

Preface

If you are a student coming to the study of vertebrates for the first time, several introductory remarks may be helpful, especially on how this textbook will support your work. First, the discipline of vertebrate biology is diverse and inclusive. It brings together themes from molecular biology, genes and genomes, evolution and embryology, biomechanics and experimental physiology, and it incorporates continuing and astonishing new fossils into the vertebrate story. Much of what you have met in earlier courses you will meet again here in an integrated way.

Second, to unify these themes, I have again written and revised this eighth edition within the unifying framework of form, function, and evolution. The first few chapters set this up, and the subsequent chapters treat vertebrates system by system. You may notice that each of these subsequent chapters begins with a discussion of morphology, followed by a discussion of function and evolution. Each chapter is therefore self-contained—form, function, evolution.

Third, as a student you likely enter this course after some background in the sciences, perhaps expecting to equip yourself with practical knowledge useful later in professional schools or in health-related careers. Certainly, this course, in part, delivers such practical information. But because vertebrate morphology is an integrative discipline, it brings together physiology, embryology, behavior, and ecology and also deploys modern methods of systematics and new finds in paleontology. Consequently, you will move beyond memorizing facts in isolation or as an end in themselves and instead begin to meet and understand larger concepts to which the morphology testifies. What may come as a surprise is that many theories, especially evolutionary theories within vertebrate biology, are still unsettled and unresolved, inviting a new idea or fresh approach open to anyone. This is one of the reasons I have included various controversies and support your efforts to become engaged in the thinking and scientific process.

For faculty who have used this textbook before, you will find it retains a familiar and inviting organization with the science updated and the student support enhanced. For those coming to this textbook for the first time, you will notice that the morphology receives generous treatment

within a phylogenetic context. But today we expect our students to develop academic and professional skills beyond just facility with anatomical terminology. In general, we expect our students to develop skills in critical thinking and a facility with scientific concepts. Each of us will find our own way of composing a course in vertebrate morphology that serves such course objectives. This textbook was written to support such course objectives as individual instructors build their courses. It is flexible. You can mix and match, change order to suit your course, and give emphasis to those systems that most suit the organization of your course. Because each chapter integrates form, function, and evolution pertinent to that system, each chapter is coherent within itself. Where information or concepts are treated in greater detail outside a particular chapter, they are cross referenced to help guide the student and clarify the discussion. Although discussed in earlier editions, let me repeat the specific strategy built into this textbook to improve student success and to help them develop skills in critical thinking and conceptual understanding.

For the Student

A number of strategic features within the textbook enhance its usefulness for students. It is richly **illustrated** with figures that include new information and provide fresh perspectives. Each chapter opens with an **outline**. Important **concepts** and major anatomical terms are boldfaced. **Cross references** direct students to other areas of the text where they can refresh their understanding or clarify an unfamiliar subject. Each chapter concludes with a **chapter overview**, which draws attention to some of the concepts developed within the chapter. **Box Essays** are included along the way in most chapters. Their purpose is to present subjects or historical events that students should find interesting and, perhaps from time to time, even fun. A **glossary** of definitions is included at the end of the book.

In addition to its practical features, the textbook also uses selected topics within vertebrate structure to develop student skills in critical thinking and mastery of concepts within a coherent framework.

Critical Thinking

Within the sciences, critical thinking is the ability to marshal factual information into a logical, reasoned argument. Especially if accompanied by a laboratory, a course in vertebrate morphology delivers hands-on experience with the anatomy of representative animals. Students can be directly engaged in the discovery of vertebrate form. But they can be encouraged to go beyond this. Instructors can lead students into larger issues: How does it function? How did it evolve? For example, early on in the textbook, students are introduced to "Tools of the Trade," methods by which we empirically examine how parts work and how we can place organisms within a phylogenetic context. After a discussion of basic morphology, each chapter discusses how these systems work and how they evolved.

I have deliberately included new, neglected, or competing views on function and evolution. Many of these ideas come from Europe, where they have been known for a long time. Personally, I find many of these ideas compelling, even elegant. Others strike me, frankly, as thin and unconvincing. Despite my own skepticism, a few contrary ideas are included. My purpose is to get students to think about issues of form, function, and evolution.

Several theories on the evolution of jaws are discussed, as are several theories of the origin of paired fins. Often students expect that today we have the final answers. Students implore, "Just tell me the answer." The debate about dinosaur physiology is a wonderful opportunity to show students the ongoing process of scientific investigation. Most have seen the Hollywood films and expect the issue settled. But we know that science is an ongoing process of refinement, challenge, and sometimes revolutionary change. One Box Essay sets forth the early case for dinosaur endothermy. That debate spawned further investigation that now returns to challenge such a view of dinosaurs as "hot-blooded" beasts. The second Box Essay on dinosaur endothermy presents this newer and contrary evidence, and thereby showcases how, even in extinct animals, it is possible to test hypotheses about their physiology, morphology, and lifestyles.

