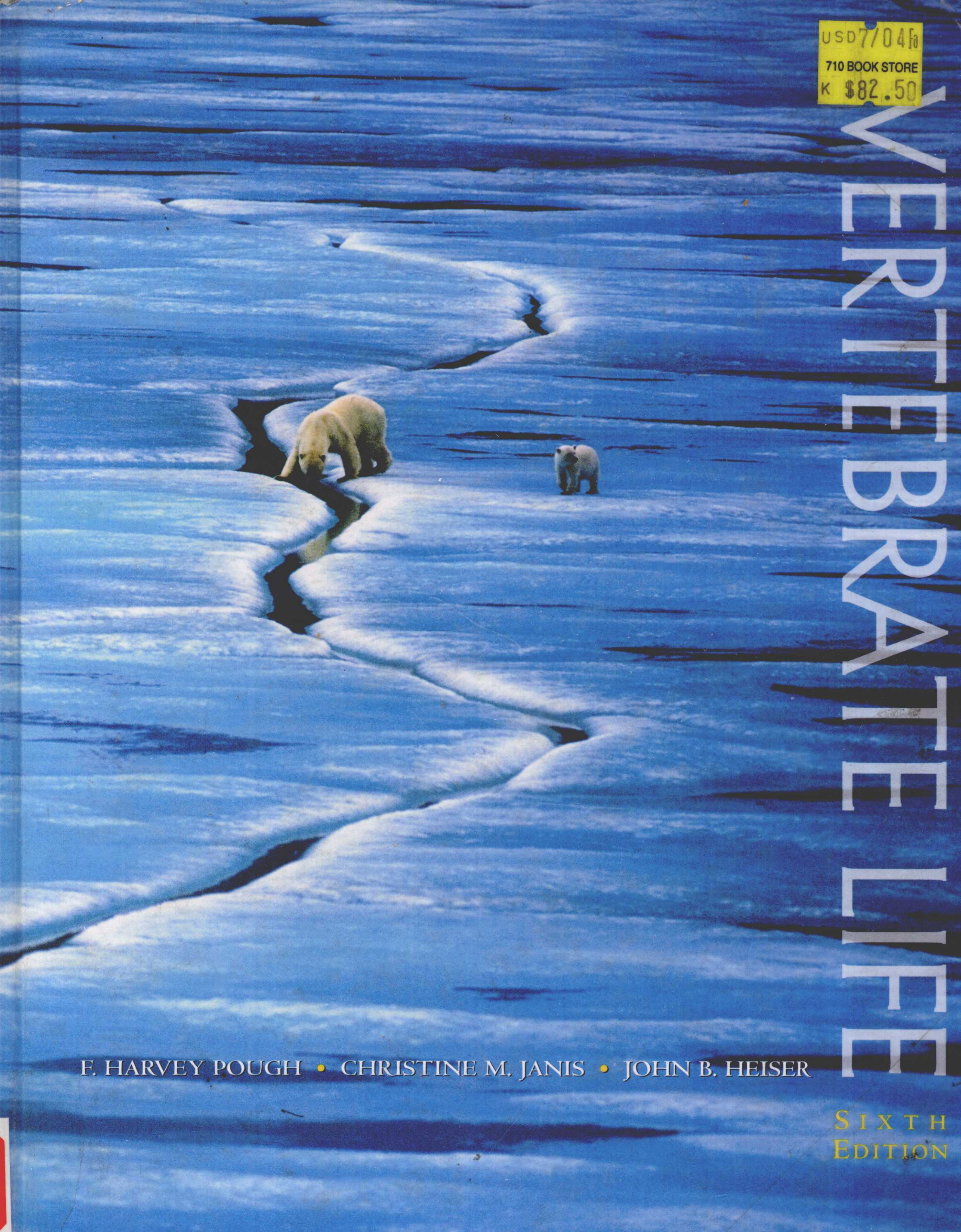
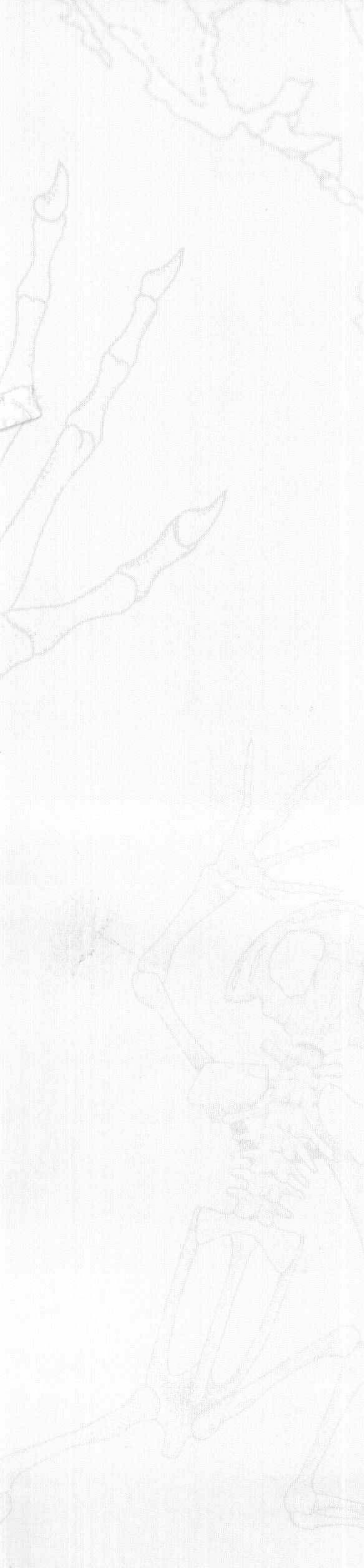


