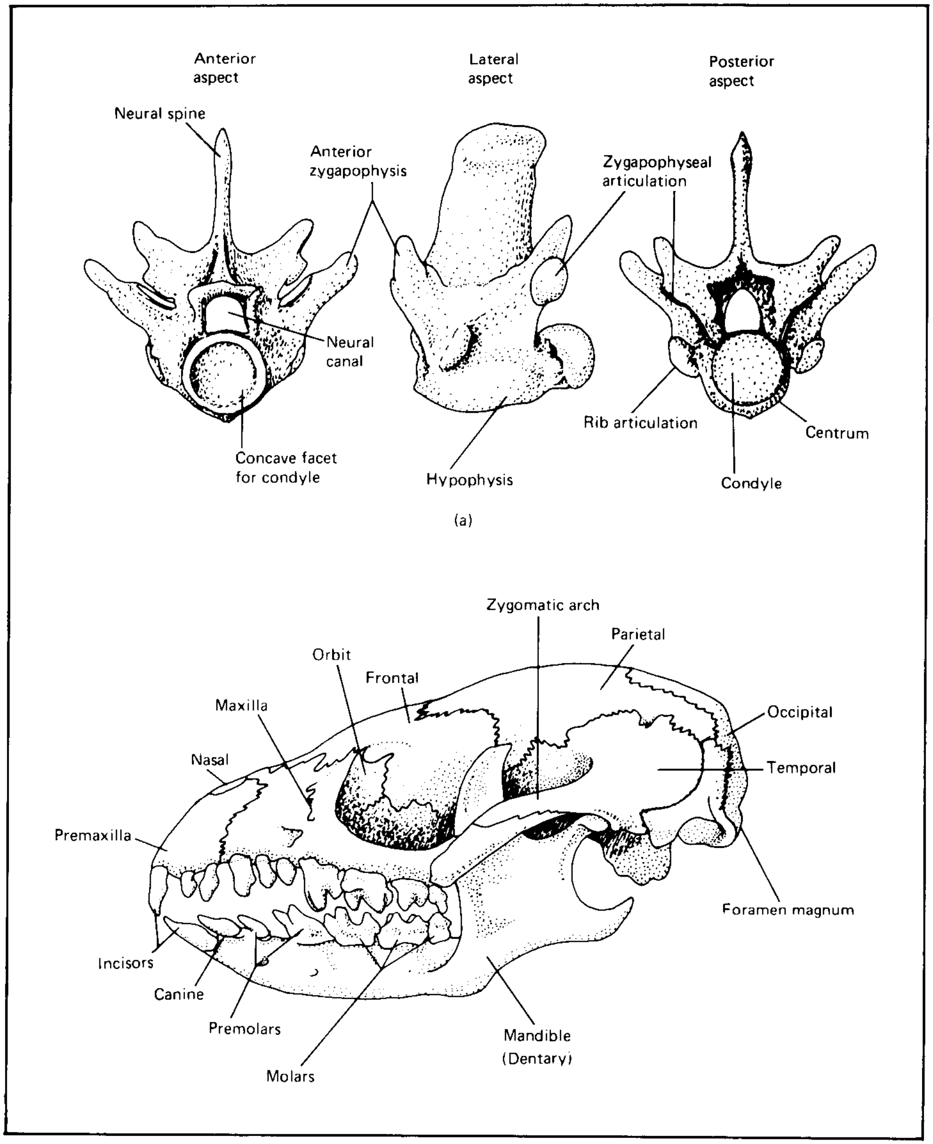

Figure 1-1 Examples of a typical reptilian vertebra and a mammalian cranium.

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

	Jaws	*Endoskeleton*	*Locomotory Appendages*	*Respiratory Surface*	*Extra-Embryonic Membranes*	*Body Temperature Energetics*	*Integument*	
AGNATHA	AGNATHA	CARTILAGE	FINS (Pisces)	GILLS	ANAMNIOTA (Yolk sac and chorion)	ECTOTHERMAL	GLANDULAR (Mucous secretions)	Naked
CHONDRICHTHYES	GNATHOSTOMATA	CARTILAGE	FINS (Pisces)	GILLS	ANAMNIOTA (Yolk sac and chorion)	ECTOTHERMAL	GLANDULAR (Mucous secretions)	Placoid Scales
OSTEICHTHYES	GNATHOSTOMATA	BONE	FINS (Pisces)	Note 1	ANAMNIOTA (Yolk sac and chorion)	ECTOTHERMAL	GLANDULAR (Mucous secretions)	Dermal Scales
AMPHIBIA	GNATHOSTOMATA	BONE	LIMBS (Tetrapoda)	Note 2	ANAMNIOTA (Yolk sac and chorion)	ECTOTHERMAL	GLANDULAR (Mucous secretions)	Naked
REPTILIA	GNATHOSTOMATA	BONE	LIMBS (Tetrapoda)	LUNGS	AMNIOTA (Yolk sac, chorion, allantois and amnion)	ECTOTHERMAL	AGLANDULAR (Dry)	Epidermal Scales
AVES	GNATHOSTOMATA	BONE	LIMBS (Tetrapoda)	LUNGS	AMNIOTA (Yolk sac, chorion, allantois and amnion)	ENDOTHERMAL	AGLANDULAR (Dry)	Feathers and Epidermal Scales
MAMMALIA	GNATHOSTOMATA	BONE	LIMBS (Tetrapoda)	LUNGS	AMNIOTA (Yolk sac, chorion, allantois and amnion)	ENDOTHERMAL	SECONDARILY GLANDULAR (Oily and watery secretions)	Hair