Concepts

Vertebrate morphology also helps develop an appreciation and understanding of the scientific concepts that unite biology and reflect on "how" science works. As John A. Moore put it, science is a "way of knowing" (Moore, *American Zoologist*, 1988). Comparative morphology throws into clear relief differences and similarities between organisms. The concepts of homology, analogy, and homoplasy help us understand the basis of these comparative and similar features. Many of the concepts were birthed in the nineteenth century and have grown into the guiding themes of biology today. Evolution, defined as descent with modification through time, is one of the foundation concepts in biology. Vertebrate morphology provides a showcase of adaptive change on the basic vertebrate body plan. But evolution is

change in a highly integrated organism, a connected system of parts and their functions. This too was recognized within the nineteenth century, suggesting constraints on evolutionary modification. Vertebrate morphology provides compelling examples of how an integrated organism might evolve. For example, a remarkable fossil record documents an undeniable change in jaw articulation within synapsids, seeing the two participating bones (articular, quadrate) of basal synapsids replaced by two different bones in derived groups, including mammals. Fossil intermediates between the two conditions mark the anatomical changes, but they also suggest how functional changes, which must accompany evolving systems, also change without disrupting performance.

Within many vertebrate systems, the close coupling of form and function with lifestyle is illustrated. Built on a basic vertebrate plan, the tetrapod locomotor system illustrates the close relationship between limbs and axial skeleton, and the type of locomotion—flight, cursorial, burrowing. The cardiovascular system, especially in organisms that exploit water and air, illustrates the close relationship between vascular morphology and the physiological flexibility that permits. The basic concepts of form, function, and adaptive evolution parade before us as we move from system to system in vertebrate morphology.

Evolution proceeds most often by remodeling, modification of a basic underlying plan, not by all new construction. This is illustrated in the skeletal system, as well as within the cardiovascular (aortic arches) system.

Organizational Strategy and Rationale

I have written this book within the unifying framework of form, function, and evolution. These are common themes that run throughout. The vertebrate groups are organized phylogenetically within each chapter, and their systems discussed within such a context. Morphology is foremost, but I have developed and integrated an understanding of function and evolution into the discussion of anatomy of the various systems. The first five chapters prepare the way.

Chapter 1 introduces the discipline, evaluates the intellectual predecessors to modern morphology, defines central concepts, and alerts students to misunderstandings they may unknowingly bring with them to the study of evolutionary processes. Chordates and their origins are covered in chapter 2. Considerable attention is given to the neglected protochordates and their evolution. This sets the stage for an extended discussion of the cast of characters in the vertebrate radiation, which occupies us for the remainder of the book, beginning next in chapter 3. Here, we discuss vertebrates, their origins, and basic taxonomic relationships. Chapter 4 introduces basic concepts of biomechanics and biophysics, preparing for their use later in understanding aspects of vertebrate design and function. Chapter 5 includes a summary of descriptive embryology and concludes with a discussion of the role embryonic processes play in vertebrate evolutionary events.

The remaining chapters develop each major system. Besides carrying overall themes, each chapter internally follows a consistent organization. Each begins with a basic introduction to the morphology and then proceeds to discuss function and evolution. This way, the overall themes are repeated in each chapter, bringing consistency of presentation to each chapter and coherence throughout.

New and Expanded in the Eighth Edition

New fossil finds, modern experimental research, and new phylogenies continue to enrich vertebrate biology, sometimes solving old questions or surprising us with a new understanding of how vertebrates function and how they evolved. Much of this is added to this new edition.

Origin of Chordates. The evolutionary arrival of the chordate body plan continues to receive fresh ideas. I have revised the end of chapter 2 to incorporate the most recent views. This revision has also helped clarify the evolution of the gnathostome “The New Mouth,” discussed in chapter 13 (Box Essay 13.1). The origin of chordates also leads into the revised summary of phylogenetic relationships within the vertebrates, chapter 3.

Phylogenetic Relationships. Thanks to continuing use of improved genetic and morphological data sets, phylogenetic relationships are becoming better resolved, and natural groups are emerging from this analysis with better clarity. This is the basis for revisions in chapter 3. Many smaller adjustments in the placement of various vertebrate taxa are incorporated, but two in particular should be noted—turtles and dinosaurs. I incorporate the new placement of turtles, not basally as done historically within the reptiles, but further advanced within the archosauromorphs (figure 3.27). The second proposed change was published recently (Baron et al., 2017 doi:10.1038/nature21700) wherein dinosaurs were significantly reshuffled with the archosaurs. I have chosen not to incorporate this proposed new revision within this chapter. It hypothesizes significant changes in early dinosaur evolution, so I would first like to see how it stands up in the hands of other systemists.

The Musculature System. I have revised chapter 10 to better emphasize its overall themes as done in other chapters—morphology, function, evolution. I hope this revised organization will help the student to better assemble the evolutionary story of the muscle system.