VERTEBRATE LIFE

F. HARVEY POUGH • CHRISTINE M. JANIS • JOHN B. HEISER

SIXTH EDITION



Vertebrate Life

Sixth Edition

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Preface

The sixth edition of *Vertebrate Life* incorporates a large number of changes, many of them the result of suggestions by colleagues who are using the book. The most conspicuous change is elimination of the overview of vertebrate anatomy and physiology that was provided in Chapters 3 and 4. With the concurrence of reviewers, we decided that a phylogenetic perspective is better emphasized by moving material from those introductory chapters into later chapters that cover the particular taxa whose characters are being discussed. Most of the material and figures in Chapters 3 and 4 have been retained, but they appear now in different locations.

Also in response to suggestions from colleagues, we have increased the emphasis on conservation, which has become a central theme of many vertebrate biology courses. We have included information about conservation issues in the chapters on extant taxa, and we have added a new final chapter that draws on information from earlier chapters to present an overview of conservation in the context of humans and other vertebrates. The historical and organismal perspectives of the book are retained in this chapter, which considers both the record of extinctions that coincides with the spread of modern humans in the past 100,000 years and current problems and conservation efforts.

We have changed the literature citations from a bibliography of papers actually cited in each chapter to a list of additional readings. This change allows us to include useful references that are not actually cited in the text. We have made greater use of websites as sources of information, and Prentice Hall maintains a web page for this book *http://prenhall.com/pough/* that includes links to Internet sites for each chapter.

As in previous editions, we have included cladograms illustrating the postulated relationships of vertebrates. In doing so, we have tried to point out areas of controversy. The cladograms include synopses of the character states on which they are based. New in this edition are simplified cladograms that emphasize the relationships of extant taxa.

Acknowledgments

As always, our editor Teresa Ryu combined support and decisiveness to keep the project on schedule, and she was ably assisted by Colleen Lee. It has been a pleasure to work with both of them. The production manager, Patty Donovan of Pine Tree Composition, kept all the parts organized. Without her skill and experience, this book would still be in pieces at sites around the Northern Hemisphere. We are fortunate to have Kandis Elliot as the artist for this edition. Her work blends so well with earlier illustrations by Laura Schuett and Carol Abrazincas that the extent of her contribution is not readily apparent.

Writing a book with a scope as broad as this one requires the assistance of many people. We are grateful to the following colleagues for their generous response to requests for information and their comments and suggestions:

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PART 1

Vertebrate Diversity, Function, and Evolution

The more than 50,000 living species of vertebrates inhabit nearly every part of the Earth, and other kinds of vertebrates that are now extinct lived in habitats that no longer exist. Increasing knowledge of the diversity of vertebrates was a product of the European exploration and expansion that began in the fifteenth and sixteenth centuries. In the middle of the eighteenth century, Swedish naturalist Carolus Linnaeus developed a binominal classification to catalog the varieties of animals and plants. The Linnean system remains the basis for naming living organisms today.