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.

Humans have pride in their uniqueness, in their *humanity*, in what some have even referred to as god-like qualities. How unique is humankind really?

1.2.1 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 see how true this assertion is by examining some of our unique and some not-so-unique features.

Table 1-2 lists the more distinctive anatomical and behavioral traits of humans. Structurally, the most crucial anatomical development for the evolution of the human condition was acquisition of a fully upright posture and strict bipedal locomotion. Many other vertebrates have evolved bipedalism, but only the human has become a fully erect bipedal strider. Other 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 been tool making and language, which in turn have been dependent upon evolution of the human hand and brain [Simpson, 1966, 1969].

The scientific name that humans have assumed—*Homo sapiens*—suggests the traits that we consider unique, our wisdom.

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 enlarged with respect to the rest of the brain, cover over most of it, and have become highly folded, thereby greatly increasing the surface area available for associational neurons (Figure 1-2). The most important component of the cerebrum—the roof or **neopallium** (*neo* = new, *pallium* = cloak)—is a structure that humans share with all other mammals. It is weakly developed in some reptiles but not at all in birds or other vertebrates[Diamond and Hall, 1969].

Probably the neopallium began to enlarge in mammal-like reptiles of the late Paleozoic, around 250 million years ago. The neopallium itself, however, derives from a still older structure, the olfactory forebrain or **prosencephalon** (*pro* = before, *encephalon* = brain). Like the midbrain and the hindbrain, the prosencephalon existed in the earliest known vertebrates, about 500 million years ago.

We can consider the human hand in a similar way. The hand of no other species compares with ours for dexterity and manipulation. One has only to watch a good typist or pianist or jeweler at work to be impressed by the subtlety and infinite variety of movements of which the human hand is capable. Clearly humans can do more things with their hands than any other animal.

The human hand is a tool-using and tool-making organ *par excellence,* and the development of human culture and civilization has been based not only on our superior intellect but also on our ability to make things and manipulate things with our hands. Our technology is quite firmly based on the evolution of our hands.

The human hand is also used for social communication. Emotive communication especially is likely to be manual. We salute the flag, we point accusing fingers, we shake our fists in anger, and we swear in a variety of finger signs. Good speakers continually add emotional content to their speeches with hand gestures. Sign language no doubt preceded vocal language in human social relations and has probably played a large role in the evolution of symbolic communication.

The human hand performs four basic movements—divergence, convergence, prehensility, and opposability (Figure 1-3). The first two are general mammalian characteristics. The first mammals evolved **divergence**, the ability to spread the toes of their paws, in association with their load-bearing function for quadrupedal locomotion. This ability in the forepaws has not been lost in forms that later evolved bipedalism. **Convergence**, or cupping of the hand, is achieved by flexion at the joints of the metacarpals and phalanges. Two convergent paws can be used like one prehensile hand, and many mammals—squirrels and sea otters are examples—manipulate their food in two convergent paws while eating. **Prehensility**, which refers to the ability to wrap the fingers around an object, has been perfected by primates in association with **brachiation**, swinging by hands and arms through branches of trees. It has been independently evolved in other arboreal mammals like the opossums. **Opposability** is the ability to pass the

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	Major factors in human adaptive achievement have been tool making and language.
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.	

From G. G. Simpson [1966], *Science* 152:474—478.

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

thumb across the palm while rotating it around its long axis to allow the ventral ball to touch the tips of other fingers. Although many primates perform this movement, the bone and muscular structures associated with it are best developed in the human (Figure 1-4).

During the course of evolution humans capitalized on prehensility and opposability, inherited from their tree-dwelling ancestors, to develop a power grip and a preci-