Lungs and the Rise of Archosaurs. The especially efficient lungs of birds are well known with air sacs and one-way flow of air. But in the seventh edition, I reported that a similar one-way air flow, even without air sacs, occurs in crocodiles. This can now be updated to see a similar possibility in other modern reptile groups. This surprising finding is tentatively attributed to Colleen Farmer, whose story of the discovery is highlighted in Box Essay 11.5. If true of archosaurs in general, it may represent a respiratory adaptation to low oxygen levels in the early Mesozoic and account for the rise of Archosaurs.

Updated and Revised. Countless changes and revisions throughout this new edition have been made, some major, some small. These changes have corrected misinformation, updated information, and often better clarified an explanation. For this I am indebted to students, reviewers, and colleagues for bringing these suggestions to my attention.

Serving the Student. Features of the textbook have been further expanded to make its presentation clearer and inviting. The use of color brightens these sections of the book. Color has also been used to better correlate and compare structures between figures in these chapters. Where feasible, I have added more color to the illustrations. Many illustrations are new, revised, or relabeled to improve clarity. The accompanying laboratory dissection guide (authored with E. J. Zalisko) is closely cross-referenced to this textbook. In addition, selective **functional laboratories** are available online to provide students with firsthand experience of working between the anatomy and its functional and evolutionary significance.

Serving Instructors. This eighth edition—new, revised, updated—can serve as reference and resource support for the course you put together on vertebrates. In addition to this, resources are available to you online. The functional laboratories may be downloaded and used as they supplement your course. **PowerPoint images**, chapter by chapter, are available online, along with additional images from McGraw-Hill that can be used to compose lectures and laboratory presentations.

Supplements

Comparative Vertebrate Anatomy: A Laboratory Dissection Guide

Newly revised, *Comparative Vertebrate Anatomy: A Laboratory Dissection Guide*, Eighth Edition, by Edward J. Zalisko and Kenneth V. Kardong is now available. At the end of this dissection guide, the authors include a Student Art Notebook. This notebook, promoted by students, is a reprinted collection of the most important and commonly used dissection figures in the current edition of the laboratory manual. It addresses a frustration inherent in most dissection guides, especially when comparing homologous systems between representative animals, of having to flip between text and distantly placed illustrations. This laboratory manual weaves the functional and evolutionary concepts from this textbook, *Vertebrates: Comparative Anatomy, Function, Evolution*, into the morphological details of the laboratory exercises. Using icons, the laboratory manual identifies cross references to this textbook, so students can quickly move from the dissection guide to this textbook to consult the expanded treatment of function and evolution. Each chapter of the dissection guide first introduces the system, makes comparisons, and demonstrates common themes in the animal systems. It also introduces central terms to be used next in the chapters. Then the written text

carefully guides students through dissections, which are richly illustrated. Anatomical terms are boldfaced and concepts italicized. The dissection guide is written so that instructors have the flexibility to tailor-make the laboratory to suit their needs.

Website for *Vertebrates: Comparative Anatomy, Function, Evolution*, Eighth Edition

A website for this textbook, available at www.mhhe.com/kardong8e, includes further useful information upon which instructors can depend and students can consult. Here can be found the **functional laboratories**, helpful in a linked laboratory, if available, or selectively in lecture. End-of-chapter **selected references**, giving students a start into the literature, are located here.

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Art and Artists

Please indulge me a final moment of lament. For illustrations, modern textbooks have substituted photographs and figures made of computer-generated plastic figures, especially when rendering molecular events. There is nothing wrong with this, but what has been eliminated is involvement of the human touch, directly, namely the artist. Preparing this textbook has given me the chance, at no expense to students by the way, of engaging some of the best artists of our day. They bring a sharp eye and traditional talent to rendering of enlightening pieces of art. Many have contributed, but one is L. Laszlo Meszoly (Harvard University), who has contributed special figures to this and earlier editions. Another is Kathleen M. Bodley, whose remarkable ability to render soft tissue in particular has enriched our dissection guide and is quite stunning. Her work also graces the cover of this textbook. My thanks to these two in particular. This is a wonderful tradition of scientific illustration they carry forward.

Acknowledgments

I am indebted to reviewers, students, and colleagues who have generously shared with me their suggestions to improve the textbook. My hope is that these colleagues will see, if not

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HISTORICAL PERSPECTIVES

The Pre-Columbian World

Early Man

Early Man

Early Man

Early Man

Early Man

Early Man

Early Man

Early Man

Early Man

THE SCIENCE OF VERTEBRATE MORPHOLOGY

George Cuvier

Richard Owen

WHAT ARE THE MAIN PRINCIPLES OF VERTEBRATE MORPHOLOGY?

PHYSIOLOGICAL CORRELATION

Amphibians

Reptiles

Amphibians

Comparative Vertebrate Morphology

Comparative morphology deals with the form and function of animals. We focus on animals in particular vertebrate groups, and the significance these organisms and their structures have. The use of comparative morphology is not just a convenience. It is a way of understanding the similarities and differences that have evolved. It also emphasizes the functional and evolutionary changes that vertebrates carry within their structures. Comparison also helps formulate the questions we must ask of structure.

PHYSIOLOGY

Early Man

Early Man

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