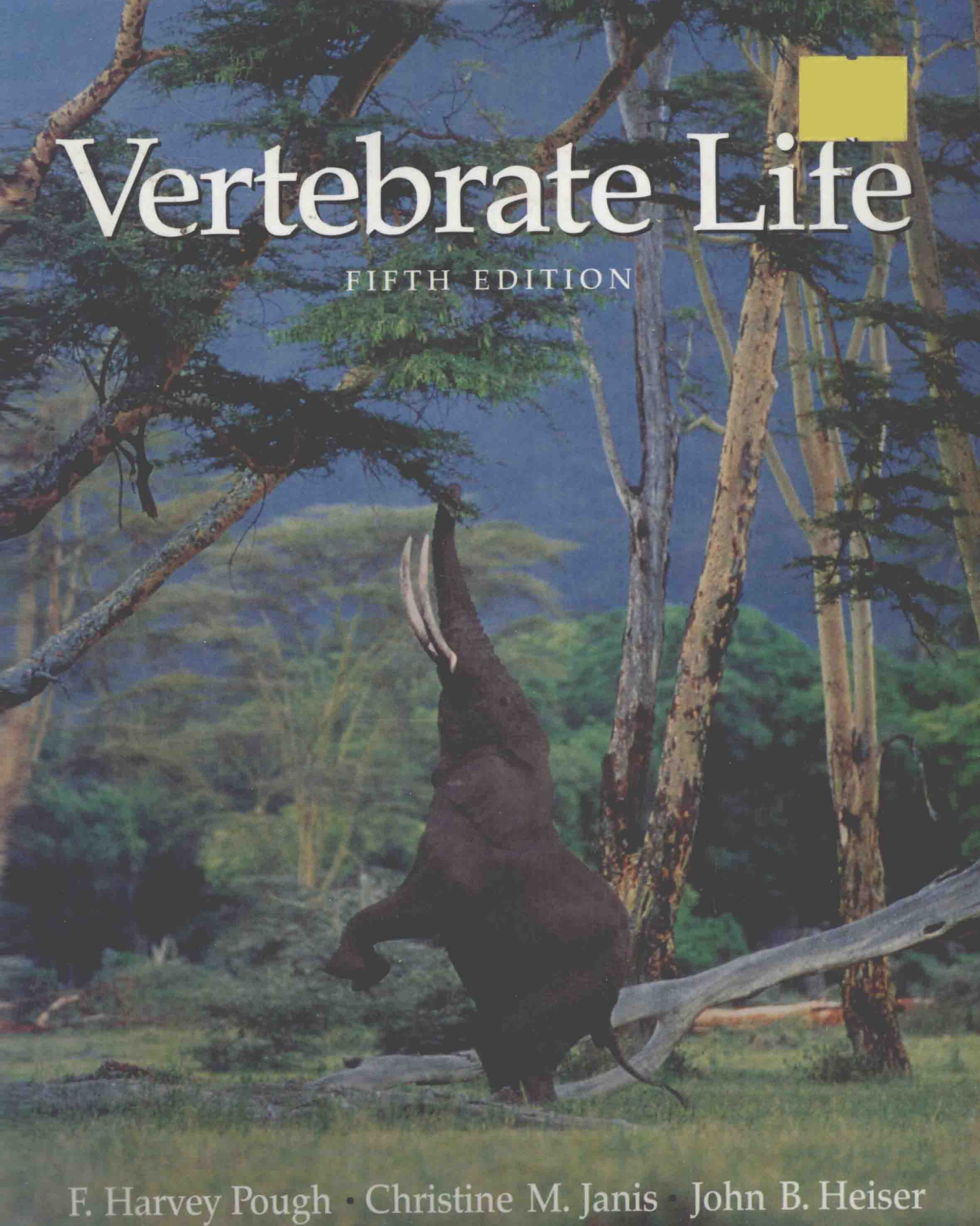

Vertebrate Life

FIFTH EDITION

F. Harvey Pough · Christine M. Janis · John B. Heiser

Fifth Edition

Vertebrate Life

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About the Authors

F. Harvey Pough began his biological career at the age of fourteen when he conducted his first research project on the ecology of turtles in Rhode Island. His reserarch now focuses on organismal biology, blending physiology, morphology, behavior, and ecology in an evolutionary context. He greatly enjoys teaching undergraduates and has taught courses in vertebrate zoology, functional ecology, herpetology, and the ecology, environmental physiology, and evolution of humans. After 23 years at Cornell University, he moved to Arizona State University West as Chair of the Department of Life Sciences to focus on the challenges of teaching undergraduates at a university that emphasizes community involvement. When not slaving over a hot computer revising *Vertebrate Life*, he enjoys walking in the desert with his labrador retriever, Martha.