A century later, Charles Darwin explained the diversity of plants and animals as the product of natural selection and evolution. In the early twentieth century, Darwin's work was coupled with the burgeoning information about mechanisms of genetic inheritance. This combination of genetics and evolutionary biology, known as the New Synthesis or neo-Darwinism, continues to be the basis for understanding the mechanics of evolution. Methods of classifying animals have also changed during the twentieth century; and classification, which began as a way of trying to organize the diversity of organisms, has become a powerful tool for generating testable hypotheses about evolution.

Vertebrate biology and the fossil record of vertebrates have been at the center of these changes in our view of life. Comparative studies of the anatomy, embryology, and physiology of living vertebrates have often supplemented the fossil record. These studies reveal that evolution acts by changing existing structures. All vertebrates share basic characteristics that are the products of their common ancestry, and the progress of evolution can be analyzed by tracing the modifications of these characters. Thus, an understanding of vertebrate form and function is basic to understanding the evolution of vertebrates and the ecology and behavior of living species.

CHAPTER

1

The Diversity, Classification, and Evolution of Vertebrates

Evolution is central to vertebrate biology because it provides a principle that organizes the diversity we see among living vertebrates and helps to fit extinct forms into the context of living species. Classification, initially a process of attaching names to organisms, has become a method of understanding evolution. Current views of evolution stress natural selection operating at the level of individuals as a predominant mechanism that produces change over time. The processes and events of evolution are intimately linked to the changes that have occurred on Earth during the history of vertebrates. These changes have resulted from the movements of continents and the effects of those movements on climates and geography. In this chapter we present an overview of the scene, the participants, and the rules governing the events that have shaped the biology of vertebrates.

1.1 The Vertebrate Story

Mention "animal" and most people will think of a vertebrate. Vertebrates are often abundant and conspicuous parts of people's experience of the natural world. Vertebrates are also very diverse: The more than 50,000 extant (currently living) species of vertebrates range in size from fishes weighing as little as 0.1 gram when fully mature to whales weighing over 100,000 kilograms. Vertebrates live in virtually all the habitats on Earth. Bizarre fishes, some with mouths so large they can swallow prey larger than their own bodies, cruise through the depths of the sea, sometimes luring prey to them with glowing lights. Fifteen kilometers above the fishes, migrating birds fly over the crest of the Himalayas, the highest mountains on Earth.

The behaviors of vertebrates are as diverse and complex as their body forms. Vertebrate life is energetically expensive, and vertebrates get the energy they need from food they eat. Carnivores eat the flesh of other animals and show a wide range of methods of capturing prey. Some predators search the environment to find prey, whereas others wait in one place for prey to come to them. Some carnivores pursue their prey at high speeds, others pull prey into their mouths by suction. In some cases the foraging behaviors vertebrates use appear to be exactly the ones that maximize the amount of energy they obtain for the time they spend hunting; in other cases vertebrates appear to be remarkably inept predators. Many vertebrates swallow their prey intact, sometimes while it is alive and struggling, but other vertebrates have very specific methods of dispatching prey. Venomous snakes inject complex mixtures of toxins, and cats (of all sizes from house cats to tigers) kill their prey with a distinctive bite on the neck. Herbivores eat plants. Plants cannot run away when an animal approaches, but they are hard to digest and they frequently contain toxic compounds. Herbivorous vertebrates show an array of specializations to deal with the difficulties of eating plants. These specializations include elaborately sculptured teeth and digestive tracts that provide sites where symbiotic microorganisms digest compounds that are impervious to the digestive systems of vertebrates.

Reproduction is a critical factor in the evolutionary success of an organism, and vertebrates show an astonishing range of behaviors associated with mating and reproduction. In general, males court females and females care for the young; but these roles are reversed in many species of vertebrates. The forms of reproduction employed by vertebrates range from laying eggs to giving birth to babies that are largely or entirely independent of their parents (precocial young). These variations range across almost all kinds of vertebrates. Many fishes and amphibians produce precocial young, and a few mammals lay eggs. At the time of birth or hatching some vertebrates are entirely self-sufficient and never see their parents, whereas other vertebrates (including humans) have extended periods of obligatory parental care. Extensive parental care is found in seemingly unlikely groups of vertebrates—fishes that incubate eggs in their mouths, frogs that incubate eggs in their stomachs, and birds that feed their nestlings a fluid called crop milk that is very similar in composition to mammalian milk.

