Preface

From the beginning to this fourth edition, I have written and revised this book within the unifying framework of form, function, and evolution—chapter by chapter. These themes run throughout to provide coherence. The organization of the book is intended to support and encourage students to be actively engaged in the material and to think critically about the functional and evolutionary significance of the anatomy introduced and explored.

Students often enter this course after some background in the sciences, perhaps expecting to equip themselves with practical knowledge useful later in professional schools or health-related careers. Certainly such a course, in part, delivers practical information. But this is also a point in undergraduate training when students should move beyond memorizing facts in isolation or as an end in itself and begin to understand larger concepts and themes. Vertebrate morphology is particularly fitted to this as it has become an integrative field bringing together physiology, embryology, biomechanics, behavior, and ecology as well as deploying modern methods of systematics and the new material arriving from paleontology. As an integrative discipline, vertebrate morphology is well suited to show the workings of science itself. Controversies are discussed herein and the organization of the book supports and encourages students themselves to become engaged in the scientific process.

Certainly new and updated information is included. But I have also included new sections that reflect changes in the field of vertebrate morphology. In this edition, for example, there is a new section on "evo-devo", the basic genomic control mechanisms that guide morphological development. This is then selectively followed up in later chapters by examining how genomes and developmental control mechanisms are the likely basis for novel evolutionary modifications between groups.

For those 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 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. Important literature is cited at the end of each chapter; and a web address connects them to further references and resources. Boxed essays are included 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, with four appendices: (A) Vector Algebra, (B) International System of Units, (C) Common Greek and Latin Combining Forms, and (D) Classification of Chordates.

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 (e.g. calcichordate origin of vertebrates). 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 boxed 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 boxed 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, 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 are 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, 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 Fourth Edition

Evo-Devo. I have added an entirely new introductory section on evolution and development to Chapter 5, based on molecular embryology but relating the importance of genomic control systems to morphological development. In turn, I selectively, in later chapters, discuss how master control genes (*Hox* genes) might provide the genetic mechanisms for major evolutionary changes in vertebrate design. This helps link modern cell and molecular biology to organismal events of morphogenesis and evolution.

Origin of Flight. After some decades of debate, fossil finds and experimental evidence have produced new ideas about the origin of flight in birds. This is discussed in a new section within the skeletal system.

Biomechanics and Aerodynamics. Getting into the air is no small feat for bird or airplane. This section in the chapter on biological design has been corrected and expanded, addressing some of the misconceptions about wings and wind.

Mode and Tempo of Evolution. The concluding chapter now includes a section integrating levels of organization from *Hox* genes to developmental processes to evolutionary change.

Update and Revised. With thanks to suggestions from students, reviewers, and colleagues, I have made many changes and revisions throughout this new edition, some major, some small. Besides the particular changes just mentioned, I have also substantially revised the chapters on biological design, life history (embryology), circulatory system, digestive system, endocrine system, and added new sections in the concluding chapter.

Serving the Student. Features of the textbook have been expanded to make its presentation more clear and inviting. The use of **color** has been expanded which brightens these sections of the book. But color has also been used to better correlate and compare structures between figures in these chapters. Many **illustrations** are new, revised, or re-labeled to improve clarity. For example, new figures are used, along with new text, in the development chapter to discuss bone growth and its significance in producing lines of arrested growth (LAGs), an important feature in the controversies over dinosaur physiology. The accompanying laboratory dissection guide (authored with E. J. Zalisko) is closely crossreferenced to this textbook. But in addition to this, selective **functional laboratories** are now available, on line, to provide students with first hand experience of working between the anatomy and its function and evolution.

Serving Instructors. This fourth 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 on line. 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 other digital images at McGraw-Hill that can be used to compose lectures and laboratory presentations.

Supplements

Comparative Vertebrate Anatomy: A Laboratory Dissection Guide

Newly and substantially revised, Comparative Vertebrate Anatomy: A Laboratory Dissection Guide, Fourth Edition, by Kenneth Kardong and Edward 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 the textbook, Vertebrates: Comparative Anatomy, Function, Evolution into the morphological details of the laboratory exercises. Using icons, the laboratory manual identifies cross references to the textbook, so students can quickly move from the dissection guide to the 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.

A website for this textbook is available at *www.mhhe.com/kardong4*. Besides links to related material, this website includes further literature references, and it also offers instructors printable pages of illustrations that may be used as transparency master. The website also includes several functional labs, and will be updated regularly to post new information on vertebrate phylogenies, function, and evolution.

Digital Zoology

Digital Zoology is an exciting interactive product designed to help you to make the most of your zoology classes and laboratory sessions. This program contains interactive cladograms, laboratory modules, video, interactive quizzes, hundreds of photographs, a full glossary, and much detailed information about the diversity and evolution of the animals that we find on the planet. To find out the latest news on this ever-expanding product, log on to *www.mhhe.com/ digitalzoology* and find out how to get your copy.

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