Christine M. Janis is an Associate Professor of Biology at Brown University where she teaches comparative anatomy and vertebrate evolution. A British citizen, she obtained her bachelor's degree at Cambridge University and then crossed the pond to get her Ph.D. at Harvard University. She is a vertebrate paleontologist with a particular interest in mammalian evolution (especially hoofed mammals) and faunal responses to climatic change. She first became interested in vertebrate evolution after seeing the movie *Fantasia* at the impressionable age of seven. That critical year was also the year that she began riding lessons, and she has owned at least one horse since the age of 12. She is still an active rider, although no longer as aggressive a competitor (she used to do combined training events). She attributes her lifestyle to the fact that she has failed to outgrow either the dinosaur phase or the horse phase.

John B. Heiser was born and raised in Indiana and completed his undergraduate degree in biology at Purdue University. He earned his Ph.D. in ichthyology from Cornell University for studies of the behavior, evolution and ecology of coral reef fishes, research which he continues today with molecular colleagues. For fifteen years he was Director of the Shoals Marine Laboratory operated by Cornell University and the University of New Hampshire on the Isles of Shoals in the Gulf of Maine. While at the Isles of Shoals his research interests focused on opposite ends of the vertebrate spectrum–hagfish and baleen whales. J.B. enjoys teaching vertebrate morphology, evolution, and ecology both in the campus classroom and in the field and is recipient of the Clark Distinguished Teaching Award from Cornell University. His hobbies are natural history, travel and nature photography and videography, especially underwater using scuba. He has pursued his natural history interests on every continent and all the world's major ocean regions. Because of his experience he is a popular ecotourism leader having led Cornell Adult University groups to the Caribbean, Sea of Cortez, French Polynesia, Central America, the Amazon, Borneo, Antartica, and Spitsbergen in the High Arctic.

Preface

The fifth edition of *Vertebrate Life* continues to reflect extraordinary activity in vertebrate biology. The most pervasive innovations have resulted from the widespread adoption of phylogenetic systematics (cladistics) as the basis for determining the evolutionary relationships of organisms. The emphasis that this system of classification places on the importance of monophyletic groupings has ramifications in many areas of biology. As an objective (albeit frequently controversial) method that reflects information about the sequence of changes during evolution, cladistics provides an evolutionary framework in which ideas from other biological specialties can be accommodated. As a result, studies of behavior, physiology, and ecology are increasingly being placed in an explicitly evolutionary context, and this common ground has fostered increased interaction among those specialties.

In this edition we have expanded the cladistic classification originally introduced in the third edition, especially in our treatment of anatomy and physiology. As in previous editions, we have included cladograms illustrating the postulated relationships of vertebrates. In doing so, we have tried to reconcile the views of various authorities and point out major areas of disagreement. We pruned excessive detail from the cladograms in this edition while retaining information about the geologic time span for the lineages illustrated. The cladograms include synopses of the character states on which they are based and citations of the primary sources used. This information will facilitate exploration of different views, and will help faculty and students to modify the phylogenies presented here as new interpretations are published.

Literature citations have been brought up to date, with many references from 1997 and later. As before, we have chosen citations on the basis of their helpfulness to students attempting to enter the literature of the subject; review articles are cited when possible, and recent references are used because students can trace earlier work through them.

■ Acknowledgments

The ability of our editor, Teresa Ryu, to combine support and decisiveness was critical to keeping the project on schedule, and it has been a pleasure working with her. Jennifer Carey, our production manager, worked tirelessly to pull the various parts of the book together. Without her organizational ability and command of the intricacies of publishing the manuscript would still be spread in pieces across the floors of the authors' houses. Laura Schuett's extraordinary ability to capture the essence of an animal or a structure has enriched the illustrations immeasurably. We are grateful to Carol Abrazincas whose thumbnail sketches make the revised cladograms more informative and more attractive than previous versions.

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

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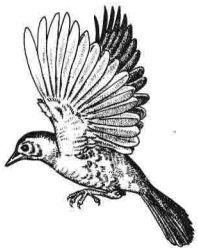


Vertebrate Life

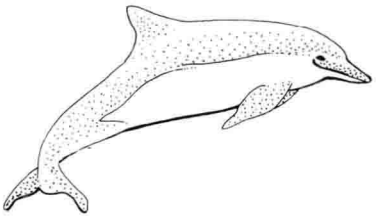
PART 1 Vertebrate Diversity, Function, and Evolution

The 45,000 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 one of the products of European exploration and expansion that began in the fifteenth and sixteenth centuries. In the middle of the eighteenth century, the 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, and 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 is known as the New Synthesis or Neo-Darwinism, and continues to be the basis for understanding the mechanics of evolution. Recent work has broadened our view of evolutionary mechanisms by suggesting, on the one hand, that some major events in evolution may be the result of chance rather than selection, and, on the other hand, that natural selection can sometimes extend beyond individuals to related individuals, populations, or even entire species. The emphasis on methods of classifying animals has also changed during the twentieth century, and classification, which began as a way of trying to organize the diversity of organisms, has become a way of 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 have basic characteristics in common that are the products of their common ancestry, and progressive modifications of these characters can trace the progress of evolution. 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, Evolution, and Classification 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.

■ 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 approximately 50,000 extant (= currently living) species of vertebrates range in size from fishes that weigh as little as 0.1 gram when they are fully mature to whales that weigh nearly 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. Some 15 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 that 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 can 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