The diversity of living vertebrates is fascinating, but the species now living are only a small proportion of the species of vertebrates that have existed. For each living species there may be more than one hundred extinct species, and some of these have no counterparts among living forms. The dinosaurs, for example, that dominated the Earth for 180 million years are so entirely different from any living animals that it is hard to reconstruct the lives they led. Even mammals were once more diverse than they are now. The Pleistocene epoch saw giants of many kinds—ground sloths as big as modern rhinoceroses, and raccoons as large as bears. Humans are great apes, close relatives of chimpanzees, and much of the biology of humans is best understood in the context of our vertebrate heritage. The number of species of vertebrates probably reached its maximum in the middle Miocene, 12 to 14 million years ago, and has been declining since then.

The story of vertebrates is fascinating. Where they originated, how they evolved, what they do, and how they work provide endless intriguing details. In preparing to tell this story we must introduce some basic information, including what the different kinds of vertebrates are called, how they are classified, and what the world was like as the story of vertebrates unfolded.

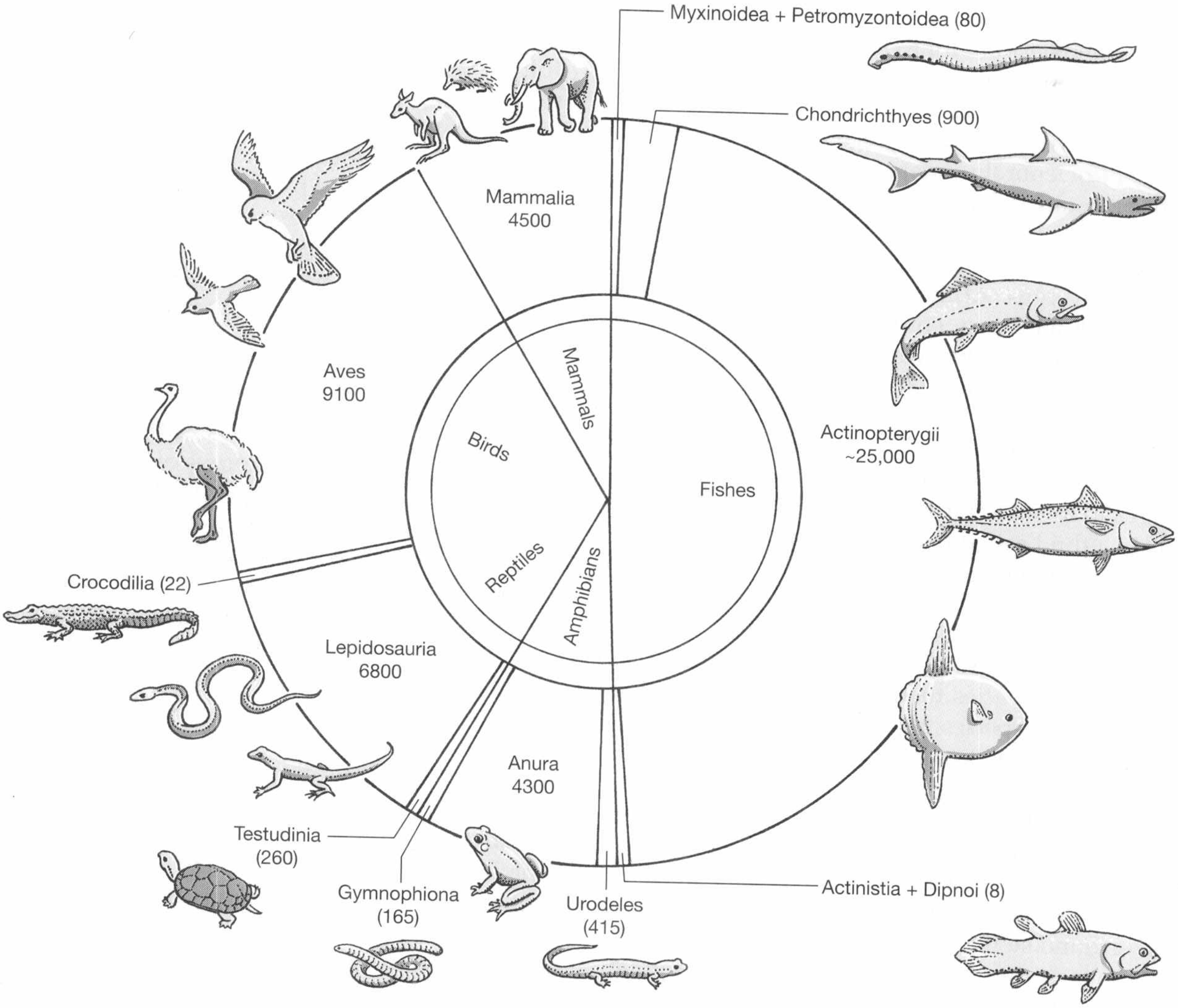
The modern approach to biological classification is popularly known as cladistics, from the Greek word *cladus,* meaning "branch."

