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 sixth 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. 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. One need not move through in the same order presented here, but chapters can be assigned in the order suited to the organization of one's own course. Because each chapter integrates form, function, and evolution pertinent to that system, each chapter is coherent within itself. 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 practical features within the textbook enhance its usefulness for students. It is richly **illustrated** with figures that include new information and provide fresh perspective. 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 morphology, function, and evolution 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," the 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 a 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 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, 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. 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 Sixth Edition

Remarkable and innovative research continues to enrich the discipline of vertebrate biology. Much of this is added to this new edition.

Feathers. We now know that the regeneration of feathers is a much more complex process than previously thought, thanks to new research. The inductive interaction between skin dermis and epidermis deep within the feather follicle establishes a zone of cell proliferation producing the feather proper, and a patterning zone where fates of newly formed cells are established in a remarkably intricate system. Feathers evolved before birds. This means that these skin specializations addressed biological roles before they addressed flight. This new description of feathers therefore opens up a new perspective on this major evolutionary event. This is discussed in the chapter on integument (chapter 6) with new supportive illustrations.

Cardiac Shunt. The hearts of living amphibians and reptiles permit a right-to-left shunting of blood, thereby bypassing a trip to the lungs, but instead blood high in CO_2 heads out directly to systemic tissues. This cardiac shunt was thought to be important during diving, where lungs quickly become depleted of oxygen and little physiological benefit attended sending blood to the lungs. This may still be true, but new and speculative research suggests another, or an additional, explanation for the shunt. This blood bypassing the lungs may bring CO_2 to digestive organs processing a meal and thereby increase effectiveness, especially in ectothermic vertebrates. This new insight is discussed and illustrated in the circulatory system chapter (chapter 12).

Evo-Devo. I have built on the genetic section on evolution and development (chapter 5) introduced in earlier editions. This has included additional illustrations and revised accompanying text. Examples throughout show how master control genes (*Hox* genes) and developmental genes preside over the construction of the vertebrate body and its various systems. In the concluding chapter, I emphasize how these special genetic gene sets provide the basis for major evolutionary changes.

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 revision in chapter 3, but these updated phylogenies are carried forward throughout the book.

Turning over Chordates. New developmental genetics, discussed in the previous edition, informs us that the immediate chordate ancestors flipped over, reversing dorsal and ventral surfaces. That view seems to hold still and therefore remains the surprising basis of the chordate body plan today.

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 more clear 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, within color signatures, for example, I have added more color to the illustrations. Many **illustrations** are new, revised, or relabeled to improve clarity. For example, besides those illustrations mentioned earlier, new/revised figures illustrate an updated full skeleton of *Ichthyostega*, pectoral girdle evolution, air bladder evolution, and cardiovascular blood flow; and various changes have been made in figures elsewhere. Scientific references are available to the students, online, if they would like to follow up or read more about a particular subject. 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 sixth 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*, Sixth Edition, by Kenneth V. Kardong and Edward J. Zalisko, is now available. At the end of this dissection guide, the authors include a Student Art Notebook. This notebook 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. 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*, Sixth Edition

A website for this textbook, available at *www.mhhe.com/kardong6e*, 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 helpful selectively in lecture. End-of-chapter **selected references,** giving students a start into the literature, are located here. Instructors can also access printable pages of **illustrations** that can be used as transparency masters, lecture handouts, or incorporated into PowerPoint presentations.

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