Cladistics recognizes only groups of organisms that are related by common descent, or phylogeny (Greek *phyla* = tribe and *genesis* = origin). The application of cladistic methods has made the study of evolution rigorous. The natural groups recognized by cladistics are easier to understand than the artificial groups we are used to, except that we are familiar with the names of the artificial groups and the names of the new groups are sometimes strange. At this point we need to establish a basis for talking about particular animals by naming them, and to relate the old, familiar names to the new, less familiar ones. Figure 1–1 shows the major kinds of vertebrates and the relative numbers of living species. In the following sections we describe briefly the different kinds of living vertebrates.

Hagfishes and Lampreys—Myxinoidea and Petromyzontoidea Lampreys and hagfishes are elongate, scaleless, and slimy and have no internal hard tissues. They are scavengers and parasites and are specialized for those roles. Hagfishes (about 40 species) are marine, living on the continental shelf and open ocean at depths around 100 meters. In contrast, many of the 41 species of lampreys are migratory forms that live in oceans and spawn in rivers.

Hagfishes and lampreys are unique among living vertebrates because they lack jaws; this feature makes them important in the study of vertebrate evolution. They have traditionally been grouped as agnathans (Greek *a* = without and *gnath* = jaw) or cyclostomes (Greek *cyclo* = round and *stoma* = mouth), but they probably represent two independent evolutionary lineages. Hagfishes lack many of the features characterizing most vertebrates; for example, they have no trace of vertebrae and sometimes are classified in the Craniata, but not in the Vertebrata. In contrast, lampreys have rudimentary vertebrae as well as many other characters they share with jawed vertebrates. The jawless condition of both lampreys and hagfishes, however, is ancestral.

Sharks, Rays, and Ratfishes—Elasmobranchii and Holocephali Sharks have a reputation for ferocity that most of the 350 to 400 species would have difficulty living up to. Many sharks are small (15 centimeters or less); and the largest species, the whale shark—which grows to 10 meters—is a filter feeder that subsists on plankton it strains from the water. The 450 species of rays are dorsoventrally flattened, frequently bottom dwellers that swim with undulations of their extremely broad pectoral fins. The approximately 30 species of ratfish are bizarre marine fishes with long, slender tails and buck-



▲ Figure 1–1 Diversity of vertebrates. Areas in the diagram correspond to approximate numbers of living species in each group. Common names are in the center circle, and formal names for the groups are on the outer circle.

toothed faces that look rather like rabbits. The name Chondrichthyes (Greek *chondro* = cartilage and *ichthyes* = fish) refers to the cartilaginous skeletons of these fishes.

Bony Fishes—Osteichthyes Bony fishes are so diverse that any attempt to characterize them briefly is doomed to failure. Two broad categories can be recognized: the lobe-finned or fleshy-finned fishes (sarcopterygians; Greek *sarco* = flesh) and the ray-finned fishes (actinopterygians; Greek *actino* = ray and *ptero* = wing or fin).

Only eight species of lobe-finned fishes survive, the six species of lungfishes (Dipnoi) found in South America, Africa, and Australia and the two species of coelacanth (Coelacanthiformes), one from deep waters off the east coast of Africa and a second species recently discovered near Indonesia. These are the living fishes most closely related to terrestrial vertebrates.

In contrast to the lobe-fins, the ray-finned fishes have radiated extensively in fresh and salt water. More than 22,000 species of ray-finned fishes have